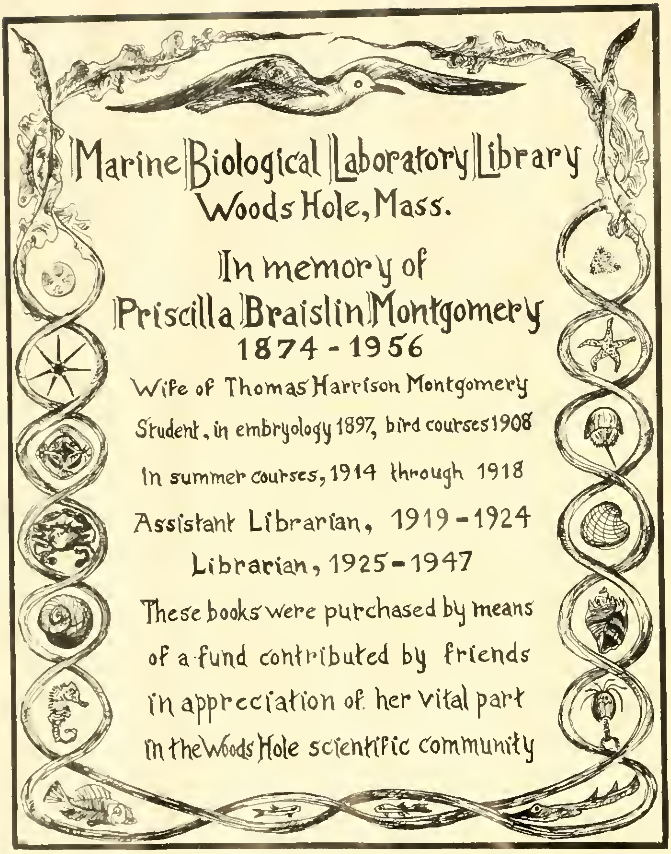

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TEXTBOOK OF THEORETICAL BOTANY. Volume I

A TEXTBOOK OF PRACTICAL BOTANY

TEXTBOOK OF THEORETICAL BOTANY

Ranunculus lyalii, from Mt. Cook, New Zealand.

TEXTBOOK OF THEORETICAL BOTANY

BY

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M.A.(Cantab.), D.Sc.(Lond.), F.L.S.

AND

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B.Sc.(Lond.), Ph.D.(Lond.), F.L.S.

VOLUME II

With Drawings by
Miss K. BENSON-EVANS, M.Sc., F.L.S.
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To the dear memories of
W.R.I.C. and F.M.McL.

FOREWORD TO VOLUME II

THE unexpected and deeply regretted death of Dr. Ivimey-Cook took place in February 1952, just after the publication of Volume I. This was not only a serious loss but it has thrown an additional burden on the surviving author which is to some extent responsible for the delay in the appearance of this Volume. Only a part of the manuscript had been prepared before Dr. Cook's death and the completion of the book without his able and careful collaboration has taken longer than was anticipated.

It is not proposed, however, to abandon the preparation of the two remaining Volumes of the complete work. They will continue to bear our joint names, as Dr. Cook left a considerable amount of material intended for these Volumes, particularly a draft of an important section on Economic Botany, which was the product of wide experience and study. Notwithstanding the increased difficulty of the task it is hoped that, if fate is kind, the work may be finished without too great a delay.

R. C. McL.

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GLOSSARY OF PREFIXES AND SUFFIXES

The following list of the more important Greek and Latin roots used in botanical terminology has been compiled to enable the student to understand the meaning of technical terms. With its aid most of those occurring in the text can be readily translated. They are arranged as prefixes and suffixes according to their usual employment, though some may occur in either position. Their derivation from Greek (G.) or Latin (L.) has been indicated in each case.

PREFIXES

a-	not, without (G.).
ab-	from (L.).
acro-	apex (G.).
actino-	radial (G.).
ad-	to, towards (L.).
amphi-	around (G.).
ana-	up (G.).
andro-	male (G.).
anemo-	wind (G.).
angio-	vessel (G.).
angusti-	narrow (L.).
aniso-	unequal (G.).
ante-	before (L.).
anti-	against (G.).
apo-	away from (G.).
arch-	primitive (G.).
asco-	sac (G.).
auto-	self (G.).
aux-	growth (G.).
basid-	pedestal (L.).
bi-	twice (L.).
bio-	life (G.).
botan-	herb (G.).
brachy-	short (G.).
bryo-	moss (G.).
carp-	fruit (G.).
caul-	stem (L.).
chaet-	bristle (G.).
chlamyd-	cloak (G.).
chloro-	green (G.).
chondro-	grainlike (G.).
chromo-	colour (G.).
chryso-	golden (G.).
circum-	around (L.).
co-, *con-*	together (L.).
coeno-	in common (G.).
coleo-	sheath (G.).
crypto-	hidden (G.).
cyano-	blue (G.).
cyto-	cell (G.).
derm-	skin (G.).
desm-	bond (G.).
di-	twice (G.).
dia-	through (G.).
dicho-	separate (G.).
dictyo-	net (G.).
diplo-	double (G.).
dys-	bad (G.).
e-	without (L.).
ecto-	outside (G.).
endo-	inside (G.).
entomo-	insect (G.).
epi-	upon (G.).
erythr-	red (G.).
eu-	well, proper (G.).
eury-	broad (G.).
ex-	out of (L.).
gam-	marriage (G.).
gamet-	spouse (G.).
gastero-	stomach (G.).
ge-	earth (G.).
geitono-	neighbouring (G.).
geno-	racial (G.).
gluc, *glyc-*	sweet (G.).
goni-	offspring (G.).
gymno-	naked (G.).
gyn-	female (G.).
hadro-	strong (G.).
halo-	salt (G.).
haplo-	single (G.).
helo-	marsh (G.).
helio-	sun (G.).
hemi-	half (G.).
hetero-	different (G.).
hexa-	six (G.).
holo-	entire (G.).
homo-, *homoio-*	alike (G.).
hyalo-	crystal (G.).
hydro-	water (G.).
hyper-	above (G.).
hyph-	web (G.).
hypo-	below (G.).

idio-	peculiar (G.).
infra-, *infer-*	below (L.).
inter-	between (L.).
intra-	within (L.).
iso-	equal (G.).
karyo- (*caryo-*)	nut, nucleus (G.).
kata-	down (G.).
lati-	broad (L.).
leuco-	white (G.).
limno-	lake (G.).
lyco-	wolf (G.).
lys-	loosen (G.).
macro-	large, long (G.).
mega-	large (G.).
meio-	less (G.).
melan-	black (G.).
meris-	part (G.).
meso-	middle (G.).
meta-	with (G.).
micro-	small (G.).
mito-	thread (G.).
mon-	single (G.).
morph-	shape (G.).
multi-	many (L.).
myco-	fungus (G.).
myrmeco-	ant (G.).
nan-, *nann-*	dwarf (G.).
necro-	dead (G.).
neo-	new (G.).
nerit-	coastal (G.).
notho-	false (G.).
nuta-	nodding (L.).
nycti-	night (G.).
ob-	inverse (L.).
oligo-	few (G.).
omni-	all (L.).
oo-, *ovo-*	egg (G.), (L.).
ornitho-	bird (G.).
ortho-	straight (G.).
oxy-	sharp (G.).
pachy-	thick (G.).
palaeo-	ancient (G.).
pan-	all (G.).
para-	beside (G.).
partheno-	produced without sex (G.).
pelagi-	oceanic (G.).
penta-	five (G.).
peri-	around (G.).
phaeo-	brown (G.).
phanero-	manifest (G.).
pheno-	appearance (G.).
phloe-	bark (G.).
photo-	light (G.).
phyco-	algal (G.).
phylo-	tribe (G.).
physo-	bladder (G.).
pinna-	feather (L.).
plano-	wandering (G.).
pleio-	more (G.).
pluri-	several (L.).
poly-	many (G.).
post-	after (L.).
pre-, *prae-*	before (L.).
pro-	for (L.).
proto-	first (G.).
pseudo-	false (G.).
psilo-	bare (G.).
ptero-	wing (G.).
quadri-	four (L.).
quater-	fourth (L.).
quinque-	five (L.).
rhiz-	root (G.).
rhodo-	red (G.).
sapro-	putrid (G.).
schizo-	splitting (G.).
scler-	hard (G.).
semi-	half (L.).
siphon-	tube (G.).
solen-	tube (G.).
soma-	body (G.).
sperma-	seed (G.).
sphaero-	spherical (G.).
spheno-	wedge (G.).
squam-	scale (L.).
steno-	narrow (G.).
stereo-	solid (G.).
styl-	column (G.).
sub-	below (L.).
super-, *supra-*	above (L.).
sym-, *syn-*, *sys-*	together (G.).
telo-	end (G.).
ter-	third (L.).
tetra-	four (G.).
thalasso-	marine (G.).
thallo-	sprout (G.).
therm-	heat (G.).
thero-	summer (G.).
trans-	across (L.).
tri-	three (L.), (G.).
tricho-	hair (G.).
uni-	one (L.).
vas-	vessel (L.).
xantho-	yellow (G.).
xeno-	stranger (G.).

xero-	dry (G.).
xyl-	wood (G.).
zoo-	animal (G.).
zygo-	joined (G.).

SUFFIXES

-androus	male (G.).
-angium	vessel (G.).
-arch	beginning (G.).
-blast	bud, rudiment (G.).
-bolic	thrown (G.).
-carp	fruit (G.).
-chasium	separation (G.).
-colous	inhabiting (L.).
-cyclic	circled (G.).
-cyst	cavity (G.).
-cyte	cell (G.).
-dendron	tree (G.).
-derm	skin (G.).
-dynamous	powered (G.).
-enchyma	infusion (G.).
-ferous	bearing (L.).
-fid	cleft (L.).
-folium	leaf (L.).
-fuge	avoiding (L.).
-gen	producing (G.).
-generous	bearing (L.).
-graphic	writing (G.).
-gynous	female (G.).
-kinesis	movement (G.).
-lith	stone (G.).
-logy	knowledge (G.).
-lytic	dissolving (G.).
-merous, *-mery*	part (G.).
-meter	measure (G.).
-morphic	shaped (G.).
-nastic	pressed (G.).
-nate	born (L.).
-nym	name (G.).
-oecium	dwelling (G.).
-oid	like (G.).
-ont	being (G.).
-phage	eating (G.).
-petal	seeking (L.).
-philous	loving (G.).
-phobic	hating (G.).
-phore	bearer (G.).
-phyll	leaf (G.).
-phyte	plant (G.).
-plasm, *-plast*	moulded (G.).
-plicate	folded (L.).
-podium	foot (G.).
-rhiza	root (G.).
-scopic	looking (G.).
-sect	cut (L.).
-some, *-soma*	body (G.).
-sperm	seed (G.).
-spore	germ (G.).
-stachys	spike (G.).
-stele	pillar (G.).
-stichous	ranked (G.).
-tactic	arranged (G.).
-taxis, *-taxy*	order (G.).
-thallic	shoot (G.).
-theca	case (G.).
-tome, *-tomy*	cutting (G.).
-tonic	tuning (G.).
-trichous	hairy (G.).
-trophic	nourished (G.).
-tropic	turned (G.).
-ula, *-ule*	diminutive (G.).
-vorous	consuming (L.).
-zoid	animal-like (G.).

CHAPTER XXIII

THE ANGIOSPERMAE: FLOWERS

Although in its widest application the term "Flowering Plant" correctly includes the Gymnosperms as well as the Angiosperms, yet it is nearly always the latter group which we have in mind when the term is used. The interpretation of the reproductive strobili of some Gymnosperms is open to question, but in the great majority of Angiosperms it is clear what we should regard as the "flower" and it is these angiospermic flowers and their organs that we are about to consider. So vast is the range of pattern among the angiospermic flowers, so infinitely varied are their forms, that it would be impossible even in a complete volume to give any full, systematic account of them and we can only touch here on some of their fundamental features and the general nature of their plan.

Fig. 1042.—Karl Eberhard, Ritter von Goebel, a great leader in plant morphology and author of the "Organographie der Pflanzen".

INFLORESCENCES

It has been claimed that the earliest type of flower is foreshadowed by the bisporangiate strobili of some of the extinct Cycadophyta, which were solitary and terminal on an axis. Without necessarily upholding the idea of the direct descent of the Angiosperms from such types, we may accept the solitary, terminal flower as our starting point for the consideration of flower-groupings. We have little or no actual information about the evolution of such groupings and our treatment of them must therefore be purely formal and geometrical, for which purpose the simplest starting point is the best.

Among the living Angiosperms such solitary terminal flowers are rarely formed on the principal axis and then only in a few annuals of slight growth, such as *Nigella* or *Papaver* among Dicotyledons, or in reduced geophilous Monocotyledons such as *Tulipa*. They are not uncommon, however, on lateral branches and it may be significant that they are found in genera which are on other grounds regarded as primitive, *i.e.*, *Magnolia* and *Liriodendron* (Fig. 1043). There is no evidence to support the idea that the condition here is due to reduction.

FIG. 1043.—*Liriodendron tulipifera* with solitary flowers, terminal on the branches.

Much more widespread is the grouping of flowers upon some more or less definitely specialized part of the shoot system and it is to such groupings that the term **inflorescence** is applied, when used morphologically.

Originally the term was applied by Linnaeus to the mode of arrangement of the flowers upon the flowering branch itself, which is more correctly described as **anthotaxy**. Modern usage has widened the meaning and Bentham and Hooker give an inclusive definition which combines both the older and the newer, less abstract ideas: "The inflorescence of a plant is the arrangement of the flowering branches and of the flowers upon them. *An* inflorescence is a flowering branch or the flowering summit of a plant above the last stem leaves, with its branches, bracts and flowers." The latter sense is that in which the word is now usually understood.

Vegetative branching is classified as monopodial or sympodial (see Volume I, p. 838), the former being considered the more primitive form. Flowering branches show a similar distinction, the monopodial types being called **racemose** or **indefinite** and the sympodial types called **cymose** or **definite**. More or less parallel with this distinction there runs a further difference, namely in the order of the opening of the flowers. In monopodial types the flowers furthest from the apex usually open first and the order of opening is therefore **acropetal** or **centripetal**, while in sympodial forms the order is reversed, *i.e.*, it is **basipetal** or **centrifugal**. This latter distinction is not however universally valid and the attempt to graft it on to the simple monopodial-sympodial differentiation has been productive of much confusion and has led to the condemnation of inflorescence classifications in general as inconsistent and unsound. No such inconsistency exists as regards the mode of branching, and if we retain a clear idea of monopodial and sympodial construction respectively, it will afford us the most useful clue to the labyrinth of inflorescence types.

The amount of distinction between flowering and vegetative branches is variable. Some plants, *e.g.*, *Geranium*, show little or none. In most cases, however, there is a distinction of foliage, the leaves of the inflorescence branches being modified, often reduced, from the foliage form. They are distinguished as **bracts**, while those on the flower stalk itself, when present, are called **bracteoles**. They belong to the class of hypsophylls and they have been discussed in the chapter on leaves in Volume I. Extreme differentiation of the inflorescence may lead to the complete suppression of bracts and bracteoles, as in many Cruciferae, producing that rare phenomenon, a leafless stem.

The inflorescence branches generally form the summit of the plant or at least of the shoot systems in which they appear. Such inflorescences are called **terminal**. A minority of inflorescences are, on the other hand, **intercalary**, that is they occur as zones in the development of the shoot, which continues its vegetative growth beyond them. Pseudo-terminal inflorescences may develop from the intercalary type, as in some Winteraceae, such as *Drimys*, by abortion of the terminal bud of the branch, so that a group of axillary inflorescences becomes congested at the apex of the branch.

Intercalary inflorescences usually consist of sympodial, axillary shoots on a monopodial vegetative axis. These may be either complex, many-flowered cymes or single flowers in the leaf axils. Numerous transitional types suggest that there has been evolution both by amplification and by reduction.

While terminal inflorescences are progressive structures and show evidences of development, the intercalary types seem rather to have originated by the gathering together and condensation, that is to say reduction, of more extensive branch systems, each with its terminal flower or inflorescence. Agreeably to our supposition that the primitive terminal flower is a starting point, we may regard terminal inflorescences as being also relatively primitive.

The fertility of flowers often varies with their position in the inflorescence and those at the base or summit may be quite sterile. Sometimes entire inflorescences may be sterile and transformed for other uses, as in *Vitis* and *Adenia* (Passifloraceae), where they become tendrils.

The curious inflorescences of many tropical trees, which spring directly from the surface of old stems (**cauliflory** or **cladanthy**), are peculiar not only in position but sometimes in origin. They are, as a rule, reduced terminal inflorescences on suppressed side-shoots and conform otherwise to the various types recognizable among terminal inflorescences generally, though often in a condensed and obscure pattern. Exceptionally, however, they are adventitious and arise endogenously from a secondary cortical meristem.

Cauliflory is a term which covers a variety of flowering habits with the common feature that flowers and fruit are borne on old, thickened branches or on the main trunk of a tree. This is in striking contrast to the habit of nearly all trees of temperate zones, whose flowers are borne only on the young branches. Cauliflory is a widespread character, both in a geographical and a systematic sense, of the trees of tropical forests, but it is notably common only among the trees of the lower stories of the canopy and is seldom found in trees which belong to the highest story. The latter sometimes display *penduliflory*, which is a condition in which the flowers are borne on long, thin, pendent shoots, which hang down below the crown. Cauliflory is found in very few trees of temperate climates, the Judas Tree, *Cercis siliquastrum*, being one of these exceptions.

Cauliflory may be general, which means that flowers may appear anywhere, either on the branches or trunk. *Ramiflory* is a modification, flowers appearing on the older branches but not on the trunk itself. The opposite condition is *trunciflory*; but neither of these terms is much used. The extreme condition is seen in certain "geocarpic" species of *Ficus*, in which the flowering shoots arise only at the base of the main trunk, which appears to be surrounded by bunched masses of fruits, partly lying on the ground, along which the flowering shoots may creep like runners, for distances of several metres.

Biologically the habit of cauliflory may be valuable in exposing the flowers much more freely than would be the case if they were immersed in the dense canopy of the forest, but we know too little of the floral biology of the tropical forests to be sure whether this is truly a gain or not. In any case there must be some underlying physiological cause, which is at present quite obscure.

The more types of plants are examined, the more clearly will it be realized that all forms of inflorescence merge into one another and that mixed forms are common. Even the two main groupings into racemose and cymose forms are not watertight. Whether or not one of them may have been derived from the other in an evolutionary sense, they do show intergrades, and are not mutually exclusive categories.

With these reservations we may proceed to the description of a number of frequently recurring types, to which a large proportion of inflorescences may be referred.

By analogy with the vegetative branch system, it has been held that the monopodial or racemose plan must be the primitive plan of inflorescence branching, but that this is not necessarily true or even probable will be perceived if we reflect that the formation of a terminal flower, that is to say the original state of flowering in its simplest manifestation, brings the growth of the axis to a stop and thus precludes any further development on the monopodial plan. Any development beyond this initial condition will therefore involve the production of lateral axes to replace the arrested apex, that is to say it will be on the sympodial or cymose plan. A comparative study of flower clusters shows that among Dicotyledons, the first stage of cymose advancement is the development of two lateral axes beneath the terminal flower, each in its turn ending in a flower and giving rise to another pair of flower-bearing laterals, and so on. This is the **dichasium.** (This and the following inflorescence types are illustrated diagrammatically in Figs. 1044 and 1045.)

Among Monocotyledons, it is commoner to find only one lateral formed at each stage of branching, providing a **monochasium**. The same condition also occurs among Dicotyledons, but apparently as the result of reduction from two laterals to one.

Monochasia present a variety of different appearances according to their mode of development. When the successive laterals come off always towards the same side of the axis we have a **bostryx.** The successive laterals of a bostryx may stand at different angles to the parent axis. Not uncommonly the directions of successive laterals show regular angular deflections either clockwise or anti-clockwise, building up a type of spiral inflorescence to which some writers limit the application of the name. When the laterals do in fact all lie in the same plane they produce a helicoid grouping known as a **drepanium**. On the other hand, the laterals may alternate successively towards opposite sides of the parent axis, thus building up a scorpioid figure called a **cincinnus**. If the laterals of a cincinnus all lie in the same plane so that they form a fan-shaped figure, they constitute a **rhipidium**, chiefly a monocotyledonous type. The terms " helicoid " and " scorpioid " have been much confused. In general both terms would apply descriptively to a curled cymose inflorescence, such as that of Boraginaceae, but strictly speaking " helicoid " should only be used of the bostryx or unilateral type and " scorpioid " of the cincinnus or alternating type.

If more than two laterals are formed at each stage of branching, we have a **pleiochasium**, which is rare as a simple inflorescence but is not uncom-

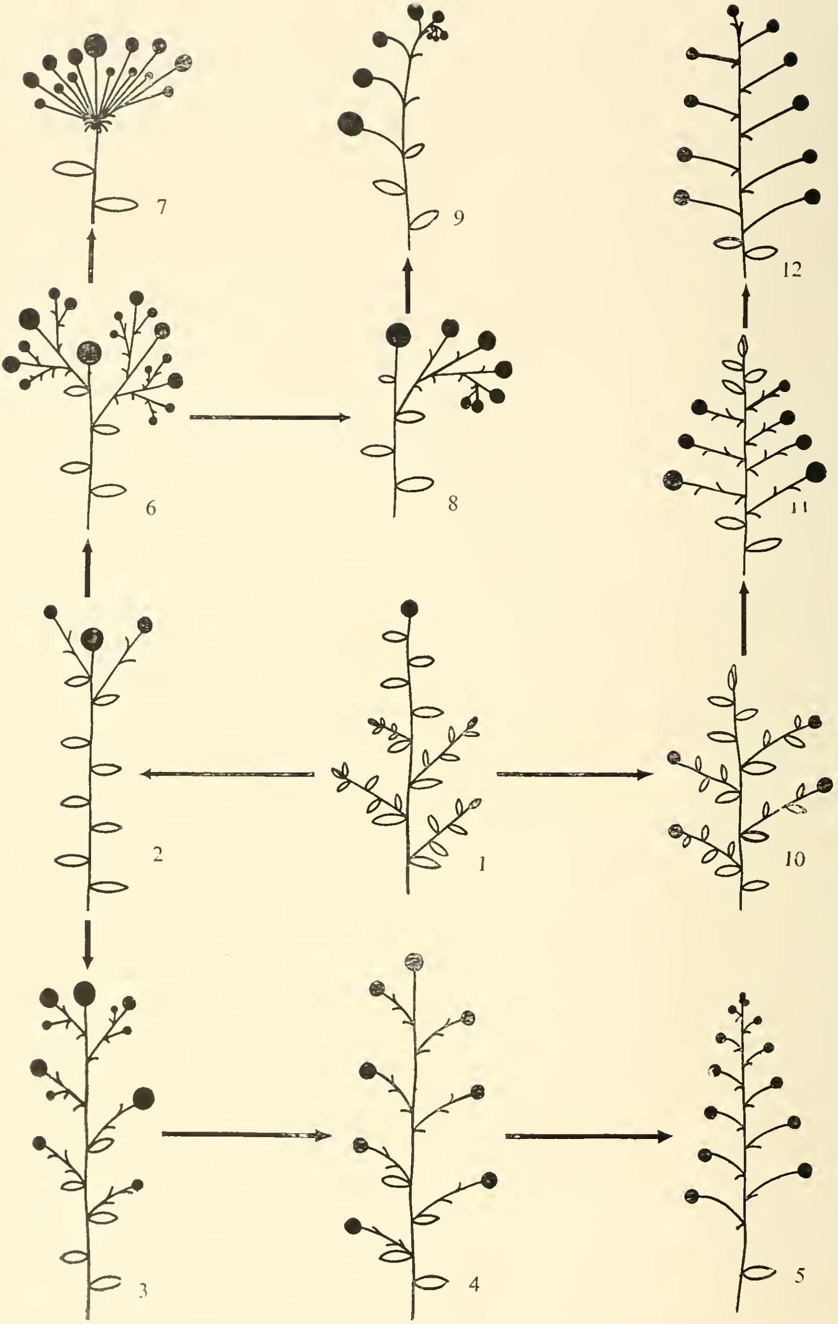

FIG. 1044.—Suggested interrelationships of inflorescence types. (1) Flowers solitary, terminal. (2) Simple dichasium. (3) Pleiochasium with terminal flower opening first. (4) Ditto, terminal flower no longer opening first. (5) Raceme with acropetal opening. (6) Compound dichasium. (7) Cymose umbel. (8) Continuous monochasium. (9) Sympodial monochasium with false axis. (10) Terminal flowers only on side branches. (11) Intercalary inflorescence derived from the previous type. (12) Pseudo-terminal inflorescence as a further derivative. (*After Parkin*, 1914.)

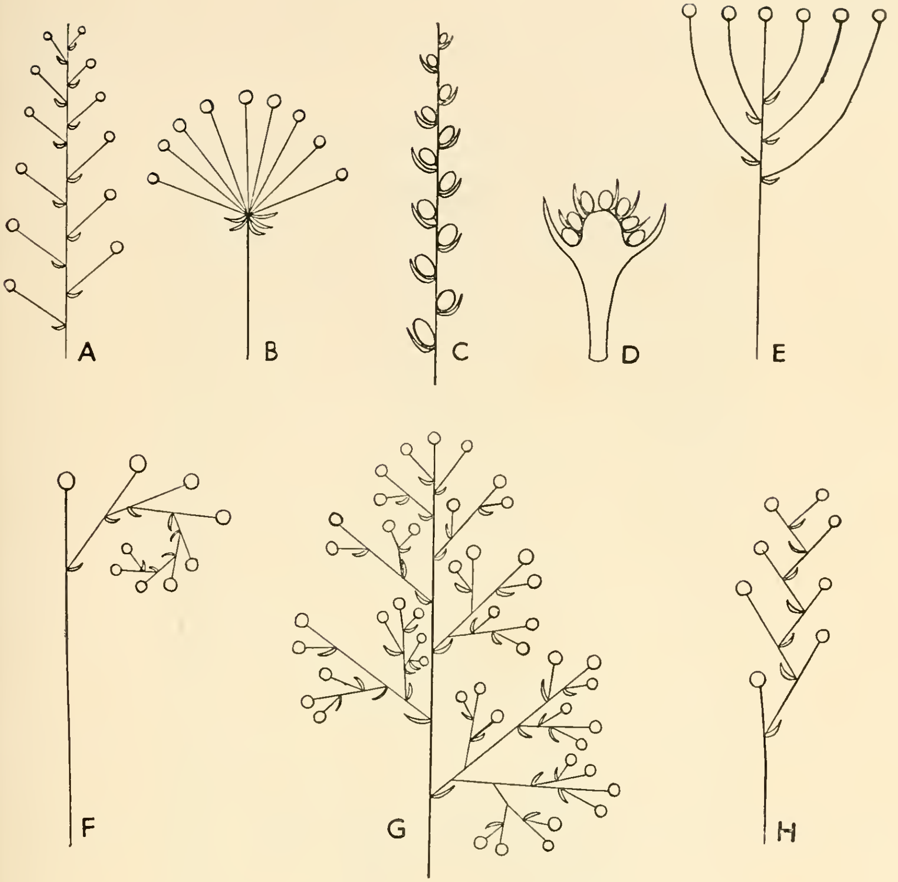

FIG. 1045.—Simple inflorescence types. A. Raceme. B. Umbel. C. Spike. D. Capitulum. E. Corymb. F. Drepanium. G. Panicle. H. Cincinnus. (*After Velenovsky.*)

mon in the compound form known as a **panicle**. This latter name has been very inexactly used. It may be taken to apply to any loosely arranged aggregate of inflorescences of which the units may be either cymose or racemose. A pleiochasium is one of the cymose types, the axis terminating in a flower, below which arise an indefinite number of laterals, each of which is itself another pleiochasial cyme with several laterals. Racemose panicles *i.e.*, compound racemes, also occur, especially among the grasses.

A mixed type of panicle also occurs, the **thyrsus**, in which the main axis is indefinite, that is, the inflorescence as a whole is monopodial, but the lateral axes are cymose. The typical thyrsus is usually somewhat condensed, as in *Syringa*. The condensed thyrsus of *Dipsacus* closely resembles a capitulum (see below), but each flower has a separate involucre and the order of opening is from the middle towards both ends, not acropetally as in a true capitulum.

Very condensed cymes are characteristic of the Labiatae, usually axillary to the leaves on the vegetative axes. As the leaves in this family are opposite, the paired cymes are contiguous around the axis, forming a false-whorl or **verticillaster** (Fig. 1046).

FIG. 1046.—*Salvia sclarea*, with flowers in verticillasters.

Monopodial inflorescences are numerous. In spite of an appearance of simplicity they are all under suspicion of being actually reduced types, and the presence in many cases of bracteoles on the flower stalks certainly suggests that the individual flowers of such inflorescences are really the terminal flowers of reduced dichasia. This is also true of many solitary flowers, *e.g.*, *Viola*, where bracteoles are present on the flower stalks, but only abnormally subtend additional flowers.

The development of monopodial from sympodial types may have followed more than one line, *e.g.*, firstly, by the reduction of lateral cymes to the status of single axillary flowers on monopodial vegetative shoots, thus giving the appearance of a monopodial sequence of flowers, or secondly, by a change in the order of flowering in a pleiochasium, the lower flowers opening while the uppermost are still in bud. Strictly considered, the latter change does not give a true monopodium, as there is still a terminal flower, however immature, but in practice it may be impossible to distinguish whether the undeveloped apex of the inflorescence was or was not a terminal flower, and in such cases we must allow ourselves to be guided by the acropetal order of flowering and place all such types under the monopodial heading.

A third method of evolution may have been through the indefinite prolongation of intercalary inflorescences, the growing point of the shoot continuing to produce bracts with axillary flowers, instead of reverting to vegetative leaves as is usual in such inflorescences.

The simplest type of monopodial inflorescence is the **raceme**, in which single flowers are borne on stalks in the axils of spirally arranged or whorled bracts. The flowers normally open in acropetal succession and the apex is either an indefinitely active growing point or else is abortive. A similar arrangement, but with sessile flowers is the **spike**, for example the inflorescence of *Plantago*, or the " catkins " of *Salix*. Where no internodes are developed these two types give rise respectively to: the **umbel**, with stalked flowers, arising from a common node; or the **capitulum**, with sessile flowers closely aggregated upon a stumpy, contracted, or even flattened axis.* Umbels may be simple or compound. In the latter each primary stalk bears a separate small umbel.

These are all relatively simple forms and where the acropetal order of flowering exists are generally recognizable.

The last of the racemose types is produced by the extra-elongation of the lower flower-stalks, which raises the flowers of the whole raceme to a common level at the top of the inflorescence. This is the **corymb**, a common type among the Cruciferae. It corresponds to the cymose rhipidium. The bracts in Cruciferae are frequently suppressed and the corymbs especially are usually without them.

It must be pointed out, indeed, that both the umbel and the corymb may be simulated by cymose as well as racemose flower groups. The order of flowering may or may not serve to distinguish them and in practice it does not seem desirable to attempt a distinction.

As we remarked above we have no direct information about the evolution of inflorescences, but we can see on biological grounds that some types offer advantages over others and we may conclude from this that they are probably more advanced. For example, compound types like the panicle afford a longer flowering period, and other things being equal this offers better opportunities for pollination, less subject to the drawbacks of temporary bad weather or accidental damage. The simple raceme may afford a similar advantage if its growth is truly monopodial and prolonged, with, in addition, some economy of material and closer proximity of the individual flowers. This latter point has often been indicated as an advantage in the condensed types, such as the capitulum, umbel, etc., but the gain in conspicuousness which, it is claimed, is thus attained by close massing,

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* The expanded basis of a capitulum is usually called the receptacle, but to avoid confusion with the receptacle of the individual flowers the term *phoranth* is to be preferred.

is usually counterbalanced by the smaller size of the flowers, and the advantage where insect visits are concerned seems to be rather in the relative ease with which cross-pollination is effected.

The most condensed types frequently resemble single flowers, particularly the capitula of various families, in which the resemblance is often enhanced by the development of pseudo-petals around the capitulum, through the alteration either of bracts or of the corollas of the peripheral flowers (Fig. 1047). The most advanced types are almost certainly the highly condensed forms in which there is specialization of function between the individual flowers, as in the spadix (spike) of *Arum* or in the cyathium (capitulum) of *Euphorbia* and in many Compositae. The degree of integration becomes, in certain cases, so great that the structure has both the semblance and the biological character of a flower while the aspect of the individual flowers is lost. The Euphorbiaceae show this in a remarkable degree. Some genera have perfect flowers arranged in catkins. In others the catkins have been condensed and show reduction. In *Euphorbia* the catkin is so reduced that it (the cyathium) has the appearance of a simple flower. In yet other types the cyathia themselves are reduced and grouped into " incyathescences ", which a further reduction again brings down to the aspect of a simple flower; two cycles of what has been called super-evolution. There are indeed numerous instances which illustrate the value and importance of the flower-model, by its re-emergence in condensed

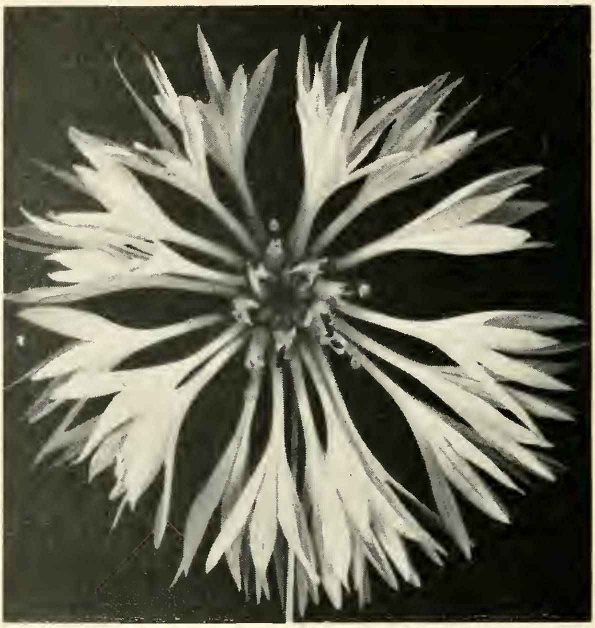

FIG. 1047.—*Centaurea cyanus.* Capitulum showing disc florets surrounded by highly modified ray florets.

inflorescences in which the structure of the individual flower has been sunk, often literally as well as figuratively, into the compound structure. The capitulum and the cyathium are the most familiar examples but cases also occur in other families.

Such a case is *Brosimum* (Moraceae). Several members of this family, notably *Morus* (Mulberry), produce short spikes in which the flowers are more or less closely united to each other and to the inflorescence axis, but in *Brosimum* this has gone so far that the male flowers of the spike are reduced to single stamens, arising from a spherical swelling enclosing a female flower, which is represented by a single carpel (Fig. 1048).

The capitulum is characteristic of the Compositae, but the same type of condensation of the inflorescence into flower-like capitula or pseudanthia, appears quite independently in Saururaceae (*Houttuynia*); Hamamelidaceae (*Rhodoleia*) (Fig. 1049); Liliaceae (*Massonia*) (Fig. 1050) and *Haemanthus*; Umbelliferae (*Astrantia*); Cor-

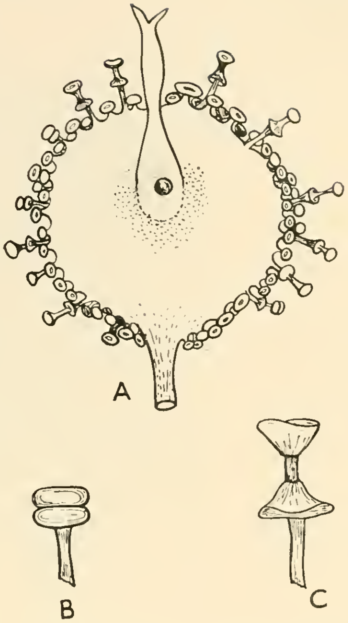

FIG. 1048.—*Brosimum discolor.* A, Median section through inflorescence with central female flower reduced to one carpel and male flowers reduced to single stamens. B, Young stamen. C, Stamen after dehiscence. (*After Velenovsky.*)

FIG. 1049.—*Rhodoleia championi.* Inflorescences simulating single flowers. (*After Velenovsky.*)

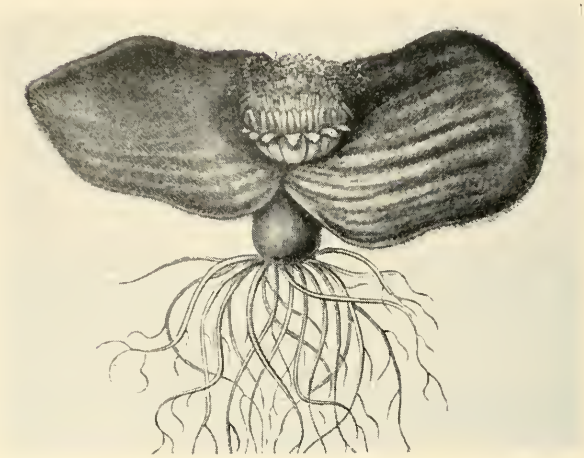

FIG. 1050.—*Massonia hirsuta*, a liliaceous plant with a terminal capitulum. (*After Engler-Prantl.*)

FIG. 1051.—*Cornus nuttalii*, inflorescences surrounded by petal-like bracts.

naceae (*Cornus*) (Fig. 1051); and Myrtaceae (*Darwinia*), and many more. An even higher level of integration may indeed be occasionally reached, as in *Echinops* (Fig. 1052) where the " flower " is actually a capitulum of single-flowered capitula, showing the flower form raised, as it were, to the third power. To approach the flower-model seems, indeed, to be a tendency pervading inflorescences throughout the Angiosperms.

FIG. 1052.—*Echinops sphaerocephalus.* A super-capitulum of reduced one-flowered capitula.

ELEMENTARY STRUCTURE OF FLOWERS AND FRUITS

The stalk of a flower, that is the internode which ends in a flower, is called the **pedicel** and the stalk of an inflorescence, on which pedicels are inserted, is the **peduncle**. At the apex of the pedicel there is an enlargement called the **floral receptacle** or **thalamus**, on which are inserted the floral parts.

The "perfect" flower comprises four sets of organs (Fig. 1053). Lowermost and outermost stand the **sepals**, which compose the **calyx** and are normally green and small. Above these come the **petals**, composing the **corolla**, usually coloured. Both sets together form the **perianth**, but either or both sets may be absent.

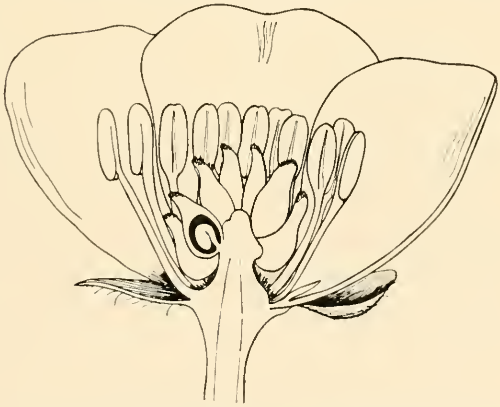

FIG. 1053.—*Ranunculus acris.* Longitudinal section of a "perfect" flower. From below in succession are seen the sepals, the petals (that on the right showing the small nectary flap), the stamens, the carpels, all inserted on the conical receptacle.

The reproductive parts come next; firstly the **stamens**, making up the **androecium,** and lastly the **carpels**, forming the **gynoecium**. The insertion of the parts on the receptacle may be wholly **spiral**, or wholly in whorls, that is, **cyclic**, or partly one and partly the other, **spirocyclic**. In most cyclic flowers there is a strict **alternation** in the position of parts in successive sets, but this is not true of spiral flowers.

Organs of one set may be **coherent** or united together, or they may be free (Fig. 1054). Organs of different sets may also sometimes be **adherent** together.

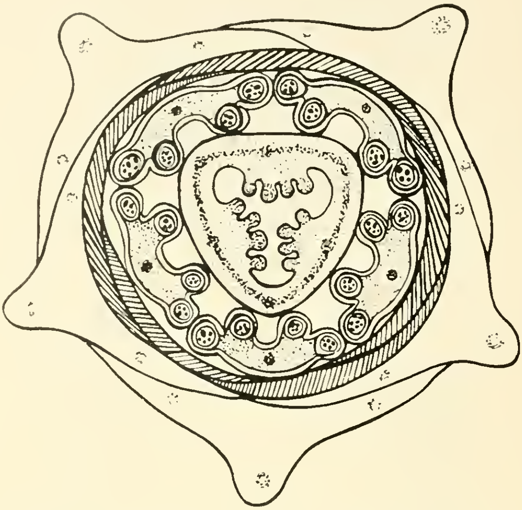

FIG. 1054.—*Passiflora coerulea.* Transverse section of a flower bud. All the parts are free except the three carpels in the centre, which are coherent. (*After Van Tieghem.*)

Cohesion affects chiefly the petals, which are either **apopetalous** (free) or **sympetalous** (joined), and the carpels which are either **apocarpous** or **syncarpous**. Cohesion of the stamens is less commonly found, but they are frequently adherent to the petals, when they are said to be **epipetalous**.

The stamen consists of a stalk or **filament**, on which is borne a head or **anther**. The anther is a four-lobed structure, each lobe containing a **pollen-sac**, and the four lobes are united round the upper prolongation of the filament, called the **connective**. Each pollen-sac or loculus contains **pollen grains**, the microspores of the Angiosperms, which are exposed when the anther splits open (dehiscence) at maturity. The carpel generally consists of three parts: the **ovary**, a hollow structure enclosing one or more **ovules**; the **style**, which is a columnar prolongation of the ovary wall, terminating in the **stigma**, an adhesive surface on which the pollen is received.

In addition to the above parts, there are also, in many flowers, **nectaries** or honey glands, which may be either outgrowths of the receptacle, or may be formed by the modification of other parts, *i.e.*, stamens, petals or sepals or of portions of these organs.

When both stamens and carpels are present the flower is said to be **hermaphrodite**. If the individual flowers contain only stamens or carpels, but both types of flowers are present on the same plant, the condition is described as **monoecious**; while if staminate and carpellate flowers are separated on different plants, it is described as **dioecious**. When all the parts of the flower are uniformly developed and arranged around a common centre the flower is said to be radially symmetrical or **actinomorphic** (Fig. 1055). If however the parts are unequally developed or arranged so as to create a bilateral symmetry, the flower is called **zygomorphic**, the single plane of symmetry, along which the flower may be divided into two equal halves, being usually vertical, that is to say in line with the inflorescence axis and the bract of the flower.


FIG. 1055.—*Tulipa sylvestris.* An actinomorphic, monocotyledonous flower. All the parts of the perianth are petaloid.

Viewed in vertical section, the arrangement of the parts, in which the carpels stand highest, *i.e.*, superior, is described as **hypogynous**. In a number of families, however, the receptacle appears to be expanded laterally, so that the perianth and stamens stand away from the carpels, on the edge of a disc, or hollow cup, which raises them to the level of the carpels or even above them. Such flowers are called **perigynous**. Finally this cup-shaped structure may completely enclose the carpels, which then appear to be embedded within a solid covering of tissue and to lie below the level of the other flower parts. The flower is then **epigynous** and is said to have an **inferior ovary**.

It is a common error of speech to refer to flowers as if they were sexual structures and to speak of the stamens as male and the carpels as female organs. While it is true that the flower serves the function of sexual reproduction, it is itself a purely sporophytic structure and its reproductive parts are sporangia. The pollen-sacs are micro-sporangia and the pollen grains are microspores. The ovules are not themselves strictly comparable to megasporangia, but they each enclose a megasporangium, containing megaspores. The gametophytic generation is represented only by extremely reduced vestiges, little more than the gametes themselves, which are produced enclosed within their respective spores. That the production and operation of the gametes are thus hidden within the organization of the flower, naturally accounts for the confusion above referred to, against which, however, the mind of the botanist should be carefully guarded. So long as the true conditions are properly understood there can be little harm in using the common parlance, which is often convenient.

The pollen grain consists of a single cell with two wall-layers; the **extine** or **exine** which is thickly cuticularized and protective, and the **intine** which is very thin. The interior of the cell is densely filled with cytoplasm and often contains abundant food reserves in the form of minute starch grains or oil-drops. When mature it contains two nuclei; one of which is the nucleus of the pollen grain itself, as a cell, while the other is enclosed within a delicate oval or lens-shaped membrane, forming a cell within a cell. This is the **generative nucleus**, from which are produced the **male gametes**. There is no trace of vegetative prothallial cells such as are found in most Gymnosperms, the pollen grain nucleus is the only vestige of the male prothallus.

The first stage in the sexual process is the transference of the pollen from the opened anther to the stigma, a process known as **pollination.** It may be brought about by movements of the parts within a single flower (**self-pollination**) but is more often carried out by external agencies, either by the wind (**anemophily**) or by insect visitors (**entomophily**) who carry the pollen from flower to flower (**cross-pollination**).

The ovules are borne upon a cushion of specialized tissue within the ovary, called the **placenta**. Each ovule consists of a central mass of tissue, the **nucellus**, which is usually surrounded by two coats or **integuments** and is attached to the placenta by a stalk or **funicle** (Fig. 1056). The integuments do not completely enclose the nucellus, but leave, at one end, a small opening, the **micropyle**, through which fertilization normally takes place. The opposite end or base of the ovule is called the **chalaza**.

Within the nucellus is the embryo sac, which is often so enlarged as to occupy most of the nucellus. At maturity it commonly contains eight nuclei; three at the micropylar end, which constitute the **egg apparatus**, one of them being the **oosphere** and the other two the **synergidae**; two nuclei lie in the middle of the sac, and are known as the **polar** or **endosperm nuclei**; while three more nuclei form a group at the other end of the sac and are called the **antipodal nuclei**. When a pollen grain has been transferred to the stigma it absorbs water and its contents begin to swell; the extine cracks and the intine protrudes from the opening as a thin-walled sac. Food reserves in the grain are hydrolysed, vacuoles are formed and growth begins. The protruding sac extends and very rapidly develops into a long outgrowth, the **pollen tube**, into which pass the contents of the grain. The pollen grain nucleus goes first and now becomes the **tube nucleus**, and the tube itself, penetrating the tissues of the style, grows towards the ovary and eventually reaches the placenta, from which it emerges and passes across any intervening space to the micropyle of an ovule, being guided apparently by chemotropic attraction (see Volume III). As the tube approaches the ovule, the generative nucleus divides into two and forms two vermiform nuclei, the **male gametes**. The tip of the tube penetrates the nucellus and on making contact with the embryo sac the walls of both structures are dissolved, possibly by the action of the synergidae. Meanwhile the tube nucleus disappears and the male gametes enter the embryo sac. One of them moves to the oosphere, the other joins the two polar nuclei. Nuclear fusion then takes place in each case, one male gamete fusing with the oosphere and the second male gamete with the two polar nuclei. During the first division of the fused nuclei the different sets of chromosomes are intermingled and fertilization is complete. There is thus a **double fertilization** of the oosphere and of the polar nuclei respectively, the latter also constituting a **triple fusion**. From the fertilized oosphere there develops the **embryo**, and from the triple polar nucleus develops the **endosperm**, or nutritive tissue, which however is sometimes abortive. During the post-fertilization developments the nucellus usually shrivels and the integuments

FIG. 1056.—Longitudinal section of the ovule of *Aquilegia*. The chalaza is above, the micropyle below. On the right is the funicle with a young vascular bundle. In the middle is the dark-coloured nucellus containing the very large embryo sac, in which may be seen one antipodal, the two polar nuclei and portions of two synergidae. The oosphere nucleus is not in the section. The two integuments can be distinguished at the micropyle end. The whole ovule is anatropous.

become altered and thickened to form the protective covering or **testa** of the seed. The matured product of the ovule is therefore a **seed**, surrounded by a testa and containing an embryo, with or without endosperm.

Simultaneously the wall of the enclosing ovary becomes altered to form the fruit wall or **pericarp**, sometimes dry and woody or leathery, sometimes fleshy, within which are enclosed the ripe seeds. The other parts of the flower are usually shed during fruit development so that finally the fruit is the only organ left on the pedicel. The fruit may, in its turn, dehisce and release the seeds, or it may be shed as a whole, with the seed or seeds still enclosed.

ARRANGEMENTS AND RELATIONSHIPS OF FLORAL PARTS

The production of flowers is generally regarded as an index of physiological maturity and the initiation of flower buds is indeed associated with biochemical changes which mark the close of a developmental phase. The onset of flowering is of course subject to influence by such external factors as temperature and length of exposure to daylight, but these factors must operate upon an organism which is, so to speak, ripe for flowering, in order to produce their effects.*

Species vary greatly in the time of onset of flowering. The ephemeral weeds, such as *Cardamine hirsuta*, may produce an inflorescence within a few weeks of germination, but some of the longer-lived forest trees may wait for thirty years before flowering for the first time. The habits of plants in this respect fall into two categories; firstly those which flower but once and then die, which are called **monocarpic**. They may be either short-lived annuals, or perennials like *Agave americana*, the giant monocotyledonous shrub which grows slowly for many years and then throws up its single immense and final inflorescence (Fig. 1057). The same habit obtains among the Bamboos and in several of the Palms. Secondly there are those which flower repeatedly, once or more every year throughout their lifetime, which are classed as **polycarpic**. This latter class have the great biological advantage that even if the period of immaturity of the individual is prolonged, there will always be a succession of new individuals reaching maturity every season. The monocarpic perennial which flowers only once after a long period of development, proceeds, as it were, by a series of jumps and is plainly in a less favourable and more vulnerable condition than the polycarpic plant, whose more nearly continuous progress from generation to generation evens out the risks from the climate or from the attacks of enemies.

Even polycarpic plants do not always flower regularly but are periodic. There are numerous examples, of which we may cite *Banksia* (Proteaceae) and the Southern Beech (*Nothofagus*). The common Beech (*Fagus*) also, though it may flower regularly, is only periodically fertile.

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* Flowering maturity is probably connected with the formation of specific growth substances in the plant, since it has been shown that naphthalene acetic acid and other synthetic growth substances can induce flowering in a number of plants.

FIG. 1057.—*Agave americana*. A monocarpic plant in flower. The upper flowers are replaced by bulbils. (Jardim botanico, Rio de Janeiro.)

Flowers are usually borne on lateral axes arising from the axil of a foliar organ called the **bract**, which is occasionally indistinguishable from a foliage leaf, but is usually different in size and often also in shape. It is not infrequently reduced to a scale-leaf, corresponding to the base of a foliage leaf, and it may rarely be entirely absent. The posture of the flower in relation to the axis and the bract varies considerably but is generally fairly constant throughout wide related groups such as Orders. This posture of the flower is defined by the position of the outermost (lowest) sepal, particularly in relation to the **bracteoles**, which arise on the pedicel in close relation to the flower. The bracteoles seem to have been primitively the bracts of further flowers, and in some cases axillary flowers arise from them, either as part of the normal branching of a cymose inflorescence or in other cases as occasional abnormalities, but in the majority of cases these lateral flowers are aborted and in many instances the bracteoles are so closely integrated with the flower which terminates the pedicel that it is impossible to say whether they ever functioned as bracts. The presence or absence of bracteoles is often very variable, even in closely related species, though whole genera, *e.g.*, in the Leguminosae, may be without them.

The lateral vegetative branches of Dicotyledons normally begin with two laterally placed prophylls and those of Monocotyledons with a single prophyll, posterior to the branch, that is, between its base and the main axis. These may be considered as the " cotyledons " of the new shoot. A similar rule holds for the flowers; Dicotyledons having two lateral bracteoles and Monocotyledons one in the posterior position. If bracteoles are absent the first sepal may either occupy the position where the first bracteole would have stood or, more frequently, the position which it would otherwise have occupied if the bracteoles had been present. For example, in Cruciferae the lowest pair of sepals lie in the plane of the axis, as if the two abortive lateral bracteoles were actually present.

Displacements of the bracteoles from their true morphological position are not uncommon. Both the bracteoles of a Dicotyledon may be displaced, anteriorly or posteriorly, and in other cases one of the two may be displaced to right or left respectively and placed at the beginning of the sequence of sepals so that in effect it becomes a sepal. This close relationship of bracteoles and sepals is shown even more clearly in those Dicotyledons which have multiple bracteoles. In these flowers a succession of bracteoles, usually paired, are closely set below the flower to form an involucre, good examples being *Camellia* and *Chimonanthus* (Fig. 1058). In many such cases it is impossible to say exactly where the involucre ends and the calyx begins. One cannot avoid the conclusion that the calyx is a progressive development from bracteoles rather than a retrogressive corolla, and the same applies to those cases in which the whole perianth is simple and consists only of sepaloid members. Such an apparent continuity between bracteoles and sepals is not however universal, for the former may sometimes be independently developed into an enlarged involucre which completely envelops

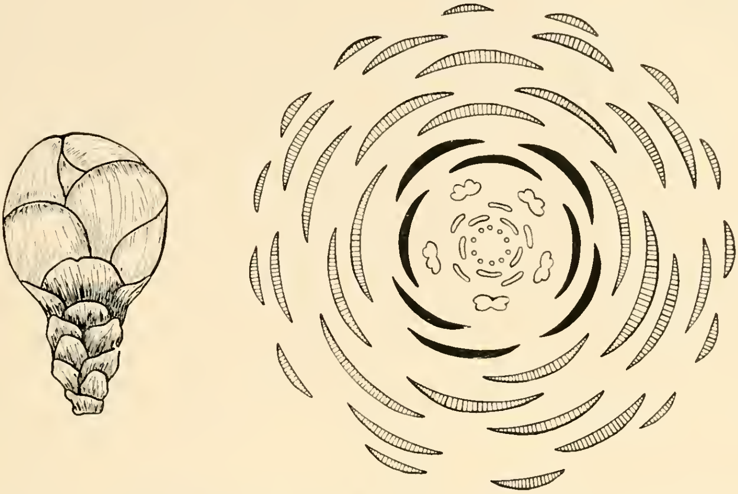

FIG. 1058.—*Chimonanthus fragrans.* A bud and a floral diagram showing the continuous sequence of bracteoles and sepals. (*After Le Maout and Decaisne.*)

the true calyx or even the entire flower bud, as in *Calystegia sepium* (Fig. 1059), but these are exceptional occurrences and do not invalidate the general conclusion of the existence of homology between the two sets of organs.

Floral symmetry is defined by the position of the flower with regard to its mother-axis. The side nearest the axis is designated **posterior** and the side away from the axis is called **anterior**. The plane passing through the axis from back to front of the flower is the **antero-posterior** or **median plane**, that at right angles to the median is the **transverse** or **lateral plane**.

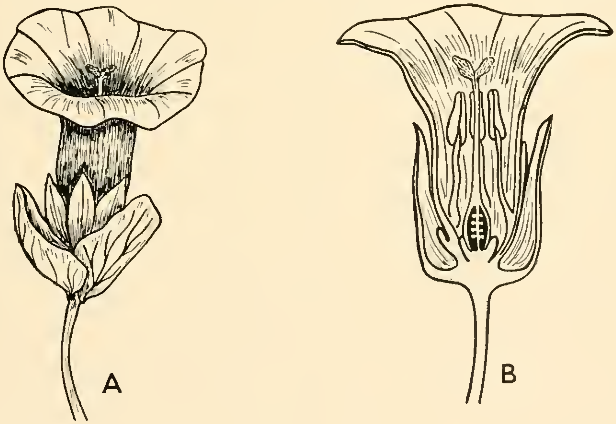

FIG. 1059.—*Calystegia sepium.* A, The flower. B, Longitudinal section, showing involucre of two bracteoles enclosing the calyx.

The **horizontal symmetry** of the flower depends in the first place on the mode of arrangement or **insertion** of the parts of the floral receptacle. Here we can distinguish three types: (1) **spiral** throughout, (2) **cyclic** throughout, that is with all the parts in distinct whorls, and (3) a mixture of both types, generally called hemicyclic or **spirocyclic**. As spiral phyllotaxy is the commonest arrangement in vegetative shoots, many morphologists have assumed that the spiral system in flowers is the earlier, more primitive, type and that the cyclic arrangement has been derived from it. Without anticipating the question as to whether a flower can be truly equated to a shoot, which we shall discuss in a later section, we may point to the fact that spiral and spirocyclic arrangements only occur in the flowers of families which, on other grounds, may be regarded as primitive, *e.g.*, Magnoliaceae Ranunculaceae, Nymphaeaceae, in whose flowers the number of parts is large and indefinite. The more advanced families, including all the Metachlamydeae, in which the flowers have a small, definite number of parts, are strictly cyclic. Even in the families mentioned the spiral arrangement is seldom complete (examples: *Caltha*, *Ficaria*). For instance, in *Nymphaea*, although all the other parts are spiral, the carpels form a whorl.

In Magnoliaceae, the perianth shows a tendency towards tripartite whorls and in Ranunculaceae to five-partite whorls, while in some of the latter family, the sexual parts, though spiral, can nevertheless be analysed into sets of three, which in species with reduced numbers of floral parts become definitely whorled.

In spiral flowers the number of parts is nearly always large and they are usually inserted on a large receptacle and are completely free from each other, but in cyclic flowers, with smaller receptacles and closer insertion of parts, modifications by **cohesion** and **adhesion** often arise. Cohesion of similar parts affects any of the organs of the flower. The sepals may be united into a calyx tube or the petals into a corolla tube, the degree of union varying in extent in both cases from complete fusion, which leaves no trace of the individuality of the members, to cohesion into a shallow ring at the base only. While the cohesion of sepals, or **synsepaly**, is a sporadic phenomenon, in regard to which even species within the same genus may differ, **sympetaly**, on the other hand, tends to run consistently through whole families and is a valuable classificatory character, due no doubt to its importance in connection with pollination. Cohesion of stamens, **synstemony**, is somewhat rarer. It is characteristic of a number of Leguminosae and is a constant feature throughout the Compositae, in both of which families the stamen tube is an essential part of the pollination

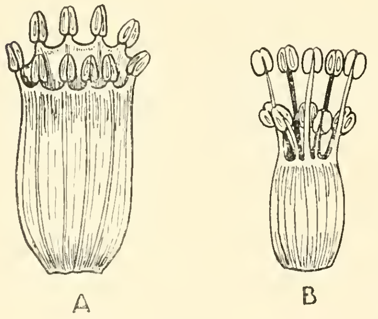

Fig. 1060.—Coherent stamens. A, *Quivisia*. B, *Oxalis*. (*After Van Tieghem.*)

mechanism. They differ in that the leguminous stamens cohere by their filaments and the anthers are free, while in Compositae the opposite obtains. Examples of synstemony occur in other families, *e.g.*, *Impatiens* and *Oxalis*, but it is on the whole an exceptional condition (Fig. 1060). Union of the carpels is, on the contrary, a common feature of floral organization. As in the other organs, it varies in extent, from union only at the base of the ovaries, as in *Tropaeolum*, to the stage where there is complete union of ovaries, the styles or at least the stylar branches remaining free, as in *Linum*, or to the further stage of the fusion of styles, but with the stigmas separate as in *Oenothera*. Finally there are innumerable cases in which union of all parts of the gynoecium is so complete that their individuality is lost in the united structure. A very unusual state is shown by *Vinca* and *Asclepias*, in which the ovaries are free but the styles and stigmas are joined.

A distinction is drawn from the developmental standpoint between various degrees of carpellary cohesion. Carpels which are wholly free are called **apocarpous**, but cases exist in which carpels really free may appear to be united, *e.g.*, *Nigella* and *Hydrocharis*, the carpels not being joined to each other but to a common axis of receptacle tissue. Carpels which are united to each other to form a compound structure are called by the general term **coenocarpous** (Fig. 1061). Where the ovary shows septation into distinct **loculi**, *i.e.*, internal spaces, corresponding in number to the united carpels, the condition is called **syncarpous**, and where there is no septation and only a single loculus, common to all the carpels, it is called **paracarpous**. The latter condition has been attributed to a shift of the fertile region, *i.e.*, the ovule-bearing placentae, into the upper portion formed by the united styles, and all stages may be observed between paracarpous gynoecia with a distinctly syncarpous base, to those in which the latter has been suppressed. The paracarpous gynoecium naturally has rarely any styles, though the stigmas may remain free. The coenocarpous gynoecium may thus be regarded as having three zones: syncarpous base, paracarpous styles and apocarpous stigmas, which may be all present, in varying degrees of development, but any of which may be suppressed. Apocarpous gynoecia are characteristic of flowers with large or elongated receptacles while the close approximation required for union of the carpels can only occur in flowers with contracted receptacles.

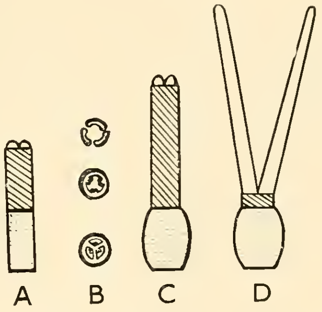

FIG. 1061.—Troll's interpretation of carpellary cohesion. A, B, Typical coenocarpous gynoecium, showing, from below, syncarpous, paracarpous and apocarpous regions, with the corresponding transverse sections. C, Typical syncarpous gynoecium. D, Syncarpous gynoecium of *Colchicum*, with long, free stylodia, which are really free, elongated stigmas, the paracarpous stylar region being almost suppressed. (*After Troll.*)

Adhesion occasionally affects the perianth members, the calyx and corolla being united, while the androecium may in some cases be united to the gynoecium. There are also certain rare instances where an inferior gynoecium is adherent to the vegetative axis or to the pedicels of neighbouring flowers (Fig. 1062), but the commonest example of adhesion is the union of staminal filaments more or less completely to the corolla. This arises from a congenital union of the two sets of primordia in the flower bud, so that for some time they appear to develop as unit structures. Separation may be so far postponed that only the anthers and the tips of the petals are free. The general term for such a congenital fusion of dissimilar organs is **adnation**, and the special, though incorrect, term applied to the stamens in this case is **epipetalous**, which should imply that the stamens are developed on the petals, but this, as we have seen, is not the case. Indeed, if, as is not uncommon, the stamens develop more rapidly than the petals, the latter may appear to arise on the stamens (*e.g.*, *Primula*), though this is only an appearance due to the different rates of development in the united rudiments.* Owing to the prevalence of strict alternation of parts in the flower, adnate stamens are generally found in sympetalous

FIG. 1062.—*Petagnia saniculifolia.* Lateral flowers adherent to the inferior ovaries of the terminal flowers. (*After Baillon.*)

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* The parallel case, of episepalous stamens, is rare, but it occurs in *Banksia* and other members of the Proteaceae.

flowers, where they are normally aligned with the sutures between the coherent petals.

In many Dicotyledons the androecium consists of two whorls of stamens, whose relative positions illustrate the principle of alternation. The stamens of the outer whorl alternate with the petals and are therefore opposite the sepals, *i.e.*, they are **antisepalous**. Those of the inner whorl are opposite the petals and are called **antipetalous**. This twofold alignment is called **diplostemony**.

Alternation of the parts in successive floral whorls is so fundamental in the structure of all cyclic types of flower that an exception to the rule calls for some explanation. Such an exception is **obdiplostemony**, which implies that the stamens of a single whorl, or those of the outer whorl if there be more than one, stand opposite the petals, *i.e.*, they are antipetalous instead of, as usual, antisepalous (Fig. 1063). This condition may be seen, for example, in *Primula*, *Vitis*, *Geranium*, *Silene* and *Viscaria* and other Caryophyllaceae and in the Chenopodiaceae, Ericaceae, Oxalidaceae, etc. Several suggestions have been made towards bringing this anomaly into conformity with the general rule. The simplest is that an outer whorl of stamens, occupying the normal antisepalous position, has been suppressed. Evidence for this is the presence in the receptacle of *Geranium maculatum* of a ring of vestigial trace-bundles outside the two extant stamen whorls and alternating with the sepals, as would be expected if they mark the position of the vanished stamens. The value of such anatomical evidence has often been doubted (see the next section) but this is a case in which it is difficult to reject it. So far as Primulaceae is concerned the hypothesis of a suppressed whorl of stamens is made practically certain by the presence of a whorl of sterile stamen rudiments in the antisepalous position in *Samolus* and *Soldanella*, both members of that family (Figs. 1064, and 1065).

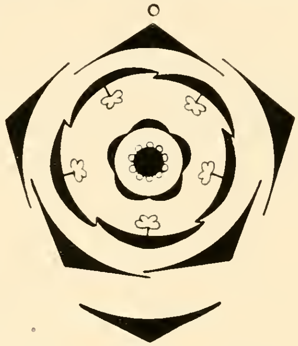


Fig. 1063.—Floral diagram of *Primula*. Stamens of the single whorl opposite the petals.

Another suggestion is that the petal and its superposed stamen are a single morphological unit, the petals in such cases being the product of the abaxial fusion of a pair of staminal stipules. Lateral outgrowths of the stamen filament frequently occur, whether they are truly stipular or not, and that these may fuse behind the stamen seems to be borne out by the formation of the " corona " or inner corolla in the flowers of some Amaryllidaceae, *e.g.*, *Narcissus*. The bifid outline of the petals in many Caryophyllaceae, especially well marked in *Stellaria*, accords with this idea and it may be the explanation in some cases, if not in all. A third theory, due to Payer and involving less supposition than the others, is that there has been an apparent inversion of the stamen whorls in the flower, due to the larger size and more rapid growth of the primordia of the antisepalous stamens and of the corresponding sectors of the receptacle, which crowd out the upper, antipetalous stamens from their proper places, forcing them outwards so that they appear to be the outer whorl. Even when fully developed the petal-stamens are usually smaller than the calyx-stamens; they are often reduced to staminodes and are sometimes missing. The petals themselves may be affected by this overgrowth of the sepal sectors of the receptacle and in obdiplostemonous flowers are often reduced or missing, as in the Chenopo-

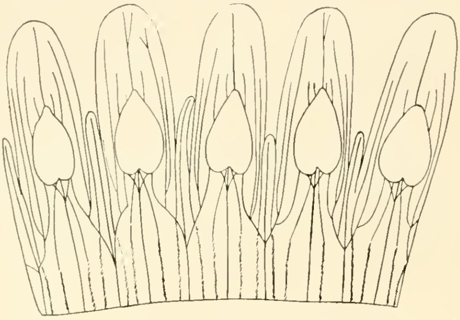


Fig. 1064.—*Samolus repens.* Flower opened out to show the rudimentary stamens of the outer whorl alternating with the petals. (*After Saunders.*)

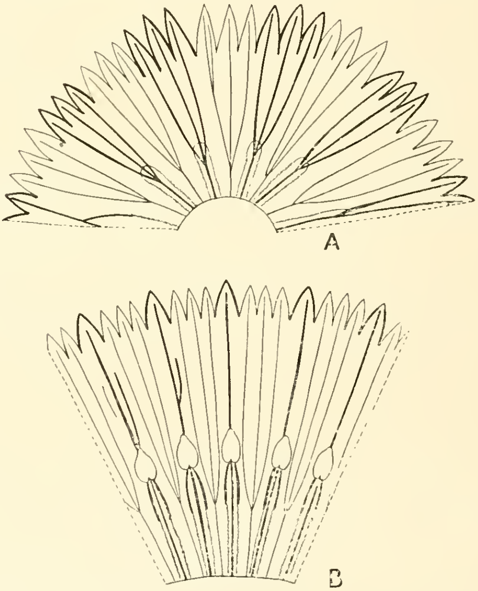


Fig. 1065.—A, *Soldanella alpina.* B, *S. pusilla.* Corollas opened out showing the outer, antisepalous staminodes incorporated into the corolla, alternate with the petals. Petals indicated by heavier outlines. (*After Saunders.*)

diaceae. This theory is supported by observations on the flower primordia and by the comparison of related genera. In *Stellaria media* variations of the normal flower occur, with petals and antipetalous stamens suppressed. This is paralleled by the normal structure in other genera. In *Corrigiola littoralis* the antipetalous stamen whorl is absent; in *Scleranthus perennis* the petals are absent and sometimes also the antipetalous stamens; in *Paronychia* species both sets of organs are absent.

The alternation rule naturally does not apply to spiral flowers, nor does it strictly apply where the number of parts in successive whorls is not the same. The carpels, for example, are often fewer in number than the stamens, and no fixed rule applies to their relative positions. There is usually the nearest approach to alternation that is compatible with the symmetry of the particular flower, for which the mechanical necessities of space-filling in the limited room available may be held accountable.

All flowers in which the arrangement of parts around the axis is symmetrical about at least two planes are called **actinomorphic**. That this is the fundamental type of flower symmetry is witnessed by two facts; in the first place by the rule of **equidistance**, which is no more than the observed fact that the insertions of floral parts are normally equally spaced around the receptacle, and by the further observation that even in irregular flowers the receptacle itself is normally circular in section, exceptions, such as the oval receptacle of *Reseda*, being relatively rare. Thus the earliest stages of development are normally actinomorphic, even in flowers where this is afterwards changed.

Actinomorphic symmetry is maintained even when the numbers of parts in the floral whorls are variable. This may be seen by comparing terminal and lateral flowers in some inflorescences (*e.g.*, *Berberis* and *Sanguisorba*) where the terminal flowers often have an increased number of parts. Variations may also arise from chorisis (see p. 1105) and in other ways. The situation is met by the redistribution of parts around the receptacle so that equidistance is maintained and the circle of 360° is equally divided between the parts.

Radial symmetry is, however, replaced in many species by bilateral symmetry about a single median plane, which may be antero-posterior, transverse, or oblique, such flowers being called **zygomorphic**. Some rare cases occur of **asymmetric** flowers, chiefly among the Marantaceae, in which there is no plane of symmetry.

The irregularities which produce zygomorphy are of four distinct kinds, which may be present separately or, more often, together. The following are instances in which they occur separately. (1) Reduction in the number of one category of parts in relation to the others. Some of these cases are doubtful. For example, the partial sterilization of three stamens out of six in *Commelina coelestis* or the suppression of two carpels out of three in *Viburnum lantana* (Fig. 1066) creates zygomorphy in these flowers, but the rest of the parts retain radial symmetry. The zygomorphy in such cases is not obvious to the eye and is only to be discovered by careful analysis.

Fig. 1066.—Floral diagram of *Viburnum*. Only one carpel of three is fertile.

The suppression of a petal, like the posterior petal in *Koelreuteria*, has an obvious effect. (2) The fusion of equal parts, especially members of the perianth, into unequal groups. This seldom occurs in the absence of other irregularities, an exception being the two-lipped corolla of *Lonicera* (see Fig. 1244). (3) Lateral displacement of parts, not associated with fusions or other irregularities, hardly ever occurs, as might be deduced from the general principle of equidistance. The appearance of such displacement, creating a superficial or positional zygomorphy, may arise from the lateral bending of mature parts, which are symmetrically inserted, as in the corolla of *Rhododendron* (Fig. 1067) and *Dictamnus* (Fig. 1068). (4) By far the most

Fig. 1067.—Positional zygomorphy of the corolla in *Rhododendron*.

Fig. 1068.—Positional zygomorphy of the corolla in *Dictamnus fraxinella*. A visiting bee is seen below.

important cause of zygomorphy is the unequal development or heteromorphy of parts. Any of the floral organs may be thus affected and the examples are countless. To cite one conspicuous example where the petals are heteromorphic although the ground plan of the flower is regular, we see in *Saxifraga sarmentosa* (Fig. 1069) a flower in which two petals are much larger and longer than the other three. A similar heteromorphy of the petals is very common in the peripheral flowers of crowded inflorescences, as in Umbelliferae, Compositae, etc., in which the outwardly directed petals are much enlarged. The flowers of those families in which zygomorphy is most characteristic, *e.g.*, Scrophulariaceae, Labiatae, Leguminosae, show, however, combinations of more than one of the above features. The more extreme the zygomorphy the greater is the number of the flower parts which are affected by irregularities and the more marked are the differences between them.

Fig. 1069.—Zygomorphy of the corolla due to heteropetaly in *Saxifraga sarmentosa*.

The plane of symmetry in zygomorphic flowers is usually the anteroposterior plane which passes through the bract and the inflorescence axis, but in many Solanaceae such as *Datura*, the plane of symmetry is oblique, due to the obliquity of the bicarpellary ovary, and in a few cases, such as *Corydalis* and *Dicentra* (in Fumariaceae), the plane of symmetry is transverse. Obliquity of the plane of symmetry may also arise during floral development through the torsion of the pedicel, as happens in *Corydalis*. The complete inversion of the flower by the torsion of its support is called **resupination**. It is met with consistently in the median zygomorphic flowers of the Orchidaceae and Lobeliaceae, though in the former case, there being no pedicel, it is the sessile inferior ovary which is twisted through 180°.

Resupination is a puzzling character, which appears here and there in a number of families, but only in insect-pollinated flowers. In some cases, it provides a better landing ground for the insect visitor, but this is not invariable. Its utility may vary in different cases, but some relation to pollination conditions is indicated.

Zygomorphy is most general in lateral flowers; terminal zygomorphic flowers are rare. It is therefore generally associated with racemose inflorescences. Occasionally terminal flowers may appear in an inflorescence of zygomorphic flowers, but they are then anomalously actinomorphic, due to the formation of compensating irregularities all round the flower, which is also sometimes monstrous. The abnormality is hereditary in certain strains, as in the well-known "Gloxinia-flowered" Foxglove (*Digitalis*) (Fig. 1070). The condition is called **peloria** (see p. 1156).

Comparison of flowers in respect of their vertical, as distinct from their horizontal symmetry, shows that this frequently varies according to the form of the floral receptacle (see p. 1103), but that variation in other respects is decidedly rare. The normal seriation of parts, for example, is highly constant. In *Malus spectabilis* carpels sometimes arise among the stamens, but this is an inconstant anomaly. In *Triglochin maritimum*, on the other hand, it is surprising to find, as a normal feature, a whorl of perianth members apparently intervening between the two whorls of stamens (Fig. 1071). A displacement of the outer staminal whorl suggests itself as an explanation, similar to that taking place, according to Payer, in obliplostemonous flowers.

Fig. 1070.—*Digitalis purpurea.* Inflorescence with large terminal, peloric flower, which is actinomorphic, while the lateral flowers are zygomorphic. (*After Velenovsky.*)

An analogous displacement during ontogeny is also probably the origin of the condition in the few observed cases (*Dichapetalum*, *Lychnis*) in which stamens and petals appear to form a single whorl, an occurrence which is otherwise at variance with the theory of zonal differentiation of the floral receptacle, which we shall speak about hereafter (see p. 1131).

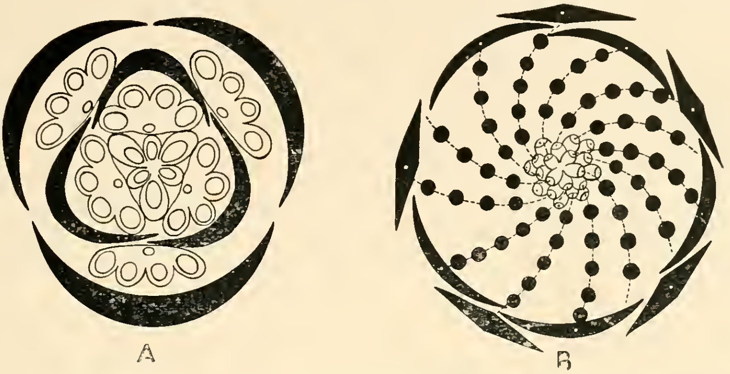


FIG. 1071.—Floral diagrams. A, *Triglochin maritimum.* The two whorls of stamens are apparently separated by perianth members. B, *Ranunculus acris.* Holospiral construction with 13 parastichies. (*After Hirmer.*)

The arrangement of parts in a flower and its horizontal symmetry can be most simply and clearly expressed in the **floral diagram**, or ground plan of the flower, on which the various parts are represented as projected in one plane. Developed by Payer and Sachs from the phyllotaxis diagrams of Schimper, the floral diagram showed itself in the hands of Eichler (1875) to be an invaluable aid in the analysis of floral structure (Fig. 1072). Sepals

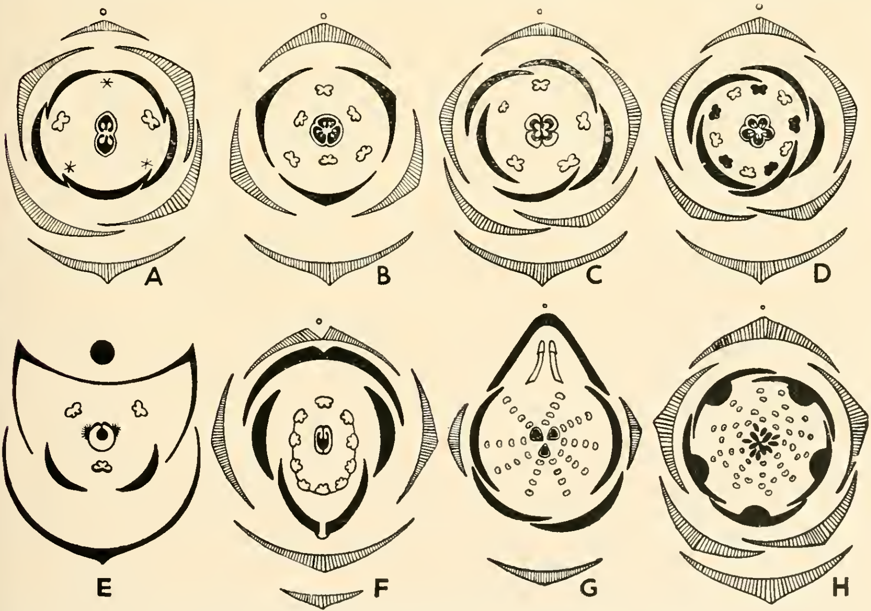


FIG. 1072.—An illustrative selection of floral diagrams. (Mostly after Eichler.) A, *Veronica*. B, *Lilium*. C, *Echium*. D, *Dictamnus*. E, *Poa*. F, *Vicia*. G, *Aconitum*. H, *Ranunculus*.

and petals are usually symbolized by conventional crescent-shaped outlines; stamens may also be symbolized by points or by outlines of the anthers in cross-section. The gynoecium is represented by a cross-section of the ovary. The positions of bract, bracteoles and axis are usually indicated outside the flower and accessory structures inside it, such as nectaries, may also be indicated. In the plan of the perianth account must be taken of the relative sizes of the members, and of course, of any departure from normal equidistance in any region. Similarly the spiral or cyclic sequence must be shown, and the cohesion or adhesion of members is indicated by lines of linkage drawn between them. Irregularities should also be shown, such as the presence of a petal or sepal spur, which is indicated by a loop attached to the back of the appropriate symbol. Lastly it may sometimes be desirable in special cases to mark with a cross or a dotted line the positions of lost or abortive members.

A floral diagram thus constructed is an abstraction, in so far as it omits all the small details which make up the specific personality of a flower. It is a generalization which, in many cases, holds good for an entire genus or even for a number of genera in a family and it is, finally, an interpretation, in obscure cases, of the morphological conclusions of its author.

Alongside the floral diagram we must rank the **floral formula**, which we owe to Grisebach. In this we summarize the numbers of the parts, under the initial letters: K (Calyx), C (Corolla), A (Androecium) and G (Gynoecium). P (Perianth) may be used where there is no distinction of calyx and corolla. Each initial is followed by the number of the respective organs, placed between brackets if they are coherent, and divided between their respective whorls if more than one whorl of any given member is present. If the number of parts is large and variable the sign α is used instead of a number. Thus:

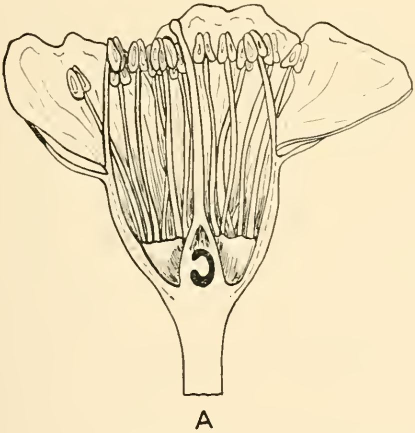
Ranunculus	K5	C5	Aα	G$\underline{\alpha}$	⊕
Convolvulus	K5	C(5)	A5	G($\underline{2}$)	⊕
Cytisus	K(5)	C5	A(5+4)+1	G $\underline{1}$	·|·
Galanthus	K3	C3	A3+3	G($\overline{3}$)	⊕

The symbol ⊕, if added, indicates actinomorphy, and ·|· indicates zygomorphy. The lines above or below the figure for the gynoecium indicate an inferior or superior ovary, respectively. If two distinct sets of parts are adherent, the figures for the two sets may be enclosed in square brackets.

A flower in which the number of parts in each whorl is the same throughout the flower is called **isomeric**, as for example in certain species of *Sedum* in which the floral formula is K5 C5 A5 G5 or in Liliaceae, P3+3 A3+3 G3. The opposite condition, where there are unequal numbers, is called **heteromeric** or **heterocyclic**, *e.g.*, *Nicotiana*, K5 C5 A5 G2.

The **vertical symmetry** of the flower, that is the relation of its parts as seen in vertical, median section, varies according to the position of the gynoecium in relation to the other parts. In the majority of flowers the receptacle is either conical or spheroidal in shape, and the order of parts is that which we have described as typical, namely, sepals, petals, stamens, and carpels, the latter occupying the highest position, around the summit of the receptacle. Such flowers are called **hypogynous** (Fig. 1073), because the other parts stand below the gynoecium. In a number of cases, however, the receptacle appears to be expanded laterally, so that a **floral disc** is formed, sometimes, as in the Strawberry, surrounding a normal conical receptacle, sometimes replacing this entirely, so that the whole receptacle is saucer-shaped or even cup-shaped. This disc has sometimes been given the status of a distinct organ, under the name of the **torus**, but this involves the idea that in hypogynous flowers it is present in a suppressed condition as a special zone or layer of the receptacle, for which there is no direct evidence. The surface of the disc is sterile and the perianth and stamens, being attached to its rim, are thereby elevated to a level with the carpels. This is the **perigynous** condition (Fig. 1074). The cup may in some cases, as in the Rose, become, in fact, a flask within which the carpels

Fig. 1073.—Longitudinal sections of hypogynous flowers. A, *Adonis*. B, *Helianthemum*.



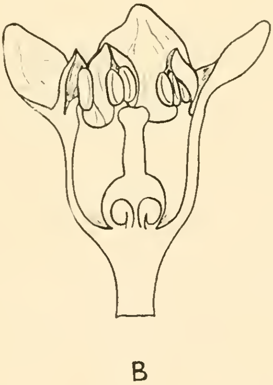


Fig. 1074.—Longitudinal sections of perigynous flowers. A, *Prunus*. B, *Rhamnus*.

are contained, though so long as the flask retains an open mouth, the flower is still called perigynous. But the extreme expression of this tendency to enclosure of the carpels seems to be reached in those flowers in which the carpels are not only enclosed, but organically fused to the inner wall of the container, whose rim, bearing the outer organs of the flower, now seems to have closed over the gynoecium and to be no longer distinguishable from the ovary walls. The perianth and stamens are thus superposed on the carpels and the flower is called **epigynous** (Fig. 1075). The relative position of the gynoecium is also expressed by referring to it as **superior** and **inferior** in the respective cases.*

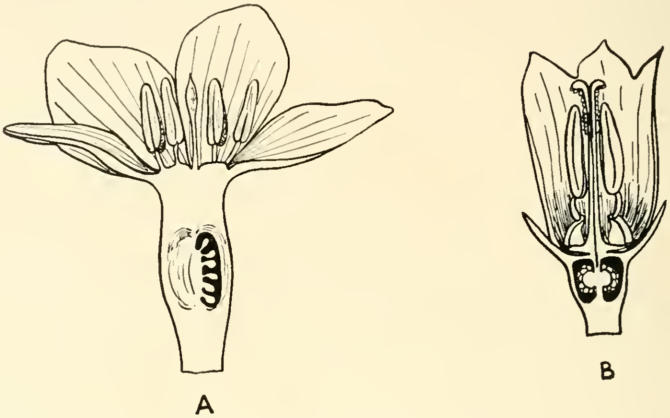


Fig. 1075.—Longitudinal sections of epigynous flowers. A, *Leucojum*. B, *Campanula*.

We have deliberately used the words " appears " and " seems " in the above description, which reflects views long current, because the true course of events in the development of epigyny has been much disputed. The one point of general agreement is that epigyny is more advanced in an evolutionary sense than hypogyny, and hence that the problem is the development of the inferior ovary from the superior, rather than the reverse.

There are three main theories, with variations. The oldest, which dates from de Candolle, looks upon the carpels as having been enclosed by the concrescent bases of the other floral parts. This is called the " appendicular theory ", since these floral parts are regarded as phyllomes and hence as appendages of the axis. The second theory considers the whole inferior ovary as formed from the hollowed receptacle, the carpels being either non-existent or else reduced to the styles and stigmas, with, sometimes, carpellary placentae in the " ovary ". This is the " axial theory ". The third theory also accepts the idea of the hollowed receptacle but maintains that the carpels are present, fused to the inside of the receptacle cup.

All three views are based upon an assumed antithesis between the axis and its appendages which now seems old-fashioned, and it may be said that

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* For a fuller discussion of the problem of epigyny see p. 1135 in the section on the floral receptacle, and also p. 1137 in connection with the inferior ovary.

an uncompromising adherence to any one of the three theories has led to some remarkably twisted interpretations of difficult cases. On the other hand evidence has been produced, especially from floral anatomy, giving support to each of the theories respectively. Considering this and considering also the great plasticity of floral organs and the vast range of variation in known floral structure, it does no violence to the probabilities if we conclude that epigyny has been reached by various means and that no uniform explanation can be devised, though modern evidence favours the view that the receptacular type of inferior ovary, which truly involves an invaginated axis, is at least uncommon.

We have referred above to the fusion of floral parts as a common phenomenon. Less common but yet not rare is the opposite event of the splitting of an organ originally single. This was first recognized by Payer in his great work on the ontogeny of flowers (1857) which provides a wealth of information on the subject. He called it *dédoublement*, but the term in general use is Eichler's **chorisis**. No genuine distinction can be drawn between the branching of an organ, which partially divides it, *e.g.*, the stamens of *Tilia*, and congenital chorisis, in which two rudiments appear in a position where only one would be expected either from the general symmetry of the flower, or from comparison with allied types (Fig. 1076). It is, however, possible to distinguish a simple splitting, such as that of the stamens of *Adoxa* (Fig. 1077) or *Carpinus*, where each portion carries only two pollen loculi and is plainly the half of a complete anther, and a true chorisis from which two, or sometimes more than two, apparently complete members results—a species of twinning—even although the twins may re-

FIG. 1076.—Androecium of *Vella* showing chorisis of stamens. (*After Velenovsky.*)

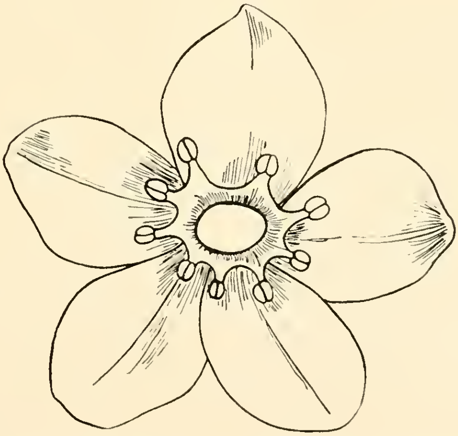

FIG. 1077.—*Adoxa moschatellina*. Flower showing chorisis of stamens. Each filament bears only a half-anther. Gynoecium omitted.

main united in their basal regions. Chorisis is most frequently observed in stamens and we shall give further examples later in this chapter under the heading of " The Androecium ". In double flowers however, both stamens and petals may be affected by it, the former being, in addition, modified into petaloid structures. Where the division takes place along the radial plane, we speak of lateral chorisis and where it is tangential to the flower it is called parallel or serial chorisis. Occasionally both may occur together. Chorisis is not to be regarded simply as a monstrosity, though it may sometimes produce abnormal forms like double flowers. On the contrary, it is often a constant or even a distinguishing feature of whole genera like *Butomus* and *Scleranthus* (Fig. 1078), or some genera in the Cruciferae (see p. 1176).

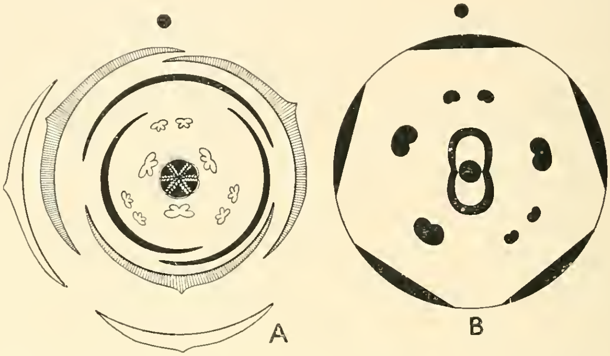

Fig. 1078.—Floral diagrams. A, *Butomus*. B, *Scleranthus*.

We have referred above to the fact that in the comparatively unspecialized spiral flowers the numbers of parts are usually large and indefinite. It is an observed fact that parts of any one kind which are numerous have smaller rudiments and less constant numbers than parts of which there are only a few. This rule is one with a widespread application and it can be observed in animals as well as in plants. Among Angiosperms, the cyclic arrangement necessarily limits the numbers of organs, unless, like the stamens of the Poppy, they are very small, and flowers of specialized structure are all cyclic and oligomerous, that is, have small numbers of parts. Floral evolution has, in fact, been accompanied by much material reduction, although it is associated with greater sexual efficiency.

When we compare extremes, such as *Nymphaea*, with very many parts, and *Galium*, with few, the general evolutionary tendency towards oligomery is undeniable, but in the intermediate regions fluctuations of the numbers of parts, or **meristic variation**, are quite frequent, involving both **meiomery** or reduction, and **pleiomery** or multiplication. Only the most advanced families show a high degree of fixity of numbers.

Meiomery may involve abortion, that is the disappearance of parts, sometimes partially, with a rudiment remaining, sometimes so completely that no trace remains, even in the microscopic anatomy.

Meiomery is more frequently due to fusion of members than to suppression, an interesting example being the transformation of a perianth consisting of two trimerous whorls into one pentamerous whorl by the fusion of a member of the outer whorl with one of the inner. In some other cases suppression certainly occurs, for example in *Ranunculus auricomus*, and *Anemone nemorosa*, where partial or total suppression of the perianth may be observed, in varying degree, even among flowers on the same plant.

Pleiomery is a natural consequence of chorisis, but it may also result from the reduction in size of organ rudiments, which permits larger numbers to be formed in a given space on the receptacle. Meristic variations of either kind may occur either sporadically within the limits of a single species or as a constant feature distinguishing whole species or genera from those most nearly related to them.

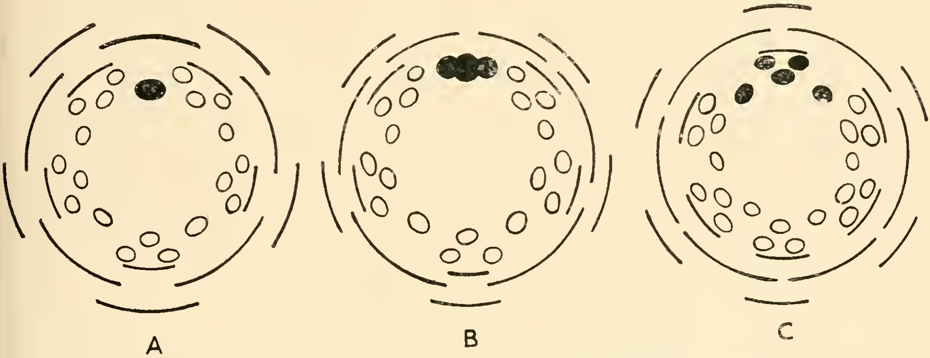

FIG. 1079.—*Comarum palustre.* Diagrams of three flowers showing pleiomery of the posterior stamen of the inner whorl causing change from pentamery to hexamery. (*After Goebel.*)

An instance of the first kind is the variation in the number of stamens in *Potentilla* (*Comarum*) *palustris* (Fig. 1079). The posterior stamen of the antisepalous whorl sometimes divides into three and this is associated with chorisis of the opposed sepal and the intercalation of a new petal, thus transforming a pentamerous flower into a hexamerous one. This exemplifies the point that meristic variation is seldom confined to a single organ, but seems to affect whole sectors of the receptacle, in which growth is either increased or decreased, relative to the other sectors, with corresponding effects on the numbers of the parts included in those sectors. Salisbury has examined large numbers of flowers in certain genera of Ranunculaceae, *e.g.*, *Eranthis*, *Ficaria* and *Anemone* (Fig. 1080), in which meristic variation is very prominent, and has shown that there is a decided correlation between the numerical condition in different parts of the flower, increase or decrease in numbers being, in general, exhibited simultaneously by the perianth, androecium and gynoecium. Branching of stamens and carpels and lobing of the petals illustrate the tending to multiplication by fission. Only in the case of the corolla is there evidence of increase occurring by the transformation of other floral organs, in this case of the stamens.

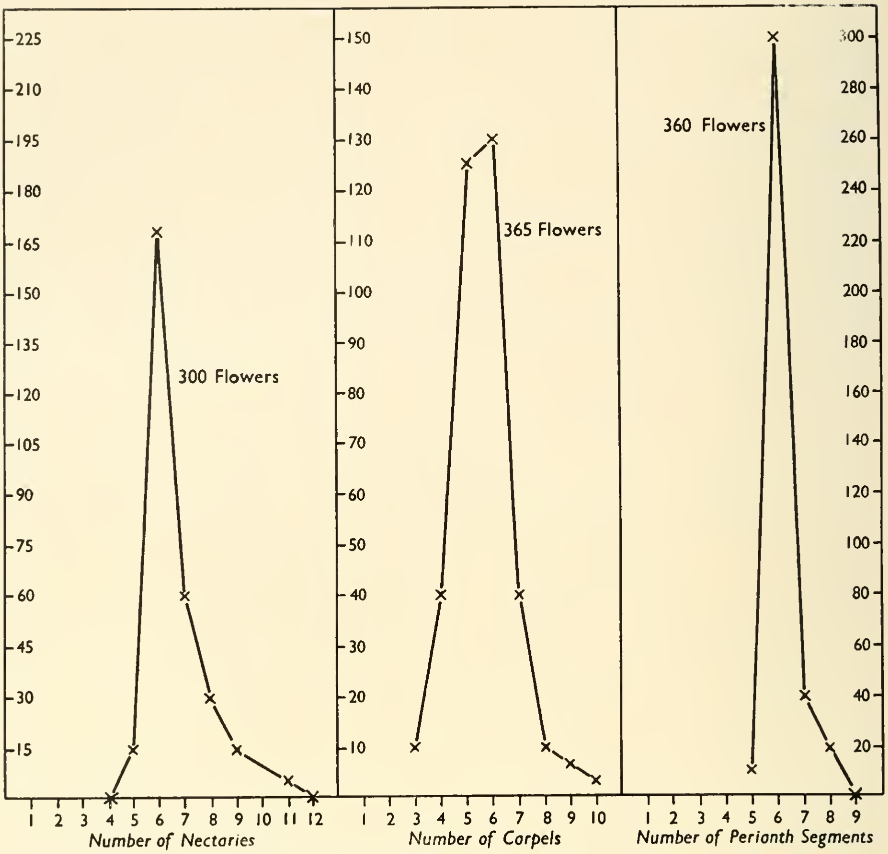

FIG. 1080.—*Eranthis hiemalis.* Graphs showing the extent of meristic variation. (*After Salisbury.*)

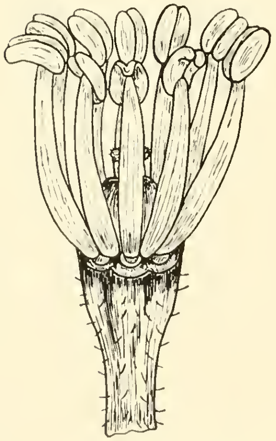

FIG. 1081.—Pleiomeric androecium in *Megacarpaea* (Cruciferae).

It is clear from these observations that fluctuating variations in the numbers of parts are continually appearing in certain species. On the other hand a particular meristic change may be a constant in some species and genera, in the sense that they are distinguished from related types either by a characteristic pleiomery or meiomery of parts. Thus *Megacarpaea* (Fig. 1081) is peculiar among the Cruciferae in having ten or more stamens instead of six and *Veronica* is distinguished by the reduction of its stamens to two instead of the five which make the full complement in Scrophulariaceae. No trace of the missing stamens remains in *Veronica*; it is an example of complete abortion, or **ablasty**, without even rudiments being formed. Numerous other genera of the same family show a reduction of stamens from five to four, and in some of these, notably in *Pentstemon*, the missing posterior stamen is represented by a partially developed rudiment, or **staminode**. Analogous abortion of parts is commonly associated with zygomorphy in many families. Flowers in which parts have been suppressed are usually called " reduced ", but the question whether apparently simple flowers are always the result of reduction has been disputed, especially by some European botanists, who have maintained that certain groups of simple flowers, with only a simple perianth or none and with only one type of sex organ developed, are in fact primitive and most nearly related to the presumed gymnospermic ancestors of the Angiosperms. This view has found less support in recent years, though it is still upheld by some palaeobotanists.

Evident reduction is shown by flowers in which whole categories of parts, present in their nearest relatives, are missing. Thus, the common Ash, *Fraxinus excelsior*, has achlamydeous, unisexual flowers, though it belongs to a family, the Oleaceae, whose flowers are normally bisexual and provided with a perianth. Similarly, in the Composite genera *Haastia* and *Xanthium*, the female flowers are reduced to a carpel with no perianth. Extreme reduction characterizes the genus *Euphorbia*, in which the male flower is reduced to a single stamen, terminal on its pedicel. In *Naias*, the male flower consists of one stamen, with a one-membered, enveloping perianth, and the female flower consists of a single, naked carpel (Fig. 1082). *Callitriche* has achlamydeous flowers, the place of the perianth being supplied by two lateral bracteoles, between which, in the male flowers, stands a single stamen, while the female flower has two joined carpels (Fig. 1083). Many similar examples could be quoted. Some families, for example, the Araceae, display a reduction series, from complete bisexual, trimerous flowers in *Orontium* (Fig. 1084) to unisexual naked flowers with one carpel or two stamens in *Spathicarpa* (Fig. 1085).

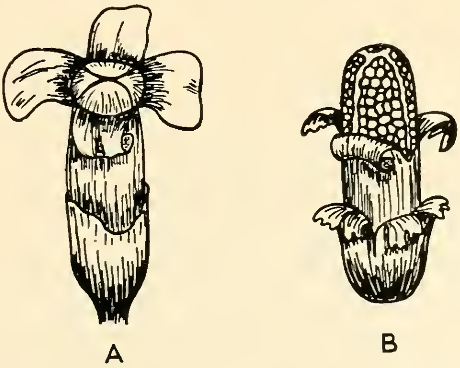

Fig. 1082.—Male flowers of *Naias*. A, Half open. B, Older flower with dehiscent anther. (*After Le Maout and Decaisne.*)

Lesser degrees of reduction, involving only meiomery of certain whorls,

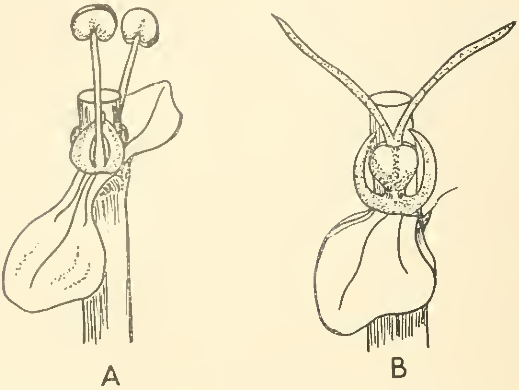

FIG. 1083.—Flowers of *Callitriche*. A, Male. B, Female. (*After Le Maout and Decaisne.*)

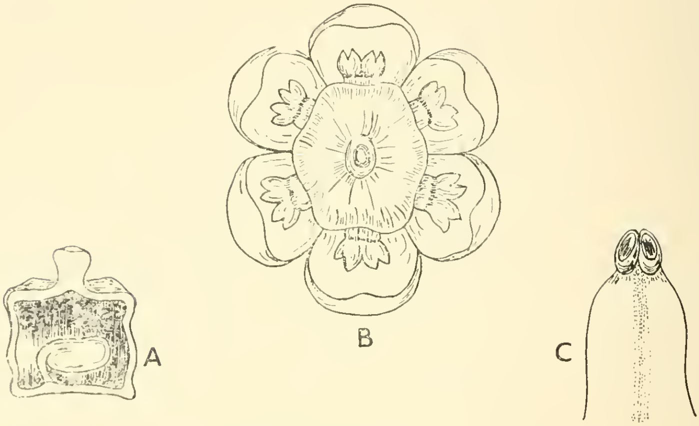

FIG. 1084.—Flower of *Orontium aquaticum* (Araceae). A, Ovary in section. B, Entire flower. C, Stamen. (*After Le Maout and Decaisne.*)

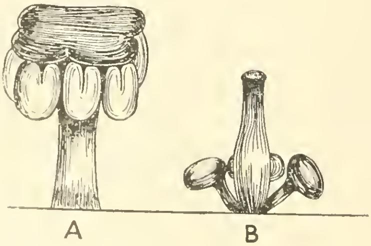

FIG. 1085.—*Spathicarpa sagittifolia* (Araceae). A, Male flower. B, Female flower. (*After Engler.*)

we have already mentioned as being a common cause of zygomorphy, and such cases are too numerous to specify.

Reduction in the most general sense seems to have been concomitant with floral evolution. Spiral flower types are usually polymerous, the cyclic flowers on the other hand show a general stabilization at the level of 4 or 5 parts per whorl in Dicotyledons and 3 per whorl in Monocotyledons. A corresponding reduction in the number of cycles takes place. Spiral flowers may have 15 or 16 tiers of parts, but the majority of Dicotyledons are normally pentacyclic with five whorls (calyx, corolla, stamens (2), carpels) and the more advanced familes are normally tetracyclic, with only one whorl of stamens.

It is a significant fact that when the corolla is suppressed the sepals often become transformed into the semblance of petals and are called **petaloid**. The change is seen in many genera of the Ranunculaceae, *i.e.*, *Caltha*, *Eranthis* and *Helleborus*, where the petals are either missing or are transformed into nectaries. Such an exchange of character affects other organs besides sepals. Petals may become **sepaloid**, as in *Empetrum*, the Crowberry, although such a modification is not very common, most flowers with sepaloid perianths being only monochlamydeous, *i.e.*, they have no true corolla.

More frequently, stamens may become petaloid, and this is the most general cause of **doubling**. The most completely double flowers show complete petalody of all the sporogenous members, both stamens and carpels, with consequent sterility, but more often only the stamens, or in polyandrous flowers, like *Rosa* (Fig. 1086) and *Paeonia*, only a variable proportion of the stamens, are affected. In such cases intermediate organs are commonly found, for example, stamens with petaloid filaments, which

FIG. 1086.—Double Rose of the "Hybrid Tea" group. ("Betty Uprichard".)

retain a more or less functional anther attached (Fig. 1087). In completely petaloid stamens pollen formation is generally suppressed or if a remnant of an anther persists, only sterile pollen is formed.

Fig. 1087.—Flower of *Rhododendron* with petaloid stamens, in front and side views.

Fig. 1088.—A double *Fuchsia*. Only the petals are affected by chorisis, which has increased their number.

Transformation of organs is not, however, the only way in which doubling of flowers occurs; additional organs may be produced by the serial (tangential) chorisis of existing organs. In the double Pink (*Dianthus*) the stamen rudiments divide repeatedly in this manner, some of the segments becoming petaloid, others developing into normal stamens. In the double *Fuchsia*, on the contrary (Fig. 1088), chorisis affects only the petals, the number of which is greatly increased, forming several whorls, without the androecium being affected. Occasionally both methods, petalody and chorisis, may be combined, with the result that double flowers are formed in which the number of petals exceeds the total number of petals and stamens in the normal flower. The double Buttercup is a good example and Pliny's "hundred-petalled Rose" (*R. centifolia*) is another. To an older generation of morphologists the phenomenon was known as "petalomania".

A minor anomaly, which may be included under the heading of doubling, is that sometimes seen in *Primula* and other sympetalous flowers, where an abnormal, petaloid calyx forms an exterior "corolla", enclosing the normal one and producing what gardeners call the "hose-in-hose" varieties.

The physiological causes of doubling are still obscure, but high nutrition seems to favour it, and although double flowers are sometimes found wild, their low fertility is a hindrance to their survival in that state. Doubling is commoner in cultivation, where, on the contrary, the artificial taste of florists ensures their perpetuation. The tendency is hereditary in certain strains, and if a double flower yields good seed, its progeny frequently produce a high percentage of doubles, *e.g.*, about 60 per cent. in the garden Stock (*Matthiola*). The character is not, however, genetically fixed and its expression depends on maintaining good cultivation and rapid growth, without which the majority of the seedlings will only display the single form.

Some species of plants habitually produce flowers of more than one form on the same individual. This is called **heteranthy**. Many instances occur of variation in the distribution or development of the sporogenous organs among flowers on the same plant (see p. 1269), but such variations do not as a rule affect the general model of the flowers, though male and female flowers in monoecious and dioecious species may sometimes differ considerably in aspect, as, for example, in *Akebia* (Fig. 1153), a well-known climber, the female flowers of which are twice as large as the male flowers. A further example is provided by *Albizzia moluccana* (Leguminosae) which has inflorescences with large, terminal, female flowers and small, lateral, male flowers.

A series of genera in the family Malpighiaceae have an exceptional kind of heteranthy, for the plants bear large numbers of reduced flowers as well as the normal ones. The former have no calyx, a small corolla or none, one abortive stamen and two carpels with an abortive style. There is here no question of cleistogamy, for these flowers are wholly sterile.

Variations of the flower model,* *i.e.*, true heteranthy, are usually associated with different positions in complex inflorescences. For instance, it is well known that in many Compositae there is a wide difference between the flowers which form the central "disc", *e.g.*, in the Sunflower (*Helianthus*), and the marginal flowers. The former are actinomorphic and bisexual, but those on the margin, called the "ray florets", are either sterile or only female and have a relatively enormous lateral expansion of the corolla, or part of it, towards the exterior, the effect being to surround the circular

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* We have used the word "model" in an effort to give an English equivalent for the German "Gestalt". The latter has secondary implications which are not entirely covered by the English word but we believe it conveys the main meaning of a somewhat difficult term.

inflorescence with a ring of petaloid " rays ", which simulate single petals in general appearance and even in details of structure (see Fig. 1878, p. 1948). The whole inflorescence thus acquires the aspect of a single flower and may be biologically regarded as conforming to the flower " model ", though morphologically quite distinct.

Sterile marginal flowers are characteristic of the genus *Viburnum* (Fig. 1089) (especially in *V. opulus*, the Guelder Rose), which has corymbose inflorescences. In this case the expansion of the corolla is sometimes unsymmetrical but in some species it is symmetrical and the sterile flowers retain their radial symmetry, though many times larger than the fertile, central flowers. An analogous appearance is presented by the inflorescence of *Hydrangea*, though in this case it is a petaloid calyx which becomes expanded. The favourite tropical shrub *Mussaenda* owes its attraction to the enormous development of one coloured sepal from each of two or three flowers on the margin of the corymbose inflorescence.

FIG. 1089.—*Viburnum tomentosum.* Marginal flowers with irregularly expanded perianths.

Excessive development of the corolla in marginal flowers, though it seems to depress the development of other parts, is not however invariably associated with sterility, for the zygomorphic marginal flowers in Umbelliferae referred to on p. 1156 are generally fully fertile (Fig. 1090).

Excessive or specialized development on the periphery of an organ or group of organs like an inflorescence, is sometimes called **exotrophy**. It is not confined to such cases of perianth development as we have mentioned, but may be also observed in bracts and fruits and in vegetative organs such as asymmetrical leaves.

Positional heteranthy is likewise not limited to cases of exotrophy. For example, in *Muscari comosum*, the terminal group of flowers in the raceme is sterile, each flower being elongated and of a brighter blue than the fertile flowers, so that the top-knot of sterile flowers makes up an "advertisement" of the inflorescence which attracts the notice of pollinating insects.

FIG. 1090.—*Heracleum sphondylium.* Umbel showing irregular exotrophic development of the lateral flowers.

THE ANATOMY OF THE FLORAL AXIS AND THE FLORAL RECEPTACLE

The anatomy of the pedicel or the peduncle does not itself call for much special remark. As a rule it shows a vascular arrangement closely resembling that of a young vegetative stem of the same plant. It is in fact a one-internode stem, with a single ring of bundles in Dicotyledons and concentric rings in Monocotyledons. Pedicels of the latter group usually have a simpler structure than the vegetative axis, frequently with only a single ring of bundles as in the stems of Dicotyledons. When several rings are present they are clearly concentric, an arrangement which is often disguised in the stem by the flexures and changes of direction of the leaf-trace bundles at the nodes. Where the pedicel or peduncle is long, it may possess a better developed stereome system, both of sclerenchyma and collenchyma, than does the stem. It is also not uncommon to find independent phloem strands, alternating with the normal bundles or scattered in the medulla or the cortex, especially where large fruits, or a large number of fruits, are developed.

Occasionally anomalous structures may be present, as in *Utricularia* and *Adoxa*, where each bundle is surrounded by an individual endodermis, producing what may be called either a polystelic or an astelic structure according to the point of view. In Dicotyledons secondary thickening may occur, especially during the ripening of heavy fruits such as those of *Cucurbita*.

If the structure of the pedicel is relatively simple, it is quite otherwise with the floral receptacle itself. Here we have to deal with a highly condensed structure upon which are crowded together a large number of varied appendages, each with a distinctive vascular structure. Moreover, the axis has only limited or determinate growth, that is to say it is without any permanent meristematic apex to which the development of structures can be related, as in a vegetative axis. The abrupt ending of the floral axis at the uppermost carpel is apparently due to inhibition from within, not to starvation. It has two elements of great value from the evolutionary standpoint; in the first place, the retention of the reproductive appendages within the protective limits of the calyx, and secondly the freedom of the ovules from the metabolic competition of any superior organs. The cessation of growth is not inevitable, as may be seen from the anomalous development known as **proliferation**, found for example occasionally in *Rosa*, in which the floral axis continues to grow, reverting to the vegetative condition and forming a leafy shoot which may eventually produce a second or even a third flower.

The vascular anatomy of the axis in the hypogynous flower is simpler than that in the epigynous flower, which we will consider later. Even in the simpler case however the variation is so great that the structure can only be described in the most general terms. As the slender pedicel enlarges into the bulbous or conical receptacle, the ring of vascular elements also enlarges proportionally and the individual bundles usually broaden tangentially so that there is an almost continuous or sometimes a wholly continuous

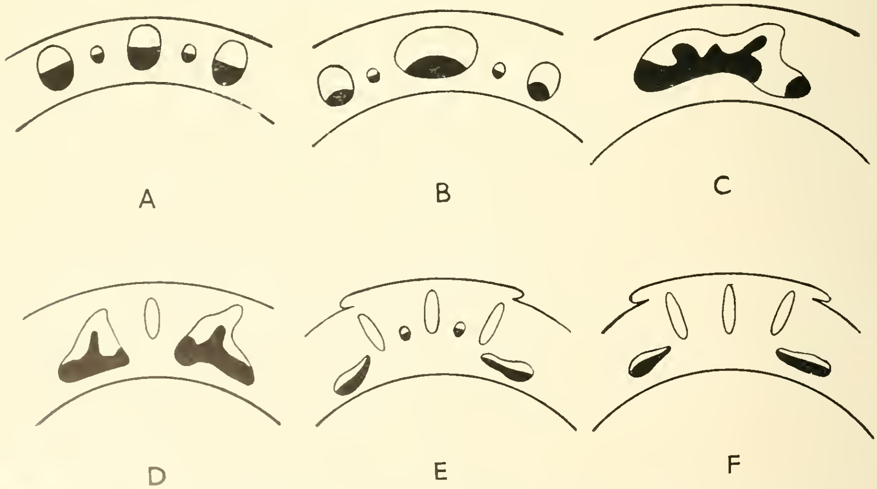

Fig. 1091.—A series of sections, of which A is the lowest, showing vascular changes from the pedicel to the receptacle. C shows a compound, fused bundle. At D, this has split to give off the median trace of a sepal. E, The lateral bundles have also split and given off the two sepal laterals, leaving three gaps. F, The lateral gaps have closed and the three sepal traces are moving outwards. *Caltha palustris*, somewhat diagrammatic. (*After* Smith.)

ring, near the base of the receptacle. From this are given off the sepal traces, normally three to each sepal, leaving gaps in the ring, which break it again into a hollow cylinder of separate bundles (Fig. 1091). Petals and stamens are alike in normally receiving one trace only. At each point where a trace is given off one of the axial strands divides radially, either into two or three. If into two, one portion becomes the trace and the other remains in the axial cylinder. If there is division into three, then the median portion becomes the trace and two axial strands remain. Such increases in the number of axial strands are counterbalanced by frequent fusions between adjacent strands, so that the whole axial cylinder is like a network of vascular bundles.

The carpels most generally receive three traces (Fig. 1092), though the number varies from one to five. The strong dorsal trace arises first, that is to say lowermost, then the two axial strands, lying on each side of the gap left by the dorsal trace, divide, and the portions lying next to the gap become the ventral or marginal traces of the carpel.

The receptacle anatomy is thus not fundamentally different from that of a vegetative stem which has limited growth and crowded appendages, though it is evident that the appendages in the flower are not of uniform nature. Were we to judge by vascular anatomy, as many believe that we may, the floral axis would be regarded as clearly homologous with a vegetative axis.

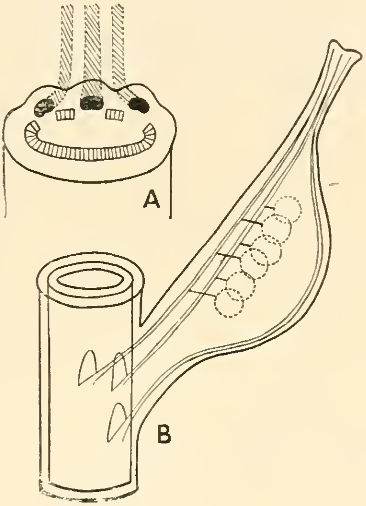

Fig. 1092.—Diagrams showing the similarity of the typical 3-trace supply to the foliage leaf, A, and to the carpel, B. (*After Eames, partly modified from Sinnott and Bailey.*)

Eames, who maintains this view, has endeavoured to typify floral vascular structures by reference to two main patterns:

1. The *Aquilegia* Type (Fig. 1093). 3-trace sepals, 1-trace petals, 1-trace stamens, 3-trace carpels. Between the last of the stamens and the first of the carpels the stele unites into a ring. Remnants of the axial cylinder may persist for a short distance above the carpels, mostly in the form of phloem and rapidly fading out.
2. *The Scheuchzeria Type* (Fig. 1094). 1-trace perianth members, all similar, 1-trace stamens. The vascular ring then re-unites and subsequently breaks to give off the dorsal traces to the carpels. The bundles left in the ring divide to form the six ventral traces of the carpels, two to each. Above the carpellary level there is no trace of vasculation remaining.

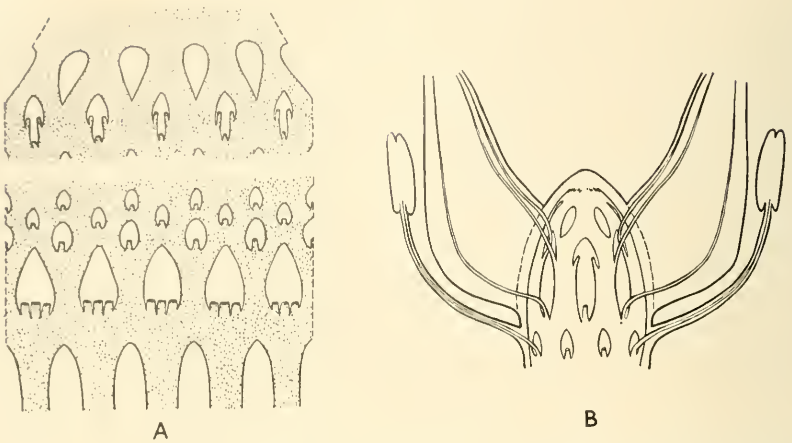

FIG. 1093.—*Aquilegia* type of flower vasculation. A, The vascular skeleton of the receptacle, spread out. The top series of gaps represent the second whorl of sterile carpel rudiments. B, Upper part of the receptacle showing the course of the traces. See text. (*After Eames.*)

The essential difference between the two types is the fact that in the second type only one kind of perianth part is present and that its vascular supply resembles the staminal type rather than the sepal type; while in the supply to the carpels the ventral traces are not simply branches from the axial system, but consist of the entire remainder of that system.

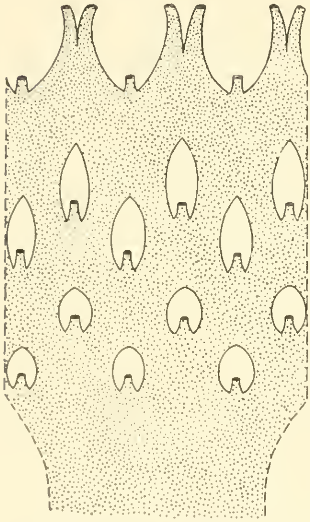

FIG. 1094.—*Scheuchzeria* type of flower vasculation. The vascular skeleton of the receptacle spread out. Vascular cylinder does not extend beyond the carpel traces. See text. (*After Eames.*)

There are normally no distinct internodes on the floral receptacle, but the axial anatomy frequently shows two intervals in the sequence of organs, firstly between the petals and stamens and secondly between the stamens and carpels. These intervals are not necessarily visible externally.

We have insisted at an earlier point that the variation in detail is just as great in the vascular anatomy of the flower as it is in the morphology of the parts themselves and that it is only in regard to the barest outline that any generalizations are possible. The outstanding conclusions from the receptacular anatomy appear to be that the two categories of perianth parts are distinct in nature, the sepals being normally 3-trace organs with three trace-gaps in the axial ring, but showing variation between a 1-trace, single-gap condition and a multi-trace, multi-gap condition, both of which are exceptional; while the petals, on the other hand, are, with very few exceptions, 1-trace structures, agreeing in this with the stamens. The sepals would be therefore interpreted as modified bracts, not as sterilized " sporophylls ", while the petals would be assumed to belong to the potentially fertile portion of the flower system.

The stamens have become consistently 1-trace organs in most flowers, but in a few primitive families, especially Magnoliaceae and Winteraceae, 3-trace stamens exist, so that presumably all the floral parts originally conformed to the 3-trace pattern, which Eames has shown good reason for supposing to have been the foundational pattern in the leaves of the vegetative axis. This is not of course to be taken as implying that the floral parts are derived directly from foliar leaves or vice versa, an outworn conception, but simply that they have a common morphological character.

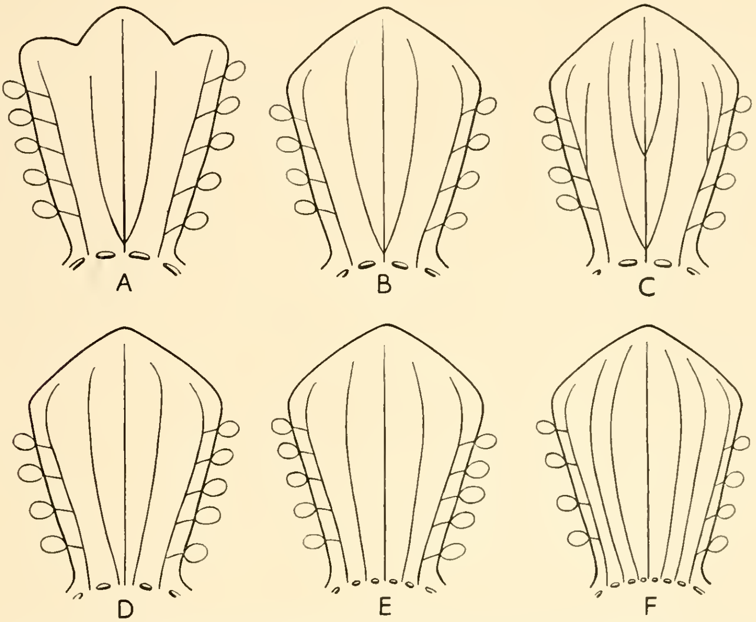

FIG. 1095.—Diagrams of theoretical primitive carpels, showing palmate venation and 3, 5 and 7 traces from as many gaps. (*After Eames.*)

The carpels share the common 3-trace structure, with variations of 1, 3 and 5 to many traces (Fig. 1095). The 3-trace condition is the commonest and is above all characteristic of follicles. The 1-trace carpels are nearly always akenes, the ventral bundles, which supply the ovules, branching off from the single trace, which is dorsal in the carpel. The ventral traces usually persist somewhat above the insertion of the ovule, if this is near the base of the akene, and in a few cases the upper parts of these traces produce branches either to abortive ovule rudiments, *e.g.*, in *Clematis recta*, or even to the places where these might be expected, but from which they are absent, *e.g.*, *Anemone*. This is credible evidence that the akene condition has been reached by reduction from multiovulate carpels of the follicle type. It is also evidence for the important anatomical consideration that the vascular supply to an organ may, at least in some cases, survive the organ itself. This is a matter of some importance as it bears upon the much-discussed question whether anatomical evidence of morphological changes should be received or be ignored as too uncertain to be valuable.

In akenes with basal ovules all three traces may be very much shortened. This affects the ventral traces earlier and more strongly than the dorsal trace. They may indeed in extreme cases disappear entirely, leaving the ovule attached to the remaining dorsal trace, a condition which never otherwise occurs.

The persistence of vasculation above the carpels, which we have noted above in the *Aquilegia* type, has some bearing on the question whether a carpel may be truly terminal on the receptacle, which in its turn bears on the further question of whether a carpel is foliar or not, since no true leaf is terminal.*

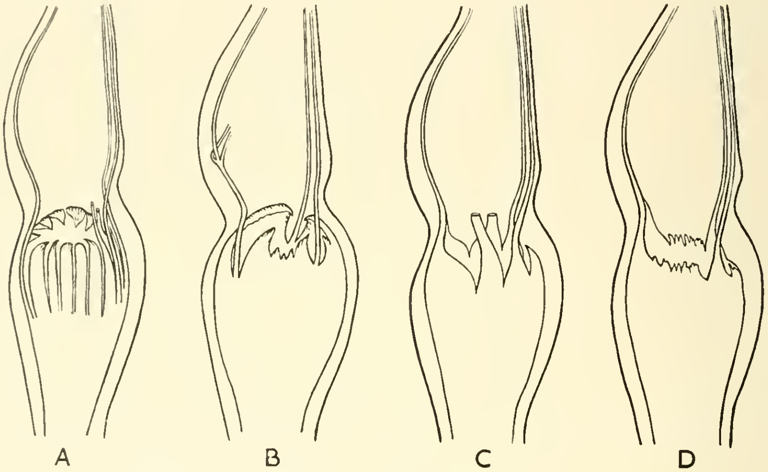

FIG. 1096.—Diagrams showing the vasculation of receptacles bearing solitary carpels. A, *Prunus avium*. B, *Actaea*. C, *Albizzia*. D, *Bauhinia*. Illustrating phases in the reduction of the "superfluous" vascular tissue. (*After Eames.*)

Most of the carpels, *e.g.*, in Leguminosae, which used to pass as being terminal, are in fact supplied by traces which are given off a short distance below the end of the receptacular stele (Fig. 1096), the remaining tissues of which come to an end in the base of the developed carpel (see also p. 1117). This is scarcely reconcilable with a truly terminal position. A similar anatomical structure occurs in the base of the uppermost carpel in some Ranunculaceae and Rosaceae, where there is no suggestion of terminality.

Where there is reduction of the gynoecium to a single carpel it usually appears to be terminal, but the vascular anatomy negatives the appearance. The residual bundles of the axial stele which would have supplied other

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* The latter proposition may sound very dogmatic, but it is simply a corollary to our accepted view of a leaf (see Volume I) which is that it is an appendicular structure. If therefore an organ is terminal it cannot, *ipso facto*, be a leaf; which is another illustration of the difficulties encountered when we try to categorize the parts of the plastic living organism.

carpels are traceable and may be disposed of in one of four ways: (1) they may disappear below the carpel level; (2) persist in the axis either separately or anastomosed; (3) fuse with the carpel trace; (4) enter the carpel as supernumerary traces (as above).

The variant conditions of cohesion and adhesion naturally affect the floral anatomy. In the cohesion of 3-trace organs, either sepals or carpels, the marginal bundles, which in the case of carpels are the ventral traces, tend to become concrescent, even down to the base. Conversely they may be concrescent at the base and free above. In a coherent calyx, *e.g.*, in the Labiatae, the varying degrees of concrescence of the traces affect the number of " nerves " or ridges displayed, which may be a generic character (Fig. 1097). The condition of adhesion is well shown in epipetalous stamens,

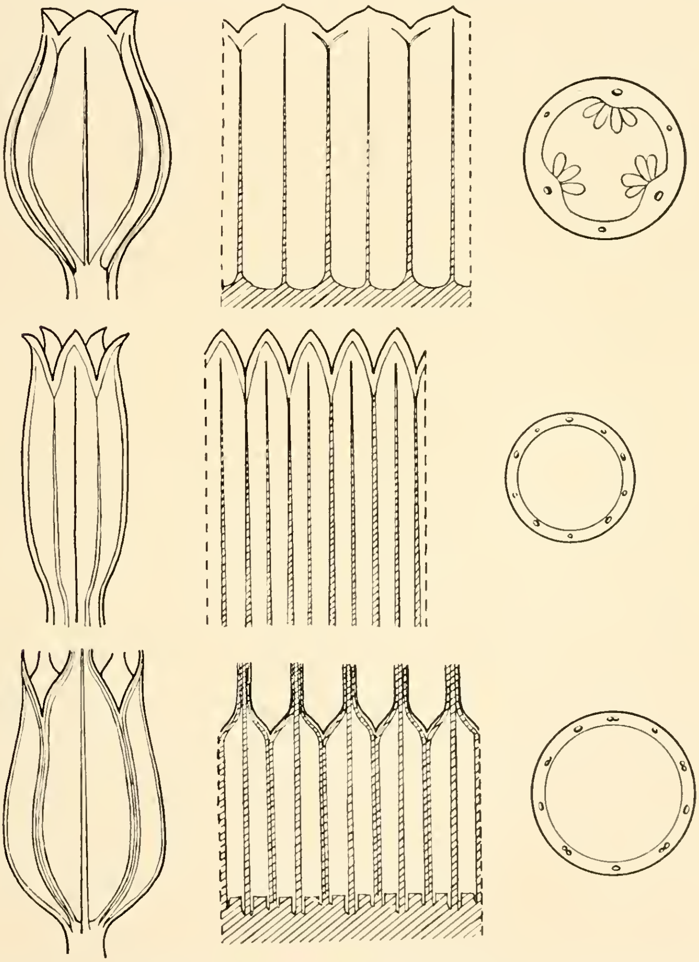

Fig. 1097.—Diagrams showing the vascular similarity under cohesion, in ovary, corolla and calyx. In each case there is cohesion of the lateral bundles. Top, ovary of *Reseda odorata*. Middle, corolla of *Helianthus divaricatus*. Bottom, calyx of *Agrostemma githago*. (*After Eames.*)

where the radially adjacent traces of the adherent stamens and petals may be either free from each other or fused to any extent.

The anatomy of double flowers may be of value in showing the nature of the extra organs. For example, in the double "Turban" *Ranunculus*, every organ above the sepals has the petal type of trace, *i.e.*, a single trace which divides into three main veins. There is no interval anywhere in the sequence and the number of petals is more nearly equal to the number of petals plus stamens of the single flower, than to the number of petals plus stamens and carpels. This points to the conclusion that the accessory petals have all been formed from stamens and that there are no altered carpels present.

In the double flower of *Caltha*, which in the single state has no petals, the accessory coloured organs have the petal type of trace and once again no carpels are present. Moreover so many accessory petals are formed that the vascular supply is insufficient for all of them and the uppermost twenty or so have no vasculation at all. A similar situation exists in double flowers of *Delphinium*, where all the parts above the sepals level have the appearance and vascular supply of petals and their number equals that of the combined petals and stamens in the normal flower. Here again petals and stamens seem to form a continuous series of mutually interchangeable units.

The validity of anatomical evidence in deciding questions of floral morphology has been frequently and powerfully disputed, particularly the evidence derived from vestigial trace-bundles, which have been often considered to indicate the former existence of vanished organs in certain flowers. Facts have been brought forward to show that the trace supply to organs of reduced development may disappear before the organs themselves. Although this is undeniable, there are, however, many instances where the opposite condition appears to be indicated by circumstances of strong probability, when interpreted in the light of comparison with related species. The classic example is that of the type of Orchid flower in which there is only one functional stamen. The vascular evidence points clearly to the disappearance of one or of two stamens, the third being present but adnate to the style. Another case has already been referred to (p. 1119), in connection with the vasculation of the carpel in certain Ranunculaceae, where vascular traces lead to the positions of upper ovules, which are not present, but whose former existence is indicated by the presence of abortive ovules in the upper part of the carpel in related genera. A further example is the ovary of *Sambucus*, which appears to consist of three carpels only, but the vascular supply for five is present, thus bringing it into line with many other members of the Caprifoliaceae. In *Salix* it is claimed that there is anatomical evidence for the former existence of a perianth, of which the nectaries (which in some species are petaloid) are surviving vestiges. Instances like these, and others which have been investigated, seem to show that anatomical evidence should not be wholly condemned. Even if not universally obtainable, or applicable, it may at least be useful in some cases.

FLORAL ONTOGENY

The ontogeny of the flower begins with the initiation of a floral growing point at the apex of the branch which is destined to become a floral pedicel. Over this development considerable controversy has centred, because it has an important bearing on the theory of floral morphology. The question at issue is whether the development of the floral axis is comparable with that of a vegetative axis or whether it is fundamentally different. In other words, whether the history of floral development supports the classical view that the flower is essentially a contracted shoot, or not.

In 1938 Grégoire published an extensive series of researches which showed, as he claimed, that the organization of a flowering apex was quite distinct from that of a vegetative apex. According to his views there are only two zones in the floral meristem; a superficial meristematic mantle and an internal parenchymatous mass. Mitosis is almost confined to the first zone, while the second has highly vacuolated cells. This growing region has no apex, and shows no regular plastochrones. The outer surface is a dome, expanding only in area. There is no group of initial cells, the central mass being added to all round by periclinal divisions in the mantle layer and adapting itself to the extending area of the latter. Furthermore he claimed that the vascular traces arise in the central core and extend towards the rudimentary organs of the young flower, whereas in the vegetative apex the vascular traces first appear at the bases of the leaf rudiments and differentiate both downwards and upwards. Such a structure, Grégoire maintained, is unique; it is in a category by itself. If homology is considered to imply ontogenetic identity, and if there is no such identity, then the floral organs cannot be homologous with any vegetative organs of the plant, but are *sui generis* or of their own kind.

Ideas of so novel a character have provoked contradiction at the hands of those who support the classical view of the flower and a number of observations which are incompatible with Grégoire's views serve to show that his theory is, at least, not of universal application. The fundamental unity of floral plan makes it improbable that structures so characteristic as flowers can differ entirely from each other in their morphological nature and consequently a true morphological explanation should either be universally valid or not at all.

One fairly obvious difficulty in the general application of Grégoire's theory is that in many species a vegetative growing point may be directly converted into a floral rudiment, in which case we cannot be dealing with two fundamentally different structures but rather with a change of one into another. For example, in *Rubus* (Fig. 1098), as shown by Engard, the alteration takes place as follows. The first step is the cessation of vertical growth, accompanied by a globose expansion of the apex. Then come a series of very short plastochrones which produce, nearly simultaneously, a group of closely related primordia, the sepals, which expand laterally into a continuous rim around the growing point. They originate from the second tunica layer (T_2) in exactly the same way as the foliar primordia on a stem.* Intercalary growth in this rim produces the perigynous disc, which is therefore of foliar origin. Alternating with the sepals, the petal primordia also arise in T_2. There is sufficient variation in the position of the primordia of the perianth members to indicate that plastochrones have not been entirely suppressed, but this initial asymmetry disappears in later development. The sepal formation is the last act of the vegetative stage and the production of the stamen-like petal rudiments marks the beginning of a new phase, or what has been called a " new route " in development.

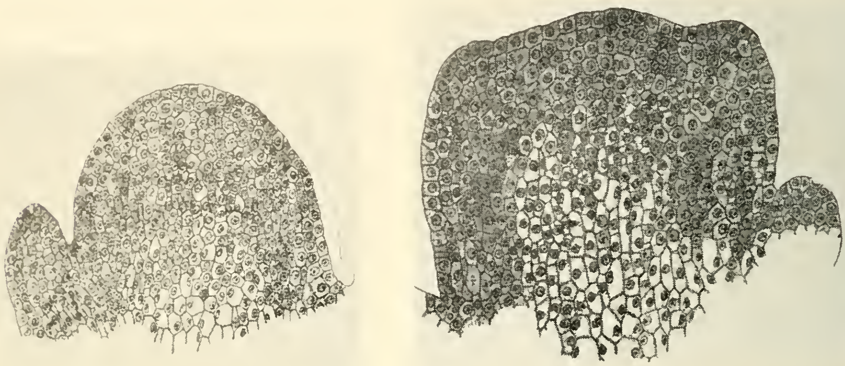

Fig. 1098.—*Rubus rosaefolius.* On the left is an apex still in the vegetative state showing the last foliage leaf primordium. On the right an apex passing over into the flowering state showing sepal primordia with virtual elimination of the plastochrones. (*After Engard.*)

The stamens also originate in the T_2 layer and the staminal archesporium develops from the T_2 layer of the stamen itself, so that the pollen possesses the characters of the second tunica layer of the apex, which may, as has been shown in chimaeras, be different from those of the first layer.

The carpels are also T_2 structures. Each appears first as a simple hump, in which the first procambial strand to appear becomes the abaxial or dorsal trace. The ovarial cavity is produced by wing-like expansion of the adaxial margins, forming a gradually deepening groove. The ovules begin in the T_2 layer of these wings and the nucellus and embryo sac belong to the T_2, but the ovular integuments belong to T_1. In *Rubus*, the vascular system of the floral apex is essentially that of the vegetative apex, but shortened.

We have not yet got so detailed an account of the above process in many other cases, but the information available shows that in a number of other flower rudiments the distinction of tunica and corpus persists from the vegetative into the floral apex. In *Vinca* there are three types of apex: 1. The juvenile vegetative apex which forms leaves only. 2. The adult apex which forms both leaves and flowers. 3. The floral apex which forms only a flower. All three are morphologically alike, with two tunica layers

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* See Volume I, p. 846, for a discussion of the apical structure of the vegetative stem.

and an active corpus, and the differentiation between vegetative and floral apices is purely physiological. In *Datura* the petals and sepals originate, like the leaves, from T_2, but the stamens come chiefly from the corpus. A study by McCoy of *Frasera carolinensis* (Gentianaceae) showed that its floral apex was homologous with that of the vegetative shoot, with a corpus and two-layered tunica, the floral organs being initiated by periclinal divisions in the T_2 layer. Other examples could be quoted, but enough has perhaps been said to indicate that it is difficult to accept the floral apex as " irreducible ", *i.e.*, inexplicable in any terms but its own.

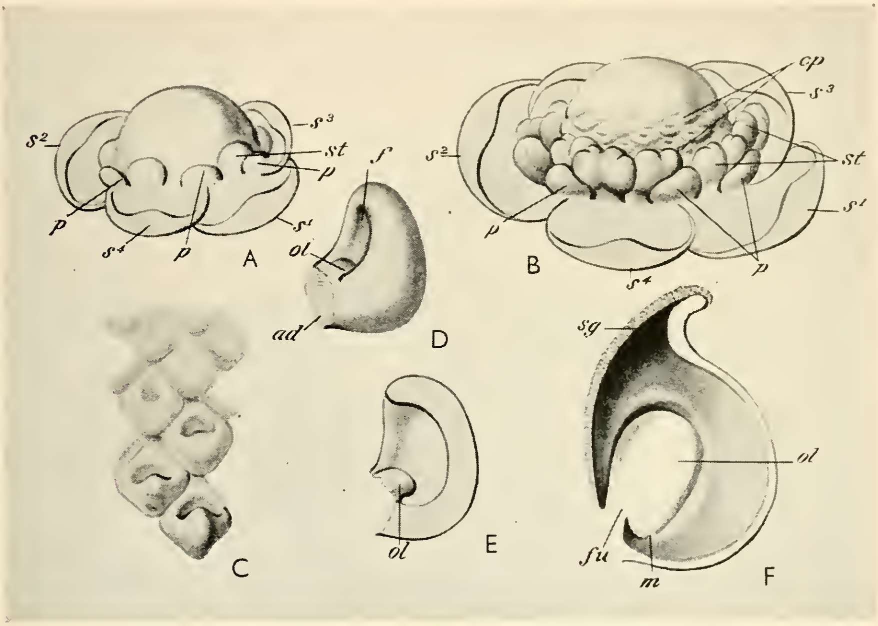

FIG. 1099.—*Ranunculus trilobus.* Floral ontogeny. A and B, Whole flower, younger and older stages. C, Carpel primordia in surface view. D, Young carpel. E, The same in section. F, Mature carpel in section.
s=sepals, *p*=petals, *st*=stamens, *cp*=carpels, *ol*=ovule, *f*=furrow of young loculus, *ad*=point of attachment of carpel, *m*=micropyle, *fu*=funicle, *sg*=stigma. (*After Payer.*)

The general rule in the ontogeny of floral parts is that they follow one another in a definite acropetal series (Fig. 1099), the youngest organs being those nearest to the growing region. Normally the latter is at the floral apex, but instances of reversal may occur, in which the apex ceases to grow while an intercalary zone continues active, thus causing a basipetal (or centrifugal, if the expression be preferred) order of development, which is most observable among the stamens. The systematic occurrence of this peculiarity in certain families is dealt with in the section on the androecium in this chapter. Where only two whorls of stamens exist and they develop in the centrifugal order it will follow that the outermost whorl of stamens, those opposite to the sepals, will arise later and lag behind the development of those which are opposite the petals, and alternate with the sepals. The latter may therefore surpass the former in growth and displace them, producing the appearance of an outer whorl standing opposite the petals. This is one of the ways in which obdiplostemony may arise, as we have explained in a previous section (see p. 1095).

Another departure from strict succession is seen in the late development of the petals in many cases. Their primordia may originate before those of the outer stamens but they lag behind them in further development and may only complete their growth after all the stamens have been completely formed. If the petals have been indeed evolved from sterilized stamens, this lag may be regarded as a check due to the " new path " along which they develop, in contrast to their fertile companions.

Those zygomorphic flowers in which the zygomorphy is due to a departure from the normal radial symmetry of the receptacle, show irregularity in the development of their parts, especially the petals, whereby one side of the flower is in advance of the other. In *Reseda*, which shows this difference in a marked degree (Fig. 1100), the side of the receptacle nearest to the inflorescence axis is, from a very early stage, higher than the opposite

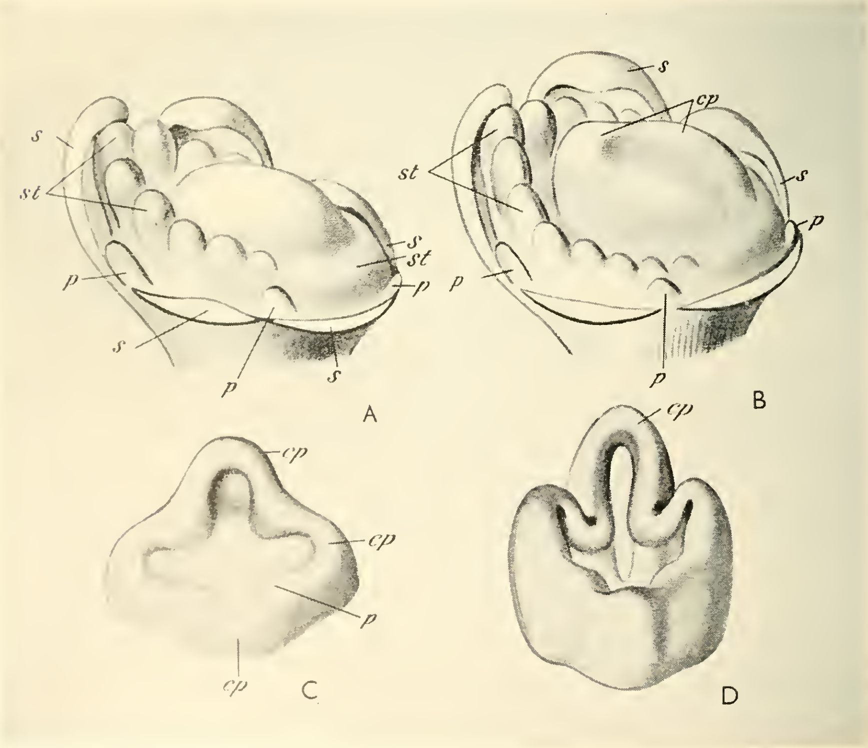

Fig. 1100.—*Reseda odorata.* Floral ontogeny. A and B, Two stages of whole flower. C and D, Two stages of the gynoecium, older than in A and B. Lettering as in Fig. 1099, except that in C, *p* = placenta. (*After Payer.*)

side and the development of parts on the higher side is correspondingly accelerated. The adaxial stamens are nearly fully formed before the abaxial petal appears. Even a flower which is ultimately actinomorphic, *e.g.*, *Parnassia*, may show this bilateral asymmetry in early stages of its development and is thereby seen to be cryptozygomorphic. Papilionate flowers of the Leguminosae show a similar unilateral development but in the reverse direction, from the abaxial to the adaxial sides.

It can be readily understood that in flowers where there is partial suppression of certain organs, such as the sterilization of part of the androecium, the reduced parts lag behind the normal parts in their growth and usually stop before arriving at the mature form. They may also, however, be initiated later, as in *Scleranthus annuus* (Fig. 1101), where the two fertile stamens are initiated considerably earlier than the three sterile stamens, which remain much smaller than the others. The subdivision of a primordium may lead to a similarly differentiated development, as in *Philadelphus* (Fig. 1102), where each of the four original rudiments divides radially into 7–9 segments. The median segment, or the median three segments, are so much more forward than the others (some of which abort altogether) that they press inwards and appear to form, in the mature flower, an inner whorl of stamens, although all the primordia formed a single whorl.

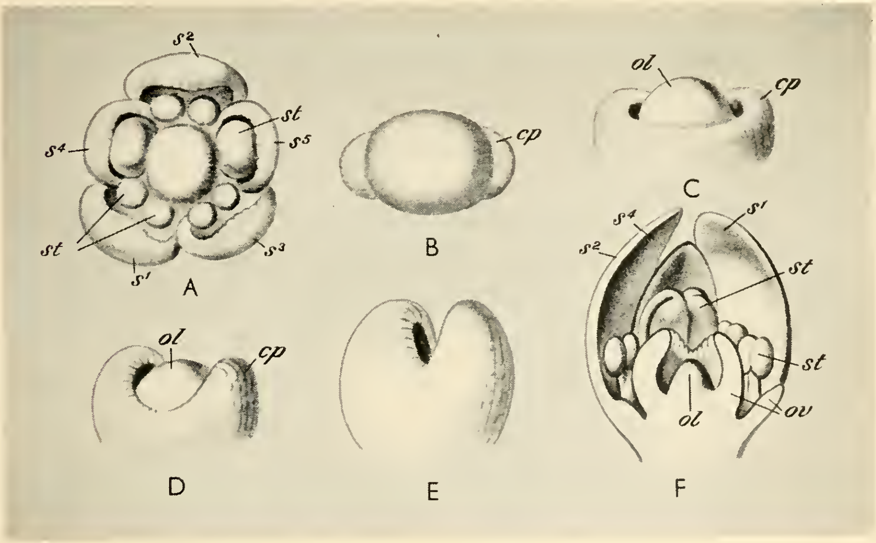

Fig. 1101.—*Scleranthus annuus.* Floral ontogeny. A and F, Early and nearly mature stages of the whole flower. The three sterile stamens have undergone chorisis. B, C, D and E, Successive stages in the development of the ovary. Lettering as in Fig. 1099, *ov* = ovary. (*After Payer.*)

Lastly, there is the important phenomenon of protogyny, the carpels maturing before the stamens. This, which is due to the enhanced rate of development of the upper zone of the receptacle as a whole, is apparently

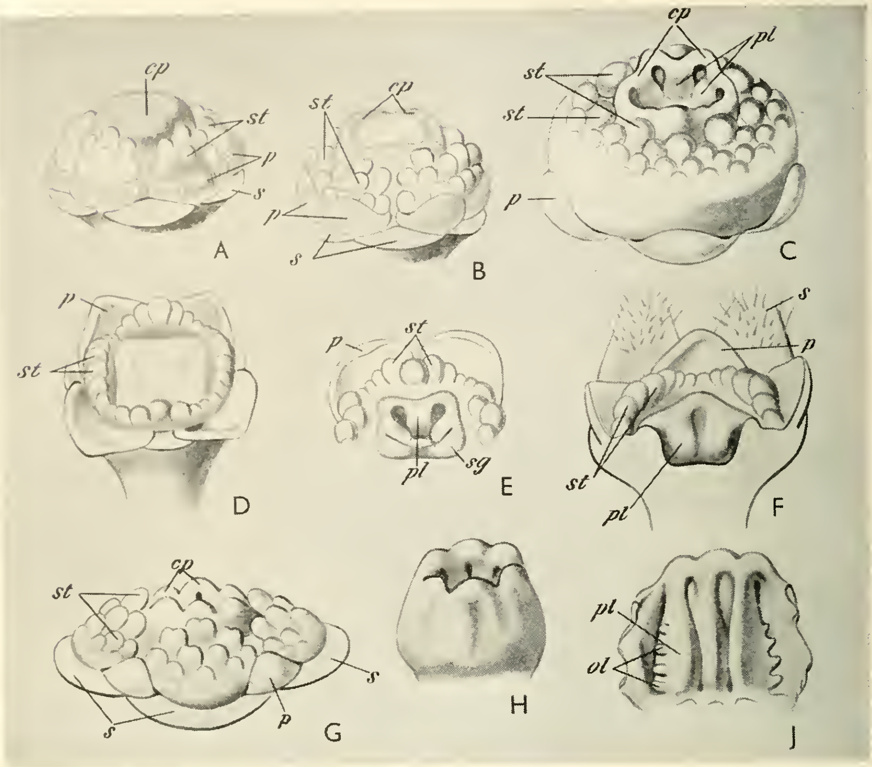

Fig. 1102.—Ontogeny of fascicled stamens. A and B, *Hypericum androsaemum*. C, *Cistus populifolius*. D, E and F, *Philadelphus coronarius*. G, *Sparmannia africana*. H and J, The same, the gynoecium only. Lettering as in Fig. 1099, *pl*=placenta. (*After Payer*.)

caused by the local concentration of growth substances, just as in the above-cited examples of local acceleration of growth in certain radial sectors only. It is of great significance in connection with cross-pollination, but its physiology is still obscure.

THE FLORAL RECEPTACLE

The axis of the flower, on which the floral organs are borne as lateral organs, is known as the **receptacle**, or the **thalamus**. It is a direct continuation of the pedicel and, in flowers with numerous parts, especially spiral flowers, it may be elongated considerably, as in Magnoliaceae, or expanded into a sphere on which the parts are distributed, as in Annonaceae. When a smaller number of parts is present the receptacle is short and may be no more than a minute cushion. The elongated receptacle has usually been held to be the more primitive form, partly from its occurrence in families regarded as primitive on the basis of their general assemblage of characters and partly on the ground of its being nearer to the character of a vegetative shoot, with which classical theory compares the flower.

Without discussing this question at the moment, we must understand that the relationships of the parts on so limited an axis as that of the flower can never be exactly similar to the relationships of the parts on a vegetative axis, even when the receptacle is as elongated as in a *Magnolia* (Fig. 1103), and that the crowding together of parts on the receptacle may give rise to doubts in some particulars as to the exact limits between axis and appendage, especially in compound gynoecia. The entire surface of the receptacle is mapped out between the various appendage organs, which originate in very close contact, and even the apex may become, at least secondarily, involved in carpel formation. This is a different thing from stating, as some do, that a single carpel may be terminal on the receptacle. We have seen in the preceding section that in many apparently terminal carpels the vascular supply in the carpel base shows that the apex of the receptacle still exists and has at least some traces of its own vasculation, but that it has become embedded in the base of the carpel and lost to sight. The same is true of some coenocarpous ovaries, as we shall see later (see p. 1229).

FIG. 1103.—*Magnolia pterocarpa*, showing the remarkably elongate receptacle. (*After King.*)

The receptacle is sometimes called the *torus*. This is incorrect, for the term was introduced by R. A. Salisbury and used by de Candolle for a peculiar concept, that of a zone of the receptacle called by the latter " the proper receptacle ", which lies between the calyx and the ovary and forms the common basis of the petals and stamens. He distinguished it from the floral axis which bears the carpels and attributed its formation to the fusion of abortive petals and stamens. It was depicted as sometimes extending itself over the calyx to form the disc or cup of perigynous flowers, or as rising round the ovary, with or without simultaneous adhesion to the calyx; in the former case leading to epigyny. Again torus and disc have often been used synonymously but the disc is only one form of expanded torus and to transfer the epithet " disc " to the torus zone in hypogynous flowers is hardly justified.

It is an interesting idea but not one for current use. At the present day the term " receptacle " is applied to the whole floral axis from the base of the calyx upwards and the torus is not regarded as a distinct organ which, indeed, de Candolle did not claim that it was.

FIG. 1104.—*Magnolia* x *soulangeana*. A three-branched receptacle.

Rare cases of branching of the receptacle are known, *e.g.*, in *Myosurus* (Ranunculaceae) and *Magnolia* (Fig. 1104) which have unusually elongated receptacles, but very little is known about the anatomy of such structures. They are, of course, quite distinct from the appearance of branching which may result from the partial coalescence of two flowers by the congenital union of their rudiments.

The interesting suggestion has been made by Burkill that the tendency towards isomery in flowers is due to the action of hormones in determining the destination of primordia, these hormones coming from organs whose nature is already determined and acting along lines of greatest proximity, that is along the parastichies.

This involves the view that an emergence on the receptacle is at first indeterminate and that it only becomes, strictly speaking, a primordium or rudiment when the course of its future development has been determined. The flower may thus be thought of as divided into a series of horizontal, biochemical zones, the lowest of which is hormonically sterilized as sepals. The balance between the zones of maleness and femaleness is closely adjusted, which may be attributed to the clear-cut opposition between the controlling influences, but the sterility control appears to spread upwards from the calyx into the adjacent male zone, leading to the sterilization of a certain number of its members as petals. This balance is not exact and some hesitancy or indefiniteness may appear at the line of junction, with the production of intermediate organs as petaloid stamens of varying degrees of sterility. There is thus no positive correlation between the numbers of petals and those of stamens. In primitive flowers with numerous free parts, such as the *Ranunculus* type, the two sets of parts are indeed vicarious, that is to say they are negatively correlated, an increase in one set corresponding to a decrease in the other, as would be expected if the petals are transformed stamens. The orderliness of the flower may therefore be due to hormonic control rather than to the geometrical requirements of close packing on the receptacle, which does not in fact begin to operate until the primordia are partially developed and their nature already determined.

The question whether the immediate ancestors of the Angiosperms were hermaphrodite or unisexual has been for long a subject of research and speculation, since on the answer depends what view we take of the evolution of the group. In the first case the receptacle produces both types of sporangial appendages and in the latter case it produces only one, that is to say that one of the reproductive zones is missing. If we adopt the comparative method we can find facts which appear to support either theory. The most widely held view has been that a hermaphrodite type with numerous floral parts, like that of the Magnoliaceae, presents the most primitive mode of organization among living Angiosperms, and that the unisexual condition has been evolved from this by a process of reduction. This fitted in well with the theory that the angiospermic flower was evolved from large bisporangiate strobili of the kind represented by the fossil Bennettitales (Fig. 1105).

Many stages intermediate between the hermaphrodite and the unisexual state can be found among living flowers. A series may be traced leading from simple sterility of either androecium or gynoecium, through regressive degrees of imperfect development, towards the complete disappearance of one or the other. It is inconceivable that such a series of intermediate stages can be read otherwise than as a process of elimination of one or other of the sets of sexual parts. The androecium is the more frequently affected but abortive gynoecia are also known. Even in the multipartite Ranunculacean flower, *Caltha palustris*, the vascular anatomy shows that the apex of the gynoecium has disappeared and that in the double variety grown in gardens it has vanished altogether.

As we shall see later in connection with pollination it is not uncommon

FIG. 1105.—*Cycadeoidea ingens.* Bisporangiate flower of one of the Jurassic Bennettitales. Stamens large and pinnate, ovules on a central, conical receptacle. The ovules are gymnospermic but otherwise there is close similarity to an angiospermic flower. (*After Wieland.*)

to find flowers of different sexual types produced not only on different plants of the same species, but even on the same individual plant. It is unnecessary therefore to labour the point that a reduction in sexual expression is not only possible but frequently occurs. The opposite view has received a stimulus of late years from the discovery of the Caytoniales, a group of Mesozoic fossil plants, possibly derived from the Pteridospermae, which have arrived at a condition of angiospermy by the inclusion of the ovules within a closed, and apparently stigmatiferous cupule. Their reproductive shoots were unisexual and the possibility that they might have been in the evolutionary line towards the living Angiosperms turned attention to the idea of the primitive nature of unisexual flowers. Acceptance of this view implies that organs of both sexes can arise where only one was formerly present.

Comparative studies show that the distinction of the two sets of sporangial parts is by no means fixed. In Conifers, where the cones are normally unisporangiate, it is not uncommon to find abnormal cones which are bisporangiate, that is to say producing both micro- and megasporangia. In Angiosperms also many anomalous cases occur of ovules borne on stamens, pollen grains formed in ovules and organs of mixed character generally, which serve to show that it is quite possible for sporangia of both types to appear in a zone which has previously been unisexual. There is however a considerable gap between such abnormalities and the beautiful regularity of the typically hermaphrodite flower, a gap which it is not easy to bridge, either by theory or observation, so that the onus of proof that floral evolution has in fact followed a course from the unisporangiate to the bisporangiate condition still lies with its supporters.

It is one of the characteristic features of the receptacle, in comparison with a vegetative axis, that it has commonly no internodes. Cyclic flowers, it is true, produce their parts in successive whorls, but they are generally not vertically separated and the plastochrone periods either overlap, so that they cannot be distinguished, or perhaps disappear altogether. Nevertheless there are enough special cases known, in which internodes are part of the floral architecture, to show that the plastochrone rhythm, though disturbed, is not lost, at least in every flower.

Elongation of the receptacle is of two kinds. There are the flowers in which the receptacle is elongated throughout, even from its inception, as in *Magnolia*, *Myosurus*, etc., and there are those in which the elongation of one or more internodes only appears during development. The latter is a fairly common phenomenon, though it does not always show itself in a striking degree. (See also p. 1139.)

An expansion of the receptacle either within the calyx or within the corolla is sometimes known as the **disc**. This is not necessarily an elongation and is more often a lateral expansion, which may or may not take the form of a disc in the ordinary sense of the word, interpolating a naked zone between perianth and stamens or between the gynoecium and the other floral parts, as in the Strawberry and other slightly perigynous flowers. In *Prunus* and *Rhamnus*, for example, the disc is cup-shaped and this is often interpreted as a stage in the evolution of highly perigynous and epigynous flowers. The term disc is however also applied to the naked zone on top of the gynoecium in epigynous flowers, *e.g.*, in Umbelliferae, where it surrounds the style and extends to the androecium, in which case it is not obviously or certainly a part of the receptacle. The disc is often associated with the production of nectaries and sometimes its whole surface may be secretory. It is true that the apparent expansion of the receptacle into a disc or cup may be interpreted, we shall see below, as a structure formed of the fused basal parts of the perianth or the androecium or of both, but in other cases there are grounds for the belief that a toral enlargement has occurred. For example in certain sections of the family Monimiaceae typified by the genus *Tambourissa* (Fig. 1106), the flower takes the form of a flattened, hollow vessel of fleshy consistency, with only a small opening above, all over the inside of which the carpels stand immersed in the fleshy tissue. This does not bear the aspect of a combination of organs, but rather that of a genuine receptacular cupule.

This latter structure, the cupule, is seen at its best development in the order formerly called the Cupuliferae and now known as Fagales. The traditional view of the cupule which surrounds the fruits in *Quercus*, *Fagus*, *Castanea*, etc., is that it is formed of a number of fused bracts, which in the two latter genera separate at maturity into four woody valves. There is

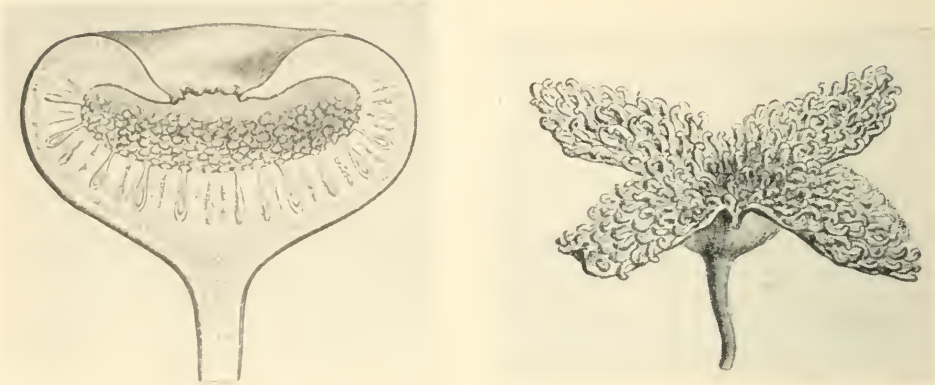

FIG. 1106.—Left, female flower of *Tambourissa elliptica*. Right, male flower of *T. leptophylla* (Monimiaceae). Expanded receptacles bearing large numbers of sporangiate parts. (*After Baillon.*)

reason to doubt this, however, and to regard the cupule as formed, at least in part, of an intercalary toral outgrowth bearing numerous bracteoles in the shape of spines or scales. In the Lauraceae very similar cupules occur which are apparently of double nature, the upper portion being calycular

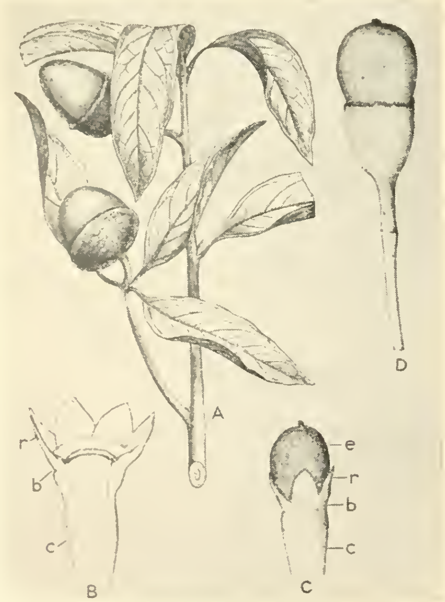

FIG. 1107.—*Nectandra puchury*. A, with cupulate fruits. *Phoebe elongata*. B, Receptacle and perianth. C, The same, with fruit in place. *b* = the zone at which the perianth is abstricted. D, After abstriction of the perianth; fruit and cupule. (*After Velenovsky.*)

and the base of the cup, which alone persists at maturity, being receptacular. (Fig. 1107.)

There are many perigynous and epigynous flowers in which it must remain a subject of research, or may indeed be altogether dubious, whether the tissues surrounding the gynoecium are composed of an axial upgrowth or of the fused bases of the floral organs or of both combined, but there are numerous instances where the origin of the enclosing cup by fusion may be assumed to be correct. Many Saxifragaceae with half-inferior or inferior ovaries appear to be in this class, likewise some members of Rosaceae (Fig. 1108), where the ovary is adherent to the side of a floral tube. The condition in Dipsacaceae is likewise significant, for here the floral tube may only be adherent to the ovary at the top, so that we have an epigynous flower with a free ovary. In *Fuchsia* and *Oenothera* the floral tube which surmounts the inferior ovary plainly consists of the fused bases of the sepals, petals and stamens.

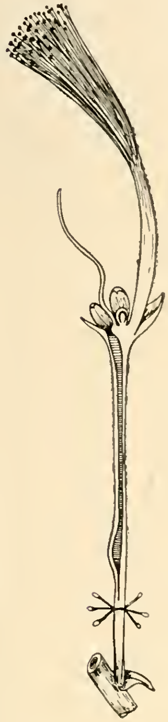

FIG. 1108.—Flower of *Acioa* (Rosaceae) in longitudinal section, showing the ovary adherent at the top of the floral tube. (*After Velenovsky.*)

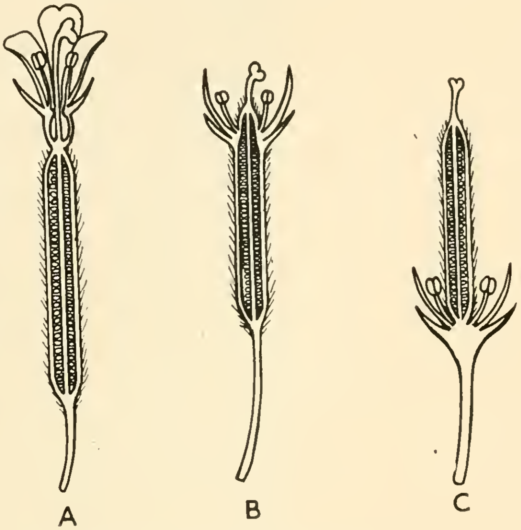

FIG. 1109.—Sections of a normal flower, A, and two abnormal flowers, B and C, of *Epilobium montanum*, showing descent of the floral parts from the epigynous to the hypogynous position. (*After Velenovsky.*)

The allied genus *Epilobium* also has a small floral tube of the same nature, and in this genus Velenovsky has observed a very interesting series of abnormalities (Fig. 1109), beginning with the disappearance of the floral tube, so that the perianth became sessile on the top of the ovary, and ending with the complete descent of the perianth and androecium to the base of the gynoecium, so that a normally epigynous flower had been transformed into a hypogynous one. The most noteworthy point observed was that the hairy surface of the ovary in the superior position was exactly the same as in the inferior position, which is hardly consistent with the idea that it had been stripped of enclosing receptacular tissue. In such cases one cannot avoid the conclusion that epigyny is brought about by the adhesion of the other floral parts to the ovary.

Anatomy may sometimes throw light on the condition, as in *Alstroemeria*, where a transverse section of the inferior ovary shows distinctly that a floral tube, with its own vascular system consisting of the independent traces of the perianth and stamens, encloses and is united to the ovary wall. The same structure obtains in *Furcraea gigantea*, where moreover the enclosed carpels are free from the inner perianth segments and have their own proper walls.

FIG. 1110. *Echinopsis tubiflora.* Long floral tube bearing bracteoles, which extend downwards over the outer wall of the ovary.

Morphology may also sometimes be decisive, as in Cactaceae, where the ovary wall may bear bracteoles and must therefore, it is argued, be of axial nature (Fig. 1110).

No question in botanical morphology has been more debated than the relationship of the axis to the carpels, especially in the inferior ovary (see also pp. 1104 and 1219), and a vast expenditure of dogmatism by the textbook writers of more than a century has not sufficed to reduce all cases to a common level or to establish any fixed principle of reference. The insistence upon the categorical separation of axis and appendage, which led, for example, to the assertion of purely imaginary axial upgrowths forming the placentae, even in superior ovaries, now seems to us, in the light of fossil evidence, quite outmoded, nor are we inclined to allow to the torus or disc, as a term applied to the receptacle lying between calyx and gynoecium, the status of a distinct and peculiar organ of the flower. We have not sufficient information to judge how frequent any one morphological condition may be among Angiosperms, nor, except in certain cases, what the condition is in individual species, but it is reasonably certain that there are various possibilities and that no one condition is universal. Including the conditions already mentioned, the following relationships are all theoretically possible as explanations of the inferior position of the ovary. They have been thus summarized by Douglas (Fig. 1111).

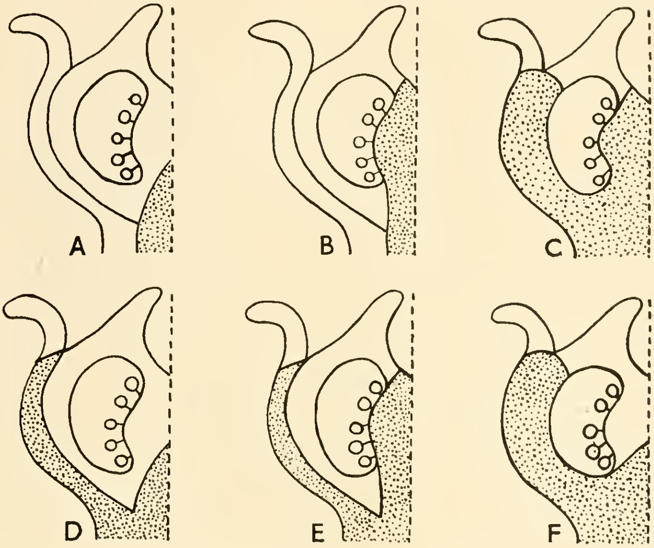

Fig. 1111.—Diagrams illustrating types of inferior ovaries with varying amounts of axial (shaded) and appendicular (unshaded) tissues, according to different constructional theories. A, Ovary wholly appendicular. B, Placenta axial. C, Ovary axial except for carpellary lid. D, Cup axial, ovary appendicular. E, Cup and placenta axial, ovary appendicular. F, Cup axial, placenta appendicular. (*After Douglas.*)

1. The outer floral whorls are concrescent around the ovary, to which they are adnate. This was the theory advanced, though obscurely, by A. P. de Candolle in 1827, later clearly advocated by Van Tieghem and recently supported by Eames as applicable to the majority of species. (Fig. 1111, A and B.)

2. The whole of the inferior ovary consists of receptacular tissue, bearing ovules, the carpellary wall being reduced to a sterile covering including little more than the styles and stigmas. This theory originated with Schleiden in 1839 and was held by most of the German school of botanists in the nineteenth century. (Fig. 1111, C.)

3. The inferior ovary consists of a concave receptacle enclosing true

carpels. This view was first advocated by Naudin in 1855 and it has attained a wider following than any other, so that it has become almost axiomatic in botanical teaching to say that the outer tissue of the apple, for example, is receptacular and the core is carpellary! Goebel was largely responsible for popularizing this view and his authority carried great weight. A variety of this theory maintains that the placental region is axial (receptacular) though admitting that the dorsal ovary wall is carpellary. (Fig. 1111, D & E.)

4. Sachs in 1870 adhered to the second theory, above, but considered that in some cases at least the central placentary region was carpellary, as well as the top, in other words, that the carpellary portion of the inferior ovary might be fertile as well as sterile. This is almost certainly true of parietal placentae such as those in the Orchidaceae and may be true of some axile placentae as well, the carpellary margins being supposed to be prolonged centripetally till they meet in the centre of the ovary. (Fig. 1111, F.)

5. The peculiar views of Grégoire on the unique character of the floral axis led him naturally to the view that the inferior ovary is also a unique organ with no parallel among vegetative organs. We have referred in more detail to this view and the criticisms brought against it, earlier in this chapter.

6. The " acarpous " theory, advocated by McLean Thompson in 1933, which is really a development of the second or axial theory, combined with some of the features of Grégoire's theory. The whole inferior ovary is interpreted as axial, produced by an excess of toral growth over apical growth, leading to an invagination of the floral axis, within which megasporangia are borne. No carpellary or foliar structure is supposed to take any part in its formation.

Investigations have chiefly followed one of two lines, either ontogeny, that is the development of the floral primordia, or else the comparative anatomy of mature flowers. Most of the research has been carried out under the influence of some theory and strained interpretations have not been lacking, but generally it may be said that ontogeny has tended to support the axial theories and comparative anatomy to support the adnation theories. In a few types, such as *Rosa* and *Calycanthus* (Fig. 1112), the vascular anatomy suggests a double nature for the floral cup. The vascular bundles from the stalk form an outer ring in the cup, surrounding an inner series of recurved bundles with a downward course (and in *Calycanthus* with reversed orientation) which supply the ovules and are connected at a higher level to the exterior bundle ring. The base of the cup, up to approximately the level of the bundle junctions, is interpreted as axial, the ovary being definitely invaginated in a hollow receptacle, while the upper portion of the cup is foliar. A few other examples

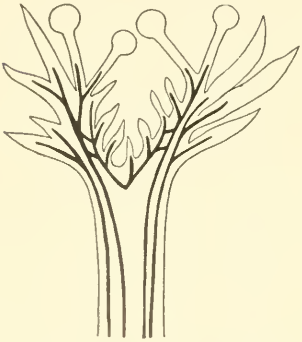

FIG. 1112.—*Calycanthus floridus.* Longitudinal section of flower with invaginated receptacle, showing carpel traces with reversed orientation passing downwards and inwards from the axial bundles. (*After Smith.*)

of this condition are also known in less familiar plants and the conclusion has been drawn that where there has been actual invagination of the receptacle the anatomy tells the story, while in the absence of such evidence the way is open to accept the concrescence of floral parts as the origin of the epigynous state. In many cases, *e.g.*, the important one of the apple, no agreement regarding status has been reached.

Invagination of the receptacle unquestionably happens in certain flowers, unconcerned with inferior ovaries. For example the receptacle in *Nelumbium* (Fig. 1113) enlarges during post-floral development, into an inverted cone, in whose upturned base the akene fruits are each, separately, embedded in a little cup. This singular development has few parallels, although something like it occurs in Monimiaceae, as was mentioned above.

FIG. 1113.—*Nelumbium nucifera.* Receptacle with embedded seeds, also seeds separately and germination. (From an unpublished pencil sketch by Sir Joseph Hooker.)

Before leaving this subject it might be well to utter a plea for the retention of the useful words, hypogyny, perigyny and epigyny, in their original meaning as purely descriptive terms and to deprecate the infusion of theory into them which has recently taken place. It should be possible to call a flower epigynous without implying any particular view as to the origin of the condition. To limit it to cases of what are called " true epigyny " according to one theory or another is a perversion of language.

Turning now to the phenomenon which is in some ways the converse of axial invagination, namely axial elongation, we find that there are various ways in which elongation of receptacular internodes may occur. The enlargement of the internode between perianth and androecium, as a torus, we have already referred to, but the internode below this, between calyx and corolla, may sometimes be elongated, as in some Caryophyllaceae, notably *Silene saxifraga** (Fig. 1114), lifting the flower partially or wholly

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* It is true that in this, as in other Caryophyllaceae, there is a basal cohesion of the floral parts, but the gynoecium cannot be borne on this and there must be a core of axial tissue.

out of the calyx. It is then called the **anthophore**. Again, if the toral internode is notably elongated and there is a marked separation between the perianth and the two upper zones of the flower, the structure is called a **gynandrophore**; examples being *Passiflora*, *Boscia* (Fig. 1115) and *Sterculia*. The family of Capparidaceae supplies several remarkable examples of gynandrophores, sometimes moreover, surrounded by an elongated tubular cupule formed of the united calyx and corolla. When the internode between androecium and gynoecium is elongated (Fig. 1116) it becomes a **gynophore** (Papilionaceae, Rutaceae, etc.). The Capparidaceae are again noteworthy for the production of such structures, the gynoecium being often raised completely out of the flower, so that in the young state it resembles a rather large stigma at the top of a rather long style. One of the most striking examples is, however, the Ground Nut, *Arachis hypogaea*, in which the enormously elongated gynophore becomes positively geotropic and drives the young fruit into the soil, where it ripens (Fig. 1117). The ovary is itself so slim and pointed in its young state that it looks merely like the apex of the gynophore, and being colourless the entire structure at first closely resembles an adventitious root. From the biological point of view we may regard this gynophore as taking the place of the elongating pedicel which in other cases of "geocarpy" accomplishes the burial of the fertilized ovary. (See p. 1570.)

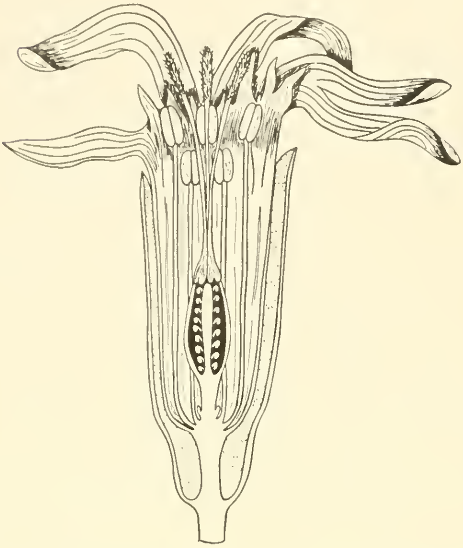

FIG. 1114.—*Silene saxifraga*. Flower in longitudinal section with anthophore, below, and gynophore, above. (*After Wettstein.*)

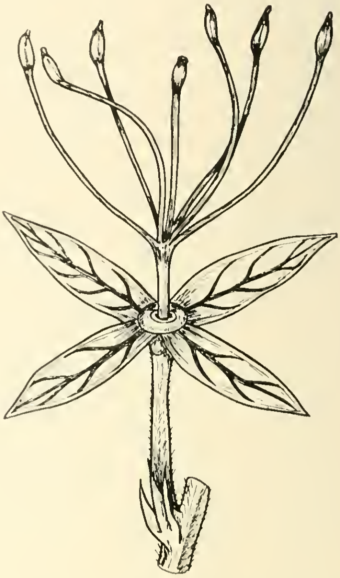

FIG. 1115.—*Boscia variabilis*. Flower with gynandrophore. (*After Collett and Hemsley.*)

A simple androphore supporting the androecium alone can only occur (unless the basal ring formed by the united stamens in flowers like *Oxalis*

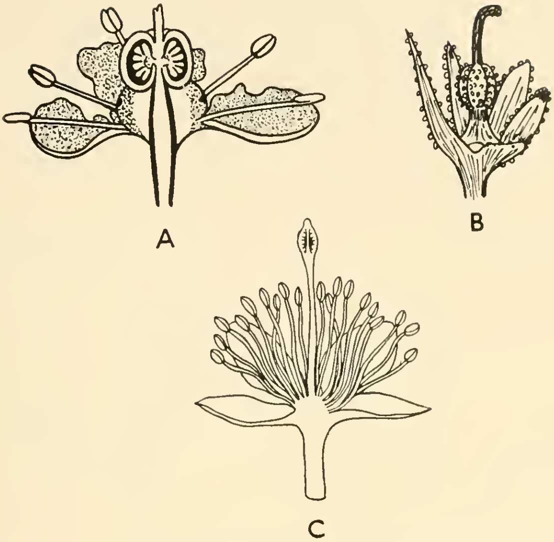

FIG. 1116.—Gynophores in: A, *Ruta*. B, *Dictamnus*. C, *Capparis*. (*After Le Maout and Decaisne.*)

FIG. 1117.—*Arachis hypogaea*. Base of plant showing long, geotropic gynophores bearing young fruits.

be so interpreted) in unisexual flowers. The male flowers of *Menispermum canadense* provide a good example, the stamens arising in a cluster at the top of a short naked stalk, almost like a male flower of *Taxus*.

A structure resembling an anthophore but apparently of different nature is that called by Velenovsky a **pericladium**. This is a sub-floral stalk found in many Liliaceae, varying from very short in *Convallaria* to a length equal to that of the pedicel in *Asparagus*. The junction of pericladium and pedicel is marked by a constriction in all these cases. The nature of this structure is revealed by *Tritileia* (Fig. 1118), in which genus the flowers of some species have no pericladium and a long gynophore, while in others there is a long pericladium and no gynophore. It would appear from the investigation of flowers of the latter type that the pericladium consists of a gynophore to which the bases of the other flower organs are adnate, that is to say they have cohered and adhered around it, forming a compound organ. The constriction below the pericladium is thus the true base of the flower.

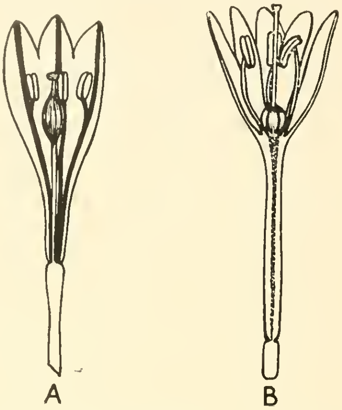

FIG. 1118.—Pericladia in flowers of: A, *Tritileia*. B, *Anthericum*. (*After Velenovsky*.)

THE FLORAL ENVELOPE

The demarcation between the vegetative, leaf-bearing axis and the flower is not always sharp or clear, especially with terminal flowers. As we have described in the early part of this chapter, there may be an assemblage of bracts or hypsophylls, below the flower, showing a more or less gradual transition between the foliage leaves below and the sepals above. The sepals may form a direct continuation of this series of bracts, or in some cases, there may be no distinguishable sepals and the series of bracts forms the outer envelope of the flower. Even where there exists a definite morphological boundary between bracts and sepals, the bracts may form a group with an evident, special relationship to the flower and constitute what is called an **involucre**. As Troll has maintained, there is no fundamental difference between an involucre surrounding a single flower and one surrounding a condensed inflorescence, such as that of the Compositae or of *Euphorbia*, which exhibits the *gestalt* or pattern of a flower. There is no need to suppose that involucrate single flowers are reduced capitula (Cf. *Scabiosa*, p. 1145). The two cases may be quite independent from an evolutionary point of view, though from the aspect of gestalt morphology they are equivalent.

FIG. 1119.—*Paeonia delavayi.* Leafy involucre.

Involucres are very varied in appearance. In *Dianthus* we have a simple involucre with four bracts, in two decussate pairs, set very close to the flower and resembling a calyx. The Ranunculaceae display all types of involucre, from the spiral series of bracts in *Paeonia* illustrated in Fig. 1119, and the wide, leafy involucre of *Eranthis*, looking like a green collar below the flower, to the loose, leafy involucres of *Anemone*, which are usually separated by some distance from the perianth. The latter genus is particularly interesting because of the series of stages to be observed between species like *A. nemorosa*, in which there is a whorl of three palmatifid bracts, each resembling a foliage leaf (Fig. 1120), which stands about half-way down the flowering stem, and *A. hepatica*, in which there is also a whorl of three involucral bracts, but so reduced in size and so close to the flower that it is difficult to withhold from them the name of sepals. Series like this support the view that the sepals are in fact involucral bracts which have become a permanent part of the flower.

The flowers of *Mirabilis* (Nyctaginaceae) are arranged in cymes of three, of which only the middle one develops. Around its base stands an involucre

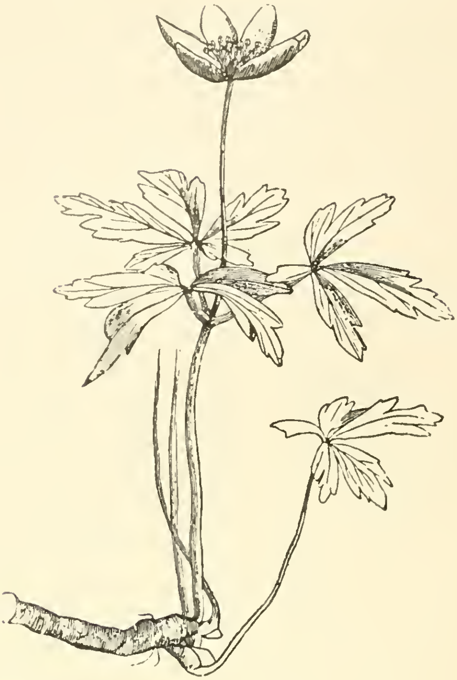

FIG. 1120.—*Anemone nemorosa.* Whorl of foliose bracts forming remote involucre. (*After Le Maout and Decaisne.*)

of five parts, which really belongs to the cyme but looks exactly like the calyx of the flower.

Another well-known example is the cupule or involucre of *Corylus*, the Hazel, which consists of a single enveloping leafy structure, developed from the minute bracteole of the individual female flower. In *Scabiosa* there is a double involucre, for not only is there a whorl of bracts around the inflorescence, but each individual flower is surrounded by a membranous cup, which, although it arises from the top of the inferior ovary, can be nothing else than an involucre (Fig. 1121). Finally there is the cupule of the Oak, *Quercus*, which is at least partly formed of closely imbricated bracts, although we have shown above that it is basically receptacular in nature and not distinguishable from the receptacular cupules found in Lauraceae.

Perianth or **perigone** is the name applied collectively to the floral envelope proper, which in the majority of flowers consists of sepals and petals. There is a certain number of flowers, usually small in size, which have no perianth and are called **achlamydeous**. At one time this condition of the flower was regarded as a mark of relationship and families thus characterized were grouped by Bentham into the class Incompletae. It is, however, fairly certain that the condition is one of reduction and that it has been reached from more than one direction. The group has therefore been broken up in recent classifications. Among families which are typically

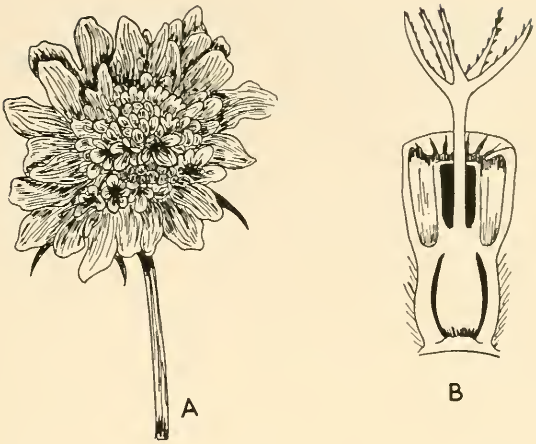

FIG. 1121.—*Scabiosa columbaria.* A, General involucre around inflorescence. B, Special involucre around a single flower. (*After Le Maout and Decaisne.*)

achlamydeous there are such diverse and unrelated types as Piperaceae, Ceratophyllaceae, Salicaceae, Myricaceae, Callitrichaceae, Typhaceae and Lemnaceae.

Many other families are partly achlamydeous. In the Betulaceae the female flowers, and in the Corylaceae the male flowers, have no perianth, although the flowers of opposite sex have one which is small and simple. A few families contain one or more genera which are exceptional in being achlamydeous. Examples of these are Naiadaceae (*Zostera*), Euphorbiaceae (*Euphorbia*) and Potamogetonaceae (*Ruppia*). A small number of genera may even contain certain achlamydeous species, *e.g.*, *Fraxinus excelsior* (Fig. 1122), although the rest of the species in that genus possess more or less complete perianths.

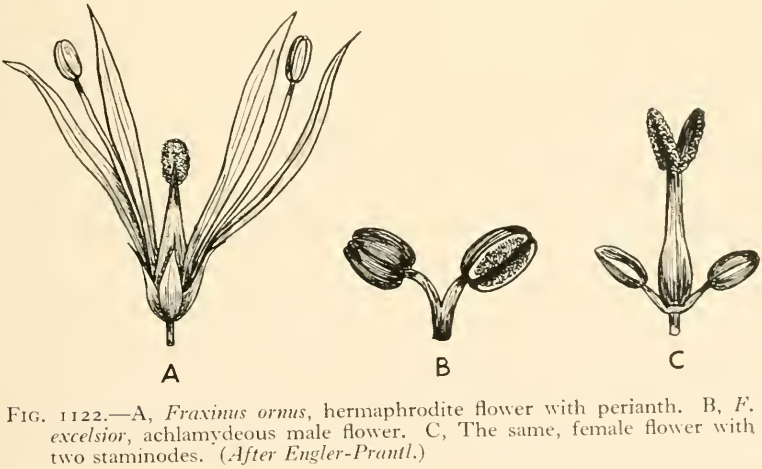

FIG. 1122.—A, *Fraxinus ornus*, hermaphrodite flower with perianth. B, *F. excelsior*, achlamydeous male flower. C, The same, female flower with two staminodes. (*After Engler-Prantl.*)

When only one type of member is present in the perianth the flower is called **monochlamydeous**, irrespective of whether the members are sepals or petals, though in the vast majority of such flowers the perianth parts are assumed, often without much positive evidence, to be sepals. If petals are present in some altered form, for example as nectaries, which in effect removes them from the category of perianth members, the flower may still be monochlamydeous and the perianth members are obviously sepals, but where no such morphological indication exists the vascular anatomy may be the only evidence available as to the nature of the existing parts. *Caltha* is a case in point, the perianth parts being coloured and petaloid in texture but having the characteristic 3-bundle trace of sepals instead of the single trace of true petals.

Where all the perianth parts are alike the flower is called **homoiochlamydeous**, a term often treated as synonymous with monochlamydeous, though it is not so in strict usage, for there are many flowers, especially among the Monocotyledons, where both sets of members are presen, though both are alike in appearance. In the Liliaceae both sets are petaloid, but both may conversely be sepaloid, as in *Rumex*.

Flowers with both sepals and petals present are called **dichlamydeous**, and if the two categories of parts are dissimilar they are, further, **heterochlamydeous**.

We have previously referred (p. 1137) to the phenomenon of concrescence between floral parts as affecting the question of the origin of epigyny and perigyny. While it remains doubtful, in many cases, whether a floral cup surrounding the gynoecium has originated by concrescence or by receptacular upgrowth, there are a few hypogynous flowers, such as *Hyacinthus* and *Asparagus*, in which a definite concrescence of sepals and petals has evidently taken place, usually also adding, as in the above examples, concrescence with stamens as well, so that all the whorls, except that of the carpels, may be adherent.

Although the placing of perianth parts around the floral receptacle follows the general principle of equidistance, to which we have already referred, there is considerable variety in their precise relations to each other. The spiral order has been very widely and perhaps rather uncritically accepted as the most primitive, that is to say, as the order which probably prevailed in the immediate ancestors of the Angiosperms. This view is admittedly bound up with the assumption that the Angiosperms have originated from gymnospermous ancestors with cone-like flowers of many sporophylls, spirally arranged, a view which, though probable, is by no means proved.

A sounder and more factual approach to the question lies in the comparative examination of the flowers themselves, and Salisbury, from extensive observations of meristic variation in the Ranunculaceae and Alismaceae, has suggested that the primitive condition is one of trimery, that is with parts in whorls, or closely placed groups, of three. This condition, he considers, is related to the mode of cell-division in the meristematic apex, which is in turn derivable from the type of three-sided apical cell that is prevalent among the Pteridophyta. We have already shown reason for doubting whether the axis in the Spermatophyta can be derived directly from that of the Pteridophyta (see Volume I, Chapter XXI), and of course, Gregoire's theory of the unique nature of the flower axis, if substantiated, would also tell against Salisbury's view.

The flowers of the Ranunculaceae, where the number of parts is large and fluctuating, afford very suitable material for the investigation of the conditions governing flower-building, and several intensive studies have been devoted to them. One of the most painstaking of such studies, by Burkill, does not support Salisbury's view of the primitiveness of trimery, but on the other hand, reveals a strong tendency to **isomerism**, that is to say towards stabilization with an equal number of parts in all four zones of the flower, calyx, corolla, stamens and carpels. This is attributed to the action of hormones, determining the character of each primordium on the receptacle, which are supposed to be equally distributed around the axis and to act most strongly along the lines of closest contact of the primordia, that is to say the parastichies.

If a trimerous, whorled flower is more primitive than a spirally arranged flower, then a shift of primordia must have taken place to bring about the change. Salisbury suggests that this occurred by the fusion of the last member of the outer whorl with the first member of the inner whorl, thus giving a single series of five members arranged serially, instead of two whorls of three. Some change of the plastochrones must also be involved, spacing out the newly arranged members in wider order on the axis. The perianth parts in Ranunculaceae, Rosaceae and many other orders with multipartite flowers, although apparently whorled, are, in fact, inserted in a very closely set series, which needs only a little elongation to produce a true spiral.

In most of the advanced families the perianth parts are, however, strictly whorled, that is to say their primordia appear simultaneously on the young receptacle, without any trace of precedence among them. The change from a spiral order, even a compressed spiral, to this ringed arrangement, is analogous to the change on the vegetative shoot between a spiral phyllotaxy and opposite or whorled leaves and has presumably come about in a similar way. It is no mere matter of shortening of internodes or of rearrangement of parts by suppression or fusion; a perfectly definite change in the growth pattern of the apical meristem is involved and of its inner physiological meaning we are still ignorant, though its consequences in flower-building have been obvious and profound. At one step it limits the number of parts of each kind, it crystallizes the tendency to isomerism and it opens up possibilities of constructive fusion on which the higher flower-forms depend.

The arrangement of the perianth parts in relation to each other is called the **aestivation** of the flower. There are two fundamental types. When the parts meet edge to edge they are said to be **valvate**, and this might be expected to be more common than it actually is, if the parts are equidistant on the axis. The valvate condition demands not only equidistant origins of the primordia but an exactly equal rate of growth among them and either or both of these conditions may be lacking in many flowers. Unequal spacing of the primordia is less common than unequal growth, but the majority of flowers are affected in some degree by these two factors, resulting in the overlapping of parts, which are then said to be **imbricate**. Sepals are less affected than are petals, so that the calyx may often be valvate while the corolla is imbricate, a condition beautifully illustrated by the flowers of *Fuchsia* (Fig. 1123). The corolla itself, in *Ailanthus*, shows both conditions, the petals being valvate below and imbricate above.

FIG. 1123.—*Fuchsia*, hybrid. Flower showing valvate sepals and imbricate petals.

Where there is a definite sequence in the appearance of primordia on the axis, the successive rudiments are separated from one another, in the great majority of cases, by an angle of about 140°, which has been interpreted, on geometrical grounds, as being an approximation to what is called the limiting divergence of 137°30′28″. If the growth of such rudiments were perfectly uniform, a uniform order of overlapping would naturally result. This is a common arrangement and is known as the **quincuncial order** (Fig. 1124).

The typical quincuncial order of imbrication is that of a $\frac{2}{5}$ spiral phyllotaxy. Parts 1 and 2 overlap at both edges, being the outermost of the spiral. Part 3 in the sequence overlaps with its backward edge and is overlapped by 1 at its forward edge, while parts 4 and 5 are overlapped at both edges, being the innermost parts of the spiral succession. Another frequent form of imbrication corresponds to a $\frac{1}{5}$ phyllotaxy, in which part 1 is the only one overlapping at both edges, and part 5 the only one which is completely overlapped, while parts 2, 3 and 4 are both overlapped and overlapping. This is sometimes regarded as typical imbrication.

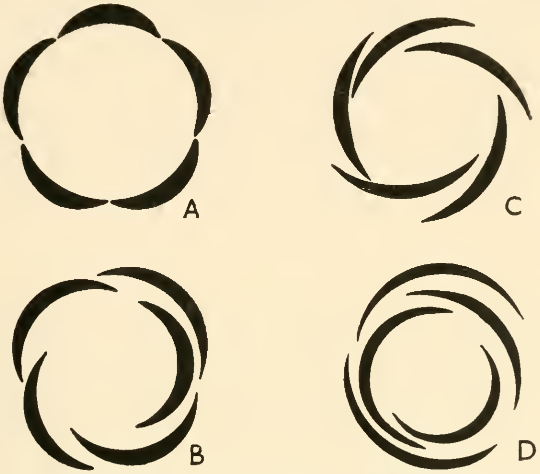

Fig. 1124.—Diagrams of aestivation. A, Valvate. B, Imbricate. C, Contort or Rotate. D, Quincuncial.

The common phenomenon of circumnutation of the vegetative apex shows clearly that the rate of growth may vary in different radial sectors of the axis and this is, no doubt, true of the floral axis also, since irregularities commonly arise through delay or acceleration in the growth rate of individual sectors. These inequalities may, in some cases, lead to the deformation of the receptacle or even to zygomorphy of the whole flower, but more commonly they lead only to departures from the typical quincuncial imbrication of the petals, due to the edges of petals slipping over or under those of their neighbours, as they expand.

The extreme case of departure from quincuncial arrangement is that in which each petal, in succession, overlaps its up-spiral neighbour and is overlapped by its down-spiral neighbour. This is called **contort** or **convolute** and it is characteristic of certain families, such as Gentianaceae. Both right-handed and left-handed convolution and imbrication occur and reversal is not uncommon. In *Saxifraga granulata* the existence of right-handed and left-handed races has been detected (Fig. 1125), an interesting case, in which not only the imbrication of the petals, but the order of opening of the flowers in the inflorescence and of the opening of stamens in the androecium, follow spirals which are reversed in the two races. Compton showed reason to believe that reversal of the overlap of the margins in the coleoptile of Barley was due purely to chance, but that can scarcely apply to so extensive a change as in the above example, where a genetic difference between the races seems to be probable. Analogous reversals in the spiral shells of Gastropods are well known.

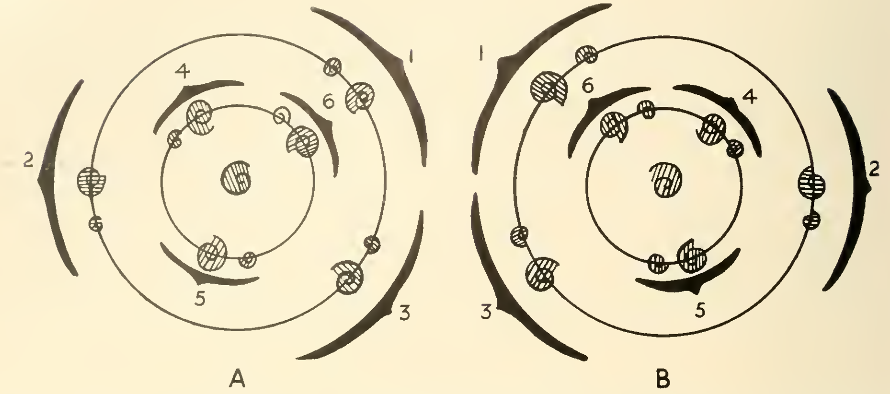

FIG. 1125.—*Saxifraga granulata.* Inflorescence diagrams of two different races showing the different distribution of right-handed and left-handed flowers in the two cases. (*After Goebel.*)

There are two other conspicuous departures from the quincuncial order. The first is the **vexillate** form characteristic of Papilionaceae (Fig. 1126). The standard petal is part 4, but instead of being internal, its superior vigour of growth renders it entirely external. The second is the **cochleate**, characteristic of the type of scrophulariaceous flowers called " personate " (see p. 1155). Here the second part, which is the anterior petal of the flower, is delayed in growth and is internal to both its neighbours.

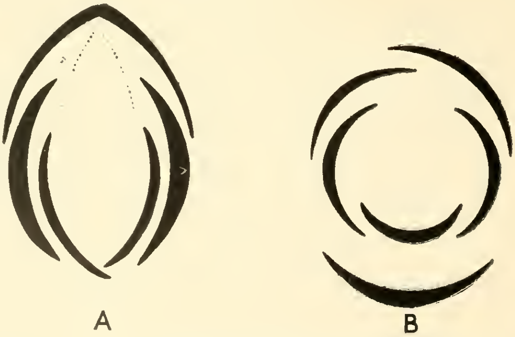

FIG. 1126.—Diagrams of aestivation. A, Vexillate. B, Cochleate.

Analogous differences occur in the aestivation of monocotyledonous flowers, with a $\frac{1}{3}$ phyllotaxy, but in this class, with the smaller number of parts in a whorl, it is not uncommon for the parts to be entirely separated, so that no question of overlapping arises.

The act of flowering is called **anthesis**. The initiation of flowers has sometimes been attributed to " flower-building substances ", but if by this is meant the action of peculiar compounds which specifically build floral tissues and no others, then there is no evidence of their existence. What is more probable is that under certain conditions the physiological system of the plant is ready or ripe for flower formation and it may be that the mechanism is put in motion or directed by the action of certain material agents, which we may think of as " flower-realizers " in the sense that they induce flower formation in a system already prepared for it. Readiness for anthesis is a definite physiological condition, localized in certain parts of the plant, as shown by the fact that plants grown from cuttings of flowering shoots, though slow to establish their own roots, give plants which grow slowly and flower freely, but cuttings of vigorous, vegetative shoots form roots quickly and give plants with luxuriant vegetative growth and few flowers. The underlying physiological factors in this disposition to flower are still little understood, but it is known that the relative lengths of exposure to light and darkness are important, and may be decisive in controlling flowering, as we shall see in our treatment of physiology in a later volume.

FIG. 1127.—*Cercis siliquastrum.* Fascicles of flowers on an older branch. An example of nudiflory and also of ramiflory, one of the forms of cauliflory.

Flowering usually precedes or follows, rather than accompanies, the period of greatest vigour in growth. Some plants indeed flower before the leaves appear, when there is no other growth in progress. Others flower, like *Colchicum*, after the leaves have died off, either condition being spoken of as **nudiflory**. Many species flower on the extending shoots of the current season, but far more flower on older shoots, of the previous or still earlier seasons. Tropical woody plants have the peculiarity, in many cases, of flowering on the oldest branches or even on the main trunk, which is called **cauliflory** (Fig. 1127). See also p. 1074.

The expansion of the flower is brought about by a change in the growth relationships of the perianth members. In the bud stage the close association of parts is due to hyponastic growth, that is growth which is greater on the abaxial than on the adaxial side. This gradually diminishes to zero and is replaced by epinastic growth, or excess growth on the upper surface, particularly at the base of the members, whereby their angle with the axis is greatly increased. In some cases, especially in sepals, this may go so far that the parts are completely bent backwards against the axis below the flower, when they are said to be **reflexed**. Salisbury has shown that the reflexed sepals in some species of *Ranunculus* are sensitive to light, and that in light of diminished intensity the epinastic curvature is greatly lessened and the sepals do not become reflexed. The same is true of the epinastic growth at the bases of vegetative leaves. These growth movements must be distinguished from the variable movements of parts in the expanded flower, such as the movements of night-closing, which are usually due to variations of turgor in the tissues, associated with changes either of light or of temperature, or else follow mechanical shock.

The range of the size of flowers is very great. Minute annuals may have flowers only 1 mm. across. At the other end of the scale are the immense flowers of *Rafflesia arnoldi* (see Fig. 1576) and *Aristolochia gigas* which may be nearly 1 metre across.

Relatively few flowers are more than 10 cm. in diameter, and most large flowers are tropical. Conspicuousness is otherwise attained by massing small flowers together, by which means the chances of cross-pollination are increased.

Generally speaking the size of flowers is in inverse relation to the numbers produced, the giant flowers being always solitary and the largest inflorescences producing, on the other hand, numerous small flowers.

The duration of flowers is also very variable. Many last for less than a day, opening only once and closing after a definite number of hours. Observation of such ephemeral flowers has enabled gardeners to construct " floral clocks " which show the time of day by the opening and closing of the various flowers of which they are composed. The most ephemeral flowering on record is that of *Hibiscus trionum*, which opens about 9 a.m. and closes by noonday, a period of only three hours.

According to Kerner there is an inverse relationship between the number of flowers produced and their longevity. If a plant produces but one flower annually, as do many Monocotyledons, the flower usually lasts for many days, thus increasing the chances of insect pollination. Conversely flowers of large inflorescences and, moreover, flowers with numerous stamens and abundant pollen are usually short lived. Longest lived of all are the flowers of some Orchids, which may last from one month to three months or more. There is a definite relation of longevity to pollination and in most flowers fading follows rapidly after pollination, even in long-lived flowers. See also p. 1480.

The physiology of the fading of flowers is a complex problem. In some cases the evanescent parts, especially petals and stamens, are cut off by abscission layers at the base and dropped while they are still fresh. In others the abscission layer is formed but the parts are not dropped. They wither because their water supply is interrupted. Many form no abscission layer but the water content of the petals is apparently withdrawn by neighbouring organs; while in a large number none of these things happen and the petals die from unknown internal causes, attributed by some writers to inherent instability of their protoplasm, which is not very enlightening.

The general functions of the perianth in anthesis may be summed up under two headings: (1) The attraction of pollinating insects and, to a more limited extent, the regulation of their entry into the flower. (2) The protection of pollen and nectar from the weather and from robbery by non-pollinating insects, such as flies. The first function is naturally limited to insect-pollinated flowers and is associated with bright colours and often with perfume. This function of the perianth as an " advertisement " and as a regulator of insect movement, we shall deal with more particularly when we speak about pollination (see Chapter XXIV). It is no longer a " naive assumption ", as Goebel calls it, that insects are colour sensitive, for much experimental evidence shows that they can have markedly selective preferences in this respect. It is true that differential coloration of the reproductive organs is a very widespread phenomenon in the plant world and is found in all groups from the Algae to the Gymnospermae, but there can be little doubt that its remarkable development in the flower is associated with the habit of insect-pollination, which has been in so many respects the *deus ex machina* of floral evolution.

De Candolle divided flowers, according to their colours, into a xanthic or yellow series and a cyanic or blue series. This classification does in fact correspond to an important difference between those flowers which carry coloured plastids displaying yellow, orange or red, due to carotenoid pigments, and those flowers which carry soluble anthocyanin pigments of red, pink, purple and blue shades. The delicate yellows of the Primrose type really belong to this latter series, as they are due to the related pigment class of soluble anthoxanthones. Grant Allen suggested that flower colours presented an evolutionary sequence, in which yellows and whites predominated among the more primitive polypetalous flowers, especially those pollinated by small flies and beetles, while anthocyanin colours are commoner among the more advanced sympetalous flowers, which are chiefly pollinated by bees. Lubbock and others having shown that bees have a preference for blue, Allen concluded that natural selection would tend to produce blues as the end of the progression. As a broad general principle this may be true, but it is an over-simplification of the facts, for the relations of the bees to flowers are very complex and by no means fully known. Some bees are monotropic, that is visit only one type of flower. The individual hive bee may also be monotropic, but the great stores of hive honey demand a wide range of flower-visits and the colony as a whole is polytropic. The choice of flowers is not controlled by colour alone, but even more importantly by the abundance and the concentration of the nectar provided. Humble bees are perhaps more influenced by flower colour in their visits, and most of the large flowers, among which blues and purples are common colours, are pollinated by humble bees, not by the short-tongued hive bees.

Colour patterns on petals are commonest in zygomorphic flowers, especially lines and streaks, which have always been regarded as "honey guides" and are not generally required in actinomorphic flowers. On the other hand patterns of scattered dots and blotches are often found in fly-pollinated flowers and they may perhaps be more readily noticed by flies than are pure colours. Flies are short-sighted creatures and the flowers which depend on their visits are usually small and relatively dull in colour. No matter how brilliant the colour of a small flower might be, it would not be visible to a fly at a distance. To attract long-sighted bees or butterflies, flowers must either be individually conspicuous or else grouped into large clusters. Colour patterns may be useful to such flowers by increasing conspicuousness through contrast. Many flowers show very striking colour contrasts in their perianths or between the perianth and the other parts, while coloured bracts, leaves or stems may also be called into use to increase the contrast effect, of which there are numerous examples (*e.g.*, *Bougainvillea*, *Poinsettia*, *Davidia*, etc.).

Troll has pointed out the interesting fact that in the Compositae, which are, of course, highly specialized Sympetalae, the colours of the ray florets, which stand around the inflorescence like a ring of separate petals, tend to resemble those characteristic of the simpler polypetalous flowers, *i.e.*, white, yellows and reds predominate, while blues are relatively scarce. It is as if the inflorescence were behaving biologically like a simple polypetalous flower.

Flower colours are subject to alteration in tone and intensity by some external factors, especially the brightness, quality and duration of light. Bright sunshine and long days increase the depth and brilliancy of colour. The same varieties, grown for comparison in Uppsala, Sweden, and in Paris, showed a consistent advantage in favour of the northern plants, grown under a longer summer day. A greater intensity of short wave-lengths in the sunlight, such as prevails at high altitudes, also increases the brilliancy of colour and enhances the attraction of alpine flowers.

The second general function, that of protection, may include the whole flower or only the pollen. The green perianths of small flowers, such as those of Chenopodiaceae, are limited in their function to protection of the young parts of the flower and sometimes of the young fruit, during growth. More highly developed, dichlamydeous perianths usually show a division of function, the calyx acting as a general protection in the bud stage and the petals, apart from their attractive function, acting to protect the pollen. In a great many flowers this is ensured very simply by the pendent or inclined position of the flower, a feature especially notable in zygomorphic flowers, when the corolla acts as an umbrella over the stamens. Actinomorphic flowers are usually vertical, however, and in them pollen protection involves, in many flowers, movements of the petals, either in moist air or darkness, which cause them to bend inwards, closing the flower and covering the anthers. Alternatively, the petals may be folded, hooded or pouched in such a way as to afford protection. (See also p. 1305.)

Pollen protection, it is true, is not confined to such means. Bracts, for example, may often act in the same way as the petals do in other cases, while a great many flowers ensure that the pollen shall not be washed away by rain and lost, through the bending of the pedicel which turns the flowers downwards in darkness or in rainy weather. Protection from robbery by small insects concerns the nectar more than the pollen and as a means to this end the flower is sometimes permanently closed to all but large and strong insects, or else the corolla is so narrowed and elongated that only long-tongued insects can reach it. A well-known example of the closed flower is the type known as **personate**, of which the garden *Antirrhinum* is a conspicuous case (Fig. 1128). The two lower petals of the tubular corolla are so humped that they fill the mouth of the tube. They are hinged at the sides, however, so that a humble bee, clasping the flower between its legs, can force the obstructive petals to bend downwards, opening the mouth of the flower for the entrance of its tongue. The common name of Snapdragon is derived from this opening and shutting of the mouth of the flower when it is gently squeezed.

FIG. 1128.—*Antirrhinum majus.* Flower with personate corolla.

We have already spoken of the symmetry of the perianth in a previous section of this chapter, but there are one or two cases deserving another mention here, in which zygomorphic symmetry is related to the special functions of the perianth in anthesis. One such case is the frequent occurrence of asymmetric perianths, especially corollas, in flowers at the periphery of a closely-massed inflorescence, in which the petals standing radially outwards are bigger than those directed radially inwards (cf. Exotrophy, p. 1114). This type of zygomorphy is quite different from that in, for example, a *Viola*, for it is not related to pollination of the individual flower. Moreover these flowers, like their radially symmetrical neighbours, are usually directed more or less vertically, whereas in typically zygomorphic flowers the opening of the flower is usually directed outwards and downwards. Such flowers are characteristic of the inflorescences of Umbelliferae and Compositae. Their function is apparently the increase of the conspicuousness of the whole inflorescence, which, in the cases cited, as in others, consists of small, individually inconspicuous flowers. (See Fig. 1090.)

Another form of functional zygomorphy is due to the development of nectar spurs, in the form of hollow sacs, as projections from one or more of the perianth parts. In rare instances, as in some Crucifers, spurs are developed symmetrically and there is no zygomorphy, but it is usual to find one spur only, developed by the invagination of one sepal or petal. The abnormality called **peloria** (see p. 1100), namely the secondary development of radial symmetry in a zygomorphic flower-type, is sometimes brought about by the production of extra spurs from all the members of a perianth whorl, instead of from one only. This is exhibited, for example, by some strains of *Linaria vulgaris*, in which the abnormality is inherited. The additional spurs compensate the natural zygomorphy and produce an actinomorphic flower.

Peloric flowers are usually produced on orthotropic axes, particularly the main axis, in species with otherwise zygomorphic flowers. Although frequently exhibited by spurred flowers it is not confined to them and a similar regular development of the petals in zygomorphic corollas is sometimes seen in *Viola* and quite frequently in certain strains of *Digitalis* (see Fig. 1070). The opposite case, namely the development of zygomorphy in species whose flowers are otherwise actinomorphic, is rare, but examples have been recorded, every case being in flowers growing on horizontal branches. A notable instance of such zygomorphy has been reported from *Fuchsia coccinea*.

A spur may be no more than a slight concavity or it may be a tubular extension several inches long. The longest are found in the orchid *Angraecum sesquipedale*, a native of Madagascar, whose spurs are more than a foot long. This limits access to its nectar to the longest-tongued Lepidoptera, with which therefore the pollination of the plant is linked so closely as almost to amount to a symbiosis.

Sepal spurs are less common than petal spurs. The Cruciferae, mentioned above, show them almost throughout the family. Several members of the Ranunculaceae also have them, *e.g.*, *Myosurus*, in which each sepal is spurred, and *Delphinium*, in which the posterior sepal and petal are both spurred, the one fitting inside the other. The garden *Tropaeolum* has a long, coloured spur which is composed of prolongations from the three posterior sepals fused together.

Petal spurs are too numerous to be specified, but we may note that they occur both in polypetalous corollas, *e.g.*, *Viola*, *Aquilegia* (Fig. 1129), and in sympetalous corollas, *e.g.*, *Centranthus* and *Linaria*.

That zygomorphy depends on the differential development of certain sectors of the flower axis is clearly indicated by these spurred flowers, thus giving point to Burkill's comparison of zygomorphic flowers to sectorial chimaeras, plants in which tissues of different genetic character as well as different growth characters are united sectorially in a single shoot.

FIG. 1129.—*Aquilegia vulgaris*, flower with spurred petals.

The calyx has a biological importance of its own, quite apart from the corolla. Its general function of protection for the inner parts during the bud stage is often supplemented by other specialized functions in this and also in other respects. One of the most important of these additional functions is the protection of the developing fruit, after anthesis. An example of this is *Hyoscyamus* (Henbane), where the base of the synsepalous calyx develops into a hard, rounded case, enclosing the fruit and surmounted by a crown formed of the free points of the sepals. A very striking example is afforded by *Physalis peruviana* (Cape Gooseberry) in which the berry is enclosed in a large, inflated case (Fig. 1130), composed of the bright orange-coloured and almost petaloid calyx. Such persistent calyces may also become agents of dispersal, but these we shall deal with later (see p. 1556). At the opposite extreme are the caducous calyces which, having no function beyond the initial one of protecting the bud, are dropped off when the flower opens, as in *Papaver*.

The calyx may often supplement or replace the corolla as a means of advertising the flower, of which there are numerous examples in the Ranunculaceae, *e.g.*, *Caltha*, *Helleborus*, *Clematis*, etc. The garden *Hydrangea* is also an example known to everyone. Instances of such modifications of the sepals are extremely numerous and the change of character is not always as simple as in the cases cited. It is notable that not infrequently the protective function, which is no longer carried out by the modified calyx, may be taken over by bracts, which surround and enclose the young flower in a manner exactly analogous to that of a normal calyx.

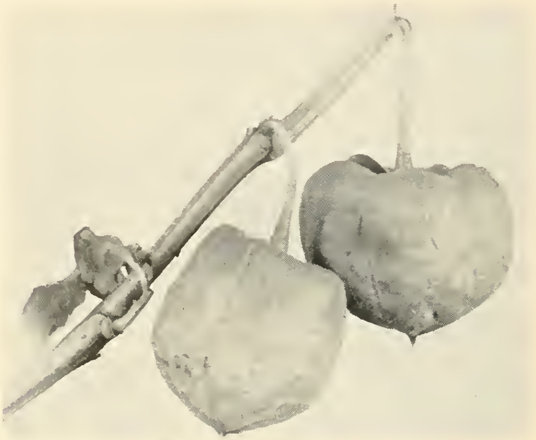

FIG. 1130.—*Physalis peruviana.* Persistent, inflated calyces enclosing the berry fruits.

A peculiar physiological modification is that known as a water calyx, in which the calyx forms a closed sac loosely enfolding the flower bud, and filled with water which is secreted from glands on the inner surface of the sepals, so that the young flower is immersed and completely protected from desiccation. These calyces are especially characteristic of tropical plants, particularly in the families Bignoniaceae and Solanaceae. Analogous water calyces enclosing the young fruits are found in some members of the Convolvulaceae.

The calyx has a generally protective function in the bud stage of the flower but in some genera the sepals persist into the fruiting stage, *e.g.*, *Rosa*, *Clerodendron*, *Ceratopetalum*, when they may fulfil other functions in connection with fruit dispersal. Marking the change of function there are very often changes of colour or consistency, correlated with the changes which fertilization brings about in the gynoecium.

Sepals occasionally bear stipules, which appear to form an outer zone of smaller sepals, known as the **calyculus**. The Strawberry and a number of related genera in the Rosaceae have a calyculus of five segments alternating with the five sepals, and formed of stipules fused laterally in pairs, two to each sepal. Such structures should be distinguished from a true **epicalyx**, in which, as in *Malva*, the outer zone is composed of small bracts in a whorl. The difference between such a whorl of bracts and an **involucre** (see p. 1142) is only a matter of degree, the bracts which form an involucre being rather less close to the calyx, as in *Anemone hepatica* and *Dianthus*, and frequently united to each other. We do not consider that a clear distinction is possible, but the two terms may be retained, as they are descriptively convenient in distinguishing cases where the bracts appear to be an addition to the calyx itself, from those in which they appear to form a distinct structure.

That the sepals are themselves of bract nature is borne out, as we have shown above, by the triple vascular trace which supplies them. They are also known to produce, occasionally, axillary buds, as in the small white flowers of *Isopyrum thalictroides* (Ranunculaceae) which has petaloid sepals and no petals. Secondary, pedicellate flowers may spring from the axils of its perianth members or alternatively sessile, incomplete flowers, standing in the sepal axils, may be included within the perianth of the primary flowers.

The **corolla**, which consists of the inner series of perianth parts in complete flowers, is generally the most conspicuous portion of the flower, usually distinctively coloured and delicate in texture. Delicate as they may seem, many corollas possess, however, a remarkable resistance to desiccation. Stomata are usually present, but, as the guard-cells contain no chloroplasts, they may not be functional.

The epidermis is often cuticularized, sometimes heavily, or covered by a thin, waxy coat. The flowers of many species, notably those of some Malvaceae, still appear fresh after having been detached and left on a table for twenty-four hours. Other species, although similar in appearance, begin to wilt almost immediately after they are cut. Comparatively little is known about the physiology of these and other characteristics of petals. We have referred to the question of the withering of flowers previously in this chapter, on p. 1152. See also Chapter XXV, p. 1480.

It is in the corolla that the character of the flower is most prominently displayed. We have already pointed out that two main classes are readily recognizable, namely those in which the petals are all free from each other (**apopetalous** or **polypetalous**), and those with the petals coherent to each other (**sympetalous**), but both these classes include the most extreme variations of form and size. Petals may, of course, be completely absent and the flower be therefore **apetalous**, or they may be transformed into nectaries, of which we shall give some examples later. Transitions between petals and stamens are not uncommon, particularly in spiral flowers such as *Trollius*, where a zone of indecision may appear exhibiting every gradation between perfect petals and perfect stamens, in a continuous series.

The anatomy of sepals shows unifacial structure at their points and that of petals at their bases, in which the latter agree with stamens. We may conclude from this that a sepal is morphologically the equivalent of a phyllopodium or leaf base and that a petal is the equivalent of the upper leaf portions. The two sets of organs are thus of distinct nature, though both fundamentally referable to the leaf category. If the petal-stamen homology is sound then this reference to the leaf category would hold also for the stamens.

There is a strong probability, as we have shown above in considering receptacular anatomy, that the petals and stamens are of the same morphological nature, and the balance of probability is in favour of regarding the petals as sterilized stamens. Intermediate forms, for example in double and semi-double flowers, indicate that it is the anther connective which contributes the expanse of the new petal and that the filament of the stamen goes to form little but the petal-base. These intermediate petals are often bi-lobed, with a minute apiculus between the lobes, and, where anthers are present on them, the two halves of the anther stand on the outer edges of the two lobes, as may be seen in double flowers of *Galanthus nivalis.* This strongly suggests that the petaloid portion of the organ is a broadened anther-connective, rather than a broadened stamen-filament. Traces of this supposedly primitive bi-lobing of the petal may be seen at the apices of the petals in a great many flowers, even where there is no indeterminacy and complete fixity of character prevails, *e.g.*, in many Caryophyllaceae.

Petals are usually somewhat late in their appearance in the ontogeny of the flower and this has been considered to be connected with their status as arrested stamens. The stamens may be well developed, with their archesporium already formed, before the petal-rudiments begin to appear. As Arber points out, in flowers like *Clematis* where the perianth is of sepal nature, its parts are well in advance of the others in development. It is as if there were a hesitation in the development of the flower at the petal stage, associated with their anomalous character, which is neither fully foliar nor fully staminal, but contains an admixture and perhaps an opposition of both characters.

FIG. 1131.—*Feijoa sellowiana.* Flower showing the dark-coloured upper surface of the fleshy petals, which are nectariferous.

The almost boundless plasticity of plant form is nowhere shown more prominently than in the variations of the corolla, especially in zygomorphic flowers. To mention particular examples is almost otiose, but the families of Orchidaceae, Leguminosae and Zingiberaceae may be cited as among those displaying the greatest diversity of form, colour and texture. The fragile texture of most petals is sometimes modified. In *Feijoa sellowiana* (Myrtaceae) (Fig. 1131) the petals are fleshy and the entire inner surface, which is bright crimson in colour in contrast to the white outer surface, is nectariferous, so that they are eaten in Brazil as sweetmeats. In the annonaceous genus *Xylopia* the petals are woody and look like the five valves of a dehiscent capsule. Petals are not often hairy, the White Dead Nettle, *Lamium album*, providing one of the best known exceptions. Hairy flowers, like hairy leaves, are usually associated with xerophytic conditions, as in many Ericaceae in South Africa, but this is not so in *Hoya carnosa* (Asclepiadaceae) (see Fig. 1798) which is a tropical climber from S.E. Asia. Sepaloid and staminoid modifications of the petals are widespread and have already been described; less common are those which are sepaloid in the middle and petaloid at the edges, as in some degree occurs in several Liliaceae. The Compositae provide a very interesting study in the modification of the corolla. The distinction between the small, actinomorphic corollas of the disc flowers and the large, unilaterally developed corollas of the ray flowers is well known, but the form of the latter is very variable, the " ray " or ligulate portion being formed from two, three, four or all five of the united petals. Troll has shown that in the details of its structure this ligulate portion often reproduces, even in small details, features characteristic of single petals, which he regards as supporting his conception of the overriding influence of the " flower model " or pattern in shaping structures of diverse morphological character.

Petals are often differentiated into a narrow basal part, called the claw, and a flat, expanded part called the limb. The petals of the Cruciferae afford a good example, the narrow claws of the four petals standing vertically, so close to the stamens and to each other that they make a good substitute for a floral tube of the *Primula* type. Some bizarre extremes of this type of petal formation are to be seen in the Sterculiaceae, the petal limbs appearing on the ends of long, delicate filaments, which gives the whole structure a striking resemblance to a stamen. The Asclepiadaceae provide numerous examples of the opposite modification, the apex of the petals being here drawn out into long filaments, which may be many times as long as the flowers (Fig. 1132).

Fig. 1132.—*Trichosacme lanata.* Petals with long hairy appendages. (*After Velenovsky.*)

One of the most striking modifications of the normal corolla is the development of an inner ring of ligule-like appendages, the **paracorolla**, which may be united into a membrane, like a belt, called the **corona**. Examples of these structures are widespread, in many families, but they are best known in the Amaryllidaceae, where the prominent corona of *Narcissus*, often extended into a long, tubular " trumpet ", is familiar to all.

Many morphological interpretations have been put upon this structure, and it is not necessary to assume that it is always of the same character. It usually arises on clawed petals at the junction of the two parts, or at the mouth of the floral tube in sympetalous corollas, which is morphologically the same situation. It has been interpreted as representing petal ligules, petal stipules, staminal stipules, simple emergences, foliar modifications of the upturned basal lobes of sterile anthers, or invaginations of the petal tissues. The last condition is obvious in *Symphytum*, where the teeth of the paracorolla are really hollow pockets, and the same explanation holds for *Lychnis*, where however the hollow structure can only be made out in sections. Although the corona, as a united structure, is best known in the above-mentioned family, the Amaryllidaceae, a paracorolla of separate segments is prominent in several dicotyledonous families, *e.g.*, Thymelaeaceae, Gentianaceae, and Passifloraceae. In *Passiflora* (Fig. 1133), indeed, the long, blue-and-white striped filaments of the paracorolla quite outshine the corolla itself in beauty. Here they have plainly no connection with the stamens and would appear to be outgrowths from the petal bases, but in *Gentiana* two different structures are apparently involved. In *G. amarella* the paracorolla filaments are like those of *Passiflora*, petal outgrowths, but in *G. verna* and some other species, staminal stipules have become united together outside the stamens filaments and have also become more or less united to the corolla, giving the same appearance of a paracorolla as in *G. amarella*.

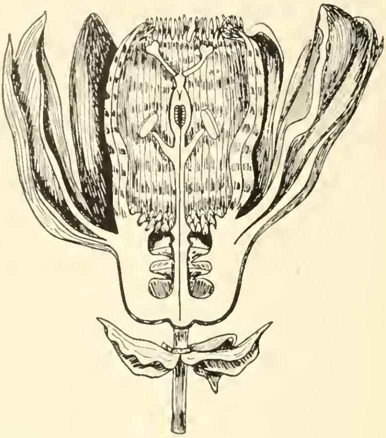

FIG. 1133.—*Passiflora coerulea*. Longitudinal section of flower showing the ring of blue-and-white striped effigurations inside the corolla. (*After Engler-Prantl.*)

In Amaryllidaceae also, both types of structure are represented. The Pancratiae have a corona which is definitely staminal in origin and mostly united to the androecium (Fig. 1134), but in *Narcissus* (Fig. 1135) the corona is explained by Arber as due to ligular outgrowths of the petals, which are reversed in orientation, as shown by their vascular bundles, so that the two

FIG. 1134.—*Eucharis amazonica.* Amaryllidaceae. Flower with staminal corona.

FIG. 1135.—*Narcissus pseudonarcissus.* Flower showing medium-sized corona.

portions of the petal face one another, like the two portions in the double-bladed leaves which are sometimes found as abnormalities in a number of plants, for example in *Bergenia crassifolia* (Saxifragaceae), well known in gardens.

Stipules in the flower are not uncommon. We have already noticed them in sepals and they are also found on petals. Many genera of the Caryophyllaceae, *Silene* and *Viscaria* for example, have narrow membranous appendages, on each side of the petal-claw, which can only be regarded as stipules. They are, moreover, quite distinct from the paired invaginations which form the paracorolla in *Lychnis*, *Melandrium* and some other members of the family.

In *Hypecoum* (Fumariaceae) the stipules of the two internal petals are retracted to a position external to the petal and are so much larger and more conspicuous than the petal itself that the latter might be mistaken for an outgrowth of the stipules, did not the floral diagram show the true position. The outer petals, on the other hand, have only two stipular wings of moderate size.

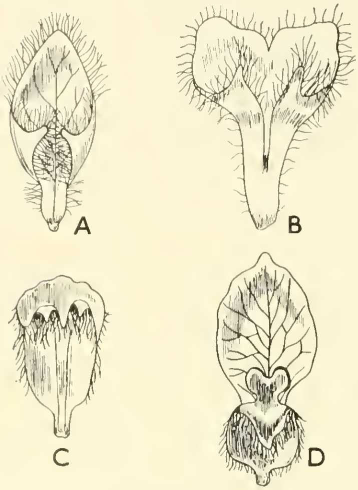

Fig. 1136.—*Serjania*, petals of various species showing the development of petal stipules from two basal lobes into a united structure opposed to the petal. (*After Velenovsky*.)

The flowers of the Sapindaceae provide a very interesting series of developments in petal stipules, beginning with two inturned marginal lobes, which in some genera become united adaxially, forming, with the petal, a cup. Finally, in *Serjania* (Fig. 1136), the fused stipules separate from the petal and stand up independently, forming an inner ring, like a second corolla or paracorolla, of small, bifid segments.

The awns on the floral parts of grasses are for the most part the terminal portions of the glumes, paleae, etc., on which they occur, the blade-like portion of these structures, which is frequently bifid at the apex, being probably stipular in nature. When the apex is not bifid it forms a crest across the adaxial side of the awn, analogous to the ligular crest on vegetative grass leaves, a structure which itself may also be either bifid or united.

The subject of fusions between corolla parts during the evolution of the flower is one we have already mentioned when considering the floral phyllotaxis. The most conspicuous category is that of tangential, *i.e.*, marginal, fusion between members of the same corolla whorl, in cyclic flowers, to produce a **floral tube**. This condition, called **sympetaly**, occurs sporadically in some families of the Archichlamydeae, namely Rhamnaceae, Crassulaceae and Papilionaceae, but is a uniform characteristic of all the families which form the group of the Metachlamydeae; *e.g.*, Primulaceae, Scrophulariaceae, Compositae, etc. Among these floral types there is an almost endless variety of forms, the description of which, by themselves, without relation to their functions in pollination, would lead nowhere. The appropriate place for their treatment is in the consideration of the families of Angiosperms (see Chapters XXVIII to XXX and Chapter XXIV on Pollination). We should remark here, however, that striking alterations in the mature structure may arise from relatively slight adjustments of the distribution of growth in the rudimentary stages. Many apparently exceptional forms can be traced on analysis to a few simple changes in the distribution of growth rates among different parts. An acceleration here, a retardation there and the outcome may seem altogether different. To take an easy example, let us suppose a young flower with five equal petal-primordia. If these grow most rapidly in their upper regions, five separate petals will result. If, on the other hand, their basal zones, where they are in contact, are most active in growth, a five-lipped floral tube will be found. Should they grow separately at first, and thereafter the growing zone shift to the bases, linking two rudiments on one side of the flower and three on the other, a two-lipped labiate corolla will be produced. Probably the commonest mode of formation of a floral tube is that of an early union of primordia into a ring, which elongates by intercalary growth.

Temporary cohesions, between the edges of valvate sepals and petals, are not uncommon in the bud stages, being subsequently ruptured when the bud opens. The red sepals of *Fuchsia* are a good example. Haberlandt has shown that these junctions are formed by the suturing of the marginal cells together by means of many minute interlocking processes, without actual tissue union existing.

The histological structure of petals is, as a rule, simple. The epidermis is often papillate, giving a velvety surface, but does not often produce long hairs. The epidermal cells, even when not papillate, are often covered with a ridged or warty cuticle which produces a matt surface. Glossy petals are, in fact, exceptional. Those of *Ranunculus*, so well known to children, owe their sheen to starch grains in the epidermis, which form a light-reflecting layer. Stomata are usually present, though they seem to be incapable of movement. The guard cells are devoid of chloroplasts and the whole structure is often vestigial. The interior tissue is generally loosely organized, with irregular cells and abundant intercellular spaces, and there is rarely any differentiation of a palisade layer corresponding to that in foliage leaves. Secretory cells and epidermal glands are commonly present and secrete the aromatic substances which give flowers their perfume. The walls of the epidermal cells are often very highly convoluted and in many cases the convolutions open into loops, leaving small intercellular passages. The whole outer surface is however covered by a continuous cuticle, which varies in thickness in different species. Chromoplasts may be present in some red and yellow flowers, but in some yellow and in most blue or purple flowers, the cells, including sometimes those of the epidermis, are filled with anthocyan pigments in solution and no plastids occur.

The vascular supply to the petal is, almost universally, a single trace bundle, but this branches pinnately from near the base, except in very small petals, and the branches form an open fan-pattern, following apparently the marginal expansion of the petal rudiment. Marginal bundles, which are common in leaves, are rare in petals and are confined to a few families and genera, notably the Primulaceae, the Compositae and the genus *Datura* in the Solanaceae, all of which are sympetalous. There is a good deal of comparative evidence to support the view that these exceptional marginal bundles, which do not originate as branches from the main petal-traces, are derived from lost stamens of an outer whorl alternating with the petals (*i.e.*, antisepalous), the persistent traces of which have become incorporated into the petal-whorl. Some flowers, indeed, show that their antisepalous stamens have become transformed into supernumerary petaloid structures which are bodily incorporated into the corolla. As all the facts tend to support the idea that the normal petals are sterilized stamens, there is nothing inherently unlikely in the addition to the corolla of these accessory members from the outer stamen-whorl. (See Fig. 1065.)

The vascular bundles which form the petal supply are usually small and of relatively weak development. Very often they are centric, with phloem surrounding a xylem strand, which, in a few rare instances, as in the corolla of some Gentianaceae, may have a central protoxylem, *i.e.*, the bundle is mesarch, a curious recrudescence of a type of vascular structure long ago lost in the ancestry of the Angiosperms. We shall refer to this again in considering the anatomy of stamens.

On the much-debated subject of the evolution of the perianth it is only necessary to recapitulate here certain evidence which has been already dealt with in the foregoing pages. The distinction between sepals and involucral bracts is not hard and fast, and in a good many flowers no boundary line can be drawn, as the succession of bracts is uninterrupted right up to the corolla. Several genera, in particular *Anemone*, also present a variety of conditions among their species, showing the approach towards the flower of a whorl of leafy bracts, from a position well down the pedicel, to a position immediately below the perianth, when it becomes sophistical to deny it the status of a calyx.

We have referred to the condition in *Mirabilis* (see p. 1143), where only the presence of the lateral flowers of the cyme distinguishes the involucre from a true calyx, and in some species of the genus these flowers are suppressed. The morphological character of sepals, their three-trace vascular supply and their histological structure, which is leaf-like, all point in the same direction, namely that they are closely related to bracts and belong to the foliage system.

Petals, on the contrary, despite their flattened dorsiventral symmetry, seem to be associated with the androecium and to have originated by the sterilization of the lower staminal members. Like stamens they have only a single vascular trace and intermediate forms between petals and stamens are often present. When, for example, members of the normal staminal whorls become partially or wholly sterilized, they assume petaloid forms and, in double flowers, the whole of the stamens may be transformed into extra petals, but not into sepals. The status of petals as sterilized stamens is also supported by their tardy appearance in the ontogeny of the flower bud and by the inverse correlation of the numbers of the two sets of organs which is shown in some species of *Ranunculus*, where an increase or decrease in the number of stamens is associated with a reverse change in the number of petals.

Although the two-fold, convergent origin of the two components of the perianth is supported by many observations in flowers of various families, it would be a mistake to regard it as a universal rule. Some of the spiral flowers of the Ranunculaceae suggest, by the absence of a clear demarcation between sepaloid and petaloid perianth members, a common origin in such cases from the androecium. In some of the small flowers of Fagales, on the other hand, it is difficult to distinguish between perianth segments and bracts, both appearing to have a common foliar nature. The same is true of some spiral flowers also, *e.g.*, *Calycanthus*. As the biological functions of the perianth are so variable in different families, it should not be surprising that its morphological nature may also be variable.

THE ANDROECIUM AND THE STAMENS

The position of the androecium, by which name we signify collectively the stamens, or the " male attire " of the flower, as some early authors called it, is typically between the innermost petals and the outermost carpels. It forms therefore the lower zone of that pyramid of reproductive organs which constitutes the second of the two main regions in the flower. Together with the gynoecium it makes up what are often called the " sexual " or " essential " organs.

We must emphasize here that to call either a stamen or a carpel a sexual organ is a misnomer. Both are sporophytic structures, bearing sporangia and producing spores. The confusion was natural enough in earlier days, because the extremely reduced gametophytes remain enclosed within the spores, and the existence of an alternation of generations was unsuspected. There is no excuse for such an error at the present day.

The stamens bear microsporangia and by common consent they are usually equated to the microsporophylls of the Pteridophyta and Gymnospermae, though we shall have to consider later whether they are in fact descended from single leaf structures or from a branch system.

The stamens of some of the least specialized flowers are arranged spirally, following the same genetic spiral as the perianth on one side and the carpels on the other. No question of the alternation of parts therefore arises. A comparatively small shift in the divergences or intervals between the rudiments of the lowermost stamens would disjoin the continuous spiral into a series of separate parastichies (see p. 1101), each pursuing a spirally curved path around the floral receptacle, thus creating a hemicyclic flower, such as that of *Nigella*. The commonest numbers of these parastichies are 8 and 13. When the higher number is present, especially if the stamens are very numerous, as in *Aquilegia* and in some species of *Helleborus* and *Anemone*, the vertically superposed stamens form close vertical rows, or orthostichies, which are more conspicuous than the oblique parastichies. In flowers with thirteen parastichies, five will begin with stamens which stand approximately alternate to the perianth members. With reduction in the size of flowers and a consequent reduction in the number of stamens, due to lack of space, it appears to be these alternating stamens, and those in their parastichies, which have been retained, while the intervening ones disappeared, thus completing the disruption of the primitive genetic spiral and leaving isolated parastichies in which the corresponding stamen members will appear to be at the same level and will appear simultaneously at the growing point. In other words they will form a series of whorls and the flower will now be cyclic. The cyclic arrangement, with stamens either limited to one whorl consisting of the first members of each parastichy or alternating in two successive whorls, is more adaptable to the conditions of close spacing, especially in smaller flowers, than the spiral or hemicyclic arrangements and has remained a constant feature of all the higher families.

The chief exception to the general rule of alternation between the outer stamens and the petals arises in the case of obdiplostemony, where they stand opposite the petals. The probable reasons for this anomaly we have already sufficiently discussed on page 1095. The case of *Potamogeton*, where the petals arise directly from the backs of the stamens, may be otherwise accounted for, as here we seem to have before us petaloid outgrowths of the stamens, and not true petals.

The small flowers of the monocotyledonous genus *Triglochin* present a noteworthy peculiarity (see Fig. 1071). The three stamens of the outer whorl stand opposite to the three outer perianth members. These are followed by a second whorl of three perianth members, alternating with the outer stamens, and to these perianth members succeed the three inner stamens which are also opposite to them. Not only is there a correspondence in position but there is also an organic connection between the stamens and their opposed perianth segments shown by their falling together as units. Flowers of *Triglochin* occasionally occur which are dimerous, not trimerous, with four stamens and four perianth parts in pairs, instead of six in threes, and these flowers so closely resemble the dimerous flowers of *Potamogeton* that we may conclude that the same explanation is applicable here, namely that the apparent perianth segments are really outgrowths of the stamens themselves and that there is no true perianth present. In the related genus *Ruppia*, which is also dimerous, the apparent perianth parts are reduced to mere scales on the backs of the stamens and the flower is naked.

A somewhat similar position exists in several other families. The flowers of the Proteaceae, for example, are usually tetramerous, with a perianth composed only of one whorl of four sepals, to which are adherent four opposite stamens, only the anthers being free and seeming to arise near the tips of the sepals, which often cover them with a sort of hood. This invites comparison with the genera mentioned above, but for the fact that the opposition of stamens and sepals would be normal, according to the rule of alternation, if any true petals were present. In *Banksia* (Fig. 1137), there are four small scales, alternating with the stamens, which can only be reduced petals, but they are seemingly interior to the stamen whorl. The development of the flower in the Proteaceae shows that the stamens and sepals spring from quite distinct rudiments but they are carried upwards together by intercalary growth of the sectors of the torus beneath them, which does not affect the rudimentary petals. The apparently exterior position of the stamens is therefore attributed to this enforced association with the sepals in the course of development and there is probably no departure from the normal order of succession and alternation.

The normal order of development in the androecium is generally conceived as being centripetal, that is to say that the outer stamens develop first and the inner whorls, if any, successively later. The idea that this is the universal order probably arises from the fact that it obtains in several of the most fully investigated families such as Ranunculaceae, Rosaceae, Papaveraceae, Leguminosae, Myrtaceae and Nymphaeaceae. Corner has shown however that in a number of families the order is reversed and is centrifugal. The families for which this has been proved are Paeoniaceae, Dilleniaceae, Hypericaceae, Capparidaceae, Tiliaceae, Malvaceae, Theaceae, Aizoaceae and Cactaceae. The position of *Paeonia* in this group is interesting. It stands apart from the majority of the Ranunculaceae in so many characters that it is now often put, as above, in a separate family. The stamen development confirms this separation and associates the genus more closely with Dilleniaceae, a family to which it shows affinity in other respects.

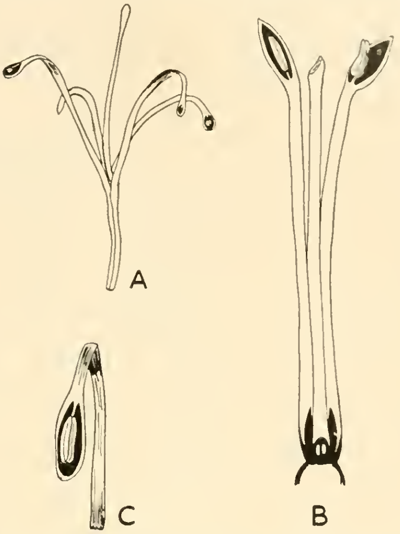

FIG. 1137.—*Banksia* sp. Proteaceae. A, Flower. B, Flower cut vertically, showing the small petal scales at the base, in black. C, Upper part of sepal with attached stamen. (*After Le Maout and Decaisne.*)

There is a much more definite hiatus in development between the stamens and the petals in flowers with centrifugal stamens than in other cases. Centrifugally developing stamens show no arrangement in parastichies. They form irregular whorls on a peripherally expanding floral disc with, frequently, a doubling of the number of stamens in each whorl outwards. Such stamens are often grouped in fascicles, a matter we shall return to later.

The adhesion of stamens to petals, especially in sympetalous flowers, is of common occurrence and is known as **epipetaly**. If the sepals are involved it is called **episepaly** (cf. Proteaceae, above). The degree of union varies between a mere junction at the base, to a complete union of everything except the anther and in a few rare cases, such as *Viscum* (Mistletoe)

(Fig. 1138), even the anther is involved, so that the separate identity of stamen and perianth segment is completely lost. The vascular supply to the stamen may remain separate even when the filament is entirely adnate to a petal, but there is much variation in this respect and union of the stamen bundle to the petal supply may take place quite low down, the anther then being supplied by a branch from the combined bundles. We have already had occasion to refer to this relationship and some of its features in the present chapter (pp. 1094 and 1166).

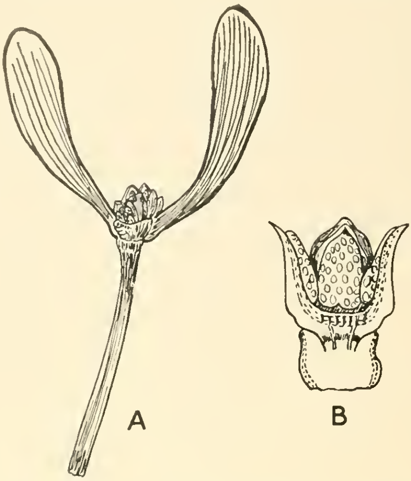

Fig. 1138.—*Viscum album.* A, Flowering shoot. B, Male flower showing three anthers with multiple loculi. (*After Le Maout and Decaisne.*)

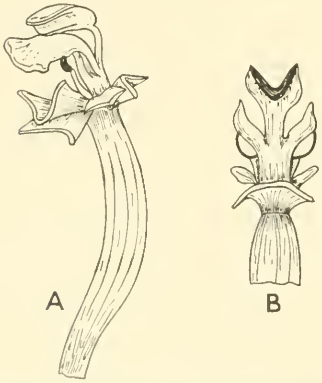

Fig. 1139.—Flower of *Cypripedium* with perianth removed to show the gynostemium. A, Side view. B, Front view. (*After Van Tieghem.*)

Union of the stamens to the gynoecium is much less common, at least in hypogynous flowers, though we have seen previously that it may be involved in at least some cases of epigyny. In epigynous flowers, however, even though there may be evidence for the fusion of the lower parts of the stamen to the wall of the ovary, the upper parts, particularly the anthers, generally remain free. A further degree of fusion, which occurs in some cases, between the anthers and the style, produces a compound structure called a **gynostemium.** The Orchidaceae provide the most conspicuous example of this structure, which is general throughout the family. One of the least reduced genera, *Cypripedium* (Fig. 1139), has two fertile stamens and a prominent, petaloid staminode, or sterilized stamen, which are all united to the style, and between which protrudes the large, flattened stigma. *Orchis*, and many other genera, have only one stamen, with two pollen-bearing lobes, the back of which is fused to an upgrowth from the top of the inferior ovary, probably representing the third lobe of a tripartite stigma, the two lower lobes of which remain functional. The united structure stands up prominently in the centre of the flower (see Chapter XXX). Another well-known case is that of the large genus *Aristolochia* (Fig. 1140), in which the anthers are united in a ring around the outside of the stylar column, to which they are dorsally fused, their enlarged connectives often surmounting the stigma. A similar condition is characteristic of the family Stylidiaceae, where there are only two stamens, their filaments being completely adnate to the style, and the anthers standing beside the stigma. Examples of cohesion between stamens and superior ovaries are much less frequent, but one striking case is *Gymnotheca* (Fig. 1141), a genus nearly related to the Pepper family, in which the six stamens are united to the ovary wall, nearly to its top. In *Passiflora* the stamen filaments are adnate to the gynophore but the anthers are below the level of the ovary.

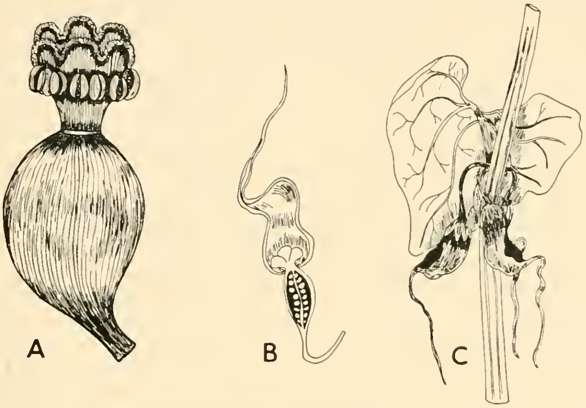

FIG. 1140.—Gynostemium in *Aristolochia*. A, Perianth removed showing anthers dorsally attached to the style. B, Flower in longitudinal section. C, Flowers in position on the plant. (*After Van Tieghem.*)

The cohesion of stamens with each other is a widespread feature of flower structure and occurs in all degrees, from simple pairing to union of all the stamens into a tube, or to a comparatively elaborate grouping into fascicles or bundles. The phenomenon bears the general name of **synstemony**. Besides occurring in a great number of isolated cases it is a general characteristic of some large families like the Papilionaceae, Malvaceae (Fig. 1142), Rutaceae, Meliaceae, Guttiferae, Cucurbitaceae and Compositae. In the last named family cohesion is by the margins of the anthers, the filaments remaining free, but in the generality of cases it is the other way about, the filaments cohering while the anthers are free.

A succession of stages may be observed in Cucurbitaceae, between flowers with all five stamens free and those in which all five are closely

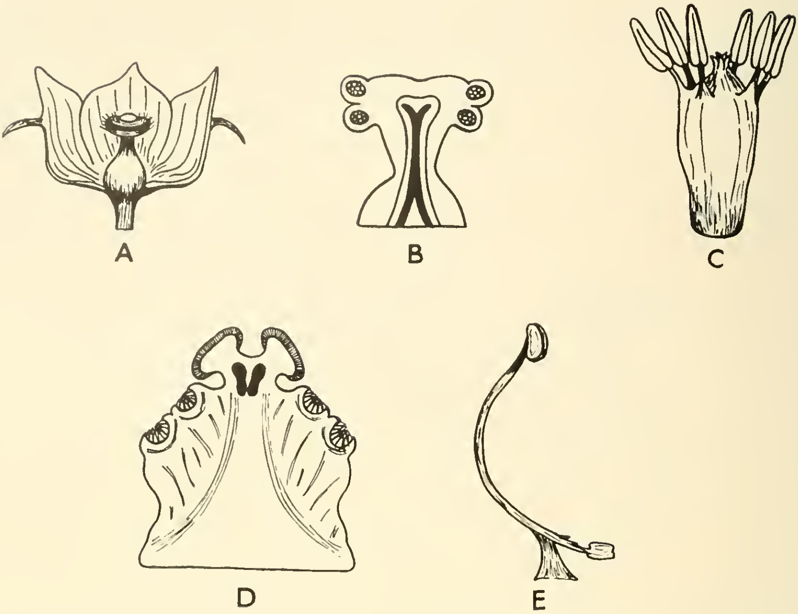

Fig. 1141.—Anomalous androecia. A, *Cyclanthera*, male flower with stamens united into one central structure. B, The same, in section. C, *Gymnotheca*, stamen filaments united to the ovary wall. D, *Clusia*, stamens united into a fleshy mass and adherent to the style. E, Stamen of *Salvia*. Short filament attached to long, curved connective with a half-anther at each end. (*A, B and D after Engler-Prantl. C after Le Maout and Decaisne.*)

Fig. 1142.—*Hibiscus schizopetalus*. Flower with long, pendent, monadelphous androecium.

united, through intermediate stages in which one stamen only is isolated, the other four being more or less united in pairs. The completest union is shown by *Cyclanthera* (Fig. 1141), the male flowers of which display a central structure, shaped rather like a collar stud and called a synandrium, in which all five stamens are completely coalescent even to the pollen loculi, of which there are two, one above the other, running horizontally around the circular cap of the synandrium.

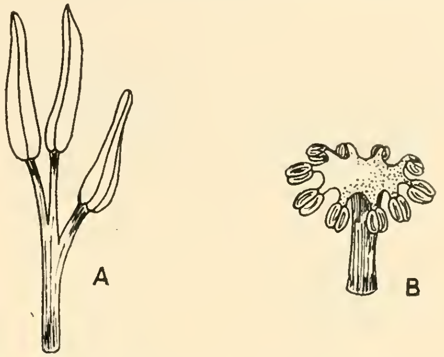

Fig. 1143.—Synstemony in: A, *Pandanus*. B, *Myristica*. (*After Le Maout and Decaisne.*)

The flowers of Cucurbitaceae are unisexual and it is noteworthy that synstemony is more generally shown by the male flowers of diclinous plants than by hermaphrodite flowers. Examples of the former are: *Begonia*, *Schizandra*, *Myristica* (Fig. 1143), *Nepenthes*, *Clusia* (Fig. 1141), *Pandanus* (Fig. 1143) and *Typha*. It will be observed that the majority of these are Dicotyledons and the phenomenon is in fact much commoner in this group than among Monocotyledons, which, indeed, are more rarely diclinous.

Staminal concrescence in hermaphrodite flowers is well exemplified by the Malvaceae, in which the filaments of the numerous stamens are united into a tube around the gynoecium. One member of the family, the frequently cultivated shrub *Plagianthus* (Fig. 1144), carries matters even further, for the petals, which are smaller than the sepals, are also concrescent with the staminal tube, from which they appear to arise. The development of a staminal tube reaches its height in the Meliaceae, where it overtops the perianth and is the most conspicuous object in the flower. It is

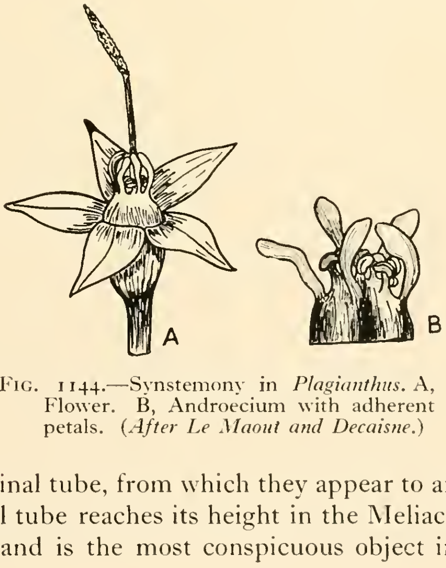

Fig. 1144.—Synstemony in *Plagianthus*. A, Flower. B, Androecium with adherent petals. (*After Le Maout and Decaisne.*)

often decorated with a sort of paracorolla round the top, surrounding the anthers (Fig. 1145).

When all the stamens are united they are said to be **monadelphous**; when in two groups, **diadelphous** and so on.

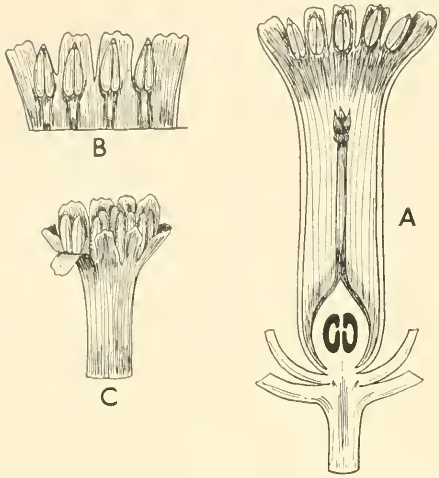

Fig. 1145.—*Azadirachta indica.* Meliaceae. A, Flower cut lengthways, showing the well-developed staminal tube. Perianth removed. B, Part of top of tube enlarged. C. Top of the tube showing the petaloid appendages to the anthers. (*After Engler-Prantl.*)

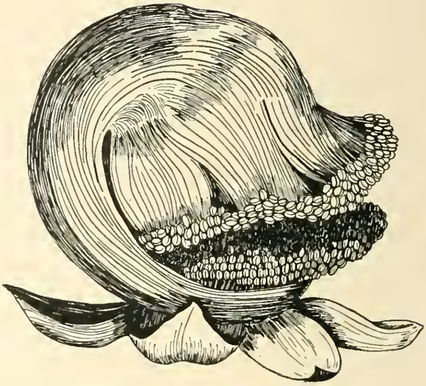

Fig. 1146.—*Couroupita surinamensis.* Androecium showing the phalanx of united stamens which is inverted over the centre of the flower. (*After Le Maout and Decaisne.*)

Couroupita, the Cannon Ball Tree (Myrtaceae) (Fig. 1146), has a monadelphous arrangement of stamens which is unique. They are very numerous and are all united by their filaments into the shape of a bowl around the gynoecium. On one side of the bowl the filaments are short and upright, but on the other side they are prolonged into a broad band, which curves up over the stigma, covering it and the whole top of the flower with a mass of downwardly pointing anthers. The Papilionaceae present varying conditions, which are of systematic significance, certain genera being monadelphous and others diadelphous, a single stamen, usually the posterior one, remaining free while the others are concrescent. The diadelphous condition is well illustrated in the Fumariaceae, where the stamens are grouped into two compound structures, or phalanges, each consisting of one middle stamen with two half-stamens attached to its sides, the filaments forming a broad band and the anthers being free (Fig. 1147).

Most of the above examples of concrescence are congenital, that is they arise by union of the organ primordia. This reaches its limit in cases where the separate identity of the primordia is lost and the united structures arise from a common, usually ring-like, basis. A later union, or growing

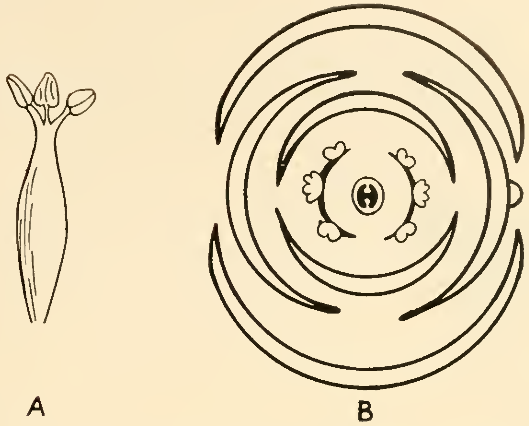

FIG. 1147.—*Corydalis.* Fumariaceae. A, Staminal phalanx with median anther flanked by two half-anthers. B, Floral diagram. (*After Le Maout and Decaisne.*)

together, of organs initially separate, is rare, though the union of anthers in the Compositae affords a good example.

The Panama-hat plant, *Carludovica palmata* (Fig. 1148), presents a striking combination of floral reduction and concrescence of stamens. The flowers are of two sexes, arranged in a dense spike, each female flower being flanked by four groups of male flowers, four in each group. Each male flower has only a rudimentary perianth of small scales, within which stands

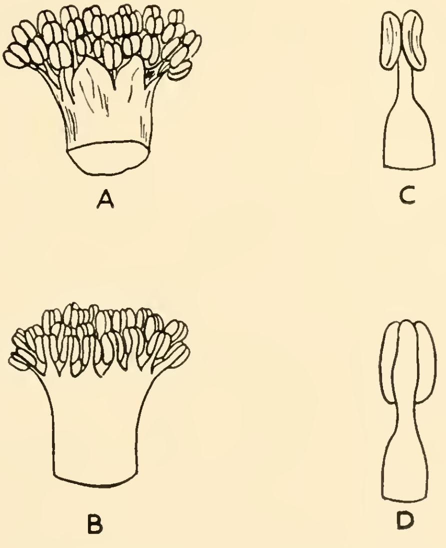

FIG. 1148.—*Carludovica palmata.* A, Phalanx of stamens, outer face. B, The same, inner face. C, Stamen, outer face. D. Stamen, inner face. (*After Le Maout and Decaisne.*)

a solid phalanx of stamens with all their filaments united and only the anthers free.

The grouping of all the stamens into coherent bundles, or fascicles, usually equal in number to the number of petals, is common in certain families, such as Guttiferae, Loasaceae, Tiliaceae and Myrtaceae. Each fascicle originates as a single large primordium, on which there arise a large number of small protuberances which elongate into individual stamens, united by a common base. This base normally remains short, but in *Melaleuca* (Fig. 1149) and some other members of the Myrtaceae it also elongates, so that each fascicle appears to be mounted on a long pedicel. The genus *Candollea* in the Dilleniaceae presents a similar peculiarity. There are five staminal filaments, in the normal antisepalous position, but each filament bears at the top a cluster of five, elongate, bilocular anthers, presumably representing a stamen fascicle with united filaments. The facts of development, however, are not known. The stamens of *Citrus* show a partial and irregular fusion into groups of from two to six or seven stamens, with their filaments united and their anthers free, but this is not fasciculation in the strict sense, as all arise in a single whorl. It seems to be a case of ordinary, though imperfect, synstemony.

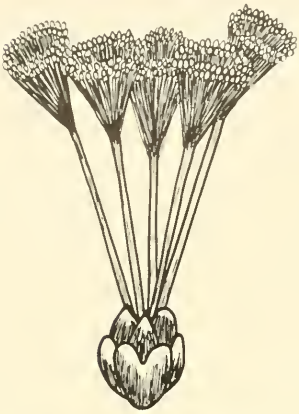

FIG. 1149.—*Melaleuca*. Fascicles of stamens with pedicels. (*After Van Tieghem.*)

True branching of stamens is of rare occurrence and the only well-known examples are in the genus *Ricinus* (Fig. 1150), and members of the family Dilleniaceae. The apparent branching in the Tiliaceae is more probably due to fasciculation. Indeed most cases of apparent branching are due to this, or to partial fusions between stamens in the same whorl, as in *Citrus* and *Gunnera*, or to a lateral expansion of the connective, separating two halves of the anther, of which there are many examples (*e.g.*, *Salvia*, see Fig. 1141). In another direction it may sometimes be due to chorisis.

The chorisis of stamens is a term which has been somewhat too widely applied, including a number of cases where pairs of stamens stand together in the flower at points where considerations of symmetry suggest that there should be only one. The facts of ontogenetic development, where they are known, may sometimes negative this conclusion, as in the cruciferous flower. The two antero-posterior pairs of long stamens in this family appear to interrupt the general dimery of the flower and have frequently been cited as arising by the chorisis of two stamens. That this is not so is shown by the existence of two separate stamen rudiments for each pair, at least in most of the genera. True chorisis implies the division, at an early stage, of a single rudiment into two, which develop completely in independence. The pentamerous lateral flowers of *Adoxa* illustrate this.

FIG. 1150.—*Ricinus communis.* Branching stamens of male flower. (*After Van Tieghem.*)

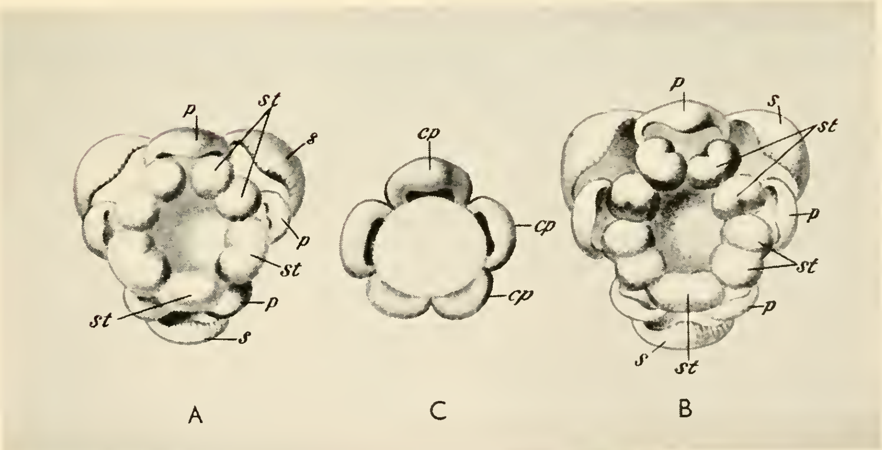

FIG. 1151.—*Adoxa moschatellina.* Ontogeny of flower. A, earlier and B, later stages showing the chorisis of the five stamen rudiments into ten half-stamens. C, Young carpels round the summit of the receptacle. See also Fig. 1077. Lettering as in Fig. 1099. (*After Payer.*)

Each flower has apparently ten stamens, but each bears only a half-anther and the ontogeny (Fig. 1151) shows plainly the radial splitting of the five primordia, each half giving rise to a separate structure. The very numerous stamens of *Papaver*, occurring in a flower of dimerous symmetry, are also due to repeated chorisis.

Chorisis occurs abundantly in the formation of some double flowers, where the extra petals may be derived, as in the Carnation, from modified stamens which have been multiplied by both radial and tangential chorisis.

The multiplication of stamens by chorisis is exceptional but on the other hand, reduction of the androecium appears to have been a general feature of floral evolution, especially in the Dicotyledons. Indefinitely large numbers of stamens are characteristic of only a few families with simple, actinomorphic flowers, while in the great majority of families the number is fixed and bears a close and constant relation to the number of perianth segments. Even so we can see a further tendency to reduction from pentacyclic flowers, with two whorls of stamens, to tetracyclic flowers which have only one whorl, the latter condition being predominant in the most advanced families. Flowers with three whorls of alternating stamens are rare. Three whorls are present in some of the Rosaceae, including *Rosa*, another example being the male flower of *Laurus nobilis*. The innermost whorl is, in this case, superposed on the outer whorl and its anthers are reversed so as to face the outer stamens.

Although the number of stamens in a whorl is generally related to the perianth numbers, there are some cases in which the number in the inner whorl is related to the number of carpels rather than to the petals. An example is the case of polygonaceous flowers with a pentamerous perianth and eight stamens, of which five form the outer whorl and three form the inner whorl, corresponding to the three (united) carpels. Here the small size of the receptacle seems to have induced reduction in the whole central region of the flower.

The biological value of reduction in the androecium, which is so constant a feature in all the advanced families, is easily understood when we recollect that pollen is an expensive product from the point of view of metabolism. Not only are the pollen grains non-vacuolate and therefore contain an unusually large amount of protoplasm, but they are also well stocked with reserve food-materials. Many flowers with numerous stamens are devoid of nectar and are only visited by bees to collect pollen, which, to the plant, is an extravagant way of ensuring cross-pollination. The contrast between the two types of flower is shown strikingly in a comparison between the related genera *Papaver* and *Fumaria*. The former is actinomorphic, has no nectar and has a large and indefinite number of stamens; while the latter is zygomorphic, produces nectar and has only two stamen fascicles, totalling four complete anthers between them.

Suppression of stamens is a widespread phenomenon and examples can be seen in most families. The suppressed stamens may be represented by vestigial organs, termed **staminodes**, which may have other functions, as we shall show later, or they may have disappeared without trace. The latter condition is sometimes constant in a whole genus, as in *Veronica*, where only two stamens are present of the five which make up the full complement in Scrophulariaceae, or in *Centranthus*, where only one out of five is present. It may, however, affect only certain individuals in a species, as in *Glechoma hederacea*, where some plants have hermaphrodite flowers and others have carpellate flowers only, a condition known as **gynodioecism**.

The suppression of stamens is indeed a tendency which we can see in various stages of fulfilment. Its beginning may, perhaps, be traced in contabescent or impotent stamens which, though normal in appearance, produce nothing but abortive pollen.

Where a parallel tendency to the reduction of the gynoecium is also operative, the extreme condition of **dicliny** may be reached, where all the flowers are either only staminate or only carpellate, or even **dioecism**, where the sexes are segregated into different plants.

The ideal in floral efficiency would be an equivalence between the number of pollen grains produced and the number of ovules to be fertilized and the complete elimination of pollen wastage. While this ideal is nowhere completely realized, we can see, by comparing advanced and primitive types of flowers, that progress towards it has been one of the keynotes in floral evolution.

The question whether the unisexual condition in the flower is a primitive feature in Angiosperms, or a secondary condition, is one that has been differently answered by systematists. Putting on one side however, for the present, all arguments based on the supposed ancestry or evolution of the Angiosperms, we can only conclude that the many evidences of the transformation of hermaphrodite into unisexual flowers show that this is a real event, while the opposite transformation remains purely hypothetical. An important part of the evidence to which we refer consists in the traces of organs of the opposite sex found in many functionally unisexual flowers. Examples of the persistence of rudimentary stamens in female flowers are fairly common; for instance in *Ilex*, *Akebia* (Fig. 1152), *Pilea*, *Liquidambar* and *Crozophora* among Dicotyledons and in *Freycinetia* and *Geonoma* among Monocotyledons.* Even where no visible rudiment of the stamens persists the space for them on the receptacle may be present, but blank, as in *Menispermum*. The opposite condition, namely the persistence of abortive carpels in male flowers, is less common, for, the carpels being situated apically, it seems to be relatively easier to cut short the growth of the receptacle and so eliminate the gynoecium altogether. Nevertheless examples occur, as in *Ilex*, *Akebia* and *Freycinetia* among those mentioned above, while in *Crozophora*, the three carpels are replaced in the male flower by three large, additional stamens. What is " normal " in this genus has also been found as an abnormality in *Oakesia* (Liliaceae), the styles of the abortive gynoecium forming perfect anthers.

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* Stamen-like structures are induced to appear in female flowers of *Melandrium dioicum*, where they are usually absent, by the attacks of *Ustilago antherarum*.

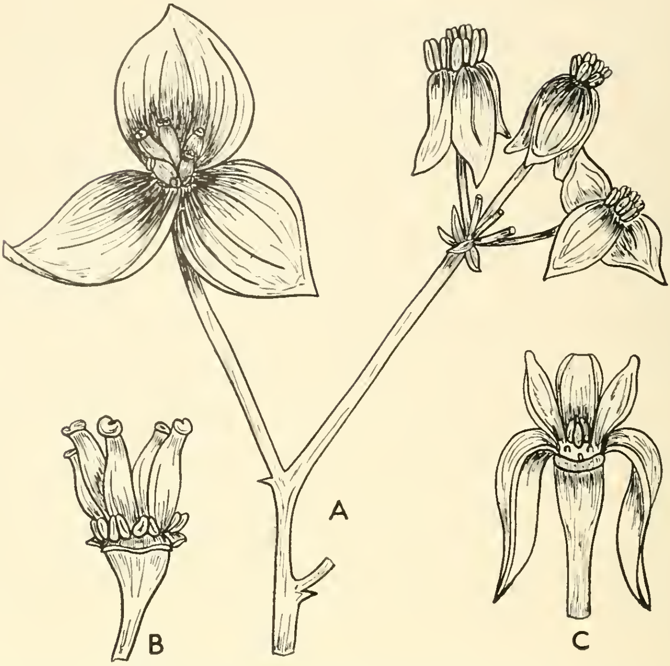

Fig. 1152.—*Akebia quinata.* A, Inflorescence with female flower (*left*) and male flowers (*right*). B, Female flower showing rudimentary stamens. C, Male flower showing rudimentary carpels. (*After Sachs.*)

An analogous replacement of a carpel by a stamen may be the origin of the apparently terminal stamens which occur in some species. The condition is rare and is limited to a few greatly reduced unisexual flowers, with frequently only one stamen and sometimes no perianth. Such are *Euphorbia*, *Callitriche*, *Naias*, *Anacardium* and *Casuarina.* We need not indulge in nice speculations as to whether these terminal stamens should be classed as axial or foliar organs, since there can be no reasonable doubt that they are of exactly the same nature as other stamens, but being fully developed on a much reduced axis, they have supplanted and suppressed its apex. That this is the true account of the matter is shown by the male flowers of *Mangifera* (Mango) (Fig. 1153), where the apparently terminal stamen is in fact one of a whorl of five, the other four being reduced to staminodes and having been manifestly pushed aside by the strong growth of the fertile stamen.

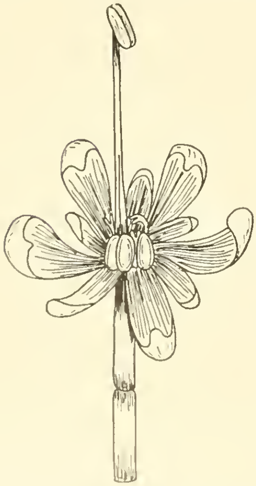

Fig. 1153.—*Mangifera indica.* Male flower with single fertile "terminal" stamen. (*After Velenovsky.*)

The presence of stamens of two or more

different forms in the same flower is called **heterostemony.** From this category should be excluded all cases of abortive or vestigial stamens, whether transformed into staminodes, petals or other forms. The term should apply only to those flowers with different forms of fully fertile stamens. Thus delimited it is not a common phenomenon and is usually associated with zygomorphy. A difference of size alone is characteristic of the stamens of Cruciferae and Labiatae and is not infrequent in Leguminosae and Scrophulariaceae. *Cassia*, a large genus of Leguminosae, shows not only a difference of size, but also sometimes of form and function among its stamens. The three uppermost are sterile and dwarf, the four lateral are longer and their pollen is eaten by insect visitors, while the three lowest are large, functional in pollination and project from the flower, sometimes to the right hand and sometimes to the left. In the Scrophulariaceae, *Verbascum* also shows a qualitative heterostemony, three stamens bearing hairs and two being glabrous. *Commelina* (Commelinaceae) has three posterior stamens with enlarged, yellow-coloured connectives which form part of the attraction of the flower. They are fertile, though with small pollen-sacs, and they are larger than the three anterior stamens. The above are all variations between stamens of the same whorl, but variation also occurs between stamens at different levels on the receptacle, as in many Lauraceae, where three distinct types of stamen may

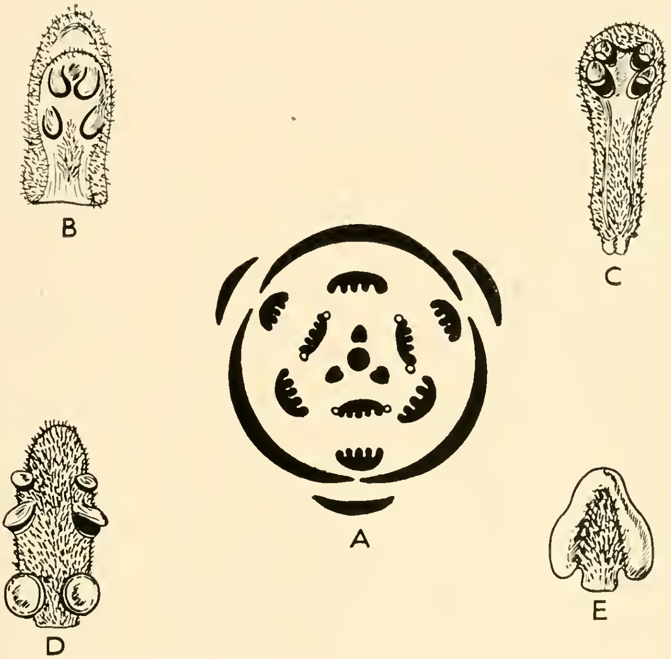

Fig. 1154.—*Caryodaphnopsis tonkinensis*. A, Floral diagram. B, stamen of second whorl, face view. C, Stamen of outer whorl, face view. D, Stamen of third whorl, abaxial view. E, Staminode of inner whorl. (*After Hooker:* ' Icon. Plant.')

be formed in sequence (Fig. 1154). See also under dimorphic flowers, Chapter XXIV, p. 1275.

The **anther** is the name applied to the fertile portion of the stamen when it is distinct from the filament. The stamens of primitive families, like the Magnoliaceae, are usually undifferentiated, the pollen-sacs, which are long and narrow, being attached to one side of or immersed in a strap-shaped structure in which filament and anther cannot be distinguished. The great majority of stamens, however, have a stalk-like filament, to the distal end of which is attached a distinct anther portion, comprising a central tissue, the **connective**, which supports and serves to unite the pollen-sacs, sometimes called **thecae**. Normally there are four of these sacs, in two pairs, one pair on each side of the connective, but at maturity the members of each pair become united by the rupture of the wall between them, so that when the anther finally opens to discharge the pollen it may be correctly called bilocular.

The traditional idea of a stamen equates it to a microsporophyll (Fig. 1155) and some discussion has arisen on the question whether, from this standpoint, the pollen-sacs, or microsporangia, are marginal or superficial. The difference has been shown to be important in distinguishing large groups among the Pteridophyta and might therefore be of some evolutionary significance. We shall return to the evolution of stamens later, but we must remark here that it would be a great mistake to assume that characters manifested by Pteridophyta or Gymnospermae must also be present in Angiospermae. The above question also begs the further question whether the stamen is, in fact, a dorsiventral structure. The stamen primordium, before the appearance of the pollen-sacs, is four-angled in transverse section, a pollen-sac being formed from each angle. Such a structure is unifacial, not dorsiventral, and, unless we are to regard it as analogous to a cruciform leaf such as that of

FIG. 1155.—Diagrams illustrating various types of microsporangial branches. A, Gnetales. B, Angiospermae. C, *Taxus*. D, Coniferales. E, Bennettitales. F, Cordaitales. G, *Rhynia*. H, Pteridospermae. (*After Zimmermann.*)

Xanthorrhoea, we cannot consider the sporangia to be marginal. The separation of the sporangial rudiments on the primordium is also evidence against the view that there are only two sporangia which are subdivided into four by trabeculae of sterile tissue. In our present ignorance of the evolution of the stamen we cannot even be sure whether the position of the sporangia is a real problem or not, but it is worth noting, in passing, that ovules may be either marginal or superficial.

The attachment of the sporangia to the connective is usually longitudinal, though transverse sporangia are also known (*Pinguicula*) as well as anthers in which the sporangia are spherical and form a rectangular group, either horizontally or vertically. Sporangia which are not only transverse but terminal, lying apparently across the top of the filament, are known in *Verbascum*, and this and some other abnormalities of position are usually ascribed to displacements during development, though little is known of the facts.

Two members of the parasitic family of Loranthaceae possess ring-like sporangia. In *Korthalsella* there are three stamens with coherent anthers. At maturity all the pollen loculi fuse into a ring. In *Arceuthobium* the one pollen loculus is annular from the beginning, surrounding a central columella.

Several anomalies of anther form are found in the Cucurbitaceae. The stamens are concrescent in most of the genera and the sporangia, which are attached to the outer surface of the connective, are very long and sinuous, forming a compressed S-shape. There is also the remarkable case of *Cyclanthera*, mentioned on p. 1173, in which the male flowers contain but one, apparently terminal, stamen, around the top of which run two transverse, ring-shaped pollen-sacs. This may be either the result of concrescence or it may be a single stamen, the other four stamens of the normal whorl of five having aborted, and the two pollen-sacs having resulted from the union in pairs of the original four. The unification may have resulted in this case from the transformation of intermediate sterile tissue into archesporium. The monosporangiate anther of *Alchemilla* has probably arisen from this latter event. It also seems to have occurred in some species of *Naias* (*e.g.*, *N. flexilis*) where there is a single terminal stamen, with a central core of archesporium, which appears to be formed by the union of four sacs, accompanied by the transformation of the central connective tissue into additional archesporium. *Naias major* has normal anthers and there are no transitional stages between the two conditions.

The number of sporangia can also be reduced by abortion. This is shown by *Piper betel*, where the number in each anther may be reduced from four to one or even none. A similar variation occurs in the anthers of the cleistogamic flowers (see p. 1351) of several genera, notably in *Viola*. The occurrence seems to be connected with general floral reduction in both the above cases. Bisporangiate anthers are not uncommon (Amarantaceae, Scrophulariaceae, Epacridaceae) and are not necessarily linked to general floral reduction. An apparently bisporangiate condition may arise through the halving of the anther by chorisis (*Adoxa*) or by the elongation of the connective (Labiatae; see p. 1189). The monosporangiate anthers of *Polygala* may also be attributed to chorisis of the anther alone, the filaments being undivided and indeed concrescent. An exceptional increase in the number of sporangia most frequently arises through transverse septation (some Annonaceae, Lauraceae and Onagraceae) or in other cases by septation in several directions, isolating numerous sporangial sacs, which may be irregularly distributed (*Viscum*, *Rhizophora*, and Mimosaceae) (Fig. 1156). This multisporangiate condition is probably a derived condition rather than a primitive one, if we have regard to the systematic positions of the plants which display it.

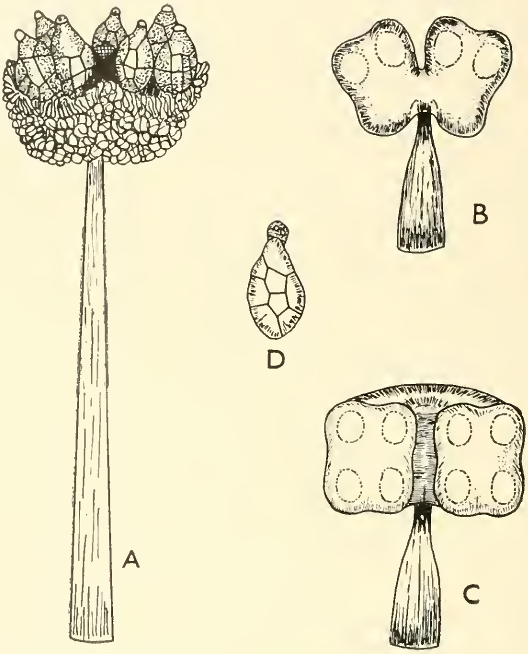

Fig. 1156.—*Calliandra tetragona* (Mimosaceae). A, Stamen after dehiscence with four pollinia in each half anther, each pollinium in a separate loculus. B, Unopened anther. C, Earlier stage before anther becomes vertical. D, Pollinium with sticky pad at top which attaches it to visiting insects. (*After Goebel.*)

When an anther is mature the outer walls of the pollen-sacs split open, exposing the ripe pollen, which is then removed by the wind or by insects, etc. This is called **dehiscence**. If this occurs on the inner (adaxial) side of the anther it is said to be **introrse**, which is the commonest condition; if it occurs on the abaxial side, which is comparatively infrequent, it is called **extrorse**. The latter condition usually implies that the sporangia themselves are directed abaxially either permanently or temporarily. Thus in some species of *Gentiana* the anther is at first adaxial but it turns over vertically into the abaxial position before it dehisces. Some flowers, *e.g.*, *Butomus*, have sporangia which are symmetrically placed around the connective and their dehiscence is neither inwards nor outwards, but lateral.

The most general mode of dehiscence is by longitudinal splitting, along the furrow between two paired sporangia. Before this happens the wall separating the pollen-sacs has itself split or broken down, so that a single line of external dehiscence opens the cavities of both the sporangia of the pair. For this reason there are scarcely ever more than two lines of dehiscence. Only in the rare cases of multisporangiate anthers (*e.g.*, *Viscum*) does each sporangium dehisce separately. The line of dehiscence may sometimes be very short and the opening formed is thus no more than a pore, there being also in this case one to each pair of sporangia, except in the Melastomaceae where only one pore serves all four. Porose dehiscence is usually confined to the distal end or only to the apex of the anther (*Solanum*) but the often quoted case of the " apical " pores in Ericaceae (Fig. 1157) has been shown to be an error. The true apex of the anther in this family is directed inwards and downwards and the portion in which the pores are formed is really a basal upgrowth.

FIG. 1157.—Flower of *Azalea obtusa* with anthers extruding pollen by terminal pores.

Transverse dehiscence also occurs, but it is rare and, except for *Alchemilla*, is almost confined to the small family

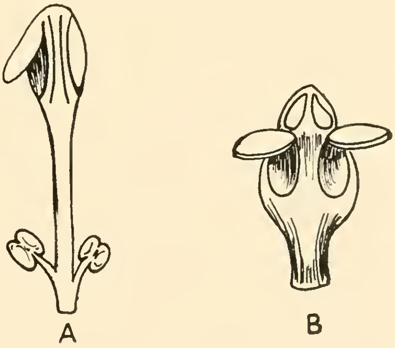

FIG. 1158.—Valvate stamens. A, *Laurus*. B, *Cinnamomum*. (*After Le Maout and Decaisne*.)

Diapensiaceae. More frequently, though almost limited to the large families of Berberidaceae and Lauraceae, the lines of dehiscence are U-shaped, and mark out either two or four flaps, or valves, which fold back, exposing large openings (Fig. 1158).

The attachment of the anther to the filament is by means of the connective. This is generally a narrow shaft of tissue, through which runs a single vascular bundle from the filament. When the connective itself forms a direct prolongation of the filament the anther is called **basifixed**. If, on the contrary, the filament is attached to the abaxial side of the connective it is called **dorsifixed**. Filaments attached to the upper end of the connective (**apicifixed**) are rare and are usually associated with widely divergent anther lobes (*e.g.*, *Lamium*). When the attachment to the filament is limited to a single point of the connective, the anther may be free to oscillate on this point, as in *Passiflora*, *Lilium* (Fig. 1159), and the Gramineae generally. It is then known as **versatile**, and in the grasses this freedom of movement is certainly useful in promoting wind-pollination.

FIG. 1159.—*Lilium martagon* showing versatile anthers.

The behaviour of the stamens at anthesis is very variable, according to the mode of pollination in particular species, and details are given of a number of examples in Chapter XXIV.

A not infrequent occurrence is the successive development and growth, either of individual stamens or of complete whorls, the later-formed replacing in turn the earlier stamens, whose pollen has already been shed. This is often accompanied by growth curvatures whereby the anthers as they ripen are brought into the appropriate position for meeting insect visitors. Well-known examples are *Tropaeolum speciosum*, *Dictamnus fraxinella*, *Gloriosa superba*, and *Parnassia palustris*. The stamens in many flowers, *e.g.*, in Myrtaceae, Rosaceae, Umbelliferae and Urticaceae, are all incurved at first, with the anthers clustered around the base of the style, or even, as in some Melastomaceae, held in pockets formed by the receptacle. An epinastic movement, due to increased growth on the adaxial side of the filament, causes them to straighten out and raise up the anthers, after the perianth has expanded. The straightening movement of the filaments in the Urticaceae is one of elasticity, not of growth, and is correspondingly sudden and explosive, the anthers being flung outwards over the edge of the perianth and a cloud of the dry pollen discharged. The well-known carpeting plant, *Pilea elegans*, has gained the name of " Artillery Plant " for this behaviour.

The specialized forms assumed by stamens are almost indefinitely variable and quite beyond detailed description. A few selected examples are shown in Figs. 1160 and 1161. Peculiarity of form is often directly associated with the requirements of pollination, but by no means always, and is

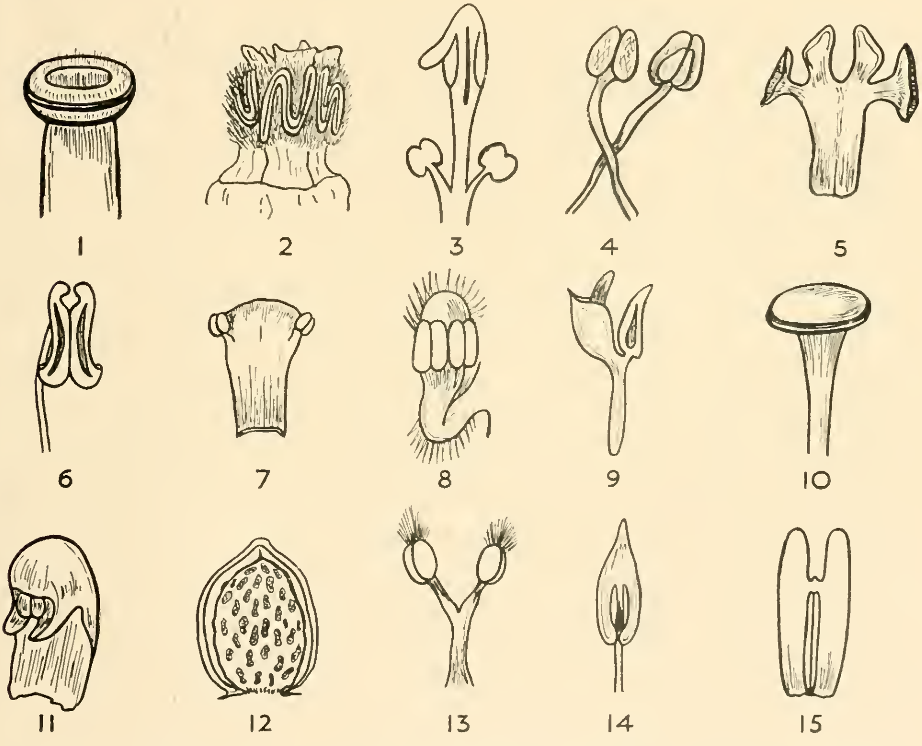

FIG. 1160.—Various types of stamens. (1) *Cyclanthera*. (2) *Cucumis*. (3) *Laurus*. (4) *Portulaca*. (5) *Burmannia*. (6) *Hydrolea*. (7) *Schizandra*. (8) *Vinca*. (9) *Asclepias*. (10) *Stephania*. (11) *Tacca*. (12) *Viscum*. (13) *Carpinus*. (14) *Hypoxis*. (15) *Barbacenia*. (*After Le Maout and Decaisne*.)

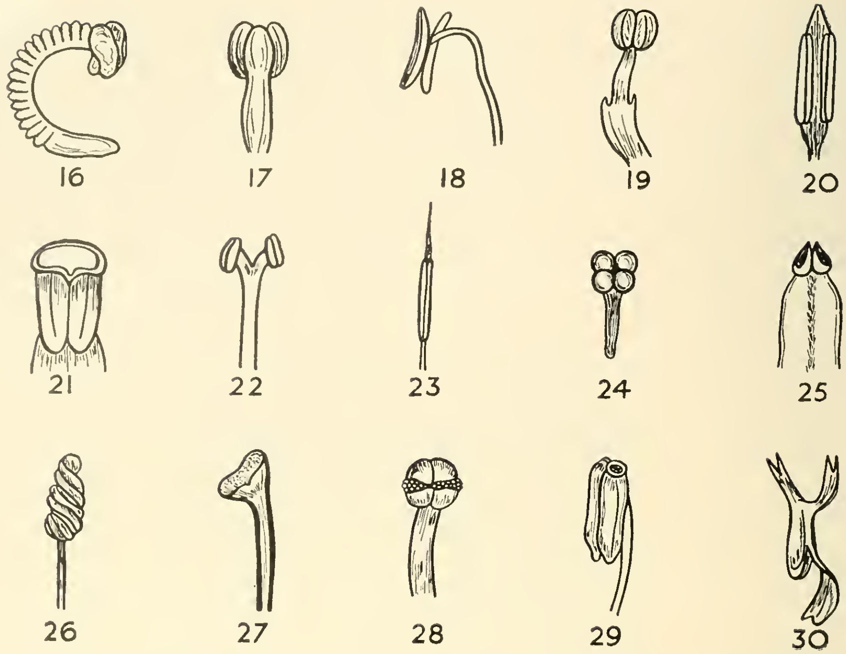

Fig. 1161.—Various types of stamens. (16) *Parietaria.* (17) *Hydrocharis.* (18) *Triticum.* (19) *Aconitum.* (20) *Magnolia.* (21) *Asimina.* (22) *Tilia.* (23) *Elaeocarpus.* (24) *Menispermum.* (25) *Orontium.* (26) *Loasa.* (27) *Pinguicula.* (28) *Alchemilla.* (29) *Rhododendron.* (30) *Vaccinium.* (*After Le Maout and Decaisne.*)

sometimes rather an expression of systematic relationship, where a certain form is constantly found in the same family.

Examples of specialization in direct relationship to a pollination mechanism are so numerous that we can only select one or two striking cases for mention. In *Asclepias* (Fig. 1162) the filaments are flattened and cohere to form a tube around the ovary. The anthers have only two pollen-sacs, opening longitudinally and each containing a pollinium or mass of united pollen grains with a viscous covering. The anthers are united by their internal faces to the edge of the stigma, with only a narrow slit between each two. From the back of each stamen arises a hood-like structure, or cucullus, brightly coloured and enclosing a horn-shaped nectary, which projects from the top of the hood. The stigma is much enlarged and has five, marginal λ-shaped appendages, one between each two anthers, which are called retinacula. The upper end is a horny clamp called the corpusculum, from which depend two divergent retinacula with adhesive glands which become attached to two pollinia, one from each of two neighbouring anthers. Nectar accumulates in the staminal cuculli and an insect seeking to get at this may catch a leg in the clamp-like corpusculum. On leaving, it withdraws the corpusculum with its two dependent pollinia and carries them to the next flower where they adhere to the glandular lower surface of the stigma. The upper surface is not receptive.

The genus *Apocynum* shows a similar but simpler arrangement. The stamens are epipetalous and the anthers closely surround the stigma, which, as in *Asclepias*, is only receptive on its under surface, so that self-pollination is prevented. Each anther is sterile at the base and is prolonged upwards into a lignified apex, which is united to the stigma. The narrow slits between the anthers are the only means of access to the nectar. The sterile base of the anther secretes a viscous fluid, and when the insect visitor withdraws its proboscis this fluid sticks to it and then picks up and removes pollen from the upper part of the anther. Unless the insect is fairly strong, it may, however, be unable to extricate itself and flies are often caught in this way.

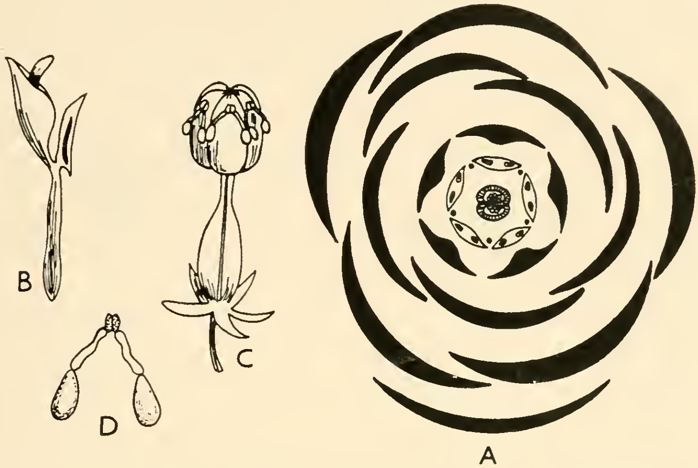

Fig. 1162.—*Asclepias curassavica*. A, Floral diagram. B, Stamen with hooded appendage. C, Gynoecium with pollinia adherent to stigma. D, Pair of pollinia with "translators" or retinacula, which are joined by the corpusculum. (*After Le Maout and Decaisne.*)

Another remarkable modification is that shown by *Salvia* (Labiatae) (see Fig. 1141). The stamens (two in number) are epipetalous and have short filaments. The anthers are versatile and each connective is greatly extended transversely into a C-form, with half an anther at each end. One limb of the connective is relatively short and its anther is sterile. The other limb extends upwards under the hood of the corolla and bears a fertile half-anther. The sterile anther stands in the mouth of the floral tube and when pushed by a proboscis it moves inwards and the upper, fertile anther is brought down forcibly on to the insect's back by the bent-lever action of the connective.

A simple example, which may stand as typical of many others, is that of *Campanula*. The base of each filament is expanded into a hood and all five of these together form a covering over the nectarial surface of the ovary. The only path to the nectar is down inside the tube formed by the close circle of anthers, which are introse.

Some staminal modifications are extremely peculiar and their relation to pollination is not clear. For instance in *Acalypha* (Euphorbiaceae) (Fig. 1163) the filament is expanded like a perianth segment, but the anther forms two curly, worm-like appendages extending out from both sides of the apex. *Cochliostema* (Commelinaceae) (Fig. 1164) has two whorls of stamens. In the outer whorl one is fertile and two are transformed into long hairy appendages. In the inner whorl, one is reduced to a vestige and the other two

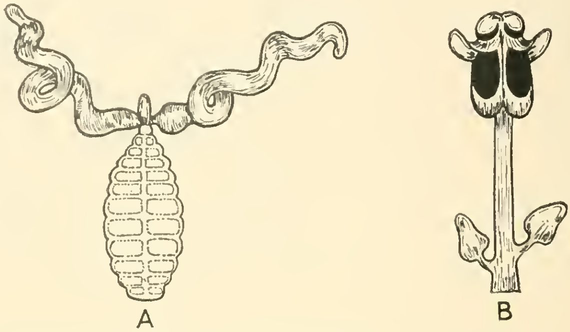

FIG. 1163.—Stamens with appendages. A, *Acalypha*. B, *Persea*. (*After Velenovsky.*)

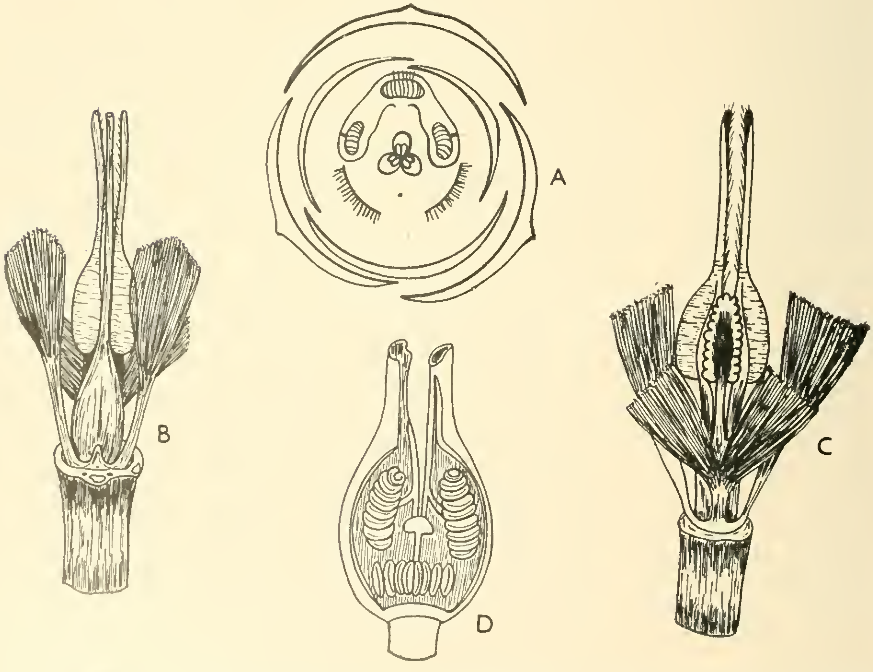

FIG. 1164.—*Cochliostema odoratissimum* (Commelinaceae). A, Floral diagram. B, Flower with perianth removed, anterior view. C, The same, posterior view, showing four fascicles of hairs and the tall sheaths enclosing the anthers. D, Sheaths separated to show the spiral anthers. (*After Velenovsky.*)

have large petaloid connectives, joined edgewise into a hood which extends far up above the anthers into two long hairy points. Inside this hood are the two anthers of the hooded stamens themselves, spirally wound and attached lengthwise to the edges of the hood. Inside is also the transversely placed anther of the single fertile stamen of the outer whorl, which is inserted under the lower edge of the hood.

As examples of staminal forms which appear to be governed by systematic relationships rather than by pollination requirements, may be cited the flat-headed stamens of some groups in the Annonaceae and the long spear-headed stamens of certain other groups in that family. There are also the sinuate stamens of Cucurbitaceae and the fascicled stamens of several families already mentioned, as well as other instances. In the magnolian alliance of families, broad, strap-shaped stamens are the rule, with no distinction of filament and connective and with the sporangia adnate on the inner surface (Fig. 1165). This is particularly well illustrated by the members of two families, Winteraceae and Himantandraceae, allied to the Magnoliaceae; by *Degeneria*, an isolated Fijian genus, with many primitive characters, in the stamens of which the sporangia are actually immersed in the flattened body; and finally by *Sarcandra* (Chloranthaceae), which belongs to the Pepper order (Piperales) (Fig. 1166).

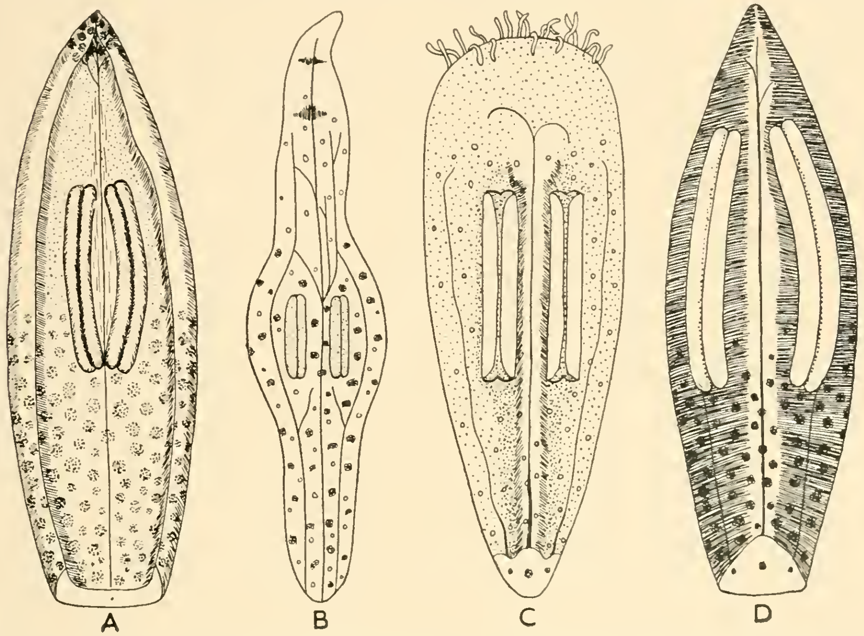

FIG. 1165.—Primitive undifferentiated stamens with adaxially attached pollen-sacs and branched or multiple vascular supply. A, *Austrobaileya*. B, *Himantandra*. C, *Degeneria*. D, *Magnolia*. (*After Canright.*)

Petaloid stamens are usually abnormalities and are generally connected with " doubling " in the flower, but in some spiral flowers they are constantly produced as part of the sequence, as in *Trollius* and *Nymphaea*, forming an intergrade zone between completely sterile petals and completely fertile stamens.

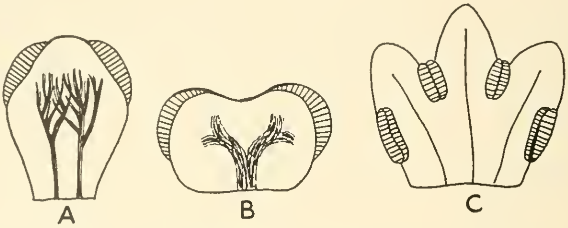

Fig. 1166.—Undifferentiated stamens in *Chloranthaceae*. A, *Sarcandra glaber*. B, *S. hairanensis*, both with branching vascular supply. C, *Chloranthus officinalis*. Three lobed stamen with three trace bundles and eight pollen-sacs. *Sarcandra* is devoid of vessels in the wood. (*After Swamy and Bailey*.)

There are a few instances of expanded stamens apart from true petalody. The uppermost stamens in *Aquilegia vulgaris* are changed into a circle of six elongated scales surrounding the carpels. They sometimes show their character by producing imperfect anthers. The Tree Paeony (*Paeonia moutan*) also has a scaly envelope surrounding the carpels, which is irregularly toothed and may be an upgrowth of the receptacle, but seems more probably to be derived from the uppermost stamens, as it sometimes bears anthers.

The sensitive stamens of *Berberis* and *Centaurea* will be dealt with below, under stamen anatomy. See p. 1196.

Staminal stipules are not uncommon and either take the form of scales or outgrowths or, frequently, glands. The stipules in the form of scales are either attached on each side of the filaments or united to each other, either adaxially or abaxially, across the filament, in a manner corresponding to that in which foliar stipules may become united across the petiole. Examples are to be found in many families, notably the Chenopodiaceae, Amarantaceae, Meliaceae and, among Monocotyledons, where foliar stipules are scarce, in several species of *Allium*. The Simarubaceae (the *Ailanthus* family) have remarkably developed staminal stipules. In *Simaba*, they are united tangentially into an elongated tube on which the stamens are borne aloft. It might be mistaken for a tubular corolla with epipetalous stamens. The Lauraceae are notable for the paired lateral appendages which nearly all its members produce at the base of the filaments (Fig. 1163). They are often glandular but are stipular in nature and are practically a diagnostic character of the family. Ligulate stamens also occur, *e.g.*, in *Alyssum montanum* where the ligule, attached to the adaxial face of the filament, is long on the short stamens and vice versa. In Melastomaceae the ligule is extraordinarily developed and protrudes from the filament in a curve, above which the filament is often sharply bent outwards.

The term staminode is applied to sterile and usually reduced stamens, one or more of which may occur in many flowers as a constant feature, not merely as an occasional and abnormal character. The degree of reduction varies, from staminodes which retain the size and, more or less, the form of normal stamens, but are sterile, to those which are merely slight emergences without any differentiation or vascular supply. The former case is illustrated by the posterior stamen in *Schizanthus*, which is smaller than the others. A further stage is shown by *Erodium*, where all five stamens of the outer whorl are reduced to their filaments only and the final condition occurs in several Scrophulariaceae and Gesneraceae, in which the posterior stamen is a mere rudiment without a vascular bundle.

The reduction or suppression of one or more stamens in a whorl may be an expression of unequal development in the sectors of the floral receptacle. If this developmental inequality is unevenly distributed, staminodes may be limited either to one side of the flower, as in the latter cases cited above, or to more than one sector, *e.g.*, *Valeriana*, where two of the five stamens are abortive and also two of the three carpels, in the same floral sectors. This is a phase of zygomorphy, which may or may not be accompanied by zygomorphy of the corolla.

Staminodes are not always reduced in the ordinary sense of that word; they may be elaborated, like the branched staminodes of *Parnassia*, or they may be, especially in Monocotyledons, transformed into petaloid organs. The Zingiberaceae are good examples of this and the petaloid staminodes may almost completely replace the sepaloid corollas as attractive organs (Fig. 1167). In this family only the anterior stamen, out of a total of six, is fertile, the other five being concrescent into one large petaloid structure. In Cannaceae, a closely related family, the five staminodes form five separate petaloid segments and even half of the single fertile anther is petaloid, leaving only two pollen-sacs functional. The flowers of *Mesembryanthemum* have a perianth which is apparently multiseriate. Actually, there are no petals but only five sepals, and all the coloured members are petaloid staminodes. A similar condition obtains, as mentioned above (p. 1159). in *Trollius*, where however there is a transition between wholly petaloid and wholly staminoid organs which suggests that there is no essential difference between the two categories of organs. A unique function for staminodes is that found in *Pilea* (Urticaceae). Inside the three perianth segments are three staminodes which are strongly bent inwards with their tips below the central akene. When the latter is ripe it

FIG. 1167.—Flower of *Hedychium* (Zingiberaceae). a, Stigma projecting beyond the anther of b, the one fertile stamen. c, Petaloid staminode. d, the narrow petals. e, Ovary. (*After Velenovsky.*)

is detached from the receptacle and the three staminodes uncurl elastically, shooting out the fruit to a distance of several metres.

FIG. 1168.—*Parnassia palustris*, flower showing the five branched staminodes.

Parnassia palustris (Saxifragaceae) (Fig. 1168) has five extrorse stamens in the outer whorl and five staminodes in the inner whorl, whose bases are attached to the petals. These staminodes have solid nectar-secreting bases, but the upper ends form a fan-shaped group of filaments (Fig. 1169), each ending in a glistening yellow knob which looks like a nectary and attracts flies by the appearance of nectar. They have also deceived botanists.

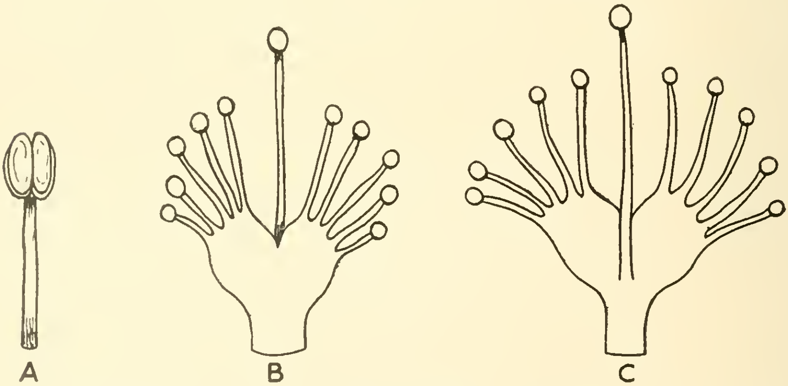

FIG. 1169.—*Parnassia palustris*. A, Fertile stamen. B, Staminode, dorsal view. C, The same, ventral view. (*After Arber*.)

All these cases are " normal " formations, that is to say they are constant throughout whole species or genera, but very curious abnormalities also sometimes turn up (Fig. 1170), especially carpelloid stamens which either bear both anthers and ovules or ovules only. Such stamens are not uncommon in *Sempervivum*. They are generally broadened, and the ovules are marginal and fully exposed. Carpelloid stamens occurred epidemically in

Barley in 1947. The condition is called " Yawning ", because of the gaping appearance of the affected spikelets. It is unsafe to read too much meaning into such monstrosities but they do emphasize the morphological unity of the floral organs.

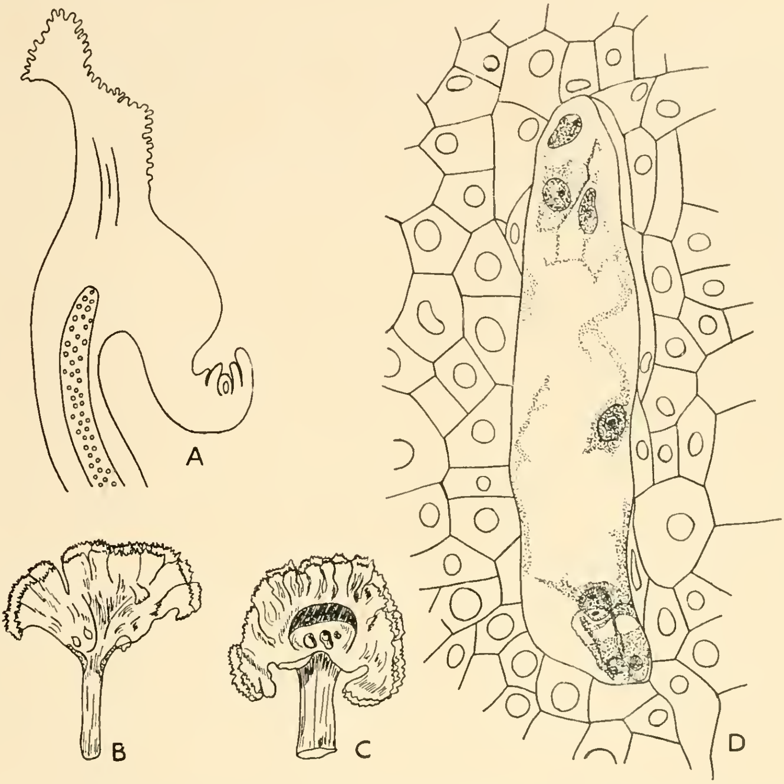

FIG. 1170.—*Podophyllum peltatum*. Carpelloid stamens. A, Vertical section showing stigmatic surface, attached ovule and normal pollen-sac. B, Stamen with stigmatic fringe and ovules. C, Stamen with stigmatic hood surrounding ovules and an open cavity. D, Mature normal embryo-sac from a staminal ovule. (*After Sawyer.*)

The anatomical structure of the normal stamen filament is very simple. There is a single, median, collateral or concentric vascular bundle and a parenchymatous cortex surrounded by an epidermis containing stomata, though no chlorophyll exists in the tissues. Where the filament bears a conspicuous appendage, such as the hood in *Asclepias*, the bundle may form a loop into it, returning on its course to pass up into the anther. Stamen appendages of stipular nature on the other hand are supplied by a branch from the main bundle, if they have any vasculation at all.

Concrescent stamens retain distinct bundles in each stamen-unit, but branched stamens have a common bundle at the base, which divides to send a branch into each segment. When stamens are adherent to petals or sepals the stamen bundle may remain separate or it may be united, in its lower part, either to the median or to a lateral bundle of the perianth member, according to its relative position. In both the latter cases the separation of the two bundles upwards produces two bundles normally orientated, with the xylems inwards.

The stamen is normally a one-trace organ, as we have previously mentioned (p. 1119) but three-trace stamens occur in some of the lower families of Dicotyledons and in a few these traces show a slight degree of branching and anastomosis, which, of course, is greatly extended in the case of petaloid stamens. Examples in normal stamens are: *Talauma*, *Himantandra*, *Degeneria* and several genera of Winteraceae, *e.g. Belliolum*; all included in the Ranales, in a broad sense. As these are all types with a distinctly primitive floral organization, it looks as if the one-trace condition in higher groups is secondary. (See Fig. 1165.)

A peculiar anomaly has been noted in *Parnassia*, the stamen bundle being diploxylic, that is having both centrifugal and centripetal xylem, the latter often forming an arc enclosing some parenchyma cells between it and the protoxylem. There are also indications of several phloem groups around the bundle. This is interpreted by Arber as indicating that the fertile stamens are reduced from stamen fascicles, which, according to this author, are still represented in the flower by the fasciculated staminodes of the inner whorl. Arber maintains that *Parnassia* should be included, on this and other grounds, in the Hypericaceae.

The primordial growth of all flower parts, it is claimed, follows the general leaf-pattern and is comparable with the growth of bracts and other leaves of limited development. Laminal growth is slight but marginal growth is prolonged and, in the stamen filaments, growth in thickness is due to a ventral meristem spread over the adaxial surface.

The structure of the stamen in the Orchidaceae is unique in several respects. There is usually only one functional stamen, adherent to the top of the ovary to form a gynostemium. The pollen grains are cemented together into a solid mass, called a pollinium, in each anther-lobe. The cementing substance between the grains, known as viscin, is derived from the breakdown of potentially sporogenous cells, and a downward prolongation of this degenerated sporogenous tissue forms a basal appendage of viscin, called the caudicula. Below the stamen is a knob of tissue, called the rostellum, supposed to be derived from the third lobe of the stigma. The interior cells of this structure undergo the same degeneration into viscin, after which its upper epidermis dissolves and the caudicula becomes adherent to the sticky mass thus exposed, which now separates from the surrounding cells and forms a cushion known as the retinaculum. It is by means of the latter that the caudicula and pollinium become attached to the head of a visiting insect, in the manner described in Chapter XXX.

The motor-tissue in irritable stamens, such as those of *Berberis* and *Centaurea*, consists of parenchyma of rounded outline, with rather large intercellular spaces, resembling the cortex in the motor pulvini of *Mimosa pudica*. The mode of operation is not definitely known but is probably the same as in the latter plant, namely by collapse of the cells following the rapid extrusion of vacuolar sap. In *Berberis* the motor-tissue is limited to the base of the filament on the adaxial side, whereas in *Centaurea* it surrounds the base of the filament. In the former the movement is therefore an adaxial curvature, while in the latter it is one of simple contraction.

The sensitive region in the stamen of *Berberis*, as in a number of other examples (*Opuntia*, *Portulaca*, *Catasetum*), differs from the rest of the filament surface in that the epidermal cells protrude as prominent papillae which are the receptors of the touch stimulus. In *Centaurea*, on the other hand, the sensitive stamens are surrounded by a belt of bristly hairs, partly united into a collar, which in this case are the touch-receptors. In *Sparmannia* the receptors are downwardly curved folds of the epidermis. All alike react to the contact of an insect's proboscis when probing the flower for nectar.

The anther begins its development as a homogeneous mass of parenchyma, in the median line of which runs a strand of desmogen that differentiates at an early stage into the vascular bundle of the connective. The outline then becomes, first, bilobed and secondly quadrilobed, each lobe being one microsporangium. In the tissue of the lobe certain cells of the sub-epidermal layer begin to enlarge, their walls becoming thicker and their protoplasm denser than in the neighbouring cells. These are the initial cells of the **archesporium**. The number of these cells is very variable. In some species of *Mentha* they form a layer almost all round each lobe of the anther. At the other extreme, in Malvaceae and Compositae, there is only one cell in transverse section and in some Mimosaceae with small anthers only one cell altogether. Generally they form a vertical file of cells running almost the whole length of the lobe, but in certain cases, where the mature pollen-sacs are not continuous but are transversely septate (*e.g.*, Onagraceae and other examples cited previously), the file of cells is interrupted by unchanged parenchyma cells.

The first division of the initial cells is periclinal, separating the **primary parietal cells** on the outside from the **primary sporogenous cells** on the inside. The parietal cells usually undergo further periclinal divisions, forming several concentric layers which constitute the **endothecium** of the anther wall.

The archesporial tissue develops by the division of the sporogenous cells, in two principal ways. The commoner method is by division in two directions, so that a solid mass of archesporium results, but in a minority of cases (*e.g.*, *Malva*, *Mentha*, etc.) the divisions are radial only and the archesporium forms a single-layered arc of cells. The subsequent growth of the archesporium cells is accompanied by the dissolution of the middle lamellae between them. At this point in development the growth of the archesporium lags behind that of the outer tissues of the anther, so that contact between the two zones is broken. In the enlarged internal space, now a **pollen-sac**, the individual cells of the archesporium fall apart and round themselves off, becoming thus the **pollen mother cells**, in which meiosis occurs, dividing each cell to form a tetrad of pollen grains. The process of pollen-grain development will be described in a subsequent chapter.

Meanwhile the superficial cells of each lobe have divided tangentially and radially to form a wall-zone, three or four cells thick. This completes the differentiation of the lobes from the central mass of the connective.

The superficial layer of cells in the wall of the anther becomes the epidermis but the sub-epidermal cells enlarge to a conspicuous size and usually become cubical or rectangular. The radial walls of these cells are thickened by a reticulum, more or less spiral in pattern, of narrow bands of lignin, leaving the inner and outer tangential walls unthickened. The bands are formed at the expense of starch stored in these cells, and they are arranged in patterns; spiral, U-shaped, ring-shaped, etc., which are characteristic of the family to which the plant belongs. Finally the protoplasm disappears and the empty cells, forming what is often called the **middle layer**, constitute, with the epidermis, the wall of the fully matured sporangium (Fig. 1171).

FIG. 1171.—*Lilium candidum*, transverse section of an anther showing four lobes with pollen-sacs and connective with vascular bundle. Each pollen-sac is surrounded by a dark zone of tapetum. The line of dehiscence between each pair of pollen-sacs is shown and the large cells of the middle layer in the anther wall.

The middle layer is sometimes confined to the walls of the sporangial lobes and sometimes it surrounds the whole anther. It does not, however, as a rule appear, at least in its characteristic form, on the inner side of the lobes, between them and the tissue of the connective. Although the anther wall in the majority of families has only one thickened middle layer, certain exceptions may show from two to five or more, the highest numbers of layers being in *Agave* and *Iris*.

Between the thickened layer and the archesporium there may be only one layer of cells or there may be several. The innermost layer always develops into the **tapetum** and if there are any supernumerary layers they are generally temporary and are sooner or later flattened and crushed. The tapetum surrounds the archesporium. Its cells divide freely and form a layer of enlarged cubical cells, which elongate centripetally as the archesporium becomes transformed into pollen mother cells. Their protoplasm becomes dense and pigmented, usually yellow or orange, but occasionally pink (*Knautia*), reddish-brown (*Pyrus*) or violet (*Anemone*). As the tapetum completely surrounds the archesporium, it follows that one sector of it originates from the sporangial wall and another sector from the tissue of the connective, but it is nevertheless uniform all round.

There are two kinds of tapetum. One is known as the Secretory Type, found only in the Lycopodiales and Isoetales, in which the cells do not disintegrate, and the other, the Plasmodial Type, characteristic of the Filicales, Equisetales and most Spermatophyta, in which the cell walls dissolve, the nuclei multiply and become distorted in shape and the liberated protoplasm, which now forms a united plasmodium, sends out long pseudopodia which penetrate between and envelop the pollen mother cells. This reversion to a state of free protoplasmic movement in highly organized plants is a very striking phenomenon. The tapetum disappears when the pollen is ripe and before the anthers open. (See Volume I, Fig. 546.)

As the pollen matures the part of the sporangial wall separating the two neighbouring lobes, on each side of the anther, is more or less completely broken down, the two pollen-sacs becoming united into one. It is in this state that the anther is described by systematists as " bilocular ". The two sporangial walls, however, remain conjoined by the tissue which lies at the bottom of the furrow between them. Here the cells of the epidermis are much smaller than elsewhere, forming a strip known as the **stomium**. Eventually they break down or disjoin, opening a longitudinal slit between the sporangia, which constitutes the line of **dehiscence**. This may be simultaneous all down the length of the anther or it may be progressive from apex to base.

These various stages may all be passed through while the flower is still a closed bud. When it opens and air and sunlight strike on the delicate anther tissue, the sporangial walls begin to lose water and to contract. This is due to the hydrostatic tension developed and the cohesion of the contained water to the cell walls. (See also under Nectaries, p. 1251.) In the important middle layer this contraction affects the unthickened outer and inner walls more than the thickened radial walls. One of two things may then happen. If, as in the majority of flowers, the thickening bands are strongest towards the inner side, then the outer cell walls contract most and the sporangial wall curls outwards, exposing the pollen. If, as in a few cases (*Butomus*), the thickening bands are strongest towards the outer side, then the inner cell walls contract most and the sporangial wall curls inwards. This also exposes the pollen, though not so effectively as in the first case.

The opening process is generally rather slow. A truly explosive opening of the anther, like that of a Fern sporangium, is only known in *Ricinus*. The so-called explosive dispersal of pollen which occurs, for example, in the Urticaceae, is not due to the dehiscence of the anthers, which is carried out normally, but to the elastic snap of the filaments straightening out when they are released, as we have described above for *Pilea* (p. 1187).

Porose dehiscence may imply only a very short stomium. The " pore " is generally longitudinal and then corresponds to a partial longitudinal dehiscence. Some Ericaceae, however, are genuinely porose, in the sense that they have no stomium and the pore is formed by the dissolution of a group of cells. The valvate anthers of Lauraceae, etc., obviously have a U-shaped stomium line and the thickened middle layer of the wall is confined to the valve flaps.

This thickened mechanical layer of the wall has been called the **endothecium** by von Goebel. He points out that although the sporangia of all the Spermatophyta belong to the eusporangiate type, the sporangia of Gymnosperms dehisce by the action of their outer wall layer, or **exothecium**, with the single exception of *Ginkgo*, while the great majority of Angiosperms dehisce by the action of the inner, endothecial layer. Exceptions to this rule among the Angiosperms are not common and in almost all

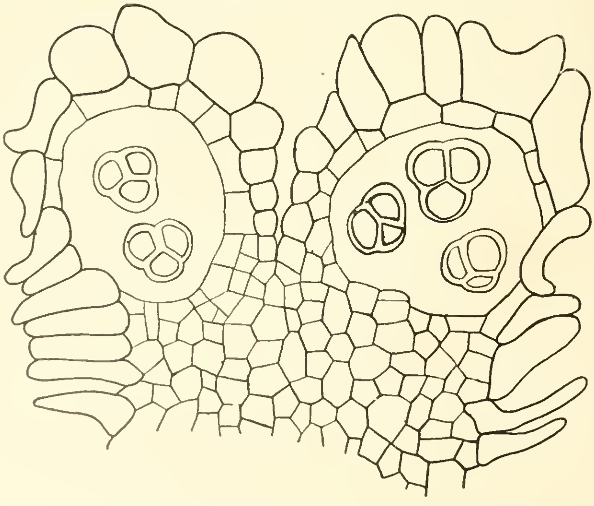

FIG. 1172.—Part of a transverse section through the anther of *Erica* showing the undifferentiated anther wall. (*After Goebel.*)

cases, if the thickened layer appears to be an exothecium it is because the epidermis has disappeared or has been suppressed. The truly porose anthers of *Erica* (Fig. 1172) and those of some very reduced water plants, such as *Zannichellia* and *Naias*, which burst by swelling, have neither endothecium nor exothecium.

On the general question of the morphology and evolution of the stamen we will limit ourselves to a few concluding words. The classical and straightforward view of the stamen regards it as a modified foliar appendage, though not, of course, a modification of the existing type of green foliage leaf. It is true that stomata are present on the stamens, as on all other floral organs, not even excepting the internal wall of the ovary, in some flowers, but stomata are not exclusively foliar structures. What their presence does suggest, however, is that the organs bearing them had in the past a photosynthetic function which the stamens, at any rate, have now quite lost.

There is, on the other hand, a school of thought which traces in the " perfect " flower the result of a process of condensation from an " inflorescence " of naked sporangia, and in the opinion of such morphologists both stamens and carpels are regarded as descended from systems of branched axes bearing sporangia. Wilson has argued ably in favour of a branched ancestry for the stamen, the nearest analogue to which at the present day would be the dichotomously branched stamen of *Ricinus*. These interpretations are bound up with the larger question whether the sporangia of the Angiosperms are **stachyosporous** or **phyllosporous**, that is, whether their sporangia are axial in origin or are borne on sporophylls. Lam has stressed the importance of this distinction in the Pteridophyta, where it divides the whole phylum into two series, and has argued in favour of its persistence in the Spermatophyta. Acceptance of the former view naturally involves rejection of the foliar, *i.e.*, sporophyll, interpretation of stamens. If it were clearer what constitutes a sporophyll or what, in terms of the Telome Theory, is exactly the difference between an axis and an appendage, such questions might have more weight. It may be true that in the course of evolution from a primitively telomic structure, some fertile telomes have passed through a foliar modification, while in other lines of evolution they have not, but this is by no means a fundamental difference and we may perhaps feel that the distinction between leaf and shoot, as between sporophyll and sporangiophore, is liable to be overstressed and to savour too much of the old formalistic morphology.

Of fossil evidence on the evolution of the stamens there is really none. A gulf exists between the microsporophylls of the Gymnosperms and those of the Angiosperms, and comparisons in that direction do not help us much. The story goes a long way back and it is perhaps among the synangia of some of the Medullosaceae that the clue to the starting point may one day be found.

THE GYNOECIUM AND CARPELS

The term **gynoecium** is applied to that portion of the flower which is composed of the carpels collectively or, in a minority of flowers, of one carpel alone, in which latter case the two terms are synonymous. The old term **pistil** was dropped because it had been applied without discrimination, both to the individual carpels, when they were free from one another, and to the compound structure formed by the fusion of several carpels.

The carpellary group is generally quite clearly delimited and occupies the morphologically uppermost part of the floral receptacle, whose restricted growth places the gynoecium usually in the centre of the flower. A distributed gynoecium rarely occurs, although in some members of the Monimiaceae, where the receptacle is concave, the carpels in female flowers may occur all over its hollow surface.

We have previously dealt with the variations of form in the receptacle which affect the position of the gynoecium in relation to the other organs of the flower, which may be either **hypogynous**, **perigynous** or **epigynous**. We shall return briefly later on to the interpretation of the inferior ovary, which has a bearing on the evolution of the flower as a whole.

As to the term **carpel** itself, we apply it to a unit structure, bearing and usually enclosing an ovule or ovules, and normally composed of three parts: an **ovary**, which is a hollow structure whose wall surrounds the ovules; a **style**, which is a column of tissue arising from the ovary; and a **stigma**, which is a receptive, glandular pad of tissue surmounting the style. The first and last of these are the essential parts, the presence of which constitutes the condition of angiospermy. The style is a convenience which aids pollination in many flowers but which is sometimes absent (Fig. 1173).

The whole gynoecium is sometimes carried upwards by the exceptional elongation of an internode of the floral axis, known as a **gynophore**, which may sometimes reach an extraordinary length, as in the Capparidaceae, raising the gynoecium completely above the flower. Similarly, individual carpels, which are generally sessile on the receptacle, may be severally elevated on pedicels, as in *Eranthis*, *Thalictrum*, *Zannichellia* and many other genera.

When all the unit carpels are separate the gynoecium is called **apocarpous**, and if they are coherent, **syncarpous** or, more correctly, **coenocarpous**. Cohesion occurs in all degrees of completeness. It may be no more than cohesion of the ovaries at their bases, as in Labiatae, or the ovaries may be united while the styles remain free as in Caryophyllaceae, or there may be a union of all parts except the stigmas, *e.g.*, Scrophulariaceae, or finally a complete union, as in Cruciferae and many other families. In coenocarpous flowers the ovary formed by the union of several carpels is called a **compound ovary** (Fig. 1174). It may be divided by **septa** internally into a number of **loculi**, or spaces, corresponding to the number of carpels involved, but in the most complete unions the dividing septa are absent and the compound ovary becomes **unilocular**, showing only traces of its

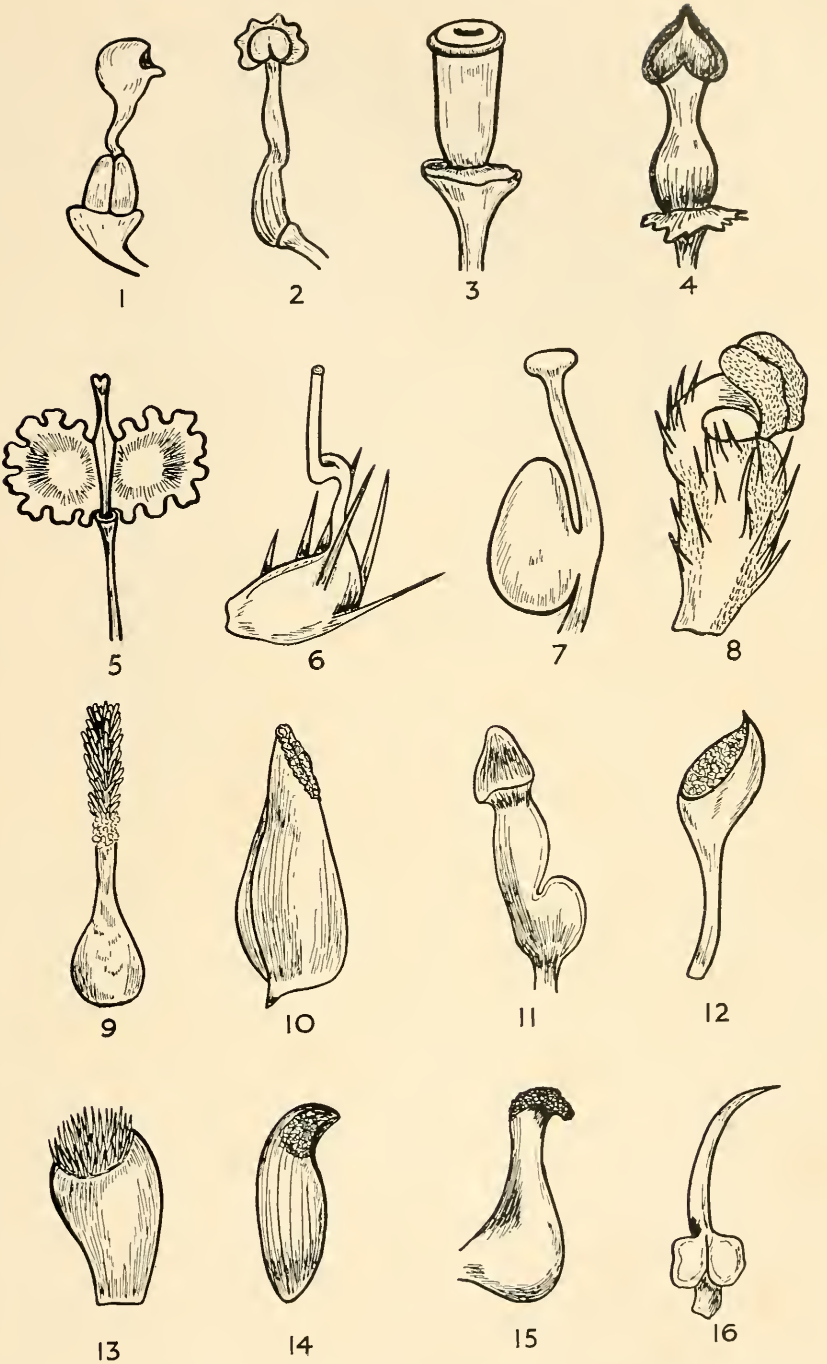

FIG. 1173.—A selection of different forms of carpels. (1) *Viola.* (2) *Corydalis.* (3) *Berberis.* (4) *Utricularia.* (5) *Cremolobus.* (6) *Geum.* (7) *Alchemilla.* (8) *Spiraea.* (9) *Plantago.* (10) *Potamogeton.* (11) *Grevillea.* (12) *Euptelea.* (13) *Peperomia.* (14) *Gyrostemon.* (15) *Adonis.* (16) *Ceratocephalus.* (*Mostly from Le Maout and Decaisne.*)

FIG. 1174.—Transverse section of a young ovary of *Lilium*, formed of three united carpels. The larger vascular bundles mark the dorsum of each carpel, the long dark bundles are the fused marginals marking the lines of division between the carpels. There is a loculus for each carpel containing two rows of ovules borne on the inturned carpel margins.

compound nature. The first case is truly syncarpous, the second is distinguished as **paracarpous**. Both are included under the term coenocarpous.

A limited number of species in certain families show an opposite kind of carpellary union, with free ovaries and with styles and stigmas united. This is to be seen in Asclepiadaceae, where it is a characteristic of the family, in some Apocynaceae, *e.g.*, *Vinca*, and in some Rutaceae, *e.g.*, *Dictamnus*, but it is an exceptional condition.

Apocarpous carpels may be spirally arranged in some of the families where that condition obtains in other parts of the flower, though even in some of these the carpels may be whorled, as they are in the majority of families both with apocarpous and with coenocarpous gynoecia. In the latter the carpels are invariably whorled.

The number of carpels is very often less than the number of parts in other floral whorls, perhaps because of the limited space available at the summit of the axis. There may often be no more than one, or there may be only one fertile carpel, with obvious traces of the abortion of others, as in *Viburnum* and *Valerianella*. Whether this be so or not, the solitary carpel must be regarded in almost every case as derived by reduction from a whorl, though it may only have been from a whorl of two. This brings up the question whether terminal carpels do exist. We have already seen (p. 1120) that in the most conspicuous case of apparently terminal single carpels, *i.e.*, in the Leguminosae, the evidence of residual vascular bundles indicates that the carpel occupies a lateral position, which has become apparently terminal by the abortion of the receptacle apex, coupled with the disappearance of the other members of the original carpellary whorl. The latter, moreover, still exists in the small genus *Affonsea* (Fig. 1175) in the Mimosaceae, which has a whorl of three. Although it is inadvisable to be dogmatic, it may be concluded that the terminal position of a carpel, like the terminal position of a stamen in a few male flowers (p. 1180), has been arrived at secondarily, in most cases, by abortion and a shift of position due to the greater growth rate of the carpel compared with the receptacle apex.

Fig. 1175.—*Affonsea juglandifolia* (Mimosaceae). Longitudinal section of flower showing whorl of carpels. (*After Baillon.*)

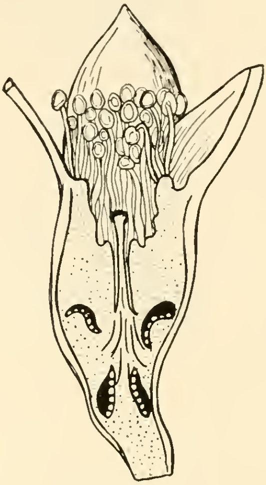

Fig. 1176.—*Punica granatum*, Pomegranate. Vertical section of flower showing two superposed whorls of carpel loculi in the inferior ovary. (*After Le Maout and Decaisne.*)

There is very rarely more than a single whorl of carpels, even when they are free and the number of other parts in the flower is large. A supernumerary upper whorl of small sterile carpels occurs as an abnormality in the Orange, giving rise to the variety called the Navel Orange, where they form a small, imperfect group at the apex of the ripe fruit. Two whorls of carpels appear, however, to be normally formed, all being fertile, in some of the lower Monocotyledons, *e.g.*, *Butomus*, *Alisma*, and *Triglochin*, in which the number of carpels is double, or more than double (*Alisma*), the number of stamens in a whorl. The Pomegranate, *Punica granatum* (Fig. 1176), presents a unique case, for there are here, in a syncarpous and inferior ovary, two completely distinct whorls of carpels, in which, moreover, the upper contains five to seven carpels with parietal ovules and the lower only three, with axillary ovules. This inversion of the normal order of diminishing numbers in the upward direction is probably due to an invagination of the whole centre of the flower into the axis, for which a parallel may be found in *Calycanthus* (p. 1138), so that the lowermost group of carpels are morphologically the upper, central group, standing on the sunken apex of the receptacle.

Spiral flowers, such as *Ranunculus*, present a great deal of variation in the number of parts in each zone, as well as in the total number of parts. The number of stamens and carpels is positively correlated with the number of perianth parts, but it may be observed that there is an inverse or negative correlation between the number of stamens separately and of carpels separately, as if there were only room for a limited number of appendages on the receptacle and when more of these are stamens then fewer are carpels, and vice versa. The number of carpels may also be reduced by abortion of the uppermost ones (cf. *Caltha*, p. 1131). Cyclic flowers show a greater stability of numbers, and in them there is often a close linkage between the number of carpels and the number of stamens, especially the number in the inner whorl of stamens, when there is more than one whorl. Variations in the respective numbers are closely linked. This may be accounted for, if we consider what has been said before about sectorial development in the flower, by the abortion of one or more sectors of the receptacle, involving the disappearance of a corresponding number of stamens and carpels together. Such variations in development are often influenced by nutrition and in starved plants there may be a general reduction of the number of parts, which may however affect the stamens more than the less numerous carpels.

When there are only two carpels, these, in zygomorphic flowers, always lie in the plane of symmetry of the flower, whether this is, as usual, the vertical plane or an oblique plane, as in Solanaceae.

The cohesion of carpels occurs, as we have seen, in various degrees of completeness. In some flowers a group of carpels which are essentially separate from each other, may be so closely pressed together, as in *Nigella* and *Butomus*, that it requires close examination to ascertain that no organic fusion exists. The carpels in *Aquilegia* and in the Saxifragaceae are united only at the base. In Apocynaceae they are united only at the top. In *Centrolepis* they are united one above the other in an alternating, vertical series; while in *Pandanus* they unite only at the fruiting stage. In the great majority there is organic union between the lateral walls, but each carpel retains a distinct, closed loculus, the fused lateral walls forming the dividing septa between the loculi (Fig. 1177). Such compound ovaries are **plurilocular**. An anomalous condition exists in *Leptodermis*, one of the Rubiaceae, in which the septa are present but are trellised instead of being solid, so that the ovary is technically plurilocular but is actually unilocular. A further degree of cohesion is that in which the lateral walls of each carpel remain incompletely developed, so that the inturned edges of each carpel do not meet each other and the loculi are incompletely separated. Finally, the carpel margins may not be inturned at all, but united to form a ring-like wall around a single internal cavity. The last two cases are classed as **unilocular**.

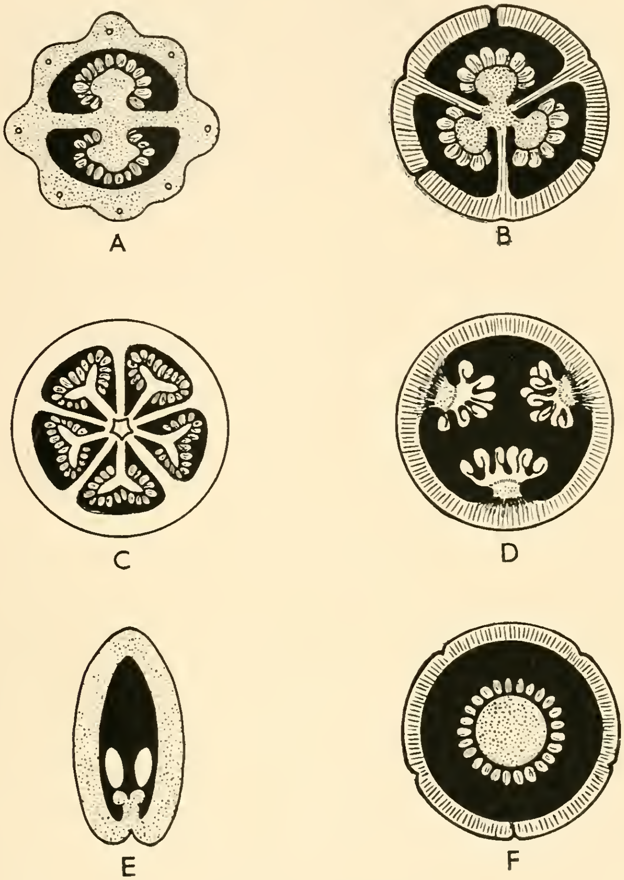

FIG. 1177.—Various types of placentation as seen in transverse sections of ovaries. A, Axile with two carpels. B, Axile with three carpels. C, Axile with five carpels. The placentae in each case represent the inturned margins of the fused carpels. D, Parietal. E, Marginal. F, Free central. (*After Goebel.*)

In plurilocular ovaries the inner margins of the united carpels are generally more or less wholly fused at the centre of the compound structure and there they form a solid column of tissues, commonly called the axis of the ovary. This is not, however, an upward continuation of the axis of the flower which does not, as a rule, extend beyond the base of the gynoecium. The tissue of the ovary axis belongs to the carpels, with at most some residual tissue of the floral axis enclosed, and the vascular bundles it contains are the ventral carpel-traces, not axial bundles. This is, as has been said, the general rule; but there are exceptions, especially in the families Oxalidaceae and Caryophyllaceae, where the summit of the floral axis is relatively broad and is not completely utilized in carpel formation. In such cases the distinct floral axis persists upwards for some distance in the centre of the compound ovary and is distinguishable by its own ring of vascular bundles, the carpellary margins being fused around it. In unilocular compound ovaries, where the carpel margins do not meet at the centre, the floral axis does not rise above the base of the ovary.

The well-known gynoecial structure in *Pelargonium* and *Geranium* presents peculiarities. It is commonly stated that the carpels, which are mechanically detached when ripe, are joined by their styles to an axial column. The floral axis is, however, only present in the lowest part of this column, at the level of the ovaries, and the upper part is formed entirely by the union of five prolongations of the carpels. These are not true styles, but sterile extensions of the ovaries, each with its separate loculus. The outer walls of these elongations are highly sclerotic and break away from the adaxial walls when the fruits are ripe, leaving the latter united in a central column.

The foregoing considerations do not, of course, apply to apocarpous gynoecia, particularly when the carpels are numerous or spirally arranged, for in such flowers the axis is prolonged to the top of the gynoecium and all the carpels are separately and laterally attached to it. Their attachment is generally sessile, but a carpellary stalk or **carpophore** is sometimes developed, which may elongate, in the fruiting stage (*e.g.*, in many Leguminosae), to more than a centimetre long. Carpels which are at first united but later separate, as in Malvaceae, are also attached directly to a central axial column.

The carpel margins, whether fused together or free, are generally the fertile portions on which the ovules are borne. They are usually to some extent swollen and consist of soft, thin-walled tissues, which form the **placentae**. The name is borrowed from mammalian embryology, but there is no true analogy with the placenta in that group, since the ovules are organically part of the parent plant. Only rarely are ovules borne superficially on the carpel walls, the Nymphaeaceae and Butomaceae being the chief examples. In these families the ovules are borne all over the inner surface of the carpels, except for the region of the mid-ribs. The Poppies appear to show a similar superficial distribution, but the septa, which do not meet centrally, are not, in this genus, the lateral walls of the carpels, but are expansions of the fused carpel margins, *i.e.*, they are really elongated placentae, as may be seen by comparison with the allied genus *Meconopsis* (Fig. 1178).

We have already, on p. 1202, discussed briefly the difference between the syncarpous and the paracarpous ovary. Paracarpous ovaries are those in which the carpels are united only by their margins, and in which therefore there are no septa. It has been suggested by Troll that the paracarpous state may have evolved in the following way (see Fig. 1061). In most compound ovaries the union is continued upward in the stylar region, the individual styles being also united, but always marginally, surrounding a central stylar canal which is never divided by septa. The placental tissue is often continued upward into the stylar canal where, however, no ovules are formed. It is possible that this upward extension of the carpel was once part of the fertile ovary and that it has been sterilized for the advantage of pollination, by elevating the stigma. If, then, the balance of growth were to shift upward, so that the stylar region regained its fertility, while the ovarial portion below was more or less suppressed, a paracarpous ovary would result. Though the theory may sound rather far-fetched, it is supported by various facts, *e.g.*, that paracarpous ovaries rarely, if ever, bear styles. Furthermore in some paracarpous ovaries, for example in *Parnassia*, the base of the ovary is syncarpous. The biological function of the missing styles may be produced either by the development of a gynophore (*Capparis*), or by elongated stigmas (*Dianthus*), or by the elongation of the ovary itself (Cruciferae).

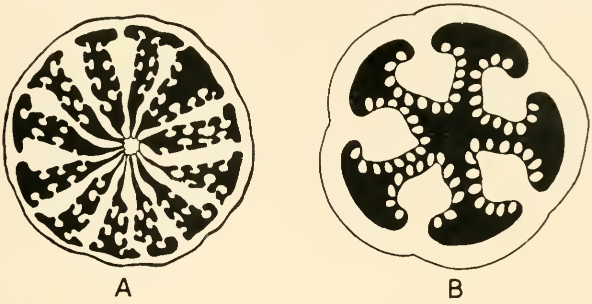

FIG. 1178. A, *Papaver*, transverse section of ovary with elongated placentae forming false septa. B, *Meconopsis* with short parietal placentae. (*After Le Maout and Decaisne.*)

The interpretation of the single carpel as an infolded (conduplicate) foliar structure is due to the theory of the flower propounded by Goethe and adopted by A. P. de Candolle (1827) who wrote: " Each carpel may be considered as a little leaf folded upon itself. " At that date it was permissible to consider the carpellary leaf as a " metamorphosis ", that is to say, a purely ideal transformation of a " typical " foliage leaf, but the study of evolution and particularly the study of fossil plants has taught us that there can be no direct relationship between a carpel and a modern foliage leaf. Each has, rather, evolved along independent lines from the primitive branch appendages of the plants of a remote past, in which the distinction of sterile and fertile appendages first become manifest. As Ozenda says, the relationship is one of fraternity not of filiation.

Both types of organ have retained some common features. They are dorsiventral, they usually contain chlorophyll, both bear stomata on one or both surfaces, and the carpel wall may contain a palisade tissue. They have branching vein-systems and they may bear closely similar hairs or glands.

These arguments for the association of the two types of structure apply with even greater force in the Pteridophyta, where the differentiation between fertile sporophylls and sterile foliage leaves is much less marked than in the Angiosperms. If therefore, as is generally accepted, the foliage leaves of Pteropsida are derived from flattened branch systems, so must also be the sporophylls. To equate a carpel to a sporophyll is not therefore inconsistent with the supposition that it had ultimately its origin in a branch system.

We have already seen that similar arguments have been advanced with regard to the stamen, and the same difficulties which we then noticed apply to the present case. Granting that originally all appendages were telomes on an undifferentiated shoot, the different views held really turn upon whether the organ passed through a foliage phase on the way to its present form, or did not. It is possible that the stamen was never laminar, but the evidence in the case of the carpel is stronger. The carpel receives typically three, sometimes five traces, but with very few exceptions never a single trace like the stamen. This accords with what Eames has shown to be the primitively three-trace foliage leaf. The suggestion is that the immediate ancestor of the carpel was a palmate, three-lobed, dorsiventral, leaf-like structure, which was in turn derived from a flat, dichotomous shoot. Hunt has distinguished two forms of carpel, based on this theory. In one, the central lobe, with only one bundle, forms the style and stigma and the outer wall of the carpel, the other two forming the lateral walls. In the other all three lobes contribute to the formation of the style and stigma, the latter being consequently three-lobed, while the style contains three vascular bundles.

A further theory of the carpel should here be mentioned, put forward by Hamshaw Thomas. He, like Eames, interprets the carpel as a triple structure (Fig. 1179). The dorsum he considers as formed from the axis

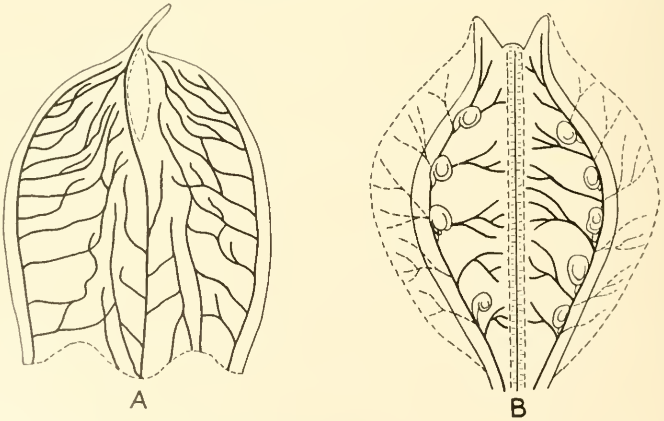

Fig. 1179.—A, Vasculation of *Delphinium* carpel. B, Diagram illustrating Thomas' theory of the derivation of a simple follicle from a palmate sporophyll. The dorsal, axial segment is shaded. The two lateral segments aborted by contact are shown with dotted lines. (*After H. H. Thomas.*)

of a fertile appendage. Its axial nature explains the paucity of branch veins coming from the dorsal bundle. The carpel walls are supposed to represent a pair of seed-bearing cupules united by their margins, in short a female shoot of Caytonialean type, reduced to two opposite cupules now concrescent. Union in this way would bring their stigmatiferous margins, supposing the cupules to have been comparable with those of *Caytonia* (see Volume III), to near the base on the ventral side of the carpel. Thomas suggests that this was the primitive position of the stigma and that its rise towards the carpel apex has been due to natural selection favouring greater accessibility of the stigma in crowded gynoecia.

To sum up this theoretical discussion we may say that the classical concept of the carpel, as a lateral, leaf-like appendage analogous to a sporophyll, with the necessary reservations as to the previous history of such appendages, is still a useful working hypothesis.

The three traces which the carpel receives from the receptacle are separate from the base. The median trace may originate at a lower level in the receptacle than the other two, and when it enters the carpel it follows a straight course upward into the style. Its course is marked, as a rule, by an external ridge or angle called the **dorsal suture**. The other traces diverge to the two margins of the carpel wall, which they follow upward, giving off branches to the ovules. Being the supply channels to the ovules they are often stronger than the dorsal bundles. They remain separate, although the parenchymatous tissues of the carpel margins become united during development. Even in a syncarpous ovary they usually maintain their separate identity, but in a paracarpous ovary they generally unite with the marginal bundles of the neighbouring carpels. They may, or may not, pass into the style. In addition, the lateral walls are supplied by a number of lateral branches from the three traces and in a large carpel the branches may form a network connecting the main bundles. It is very notable, however, that the majority of these branches originate from the marginal bundles and few, if any, from the dorsal bundle. This is the direct opposite of the mode of branching of veins in the leaf, which is away from the mid-rib, not towards it. Whether this difference is attributable to the superior physiological importance of the marginal bundles in the carpel, or whether it is a relic of the previously three-lobed condition of the carpel, cannot be decided, but the fact itself affords support to those who deny that the carpel is a simple leaf.

The orientation of tissues in the dorsal bundle is normal, that is to say the xylem is adaxial, but in a compound ovary the orientation of the bundles at the points corresponding to the inturned margins of the carpels is inverted, as would be expected if the carpel is an infolded structure. This inversion distinguishes the carpel bundles from those of the floral receptacle, if this is present in the centre of the ovary axis, since the receptacular bundles preserve their normal orientation (Fig. 1180).

A theory has been put forward by Saunders, under the name of " Carpel Polymorphism ", to the effect that there are three distinct types of carpel

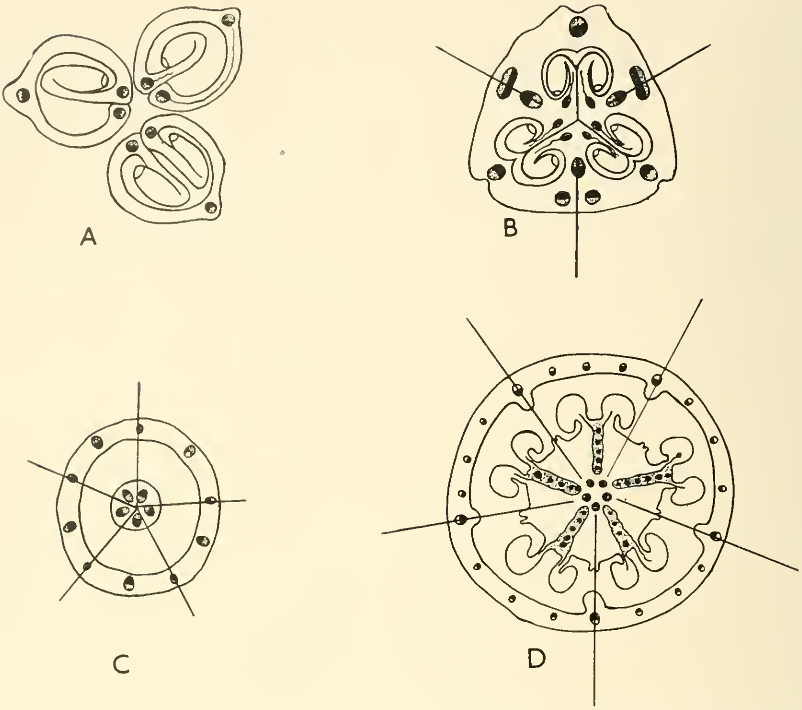

Fig. 1180.—Vasculation of carpels in transverse section. Xylem in black. The radial lines show the carpel boundaries. The marginal bundles of the in-turned margins show reversed orientation. A, *Eranthis hiemalis.* B, *Tulipa gesneriana.* C, *Anagallis arvensis.* D, *Melandrium dioicum.* The last shows a ring of axial bundles with normal orientation in the centre of the placenta. (*After Van Tieghem.*)

structure. The first type, called the " Valve Carpel ", is the one generally recognized, and it is accepted by Saunders as a foliar type of organ. In apocarpous gynoecia it is said to be the only type present and in such cases is usually fertile. It bears only one style and one stigma. The second type, the " Solid Carpel ", is present in most syncarpous gynoecia and in such cases is said to be usually fertile while the valve carpels present are sterile. The solid carpel is supposed to be reduced, in its most extreme form, to no more than a vascular bundle, but it may also have a surrounding area of ground tissue proper to itself. It may contain either one or two bundles, with one or more corresponding rows of ovules. If there is a style it may be either single or bifid. The third type is the " Semi-solid Carpel " or Pseudo-valve, which combines some of the features of both the others. It may have the lateral expansion of a valve carpel, but the ovules are not borne marginally as in that type, but are borne on either side of the central line. When a style is present, the twin dorsal bundles are both continued upward into it and there is a bifid stigma.

The standard example of a combination of solid and valve carpels is said to be the gynoecium of the Cruciferae, in which the ovules are borne on two " solid " carpels, which form the replum and are extended centripetally to form the false septum. The lateral portions of the ovary, those which are detached at maturity, are said to be two sterile valve carpels, the whole structure being thus quadricarpellary, not bicarpellary, as usually understood. The pseudo-valve type is said to be typical of most Papilionaceae and in combination with valve carpels it occurs in some Berberidaceae, and in combination with solid carpels in Orchidaceae.

A brief statement of the theory cannot do justice to the considerable array of detailed evidence which Saunders has presented in support of it, in spite of which the theory has been adversely criticized, and has obtained little credence. This is not the place to attempt to weigh up the merits of the controversy, but we should point out that the analysis of the compound ovary, on any carpellary basis, is theoretical and any theory, even the classical theory, despite its respectable antiquity, can only be maintained so long as it is not inconsistent with observation (Fig. 1181).

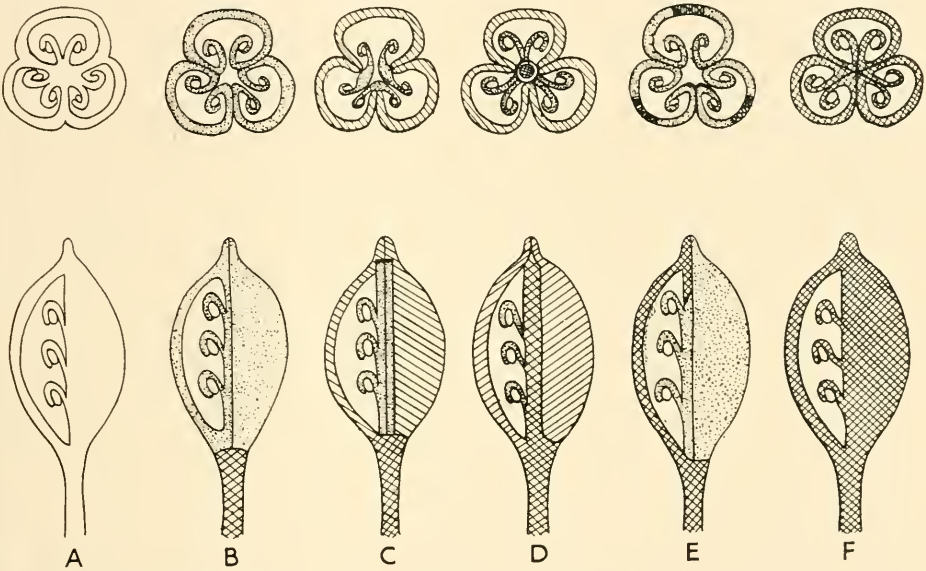

FIG. 1181.—Various theories of carpel structure. Transverse and longitudinal sections. A, Formal sections. B, Van Tieghem. C, Saunders. D. Hagerup. E, Thomas. F. Thompson-Gregoire. (*After Ozenda.*)

▩ Axis. ░ Fertile carpels. ▨ and ▧ Sterile carpels or Bracts.

Polymorphy of carpels, in a factual sense, may be seen in certain genera and is better described as **heterocarpy**. It is, however, rare, except in the Compositae, where there is frequently a difference between the carpels, or rather the fruits, of the ray florets and those of the disc florets. Though usually slight, the difference is very marked in *Dimorphotheca* (Fig. 1182), while in *Calendula*, although only the ray florets produce fruits, there are three different forms among them. In some species of *Atriplex* and *Cheno-*

podium, fruits of two different forms are produced at different points in the inflorescence and in *Polygonum* fruits which are either two-angled or three-angled are formed apparently indiscriminately. The biological reasons for these differences are not known, but in cleistogamic flowers (see p. 1355) the fruits are often different from those produced by the flowers of the same plant which are openly pollinated.

FIG. 1182.—Dimorphic fruits of *Dimorphotheca*. The ray florets produce cylindrical fruits, the disc florets produce flattened fruits.

The ontogeny of the carpels from the receptacle is best illustrated by the free carpels of apocarpous flowers. The earliest stage is a hemispherical protuberance closely resembling the primordium of a leaf. The further development in many cases resembles that of a peltate leaf rather than that of a leaf of normal type, though the three modes of growth characteristic of leaf primordia, namely, longitudinal growth, marginal growth and growth in thickness, proceed in the same order.

Troll has shown that the growth of the carpel in breadth proceeds from sub-marginal cells as in the foliage leaf and that it is only in the stylar region that there is any considerable growth in thickness. The carpellary stalk, when present, has a unifacial structure like that of the petiole of a peltate leaf and he uses this as an argument in support of the peltate character of many carpels, even where, as in some peltate leaves, the subsequent growth is not fully peltate.

The development of the typically peltate carpel has been compared with that of the abnormal ascidial leaves which occur in many genera, and with that of the pitcher leaf in *Sarracenia*, which is a very pronounced ascidial leaf. A depression appears at the apex of the primordium, and the opposite sides of the depression develop unequally. The abaxial lip grows rapidly in length, and forms the back or dorsum of the carpel, in which the dorsal bundle lies and which is produced upward into the style. The adaxial lip grows more slowly and forms a sort of ridge, called by Goebel the " sill " (*Sohle*)* of the carpel (Fig. 1183). If it extends itself upwards it forms the two margins of the carpel, which are thus united from the start. Where the ovules are reduced to one, this usually arises from the sill and is median in

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* The word *Sohle* was used by Celakovsky to denote a hypothetical plinth on which the carpel was supposed to be based, but in the sense in which it is applied to peltate carpels by von Goebel, it is better translated by " sill " than by " sole ".

position, but where numerous ovules are produced, they form two rows, one arising from each margin, and the sill in such cases remains small and is sterile.

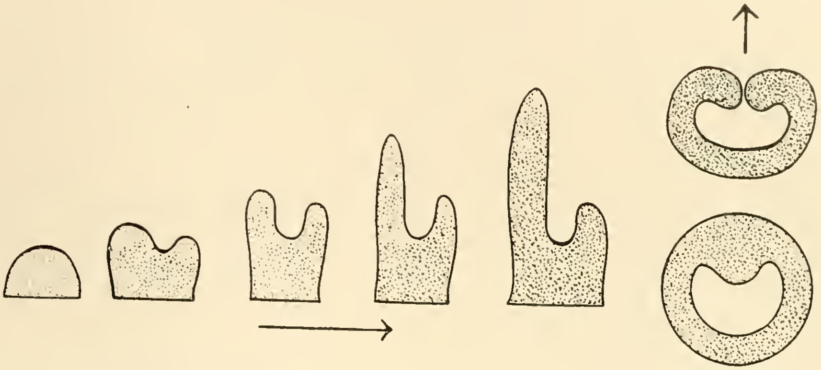


FIG. 1183.—Peltate development of the carpel rudiment. Arrows indicate the direction of the floral axis. (*After Goebel.*) Theoretical.

The above represents the most characteristically peltate carpel-form, which is to be seen in some Ranunculaceae and Rosaceae. In other members of these families and indeed in the majority of free carpels, the development may be called semi-peltate. A peltate primordium is formed in the earliest stages, with dorsum and sill, but the latter remains relatively small and is sometimes fused to the receptacle tissue. The dorsum becomes concave, often hood-shaped, and its edges approach and subsequently coalesce above the top of the sill (Fig. 1184). The extent to which the sill grows

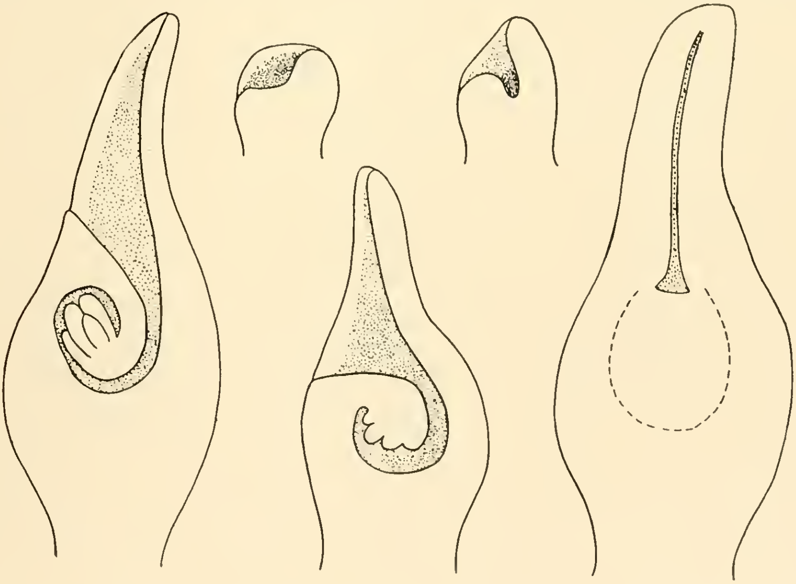


FIG. 1184.—Peltate development of the carpels in *Thalictrum*, showing the union of the margins of the dorsum above the top of the ovulate sill. (*After Troll.*)

seems, in these carpels, to determine the extent of their fertility, since the further up it extends itself, the shorter is the length of fertile carpel-margin left in the closed structure. Either the sill or the carpel-margins may bear the ovules, but not usually both.

Some of the lower Monocotyledons show a carpel development which is entirely non-peltate (*e.g.*, Butomaceae) (Fig. 1185). The carpel primordium, like that of the monocotyledonous foliage-leaf, is not a hump but a horseshoe and this shape is maintained throughout development, there being no adaxial sill (Fig. 1186). The margins only cohere when the carpel is almost fully formed, and even then not very firmly.

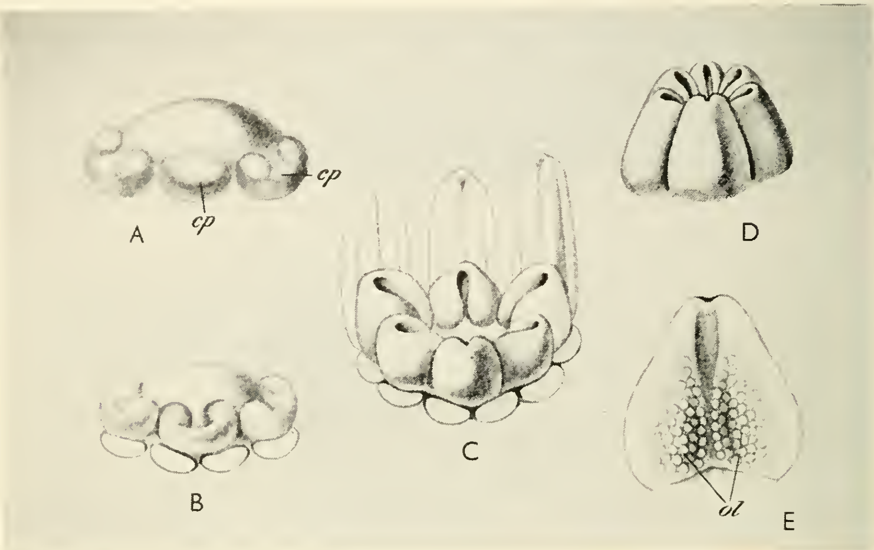


FIG. 1185.—*Butomus umbellatus*. Ontogeny of the flower. Showing non-peltate development. A, B, C and D, Successive stages of carpel development. E, Interior of carpel showing parietal distribution of ovules. (*After Payer*.)

Syncarpous ovaries may begin with a whorl of disconnected primordia which develop independently until lateral growth brings their margins into contact. From this point onwards growth becomes uniform all round the whorl so that a ring-like wall arises, crowned by the apices of the originally separate primordia (Fig. 1187). Occasionally, however, the development of each carpel proceeds individually, the lateral walls only cohering at a more advanced stage. The most general condition is that of complete cohesion of rudiments, from the beginning, so that the wall of the ovary arises and progresses as a ring, especially in paracarpous ovaries, the position of the joined carpellary margins being marked by internal folds in the ring. If the mature ovary is septate, these folds extend themselves centripetally and eventually unite at the centre, beginning from the base (where they are often in contact with the axis or with each other from an early stage) and progressing upwards. If, on the other hand, the ovary is paracarpous and

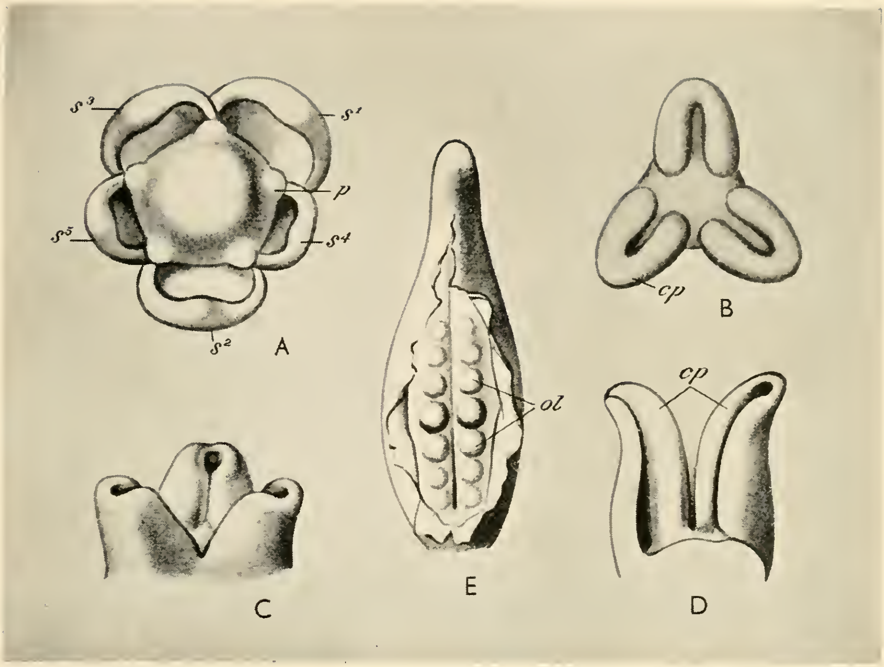


FIG. 1186.—*Helleborus foetidus.* Ontogeny of the flower. Non-peltate development. A, B, C and D, Stages in development of the carpel rudiments. E, Interior of carpel seen through the dorsum, with two marginal rows of ovules. (*After Payer.*) Lettering as in Fig. 1099.

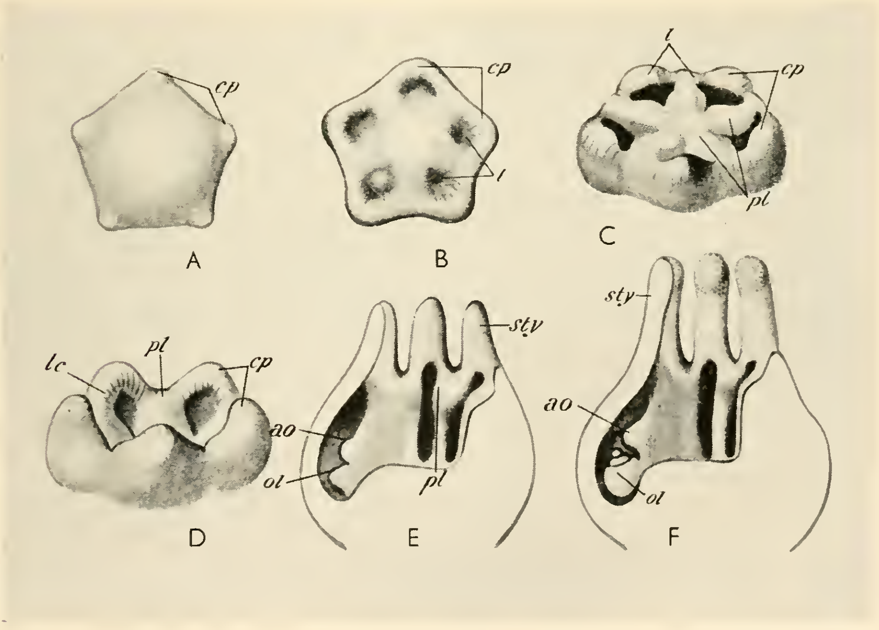


FIG. 1187.—*Linum perenne.* Ontogeny of the flower. Successive stages in development of the syncarpous ovary from independent rudiments which spread laterally and unite to form a ring wall. Lettering as in Fig. 1099 *sty*=style, *l* and *lc*=loculus, *ao*=abortive ovule. (*After Payer.*)

consequently non-septate, the folds do not extend but become directly transformed into placentae.

Where the receptacle has a particularly broad apex, as in Caryophyllaceae and Phytolaccaceae, the carpels may arise as a whorl of horseshoe-shaped loops around the periphery of the receptacle, to which their ventral margins are joined from the beginning, and the receptacle persists as the axis of the mature ovary, to which the placentae are fused.

The Nymphaeaceae afford particularly interesting examples of this arrangement. In *Cabomba* and *Nelumbium*, the carpels are free, but in the latter genus they become embedded in an obconical development of the receptacle, only the stigmas being left visible. In *Victoria* a single whorl of carpels is formed around the receptacle, leaving its apex free, which sticks up nakedly in the centre of the flower. The base of the receptacle is expanded into a cup, enclosing the carpels, which are fused to it by their dorsal walls. The divisions between the individual carpels are, however, clearly marked on their ventral surfaces. In *Nymphaea* and *Nuphar* the receptacular cup has closed in towards the axis, thus causing the ventral sides of the carpels to adhere to the apex of the receptacle, so that it now forms the axis of the gynoecium. The carpels in this apparently coenocarpous gynoecium of *Nymphaea* are not completely coherent, but are separated by narrow sinuses. In *Nuphar* these are absent and the ovary appears to be truly compound, but it differs from that of *Nymphaea* in being seemingly superior. That the outer wall of the ovary is, however, really receptacular is shown by two phenomena. About 20 per cent. of the stamens in *Nuphar*, and all the stamens in *Nymphaea*, arise from this outer wall, which is one indication of its receptacular character. The matter is rendered certain, however, by the behaviour of the fruit of *Nuphar*. It is detached at maturity and floats; the inner tissues of the ovary wall become highly turgescent and expand, causing the enclosing coat to split into lobes, which bend outwards, revealing the true carpels. The interstitial tissue between the carpels disintegrates and they separate as individuals. Despite their enclosure by the receptacular cup, they have never, in fact, lost their individuality.

All the carpels of the above family, with the exceptions of *Victoria* and *Euryale*, arise from peltate primordia; they are, in fact, pouch-like carpels, and they retain their pouch-like character throughout, having no suture and a stigmatic surface all round the lip of the pouch. This is uncommon, but is seen also in *Zannichellia* among the Helobiae, which has peltate carpels with peltate stigmas. In the majority of carpels which have peltate primordia, the dorsum extends much above the ventral portion and forms a conduplicate sac, whose margins join in the ventral line to form a suture and bear the stigmatic surfaces. Thus only the lower part of the carpel is truly pouch-like. This is the semi-peltate type already mentioned. In the earlier stages, however, there is a great measure of similarity between these peltate structures. The carpel of *Ceratophyllum*, for instance, closely resembles, in its early stages, that of *Nelumbium*, a matter of systematic interest in view of the disputed relationship of the former genus.

Just as some foliage leaves which have a pouch-zone at the base of the lamina do not retain the peltate form as they develop, so the semi-peltate carpels only show a true, unsutured pouch in their earlier, lower portions. Peltation in leaves is associated with a unifacial, *i.e.*, centric, structure in their petioles; similarly centric structure is characteristic of the gynophore stalks of peltate carpels.

The type of carpel with a peltate primordium and a marked ventral sill, such as those of many Ranunculaceae, is generally uniovulate, with the ovule borne medianly on the ventral sill, the dorsal portion of the carpel being sterile. Uniovulate carpels are exceptional in syncarpous ovaries and when they are pluriovulate it is the carpel margins which are fertile and extend almost the whole length of the carpel. The sill in such carpels is sterile and much reduced or even sunk in the tissue of the receptacle apex. Uniovulate peltate carpels do sometimes, nevertheless, compose syncarpous ovaries, notably in the Umbelliferae, where the tissue between the joined carpels originates as a combination of the ventral sills of the carpels, which extend upwards unitedly from the base during development and mature a single median ovule on each side.

It is evident from what has been said above that carpels are, in origin, of at least two kinds, those showing a peltate and those showing a folded or conduplicate mode of development. Theories of the morphological nature of the carpel should take cognizance of these differences and they should be remembered if one adopts any particular view. There is also the further possibility that the carpel may have been evolved along more than one line of descent from the immediate progenitors of the Angiosperms, despite the many other characters which seem to link them into a unitary group.

The **inferior ovary** is a structure about which much controversy has centred. To nineteenth-century botanists, working on the theory of the flower as a metamorphosed shoot, it seemed self-evident that epigyny had been derived from hypogyny and that perigyny was an intermediate condition. This presumed succession is exemplified within the limits of several distinct families, notably the Rosaceae and Saxifragaceae, while a number of families of very different affinities, *e.g.*, Onagraceae, Umbelliferae, Vacciniaceae and Orchidaceae, are characterized by predominant epigyny, which suggests that the condition has arisen independently in several lines of descent.

It was perhaps natural that the first view to be propounded about epigyny was that it was due to the well-known phenomenon of adnation, the carpels being supposedly enclosed by the coalescence of the outer floral parts among themselves and with the conjoined carpels. This theory orginated with A. P. de Candolle and was strongly supported by Van Tieghem. Towards the end of the century it lost ground to the " axial " theories. The cup in perigynous flowers seldom shows any external evidence of being a compound structure and the idea arose with Schleiden that it was a hollow axial upgrowth. In Schleiden's original view, the carpels as well as the other parts were upborne upon the margin of the cup; the carpels being reduced to little more than their stigmas, roofing in the cavity. An amplification of this theory regarded the carpellary placentae as extending downwards into the cavity or, in plurilocular inferior ovaries, as having remained in the form of an axial column in the cavity, while the dorsal parts of the carpel had been elevated by the upgrowth of the cup. This was the position maintained by Sachs. Its influence gave rise to much controversy regarding the nature of the placentae, as to whether they were of carpellary or axial nature in various cases.

The lack of any structural sign of compound nature, which it must be admitted is the case in most toral cups, is not conclusive against their origin by cohesion, since there are structures where cohesion must have taken place, where there is equally no sign of it observable. Such instances are the calycular cap which covers the bud in *Eupomatia*, later shed by circumscissile dehiscence, and the naked portion of the spadix in *Arum* which Diels has shown to be formed by the complete cohesion of flower rudiments, the individuality of which is entirely lost in a uniform surface.

There seems to be a strong case for adnation in *Doryanthes excelsa* (Amaryllidaceae), where the carpels arise on the floor of a slight depression in the receptacle and are not overgrown until a comparatively late stage in their development. In the floral cup which eventually surrounds them the stamen and perianth traces are separate from the carpel traces all the way down. There are no distinctively axial features in the cup. The carpels have their own epidermis and remain distinct. The degree of union is slight both between the carpels and with the cup, to which they become adnate.

We may pass over the theories which regarded the inferior ovary as an organ *sui generis*, that is to say without homologies, since they are involved with the view of the flower as an entirely novel structure, proposed by Grégoire, which we have dealt with earlier (see p. 1123). These views are related to the " acarpous " theory of McLean Thompson, which we shall speak of presently.

Another view of some antiquity, rivalling that of Schleiden, regarded the axial cup as having arisen around the gynoecium, which was enclosed by it, the carpels remaining intact but enclosed. The gynoecium, therefore, in this case, did not differ essentially from a superior gynoecium, and as in the latter case, there might, or might not, in different genera, be an extension of the axis upward in the centre of the carpellary whorl.

This theory is associated with the name of Celakovsky and von Goebel. The extent of enclosure of the carpels might be variable and while, in general, only the styles, if any, and the stigmas remain free, there are examples such as *Alstroemeria* and *Moraea* in which there is a substantial part of the top of the ovary left unenclosed. Of course, such variations might also be expected under the appendicular theory.

This theory eventually held the field and has only been challenged, in recent years, by the revival of the appendicular theory of de Candolle, by Eames.

Lastly, there is the theory advanced by McLean Thompson on the basis of ontogenetic evidence provided by members of the higher Monocotyledons. This has led him to the view that there are no carpels involved in the formation of an inferior ovary and that the invagination of the receptacular apex which gives rise to the loculi has a surface which is a continuous potential megasporangium. Continuous ovulation is, however, never achieved and ovulation occurs only on lines of nutritive advantage, which are considered to be the placental emergences.

From this theory of " acarpy " the author advances to a much wider generalization which might almost be called " ananthy " since he proposes to reduce the fertile organs of all flowers, both stamens and carpels, to the status of sporangiferous emergences. The flower becomes, in his eyes, only a specialized heterosporous strobilus, of which the lower part is sterilized and the upper part is potentially completely sporogenous, but in actuality is limited by physiological causes to the production of sporangia on localized emergences. Whether the strobilar axis develops as a cone or as a cup is immaterial and depends on whether growth is localized at the apex or is predominantly " toral ", that is, intercalary.

The word " torus " used by McLean Thompson and by many other writers on floral morphology would be better dropped, since it has been used in several senses (see p. 1129).

The revolutionary views of McLean Thompson have not, as yet, commended themselves widely to morphologists; for they are confronted by many contrary indications as well as the general coherency of plan which comparative morphology reveals. What is involved is not so much the abolition of the word " carpel ", since structures called by that name do exist as recognizable entities, but rather the abolition of the theoretical halo surrounding the structure, and its acceptance instead as *sui generis*, something without homologies and without a history. The abolition of the idea of the carpel can only with difficulty be limited to the inferior ovary, with which we are immediately concerned, since ontogeny and comparative morphology show that carpel-like structures are, at least in some cases, formed inside the supposed invagination of the receptacle which becomes the ovary in epigynous flowers (Fig. 1188). There are so many resemblances between the carpels in the hypogynous and epigynous forms within single groups, such as the Liliales, that logically the existence of carpels ought to be accepted in both, or denied in both. As regards the inferior ovary, however, McLean Thompson does claim that even the structures elsewhere known under the name of carpels do not exist but are simulated by axial emergences behaving as placentae. His position is that it is only in superior gynoecia that the emergences assume the form known as carpellary.

The idea of ring-like " toral " growth of the floral axis, as postulated in some of the above theories of epigyny, rests on little besides assumption. It is based upon the hypothesis that if the upward growth of the vegetative point be checked, the " growth energy " of the axis will find expression in lateral expansion, producing a ring-like emergence, which does not continue to expand laterally, but turns upward to form a cup enclosing the

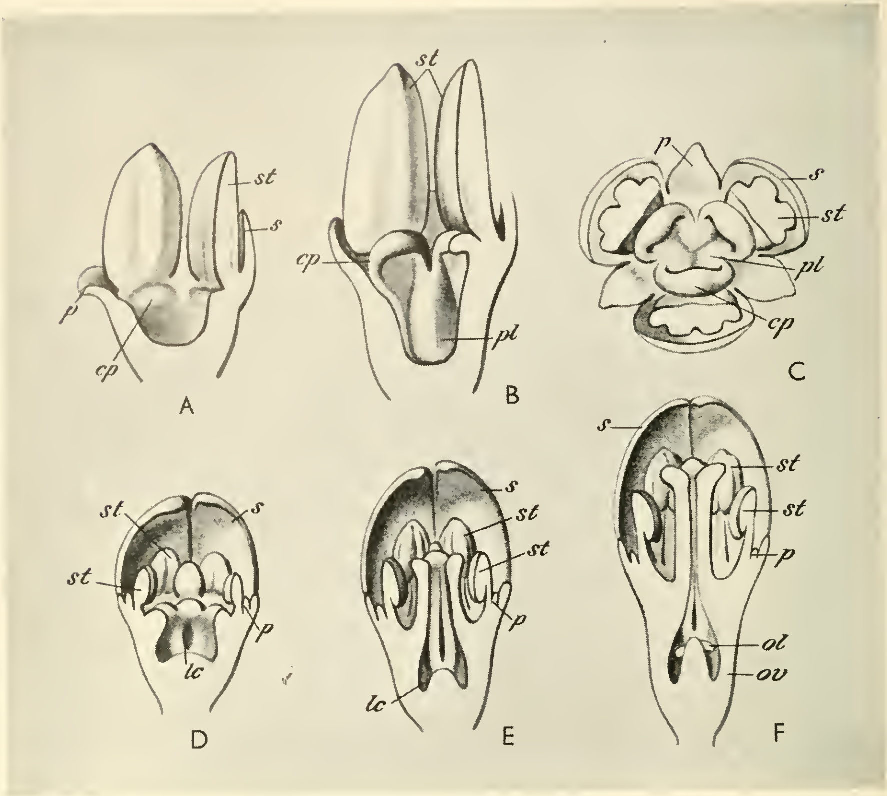


Fig. 1188.—Ontogeny of inferior ovaries. Carpels adnate to inner surface of floral cup. A, B and C, *Gladiolus communis*. D, E and F, *Gaura biennis*. (*After Payer.*)

original apex and the carpels (or at least the ovules, if we believe that no carpels are formed) in inferior ovaries, and bearing upward with it some or all of the outer whorls of floral parts. There is much in this that is gratuitous. It has no analogy among vegetative axes, nor does it accord with what is known of the processes of growth regulation. The idea of emergences generally, and not in this particular case only, runs contrary to the experience of comparative morphology, which supports the belief that no organ is wholly new but is produced by the modification of pre-existing structures through a relatively limited number of processes, which recur in innumerable examples. Such are: subdivision, cohesion, concrescence, adnation, changes of symmetry, reduction, suppression, etc.

If we subscribe to this doctrine, which is very broadly based in nature, we may call it the principle of precedence. It would at least lead us to doubt the production of a new cupped formation of axial tissue emerging from an otherwise terete axis, and not associated with the tangential cohesion of existing appendages.

To deny the possibility of such a structure on the basis of a general theory such as that we have just suggested would be, however, to beg the question. At most it can be said to place on those who believe in such an emergence the onus of proving that it occurs. Fortunately, there are other and more direct reasons for doubting it. First let us make clear that basal or intercalary growth of appendages certainly does occur, and that the basal growth of a whorl of coherent appendages will produce a cuplike or tubular structure, as we have already pointed out in speaking of the perianth. Furthermore, such a cup or tube may closely simulate a hollowed axis, though it is morphologically a very different thing. To distinguish the two structures may not always be possible, and it will, in any given case, involve the application of all three methods of morphological inquiry, namely, comparison, anatomy and ontogeny. Of these, ontogeny, although the most direct, is perhaps the least trustworthy, owing to the difficulties of the interpretation of embryonic appearances, but where it does give positive evidence it can be decisive. There may well be a residuum of cases in which no available method will distinguish the two alternative hypotheses, but we can generally establish a strong probability.

The appendicular theory rests chiefly on anatomical evidence, about the value of which opinions differ. Its negative findings are perhaps of little consequence, but where, for example, the vascular structure offers positive evidence of morphological changes, it is not to be lightly set aside, unless we are prepared to believe that the course of vasculation is quite fortuitous or that it can be easily and radically changed by physiological circumstances. Against such assumptions stands the whole of stelar history, to be seen in fossil and recent plants, which shows a surprising degree of conservatism in vascular structure and that changes have come about by slow modifications of pre-existing structures, often lagging behind organismal changes, rather than by wholesale rearrangements, abolitions and fresh creations.

Van Tieghem based his view of epigyny on the departure of the trace-bundles from the axial stele. He maintained that the position of departure marked the true level of insertion of the appendages, which might be either below or above their points of apparent insertion. If this were not so, he argued, then the corolla tube of the Primrose must be regarded as axial in the same way as the supposed axial cup of the inferior ovary. In some flowers, as in Compositae, the separate trace-bundles of the floral appendages can be followed throughout the ovarian wall and here there can be little doubt of its appendicular character. In other flowers, as in Umbelliferae, the vascular strands in the ovary wall divide into the individual appendage traces only near the top of the ovary. The appendicular interpretation of the latter condition would be doubtful were it not that Eames and his co-workers have shown that all intermediate stages can be found, even within the limits of a single genus, *e.g.*, *Vaccinium*, thus demonstrating that there is no essential difference between the extremes, and that the fusion of the appendicular traces in the ovary wall does not make them any the less trace-bundles. We may recollect the parallel case of the fusion of bundles in epipetalous stamens. On the other hand recurved bundles, which turn downwards from the system in the outer tissues to supply the carpels, have been held to show that in such cases the ovarian wall is indeed receptacular up to the level at which these bundles become separated, even if it is appendicular above.

We have no space to follow all the involved arguments which have marked this controversy during at least a hundred years. As it implies the question of the morphological nature of carpels, placentae and ovules, it is obviously a matter of some importance and every kind of evidence has been looked for and usually found. We can only say that weight of evidence, even in the classic case of the Apple, seems to be on the side of the view that the enclosure of the gynoecium in most inferior ovaries is brought about by the concrescence of the lower portions of the outer floral members to a greater or less degree, and their adnation to the ovary wall. There is even the surprising condition in the Dipsacaceae, where in some species the gynoecium is enclosed by a floral tube which is not united to it except at the very top and where the appendicular condition is scarcely open to doubt. The analogous case of *Furcraea* has been cited on p. 1136. We may also cite Velenovsky's famous *Epilobium* anomaly, already described on p. 1135. Velenovsky noted that the free surface of the abnormal superior ovary bore hairs exactly like that on the outer surface of the normal inferior ovary from which he inferred that the external tissues in both cases were morphologically identical.

It would be a mistake to assert that circumferential growth of the receptacle never occurs. One can say, however, that in most of the cases where it has been alleged, the alternative explanation of cohesional growth of the floral appendages is possible and in some instances it may be regarded as proved. No case in which this explanation is ruled out has yet been produced. The evidence in favour of receptacular hollowing is weaker than would be supposed from the frequency with which it is invoked.

To sum up, we may conclude that the receptacle may have played a relatively minor part in the production of inferior ovaries. Although thus leaning towards a not too exclusive acceptance of the appendicular theory, we must recognize that the question remains one for interested consideration.

The mode of attachment of the ovules within the ovary, generally called their **placentation**, is a matter to which considerable importance is attached in the classification of Angiosperms. The comparative study of the structure of the placentae themselves apart from their vascular supply has, on the other hand, attracted little attention.

Placentation seems to be a character of some constancy and it is very often uniform throughout whole families, thus being useful in classification. If the carpel is regarded, formally, as a phyllome, then we may say that the ovules are borne either on its margins or on its adaxial side. Only one case of definitely abaxial ovules has been recorded, in *Doryanthes* (Amaryllidaceae) where they are situated on the abaxial sides of the infolded margins. The exact position in many other cases is obscure. When the carpel or carpels develop singly they usually show the form of an infolded leaf with its margins united adaxially (or ventrally) and it is common to find a single row of ovules on each of these margins. Much less commonly one or more rows of ovules may lie along the dorsal side, attached to what would be regarded as the mid-rib of the carpellary " leaf ". Two other modes of attachment are to be found in single carpels, namely basal placentation, where one or, more seldom, several ovules are attached to the bottom of the loculus, or pendulous placentation, where the ovule or ovules appear to hang from the top of the loculus. A fifth method of attachment is also possible, in which the placenta appears to cover the whole inner surface of the carpel, and ovules are distributed all over it, or, when only a few are formed, are scattered irregularly. These five modes of placentation comprise between them all the possibilities and they are all to be found in single carpels. The very various placentations found in compound ovaries are all derivable from them, or in other words, the carpel as a unit of a compound ovary does not differ from a free carpel in its modes of ovulation, except in one respect, that where carpel margins have become fused to those of neighbouring carpels in a compound ovary, the number of ovules which they bear may be greatly increased, perhaps as a result of more effective nutrition.

Basal placentation has always attracted theorizers because ovules in this position, particularly where there is a single carpel, often appear to be direct upgrowths from the floral axis and thus in a different category from those which are borne on the carpels. At a time when ovules were held to be the equivalent of buds it was not permissible to regard them as borne on carpellary " leaves ", because it was a dogma of the older morphology that leaves cannot produce buds. Therefore, it was argued, all ovules must be of axial origin and, beginning with the simple and apparently obvious case of the basal ovule, placentae of axial nature were supposed to have grown up and attached themselves variously to the carpels. When eventually it was demonstrated that ovules were not buds but sporangia, opinion swung in the other direction; the carpels were interpreted as sporophylls and the attempt was made to show a foliar origin for all ovules. Under this interpretation the basal ovule was an outstanding difficulty. Celakovsky endeavoured to get over it by comparing the carpel to an ascidial leaf, growing from a hypothetical *Sohle*, a sort of basal plinth which, although united to the floral axis, was really a part of the carpel itself. From this grew the idea that carpels could be compared to peltate leaves, which, as we have seen above (p. 1215), does in fact appear to hold good in many cases, though not in all. Goebel and Troll have both supported this view and the former retains the term *Sohle* for the adaxial lip of the peltate carpel, which is often so little developed, in comparison with the dorsum, that it scarcely rises above the base. Ovules (usually single) borne on it may appear, in the mature carpel, to be basal, the dorsal portion of the carpel being sterile and its margins only infolded above the level of the adaxial *Sohle* or " sill " as we have translated it, following Goebel's view (see footnote, p. 1214). Troll, indeed, has pointed out that the facts of development in such cases oblige us to recognize another mode of placentation, namely median, applied to ovules borne singly on the lip of the sill, although he rejects Goebel's use of Celakovsky's term as being in a different sense from that in which the latter author used it. It is not clear, however, whether all solitary basal or pendulous ovules are, in fact, also median in Troll's sense.

These arguments and distinctions may strike the modern student as savouring of scholasticism, but they sprang from a deep conviction of the unity of the Angiosperms and a belief that there must be a fundamental uniformity in their reproductive structures, however varied its expression might be. So multiform are the Angiosperms that any theory of uniformity is certain to encounter difficulties, and suggestions of a diphyletic or polyphyletic origin of the group have frequently been made.

It might be supposed that the former axial theory of ovulation would have died out with the view that the ovule is a bud, but Sahni, from his studies of Gymnospermae, came to the conclusion that there were two evolutionary series among them; those in which the sporangia were axially borne and those in which they were borne on sporophylls. These he termed Stachyospermae and Phyllospermae respectively. This called in question the view that all sporangia were associated with foliar organs. Recently Lam has generalized this view and proposes to divide all cormophytic plants into stachyosporous and phyllosporous series. Basing himself on Zimmermann's telome theory, he holds that the stachyosporous condition, in which sporangia are borne on axial structures, is the original condition and that the phyllosporous condition, in which sporangia are borne on a leaf which has developed in one way or another from telomes, is relatively advanced. He has extended his theory to include the Angiosperms and maintains that certain orders, *e.g.*, Arales, Polygonales, Fagales, Urticales and Euphorbiales, are stachyosporous, while others, *e.g.*, Ranales, Rosales, Guttiferales and Liliales, are phyllosporous. The distinction is, in his opinion, an ancient one, traceable to the beginnings of the Angiospermae in the late Jurassic. It cuts across the differences between Dicotyledons and Monocotyledons and implies at least two separate lines of ancestry from very early times.

When we come to consider placentation in coenocarpous ovaries, we find that it is divisible into two main types, called **axile** and **parietal** respectively. Syncarpous ovaries are divided into loculi separated by septa, the latter being regarded as the infolded side walls of the component carpels, more or less completely fused to those of the neighbouring carpels on each side, the number of loculi corresponding to the number of carpels; except where " false septa " are developed, as in *Linum*, Labiatae, etc., whereby the loculi are subdivided and their number apparently increased. There may even be horizontal septa secondarily formed, which produce two-storied loculi.

The carpel walls thus meet in the middle of the ovary, where they are generally united together. The ovuliferous margins are, however, usually recurved into the cavity of the loculus, where they develop unitedly or separately into placentae, which may sometimes (Solanaceae, Scrophulariaceae) grow to occupy a large part of the loculus and bear very numerous ovules. These placentae appear to arise from the central, fused tissues of the ovary, hence they are called axile. Only in a minority of cases is any genuinely axial tissue included in the ovary axis. Some flower-rudiments have a broad top to the receptacle, which is not all used up in carpel formation, and in such flowers the apex of the receptacle may rise between the carpels and form part of the ovary axis. Examples are: Nymphaeaceae, Alsineae (Caryophyllaceae), *Nigella*, *Oxalis*, etc. The vascular bundles in the recurved placental margins of the carpels show, as would be expected, a reversed orientation, with the xylem outward. They are thus distinguishable even when they are embedded in the united tissues at the centre of the ovary. Where the receptacle tissue forms a core, so to speak, in the ovary axis, it may sometimes be distinguished by its vascular bundles with normal orientation. This depends, however, on its extent, for the vasculation may be reduced to a single concentric strand, or even be absent altogether when there is little axial tissue. In the great majority of cases, therefore, the placentation in truly syncarpous ovaries is based upon marginal placentation in the individual carpels. The degree of union between the carpels varies considerably. In many genera there is no actual fusion of tissues at the centre and the placental margins of the carpels are free and easily recognizable (*e.g.*, *Campanula*, *Erythraea*), although the lateral walls are completely united in the septa.

The parietal position of the ovules in truly syncarpous, septate ovaries is rare, just as the dorsal attachment of ovules in single carpels is rare. Examples are found in the Aizoaceae and in *Punica granatum* (Pomegranate) but they are subject to doubt as possibly produced by secondary shifting of the placentae. In *Mesembryanthemum* (Aizoaceae) the early stages of the carpel show axile attachment of the ovules, which are apparently later carried outwards and upwards on to the outer walls by intercalary growth. *Punica* is also peculiar, for here there are two whorls of carpels, the inner whorl of three having axile placentation, while the outer whorl of five, which are eventually raised above the inner whorl by intercalary growth, has parietal placentation.

Some examples of uniovulate loculi occur and it is commonly found in such ovaries that the single ovule springs either from the base or from the top of the ovary axis. There is always the possibility in such cases that we may have to do with ovules which are medianly placed on the sill of a peltate carpel, rather than with the reduction of fertility in true marginal placentae. There is, however, in some syncarpous ovaries a tendency for one or more of such uniovulate loculi to become abortive, as we see in *Viburnum*, *Valerianella* and *Stilbe*, which may be looked upon as indicating reduced fertility, at least in some cases.

Parietal placentation on the septa, which appears to be quite distinct from marginal placentation, occurs in *Cytinus*, a member of the Rafflesiaceae, which is found in southern Europe. Numerous branching placentae are scattered over the septa and bear a great number of small ovules. (See Fig. 1579.)

The case of *Butomus*, where ovulation is distributed all over the lateral walls of the carpels, which correspond to septa, but not on the outer, dorsal walls, has already been mentioned, but here we are really dealing with practically free carpels, slightly coherent only at their bases. In the related genus *Hydrocharis*, however, the ovary is inferior and syncarpous and although ovulation is much reduced as compared with *Butomus*, the same scattered, parietal placentation exists.

When we come to deal with paracarpous gynoecia we find that placentation may be either marginal or truly parietal. Many examples of unilocular paracarpous ovaries have placentae described as parietal which are really marginal, the infolded margins of the carpels being only slightly, if at all, developed. All intermediate stages can be found between completely syncarpous ovaries and those in which the lateral carpel walls are absent, the intermediates having all degrees of imperfect septation. Such incomplete carpels are in fact open, the margins of each individual carpel being separated and never united. In this respect they might be considered more primitive than closed carpels, but it is unlikely that the condition has any phylogenetic significance. The extreme instance of the open condition is found in *Reseda*, which is in no other way primitive, the whole paracarpous ovary remaining open at the top. The ontogeny of paracarpous ovaries shows that the receptacular apex is broad and that the carpel rudiments arise on its flanks, leaving a central area of the receptacle which is not absorbed into the carpel structure, as usually happens in the more closely knit syncarpous ovaries. Yet it is not unusual to find septa at the base, even in ovaries which are typically paracarpous in their upper portions, making contact with each other by means of the residual apex tissue and thus forming a plurilocular lower portion, while diminishing at a higher level so that they no longer make contact and may be no more than ridges on the inside of the ovary wall. Some ovaries of this kind may also (Capparidaceae) possess a septate upper portion, where the septa again make contact with each other, due, in part, to the narrowing of the whole ovary towards its summit.

Truly parietal, that is dorsal, attachment of the ovules occurs in paracarpous ovaries more frequently than in syncarpous types. A conspicuous case is *Begonia*, where the three angles of the ovary have been clearly shown to be the joined carpel margins, with the ovules on dorsal placentae. The genera of Lardizabalaceae afford other examples. The carpels of *Orobanche* have each two such parietal placentae. This decidedly unusual circumstance might be interpreted as a modified form of marginal placentation, the placentae having been secondarily displaced from the morphological margins, or else false margins have extended beyond the original fertile margins, in a manner analogous to the false indusium at the leaf margins in *Pteridium*. Such interpretations may apply here but they can scarcely apply in *Gentiana*. Assuming the orthodox view that there are two carpels in this genus, there are three or four distinct series of ovules attached to each carpel, each series being supplied by branches from corresponding vascular bundles in the carpel wall. This seems to be evidence for the occurrence of multiple placentae, though such cases are rare.

The gynoecium of *Papaver* has several striking peculiarities, which have been the subject of much discussion. The ovary is paracarpous, but, as is often the case in other paracarpous genera, the carpels have closed loculi at the base and apex. The partial septa which occupy the main part of the ovary are really placentae, each being a duplex structure arising from the lines of marginal fusion of the carpels. They thus equal the carpels in number. As the crown of the ovary is approached the carpels separate by the splitting of each placenta along its median plane. The surfaces thus freed become stigmatic, so that each stigmatic ray on the crown of the ovary is composed of the adjacent faces of two placentae and shows its double nature clearly.

The **commissures** where the carpel margins are joined, in paracarpous ovaries, may be more or less distinctly marked by grooves. The marginal vascular bundles may remain separate, forming a pair at each commissure, or they may be united, as are the marginal bundles of the united petals in some gamopetalous corollas.

The vascular bundles which supply the placentae, whether marginal or otherwise, are often markedly larger than the dorsal bundle, which has sometimes been urged against the foliar interpretation of the carpel, since the dorsal bundle would represent the mid-rib of the carpel leaf and this is normally the principal bundle in a foliage leaf. The enlargement of marginal bundles where these are connected to the placentae follows an obvious physiological necessity and carries no morphological weight. Moreover Arber has shown that a similar reversal of importance between mid-rib and lateral bundles may occur even in foliage leaves.

Finally we must refer to the peculiar type known as **free-central placentation**, in which the ovules are distributed over the surface of a dome or column of tissue which rises up from the base of the loculus in some paracarpous ovaries. It is a constant feature of the Primulaceae and of many Caryophyllaceae and a few other families such as Lentibulariaceae and Santalaceae, as well as certain genera such as *Dionaea* (Droseraceae). Formerly this was attributed to an upgrowth of the receptacle on which the (axial) ovules were borne, in contradistinction from the carpel-borne ovules of the majority of genera. There seems good reason to believe that the axis does sometimes take part in the formation of these placentae, but that if present, it forms only the central core and is surrounded by the adnate adaxial portions of the carpels, on which the ovules are formed. It is probably a reduced condition, since in the Silenoideae (Caryophyllaceae), the free state is only reached ontogenetically by the detachment of the placental column from the carpel walls to which it is originally joined by septa. In *Melandrium dioicum* the ovary remains septate at the base, but the placenta is free above and, although originally joined to the top of the ovary, breaks away at maturity. The presence of an axial core is shown not only by the vasculation in some cases, but in the above species by the fact that in the male flowers an axial column rises in the centre of the flower, though no carpels are formed on it. In *Osyris alba* (Santalaceae) there is only one placental bundle, but it is formed by the fusion of the three median, ventral carpel traces, which is fairly good evidence that the carpels do take part in forming the free placenta, with or without an axial core, and that the carpels are of the peltate type.

The **style** is a columnar structure arising from the ovary and bearing the **stigma**, which is a secretory area on which pollen grains are deposited and where they germinate (Fig. 1189). Although the stigma has a distinctive name, it is not always a distinct organ and cannot be properly considered apart from the style, of which it may be only a specialized area, or, in the absence of a style, an area of the ovary wall itself.

The style is the product of intercalary growth and is therefore a secon-

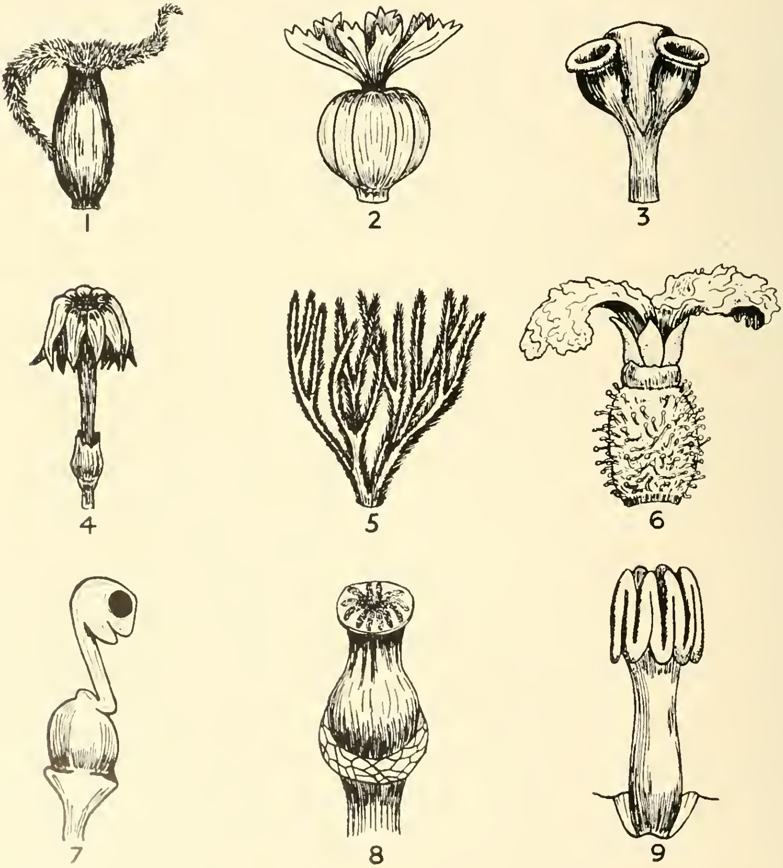


FIG. 1189.—A selection of various types of stigmas. (1) *Celtis*. (2) *Empetrum*. (3) *Burmannia*. (4) *Hura*. (5) *Begonia*. (6) *Juglans*. (7) *Viola*. (8) *Nuphar*. (9) *Opuntia*. (*From Le Maout and Decaisne.*)

dary development in the ontogeny of the flower. Considered functionally, its value lies in placing the stigma in the position where it will be most effective in pollination and its existence and the amount of its development seem to depend on this need. Thus, we generally find that there is little, if any, stylar growth in open, actinomorphic flowers with simple pollination mechanisms and that its development is greatest in sympetalous and especially in zygomorphic flowers. Its function may, indeed, be taken over by other parts, as for example by the elongated ovary itself or by the development of an axial gynophore, which may raise the stigma to an appropriate level without the intervention of a style. Alternatively, the stigma itself can become elongated so that it replaces the style, though it is a matter of words only whether one describes such elongated structures as style-less stigmas or as styles which are stigmatiferous throughout their length. They are sometimes distinguished as **stylodia** and are to be found in their highest development in wind-pollinated flowers.

Let us consider first the case of the single, free carpel. In many, perhaps in the majority, the suture runs up to the carpel apex and both the margins are either wholly or partly stigmatiferous. The stigmas may be united into a single structure or remain divided into two by the carpel suture, depending upon the degree of union obtaining between the carpel margins. The stigma therefore, even when it appears unitary, is of double origin. Robert Brown believed this to be true of all stigmas, but although widespread, the condition is not universal. In the alternative case the carpel suture does not extend to the apex, the carpel primordium terminating in a hood, and it is this structure, more or less extended into a solid column, or a tube if the loculus is involved in the extension, which bears the stigma terminally. As the hood belongs to the dorsum of the carpel, such stigmas may be called dorsal, as opposed to the ventral stigmas which originate from the carpel margins and in which the dorsum may play no part, as shown by the absence of the dorsal vascular bundle. The dorsal stigma is, moreover, a single structure from the beginning. We may say that in the second case a style has been formed, and none in the first case.

Not that this is the only way in which a dorsal stigma may be formed. In *Helleborus*, for example, we can see transitions between ventral and dorsal conditions. Here the ventral suture runs right up to the carpel apex. The dorsum is elongated into a style and the suture forms a groove along it, while the stigmatic surface in different species may be produced either on the edges of the groove (the ventral condition), or may extend on to the dorsal region and finally become localized on the dorsally produced style, where it usually forms a single structure. In *Drimys* (sect. *Tasmannia*) (Fig. 1190), where ventral stigmas are primitive, the carpel margins are fully stigmatic in some species, while in others the stigma is confined to a small crest near the apex. In the related genus *Zygogynum* the dorsum remains short and the ventral portion overgrows it, carrying the stigmatic crest over to the dorsal side, though it is not of dorsal origin. The dorsal stigma may therefore be either primary or secondary, according to the type of carpel which produces it. It is probable, nevertheless, that the ventral condition is the primitive one in Angiosperms, as it is shown by most of the " primitive families " in the group, such as Ranunculaceae, Butomaceae, Alismaceae and especially by the Winteraceae and some of the Magnoliaceae, as we shall see below. Rare exceptions to these general conditions do occur, in the case of fully peltate pouch-carpels, such as those of *Chloranthus* and other Piperaceae, where there are neither ventral nor dorsal sides, nor indeed any suture, but there is only a sessile stigmatic area at the apex. Peltate stigmas, on the other hand, where they are formed at the end of a true style (*e.g.*, *Rheum*), are not necessarily an indication of peltate carpel structure, but do not differ fundamentally from the globose or knob-like terminal stigmas, which are quite common.

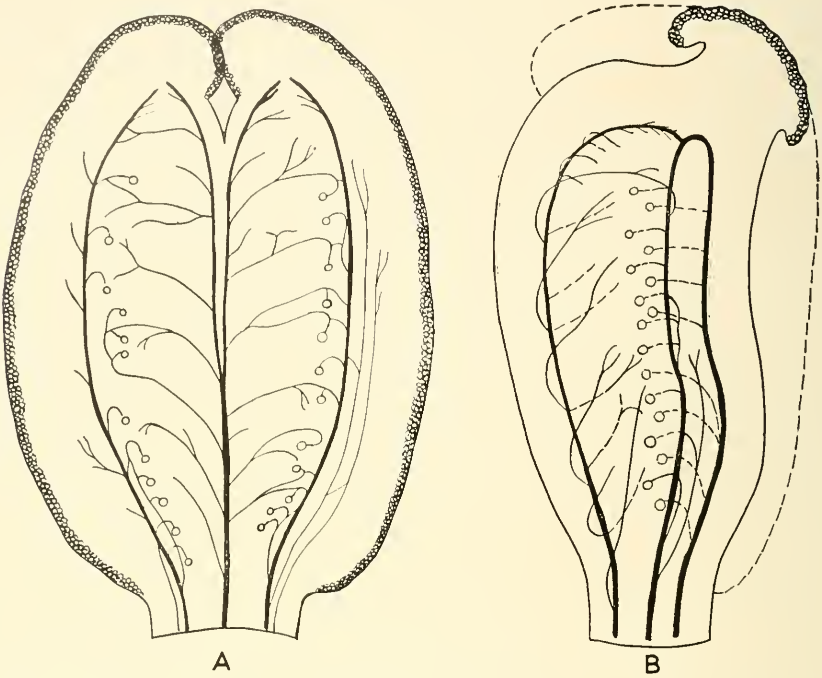


FIG. 1190.—Carpels of *Drimys*. A, Sub-gen. *Tasmannia*, carpel opened showing palmate three-veined vasculation and margins entirely stigmatiferous. B, Sub-gen. *Wintera*. Side view showing restricted stigma. Dotted line shows comparative length of stigma in *Tasmannia*. (*After Bailey and Nast.*)

The two modes of formation of the dorsal stigma and its supporting style, which we have detailed above, correspond in fact, and perhaps in origin, to the two types distinguished by Hunt on the basis of the theory, put forward by Eames, of the origin of the carpel from a palmately three-lobed structure, originally a dichotomous syntelome. Hunt distinguishes first, stigmas which are formed from the middle (dorsal) lobe only, our first dorsal type, which contain only one vascular bundle, and secondly those which are formed by the approximation of all three lobes and contain three bundles. The latter corresponds to our second dorsal type in which the suture continues as a groove along the style, which therefore contains the carpel margins and their vascular bundles, as well as the dorsum. This type is illustrated by the instance of *Helleborus* which we have quoted above. Lobing or division of the stigma where it occurs is generally associated with this compound origin. Whether one accepts the evolutionary thesis of Eames or not, the two types exist among living plants and show that solid and grooved or hollowed styles, unitary or compound stigmas have distinct origins and history.

We may briefly recapitulate the foregoing argument thus: Stigmas may be either purely ventral, when only the carpel margins are concerned, or purely dorsal, when they are formed only at the apex of the carpel; or secondarily dorsal, when both margins and apex are associated in the style, but the stigma is confined to the apex. The last condition may be developed, through intermediary stages, from the first. Styles are usually slender organs but in some Euphorbiaceae (*e.g.*, *Astrococcus*) they are fantastically enlarged and thickened and the ovaries are hidden beneath them, the group of styles looking like a whorl of carpels.

When we turn to consider coenocarpous gynoecia we see that the styles may be either free or may share the union of the ovaries to a greater or lesser degree. Where the styles are united, the stigmas may be also united, or may remain free, corresponding usually in number to the united carpels, though sometimes branched or variously lobed. The organ formed by the combined styles is, of course, not the same thing morphologically as a simple style and the use of the same name can be a source of confusion. Whatever name we apply to the compound structure, it is manifestly right that the word " style " should continue to be applied to the primary object of that nature, namely, the style of the single, free carpel.

Compound styles may be either solid or hollow. If the former, there is almost always one or more strands of conducting tissue leading from the stigma downwards to the placentae, forming a path for the penetration of the pollen tubes. If the compound style is hollow the canal is lined with a secretory layer of **conducting tissue** and this is the path which the pollen tubes follow. One cannot say definitely which condition is the primary one. Schleiden believed that all compound styles were originally hollow, but that the hollow became filled with conducting tissue. This is true of many cases, notably of *Anagallis*. Joshi on the other hand claims that in solid styles the conducting tissue is a continuation upwards of the ventral (marginal) bundles of the ovary wall and concludes that primitively the pollen tubes followed the course of these bundles and their placental branches, towards the ovules. Generally the two bundles, or the conducting strands arising from them, unite upwards, so that there is a single axial strand in the style. The canal of the hollow style is supposed by him to have originated from this axial strand.

The conducting tissue itself is generally composed of rather small thick-walled cells, without intercellular spaces, and it produces the sugars which both guide the pollen tubes chemotropically and nourish them as they grow. The cells are sometimes elongated longitudinally to the style, but not often. The thick walls are soft and in many cases become gelatinized, the cells then appearing to be isolated in a colloidal matrix. The term conducting tissue is however extended to those cases in hollow styles in which it consists only of a modified epidermis or of an epidermis and several subjacent layers. All the cells have dense, granular protoplasm and those on the surface become papillose and closely resemble the cells of a stigma. In free carpels superficial conducting layers line the carpel margins and the stylar groove, when these are stigmatiferous, and extend inwards through the line of the suture to the placentae.

Conducting tissue strands do not always follow a direct course. For example, in some Rosaceae with laterally attached styles, the conducting strand is continued below the point of attachment of the style and it has been observed that pollen tubes continue their growth downwards to the end of the strand and then turn upwards towards the level of the ovule. In some families the top of the expanded stigma is not functional, and the receptive areas are at, or below, the margin of the stigma cap. Such is the case in Asclepiadaceae, Apocynaceae, many Saxifragaceae and in *Sarracenia* and *Berberis*. How this may have come about does not immediately concern us, but it is significant that in many of these styles the conducting strand or its branches are sharply flexed below the apex, which is now passive, and bend outwards and downwards towards the active stigmatic surfaces.

A curious downward development of the conducting strand, from the base of the style into the ovary loculus, is found in Plumbaginaceae, in almost all Portulacaceae, in *Euphorbia*, *Ricinus* and in Phytolaccaceae. The majority of these examples have uniovulate loculi and the conducting tissue enlarges in the loculus into a brightly coloured plug which covers the micropyle of the ovule and is called an **obturator** (Fig. 1191). Against it the nucellus sometimes grows, into intimate contact. The name is a bad one, for, so far from blocking the micropyle, the obturator acts as a bridge for the pollen tubes from the base of the style to the ovule.

Styles as we have described them are terminal or dorsal outgrowths, but there exist styles, called **gynobasic**, which arise from the base, or at least from near the base of the carpel and on the ventral side. The Labiatae and the Boraginaceae possess this character almost uniformly and it occurs sporadically in many other families, such as Ranunculaceae, Rosaceae, Celastraceae and Phytolaccaceae (Fig. 1192). Ontogeny shows that we have here a specialized type of development of peltate carpels. In the earliest stages of the rudiment the single ovule stands on the adaxial carpel sill, not covered by the dorsum, which is at first quite small. Presently, however, the dorsum begins to grow rapidly, developing a hood, from the margin of which arises a vertical style. The hood grows over and encloses the ovule, and its margin, bearing the style, fuses with the placenta. In this way the point of origin of the style is carried over and downwards onto the

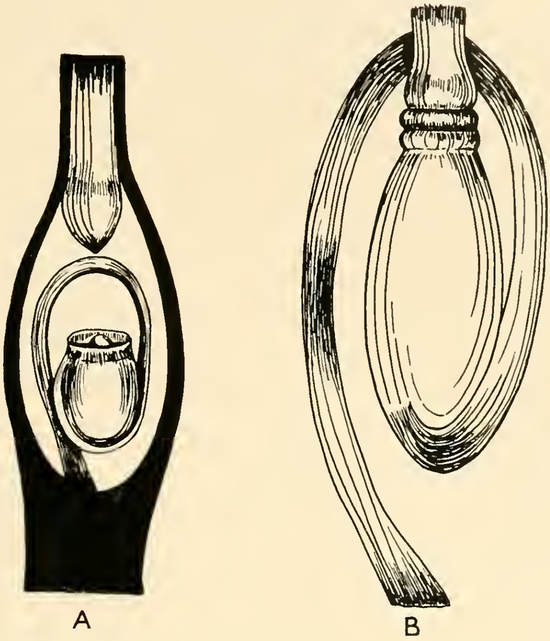


Fig. 1191.—Development of obturator in *Statice*. A, Section of ovary showing downward growth of obturator towards the ovule. B, Later stage, obturator in contact with micropyle. (*After Le Maout and Decaisne*.)

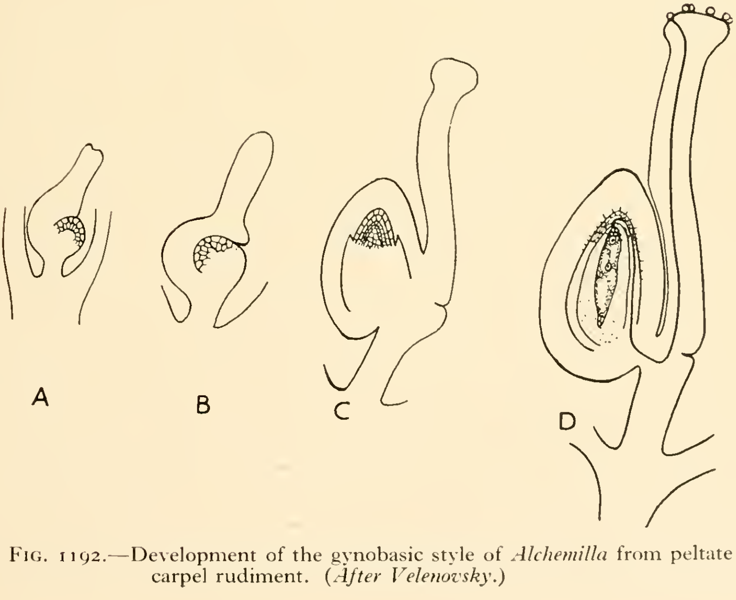


Fig. 1192.—Development of the gynobasic style of *Alchemilla* from peltate carpel rudiment. (*After Velenovsky*.)

adaxial side of the carpel, from which, at maturity, it appears to arise. The appearance may be accentuated by subsequent upward swelling of the dorsum as the ovule develops. In the bicarpellary gynoecia of Labiatae and Boraginaceae the two styles unite secondarily on reaching the gynobasic position, only the stigmas remaining free, though in other cases (*e.g.*, *Dictamnus*, *Nolana*) the union may be no more than a close adhesion. The united styles stand over the axis of the receptacle and look like a direct continuation of it. The whole process is only an exaggeration of what commonly occurs in the development of peltate carpels, for example in Umbelliferae, where, however, the adaxial sill grows up to meet the dorsum, so that the style remains at, or near, the carpel apex.

The receptive surfaces of stigmas are generally papillose or covered with short, unicellular hairs from which a mucous fluid, containing sugars, is excreted when the flower is ready for pollination.

The period of excretion may be quite short and the time during which pollination is possible is correspondingly limited. Absence of excretion except at the appropriate time is one of the most general safeguards against self-pollination in hermaphrodite flowers. The fluid serves the double purpose of retaining pollen grains and facilitating their germination. The surface of the stigma is morphologically the termination of the conducting tissue, with which it is continuous, and has similar characteristics. The stigmas of wind-pollinated flowers have much longer hairs than those of insect-pollinated flowers and these hairs are often multicellular. They act mechanically as pollen-collectors and produce little or no excretion.

Hairs of another sort are produced on the styles or stigmas of many plants as a sweeping apparatus or collector of pollen from the anthers of the same flower. Sweeping hairs around and below the stigma are well known in many Papilionaceae, *e.g.*, *Phaseolus*, *Galega*, *Cicer*. They sweep upwards pollen already shed from the anthers, when the keel, which encloses the style, is depressed. The stigmas of many Compositae have a mop of bristles which effectively sweep the pollen out of the tube of introrse anthers, through which the style grows upwards. An analogous action in some Lobeliaceae is performed by a saucer-shaped outgrowth around the style, below the stigmas. In many Campanulaceae the whole style is thickly covered with collecting hairs, against which the anthers dehisce introrsely. Both here and in some Compositae the sweeping upwards of the pollen may be assisted by contraction movements of the stamen filaments.

Pollen collection may also be assisted by expanded flaps around the stigma (Fig. 1193). The Goodeniaceae and Brunoniaceae have their stigmas surrounded by a pollen chamber enclosed by two such flaps, which are in part united at their edges. They are said to be due to an upgrowth of the floral disc, united to the style. Before the flower bud opens they are closed over the stigma, which led to the name " indusium " being applied to them, a reminiscence of the Hymenophyllaceae. The well-known shrub of tropical beaches, *Scaevola koenigii*, may be taken as an example of the operation of the pollen chamber. The chamber opens and receives pollen falling from the over-arching anthers. The style then elongates and the marginal hairs on the flaps sweep out the last of the pollen from the anthers. The flaps then close and the style bends downwards. In this position contact with the back of a visiting insect may squeeze out some pollen, but later the stigma itself elongates and pushes out the remainder of the pollen from the chamber, from which the stigma now protrudes. Finally the stigma itself becomes receptive and self-pollination is practically excluded. Analogous methods of pollen collecting are to be found in several other families, for instance, Proteaceae, Marantaceae and Polygalaceae, some portion of the style collecting pollen from the anthers and holding it for removal by insect visitors before the stigma ripens. A noteworthy feature of these specialized methods of pollen presentation is that they are in many cases associated with comparatively sparse production of pollen and hence with a need for economy in its use.

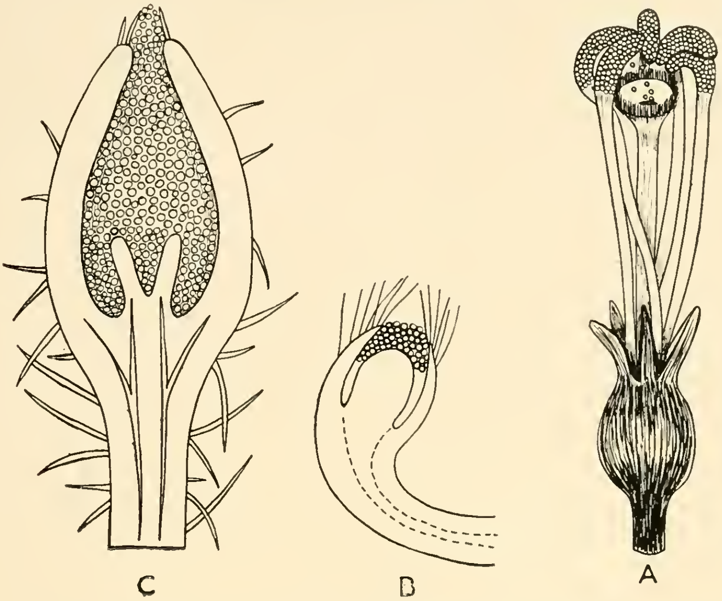


Fig. 1193.—" Pollen chamber " in Goodeniaceae. A, *Scaevola*. Flower with corolla removed to show anthers dropping pollen into the stigmatic cup. B, The same, stigmatic cup in section at a later stage, the growth of the stigma pushing the pollen out. C, *Selliera*. Stigmatic cup in section, containing pollen from the same flower. Growth of stigma beginning. (*Partly after Goebel.*)

Tubular styles, such as those of *Viola*, are hollow compound structures with a tubular opening and without any receptive stigma but with the interior filled with a mucous excretion from the lining membrane. The style has a sharp elbow-bend near its base, with a narrowed lumen, and at its apex is also bent downwards at right angles, ending in an opening which may be formed by one of the three component stigmas. When the style is pressed by an insect it bends easily at the elbow, closing the lumen. The

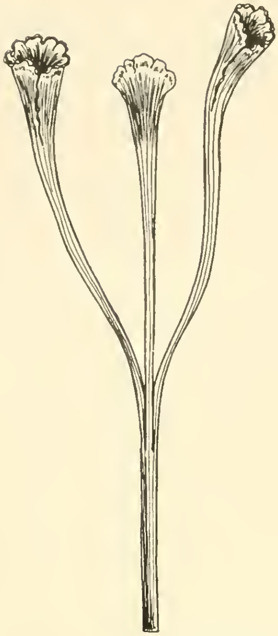


FIG. 1194.—Tubular stigmas of *Crocus*. (*After Van Tieghem.*)

pressure forces out some of the slimy contents which collect pollen, in the same manner as the pollination-drop of a Gymnosperm. On release of the pressure the style springs back into its normal shape and the drop of mucus, with the pollen, is withdrawn into the interior, where the pollen germinates. *Viola* is not unique in this mechanism, but it is rare and *Burmannia* is the only other example which can be cited.

The stigmas of *Crocus*, though tubular in form, are quite different from the above (Fig. 1194). The three styles are united below but free above and the three branches are flattened, with inrolled edges, forming three brightly coloured funnels. The actual stigmas are only at the upper rims of these, where receptive papillae are developed. Pollen tubes grow rapidly down the interior of the funnels, a matter of some importance as the styles are exceptionally long.

Allied in nature to the above are the petaloid styles of *Iris* (Fig. 1195). These three organs,

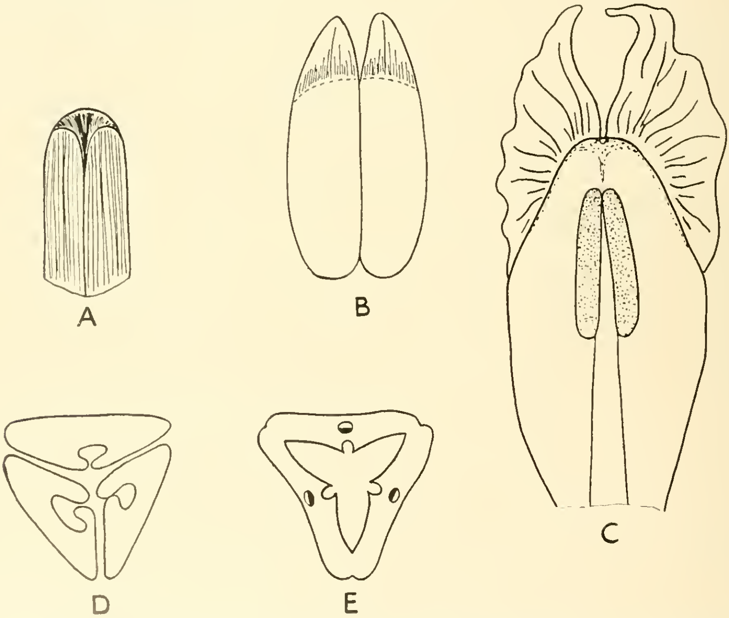


FIG. 1195.—Development of the stylar branch and stigma in *Iris*. A, Young stage with dorsal stigmatic groove. B, Later stage with free margins growing out. C, Mature branch-style, abaxial view with stamen in front; stigma dotted. D, Section near base of styles showing downward continuation of stigmatic grooves. E, Section at top of ovary; styles united. (*After Engler-Prantl and Goebel.*)

which are broad and petaloid at the top, narrow downwards until in cross-section they are flattened triangles, which ultimately become joined at their edges to form the compound style. The apex of each triangle is occupied by a furrow, with overlapping margins, and in the early stages of development the whole structure has this form, resembling the funnels of *Crocus*, with their inrolled margins. As development proceeds, the free edges of the upper portions extend greatly, right and left, and become coloured like the perianth. The two margins of the furrow also grow upwards, overtopping the apex, which becomes the stigma, and forming a pair of upwardly directed wings. The stigma in the mature structure thus has the appearance of being merely a narrow flap on the abaxial side of the style-branch. The upper end of the furrow, which is on the adaxial side, lies between the two wings and close to the stigma, and it is by this channel that the pollen tubes grow downwards to the inferior ovary.

Placental stigmas are characteristic of the Ericaceae and are found occasionally in other coenocarpous families. The compound style has a central canal into which the placentae extend upwards from the loculi to the apex, where they form the stigmatic lobes. Naturally they are sterile in their upper portions. They have in this way replaced the carpel apices as stigma-formers, and have made conducting tissue needless, since they themselves function as conductors of the pollen tubes. The vascular bundles of the style supply these placental stigmas, opening out into a crown of storage tracheids below the stigmatic surface. Considering the close association of placentae with the carpel margins, which so frequently take part in the formation of both stigmas and styles, it is surprising that placental stigmas do not often occur in more primitive families than the sympetalous Ericaceae, and one is tempted to wonder if perhaps it is not an ancient feature which has been lost along the majority of evolutionary lines.

Sensitive stigmas are of occasional occurrence. Examples are *Mimulus* and *Martynia*, in both of which there is a bilobed stigma, the lobes of which are normally wide apart. On being touched they clap together suddenly and thus entrap any pollen which may be carried by the visiting insect which has touched them.

Lastly we must mention the vexed question of the commissural stigma, that is to say the stigma which stands over the line of carpel suture in a coenocarpous ovary and not over the loculus as is usual. Some of the best known examples are to be found among the Papaveraceae and the Cruciferae, in which families it is one of the outstanding characters. The usual explanation of the peculiarity, with reference to the Cruciferae, is that the median portion of the formerly dorsal stigmas has lost its receptive surface and that the receptive margins have fused together with their neighbours, over the line of suture. Each commissural stigma is therefore produced by the union of two stigmatic margins. According to Arber the stigmas in *Papaver* arise rather differently. The upper part of each placental wall, itself, as we have mentioned above, a double structure, divides, and the two free surfaces become stigmatic where they are nearest together, thus forming a double stigmatic line above each placenta.

Leaving now the style and stigma, we must refer to one or two special features of the gynoecium as a whole. First, there is the question of reduction in the gynoecium. Reduction in the number of carpels, often associated with reduction in the number of ovules, is, as we have seen, a general tendency in floral evolution. Thus pentamerous flowers often have only three or two carpels, or even one, with consequent disarrangement of the usual alternation of parts in successive whorls. Reduced numbers may be stable throughout large circles of affinity. The dimerous gynoecium, for example, is characteristic of most of the more highly evolved families of Dicotyledons. Reduction may, however, occur as an exception. Thus, in Cucurbitaceae, which have normally a trimerous gynoecium, reduction to two or to one carpel may appear only in certain genera, by the suppression of one or two of the carpel rudiments.

In Compositae the double stigma raises a suspicion that two carpels are concerned in forming the single ovary and Small has recorded cases in which two ovules were formed, either with or without a septum between them. The Gramineae likewise have generally only a single ovule, although the double stigma and the structure of the ovary wall indicate the presence of two carpels. A very much reduced third carpel may, however, sometimes take part in forming the ovary wall and in the Bamboos and in a few other genera it is comparatively well-developed and bears a third stigma. Reduction to a single carpel does occur, though rarely, an example being *Nardus*. The conclusion is that the typical Grass ovary has been reduced from the trimerous condition which is general among Monocotyledons.

In *Cocos nucifera* the familiar three depressions at one end of the woody endocarp apparently represent a vestige of the three-carpellate condition. Two of the depressions are woody and non-functional, but the third is soft and provides a means of exit for the single seedling, through the hard endocarp.

In the above examples only traces, at the most, of the lost carpels are retained, but there are numerous cases of carpels which fail, more or less completely, to develop, although their rudiments are present in early stages, occupying their appropriate places according to the symmetry of the flower. Thus in *Triglochin palustre*, three of the six carpels are solid and sterile, though they continue to grow until the fruiting stage. In *T. laxiflorum* all six carpels are alike and fertile. In *Fedia*, in *Valerianella* and in *Pontederia*, two sterile carpels are found, which, although they retain a small loculus, produce no ovules. In *Viburnum* only one sterile carpel occurs, while in *Valeriana* and *Centranthus* only one carpel is formed and the two sterile carpels have disappeared. All stages in suppression may, therefore, be seen by comparison, from complete suppression of carpels to the relatively minor degree of reduction in which one or more of the carpels, although normally developed and producing ovules, are suppressed during post-fertilization growth. The latter condition is exemplified by *Aesculus* *hippocastanum*, the Horse Chestnut, where the three-carpellary capsule contains generally only one seed, although all three carpels produce ovules. The familiar definition of a nut-fruit, that it is an akene by reduction, is illustrated by *Corylus*, which has two carpels and a unilocular ovary with two large placentae, only one of which bears ovules, the other remaining sterile. By analogy with staminodes such sterile or vestigial carpels may be called **carpellodes**.

The genus *Carex* shows the peculiarity of a sac around the gynoecium, fitting more or less closely and rising above the ovary to an apical opening through which the long stigmas emerge. This sac is called the perigynium or utricle and it is a development of the upper palea. Its sheathing character may be compared to the basal sheaths of the foliage leaves, which in this genus are tubular and not split like those of the Grasses.

Among the Compositae the genus *Xanthium* and especially *X. spinosum*, also has sheathed gynoecia, which, however, arise in quite a different way. The much reduced female capitulum is surrounded by an involucral tube, covered externally with hooked processes (Fig. 1196). The involucre encloses two naked, female flowers, which stand in the axils of two modified bracts which are united to form a sheath around each flower. These bracts are prolonged upwards into two tubular, hooked processes, very like the others but much bigger, which protrude from the involucre. The styles grow up inside these tubes and the paired stigmas emerge from them through a lateral opening. The inflorescence is interpreted as a dichasial cyme, one of the two flowers being terminal and the other lateral, while a third, smaller bract is usually present and is held to mark the position of a suppressed, second, lateral flower.

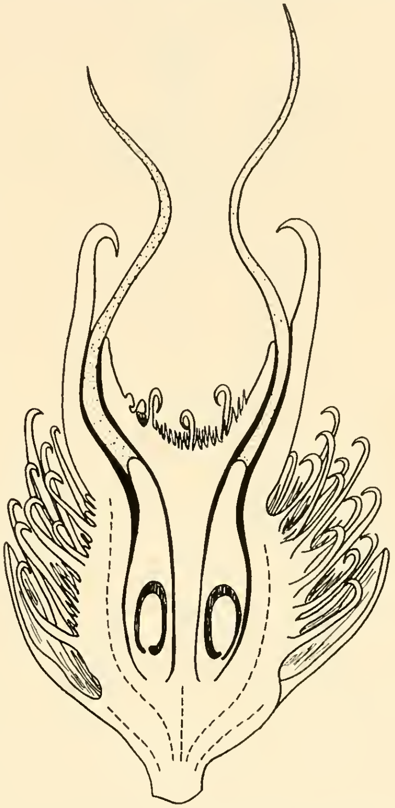


Fig. 1196.—*Xanthium spinosum*. Vertical section through a female capitulum showing the spiny involucre and the two female flowers sheathed in the united bracts. (*After Baillon.*)

A **syngynium**, or union of two or more gynoecia belonging to separate flowers, is of rare occurrence. It may be produced by the fusion of two closely placed, inferior ovaries, as happens in many species of *Lonicera* (Fig. 1197), or it may occur between superior gynoecia if the flowers are unisexual, naked and closely associated, a combination of factors which does not often occur. Examples are, however, available in the section *Faya* of the

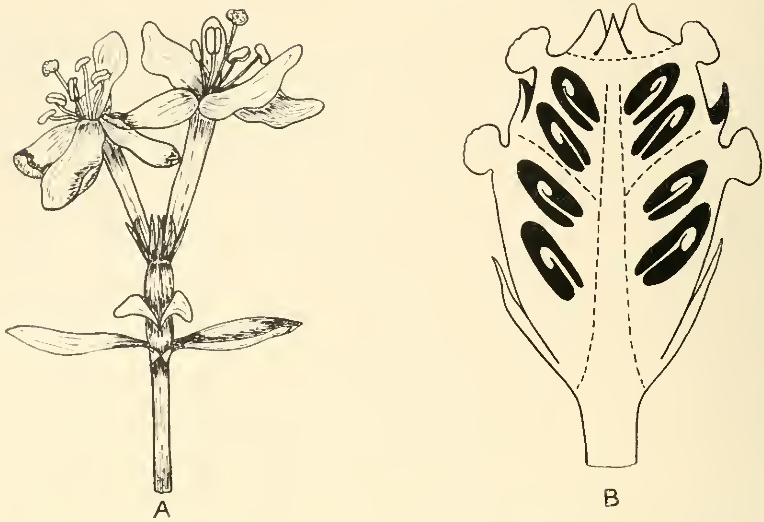


FIG. 1197.—Syngynia in A, *Lonicera* and B, *Batis*. (*After Velenovsky and Le Maout.*)

genus *Myrica* and in *Batis*, which forms a monotypic family in the Centrospermae. There is also the case of *Cryptocoryne*, one of the Araceae, in which the five naked, female flowers around the base of the spadix become united and grow into a fruit which has all the appearance of having been formed from five syncarpous carpels in one flower.

It may be justly said that the essential feature of a carpel is that it is a closed structure containing the ovules, but in some cases the closure is incomplete. The best-known example is that of *Reseda*, in which the three carpels are joined into a paracarpous ovary but their apices remain free. The upper margins are stigmatic and soon separate, leaving the top of the ovary open. A similar condition obtains in *Salix*, although only two carpels are associated. This singular and, one might say, primitive, condition is probably secondary in the otherwise somewhat specialized flowers of *Reseda*, but there are other instances in which this is less probable, because of the low evolutionary status of the families in which they occur.

Both ontogenetic and phylogenetic evidence leads to the belief that the carpel was once an open structure which has become closed by marginal union in a variety of ways. It is therefore of interest to find examples of unclosed carpels in living families of a primitive grade. Such, for instance, are the Winteraceae, closely allied to the Magnoliaceae, in which a morphological series, showing various degrees of closure, may be traced among the genera. The most primitive type is *Degeneria* (Fig. 1198), a Fijian genus, placed in a monotypic family, which has carpels formed like a conduplicate leaf, with long stigmatic margins, which only unite in the developing fruit. The stigmas extend as far inwards as the placentae, which are laminar as in the following case.

The Butomaceae, again, are primitive Monocotyledons, primitive, that

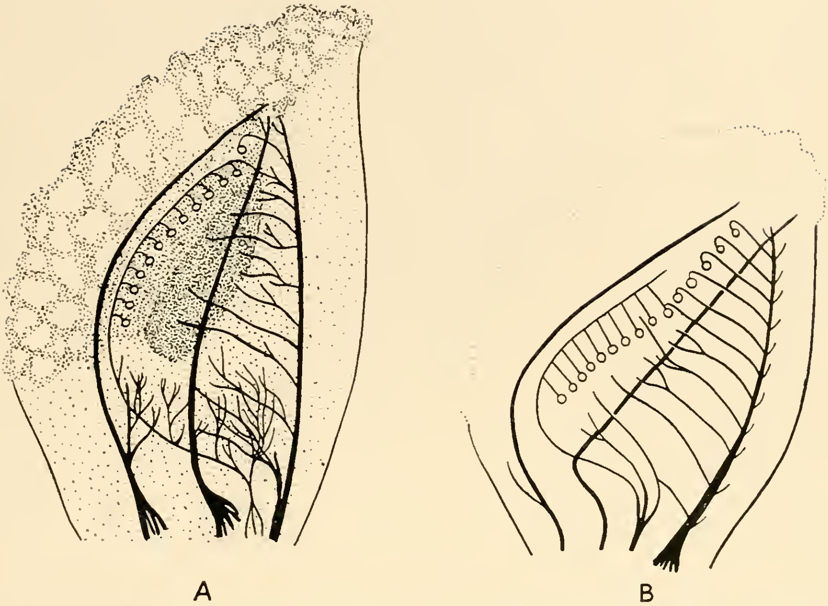


FIG. 1198.—*Degeneria vitiensis.* Longitudinal sections through carpels. A, Outline showing position of the stigma and its extension inwards to the line of ovules, shown as small circles. Note exceptional degree of branching of the dorsal bundle and the ovules supplied by branches of a bundle coming from the dorsal side of the carpel. B, Vascular system showing relatively weak, unbranched ventral bundles and ovules supplied by branches from the dorsal system. (*After Swamy.*)

is to say, in a number of characters, among which is the absence of union between the carpel margins. The carpels are closely set in two trimerous whorls and resemble those of *Degeneria* in form but with the marginal stigmas confined to the summit of a short, stylar prolongation. Although the absence of marginal union is exceptional among free carpels it is a commonplace among united carpels. The paracarpous condition, in fact, exists because the margins of the constituent carpels are united to those of their neighbours rather than to each other, so that each carpel is completely open inwards.

It has not been our practice in this book to refer to teratological abnormalities, which are too various and peculiar to be adequately considered in a general text. An exception may be made here, however, in referring to the intergrades or combinations of stamen and carpel which have been recorded in a number of plants; *e.g.*, *Ranunculus*, *Salix* and *Podophyllum*. Some of these intergrade organs are staminate but in addition to pollen-sacs they bear ovules, either superficially or partially enclosed; others are apparently carpellate but bear pollen loculi as well as ovules. Rainio has maintained that there is order in this seeming disorder and that the pollen-sacs and ovules develop at different and definite points on the appendages, which he regards as truly amphisporangiate sporophylls. No change of fertility is evident; both the pollen grains and the ovules, though formed in novel positions, appear to be normal and functional (see also p. 1195). Too much weight can easily be given to such phenomena as evidence in questions of phylogeny. Their immediate causation is practically unknown and their ultimate causation purely speculative.

The morphology of carpels has been treated at some length because they are, of all the organs of the plant, the ones most essentially characteristic of the Angiosperms, and this remains true whatever theory of their origin we may adopt. It is for this reason that so much importance has been given to them in classification, where they have sometimes been overweighted while other parts, such as the stamens, have been accorded too little significance. To separate families on the ovarial structure alone smacks of artificiality.

It may be useful here to sum up the classical theory of the flower, as it has been redefined by Eames, as being at least a good working hypothesis.

The flower is a determinate shoot with phyllome appendages. Pedicels and receptacles have typical stem anatomy and the appendages are leaf-like in their anatomy and development. Sepals are three-trace organs and are morphologically bracts and not sterilized sporophylls. Petals are one-trace organs and, though showing some leaf characters, mostly appear to be sterilized stamens. Stamens are one-trace organs, like petals, and are only three-trace in a few primitive families. Carpels are predominantly three-trace organs and are only abnormally one or many-trace. Both stamens and carpels appear to be sporophylls.

Fusion of organs may lead to the fusion of their vascular supplies, either radially or tangentially.

NECTARIES

The nectar glands, on which depend the pollination of the great majority of flowers, form a category of organs of doubtful homogeneity, since some are obviously produced by the modification of other parts of the flower, while others have the appearance of being special structures or specialized outgrowths of existing structures. They are by no means always insignificant in size but may rival or even exceed the dimensions of the gynoecium, although they may be nothing more than emergences. Outgrowths in the flower which have the character of trichomes or emergences are called **effigurations**. Some structures of this kind may serve as nectaries (Fig. 1199) but others appear to be functionless or to have only secondary functions in connection with pollination. Like the nectaries, effigurations are of mixed origin and may occur in any part of the flower. It is an unsatisfactory category, something of a rag-bag, to which all sorts of unexplained structures may be relegated.

Despite the varied origin of nectaries, those of certain families, for instance the Cruciferae, are so characteristic that they have been made use of in classification, especially within the family. Bayer proposed to subdivide the Cruciferae on the basis of the nectary forms, which are illustrated in Fig. 1200. He concluded that the whole surface of the receptacle

FIG. 1199.—*Xanthoceras sorbifolia.* Flower in vertical section showing the nectary processes (dotted) arising from the receptacle.

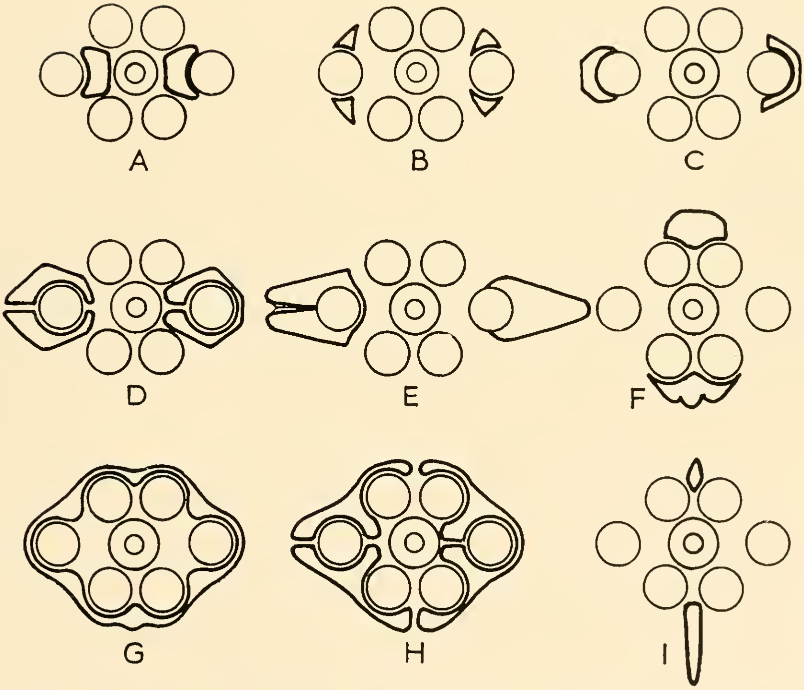


FIG. 1200.—Nectaries in Cruciferae, shown in plans of flowers. Nectaries with heavy outlines. A–E, Various forms of lateral nectaries, inside, outside and around the stamen bases. F and I, Median nectaries. G, Ring nectary. H, Complete nectary. (*After Gunthart.*)

is potentially nectariferous. Gunthart has supported this but he maintains that the various forms are attributable to space restriction due to the relative development of the other floral parts. The form of the nectary is therefore a " passive " character in his sense, being dependent on the operation of three " active " characters: the form of the gynoecium, the constriction of the calyx and the raising of the median sepal insertion level. The ring-form is apparently the original and the others are regarded as derivative. Because of the dependent status of the nectary form, Gunthart rejects Bayer's classification as artificial.

We are here treating only of nectaries which are included in the flower, but extra-floral nectaries are not uncommon. They may be formed on leaves, on stipules or on the stem (see Volume I, pp. 505 and 1028), or they may be formed in close connection with the flower, on the outside of the sepals in Malpighiaceae, on bracts or on the pedicel, in which position they may play a part in pollination analogous to that played by the true floral nectaries. A good example is afforded by *Euphorbia*, where the nectaries are formed on the margin of the involucre of the cyathium.

It is first necessary to draw a distinction between nectaries proper and nectar-holders, for, although the two things may sometimes be combined in one structure, *e.g.*, *Ranunculus*, they are frequently quite separate and indeed one may be present without the other. Nectaries are frequently present without any nectar-holder and, on the other hand, the spurs of some flowers, especially among Orchids, are apparently nectar-holders, although the nectaries have disappeared. This view is supported by the presence of both structures in other Orchids, in which the spurs function as suggested.

From the point of view of floral biology nectaries may be divided into two types: those with exposed nectar and those with concealed nectar, which is a very important difference with regard to pollination. These types occur, however, irregularly distributed among flowers of all groups so that to classify nectaries it is best to proceed on a topographical basis, according to the parts of the flower in which they are formed, which allows of a much more systematic treatment. (Adapted from Fahn.)

1. *Toral Type.* Nectar produced on the surface of the receptacle or from some part of it.
    (*a*) Marginal. Nectar produced near the base of the sepals and collecting in or around them.
    Example: *Capparis.*

    (*b*) Discoid. Nectar produced from a ring or portions of a ring around the receptacle.

    Examples: 1. Complete ring in Boraginaceae and Labiatae.
    2. Partial ring in Rhinanthaceae.
    3. Ring of small swellings in *Cistus* or of scales in Crassulaceae.

4. Ring in form of a disc in *Rhamnus*, *Thea* and *Ribes*.
5. Ring of club-like upgrowths from the disc in *Xanthoceras*.
6. In perigynous flowers the nectary either forms a thickened rim to the floral cup (*Alchemilla*, *Scleranthus*), or it may form an interior zone of the cup in Prunoideae and Cactaceae.

(*c*) Tubular. A somewhat heterogeneous class.

Examples: 1. *Bauhinia purpurea*. Nectary takes the form of a spur sunk in the pedicel and lined with secretory cells.

2. *Cristatella erosa* (Capparidaceae). Nectary takes the form of an open tube rising from the receptacle alongside the ovary.

2. *Ovarial Type*. (*a*) The carpel walls themselves secrete nectar.

Examples: 1. At the apex in *Androsace*.

2. At the base in *Gentiana* and *Clethra*.
3. In depressions in the lateral walls in *Caltha*.
4. All over the free surface of the carpels in *Tofieldia palustris* and *Sarracenia*.
5. In the furrows between the carpels in *Tofieldia calyculata* and *Ornithogalum*.

(*b*) The nectaries may form processes from the carpels.

Example: The nectary forms a cup made up of united scales, around the base of the ovary in Convolvulaceae.

It is a difficult matter to decide, in some cases, whether these outgrowths from near the base of the ovary should be classed as toral or ovarial; nor is it of great importance.

(*c*) The nectaries may be formed in the septa of syncarpous ovaries. This occurs exclusively in Monocotyledons.

Examples: Septal nectaries are found throughout the Liliales and in the Musaceae and its related families. There is a slit in each septum lined with secretory cells. The slit opens at the top of the ovary and from this opening the nectar issues and flows down the outside (Fig. 1201). In *Allium* an open canal connects with the top of the nectary slit and conducts the nectar to the base.

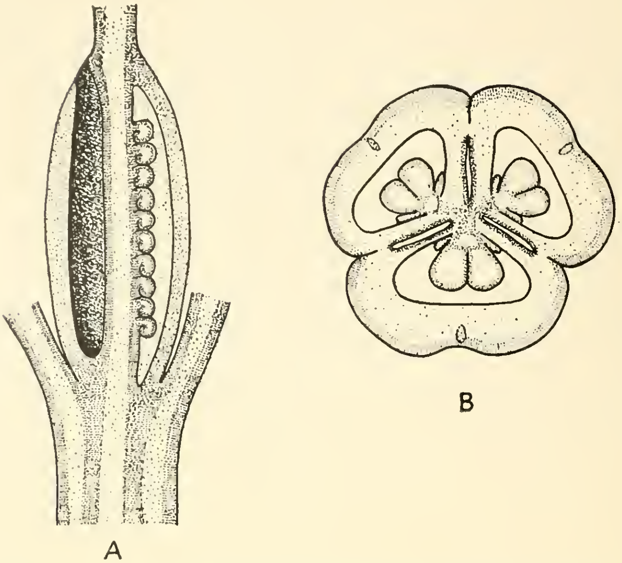


FIG. 1201.—*Haworthia reinwardtii.* Septal nectaries. A, Longitudinal section of ovary with nectary slit shown on left, opening at apex of ovary. B, Transverse section showing nectary slits in septa. (*After Brown.*)

3. *Stylar Type.* This is not clearly distinguishable from the preceding, but the base of the style is included in the nectary.

   Examples: 1. In Umbelliferae the nectary takes the form of an enlarged cushion on the top of the inferior ovary and includes the base of the style, the so-called stylopodium.

   2. A similar structure is found in Saxifragaceae with inferior or semi-inferior ovaries and in *Cornus.*

4. *Staminal Type.* Nectar is secreted by or in close association with the stamens.

   (*a*) Nectar is secreted by the bases of the stamen filaments.

   Example: From the united stamens in many Papilionaceae.

   (*b*) Nectar is secreted in grooves on the filaments.

   Examples: 1. The groove is on the abaxial side in *Vaccinium* and *Tulipa.*

   2. The groove is on the adaxial side in *Atragene.*

   (*c*) Nectar is secreted by processes at the base of the stamens.

   Examples: 1. The nectaries form swellings at the base of the stamens in Alsinoideae and in Geraniaceae.

2. The staminal nectaries are united into a ring in Silenoideae.

3. The nectaries form swellings which may be either isolated or united in various ways, in Cruciferae.

The nectaries in Cruciferae have been used as a means of classification by Bayer. It is open to question whether these nectaries are outgrowths of the receptacle around the bases of the stamens or whether they belong to the stamens themselves. As the nectaries in the closely related Fumariaceae are undoubtedly staminal, the latter alternative seems the more probable.

(*d*) The nectaries form appendages of the stamen filaments.

Example: Paired appendages, like stipules, in many Lauraceae.

(*e*) The nectaries are staminodes.

Examples: 1. Nectar is secreted from the connective in *Anemone pulsatilla*.

2. Nectar is secreted from staminodal appendages in *Sassafras* and *Persea*.

3. Nectar is secreted adaxially at the base of palmately branched staminodes in *Parnassia*.

4. Nectar is secreted by a ten-lobed cup with ten vascular strands, in Phaseoleae. Probably a reduced whorl of stamens.

(*f*) The nectaries are formed at the junction of stamen and petal in epipetalous stamens.

Examples: Nectar is secreted by a yellow-coloured nectary surrounding the base of the free part of the filament in *Colchicum* and *Trillium*. The nectar collects in a channel of the petal.

5. *Perigonial Type*. Nectar is secreted by the perianth members.

(*a*) Nectar is secreted by the sepals, a rare phenomenon.

Examples: 1. Secretion from the coloured, fleshy calyx in *Cuphea*.

2. Secretion from the base of the sepals in *Atragene*.

3. Secretion in the spur in *Tropaeolum*. This spur appears to be attached to the posterior sepal but developmentally it seems to belong to the receptacle, so that its status is doubtful (cf. *Pelargonium*).

(*b*) Nectar is secreted by the petal surfaces.

Examples:
1. Nectar exudes in small droplets from the stomata of the large anterior petal in *Verbascum*.
2. Nectar exudes in small droplets from inside the lower part of the tubular corolla and collects into a large drop, in *Lonicera*, *Pyrola*, *Narcissus* and *Iris*.
3. The whole adaxial surface of the petal is secretory in *Feijoa* (Myrtaceae).

(*c*) Nectar is secreted in grooves, pouches or spurs.

Examples:
1. Each perianth part has a longitudinal channel filled with nectar in *Lilium*, or on the labellum only, in some Orchids.
2. There is a secretory thickening on the petals, continued downwards into a groove in *Rhododendron*.
3. Nectar is formed in spurs in many Orchids, in *Valeriana* and in *Viola*, *Linaria* and *Aquilegia*.
4. Nectar is formed in pouches on the perianth parts, uncovered in *Fritillaria* but covered by a flap in *Ranunculus*. In *Garidella* (*Nigella*) the pouch is formed at the junction of the limb and claw of the petal.
5. Nectar is secreted in sacs or tubes formed by the modification of entire petals or possibly of stamens, in many Ranunculaceae, *e.g.*, *Helleborus*, *Trollius* and *Nigella*, and in *Epimedium* in Berberidaceae. These structures are often called " honey leaves " and they may be of quite complex structure.

The histological structure of floral nectaries is very varied, even within the limits of a single genus such as *Iris*. Generally speaking the tissue consists of small-celled parenchyma, both with and without air spaces, and there is usually a vascular supply in close relation to the nectary, frequently a special bundle or bundles which may branch throughout the secretory tissue if this is massive. The surface layer may have the columnar " epithem " structure or it may be undifferentiated. Frequently there is a cuticularized epidermis, in which case the excretion of nectar takes place either through stomata, which resemble water-stomata in being permanently open, or through cracks in the cuticular covering.

The quantity of nectar excreted is likewise very variable. There may be no more than a surface film or there may be several cubic centimetres collected in the spurs of some flowers. Where excretion is copious it may drip from the nectary, as in *Phygelius capensis* or in the Orchid, *Coryanthes*, where as much as 30 c.cs. may be produced.

A mixture of sugars is present, fructose, glucose and sucrose being of regular occurrence. The total sugar concentration varies greatly and is roughly inverse to the volume of nectar excreted. Rough quantitative measures show that the concentrations of fructose and glucose are closely correlated but the concentration of sucrose shows an inverse relation to that of the other two sugars. In some species three other sugars, maltose, raffinose and melibiose, may be present in small quantities, though they tend to be irregular. The last named is non-nutritive for bees but it attracts them and in years of scarcity they have been known to collect it extensively from honey-dew on leaves.

The relation of nectar concentration to bee-visits will be dealt with in the section on Pollination (see p. 1258).

A curious relation between nectary excretion and the dehiscence of the anthers has been suggested by Burck. It can be shown that, when ripe, the anthers of many flowers lose remarkable amounts of water, not, as he showed, by transpiration but by withdrawal of water internally to other tissues. This, he suggests, is due to the nectaries, then beginning excretion, which has the double advantage of attracting insect visitors at the right time and of creating the conditions of hydrostatic tension in the anther wall which lead to dehiscence.

Porsch has pointed out an interesting systematic relationship in the distribution of nectaries. The more primitive families of the Dicotyledons, the twenty-three composing Wettstein's Polycarpicae, rely chiefly on the perianth and the androecium for nectar production and seldom have toral nectaries, which, on the other hand, are characteristic of Sympetalae. The Monocotyledons agree with the Polycarpicae in this respect and display close resemblances to them, even in details, another feature connecting the Monocotyledons with the lower Dicotyledons.

Lastly we may mention the existence of false or substitute nectaries, that is soft and juicy tissues, such as the cushion surrounding the base of the style in *Leucojum* or juicy hairs like those on the stamens of *Anagallis* and *Tradescantia*, which can be sucked or eaten by insects. Even the pulpy and discoloured old petals in short-lived flowers like those of *Eremurus* or *Calandrinia*, which have passed their anthesis, may attract juice-sucking insects who may, by their visits, bring pollen to the still receptive stigmas.

CHAPTER XXIV

THE ANGIOSPERMAE: POLLINATION; AN INTRODUCTION TO FLORAL BIOLOGY

When we speak of Floral Biology we imply the study, both by observational and experimental means, of all the phenomena of organization and function in the flower which serve, either directly or indirectly, the transfer of conspecific pollen from anther to stigma. The term " Floral Biology " is obviously not an ideal one, for it seems to suggest more than is covered by the above definition, but it is now firmly fixed in botanical terminology with this acceptation: the process of pollination. The term " flower ", also, must here be understood in a biological rather than a morphological sense, as applying to any floral organization which functions as a unit for purposes of pollination, whatever its morphological nature may be.

The subject is one in which a critical outlook is essential, for the interpretation of floral structures from a functional standpoint abounds in pitfalls. In no other study, perhaps, is there a greater temptation to use teleological ideas and expressions, and in unscientific hands it has often become a mere hunt for supposed " adaptations".

That the harmonies called adaptations exist must be admitted by the most critical. Many complex floral structures can be understood in no other way, such as the relationship of the structure of the *Strelitzia* flower to pollination by birds (see p. 1300), but of the history of these structures we know nothing, and we must not rashly assume that because a certain structure is related to a certain function, the structure was developed with that end in view. That is the essence of teleological adaptationism and it should be abjured in favour of the strictly guarded conclusions derivable from observation and experiment. Only in the sense of an observed harmony between structure and function can we speak of an adaptation existing. The word itself should indeed be avoided as much as possible, for it conveys the dangerous idea of " making-fit-for ", of which we should beware.

The separation of microspores and megaspores on different members of the flower, combined with the retention of the megaspore in the megasporangium, makes pollination a necessary preliminary to fertilization, except in the special case of cleistogamous flowers of which we shall speak later. It is thus a process confined to the Spermatophyta. An analogy may be found in the conveyance of antherozoids to the neighbourhood of the archegonium in dioecious Bryophyta, which also involves agencies beyond the mobility of the antherozoids themselves; but about these we know very little.

Only a small minority of flowers are pollinated by their own pollen as a regular occurrence. For the vast majority pollination means cross-pollination, that is the conveyance of pollen from other flowers, either of the same plant or of another plant of the same species. For this, three natural agencies are available: wind, animals and water, and all are used to a greater or less extent. The Gymnospermae, as we have described in Volume I, depend on wind, with the doubtful exception of *Welwitschia*. With this in mind we might conclude that this is the primitive method and therefore the one likely to prevail among primitive Angiosperms. This may possibly be true, but it would be illogical to argue that flowers which are wind-pollinated are therefore primitive. Our attitude will depend on what we believe about the evolution of the Angiosperms. If we accept the theory proposed by Wettstein and elaborated by Engler, that the most primitive flowers are small, achlamydeous and generally unisexual, like those of the Gnetales, then we will agree that wind-pollination is the primitive method in the Angiosperms. A contrary view is, however, possible, namely that the evolution of angiospermy and the development of insect pollination were closely linked.

The geological record shows that the Angiosperms assumed their present position of dominance rather rapidly and that an astonishing multiplication of genera took place within a comparatively short time. It is at least plausible that this rapid evolution went hand-in-hand with the rapid evolution of pollinating insects and that it was on this connection that the biological success of the state of angiospermy depended. Not many of the orders of Insects are ancient. The Neuroptera and Orthoptera can be traced back to the Palaeozoic era; the Coleoptera were the principal insect order during the Mesozoic, with Diptera and Hymenoptera as relatively minor groups. The Lepidoptera and the bees, wasps and Syrphids only appear at the beginning of the Tertiary. It seems reasonable to conclude that the flowers and their pollinators were evolving side by side during the Tertiary period and that this accounts for the complex yet harmonious balance that exists between the structure of so many flowers and the insects which pollinate them.

There is a general, though not universal, relationship between insect-pollination and the presence of a coloured perianth. The Ranunculaceae, for example, though having for the most part unspecialized flowers, are insect-pollinated and have conspicuous perianths. Genera like *Ranunculus*, *Caltha* and *Ficaria* have coloured perianths, but the flowers are regular and open and offer nectar freely to almost any visitor. In the same family, on the other hand, genera like *Delphinium* and *Aconitum*, also with well-developed perianths, are zygomorphic and specialized to the visits of only humble bees and in the latter flower, to only one species of humble bee. *Thalictrum*, which is only conspicuous from its abundance of coloured stamens, is visited for the sake of its pollen. Within a single fairly primitive family there is, therefore, a considerable range of flower-pollinator relationships which suggests that in the early phases of floral evolution many diverse relationships may have sprung up, to form the starting-points of distinct lines in floral evolution.

We may contrast with pollination in the Ranunculaceae the state of affairs in the Gramineae, where wind-pollination is the rule. The grasses certainly do not represent a primitive type of Monocotyledon and the adoption of wind-pollination is therefore probably secondary. Their floral structure is both reduced and specialized and they have either no perianths or only vestigial ones, but there can be no question that among them this supposedly primitive mode of pollination is highly successful, as is testified by their numbers and their cosmopolitan distribution.

We have remarked that the majority of flowers are cross-pollinated. Where flowers are unisexual this is naturally inevitable, but most hermaphrodite flowers show arrangements which favour cross-pollination and either prevent self-pollination, or at least greatly reduce it. Considering the proximity of anthers and stigmas in most hermaphrodite flowers, and the ease with which self-pollination could be brought about in such flowers, the avoidance of it in nature struck early observers and suggested that it might carry with it something like the drawbacks of inbreeding among animals. Consequently it was not surprising that Charles Darwin was able to show from his experiments, published in 1876 as " The Effect of Cross and Self Fertilization in the Vegetable Kingdom ", that cross-pollination produces; (*a*) more seed (*b*), heavier seed, and (*c*) better germination capacity, than does self-pollination.

We have shown, in the previous chapter, that there is reason for regarding the unisexual condition in flowers as derived from the hermaphrodite condition, rather than the reverse. If this be so, we may regard the unisexual state as the extreme term of the trend towards ensuring cross-pollination. This does not imply that self-pollination is the more primitive of the two. Separation of the sexes is the rule among lower plants, and among higher plants the hermaphrodite condition is only to be found, Angiosperms apart, in some of the higher Cycadophyta. If the Angiosperms originated with a hermaphrodite constitution, they started with a handicap in regard to self-pollination, the need to minimize which may have been an important cause of their multifarious variation. These are speculative matters, but not without interest.

It must be borne in mind that there are some plants which are habitually self-pollinated and which have therefore become homozygous, without apparently suffering any penalty. Some of these types are among the Grasses and they may be widely successful, but despite the appearance of success, the genic impoverishment which their condition implies must limit their capabilities, as it leaves them dependent on chance mutations for the appearance of any heritable variations (see also *Pedicularis*, p. 1324).

The need for pollination, as a preliminary to seed and fruit production, has been known from very early times and the ceremonial pollination of the Date Palms was carried out as a religious act by Assyrian kings. In spite of the long experience of cultivators with certain crop plants, no idea of the universality of pollination in flowers found a place in botanical science until it was propounded by Thomas Millington towards the end of the seventeenth century. Nearly half a century later it was still possible to question its sexual significance.

The first person to publish records of experiments on the necessity for pollination and to distinguish the anthers as the male parts and the carpels as the female parts of the flower was Rudolph Jacob Camerarius (1665–1721). He thus gave a scientific foundation to the doctrine of sexuality in plants, but the erroneous notions regarding the nature of fertilization which prevailed until long after his day prevented the general understanding or acceptance of his views. He raised the question whether cross-fertilization is possible between two different species of plants, but the question was not answered until the work of Joseph Gottlieb Koelreuter (1733–1806) (Fig. 1202), whose publications: "Vorlaüfige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen" appeared between 1760 and 1770. He studied the manner in which pollination must take place in order to be effective. He also first recognized the general importance of insects as natural pollinators, though he thought them secondary in importance to the wind. He observed dichogamy (see below) in the hermaphrodite flowers of *Epilobium* and, most important of all, he created a number of inter-specific hybrids and showed that the offspring shared the characters of both parents.

These, however important, were discoveries relating to fertilization rather than to pollination as such, and the founder of floral biology in the present sense was undoubtedly Konrad Sprengel (1750–1816), who turned his attention to Koelreuter's neglected observations on the part played by insects in pollination and made a most remarkable series of discoveries, which he published as "Das Neu-entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen", in 1793. He not only showed the prevalence of dichogamy in hermaphrodite flowers but unravelled many of the pollination mechanisms which since his day have become familiar to botanists. He is said to have been personally eccentric and this, combined with the surprising novelty of his ideas, led to the neglect of his work by his contemporaries. It was not indeed recognized at its real value until Darwin's day. The principles of interpretation which he established still serve us for the understanding of flowers as functioning mechanisms, though his teleological deductions are out of date.

FIG. 1202.—Joseph Gottlieb Koelreuter.

Among the principal contributors to the knowledge of pollination since Sprengel may be mentioned, in the first place, Charles Darwin himself, whose work on cross-fertilization we have already mentioned. Apart from this, his discovery of the importance of heterostyly and of the manifold and wonderful pollination mechanisms among Orchids stands out conspicuously.

Fig. 1203.—Hermann Müller. Author of "The Fertilization of Flowers."

A vast amount of detailed knowledge was brought together by Hermann Müller (Fig. 1203), especially from his experience of the Australian flora, and the great compendium of information by Knuth (Fig. 1204) is still the chief work of reference on the subject. The most readable and humane account of floral biology is, however, to be found in Kerner's (Fig. 1205)

Fig. 1204.—Paul Knuth. Author of the "Handbook of Flower Pollination".

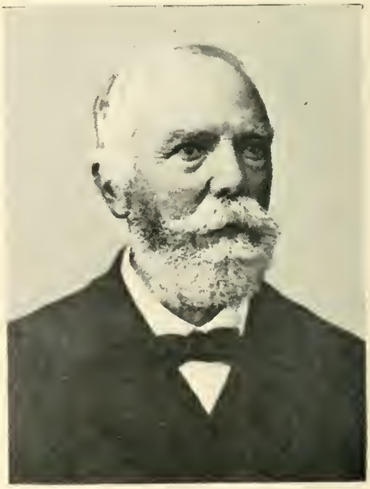


Fig. 1205.—Anton Kerner von Marilaun. Author of "The Natural History of Plants".

great " Natural History of Plants ", much of it based upon original observation. The astonishing discoveries by von Frisch of the organization of nectar or pollen collection by the honey bees, belong rather to Entomology than to Botany, in spite of their obvious bearing on pollination. They have now been expounded in more than one popular work in English.

Bees visit flowers either to collect nectar or pollen for the food stores of their hives, on which their broods must depend during the winter, while less social insects pay their visits for the same ends, but consume their finds on the spot. But were these the primitive attractions? Diels thought not and pointed out that many insects at the present day bite or suck juice from the tissues of flowers either where no nectar is formed or else is inaccessible to them. He suggests that the first insect visitors to the flowers of the earliest Angiosperms were probably beetles, the principal order of insects in Jurassic times, which came to eat the tissues, as beetles now eat the staminodes of *Nymphaea*, *Victoria*, *Calycanthus* and *Eupomatia*, at the same time bringing about pollination. The beetles were probably the only important group of flower-visiting insects before the Tertiary period and it is significant that at least one Cycad, *Encephalartos*, is pollinated by a beetle which lays its eggs in the ovules. Many are thereby destroyed, but the rest are effectively pollinated.

Diels calls beetle-pollination **cantharophily.** Although few, if any, flowers now rely exclusively upon beetles, they are sufficiently common visitors to have at least a secondary importance in many species. Recently an interesting relic fauna of beetles has been found to be exclusively associated with the giant Lobelias in central Africa. Both the plants and the insects are survivors of vanished forest conditions and it may well be that a mutual dependence has been established.

The line between false nectaries or juicy outgrowths which may be eaten or sucked and the nectaries which secrete actively, is not a hard and fast one. Some of the false nectaries contain sugary sap and on the other hand some structures which have all the appearance of nectaries are devoid of secretion. (See also under Nectaries, p. 1251.) Once nectar secretion was established in flowers its overwhelming attraction for a variety of animals would ensure that it survived and spread. Its appearance was one of the momentous steps in plant evolution, comparable in importance to the evolution of the seed.

At the present day nectar is the chief cause of the frequentation of flowers by insects, exceeding even pollen as an attraction. Its attractiveness varies, however, considerably, with regard to both its quantity and quality. The quantity produced is affected not only by internal factors but also by the weather, by the season, and by the time of day. In the early morning there may be little nectar present and the bees may visit flowers for pollen only, which later in the day they will visit for nectar. On the other hand, *Fagopyrum*, the Buckwheat, produces its dark-coloured nectar only in the mornings and is not visited by bees in the afternoon. *Fagopyrum* nectar is attractive to bees, but each flower contains very little. A bee visits about

90 flowers in one journey and a colony working a field of Buckwheat would visit about 50 million flowers for every pound of honey collected. This gives some idea of their value as pollinators.

There are relatively vast differences between the amounts of nectar secreted by different flowers. *Fagopyrum* only secretes an average quantity of 0·3 mg. per flower. At the other extreme is *Liriodendron*, which secretes nectar only on the first day of opening and on the following morning. Its average production is 1·64 gms., varying between 3·16 gms. and 0·47 gm.

Nectar flow is frequently intermittent and the factors which control it are not fully known. Some species may only produce a copious flow every few years. Both amount and concentration may vary independently. In *Antirrhinum* it has been observed that a dry or badly aerated soil reduced the yield but increased the concentration of the nectar, while cold reduced the yield but did not affect the concentration. In qualitative terms, temperature, relative humidity, soil moisture, soil type, day length and possibly altitude, all play a part in determining the amount of the nectar flow.

Differences in quantity are, however, of less importance than differences in the concentrations of sugars, to which bees are remarkably sensitive, ignoring copious but dilute secretions in favour of richer yields. Thus Pear blossom seems to offer no attraction to bees except in the morning. As the day goes on, the Apple and the Plum offer better fare as the concentration of their nectar increases. Blow-flies on the other hand always find the Pear attractive. There is thus a good deal of " competitive bidding " between species for insect visitors.

When one considers that the average water content of ripened honey is about 10 per cent., while that of the fresh nectar may be 75 per cent., so that the weight of nectar collected is about four times that of the honey produced, the need of economy of labour by the bees is evident.

In a fully grown colony of 50,000 bees there may be 30,000 field workers. If each of these makes ten journeys per day this means 300,000 loads of nectar. An average bee-load of nectar is about 0·25 mg. and about 70,000 loads of nectar go to make one pound of honey, so that a full colony may win about four pounds of honey each good day. The more concentrated the nectar collected the greater will be the return in honey for a given number of journeys. Average concentrations, under a variety of conditions, for the principal fruit blossoms are given below:

Apple	35–55%	Plum	10–40%
Cherry	20–50%	Pear	2–17%
Peach	20–25%		

Nectars with less than 5 per cent. of sugars have little or no attraction for hive bees. The table below, taken from Vansell, gives some average figures for the concentrations in a number of common plants and illustrates the wide variation which exists.

Origanum vulgare	76%	*Trifolium repens*	41%
Erodium cicutarium	65%	*Melilotus alba*	36%
Salix spp.	60%	*Persica vulgaris*	30%
Onobrychis sativa	55%	*Liriodendron tulipifera*	20%
Taraxacum officinale	51%	*Pyrus communis* (about)	4%
Stellaria media	50%		

All the above concentrations are subject to considerable changes, especially if the nectar is exposed. For example, in *Epilobium angustifolium* with exposed nectar, the concentration varies between 60 per cent. at a relative humidity of 30 and 19 per cent. at a relative humidity of 79.

The following figures show how the concentration varies with the time of day, in the Plum, at the University of California Agricultural Station at Davis, California, on 1st March.

Time	*Concentration*	*Temperature*	*Rel. Humidity*
7–8 a.m.	6·2%	52·0° F.	100%
9.40 a.m.	8·1%	59·0° F.	85%
2.00 p.m.	25.8%	70·5° F.	55%
2.50 p.m.	24·1%	71·0° F.	53%

The Hive Bee, considered as a community, is polytropic, that is to say that a variety of flowers are visited by members of one hive during the season. The individual bee is oligotropic or may even be monotropic if the flying season is short. When there is a long flying season successive broods will work different species of flowers, with different flowering seasons. No species of flower is adapted only to the Hive Bees. The great stores of honey needed demand a wide range of visits and specialization would be a great hindrance. Its medium length of tongue is best suited to open flowers or those with only short tubes, while long-tubed flowers such as *Digitalis*, *Antirrhinum*, *Gladiolus*, or *Pentstemon* are pollinated by Humble Bees, to whose visits they are better suited.

Even a small difference in the length of the floral tube may be a serious barrier, as is shown by the Clovers. The tongue of the Honey Bee averages 6 mm. in length, that of Humble Bees varies between 7·5 and 20 mm. The tube of the Red Clover flower averages 9 mm. in length. It is therefore much frequented and pollinated by Humble Bees, although in dry seasons its flowers may become short enough for the tongues of Honey Bees (see also p. 1322). The White Clover, on the other hand, with a 6 mm. corolla tube, is one of the favourites of the Honey Bee and one of its most important sources of honey. There is a famous anecdote of Charles Darwin's which relates the production of Red Clover seed to the number of cats in the neighbourhood The cats control the number of field mice and the field mice control the number of Humble Bees available for pollination. It has been cynically added that the number of cats depends on the number of maiden ladies.

Humble Bees have not the same responsibilities as the Hive Bee for large honey stores and some of the species are monotropic. For instance, both Hive Bees and Humble Bees visit the flowers of *Salix*, for pollen and nectar, but four species of the big genus *Andrena* get the whole of their supplies from this genus alone. In the big North American genus *Perdita*, all the species are monotropic, one species of bee going only to one species of flower.

Certain flowers, whether producing nectar or not, are frequented principally, and in the latter case exclusively, for their valuable stores of pollen, which is used by the bees for brood-rearing. Such flowers are: *Clematis*, *Anemone*, *Papaver*, *Thalictrum*, *Hypericum*, *Taraxacum*, *Sambucus* and *Cistus*. They may have coloured corollas, but in some, like *Salix*, *Thalictrum* or *Metrosideros* in New Zealand, it is the prominent, coloured stamens which are the flowers' chief visible attraction. In all these flowers the stamens are so numerous and the production of pollen is so far in excess of the amount required for pollination, that the sacrifice of even large quantities does no injury to the flowers, provided that the pollen-dusty bee will come and scramble over the waiting stigma. The loads of coloured pollen which burden the returning bees at certain seasons are the best evidence of the satisfaction of both parties to the arrangement! Pollen yields the bees their chief protein ration. A full-grown colony requires between 44 and 70 lbs. in a season.

Given that the pollen is plentiful in the flowers they frequent, the bees prefer it to be small-grained and rather dry. They moisten it as they pack it, with honey they provide themselves. Large and sticky grains embarrass the pollen collectors and are not popular with them, although such types of pollen are easily picked up by the nectar-sucking visitor and conveyed by it as an unintentional incident of its routine.

Pollen-flowers are generally actinomorphic and flowers of this form are usually held vertically and are fully open. Many nectar flowers are in the same category, but zygomorphic flowers are practically all nectariferous, and such flowers are generally held horizontally or are pendulous. In either case there is often some structural provision which protects the nectar, and, not less importantly, the pollen, so that it is not too much exposed either to robbery by small and useless flies or to wastage by stormy weather. Even in the open and actinomorphic flowers the nectar may be concealed at the base of the ovary as in *Clethra*, or arched over by the bases of the stamens, as in *Campanula*, or by the connivent anthers, as in *Solanum*, or concealed by flaps of tissue, as in *Ranunculus*, or held in specialized nectar grooves, as on the petals of *Lilium*, or in special nectar-holders, as in *Helleborus* and *Nigella*. Finally the whole flower may be pendulous, as in *Fuchsia*, *Atragene* and *Soldanella*. The last-named also possesses a ring of scales, below the insertion of the stamens, which shuts off a chamber containing the ovary, and in which the nectar is concealed. Flowers with a narrow entrance to the floral tube may partially occlude the entrance, either with the enlarged stigma (pin-eyed *Primula* and some species of *Gentiana*) or with the anthers (thrum-eyed *Primula* and species of *Erica*) or by folding of the petals (*Antirrhinum* and the alae in Papilionaceae). The result of all such contrivances is that only strong and long-tongued insects can force an entrance to the nectar, and in doing so cause pollination. Horizontal zygomorphic flowers may provide sufficient shelter for their nectar by means of the perianth alone, especially if this is sympetalous, the tube forming a natural concealment. Even in these flowers there may be additional protection afforded, sometimes by stiff hairs in the tube, sometimes by the infolding of the petals, as we have already mentioned, and often by spurs, bags or pouches either formed from parts of the perianth, or sunk in the tissue of the receptacle, in which the nectar collects until an insect of the right type comes to find it.

Hermann von Müller in his observations on the pollination of alpine plants, published in 1881, sought to establish a hierarchy of colours among flowers, as related to pollinating visitors. He regarded yellow and white as relatively primitive colours and blue as the most highly evolved. There is much in this which is perhaps too fanciful, but Loew, working in the environment of the Berlin Botanic Gardens, where a great variety of flowers and insects, many of them strangers, are brought together, determined that pollinating insects visited mostly the darker-coloured flowers, while " unbidden guests " such as flies preferred the lighter colours.

Investigations on the Hive Bee show that it has no innate colour preferences, but that it quickly learns to associate a particular colour with nectar and can select that colour from a number of others. Bees have, however, very short sight, and it seems probable that they are only guided by colour at short range. On the other hand many insects have an extraordinarily keen sense of smell, which is probably the guiding influence at long range. Some flowers have markings on the corolla which have been known as " honey guides " ever since they were first pointed out by Sprengel, and it has been claimed that these markings have scents differing from those of the rest of the corolla. If this is true their smell may also be important at short range.

It is not only the colours themselves but their contrasts which lend conspicuousness to a flower and many striking contrasts exist. Such are, for example, the brilliant colour-patterns on the petals of *Tigridia*, the differently coloured standard and fall petals in many Irises, the contrasting colours of disc and ray-florets in many Composites, or the contrast of green flowers and coloured bracts as in *Poinsettia* and some *Euphorbias*. Even a dimly coloured flower may be made to stand out strikingly if provided with the right background, and this may frequently be noticed, as for example in the widely spread Composite genus *Helichrysum*, where the disc-flowers are weakly coloured, but the many bracts of the involucre are white or brilliantly tinted with red or yellow.

Among Butterflies, some similarity between the colour of the insect and the colour of the flowers it visits was noted by Hermann Müller in the Alps. Many alpine Butterflies are red-coloured and appear to choose red flowers. Some blue Butterflies, on the other hand, select blue flowers. This selectivity, even if it be only partial, may be related to another form of attraction which is reputed to occur among Orchids, namely that the labellum of the flower in such species as the Bee and the Spider Orchids resemble a female insect of a species frequenting the flower, which suggests that the attraction is sexual and that the insect is deceived by the resemblance. So far as the Bee Orchid is concerned the suggestion can scarcely hold good, since the flowers are habitually self-pollinated and are rarely visited.

It must not be overlooked that the insect has an interest to be served in visiting a flower and that it will prefer those flowers that best suit its size and capabilities, *i.e.*, with regard to strength and length of tongue. Such flowers, moreover, are less likely to have been visited and emptied by other types of insects with different capabilities. Butterflies, which have longer probosces than has any bee, prefer flowers with unusually long or narrow floral tubes, in the frequentation of which they have a

FIG. 1206.—*Lilium philadelphicum.* Flowers visited by a large moth. The wings gather pollen from the freely suspended anthers. Later this may be transferred to the stigma of an older flower. The stigma is presented laterally by the bending of the style. (*After Dodel-Port.*)

monopoly. As they have only themselves to look after, they are not so particular about the quality of the nectar they obtain, and like flies may be satisfied with nectar that would not attract the Honey Bee.

Butterfly and moth flowers are easily noticed on account of their visitors. Among them are *Dianthus*, *Phlox*, *Buddleia*, *Globularia*, and some species of *Lilium*, *e.g.*, *L. philadelphicum* (Fig. 1206). Other Lilies, like *L. canadense*, are bee flowers and it is noteworthy that the latter have fixed, not versatile anthers. The versatile anthers are better suited to contact with the large, beating wings of the Butterfly.

A striking case of close association between a flower and a particular type of insect is that of the Red Clover cultivated in New Zealand. When the plant was first introduced there, none of the local insects would visit it and the plants remained sterile. To get seed it was necessary to import English Humble Bees who felt at home with the Clover flowers and long remained faithful to it in spite of the competing attractions of the native flora.

Fig. 1207.—*Yucca whipplei*. A, Part of a flowering shoot. B, Flower open and ready for pollination. C, Female of *Pronuba yuccasella* placing a ball of pollen on the stigmas. (*Partly after Kerner.*)

This mutual dependence may reach a stage where neither plant nor insect can thrive without the other. The case of the Fig will be described later. Two other famous examples are those of *Yucca* and of *Silene nutans*.

The flowers of all species of *Yucca* are borne in large panicles and as they are white they are easily visible at night. The fresh buds open at sundown and the flowers form pendent bells (Fig. 1207). They are visited by a small yellowish-white moth named *Pronuba yuccasella*, the females of which creep into the flowers and collect pollen from the small anthers, which are borne on large, woolly filaments. This pollen the insect rolls up into a tight ball, aided therein by the sticky nature of the pollen itself, and by the use of its elongated maxillary palp, which can be rolled up to hold the pollen-ball. Having collected all the pollen it can carry, the moth departs to another flower, where it alights on the stamen filaments, pierces the ovary wall with its ovipositor and lays a batch of eggs alongside the ovules of the plant. Lastly it crawls up the style and pushes its ball of pollen firmly into the cavity between the lobes of the stigma.

The moth eggs hatch in four or five days and the grubs eat the *Yucca* ovules, each of them eating some twenty ovules. When fully developed they bite their way out of the ovary and lower themselves to the ground, where they pupate until the next flowering season of the *Yucca*.

Only about 20 per cent. of the ovules are destroyed, while the rest develop into seeds, and as no seeds are formed in the absence of the moth, it is plain that the survival of the genus *Yucca* depends on the operations of *Pronuba*. Likewise, the grubs are ensured a supply of food from the developing ovules by the act of pollination, without which *Pronuba yuccasella* would also perish. Apparently nearly all the species of *Yucca* are in a similar position of dependency, for only in one species has a transference of pollen in any other way been observed to occur.

A similar though much less striking case of mutual dependence is that of *Silene nutans* (Fig. 1208), which is typical of a number of other Caryophyllaceae and some Leguminosae and Rosaceae. This plant is a night-bloomer, the flowers being closed all day and showing only the brownish outer sides of the sepals and petals. At dusk its flowers open and display a

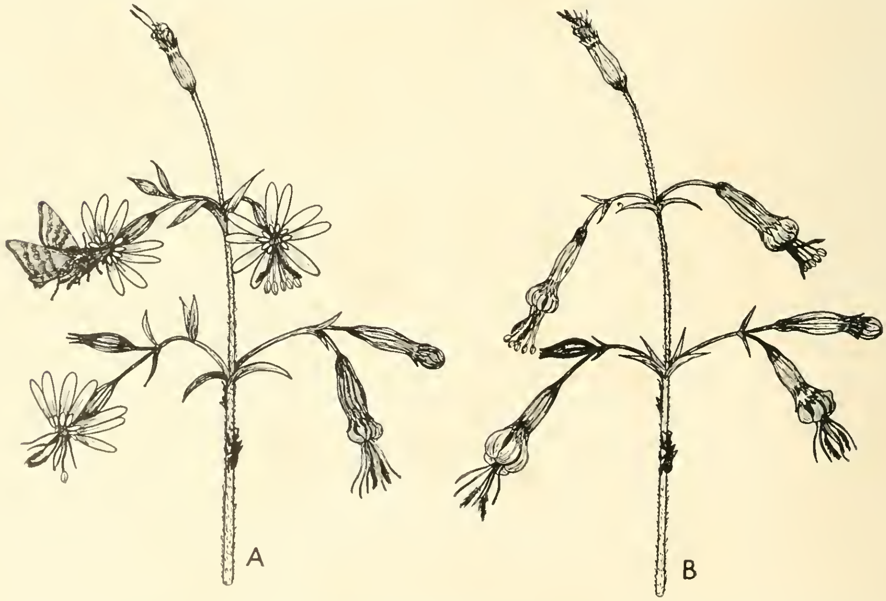


FIG. 1208.—*Silene nutans.* A, Night condition. B, Day condition. The moth *Dianthoecia albimacula* is shown pollinating a night flower. Notice also an ant caught by the sticky glands on the stem. (*After Kerner.*)

corolla of luminous white colour and five exserted anthers, at the same time diffusing a rich scent. It is pollinated by a moth, *Dianthoecia albimacula*, the males of which come for nectar. The females, however, lay eggs in the ovary of the flower and the larvae consume some of the ovules, though the remainder mature normally. The insects can only come flying, as the plant is covered with sticky hairs, and as the stamens ripen some time before the carpels, cross-pollination is ensured, for the stigmas alone are exposed on the third night of opening.

A species of Orchid from Madagascar, *Angraecum sesquipedale*, has a spur which reaches a length of nearly 30 cms., the longest known. It is supposed to depend for pollination on some species of moth with a proboscis long enough to reach the stored nectar. No such insect is known, though some Sphinx moths in Brazil have probosces over 15 cms. long. There may be here, also, a state of dependence between flower and insect, though it has not been proved. The contrary suggestion has been made that *Angraecum* is pollinated by small flies which creep bodily down the spur.

There are numerous night-flowering species, like *Silene nutans*, which was referred to above. Several species of *Nicotiana*, *Matthiola tristis*, the night-scented stock, and the night-flowering Cactus, *Cereus nycticalus*, are all well-known plants in this category. Most of them have white or pale yellow or lavender flowers, colours which have a luminous quality in dim light and are easily picked out at night. Some species are also night-scented and all are pollinated by night-flying insects, particularly moths. Some observers have remarked that flowers of bright red and orange-red shades, which are normally invisible at night, shine with intermittent phosphorescence, like some of the wood-destroying Fungi. This has been called the Elizabeth Linnaeus Phenomenon, after the sister of Linnaeus, who first noticed it in a garden bed filled with *Tropaeolum speciosum*. Another plant supposedly phosphorescent is *Lychnis chalcedonica*, whose flowers are one of the brightest reds in nature. The luminosity comes and goes in periods of a few seconds, is greatest during dewfall and fades later in the night. There is, however, a strong suspicion that the effect is only an illusion of the eye.

Some night-flowers only last for one night, as in the *Cereus* mentioned, which is common in many tropical parts of America and the Pacific islands, where it is called " Queen of the Night". Other species may open successively for several nights, as in *Silene nutans*, the flower being closed to visitors during the day, by the incurling of the petals, so that the flower resembles an unopened bud.

Many flowers which have an unusually short life, opening only for a few hours, whether by night or by day, have the further peculiarity that the petals, on withering, become crumpled and pulpy, their cell-sap exuding to the surface. The petals in this condition are visited by flies which suck up the exuded sap and at the same time cover themselves with pollen from the anthers, which they convey to other flowers. The flowers of the immense spikes in *Eremurus*, a liliaceous plant frequently cultivated, fade quickly, the petals shrivelling soon after the anthers open. In doing so they expose the swollen green veins on their under surfaces, which resemble Aphides so much that they attract Hover-flies to pierce and suck the veins as they normally do to green-flies. At the same time they become covered with pollen, which they carry away.

Variations of colour may sometimes play an important part in the attraction of insect visitors. A change of colour with age is not uncommon and if the flowers are closely massed the resulting contrast is more striking than if all the flowers were of one colour. A familiar example is the Apple, in which the petals in the bud may be bright red, but the expanded petals show only a faint flush of pink. Mixed together in the umbel the two states of the flower contrast strongly. An analogous change may take place in withering. Many yellow flowers turn white with age or blue (*Myosotis versicolor*). Blue flowers, such as those of *Myosotis*, may turn pink or white. Flowers, after pollination, may bend downwards and so display a differently coloured reverse. Lastly, the colour change may correspond to the sexual condition of the flower, as in the varieties of the Sweet William (*Dianthus barbatus*) whose flowers are white in the stage when pollen is being shed from the anthers, but turn red in the female stage, when the stigmas are receptive.

There may be a seasonal progression of colours, if the season is long, corresponding to the prevalence of different kinds of insects with diverse colour preferences. There is even a geography of flower colour, scarlet flowers, for example, being common in the Tropics, where they attract humming-birds as pollinators, though scarlet is a rare colour in temperate floras. These ideas open up interesting fields for consideration, but the facts are almost unknown.

Tubular or bell-shaped flowers, especially if they are pendent, need offer no other inducement to ensure nocturnal visitors, for they are welcome shelters for many small beetles, flies and Hymenoptera, which have no permanent homes. Composites like *Calendula* which close their capitula at night, are also favourite refuges. No special modifications have been observed bearing on these visits, but there can be no doubt that the refugees do carry pollen about from flower to flower.

Flowers pollinated by flies often have strong odours, suggestive of decay, which are repellent to us but must attract some types of fly. One would imagine that such smells would be enough in themselves to ensure attraction, but many of the tropical flowers which attract flies in this way (Aristolochiaceae, Rafflesiaceae, Araceae, etc.) are coloured to correspond with decomposing flesh, excreta, etc. The odour may act as a distant signal to the insect, but finding the source of the smell apparently depends, at least partly, on sight.

These odours are called indoloid, from their relationship to indol, though it is probable that some of them are really diamines. Amine odours are fairly plentiful in flowers and not all are obnoxious, at least when well diluted. The Hawthorn (*Crataegus*) owes its attractive scent to trimethylamine, which, when concentrated, creates "an ancient and fish-like smell". The same scent, with modifications due to admixture with other materials, is repeated in many Rosaceae, and some Cornaceae and Caprifoliaceae (*Sambucus racemosa*). Aromatic alcohols form a third group of distinctive perfumes, such as eugenol (oil of cloves) in *Dianthus* and cinnamyl alcohol in *Hyacinthus*, and the group includes many other well-known scents, *e.g.*, *Heliotropium*, *Jasminum*, *Reseda*, *Convallaria*, *Lonicera* and *Viola*, all delightful to our senses. The distribution of these perfumes follows no systematic grouping. The same or closely similar scents are to be found in flowers that have no systematic affinity and, on the other hand, different species of one genus may produce quite distinct perfumes; for example, *Sambucus racemosa* has a hawthorn scent, *S. ebulus* a vanilla scent, and *S. nigra* a paraffinoid scent. Acids and alcohols derived from paraffins form a different group of odours from those containing a benzene ring. To this group belong the perfumes of *Valeriana*, *Rosa*, *Ruta*, *Tilia*, *Phlox* and many Umbelliferae and Cruciferae. To this group also belongs the honey-scent which is so common, for example in *Trifolium*. The last group of perfumes are those belonging to the terpenes, such as oil of neroli in *Citrus*, oil of lavender in *Lavandula* and oil of citron in *Thymus*, *Verbena*, etc. They are almost always produced in internal glandular cavities.

We have already mentioned the production of perfume only after dusk by flowers pollinated by night-flying insects. The opposite event also occurs, some flowers which are day-pollinated giving out perfume only during daylight, when bees are flying, and becoming scentless at night. Such are *Spartium junceum*, *Parnassia palustris* and some species of *Trifolium* and *Daphne*.

Besides the insect visitors which are valuable as pollinators, flowers get many " unbidden guests ", insects of either the wrong shape or the wrong size to be satisfactory pollinators. There are a number of structural peculiarities which have the effect of discouraging these intruders, or at least the little ones. First the stems or the pedicels, or both, may be sticky, usually from numbers of glandular hairs, which prevent creeping insects from reaching the flowers. This may also extend to the calyx and in *Cuphea* (Fig. 1209) the protection is limited to a barrier of sticky hairs on the ends of the sepals, around the entrance to the flower. Against flying insects of small size there are often internal barriers, most frequently of hairs, either on the inside of the corolla, on the stamen filaments or along the style. Sometimes the protection takes the form of narrowing the channel to the nectar by contraction of the floral tube, or by the inrolling of some parts of the flower, in such a manner that only the proboscis of a large insect can penetrate it. In *Centranthus ruber* both methods are combined (Fig. 1210). The tube of the flower is divided longitudinally and only one of these channels leads to the spur where the nectar is held. It is lined with hairs, while the other channel, which leads to the ovary, has none.

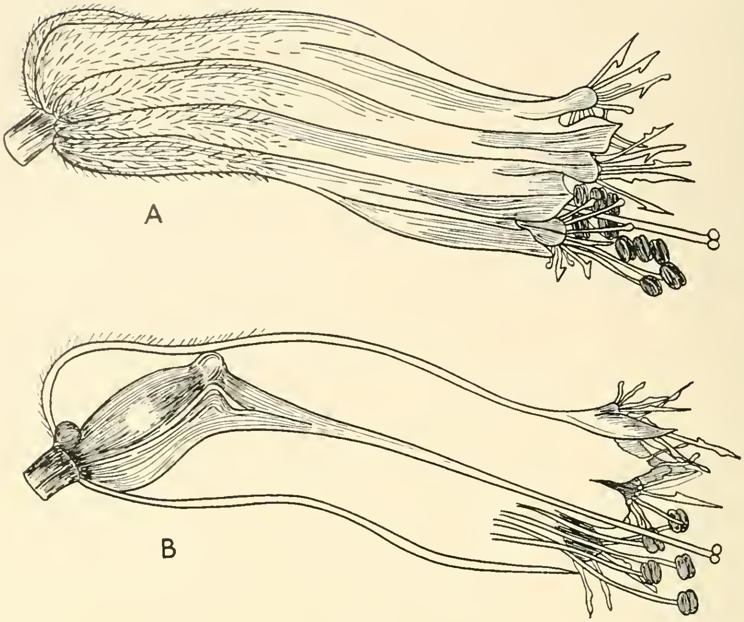


FIG. 1209.—*Cuphea micropetala.* A, Side view of flower. B, Flower in longitudinal section. The entrance to the flower is guarded by the sticky hairs at the ends of the sepals. (*After Kerner.*)

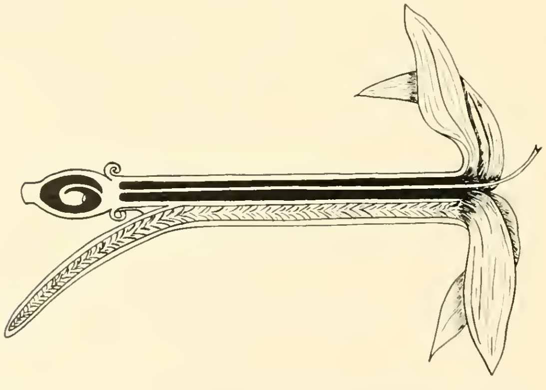


FIG. 1210.—*Centranthus ruber.* Longitudinal section of flower, showing separate nectary spur lined with hairs. (*After Kerner.*)

THE SEXUAL STATUS OF FLOWERS

Errera and Gevaert in 1878 drew up the following classification of the distribution of the sex organs in flowers, covering all observed variations. It well illustrates the differences which exist in this respect. The personal names in brackets denote the introducer of the term referred to.

I. Individual plants, monomorphic, *i.e.*, all alike in regard to the flowers they bear.
  1. Flowers monomorphic. All flowers alike, hermaphrodite.
  2. Flowers heteromorphic. Flowers of two or more kinds on each plant.
    A. Monoecious. Flowers on each plant either male or female. *Zea, Cucurbita.*
    B. Dimonoecious. Flowers of two kinds on each plant, hermaphrodite and another kind.
      1. Andromonoecious (Darwin). Flowers hermaphrodite and male. *Aesculus.*
      2. Gynomonoecious (Darwin). Flowers hermaphrodite and female, *Atriplex, Parietaria.*
      3. Agamonoecious. Flowers hermaphrodite and sterile. *Viburnum, Centaurea.*
    C. Trimonoecious, or Coenomonoecious (Kirchner), or Monoecious polygamous (Darwin). Flowers hermaphrodite and male and female, on each plant. *Acer, Ricinus.*

II. Individual plants, heteromorphic. Two or more kinds of individual, distinguished by their flowers.
  1. Heterostyly (Hildebrand). Flowers on different plants differing in the development of their sexual parts.
    A. Distyly (Dimorphism). Two kinds of individuals, bearing long-styled and short-styled flowers respectively. *Primula.*
    B. Tristyly (Trimorphism). Three kinds of individuals, bearing long, short and medium-styled flowers respectively. *Lythrum.*
  2. Polyoecism. Individuals of different sexual status.
    A. Dioecious (Linnaeus). Individual seither wholly male or female; true dioecism. *Salix.*
    B. Androdioecious (Darwin). Some individuals male, others hermaphrodite. *Dryas, Caltha.*
    C. Gynodioecious (Darwin). Some individuals female, others hermaphrodite. *Thymus.*
    D. Trioecious or trioecious polygamous (Darwin). Some individuals male, others female and others hermaphrodite. *Fraxinus, Ruscus.*

The following exceptional cases should be noted as modifications of the general scheme.

1. Some individuals hermaphrodite, others with both male and female flowers. *Callitriche.*
2. Some individuals male, others with both male and female flowers. *Arctopus* (Umbelliferae).
3. Some individuals female, others with both male and female flowers. *Morus.*
4. Some individuals female, others with both male and hermaphrodite flowers. *Gleditschia.*

STATUS OF FLOWERS WITH REGARD TO POLLINATION

The classification of the sexual conditions of flowers as originally presented by Errera and Gevaert had the disadvantage of bringing together in one scheme, both structural differences and behavioural differences, which led to complication and some lack of clarity. We have attempted here to separate the two ideas. We have presented the scheme of structural differences above and we must now consider differences of sexual behaviour in regard to pollination. The following scheme is based mainly on that of Errera, but with some modifications, to avoid, so far as possible, the overlapping of groups.

I. Cleistogamy (Kuhn). Flowers do not open and are internally self-pollinated or self-fertilized. This condition will be more fully considered later.

II. Chasmogamy (Axell). Flowers are pollinated in the open condition.

1. Autogamy (Delpino). Homogamy (Sprengel). Self-pollination. This is naturally only possible in hermaphrodite flowers. It is only effective if the species is self-fertile, *e.g.*, *Trifolium arvense.* If the species is self-sterile, *e.g.*, *Trifolium pratense*, autogamy is ineffective and cross-pollination must occur. The mode of autogamy has been distinguished as:
    A. Direct autogamy. Pollen deposited directly from the anthers on to the receptive stigma.
    B. Indirect autogamy. Pollen has to be conveyed to the stigma by an external agent.
2. Allogamy (Kerner). Cross-pollination, by pollen from another flower of the same species. This may happen in either of two ways : Geitonogamy (Kerner), which implies pollination by another flower of the same inflorescence or the same plant. Xenogamy (Kerner), which implies pollination from another individual. Either of these events may occur in unisexual or in hermaphrodite flowers, but in the latter, allogamy requires that there shall be some means of avoiding primary self-pollination. This is secured by one of two methods :

A. Herkogamy. The separation of anthers and style in such a way that direct autogamy is mechanically impossible. *Anacamptis* (*Orchis*) *pyramidalis.*

B. Dichogamy. The separation of the sexes by different times of ripening. Under this heading there are two alternatives :

1. Protandry (Hildebrand) or Proterandry (Delpino). The stamens ripen before the stigmas. Many examples. *Eremurus* (Fig. 1211).

FIG. 1211.—*Eremurus bungei.* Part of an inflorescence showing protandry. Above are unopened flowers, next, a zone of flowers with ripe stamens, and below, flowers with mature styles.

2. Protogyny (Hildebrand) or Proterogyny (Delpino). The stigmas ripen before the stamens. *Plantago* (Fig. 1212).
The second alternative is less common than the first, in hermaphrodite, but it occurs in all monoecious and most dioecious plants.

3. Heterogamy. Individual plants vary in regard to the method of pollination of their flowers.

A. Allo-autogamy. Some individuals are predominantly self-pollinated, others are cross-pollinated. *Viola tricolor.*

FIG. 1212.—*Plantago media.* Inflorescence showing protogyny. Upper flowers with long stigmas, lower flowers with long stamens and versatile anthers.

B. Homodichogamy (Errera). Some individuals are autogamous, others dichogamous. *Ajuga reptans.*

C. Heterodichogamous. Some individuals are protandrous, others are protogynous. *Juglans.*

III. Chasmocleistogamy (Delpino). Flowers are hermaphrodite, but some are chasmogamous and some cleistogamous. *Viola*, *Oxalis*, and many other examples.

Direct autogamy stands somewhat apart from other methods of pollination because it involves only the internal arrangements in the flower itself and is not dependent upon visitors. It seems paradoxical that autogamy should take place at all, considering the extraordinary variety and abundance of the contrivances which exist to promote allogamy. There can be no doubt that allogamy has certain important advantages, but this does not mean that autogamy is excluded and it very often happens that both events may occur in the same flower. Autogamy pure and simple is comparatively rare except in cleistogamous flowers, but it often occurs secondarily as a concomitant of allogamy, being, as it were, a safety mechanism which ensures that self-pollination shall occur if the biologically preferable cross-pollination should fail.

Some chasmogamous flowers with a structure from which one would infer allogamy have nevertheless adopted the habit of self-pollination, as if by retrogression they had abandoned allogamy and adopted autogamy as a short cut. This is the case in the Sweet Pea, whose stigmas are already receptive, and pollinated, before the flower opens. Some of the cereal Grasses also, although members of a family which habitually uses wind-pollination, are self-pollinated in the bud state. Even if cross-pollination occasionally occurs at a later stage in such flowers, the start obtained by the pollen-tubes of the flower itself would practically ensure that self-fertilization resulted.

In cold northerly climates, where insects are very scarce, autogamy is prevalent among many plants which are allogamous in more favourable regions. In such climates Diptera may be locally plentiful near human settlements and they may serve as pollinators for a number of plants usually dependent on bees, *e.g.*, *Thymus*, *Geranium*, *Melandrium* and *Iris*. This pollination by flies may be allogamous but is more generally autogamous. Gunthart observed that in Cruciferae and Crassulaceae and in the genus *Saxifraga*, all entomophilous species were also capable of autogamy and that the nature of the pollination might vary with the locality, protogyny changing into protandry and vice versa.

Obviously, without self-fertility autogamy is useless, and it may frequently occur without result. Self-fertility does not seem to cause any debilitation of the plant, but it must very seriously limit the gene-content and impoverish the plant from the point of view of variation, except for the comparatively rare occurrence of gene mutations.

Autogamy may be brought about in a great many ways. Indeed there are almost as many devices working for autogamy as for allogamy. One of the simplest principles is that of an overlap in time between the ripening of stigmas and anthers in dichogamous flowers, without any other arrangement. There is thus provided a period during which self-pollination is possible and usually occurs, if the anthers are close to the stigma. This is to be seen in many Liliaceae, Amaryllidaceae and Iridaceae and in some Dicotyledons such as *Geranium* and *Lithospermum*. The principle of an overlap in time is indeed inherent in the following more complex arrangements, since without it autogamy would be difficult and rare.

Movements of the floral parts often assist autogamy and these may be divided into movements of growth and movements due to bending or folding of organs. In the first category we have those upright flowers where the stigmas are at first above the anthers and so out of the way of their pollen. Subsequently, however, the stamen filaments may elongate and place the anthers either beside or above the stigmas, which are still receptive. This is common in Cruciferae, Caryophyllaceae and a variety of other families. The opposite case of elongation of the style occurs in *Epimedium*. The flowers are more or less pendent and the valves of the open anthers, loaded with pollen, are below the level of the stigma, which is only brought into contact with them by growth of the style.

Movements of elongation are often associated with bending movements, particularly in the style, which by such means places the stigma among the anthers. This is to be seen in most of the Rhinanthaceae and also notably in *Malva*. Bending movements, pure and simple, may also affect the style, as in some Labiatae, but are more often seen among stamens, which either bend in towards the stigma (*Lepidium*, *Paris*, *Lysimachia*), or arch themselves over the stigma and drop pollen directly on it (many Umbelliferae). In some of the Cactaceae, *e.g.*, *Cereus*, the stigma is at first thrust out well beyond reach of the pollen from the numerous stamens, but later is retracted by shrinkage of the long style, so that it is finally surrounded by pollen-laden anthers. Bending of the stigma is common among the Compositae. The long stigmatic lobes, which are receptive only on the upper surface, curl over so that this surface touches the style or the top of the anther tube, below the stigma, and thus picks up any remaining pollen.

Some actinomorphic flowers which are freely exposed may be autogamously pollinated by rain. A large drop collects in the flower and on this drop the pollen floats and finds its way to the stigmas. Hagerup has observed this in various species of *Ranunculus*, *Caltha* and *Narthecium*.

Lastly there are the instances of the corolla aiding in autogamy, which are often striking. Where the stamens are attached to the wall of a floral tube, the anthers may be brought against the stigma by the closing of the flower at the end of anthesis. The infolding of the petals in a sleep-movement may cause pollination, if pollen has previously been shed upon them. A good example in the Papaveraceae is *Argemone mexicana*. In flowers with tubular corollas, even if the tubular portion is very short, the abscission of the corolla as a whole allows it to slide forward along the stamen filaments, thus forcing the anthers into contact with the stigma. This occurs in several well-known plants, such as *Rhododendron*, *Anagallis*, and *Digitalis*. Even without abscission, the elongation of the corolla tube may carry pollen held on its surface upwards to the level of the stigmas.

These are only a few of the multitudinous devices which have been noted, but they make clear the general importance of the process among the flowering plants.

We have already dealt with the probable origin of dioecism in the previous chapter (p. 1131) and have shown reason to believe that the unisexual condition is secondary and derived from the hermaphrodite condition. As an example of the complexity which may exist in flowers in a transitional state, we may take the Trailing Arbutus, *Epigaea repens*. The flowers may be divided into two groups. The first group has large, well-developed, radiate stigmas, which are glutinous and retentive of pollen. The second group has small, erect, dry stigmas, on which pollen does not germinate. In both these groups there is a continuous variation in the length of the style, between the middle level of the corolla tube and exsertion of the stigma above the flower. The first group rarely produces pollen and rarely has more than sterile stamen filaments. The second group has good pollen and stamens which vary in length like the styles. The suggestion of heterostyly is negatived by the continuous nature of the variation in length and the fact that any length of style may be combined with any length of stamen. The flowers with dry stigmas never set seed, although the ovary and ovules appear perfect and the species is therefore functionally dioecious though structurally hermaphrodite.

Dioecism is usually associated with some degree of protogyny and the female plant not only flowers sooner but often lives (*Cannabis*, *Trinia*) longer than the smaller and slighter male. There may be quite a marked difference in the growth-habit and appearance of the two sexes. *Cannabis indica* is a case in point (see Fig. 1630). Other examples are *Osyris* (Santalaceae) and *Myzodendron* (Myzodendraceae) where foliage and habit are quite distinct.

Flowers which are dimorphic or heterostylous are sometimes regarded as being on the road towards dioecism. True **heterostyly**, however, as Darwin showed, is not definable purely on the morphological differences between flowers in respect of the length of style, but includes the physiological difference that neither type is fully fertile unless pollinated by the other. The condition is remarkably widespread and has been recorded from seventeen families, including Primulaceae, Oxalidaceae, Polygonaceae, Lythraceae, Plumbaginaceae, Gentianaceae, Boraginaceae and Rubiceae. In only a relatively small number of cases has the effectiveness of pollination been tested.

The classic case of *Primula* (*P. veris*) (Fig. 1213) was the first to be described in detail, by Darwin, who sums up the differences thus : The *long-styled* flowers have globular and much rougher stigmas, covered with papillae which are twice to three times as long as in the short-styled flowers, and standing high above the anthers. The stamens are short, the grains of pollen smaller and oblong in shape, though the anthers are the same size in both types of flower. The upper half of the corolla tube is more expanded. The number of seeds produced is smaller and the ovules larger. The plants tend to flower first.

The *short-styled* flowers bear the stigma at about half the height of the corolla tube, with a smooth, depressed stigma standing well below the anthers. The stamens are long, the grains of pollen are spherical and larger. The tube of the corolla is of uniform diameter except close to the upper end. The number of seeds produced is larger.

There are no intermediate forms, the two types are always borne on different plants, and plants of one type never change into the other. The two types exist in nature in approximately equal numbers. Most species of *Primula* have analogous differences between their flowers, but a few are homostylous and self-fertile, including the British species *P. scotica*. Dar-

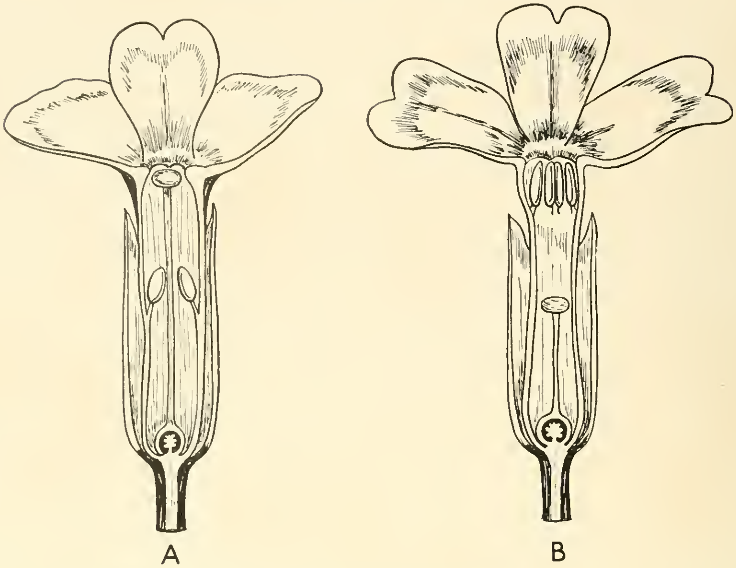


Fig. 1213.—*Primula veris.* Heterostyly. A, Long-styled flower. B, Short-styled flower. The two forms are known traditionally as " pin-eyed " and " thrum-eyed " respectively. (*After Darwin.*)

win showed in *Primula veris* that pollination of short-styled by long-styled flowers, or vice versa, gave more than twice the number of good capsules per hundred, and more than three times the weight of good seed, in comparison with the pollination of each type of flower with pollen from the same type. Here there is a specialized kind of sexual segregation. Pollination, even from another individual, is relatively ineffective if the flowers are of the same type. Not cross-pollination with any other individual, but only with a limited class of individuals carries with it the benefits of crossing. We shall see presently that a similar limitation obtains in some other plants where no difference in flower type is present.

The two types of flower are determined by a single Mendelian character. The long-styled type is homozygous and recessive, the short-styled type is heterozygous and dominant. Short-styled plants if self-pollinated give short and long-styled offspring in the 3 : 1 ratio. Long-styled plants if selfed give only long-styled plants.

Darwin called the fully fertile pollination " legitimate " and the less fertile one " illegitimate ", and he showed that the disproportion in the fertility of the two kinds of union was even greater in some other species of *Primula* than in *P. veris.* The Oxlip, *P. elatior*, is exceptional in that it produces *equal-styled* as well as heterostyled flowers and that both long- and short-styled flowers may occur on the same plant. The same kind of relationships in regard to pollination hold good, however, as in other species.

The impression that heterostyly was an approach towards morphological dioecism, Darwin showed was incompatible with the observation that the short-styled flowers, which might be supposed to be tending towards maleness, were actually more fertile than the others, producing a significantly greater weight of seed per hundred capsules.

Despite these arrangements for cross-pollination in *Primula*, Darwin was aware that very few visitors can be seen on some species, notably the Primrose (*P. vulgaris*), which he surmised was pollinated by night-flying moths. There has never been a definite solution of this question, but careful observations by Dallman showed that moths can be ruled out. He found that in cold and cloudy weather the Primroses are neglected, but that in sunny warmth there are a number of visitors, especially the large dipterans, *Bombylius major* and *B. discolor*, which are probably the chief pollinators, assisted by small beetles and perhaps nocturnal slugs.

The Buck Wheat, *Fagopyrum esculentum*, is generally heterostylous, but equal-styled flowers may occur on plants of either type. There is seldom more than one such flower on the plant and it is usually the first which opens. By " equal-styled " is meant the condition where stigmas and anthers are both at the same level. It is notable that on short-styled plants the equal-styled flowers have both styles and stamens long, and the reverse on long-styled plants. Stevens showed in this species that after legitimate pollination, the embryo had already begun development after 18 hours, while at this time the pollen tubes in illegitimate pollination had scarcely begun to grow. Between 72 and 96 hours were required in the latter case for embryo development to begin, irrespective of whether the styles were long or short. These flowers are so constantly visited by insects for the sake of their nectar that, in nature, illegitimate fertilization would practically never occur, owing to the prepotency of the " legitimate " pollen.

An interesting case of dimorphism is presented by the tribe Staticeae of the Plumbaginaceae, especially the genera *Armeria* and *Limonium*, which have been investigated by Iversen and Baker. They are dimorphic both in regard to styles and to pollen. In *Limonium* the styles differ in length but in *Armeria* they are all the same length and the difference is limited to the stigmatic papillae. *Armeria maritima* exists in two types, A and B (Fig. 1214). The type A has relatively smooth stigmas and large, rough-coated pollen grains. The B type has markedly papillose stigmas and smaller, less rough pollen grains, but there is no difference in length of style between the types. They are described as para-sterile, because the A pollen will only germinate on the B stigmas and vice versa. Only the species of *Armeria* native to the European-Mediterranean region are dimorphic, those in the Arctic and in America and Asia are all monomorphic. In the Arctic species *A. labradorica*, which is monomorphic and self-fertile, both A and B pollen of *A. maritima* will germinate on the stigmas, but its own pollen will only germinate on the stigmas of *A. maritima*, type B. This seems to indicate that the monomorphic species has originated from the A type of a dimorphic ancestor.

More complex conditions exist in some other flowers. For example, *Eschscholtzia californica* possesses four styles. Certain larger flowers produce two long and two short styles. The longer ones stand above the anthers

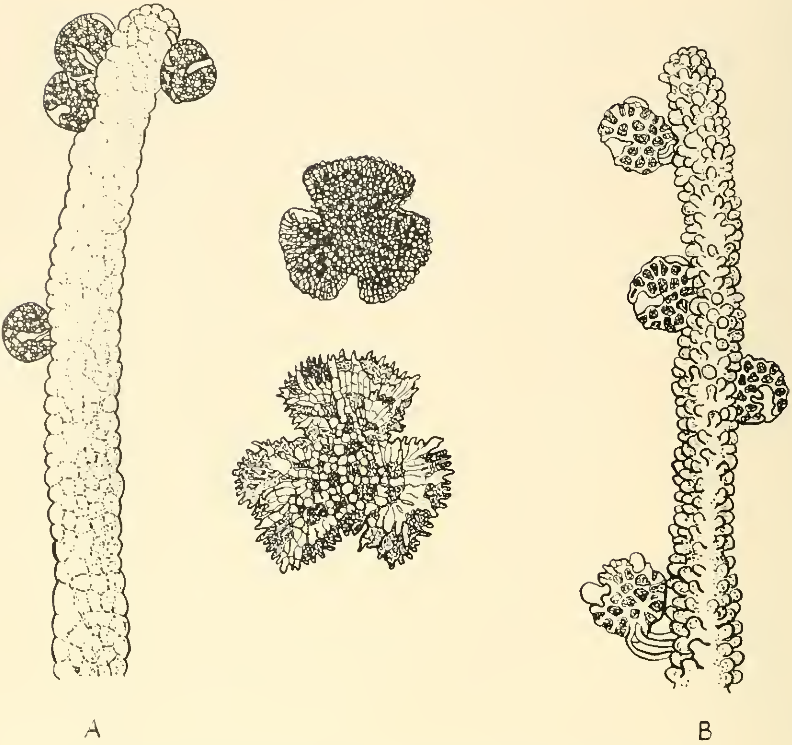


FIG. 1214.—*Armeria maritima*. A and B, The two respective types of stigma, each carrying the opposite type of pollen. In the centre, A-type pollen below, B-type pollen above. (*After Iversen*.)

and are cross-pollinated. The shorter ones lie among the anthers and are directly self-pollinated. Smaller flowers may have all four styles short and self-pollinated. Several species in Ranunculaceae and Rosaceae have heterostylous hermaphrodite flowers and produce male flowers with abortive carpels. The classic case of higher complexity is, however, that of heterotristyly or heterostylous trimorphic flowers, best known in *Lythrum salicaria*, the Purple Loosestrife (Fig. 1215), but also found in several other genera. Here again Charles Darwin gave the first account of the mechanism of pollination. There are three kinds of flowers: first, the *long-styled*, with six mid-length and six very short stamens and the style projecting considerably beyond all of them. Secondly, the *mid-styled* flower, which has six very short stamens, six which are as long as the style in the first type of flower, and a style which is mid-length. The third flower is *short-styled* and has six mid-length and six long stamens, while the style is only as long as the short stamens in the other flowers. The long style is more than three times as long as the shortest one, and the stigmas and anthers are also graduated in size according to the development of the respective styles and stamens. A striking peculiarity is that the short and mid-length stamens have yellow pollen, but the longest

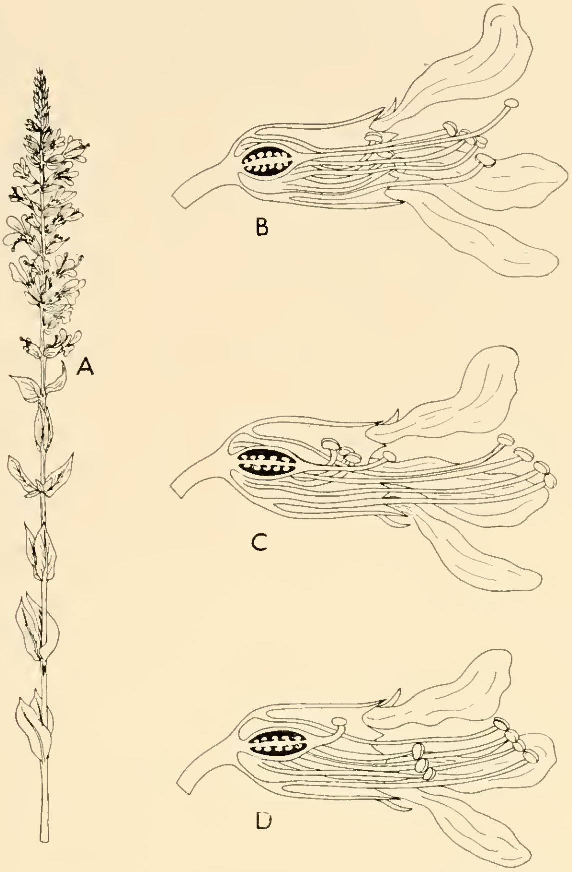


FIG. 1215.—*Lythrum salicaria*. Trimorphic flowers. A, Inflorescence. B, Long style, long and medium stamens. C, Medium style, long and short stamens. D, Short style, long and medium stamens. (*Partly after Darwin.*)

stamens have pink filaments and bright green pollen. The seeds of the long-styled ovaries are the biggest, the ratio being 1 : 0·83 : 0·70, and the same difference of size is shown by the pollen grains. All three types of plant are about equally common.

As there are nine different sets of sex organs among the three types and as each set of stamens occurs twice over, there are eighteen possibilities in pollination. Thus the stigma of the long-styled flower may be pollinated in two ways "legitimately", *i.e.*, from the long stamens of both the other types of flower, and in four ways "illegitimately", from the short and mid-length stamens. The first two unions are abundantly fertile, the latter four are highly sterile. The same is true of the flowers with mid-length or short styles, although the mid-styled form is more generally fertile.

We have already spoken of the importance of autogamy, or self-pollination, as a secondary means of securing pollination in case of the failure of cross-pollination. Later investigations have shown that heterostylous plants are no exception, but autogamy seems to be confined to one only of the flower-types produced by each species. Where this is the short-styled form, the stigma receives pollen falling directly from the anthers above it, provided that the position of the flower is vertical. Where the flower is not vertical, it is usually the long-styled flower which is autogamous. The corolla may dehisce as a unit and in slipping over the style bring the short stamens up to the stigma, which is thus pollinated by the remaining pollen. Various devices of bending or growth of the floral parts may also operate in heterostylous as in other types of flower to bring about self-pollination.

It has been pointed out that in dichogamous flowers the first protogynous flowers and the last protandrous flowers cannot be pollinated by their own species and hence are amenable to hybridization. The more complete dichogamy is, the greater are the chances of foreign pollination, which may sometimes be effective. Similarly the pollen of the first flowers in protandrous species cannot be used to pollinate flowers of their own species, since no stigmas are yet receptive. Variation in the flowering times of different plants of the species may alleviate this difficulty but cannot altogether overcome it and an ineffective phase must exist, if only a short one. Hence the importance of incomplete dichogamy, which allows an overlapping period when both sexes are active. It is much commoner than complete dichogamy. Indeed if a dioecious species, such for example as a Willow, were completely dichogamous it could hardly continue to exist. Even the incomplete dichogamy of *Salix* allows for a high frequency of hybrid pollination. The Dutch Elm, *Ulmus hollandica*, var. *belgica*, shows an extreme case of this difficulty. The flowers are hermaphrodite but highly protandrous and all the flowers shed their pollen at the same time. As none of the embryo-sacs are then ready for fertilization a large proportion of the pollen is wasted and most of the pollination is from other species of Elm, with a high degree of sterility in consequence.

We have seen above that illegitimate pollinations in heterostylous flowers are usually ineffective. This is only a special case of the general phenomenon of **self-sterility** or its analogue, **incompatibility**. Self-sterility is known to exist in many plants and probably is widespread. Among cultivated plants, especially in fruit trees belonging to Rosaceae, it may be of great economic importance. It is not, as a rule, a uniform feature throughout a whole species, but may vary from population to population or from individual to individual. It may coexist with regular self-pollination, which, of course, it renders useless, and it is a complete barrier to autogamy. The allied condition of incompatibility is one in which the flower, generally self-sterile, is also sterile to pollination by certain other strains of its own species. We are not simply dealing, in such cases, with two sexes, but with a number of specialized strains in each sex, among which sexual unions are limited to certain strains only. There is more than a hint here of analogy with the condition of multiple heterothallism which obtains among the higher Fungi. Heterothallism itself indeed is, basically, self-sterility

Whatever its cause, and among Angiosperms it is not always due to the operation of the same factors, it is a phenomenon of great biological importance and its recognition underlies all consideration of pollination. We shall deal with it more particularly in the Chapter on Sex in Volume III.

The relative fertility of species has been too little studied in relation to their reproductive power. It is obvious that successful pollination is only one of the conditions involved. Observation shows that flowers in different parts of an inflorescence may vary greatly in fertility, some being invariably sterile, and the same is true of whole individual plants. There may also be long-term causes at work to reduce the fertility of entire species. Perttula has shown that there is a negative correlation between the power of vegetative propagation and the power of producing fertile seed, and this may be connected with the types of plant association in which a species lives, plants of the more advanced and highly integrated associations having, in general, a lower seed-fertility, and greater activity in vegetative reproduction (see also p. 1351).

MODES OF POLLINATION

We have already spoken (p. 1253) of the necessity of an external agent to ensure pollen-transport in cross-pollination, to wit either wind or water or animals, especially insects. We must now consider in more detail those relationships between the floral structure and the pollinating agent, which are generally referred to as " pollination mechanisms ". For this purpose we shall use the following outline classification of the chief types of pollination mechanism, which is modified from that of Knuth. The named types have been selected as far as possible from among the less common examples. Further examples will be described in the following chapters dealing with the Families of the Angiospermae and as far as possible repetition has been avoided.

Types of Pollination Mechanisms

I. **Anemophily** (Wind Pollination)	
(*a*) Flowers with no stigma (Gymnospermae)	*Pinus*, *Taxus*, *Cycas*
(*b*) Flowers with stigma	
1. Catkin type	*Quercus petraea*
2. Pendant type	*Rumex crispus*
3. Long filament type	*Plantago major*
4. Explosive type	*Urtica dioica*
5. Motionless type	*Sparganium ramosum*
II. **Hydrophily** (Water Pollination)	
(*a*) Pollination below water level	*Ceratophyllum demersum*
(*b*) Pollination at water surface	*Ruppia maritima*

III. **Zoidiophily** (Animal Pollination)	
A. *Chiropteriphily* (Bat flowers)	*Bauhinia megalandra*
B. *Ornithophily* (Bird flowers)	
1. Direct Bird flowers	*Bignonia* spp.
2. Indirect Bird flowers	*Marcgravia nepenthoides*
C. *Malacophily* (Slug and Snail flowers)	
1. Land plants	*Chrysanthemum leucanthemum*
2. Water plants	*Lemna* spp. (?)
D. *Entomophily* (Insect Pollination)	
(*a*) Flowers visited for pollen	
1. Actinomorphic flowers	*Verbascum nigrum*
2. Zygomorphic flowers	*Cassia marylandica*
(*b*) Flowers visited for nectar	
1. Flowers with exposed nectar	*Euonymus europaeus*
2. Flowers with partly concealed nectar	*Berberis vulgaris*
3. Flowers with concealed nectar	*Vaccinium myrtillus*
4. Social flowers with concealed nectar	*Scabiosa arvensis*
5. Flowers visited by special groups of insects	
i. Hymenopterous flowers	
(*a*) Hive Bee flowers	*Trifolium repens*
(*b*) Humble Bee flowers	*Trifolium pratense*
(*c*) Bee-Humble Bee flowers	*Calamintha alpina*
(*d*) Bee-Butterfly flowers	*Rhinanthus hirsutus*
(*e*) Wasp flowers	*Scrophularia nodosa*
(*f*) Ichneumon Fly flowers	*Listera ovata*
ii. Lepidopterous Flowers	
(*a*) Butterfly flowers	*Phlox paniculata*
(*b*) Moth flowers	
(*a*) Flowers opening by day	*Lilium martagon*
(*b*) Flowers opening by night	*Nicotiana affinis*
iii Dipterous Flowers	
(*a*) Nauseous flowers	*Saxifraga aizoides*
(*b*) Pitfall flowers	*Asarum europaeum*
(*c*) Pitfall inflorescences	*Arum maculatum*
(*d*) Pinchtrap flowers	
(*a*) Clip type	*Asclepias curassavica*
(*b*) Orchid type	*Pterostylis longifolia*
(*c*) Bristle type	*Pinguicula alpina*
(*d*) Explosive type	*Crucianella stylosa*

(*e*) Deceptive flowers	
(*a*) Deceptive nectar flowers	*Parnassia palustris*
(*b*) Deceptive nauseous flowers	*Paris quadrifolia*
(*f*) Hover Fly flowers	*Veronica chamaedrys*
iv. Small Insect Flowers	*Herminium monorchis*

I. Anemophily or Pollination by Wind

The way in which wind could effect pollination was first described by Sprengel in 1793. Plants which adopt this mechanism exhibit certain peculiarities. In the first place the stigmas are often branched or are provided with brush-like or feathery outgrowths which are suitable for catching wind-blown pollen. Further the pollen grains are usually smoothed-walled, dry and light in weight so as to render them buoyant.

In general, the flowers of wind-pollinated plants are devoid of showy parts, calyx and corolla are either absent or are much reduced, and in the case of monoecious inflorescences there may be a marked difference in the form and arrangement of the male and female flowers. The male flowers are usually more numerous than the female ones; they may be aggregated into catkins or may form independent inflorescences of various forms. The anthers are often loosely suspended from the tips of long filaments and may hang outside the limits of the flowers. In some instances the individual flowers are pendulous, allowing the whole flower to be swayed by the wind. More rarely the floral parts are immobile, but the anthers are explosive.

In wind-pollinated flowers the sexes are often separated, so that self-pollination is entirely prevented, but in hermaphrodite flowers the anthers usually mature well before the style is ripe for reception.

There is often a direct correlation between the exposure to wind and the composition of the flora of an area. It is found that in exposed, windy situations a larger proportion of the plants are wind-pollinated as compared with more sheltered situations, which favour plants adapted to insect pollination.

Some plants which are adapted to insect pollination may be at times wind-pollinated. Examples of this are seen in such genera as *Erica*, *Calluna* and *Bartsia*. In these flowers the corolla is so constructed that when the flowers first open wind pollination is impossible, but nectar is secreted and the flowers are normally pollinated by insects. Should insect pollination fail, due, for example, to unfavourable weather conditions, the supply of nectar may become exhausted before pollination has been effected. In such cases the filaments subsequently elongate sufficiently to push the anthers out beyond the limits of the corolla and when the pollen is liberated in this way it can be carried by wind to the stigma of the same or a different flower.

A similar adaptation is exhibited by some species of *Cyclamen*. In their early state the flowers are adapted to insect pollination and the pollen grains are covered with a sticky oil which ensures that they adhere to the body of a visiting insect. If insect pollination fails the pollen becomes powdery, the stickiness disappears and the grains become adapted to wind dispersal.

Most pollen readily absorbs water, so it may be spoilt by moisture and it is important to protect it from damp. Moreover in damp weather the distribution of pollen by wind will be less effective. Various methods are known which prevent the discharge of pollen in wet weather or preserve it in a dry state if it is shed. The anthers of some plants, for example, open only in dry air. The pollen of many catkin-bearing trees is not actually scattered when it leaves the anther. As the pollen is discharged it accumulates in the flowers in a position protected from moisture and is subsequently scattered by the shaking of the catkin by the wind. In a similar manner the pollen of various Conifers collects on the under side of the stamens and it is from this that it is finally distributed. In *Hippophaë rhamnoides* the pollen is concealed in two shell-like scales which meet at the top and open only at the sides in dry weather. In *Triglochin maritimum* the pollen collects in boat-shaped pockets situated under the anthers and it is from here that it is scattered by the breeze. (See also p. 1101.)

(*a*) *Flowers with no Stigma*

In this group are included the Gymnosperms, in which no stigma exists and the pollen grains find a way between the scales of the female cone to the ovule itself. The pollination of *Pinus* and *Taxus* has already been described in Volume I.

Although the possession of a stigma is one of the distinguishing marks of the Angiosperms, there is at least one species in this class whose stigma is functionless and in which pollination is directed to the ovule as in Gymnosperms. This is *Rheum australe* (Polygonaceae), which has the usual three large stigmas of its genus. There is only one, erect ovule, whose nucellus protrudes through the micropyle of the integument and also through the apex of the ovary. Thus exposed it becomes adhesive and receives pollen directly, the stigmas taking no part in the process (Fig. 1216).

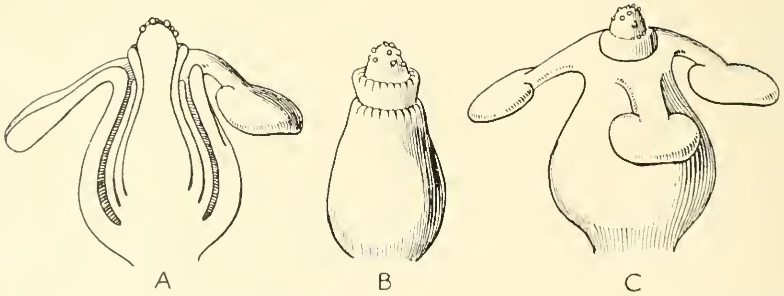


FIG. 1216.—*Rheum australe.* A, Vertical section of the gynoecium with open top from which the apex of the solitary ovule protrudes. B, Ovule with nucellus protruding from the micropyle. C, The gynoecium with three functionless stigmas and the protruding apex of the nucellus, bearing pollen grains. (*After Velenovsky.*)

(*b*) *Flowers with Stigma*

It is to this group that all the wind-pollinated Angiosperms belong. There are a number of different types which are best treated separately.

1. *Catkin Type*

This type of pollination is often referred to as the amentiferous type because the great majority of the species which exhibit it belong to the Benthamian group of the Amentiferae. In these species the male inflorescence is a catkin, that is a long inflorescence made up of male flowers which are individually immobile, but are collectively attached to an elongated axis which can be readily shaken by the wind. The female catkins are shorter and relatively immobile, but with large stigmas (see Fig. 1189, p. 1230). Good examples are seen in such common catkin-bearing trees as *Corylus avellana* (Hazel) and *Betula verrucosa* (Birch). Although the catkins of *Salix* (Willow) are usually bee-pollinated there are a few species in which the nectaries have become petaloid and they are therefore wind-pollinated.

As a standard example of this type we may instance the Oak, *Quercus* (Fig. 1217). The trees are monoecious, the staminate and carpellary flowers

Fig. 1217.—*Quercus petraea*. A, Flowering shoot; male catkins on left, sessile female flowers on right. B, Young male flowers. C, Female flower. D, Older male flower. E, Female flower in vertical section (B, C and E *after Le Maout and Decaisne*.)

being borne in separate inflorescences. The staminate inflorescence consists of a pendulous catkin up to 10 cms. long, bearing about a dozen flowers, each solitary in the axil of a small bract. The catkins themselves are formed in the axils of the uppermost bud scales, or lowest foliage leaves, so that they hang from each opening bud. Each staminate flower consists of a perianth of 5–7 minute, green segments, enclosing 5–12 stamens which are situated more or less opposite the perianth segments. Both filaments and anthers are short and there are no nectaries present. The female inflorescence consists of a spike, comprising 2–3 flowers, and borne in the axils of leaves near the end of the twigs. Each flower is surrounded by a cupule of concrescent scales and consists of a perianth of 6 greenish scales surmounting the ovary, which is inferior and syncarpous, with three loculi each containing two ovules with axile placentation. The style is short and stout and bears three stigmas the tips of which curve outwards.

The pollen is powdery and dry and is produced very freely by the pendulous catkins. It is scattered by the action of the wind. Pollination takes place in May, at which time the ovaries of the female flowers are only rudimentary and the pollen tubes grow slowly down the style, where they wait until late June or early July of the following year before the ovules are ready for fertilization.

Just as *Salix* is occasionally wind-pollinated, so certain species of *Quercus* in Malaya are insect-pollinated, the attraction being perfume rather than nectar and pollen presumably the material sought by the visitors.

2. *Pendant Type*

The best example of this type is found in the genus *Rumex* where the small, pendulous flowers are adapted for wind pollination (Fig. 1218). In *R. crispus* three forms of the plant often occur : those with large, hermaphrodite flowers in which the stigma is immersed in the perianth segments; those in which there are small female flowers scattered among hermaphrodite ones, and lastly those possessing only small female flowers, in which the stigmas project beyond the perianth segments.

The flowers consist of five or six perianth segments enclosing from 5–9 stamens, which surround the ovary. This ovary is unilocular with three styles and a single basal orthotropous ovule. The flowers are protandrous and the anthers project well beyond the limits of the perianth. The flowers being pendulous, the anthers freely discharge their pollen, which is at the same time protected from rain by the perianth. For the same reason self-pollination is prevented as the anthers hang below the stigmas. In the hermaphrodite flowers, only after the anthers have discharged their pollen do the stigmas elongate, their branches projecting widely beyond the perianth. In purely female flowers there may be the vestiges of six stamens, suggesting that these monoecious flowers have been derived from hermaphrodite ones. Even in hermaphrodite flowers some of the stamens may be functionless or reduced. Though self-pollination is excluded, geitonogamy may occur, for the flowers are generally arranged in dense panicles.

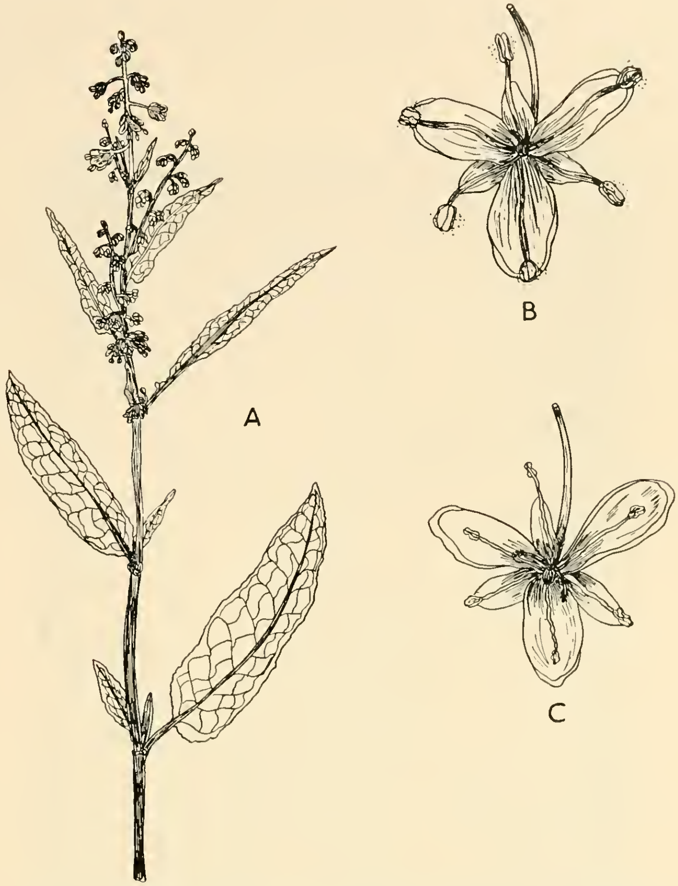


FIG. 1218.—*Rumex crispus.* A, Flowering shoot. B, Hermaphrodite flower in male stage with inconspicuous stigmas. C, Later stage after pollen shedding, with stigmas beginning to elongate.

3. *Long Filament Type*

This type of mechanism is very common and occurs in plants belonging to a number of widely separated families. It is the typical mechanism found in the Gramineae (Fig. 1219), Cyperaceae and Juncaceae (see Chapter XXX), though it is also adopted by members of the Euphorbiaceae, *i.e.*, *Mercurialis* and *Ricinus*, by *Callitriche*, *Myriophyllum* and *Hippuris* among water plants and also by such genera as *Plantago*, *Humulus* and *Cannabis*.

We can take *Plantago* as a common example (Fig. 1220). In *P. major* the inflorescence is a racemose spike up to 30 cms. in length and bearing a large number of hermaphrodite, actinomorphic flowers. The calyx consists of four sepals diagonally arranged, green in colour and surrounding a sympetalous corolla. This is represented by four acute teeth which are at first erect, but become subsequently reflexed to expose the essential organs. These consist of four stamens and a superior, bilocular ovary. The stamens arise from the base of the corolla opposite the sepals and each is made up of a long, slender filament bearing at its top a reddish-purple or yellow anther which is attached at its centre, with the pointed end of the connective directed downwards. The anther dehisces by lateral slits. The flowers are strongly protogynous (see Fig. 1212, p. 1272), and the central style projects beyond the corolla teeth while these are still in the erect position. The style is unbranched, but is slender and covered with long hairs to which the pollen grains readily adhere. During this stage the stamens remain enclosed by the corolla and begin to elongate only after the style has started to wither. The corolla teeth bend back and the filaments elongate, so that the anthers hang out freely from the flower. They swing about easily on their points of attachment and when the loculi open the pollen is freely distributed.

FIG. 1219.—*Dactylis glomerata.* Wind-pollinated grass. Spikelets in anthesis, showing the long stamens with versatile anthers and the feathery stigmas.

Since the inflorescence is a spike, the flowers along the axis are of different ages. Those at the top, being the youngest, will be in the stigmatic, or female stage at the time when the flowers in the middle of the inflorescence are shedding pollen, while at the bottom the ovules may be already fertilized. Cross-pollination is favoured by this protogyny, but there is a

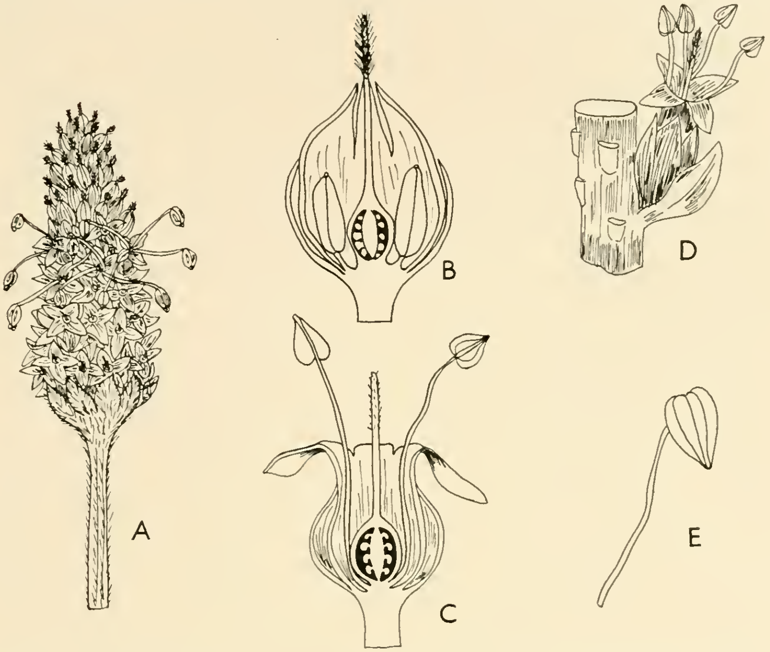


Fig. 1220.—*Plantago lanceolata.* A, Spike with flowers in the stigmatic, staminate and post-pollination states. B, Flower in stigmatic state, anthers immature. C, Flower in open, staminate state, vertical section. D, Flower with mature stamens. E, Single stamen. (C and D, *after Le Maout and Decaisne.*) (*See also* Fig. 1212.)

brief period of overlap, when pollen may be blown on to the stigma of the same flower. Such a flower, however, will have had an opportunity to be cross-pollinated and self-pollination is only a secondary possibility.

4. *Explosive Type*

The discharge of pollen by explosion of the anthers is known in a number of insect-pollinated flowers, but it is rare among wind-pollinated ones. Indeed the mechanism is known chiefly from the members of the Urticaceae and we may cite *Urtica dioica* as an example (Fig. 1221).

As a rule the male and female flowers are borne on separate plants, though cases are not uncommon in which both sexes occur on the same plant. In this case there are usually female inflorescences at the top, mixed inflorescences in the middle and male ones towards the bottom of the plant. The female flowers consist of a four-parted perianth enclosing a single ovary which bears a brush-like stigma and contains one ovule. The male flower also consists of four perianth segments, opposite each of which a stamen develops. Each stamen is bent inwards in such a way that the anther lies in the base of the flower with the curved filament held in a state of compression and the anther pressed against the abortive ovary, which stands in the centre of the male flower. Due apparently to the motion of the wind, the anthers are finally released and the filaments straighten out suddenly, like a spring, accompanied at the same time by the splitting of the anthers. This simultaneous dehiscence and ejection scatters the powdery pollen widely enough to reach adjacent plants in which the stigmas are receptive. The same explosive mechanism is exhibited by the allied genera *Parietaria* and *Pilea* (the Artillery Plant (Fig. 1222)), where the discharge is even more vigorous.

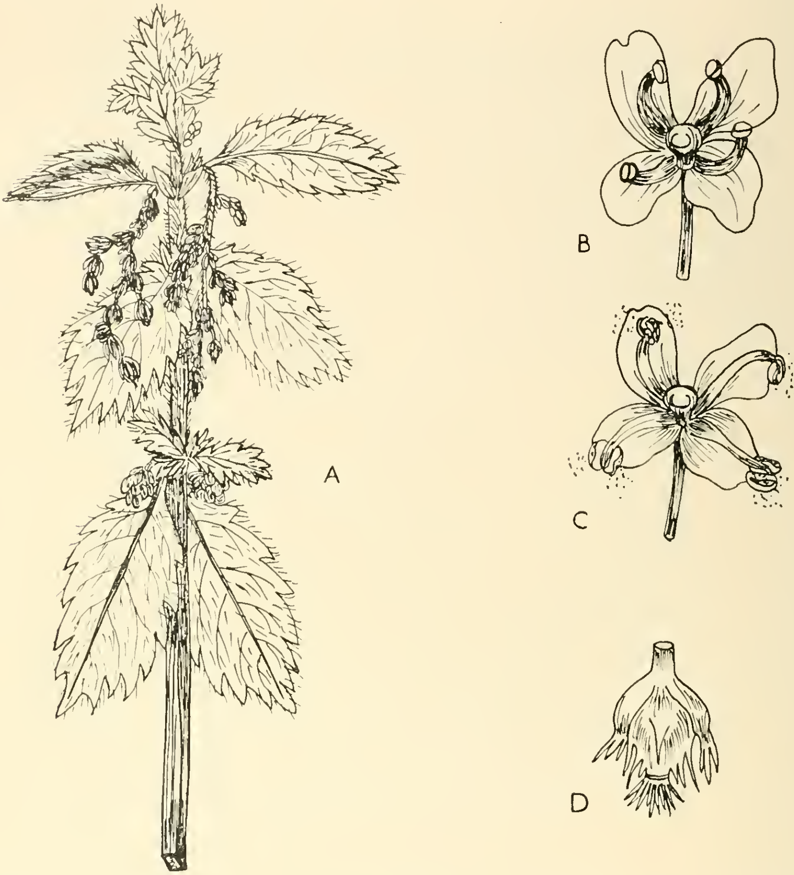


Fig. 1221.—*Urtica dioica.* A, Flowering shoot. B, Young male flower. C, Mature male flower with stamens recurved and discharging pollen. D, Female flower with pendent, bushy stigma.

5. *Motionless Type*

This type of wind pollination is exhibited by two contrasting groups, both of which belong to the Monocotyledons. The first includes a large

FIG. 1222.—*Pilea muscosa.* "Artillery Plant." The male flowers with four recurved stamens which have discharged their pollen, are plainly seen. The bushy stigmas of female flowers are less conspicuous. (× 4.)

number of Palms (see p. 2047) and the second a small group of water plants such as *Sparganium*, *Typha*, *Triglochin* and *Potamogeton*.

Sparganium ramosum (Fig. 1223) is a common aquatic plant in this country. The stems project above the water and bear spherical heads of flowers, each head being composed of either male or female flowers only. The male heads are usually formed higher up on the flowering stem than the female ones. In both male and female flowers there is a perianth of from 3–6 scaly segments. In the male flowers there are 2–3 stamens which alternate with the perianth segments, while in the female flower the ovary is formed of a single carpel and contains one or two pendulous ovules. The style is long and projects beyond the limits of the flower. Each male inflorescence contains about 100 anthers, each of which is attached to a flexible filament. Each female inflorescence is made up of about 150 flowers and, owing to the long stigma which develops on the tip of the style, the female

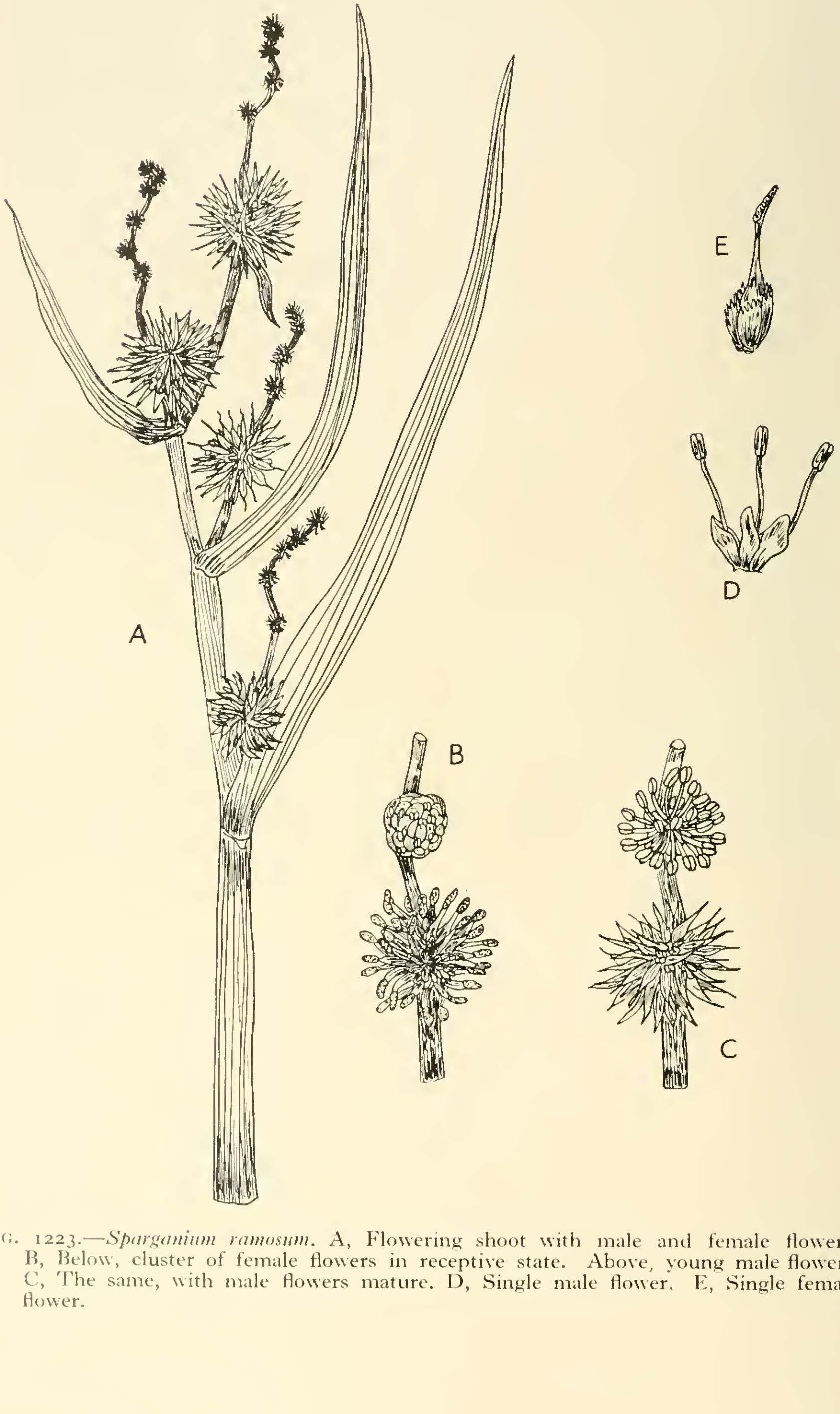


FIG. 1223.—*Sparganium ramosum*. A, Flowering shoot with male and female flowers. B, Below, cluster of female flowers in receptive state. Above, young male flowers. C, The same, with male flowers mature. D, Single male flower. E, Single female flower.

inflorescence appears to be considerably larger than the male. The pollen grains are rounded tetrahedra, covered with a network of tubercles, and are shed only after the female inflorescences on the same stem have already passed maturity. In this way geitonogamy is prevented and the pollen is blown by the wind to adjacent plants.

II. Hydrophily or Pollination by Water

Although it might be expected that water would provide a ready means of transport, especially for aquatic plants, it is remarkable how few plants may make use of this medium for pollination. Many submerged water plants utilize wind pollination, raising their inflorescences to this end above the water surface. Such are, for example, *Potamogeton* and *Myriophyllum*. Possibly because damp pollen is liable to germinate prematurely or because of the effect of surface tension, we find hydrophily employed only in the case of plants whose flowers are permanently submerged below the water. A second type, in which pollination is effected at the surface of the water, is somewhat different and as will be explained later might be more correctly regarded as a highly specialized type of wind pollination.

Hydrophily cannot be regarded as a primitive mechanism. It is almost certainly a secondary adaptation of a wind mechanism, used by plants which have taken to an aquatic habitat from a terrestrial one. For successful pollination to occur there must be a close correlation between the position of the flowers and the specific gravity of the pollen grains. If the female flowers are produced low down in the water then the pollen must have a specific gravity equal to or slightly greater than that of the water. If the female flowers develop at the surface of the water then the specific gravity of the pollen must be less than that of the water, so that it shall rise, if liberated below water, and float on the surface. These changes in the specific gravity of the pollen grains appear to be regulated by the formation in them of one or more large starch grains.

(*a*) *Pollination below Water Level* (Hypohydrogamic)

Two of the best examples of this type of pollination are provided by the genera *Naias* and *Ceratophyllum*, both of which are represented in the British Flora.

Ceratophyllum demersum is monoecious (Fig. 1224). The male inflorescence consists of a cluster of 12–16 stamens with very short filaments, each bearing a two-lobed anther which opens laterally by longitudinal slits. The tip of the anther is prolonged into a double, horned process which is composed of aerenchyma. When the stamens separate from the involucral base to which they are attached, the aerenchyma serves as a float and raises the anther to the surface of the water. The pollen grains are rounded and are enclosed in a delicate intine, the extine being absent in this and other pollens adapted to hydrophily. The pollen has just the same specific gravity as the water, consequently, when the anther opens during the period when it is rising to the surface of the water, pollen grains are freely distributed through all layers of water. This mixing of the pollen through the water is further assisted by bending movements of the plant's stem.

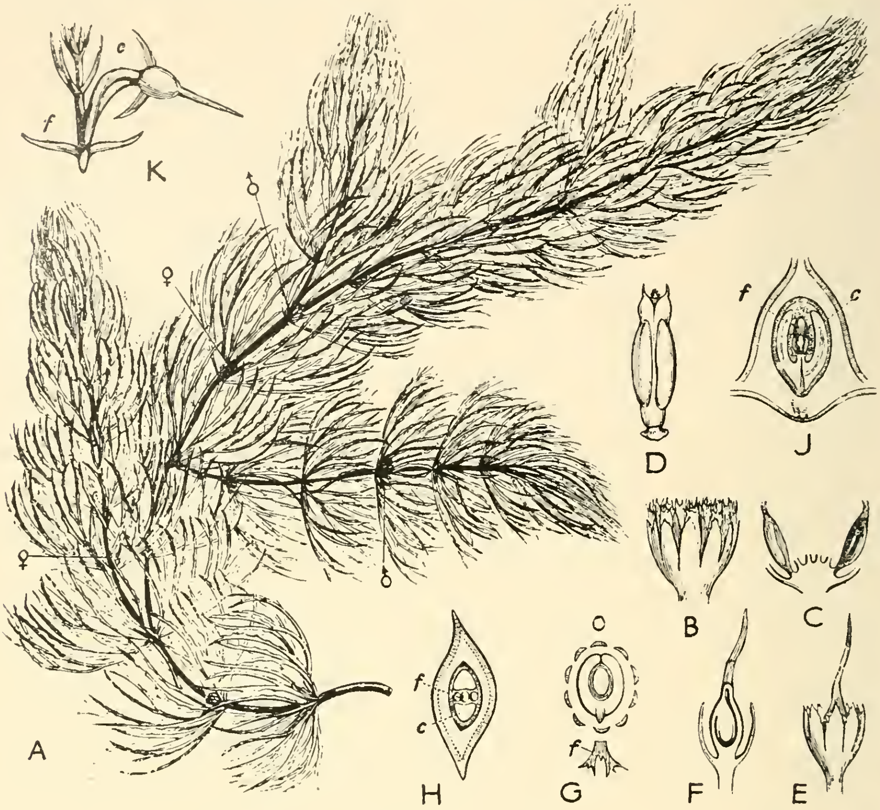


FIG. 1224.—*Ceratophyllum demersum.* A, Plant with male and female flowers. B, Male flower. C, The same in section. D, Single stamen. E, Female flower. F, The same in section. G, Diagram of the female flower. *f* = bract. H, Transverse section of fruit. J, Median vertical section of fruit with embryo. K, Germinating fruit. [In H, J and K, *c* = cotyledon; *f* = first leaf pair.] (*After Engler.*)

The female flowers are produced in much smaller numbers than the males. Each consists of a many-parted perianth surrounding the ovary, which is unilocular and contains a single orthotropous ovule. The style projects about four times the length of the perianth and is bent like a hook which tapers to a point. The whole lower surface secretes a sticky substance and serves as a stigma. The movements of the stem not only help to distribute the pollen, but may also help, by moving the attached female flowers, to increase the chance of the stigmas coming into contact with the pollen grains which are dispersed in the water.

(*b*) *Pollination at the water surface* (Epihydrogamic)

This type of pollination is more common than the last and is found in a number of unrelated genera of water plants. *Callitriche autumnalis* or *Ruppia maritima* serves to illustrate this mechanism. In both these types the pollen grains are less dense than the water and float up to the surface where they come into contact with those flowers which mature at the water surface.

In *Ruppia maritima* the flowers are produced below the water and are hermaphrodite but markedly protandrous (Fig. 1225). The flowers grow in pairs on a common stalk. Each flower is entirely naked and consist of two stamens and four carpels, arising from a spathe-like leaf-sheath. In the early stages of development the flowers are functionally male and are extremely short, scarcely projecting beyond the enveloping sheath. Each anther as it matures discharges its pollen into the water. These pollen grains are light and float to the surface and as in the last example are devoid of any extine. Each grain is tubular in shape, but bent at a right angle. After the discharge of the pollen the inflorescence functions as a pair of female flowers. Its stalk elongates greatly and the carpels, which also develop long pedicels, are carried up to the surface of the water, where the stigmas come into contact with floating pollen, which is moved about on the surface by wind and water currents. After pollination has occurred the stalk again contracts

FIG. 1225.—*Ruppia maritima.* A, Flowering shoot, showing the spiral peduncles of the female flowers. B, Inflorescence with male flower above and female flower below. (A *after Butcher and Strudwick.* B *after Le Maout and Decaisne.*)

so that the developing ovaries mature below the water and it is there that the fruit is produced.

The case of *Vallisneria spiralis* (Fig. 1226) differs from that of *Ruppia* in that the whole male flower, not only the pollen, is detached and floats to the surface of the water. The movement thereon of the male flower is due more to the action of the wind than to the water. The female flowers are not detached but are raised to the surface on long spiral stalks. There they open, but as they are waxy they are not wetted and cause a slight depression in the surface film of the water. The male flowers are produced in large numbers. They are released below water and open on the surface. Their three sepals open widely and are slightly reflexed so that they rest on the surface film and the two anthers are held vertically. The pollen from both anthers clings together into one sticky mass. As the males float about, numbers of them slide into the depressions around the female flowers, where they tend to tip over, bringing the pollen into contact with the stigmas. If a wave submerges the female flower, it and the surrounding males are closely confined in a little bubble of air, thus assisting in pollination.

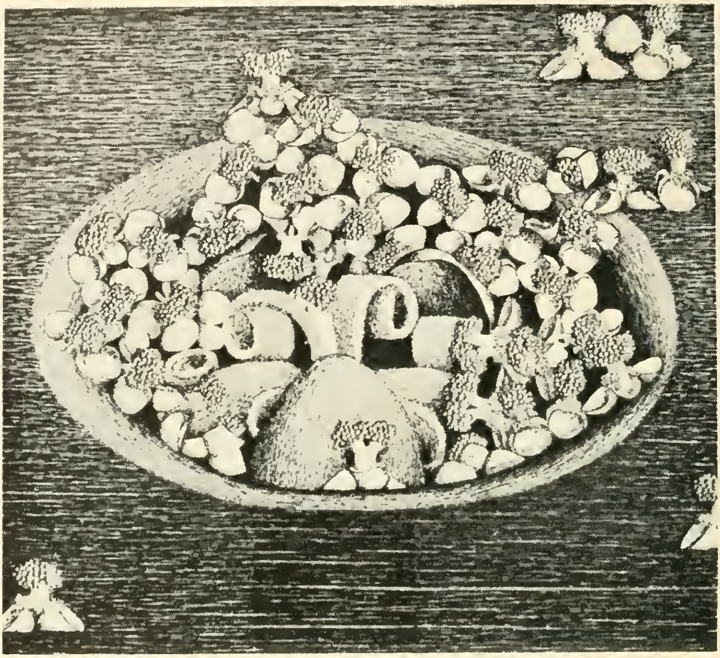


Fig. 1226.—*Vallisneria spiralis.* Female flower with curled stigmas, held in the centre of a surface depression of the water, and free-floating male flowers trapped in the depression. (*After Wylie.*)

In *Elodea* the female flowers produce similar depressions in the water surface but the male flowers explode when they reach the air and it is the free-floating pollen which is caught in the depressions.

III. Zoidiophily or Pollination by Animals

This undoubtedly represents the highest stage in the evolution of pollination mechanisms and occurs in far the greater proportion of Angiospermae. It is important, however, to realize that, although insects are the most frequent agents, several other groups of animals are to a minor extent concerned in pollination. Three groups are active agents, the bats, birds and molluscs, and, although they are treated separately, it should be realized that, at least as far as birds are concerned, most of the same factors operate that we shall consider under insects.

A. *Pollination by Bats* (Chiropteriphily)

The number of authentic cases of bat pollination is small. Bats move extremely rapidly and often at night and in some instances it has proved difficult to determine whether the bat visiting flowers was really assisting in pollination or whether it was engaged in catching night-flying insects, who were really responsible for pollination, the presence of the bat being merely incidental.

Most of the available information rests on observations made in the Royal Botanic Gardens in Trinidad, although the first recorded case came from the Botanic Gardens at Buitenzorg in Java. The following description of the pollination of *Bauhinia megalandra* illustrates one mode of operation.

Bauhinia megalandra is a tropical American tree, reaching a height of about 30 ft. It produces long white flowers which only open in the evening, between 4 p.m. and 6 p.m., in the month of January. About 5.30 p.m. bats of various species were seen flying very rapidly from flower to flower. It was observed that their visits were immediately followed by a cascade of white petals. Next morning the tree was examined and it was found that not a single complete flower remained. In almost every case not only the petals, but also the stamens had been removed. Apparently the bat settles on the flowers by holding on to the stamens, at the same time getting a grip with its legs on the recurved petals.

The cause of their visits however, remains obscure, for the flowers secrete no nectar and it can only be assumed that the bats were attracted by the presence of night-flying moths which had been drawn to the flowers by their pure white colour. Despite the damage caused to the flowers it was observed that in almost every case the style was undamaged, and since in the course of their activities the bats became liberally dusted with pollen it was inevitable that some would be scattered on the stigmas by so violent a disturbance.

Another case concerns the leguminous tree *Eperua falcata* in British Guiana, regularly visited by bats. In this case only one particular species of bat was concerned and it was found to have a brush-like tongue, resembling that of a Humming Bird. Its behaviour, when visiting the flower, was so similar to that of a moth that it seems clear that it did effect pollination.

One of the most striking instances of bat pollination is that of the cultivated banana. Both male and female flowers are open at night and have a rank odour and copious nectar which attract numerous bats. They hold on to the bracts and thrust their heads into the flowers. As the cultivated banana is parthenocarpic and seedless, no advantage accrues to the plant and in the wild species, where pollination is needed, visits by bats have not been observed. In *Oroxylum indicum* (Bignoniaceae) in Malaya the flowers have the same characteristics as those of the banana, namely dull colour, rank scent and copious nectar, and they attract such numbers of bats that the tree has been dubbed the " Midnight Horror ".

The extent to which bats play a role in pollination still requires investigation by botanists in the tropics. Observations hitherto have been few, but there are arguments in favour of bats as pollinators which make them at least worth consideration. Their addiction to eating sweet fruits, the actual observation of nectar collection in some species and the long extensible tongue, show that they have functional possibilities. Some Australian marsupials have also been known to seek nectar, including both the non-flying *Tarsipes*, which uses chiefly a honey diet, and the flying *Petaurus sciureus*, known in New South Wales as the " Sugar Squirrel ", but their relationships to the flowers they visit are unknown.

The Flying Fox, *Pteropus edulis*, in Java, which feeds on the fleshy bracts of *Freycinetia* species, may be another animal pollinator.

B. *Pollination by Birds* (Ornithophily)

The number of birds which effect pollination is small and is restricted to a few tiny species, referred to collectively as the Humming Birds and Honey Thrushes. These birds, often only an inch or so in length, hover in front of flowers, thrusting in their long slender beaks to sup up the abundant nectar. In most instances the pollination is effected directly by the bird, which carries the pollen which is shed on to its head to another flower where it comes into contact with the stigma, but certain types are known in which the mechanism is indirect. In these latter cases the amount of nectar secreted is often small and is produced in a position unsuitable for the long beak or tongue of the bird. Such flowers, however, may attract insects. By themselves these insects could not effect pollination, for the shape of the flower is not suitable, but the presence of the insects attracts small birds, who, while catching the insects, themselves bring about pollination.

Many flowers which are visited by nectar-hunting birds are not dependent on them for pollination. Most of the true ornithophilous flowers are coloured scarlet, a colour which is common in the tropics but rare elsewhere. Nectar secretion is usually prolific but perfume plays little part in the process of attraction. Another characteristic feature is the tough consistency of the flower parts to withstand the onslaughts of the powerful little visitors.

The Honey Thrushes are direct pollinators, for nectar is their main diet and they are not insectivorous. Their beaks form sucking tubes and are not adapted for solid food. The true Humming Birds, on the other hand, are often insect eaters and it is for the sake of the insects rather than for the nectar that the flowers are visited. Others are honey eaters, like the colibri species observed by Müller in Brazil, which consumes the sweet petals of *Feijoa* (see p.1160).

1. *Direct Bird Flowers*

Many of the earlier travellers in the Amazon basin have described in meticulous detail their observations on the part played by Humming Birds in the Brazilian jungle. We may cite here an account given by Bates. He first observed the activity of these Humming Birds in the neighbourhood of Caripi where he found that they were at work, day after day, on a species of *Bignonia*, which forms trees of considerable size and blooms most freely

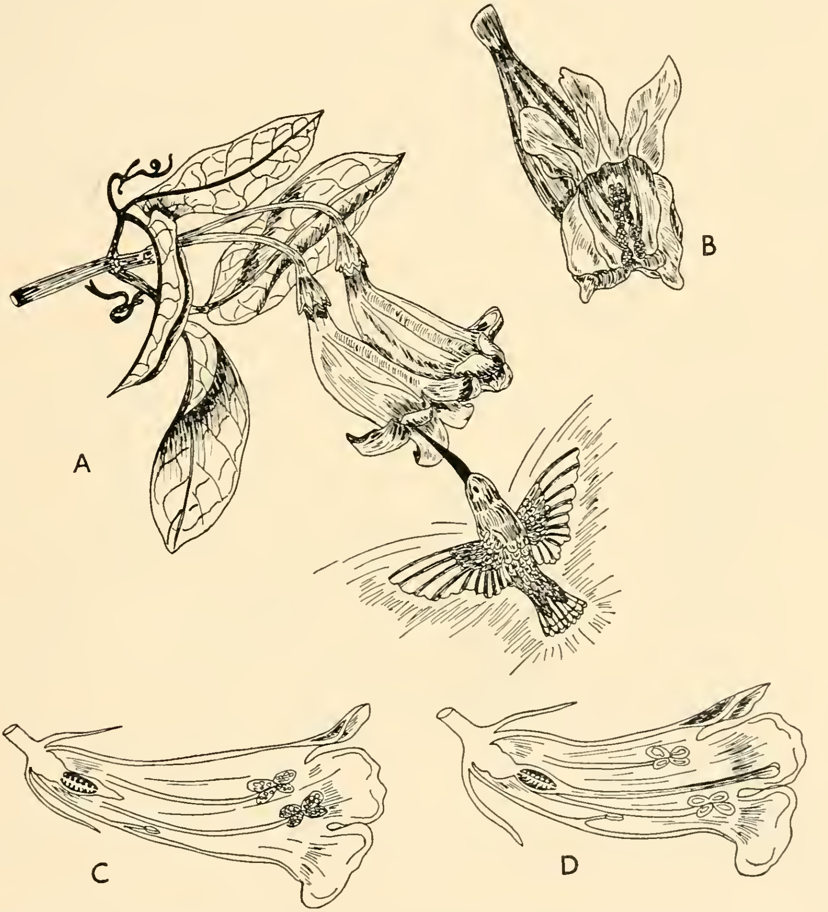


FIG. 1227.—*Bignonia capreolata*. A, Poised Humming Bird feeding from a flower. B, Front view of young flower with anthers presented. C, Young flower in section with anthers in forward position. D, Older flower in section, with stigma forward. (*After Bates*.)

in January. Each day, during the cooler hours of the morning and again in the evening, Humming Birds gathered in scores around the trees. He noted that unlike insect visitors the birds dart from flower to flower in no methodical manner. The movement of the wings is amazingly rapid, so rapid as to be imperceptible to the human eye, yet in this way the birds can hover almost stationary in front of a flower for sufficient time to gather the nectar and in doing so to become dusted with pollen. The corolla of the *Bignonia* flower (Fig. 1227) is very long and tubular, being composed of five fused petals which diverge at the tip to form a two-lipped expanse. There are four stamens together with one staminode, inserted on the corolla tube with the anthers opening inwards, towards the centre of the flower. The ovary is superior and bilocular and is prolonged into a very long slender style with a pointed, apical stigma. In the young state the stamens move towards the centre of the flower so that they more or less block the entrance. During this stage, the style, which is not yet mature, lies against the lower side of the corolla tube. Later, after the anthers have discarded their pollen, they move back against the wall of the corolla, while the style occupies the centre of the floral tube. Nectar is secreted at the base of the corolla tube and, owing to the great length of the tube, can only be reached by the long beaks and tongues of the Humming Birds. Even they must thrust their heads deep into the flower to reach the nectar and in so doing the feathers

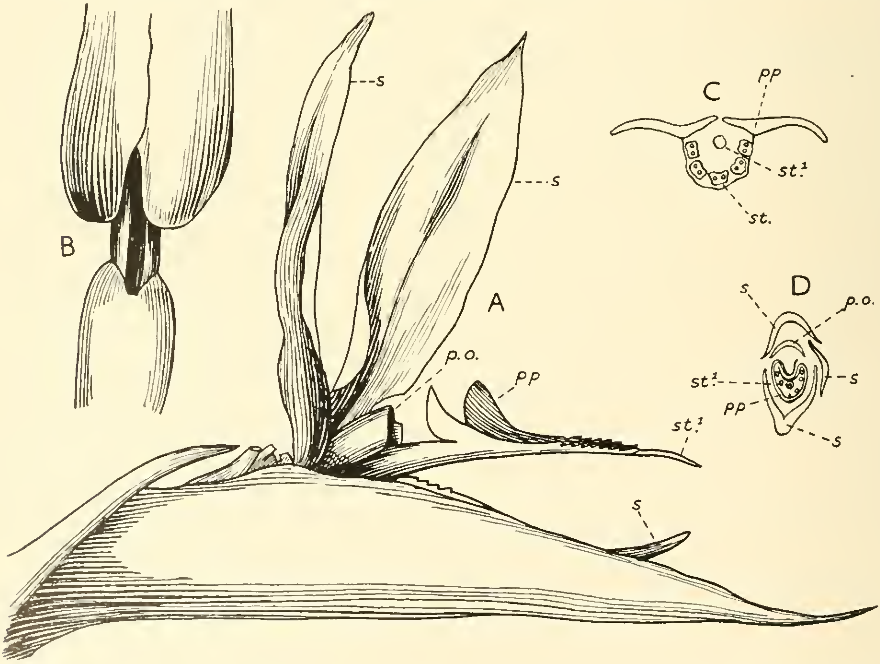


FIG. 1228.—*Strelitzia reginae.* A, Flower emerging from spathe. *s*=sepals, *st*=stigma, *pp*=two united petals covering the stamens and style, *po*=domed petal over nectar. B, View of *pp* and *po* from above. C, Section of *pp* towards apex. D, Section of *pp* and *po* near base. (*After Scott Elliott.*)

become covered with pollen which they later transfer to the stigma of another flower.

The very striking flowers of *Strelitzia reginae* (Musaceae) are enclosed by a tough spathe and emerge from it in succession. Each flower has large orange sepals and bright blue petals which make a very conspicuous colour contrast. Two of the petals are long and are united into an arrow-shaped structure, of which the two flanges overlap above, covering the six stamens and the style, the stigma protruding at the distal end. The third petal is short and dome-like and covers the entrance to the nectar (Fig. 1228). The pollinator is a Honey Bird, *Nectarina afra*, which bears on its breast the same brilliant colours as the flower. It alights on the united petals and walks along the flanges. When bending down beneath the dome-shaped petal it presses the flanges apart, so exposing the stamens and getting pollen on its breast. The protruding stigma is touched first on alighting and receives any pollen which may have been brought from another flower. Insects visit *Strelitzia*, but are very unlikely to accomplish pollination.

2. *Indirect Bird Flowers*

As an example of this type we may take the very remarkable flowers of *Marcgravia nepenthoides* whose pollination is described by Belt in his account of his wanderings in Nicaragua (Fig. 1229). *M. nepenthoides* is not

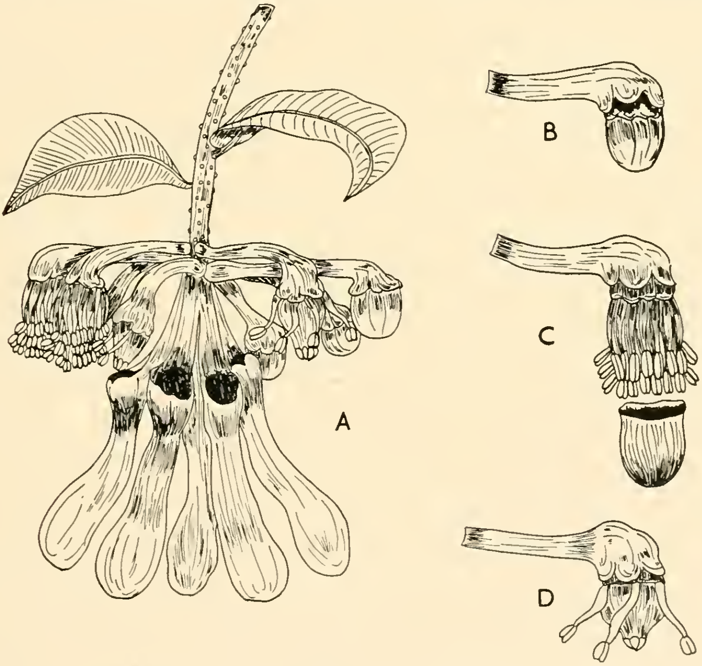


FIG. 1229.—*Marcgravia nepenthoides.* A, Inflorescence with nectary pouches and circle of pendent flowers. B, Flower bud. C, Young flower with corolla cap dropping off. D, Older flower with stamens nearly all gone and stigmas exposed. (*Modified from Le Maout and Decaisne.*)

uncommon in the jungle and bears remarkable inflorescences. The plants are epiphytic climbing shrubs which produce two kinds of shoots, the one producing clasping roots and the other forming vegetative branches bearing sessile leaves and terminating in cymose umbels of flowers. In these inflorescences the central flowers are abortive and their bracts become transformed into large-stalked, pocket-like nectaries which form a more or less radiating cluster below the inflorescence. The fertile flowers form a circle above these nectaries, each flower borne on a long, horizontal pedicel and facing downwards. The flowers are hermaphrodite, and each consists of 4–5 sepals inside which is a fused corolla which is shed like a cap to disclose a large group of stamens, united to one another and to the base of the corolla. In the centre lies the unilocular ovary containing numerous anatropous ovules and with a simple style.

The flowers are protandrous and when mature both they and the nectaries are brightly coloured. The whole inflorescence is therefore attractive to Humming Birds and also to many types of insects. Some Humming Birds probably sup the nectar directly, but various insectivorous species also visit the flowers to catch the insects. Both types of birds alike may cause pollination, for in their efforts to reach the central nectaries the tops of their heads come into contact, either with the pendulous anthers or the stigmas, according to the age of the flowers, and cross-pollination is effected.

Belt records an unnamed species of *Marcgravia* in which the nectaries had developed close to the pedicels of the flowers, which were themselves turned upwards so as to form a kind of fence around the nectaries. In this type he pointed out that the birds visiting the flowers would have their breasts, rather than their heads, dusted with pollen.

The species of plants visited by small birds belong to many genera, among which the following contain species which are more or less completely ornithophilous: *Antholyza*, *Malvaviscus*, *Protea*, *Phrygilanthus*, *Feijoa*, *Strelitzia*, *Musa*, *Ravenala*, *Fuchsia*, *Salvia*, *Hibiscus*, *Erythrina*, *Bignonia*, *Aloe*, *Kniphofia* and *Lobelia*.

How many of these and other cases of ornithophily are obligatory and how many are simply facultative is not known, for the boundary line with entomophily is not clear. Some of the larger moths could, and probably do, function in many flowers, equally as well as the smallest birds.

The whole question of pollination by birds has as yet been very incompletely investigated. It seems probable that in the tropics a considerably larger number of birds are concerned in this process than the records suggest. It must be remembered that there is a superficial resemblance both in form and in motion between some of the smaller Humming Birds and the larger Hawk Moths. Indeed Bates records that occasionally he shot these great moths in mistake for Humming Birds. Among the other birds involved in pollination are the Honey Suckers. These birds are common in South Africa and Madagascar and it has been reported that they are responsible for the pollination of a large number of different plant species.

Pollination by larger birds, including some of the smaller Woodpeckers and Starlings, has been recorded in several instances, for it is known that these birds are attracted by sweet juices and it is not improbable that they would be attracted by nectar as well.

Quite apart from such examples, a considerable number of insect-catching birds may perform pollination in cases like that cited above where insects are attracted to the nectar, but owing to the shape of the flower, would not themselves perform pollination. The modifications of structure in a flower or an inflorescence which produce such a complicated indirect pollination mechanism are difficult to interpret and it will require a far more critical and extended study of the subject in the tropics before the full story can be given. When it is unfolded it is probable that, not only will the number of examples be greatly increased, but the variety of mechanisms will require a more elaborate grouping than is possible at present.

C. *Slug and Snail Pollination* (Malacophily)

To what extent slugs and snails actually perform pollination is a matter of some doubt. It is true that their slime trails on examination have been found to contain pollen grains. It is therefore reasonable to assume that, if the animal crawls from the anther to the stigma of a flower, it may transfer the pollen to the stigma. Such a pollination is, however, fortuitous and there is no evidence that flowers are in any way specially modified to assist the animal to perform pollination. Indeed the activity of slugs and snails being what it is, it seems likely that in general the harm they do to plants exceeds any beneficial pollination which they may occasionally effect.

It is difficult therefore to consider slug or snail pollination from the same standpoint as other types of animal pollination. There are few, if any, structural adaptions on the part of the plant which can be considered to promote this method of pollination. Many flowers for one reason or another cannot be pollinated by these animals because the shape of the flower is unsuitable. A possible exception is the well-known *Aspidistra lurida*, an East Asiatic plant whose flowers are produced from below the ground and open level with the surface of the soil. The stigma forms a large flat plate almost filling the opening of the perianth and seems well suited to molluscan pollination, but it cannot be said with certainty if this is the normal process. There is no evidence that Molluscs are attracted by sugary secretions, nor that any tissues are developed which specially attract them. On the other hand very damp, rainy weather, when slugs and snails abound in vegetation, is just the weather most unsuitable for insect visits. Plants, therefore, which are in flower at such times, might fail to receive insect visits but might, if the shape of the flower were suitable, benefit from the visit of a slug or a snail.

1. *Land Plants*

The most suitable type of flower for these animals is one which is as flat as possible and in which the anthers project but little above the rest of the organs. The capitulum is obviously a very suitable arrangement for this process. Here there are a number of separate flowers closely grouped together, which discharge their pollen in such a position that it could readily be transferred from one flower to another by a mollusc crawling across the inflorescence. Indeed it is among the Compositae that most of the recorded cases occur.

FIG. 1230.—*Chrysanthemum leucanthemum.* Malacophily. Capitulum visited by a slug.

For example Ludwig has observed small slugs pollinating the capitula of *Chrysanthemum leucanthemum* (Oxeye Daisy) (Fig. 1230). It should be pointed out, however, that these observations were made in damp weather when insect visitors were absent and it should not be regarded as the normal method whereby this plant is pollinated.

Several instances have been cited of slugs and small snails seeking refuge from inclement weather by crawling into the spathes of certain Aroids. In the course of their wanderings they can effect pollination in much the same way as do small flies (see p. 2017). There is, however, no evidence that the structures clearly suitable for trapping flies are in any way connected with visits by slugs.

2. *Water Plants*

The part played by water snails is rather different, for here there is some evidence that their activity does normally promote pollination. It has been repeatedly claimed that water snails are responsible for the pollination of species of *Lemna*. Observations on the pollination of the Duck Weeds is rendered particularly difficult because of the infrequency of flowering. The inflorescence is monoecious. The male flower consists of a single stamen, while the female flower is represented by a gynoecium consisting of a single carpel with 1–6 ovules. Each inflorescence is composed of one female flower and two males, the male flowers sometimes maturing before the stigma is ripe. Observations on this point are, however, contradictory, and it appears to differ in plants growing in different localities. Some observers find that one of the male flowers matures before the female, while the second anther discharges pollen only after the style has died. The pollen grains are prickly and beset with protuberances, which suggests that they are designed for insect pollination and it is a fact that small flies do often settle on Duck Weed and may effect pollination. Various types of water insects such as the water skaters may also assist. Water snails, however, are frequently found crawling among *Lemna* plants and have been frequently observed to pollinate the flowers. This is particularly interesting because these plants are protected by the presence of raphides from being eaten by water snails.

D. *Pollination by Insects* (Entomophily)

The first observations which led to the realization that insects were responsible for pollination were made by Koelreuter and published by him in 1761. This preliminary account was followed by two further papers which appeared in 1764 and 1766. Koelreuter's first observations were made upon the Fig and it was he who first appreciated that insects were essential for the production of its seeds. In his later writings he records that it came as a great surprise to him to discover that what was true of the Fig was equally true of a number of other plants, and he mentions particularly the Cucumber, the Sword Lilies (Iridaceae) and the Mallows. As his observations multiplied he gained a clear conception of the principles of cross-pollination and of the significance of dichogamy. Koelreuter's observations, however, were soon surpassed by those of Sprengel, whose investigations were carried out on a far wider scale, and the accounts which he gave of his results raised the subject to an important branch of botanical work.

There are certain fundamental differences in the structure of the pollen grains, which in general distinguish those which are destined to be distributed by wind, water or insects. Wind-distributed pollen grains are generally small and smooth-walled, while the grains of water-distributed pollen usually lack an extine. On the other hand, the pollen which will be distributed by insects is far more variable in form. Generally it is adhesive, the extine being beset with small spines, warts, pits and grooves, while in some cases the grains are oily or are bound together with threads of a sticky substance which also assists in attaching the pollen to the stigma. Further, with the exception of hydrophilous forms, the pollen of most Angiosperms is immediately affected by water. In most instances, if water reaches mature pollen grains, they are damaged beyond recovery and cease to be viable. For this reason we find many ways in which plants contrive to protect the pollen from the effects of rain and dew. It is impossible here to list all the methods of protection which have been recorded, but mention may be made of a few of the more typical. (See also p. 1154.)

In many flowers the anthers are sheltered by a covering which may either be formed by the flower itself or may be produced from some adjacent structure. Among the former there are types in which the flower bends over so that the anthers hang downwards and are protected by the calyx or corolla. Alternatively either the flowers or the inflorescence may bend over periodically, curving downwards at night and in bad weather. Other methods of protection are achieved by the presence of a spathe, by the covering of the anthers by the petals or by the complete enclosure of the essential organs, as is so well illustrated by members of the Papilionaceae. Another method exhibited by certain flowers is for the pollen to be discharged only in dry weather, while under damp conditions the anthers close up again, thus preserving the pollen for a future occasion. This is well illustrated by such flowers as *Sambucus*, *Vitis*, *Helianthemum* and many others. A possibly unique method is exhibited by *Cobaea*, in which the pits in the pollen grains are sufficiently deep to prevent the air contained in them from being removed by water, so that the air forms a layer preventing the water from coming into contact with the absorptive surface of the grain. In many plants more than one such protective mechanism may be present, for example the anthers may both close in damp weather and at the same time the flowers may be pendulous.

There are a number of ways in which a flower may attract and induce insects to visit it, though it would probably be wrong to assume that the visit of an insect is exclusively conditioned through the agency of the flower. Anyone who has watched the activities of an insect striving to discover the means of gaining entry into a flower cannot but conclude that it knows that nectar is present if only it can find the way to reach it. On the other hand it is equally obvious that flowers which are visited by insects exhibit certain characters in common and these features can reasonably be regarded as having been developed to attract the animals to those particular flowers. Among the more important of these features are the following: conspicuousness; scent; secretion of nectar; presence of edible sap; provision of a platform upon which the insect may alight; shelter from wind; edible pollen. We have already dealt with these features in general terms (pp. 1253–1262) but further particulars are subjoined, in especial relation to insects.

Conspicuousness

There are two chief ways in which this may be achieved; either the individual flower may become conspicuous by the development of the perianth or adjacent structures into large and noticeable organs, or the flowers, small in themselves, may be aggregated into closely packed inflorescences which collectively may become very conspicuous. In some cases the flowers which make up such inflorescences vary in form, the inner flowers remaining small and inconspicuous, while the marginal flowers are considerably larger and increase the conspicuous appearance of the inflorescence as a whole. These marginal flowers may themselves be actinomorphic, like the inner flowers, or they may become zygomorphic, this zygomorphy increasing still more the contrast between the periphery and the centre of the inflorescence.

Quite apart from the shape of the flower its visibility may be greatly increased according to the colour assumed by these supplementary structures. Colour in flowers is not one of the primary attractions, such as the need for food or shelter, which bring insects to flowers, but it has considerable secondary value as a means whereby flowers may be distinguished from one another and in this sense it is an attraction to an insect like a bee which is engaged in working one particular type of flower. The colour perceptions of insects appear, however, to be limited and in some cases differences of colour may mean no more than variations in brightness to the eye of the insect. It is important to remember that the eye of an insect does not recognize colour as we do and that some colourings which to us look similar may to the insect visitor seem sharply contrasting, while in other cases colours which to us appear quite distinct may to the perception of the insect appear almost alike. (See also p. 1261.)

Flower colour is frequently not restricted merely to the petals. In many cases, both petals and sepals become coloured. Very often they assume the same basic colour, though the tint may vary, but in other species the two whorls of floral parts may develop contrasting colours. In certain cases the filaments of the stamens become coloured and may contrast with the colour assumed by the anthers or the perianth.

Müller originally suggested, what has subsequently been largely proved to be true, that insect visitors show a preference for certain colours. Bees in general seem to prefer blue flowers; butterflies, red; hover flies, yellow; and carrion flies, brown or purple. In early times considerably greater importance was attached to these matters than is done today. Indeed it has been questioned whether insects can distinguish colour at all. Experiments by von Frisch with Hive Bees have, however, proved that they have the ability to recognize different colours and there is therefore no reason to suppose that a similar faculty is not shared in some degree by other insects.

Some plants, like the Foxglove, produce one-sided inflorescences even when growing in entirely open situations. It has been suggested that such inflorescences ensure that more flowers are pollinated, because insects tend to travel upwards from the bottom to the top of a spike rather than to work round it. Radially arranged inflorescences are not so uniformly pollinated and there is a marked difference in the number of fruits developed on the symmetrical inflorescence of a Lupin compared with the one-sided spike of a Foxglove.

Scent

To what extent the scent or odour of flowers assists in pollination is a matter of some dispute. The question as to the ability of insects to distinguish different odours has not been fully settled. There seems to be little doubt, however, that flies are attracted by the nauseous odours emitted by some flowers. Many such flowers combine purple and dull red colours and are much sought after by carrion flies. Other yellowish-green or white flowers emit malodorous scents to which dung flies and some beetles are attracted. Both smell and colour seem necessary to attraction. On the other hand many flies are equally attracted to strongly scented, but not malodorous flowers. It is obvious, however, that smells may produce entirely different sensations in an insect from those they cause in ourselves. Just as a dog can recognize and distinguish smells which are imperceptible to man, so may odours which we cannot appreciate be detectable by insects. The flowers of *Ampelopsis* are hidden from sight by the leaves and, unlike its relation the Vine, they have no perfume detectable by man, but they are regularly thronged with insects, including Hive Bees, which must have been guided to them by their perception of an odour. (See also p. 1266.)

It has been noted that some flowers are scentless by day, but emit a strong odour at night. In almost every recorded instance such flowers are pollinated by night-flying moths. It is therefore reasonable to assume that moths are able to recognize these odours and may be guided to the flowers thereby.

Secretion of Nectar

The nature and position of nectaries both as floral structures (see p. 1244) and also extra-floral glands (see Volume I, p. 472) have already been discussed elsewhere. The question of nectar secretion and the factors influencing its discharge have also been dealt with (see p. 1257), so that we need only now refer to this very important factor in pollination.

Edible Sap

Certain flowers, for example *Orchis morio* and *O. mascula*, have the appearance of nectar-secreting flowers, but on examination are found to possess no nectaries. In these instances it has been shown that there is in the spur a tissue which contains a juice attractive to certain insects. In these examples, as in other flowers, such as *Hyacinthus orientalis* and *Erythraea centaurium*, where the petals provide the juice, bees and butterflies bore into the tissues and suck the sap. In certain species of *Portulaca* tiny knobs are produced on the floral disc which become distended with sap, while in species of *Verbascum*, *Anagallis* and *Tradescantia* succulent hairs are developed on the stamens, which are eaten by insects, or they may secrete a sticky substance which becomes adherent to the visitors and causes pollen to stick to them. Such flowers, which provide a juice, other than nectar, which attracts insects, are referred to as False Nectar Flowers.

Shape of the Flower

The shape of the corolla has an important bearing upon the method of pollination. In flowers with tubular corollas there is a direct correlation between the length of the tube and the length of the proboscis of the visiting insect. There are many tubular flowers whose nectar can only be reached by long-tongued insects. Flowers of this type do not invite any other kind of visitor and thereby they avoid the robbing of their nectar by insects which by their shape or size cannot perform pollination. In some flowers, in which the corolla is completely closed, entry is only possible to insects sufficiently large or strong to be able to force apart the petals, as in *Antirrhinum*, where entry is precluded to all insects other than Humble Bees.

Many zygomorphic flowers provide a platform upon which the insect may alight before entering the flower. Examples of this are found in many of the Labiatae, *Aristolochia*, the Orchids and some of the Scrophulariaceae. The arrangement of the wing and keel petals in Papilionaceae also affords a seat, but since the keel is often movable it also serves as a pollination mechanism, for the depression of the keel may at the same time cause the release of pollen which strikes the insect. Some flowers on the other hand provide no alighting platform and the visiting insect is forced to hang on to the most exposed structures, possibly the stamens, thereby receiving pollen during the act of alighting on the flower. An example of this is seen in species of *Veronica*. The capitula of the Compositae and the flat, actinomorphic flowers of various species provide an open surface on which the insect may settle. Where this surface consists of a single flower the insect may receive pollen or may pollinate the stigma according to the stage of floral development. In the capitulum or in the umbellate type of inflorescence, an insect crawling over it in search of nectar will visit one flower after another and may in this way pollinate a number of separate flowers.

Pendent, bell-shaped flowers like those of *Fritillaria* and *Soldanella* are unattractive to insects which hover, but they are accessible to Humble Bees which can climb up the stamens to reach the nectar.

Floral shape may not only assist the desirable insect to perform pollination, it may in many instances protect the nectaries from thieving by useless or unwanted visitors. Constrictions or the development of stiff hairs may prelude the entry of crawling insects. Tiny flies may fail to reach to the bottom of the floral tube, for viscid substances may prevent their movement. Hairs may be developed either on the inside of the petals or on the filaments of the stamens. They may be permanent or may wither at some period in the floral development, thus opening a passage to the inside of the flower which they had previously closed.

The robbing of nectar by insects, especially bees who eat through the corolla tube in the neighbourhood of the nectaries and sup the nectar without entering the flower, is sometimes prevented by the development of a large baggy calyx. Similarly the collecting of water by funnel-shaped calyces will preclude crawling insects from reaching the flower. A curious example of such protection against robbery is offered by the Orchid, *Coeloglossum viride*, in which the entrance to the spur is closed by a membrane which must be pierced by the proboscis of the insect visitor before the nectar can be reached.

Kerner, in his book on " Flowers and their Unbidden Guests ", records many other structures which can be interpreted as preventing or restricting this type of insect visitor. For example he suggests that spines and prickles may prevent soft-skinned creeping animals from visiting flowers; waxy coattings may interfere with the movements of ants and similar walking insects; while sticky stems such as occur in *Silene* may catch small unwanted insects. It would be unwise to interpret all such structural modifications as explicable in terms of protection against unwanted visitors. Some at least of the structures mentioned serve other and equally important ends.

Shelter from Wind

The shape of the flower or its associated organs may often provide protection to visiting insects against wind or cold. Many small insects seek shelter in the flowers and inflorescences of certain plants. The gall wasps, which are responsible for fertilization of the Fig, afford a good example which will be referred to later (p. 1327). Many small flies obtain protection within the spathes of Aroids and during their sojourn there perform pollination. This mechanism will be discussed on p. 2017. Apart, however, from these highly specialized examples, flowers with large corollas, especially when not joined into a narrow tube, do provide shelter either from wind by day or cold by night. Beetles are often found in the flowers of species of *Magnolia* and ants have been observed resting in the flowers of *Tropaeolum* and *Trollius*. Various small insects shelter in the capitula of Compositae which close at night. To what extent these insects contribute to pollination is, however, doubtful.

Edible Pollen

Although the majority of insect-pollinated flowers offer their visitors nectar or sweet sap, there are some flowers which provide pollen. Such flowers are often types with regular, radially symmetrical corollas and the pollen is fully exposed. Some of these flowers, *e.g.*, *Anemone*, open early in the year when insects are short of food. Bees use considerable quantities of pollen to nourish their young and in early spring probably collect more pollen than nectar. Such flowers produce great quantities of pollen and consequently can well afford to spare a large proportion of the pollen they produce to provide food for the visitors, in return for the essential service of pollination. Pollen is not always edible and only a comparatively small number of plant pollens are used for food by insects. Many are largely ignored, while certain pollens (*e.g.*, *Aesculus*) are definitely poisonous to bees.

Before commencing a description of entomophilous pollination mechanisms we may outline the classification of the Insects as follows:

1.	Hymenoptera	Bees, Wasps, Ichneumon Flies, Ants.
2.	Lepidoptera	Butterflies, Moths.
3.	Diptera	Hover Flies, Two-winged Flies.
4.	Coleoptera	Beetles.
5.	Thysanoptera	Thrips.
6.	Hemiptera	Bugs.
7.	Neuroptera	Dragon Flies, May Flies.
8.	Orthoptera	Earwigs, Grasshoppers, Locusts, Crickets.

These eight orders of insects have been arranged in series according to their importance as pollinators. The last two orders, which geologically are probably the most ancient, play no part in any pollination mechanism so far as is known.

The main types of entomophilous pollination have already been enumerated on p. 1282.

(*a*) *Flowers sought after for Pollen* (see also p. 1260)

It has already been pointed out that the majority of insects visit flowers chiefly to obtain nectar. The insect may use this nectar personally, like a butterfly, or it may gather the nectar, carry it away to its nest, and use it to feed its young, as is done by the bees. Among the latter, however, the grubs and the adult workers are not nourished exclusively on nectar, they require a supply of protein and this is provided by pollen, which contains 7–26 per cent. of protein. Thus we find that, where the grub depends upon the parent insect for its food, as opposed to a caterpillar which finds its own, pollen, as well as nectar, is supplied.

1. *Actinomorphic and Other Open Flowers*

These flowers are often simple and regular in form and many open early in the year at the time when the young grubs have been hatched after the winter rest period. Examples of such flowers are *Anemone*, *Thalictrum*, *Papaver*, *Hypericum*, *Helianthemum*, and *Verbascum* in all of which the pollen is abundant and very freely exposed.

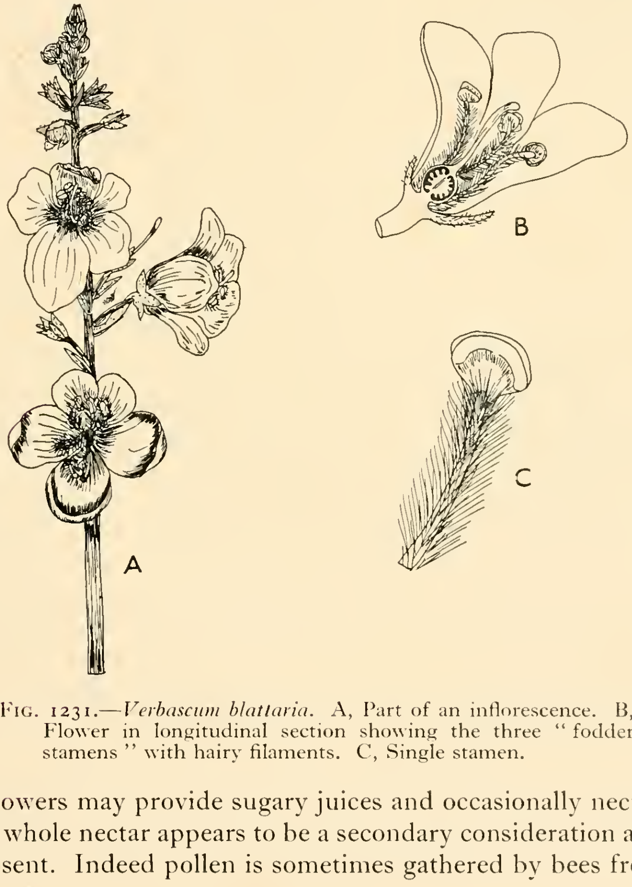


FIG. 1231.—*Verbascum blattaria*. A, Part of an inflorescence. B, Flower in longitudinal section showing the three "fodder stamens" with hairy filaments. C, Single stamen.

Such flowers may provide sugary juices and occasionally nectar as well, but on the whole nectar appears to be a secondary consideration and is often entirely absent. Indeed pollen is sometimes gathered by bees from flowers which are really adapted for wind pollination and in such cases it is doubtful whether the insect performs any useful service to the flower.

Some plants are good for both pollen and nectar, *e.g.*, the White and Red Clovers, which are worked by bees for both materials. A bee visits 300–400 flowers to collect one load of pollen, which takes from 20–30 minutes, carrying off about 1,000 grains from each flower.

Pollen flowers are generally white, yellow or red in colour; violet or blue flowers rarely provide a surplus of pollen.

Some pollen flowers are peculiar in that the stamens are beset with fine hairs, as for example in *Verbascum* (Fig. 1231), where the three posterior stamens are hairy and the anterior pair, which lie close to the stigma and provide most of the fertilizing pollen, are naked. The hairs provide a good foot-hold for the visitors, especially Hover Flies, which suck juice from the hairs and eat the pollen of the posterior stamens, while the abdomen is dusted with pollen from the anterior stamens. The flowers are incompletely protogynous and self-pollination may occur.

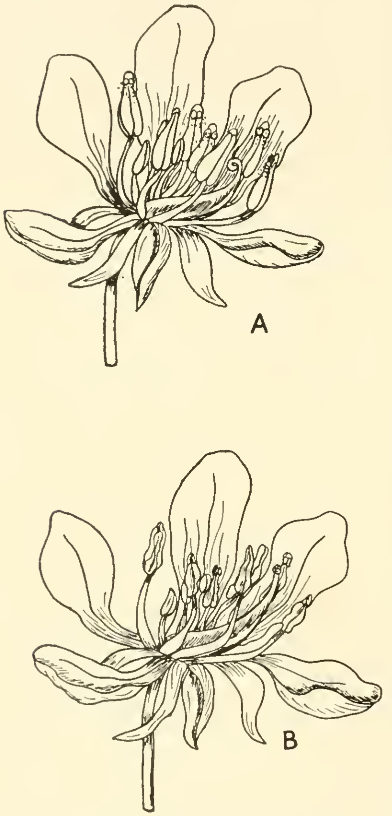


FIG. 1232.—*Cassia marylandica.* A, Young flower with two long, pollinating stamens in front and shorter "fodder stamens" behind. B, Older flower after all pollen has gone, showing receptive stigma uncurled. (*After Engler.*)

2. *Zygomorphic Flowers*

Ludwig has drawn attention to the peculiarities in certain species of *Cassia.* The differences in the position and character of the stamens in these flowers can be best explained on the assumption that some provide pollen for the visitor while others are concerned with the cross-pollination of the flower.

In *Cassia marylandica* (Fig. 1232), a member of the Caesalpinaceae, the flower is visited by Humble Bees. The flowers are zygomorphic, with a calyx composed of five sepals enclosing five free and almost equal petals. The arrangement of the ten stamens is peculiar. The three upper ones are much reduced in length and have no anthers. In some species they may be absent, but in this species they may play the part of nectar guides, though no nectar is actually secreted. The four lateral stamens are also short and the anthers open by lateral slits. They produce abundant pollen which is readily gathered by the bees as a source of food. The lower stamens are much longer, greenish in colour and are neglected by the visiting insects. These stamens, however, have anthers which also open by longitudinal slits and discharge pollen on to the body of the visiting insect. These long stamens vary in position, they may project either to the right or to the left and since both types occur on the same plant they afford a peculiar case of dimorphism. In either case, when the insect visits another flower the pollen discharged on its body will be dusted on to the stigma if the flower is in a later stage of development, for the flowers exhibit a marked protandry.

(*b*) *Flowers sought after for Nectar*

It is possible to trace a series of stages in the evolution of nectar-secreting flowers from simple types in which the nectar is fully exposed to those in which the nectar is so concealed that it can be reached only by insects of a particular shape. In this way the variety of insect visitors can be limited and the chances of cross-pollination correspondingly increased. Though the development of nectar is probably a stage in the change from anemophily to entomophily, it must not be assumed that nectar-less flowers necessarily represent a primitive condition. Flowers such as we have just been considering, in which pollen is offered to the insect, may be specialized and derived from nectar-secreting types. There is some evidence in *Verbascum*, for example, that those species in which no nectar is present and pollen provides the attraction, may have been derived from nectar-secreting forms. Even false, *i.e.*, non-excreting nectaries, may not always be primitive, but may in some cases have been reduced from active nectaries, the presumption being that nectar production as a physiological process antedated the development of special nectary structures.

1. *Flowers with Exposed Nectar*

Flowers in which nectar is freely exposed are usually actinomorphic; they are simple, open flowers, generally white, greenish white or yellow in colour. Attraction may be achieved by the individual flowers or by their aggregation into conspicuous inflorescence, as for example in the Umbelliferae, which are all in this class. Other examples of simple flowers with exposed nectar are *Ilex aquifolium*, *Galium verum*, *Acer campestre*, *Euonymus europaeus*, *Alchemilla vulgaris*, *Chrysosplenium oppositifolium* and various species of *Cotoneaster*, *Saxifraga* and *Euphorbia*.

According to the position of the nectar, the flowers may be visited by any insect with a proboscis of suitable type. The quantity of nectar is usually small and such flowers are often neglected by long-tongued insects such as the Hive Bee, who can make use of more specialized flowers. Furthermore the shape of the flowers is unsuited to large insects such as butterflies, which rarely visit them, even in the regions where these insects are common.

Some flowers with dull yellow petals but fully exposed nectar are visited only by flies and beetles who can suck nectar from a thin layer, but the principal visitors appear to vary in different parts of the world. For example, in Westphalia, Müller observed that the flowers of *Anethum graveolens* were only visited by flies and bees, whereas in Silesia, Loew records that they are chiefly pollinated by beetles.

Euonymus europaeus may be taken as an example of this group (Fig. 1233). The flowers are relatively inconspicuous and comprise four sepals and four small, greenish-white petals which are inserted on the edge of the rectangular disc. There are four rather squat stamens which stand up at the four corners, between the petals. The ovary rises from the disc in the form of a pyramid the top of which consists of a short, blunt style. The four stamens are remote from the style and the anthers are situated at about the same level as the stigma. Nectar is secreted all round the base of the ovary, between it and the disc, and is therefore accessible to any short-tongued insect. The flowers are markedly protandrous. The anthers dehisce extrorsely, while the stigma is still immature. When the stigma is ripe its tip opens out to receive pollen, but closes again as soon as it has done so. Some bushes bear only female flowers, with abortive anthers. Other bushes bear flowers which are structurally hermaphrodite, but which are functionally male and rarely set fruit. Cross-pollination normally occurs as a result of insect visits and self-pollination is almost impossible. Most observers agree that the flowers are chiefly pollinated by dipterous flies, small hymenoptera and beetles, the last being somewhat rare visitors.

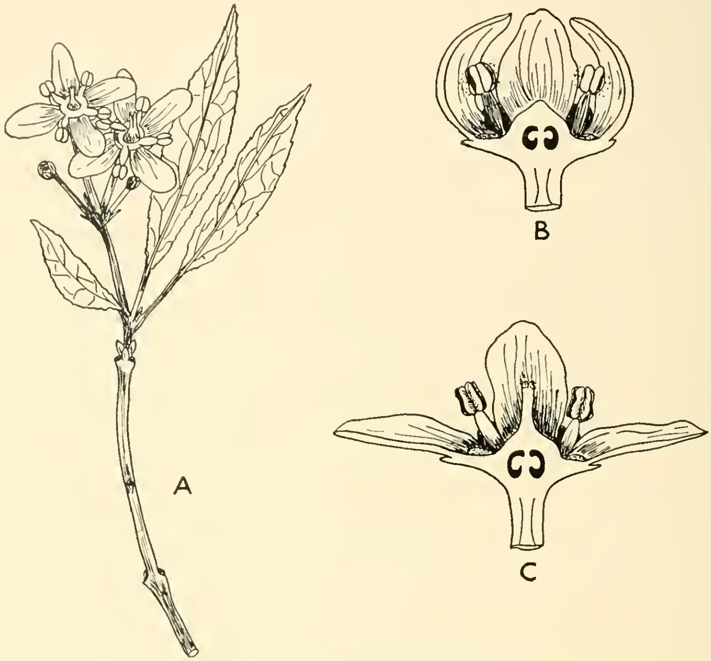


FIG. 1233.—*Euonymus europaeus.* A, Flowering shoot. B, Flower in early stage with anthers dehiscing. C, Flower in later stage, widely open, with receptive stigmas.

2. *Flowers with Partly Concealed Nectar*

It is obviously impossible to draw a hard and fast line between nectar which is exposed and concealed nectar. The two states must be connected by many intermediate gradations. The criterion upon which the present group is distinguished is whether, on a bright sunny day, the nectar is directly visible. Most of the flowers included here are actinomorphic, opening completely on sunny days but closing in dull weather, thereby hiding the nectar from view. White and yellow flowers predominate also in this group, which includes members of such genera as *Ranunculus*, *Caltha*, *Berberis*, *Anagallis*, *Potentilla*, *Sanguisorba* and many members of the Cruciferae.

The insect visitors belong to quite different groups to those mentioned in the preceding section. The flowers are often visited by the Honey Bee and other species of medium-tongued insects, but the type of visitor is to some extent dependent upon the local insect flora. For example, in the Alps, where members of the Lepidoptera are common, they often pollinate flowers with partly concealed nectar. On the other hand in areas where flowers more suited to these insects abound, the butterflies tend to leave these flowers alone, since they are not ideally shaped for their use.

We may regard flowers of this type as being at a higher stage in development than the last, for they represent a step towards specialization to a restricted type of insect visitor. A few purple flowers belong to this group, *e.g.*, *Sanguisorba officinalis* and *Comarum palustre*; they are almost entirely visited by flies.

As an example of the group we may consider the flowers of *Berberis vulgaris* (Fig. 1234), not only because they have partly concealed nectar, but also because of the movable stamens which are characteristic of the genus.

Berberis vulgaris is an uncommon British wild shrub, though it and many other species and varieties of the genus are frequently grown in gardens. Individually the yellow flowers are small and not very showy, but they are aggregated together into racemes which are very conspicuous. Each flower has a perianth made up of a number of whorls, each consisting of three members. The two outer whorls are usually regarded as representing the perianth proper, while the inner segments are referred to as the " honey leaves " and bear the nectaries at their bases. These nectaries take the form of a pair of thick, orange-coloured bodies lying at the base of each honey leaf. Standing immediately against these nectaries are the filaments of the stamens, so placed that nectar collects around the foot of each filament. The filament bases are sensitive to touch on the inner side and are readily stimulated by an insect in search of nectar. The central stigma is a rather massive discoid body with a receptive margin. An insect probing for nectar stimulates a sensitive filament, which contracts causing the anther to strike inwards and discharge its pollen against the side of the insect's head. This movement of the stamen usually disturbs the insect, which immediately leaves the flower. If it visits a new flower and presents the other side of its body to the stigma the pollen which it had previously collected will be wiped off on the stigmatic margin. The anthers themselves are peculiar. Initially they are extrorse, but open by two valves situated at the sides. These valves with the pollen attached to them turn inwards so that finally the pollen faces towards the centre of the flower. Should cross-pollination fail, self-pollination is possible by the anthers coming into contact with the stigmatic surface, though there is considerable doubt as to whether successful fertilization follows automatic self-pollination.

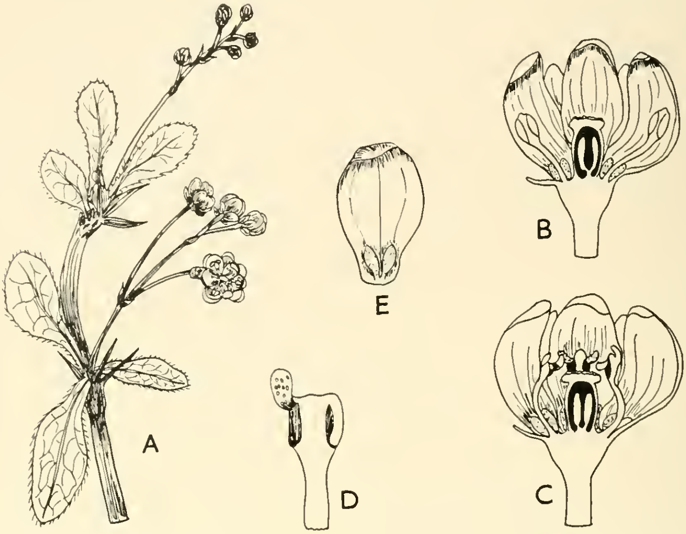


Fig. 1234.—*Berberis vulgaris*. A, Flowering shoot. B, Vertical section of flower, early stage with stamens extended. C, The same, later stage with anthers open and stamens contracted. D, Single stamen showing valvular dehiscence. E, Honey leaf of perianth with two nectaries at its base.

3. *Flowers with Concealed Nectar*

The flowers belonging to this class are the most highly specialized, though they are connected with the last by many transitional forms. The characteristic feature of the group is that the nectar is not merely out of sight, but is structurally concealed either in pouches or sacs or by being covered by hairs or other floral parts. Moreover these structures cover the nectar even when the flower is fully expanded. Though many of the flowers are actinomorphic there is a marked tendency towards zygomorphy in this group. Similarly, though a few white and yellow flowers exhibit the condition, by far the greater number of flowers with concealed nectar are red, blue or violet in colour.

Many of the flowers belonging to this class are visited only by a single group of insects, some indeed only by a single species. *Lythrum salicaria*, for example, is usually only visited by a single species of bee, which rarely visits anything else. *Scrophularia nodosa* is almost universally visited by wasps and by few other insects. We shall deal with such examples later when considering the types of flowers suited to particular groups of insects.

Among the actinomorphic flowers with concealed nectar we may cite the following: *Trollius*, *Malva*, *Rubus*, *Oxalis*, *Epilobium*, *Ricinus*, *Myosotis*, *Vaccinium*, *Calluna* and many others, while among the countless zygomorphic types are nearly all the Labiatae, and many members of Scrophulariaceae and Orchidaceae as well as other families.

As an example of the actinomorphic type of flower we may describe *Vaccinium myrtillus* (Fig. 1235). The flowers are pendulous and bell-shaped, greenish in colour with a pink or red tinge and completely lacking in scent.

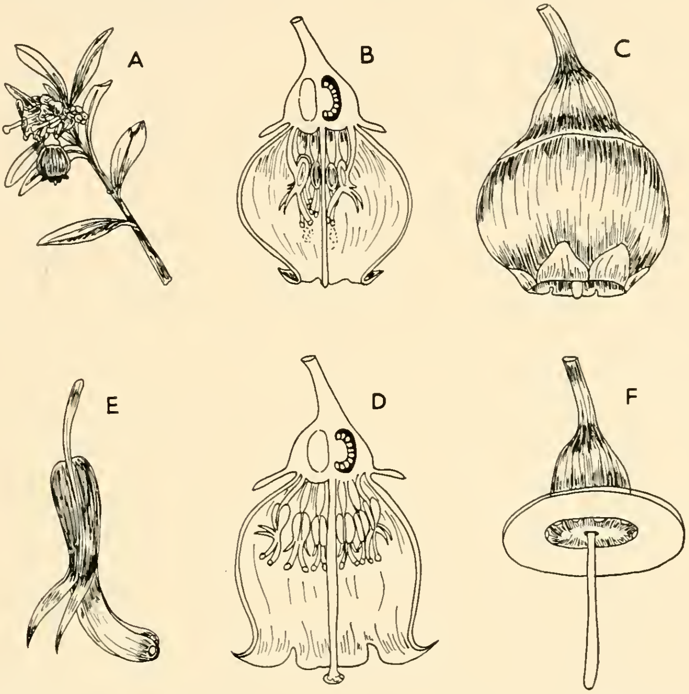


FIG. 1235.—*Vaccinium myrtillus*. A, Flowering shoot. B, Vertical section of flower during pollen discharge. C, External view of flower showing unexpanded stigma. D, Vertical section of flower in female state, with expanded stigma. E, Single stamen. F, Flower with calyx after abstriction of corolla and stamens.

Despite their inconspicuous nature they are very rich in nectar and are sought after by bees. The corolla is made up of five petals which are fused together, except at the tips, to form a bell into which only a fairly long-tongued insect can thrust its proboscis with a hope of reaching the nectar. The centre of the opening is partly blocked by the capitate stigma. An insect trying to enter the flower will therefore touch the stigma with its head. The flowers are protandrous and the stamens are situated around the style in the lower part of the flower. Each stamen consists of a short curved filament bearing an anther with two tubular extensions, the outer ends of which open by pores. Attached medianly to the anther are a pair of stiff spines which spread across the space between the anther and the wall of the corolla. The nectar is secreted on a white swelling formed on the ovary. When an insect inserts its head into the flower and thrusts up its proboscis, the latter is almost certain to touch one or more of the outer spines. The movement causes pollen to fall out of the tubes on to the head of the visitor. In this way pollen is collected in a position where, on reaching another flower, it will be brushed off on to the stigma. In later stages of anthesis pollen may fall directly from the anthers on to the stigma, thus causing automatic self-pollination, but this will only happen when the pollen has become completely dry and powdery, as it finally does.

4. *Social Flowers with Concealed Nectar*

The separation of this group from the previous one is due to Hermann Müller. He used it to distinguish the type of floral arrangement found in the Compositae and in a few other genera such as *Scabiosa* and *Armeria*. In these cases the whole inflorescence is concerned in forming a conspicuous floral structure, the flowers being individually inconspicuous. So far as colour is concerned we have two distinct types. First, there are yellow or white flowers, or a combination of the two, in which case the insect visitors are similar to those of flowers with partly concealed nectar; and secondly there are red, blue or violet flowers in which the insects are those which visit flowers with completely concealed nectar.

We may consider as an example of this group the case of *Scabiosa* (*Knautia*) *arvensis* (Fig. 1236). All the members of its family, the Dipsacaceae, are regarded as having flowers belonging to this pollination group. The purplish flowers form capitula of about fifty flowers and are usually protandrous, with nectar secreted from the surface of the ovary and concealed by the corolla tube. There is a marked difference in the size of the component flowers, those around the margin being much larger and their corollas markedly zygomorphic, a feature even more obvious in the allied garden species *S. caucasica* (See Fig. 1874, p. 1945). The calyx is extremely short and bears 8–16 deciduous bristles, which extend only about half-way up the corolla tube. This tube is made up of four petals, is about 10 mm. long, and may be somewhat two-lipped. Nectar is secreted at the base of the corolla tube and is protected by hairs, which line the inside of the tube. In the shorter flowers, it is readily accessible to all but very short-tongued insects. The flowers are markedly protandrous and in the first stage the stamens project well beyond the corolla. The anthers mature in succession and they turn on their filaments so that the longitudinal slit is directed upwards. After the pollen has been shed the anthers fall off and the filaments wither. When the four stamens have completed their development and disappeared, the style, which had previously remained short and immature in the centre of the corolla tube, begins to elongate and grows until it is almost twice as long as the corolla. It is a club-shaped structure with a large, apical, stigmatic surface. Since it only begins to grow after the last anther has withered, dichogamy is complete. Insects visiting the young flower must be dusted with pollen, while those working in an older flower will discharge their pollen on the newly grown stigma. Automatic self-pollination is impossible, but occasionally the style of one flower may touch the anthers of an adjacent one.

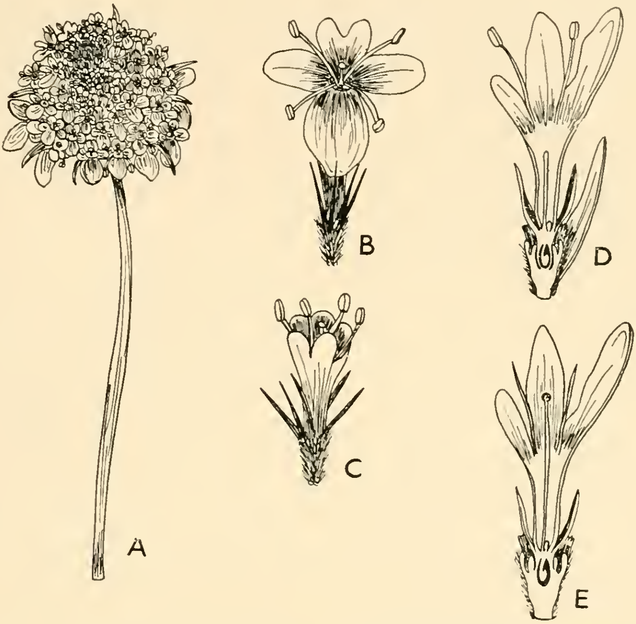


Fig. 1236.—*Scabiosa arvensis.* A, Capitulum. B, Marginal flower. C, Disc flower. D, Vertical section of flower in first, male state. E, The same in later, female state.

From time to time examples of gynodioecism have been recorded in this flower. In some parts of the country plants have been observed in which all the flowers were female, while nearby, typical hermaphrodite plants could be found. Indeed, in many plants the florets of some inflorescences exhibit incomplete hermaphroditism, the stamens being much reduced and producing no pollen. Such heads are often smaller than the fully hermaphrodite ones and are often produced early in the year.

Scabiosa arvensis appears to be pollinated almost entirely by a single species of bee, *Andrena hattorfiana*, which rarely visits any other flower, and it is probable that the plant and the bee have a common geographical distribution, though the details have not been worked out. On the other hand this bee is not the only insect visitor to the plant, though other visitors are rare and doubtfully effective as pollinators.

5. *Flowers visited by Special Groups of Insects*

i. *Hymenopterous Flowers*

Flowers belonging to these groups are pollinated only by members of the Hymenoptera. This group includes the Hive Bees, Humble Bees, Wasps, Ichneumon Flies and Ants. The flowers which are pollinated by these insects are varied in form but the majority are zygomorphic, and red, blue or violet colours predominate. Many of the flowers are so specialized that they can be pollinated by no other type of insect. Some flowers, indeed, are suitable only for the heavier and more massive bees, or those with extra long probosces. Finally we have a number of cases where the flower is so constructed that it is only possible for one particular species of bee to effect pollination, *e.g.*, *Aconitum*, *Delphinium* and several species of *Corydalis*.

Hymenopterous flowers fall naturally into six groups according to the type of insect which pollinates them:

(*a*) Hive Bee Flowers	(Such flowers can be pollinated by bees with a proboscis of 7 mm. or less), *e.g.*, *Trifolium repens.*
(*b*) Humble Bee Flowers	(Such flowers can be pollinated by bees with proboscis of more than 7 mm.), *e.g.*, *Trifolium pratense.*
(*c*) Bee and Humble Bee Flowers	(Plants with two types of flowers, with corolla tubes of different lengths), *e.g.*, *Calamintha alpina.*
(*d*) Bee and Butterfly Flowers	*e.g.*, *Rhinanthus hirsutus.*
(*e*) Wasp Flowers	*e.g.*, *Scrophularia nodosa.*
(*f*) Ichneumon Fly Flowers	*e.g.*, *Listera ovata.*

(*a*) *Hive Bee Flowers*

Under this heading must be included not only the true Hive Bee, but also a number of fairly long-tongued bees with a proboscis up to 7 mm. in length. Most of the flowers which are normally pollinated by these insects are rarely visited by any others, except occasionally by butterflies. The long probosces of the latter make it possible for them to reach the nectar, but their bodies remain so far out of the flower that they rarely effect pollination and they must therefore be regarded merely as robbers of the flowers.

The Hive Bee, as already pointed out, does not visit a wide variety of flowers and as far as Britain is concerned it shows a marked preference for a relatively small number of species. Early in the season, when pollen and nectar are scarce, it may be obliged to visit a wider range of plants than it does later on when it is freer to choose. The greater part of the honey stored in a hive is obtained successively from the cultivated fruit trees, the White Clover, the Blackberry, the Lime and later, in appropriate localities, from Heather. These flowers provide the bulk of the honey, but many other flowers are visited, depending very largely on local circumstances. A colony of bees may make use of any suitable flower if it is available in the neighbourhood of the hive in sufficient quantity and the sources of some local honeys are still uncertain. Seasons may make a profound difference in the nature of the honey obtained. For example, in some seasons, when there is a gap between the end of the Apple flowering and the beginning of the White Clover, bees may collect large quantities of nectar from Hawthorn. If, in another season, the White Clover is early, the bees may neglect the Hawthorn nectar entirely and concentrate upon the Clover, which is often the most important honey-plant. The flowers of *Trifolium repens*, the White Clover (Fig. 1237), are grouped in a dense racemose head, which bears several dozen flowers. Each flower consists of a short calyx, made up of five sepals, which are fused into a tube about 3 mm. long. The corolla is composed of five petals which are white in colour, but often tinted with pink. The vexillum is large and bent so as to cover over the other four petals. The alae are quite small and lie on either side, within the two lateral lobes of the vexillum. The carina petals are fused along their anterior edges to form a keel lying within the alae. The stamens are diadelphous, nine stamens being united together in a staminal tube surrounding the gynoecium, with short filaments and introrse anthers. The tenth stamen is free and occupies the posterior position. The gynoecium consists of a single carpel with a long, tapering style. Both stamens and style are enclosed within the keel and anthesis begins while the corolla is still closed and has scarcely extended beyond the calyx.

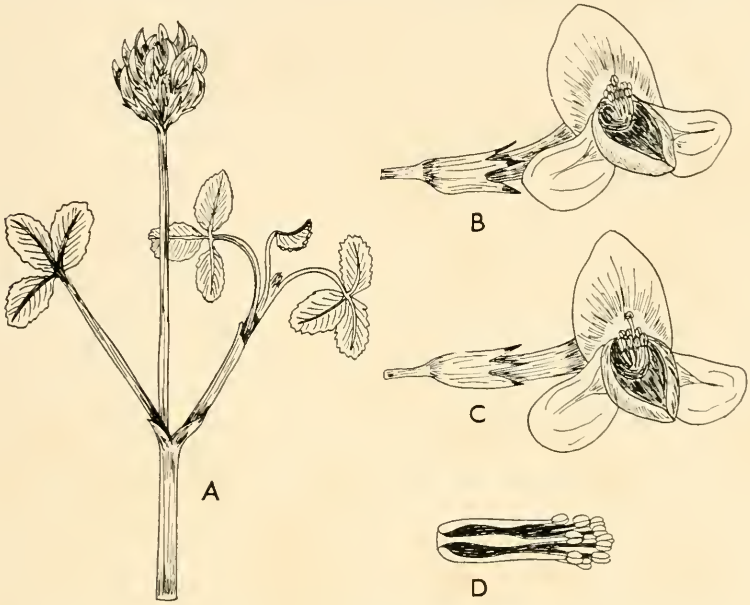


FIG. 1237.—*Trifolium repens*. A, Flowering shoot. B, Flower in young staminate state. C, Pistillate or female state, with protruding stigma. D, Androecium showing posterior, separate stamen.

When an insect visits the flower it alights on the wing petals. Since these petals are adherent, at the base, to the keel petals, its weight causes the wing and keel petals to be depressed simultaneously. The bee now thrusts its proboscis into the flower in search of the nectar, which is copiously discharged into the cavity between the ovary and the staminal tube. In so doing the keel is further depressed and the young stamens discharge their pollen underneath the body of the bee. In a later stage of anthesis, when the stigma is ripe, it occupies a position similar to the anthers, but the tip projects above them so that it is the first organ to touch the body of the visiting insect. It will therefore tend to receive foreign pollen. After the insect has left the flower, the weight being removed from the wing petals, the keel closes up again over the stamens and once more protects them. Both keel and vexillum efficiently protect the pollen from rain or dew, as well as preventing small insects from robbing the flower of its nectar.

(*b*) *Humble Bee Flowers*

These flowers have longer corolla tubes than those of the bee flowers, that is to say the tube is more than 7 mm. long, thus precluding any shorter-tongued insects from reaching the nectar. Such flowers may however be pollinated by Butterflies and Moths, while some Hover Flies seem to visit the flowers as well. Bees with short probosces, however, often rob the flowers by biting through the corolla tube and reaching the nectar that way. The Hive Bee will sometimes rob Red Clover, making use of holes already cut by short-tongued Bees who are excluded from the flowers. In many instances Lepidoptera with very long tongues can reach the nectar through the natural entrances but fail to cause pollination. In some instances pollination is restricted to a single species of Humble Bee, owing to the depth at which the nectar is secreted, and such flowers are restricted in their distribution to those parts of the world where the natural pollinator occurs.

Among the common Humble Bee flowers we may mention the following: *Trifolium pratense* (Red Clover); *Aquilegia vulgaris* (Columbine); *Antirrhinum majus* (Snap Dragon); *Digitalis purpurea* (Foxglove); *Atropa belladonna* (Deadly Nightshade); *Pedicularis sylvatica* (Lousewort); *Salvia pratensis* (Sage) and many others.

The Red Clover is by far the most valuable fodder plant for store cattle. About 40 per cent. of the bee visitors to this flower are seeking pollen. It can be worked for nectar by the Hive Bee only when the nectar has accumulated to a depth of 1·7 mm., which may happen after nights of heavy dew. In spite of this limitation and the old belief that the Humble Bee is the most important pollinator, careful observation shows that about 80 per cent. of the flowers are Hive Bee pollinated during pollen-collecting flights, and only about 15 per cent. by the Humble Bees, which are much less energetic.

Butler after careful investigation found only about 7 per cent. of the pollen loads of the Hive Bee containing mixed pollens, so the bees must be remarkably species-constant on their journeys and hence are most effective as cross-pollinators.

The case of the Red Clover is so important that we shall describe the pollination mechanism, though to a large extent it resembles the White Clover already referred to. The flowers of *Trifolium pratense* (Fig. 1238) are produced in racemose heads similar in shape to those of *T. repens*, but considerably larger. The calyx is short, with five pointed sepals, fused basally into a tube. The corolla consists of five petals, the vexillum being rather elongated and oval in shape. The alae are shorter than the vexillum and are enclosed by it, while the carina is shorter than the alae and the two petals which form it are fused marginally together. The basal parts of all five petals are united to form a tube up to 10 mm. long. The stamens are diadelphous, nine of them being fused to one another and also to the corolla tube. The upper, free stamen lies to one side of the flower and the opening it leaves in the staminal tube forms a passage to the nectar, which is secreted in the base of the corolla tube. Both the stamens and the stigma are enclosed in the carina, where they are completely protected. When a Humble Bee visits the flower it settles on the alae, which are united to the carina, and the whole is depressed. This liberates the stigma, the tip of which comes into contact with the underside of the insect. Meanwhile the bee thrusts its proboscis into the flower and the anthers, which dehisce introrsely,

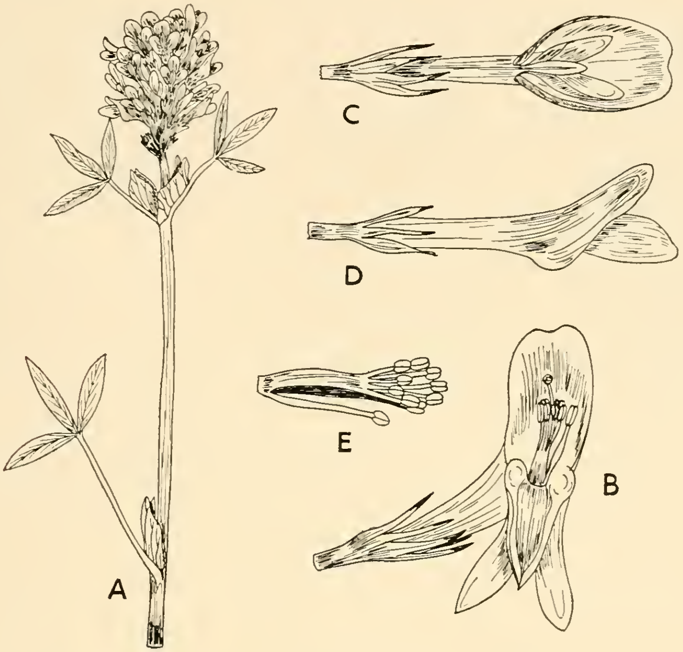


Fig. 1238.—*Trifolium pratense.* A, Flowering shoot. B, Flower after pollination with depressed carina. C, Young flower showing vexillum, alae and carina. D, Flower from side showing protruding carina. E, Androecium showing single, free, posterior stamen. The drawing is reversed.

scatter their pollen on the lower side of its thorax. When the insect withdraws its head, the alae and carina return to their original position.

Though this type has been selected because of its economic importance, all Humble Bee flowers do not work in the same way. Even in the family Papilionaceae there are a number of different mechanisms, such as the piston and explosive mechanisms, which are operated by Humble Bees, and further mechanisms can be seen in other families. Reference to some of these will be found in the account of the Families of Angiosperms in Chapters XXVIII, XXIX, XXX.

The corollas of certain flowers are so closely folded or the petals so adpressed that only a Humble Bee is strong enough to force an entry. The case of the Snapdragon (*Antirrhinum*) is very familiar in this connection. Less known is that of *Pedicularis*, where the stamens are closely covered by the infolded upper lip of the flower and the lower lip affords a landing-stage. As the bee presses its head into the flower, the edges of the upper lip are forced apart and the pollen is showered down on to the insect.

Pedicularis lanata, a species in which these conditions obtain, whereby only a Humble Bee could effect pollination, grows nevertheless in Spitzbergen, where there are no Humble Bees. Self-pollination is regularly ensured by the backward bending of the style, so that the stigma makes direct contact with the anthers. The same thing occurs in *Euphrasia minima* and other small-flowered high-alpine species of that genus. No cross-pollination is possible, yet these species do not seem to have suffered, either in seed production or in the vitality of their offspring (see also under Cleistogamy, p. 1351).

(*c*) *Bee-Humble Bee Flowers*

Several kinds of intermediate condition exist in which flowers have become adapted to visits of more than one type of insect, which differ in the length of their probosces. These are mostly exceptional cases and of considerable interest. There are two distinct principles involved. The first is illustrated by *Calamintha alpina*, in which there are two distinct forms, differing in the length of the floral tube. The long-tubed form is regularly visited by Humble Bees, while the short-tubed form is pollinated by Hive Bees. Both stocks are alike in other respects and both produce hermaphrodite, protandrous flowers.

(*d*) *Bee-Butterfly Flowers*

The second case is that illustrated by species of *Rhinanthus* of the *R. hirsutus* group (Fig. 1239). These are alpine species, the flowers of which are adapted to pollination both by Humble Bees and by Butterflies. There is a very narrow opening in the corolla immediately under the stigma, through which a butterfly can insert its proboscis and obtain nectar, in the course of which it brings about pollination. Lower down the corolla tube is a second, wider opening, which is so situated that a shorter-tongued insect, like a Humble Bee, can reach the nectar. The anthers are pendent

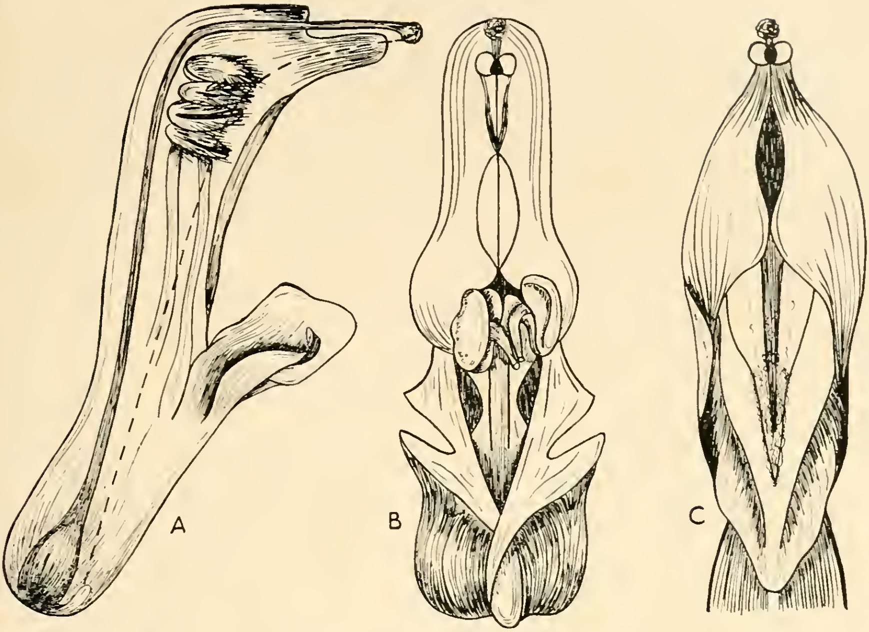


FIG. 1239.—*Rhinanthus angustifolius* (*alpinus*). A, Vertical section of flower. The dotted line shows the route from the upper corolla opening to the nectary. B, Flower from front. Above, the butterfly door, open; below, the humble bee door, shut but often forced open by the bees. C, *R. major* (*hirsutus*). Front view of upper lip, with both doors open. (*After Muller-Lippstadt.*)

and movable and the pollen is shaken out of them by contact with the insect, while a fringe of hairs on the anthers prevents the pollen from scattering.

(*e*) *Wasp Flowers*

Many flowers may be visited by wasps as well as by bees and the identity of the pollinator seems to depend upon the district. For example, in certain parts of Europe *Symphoricarpus racemosus* is chiefly pollinated by wasps, whereas in other areas its pollinator is usually the Hive Bee, although wasps may occasionally visit the flowers. Such flowers can scarcely be regarded as true wasp flowers and the number of flowers which are normally and almost exclusively pollinated by wasps is quite small. True wasp flowers are not very conspicuous, the prevailing corolla colour is reddish-brown, which contrasts somewhat with the yellow anthers, but this colour may be more conspicuous to wasps than it is to human beings. One of the most common wasp flowers is *Scrophularia nodosa;* indeed all the members of the genus which have been studied appear to rely upon wasps for their pollination. The dull purple flowers of the orchid, *Helleborine*, are also constantly frequented by wasps, the nectar being easily accessible.

In *S. nodosa*, which we may take as a type (Fig. 1240), the flowers are quite small and are arranged in dichasial cymes, which are often incomplete.

The calyx consists of five fused sepals, inside which is a globular corolla, composed of five petals completely fused together except at their apices. The corolla is brownish in colour but the inside is darker in tint and may serve as a nectar guide. The corolla is bilobed, the two posterior petals standing more or less erect, while the three lower ones form a drooping, outwardly projecting lip. There are four stamens and a staminode, the latter attached to the petals. The two anterior stamens are longer than the two posterior ones and in the early stage the filaments are so curved that they bring the anthers down almost to the floor of the corolla tube. The staminode occupies a posterior position and is brown in colour. It may also serve as a nectar guide. The gynoecium consists of two carpels, and the style is curved forward so that it rests against the posterior part of the corolla tube, and, in the early stage of flowering, it projects above the opening, in the median position. Nectar is secreted in the base of the corolla. The flowers are markedly protogynous and in the first stage a wasp visiting the flower will, when it inserts its head, come into contact with the stigma and any

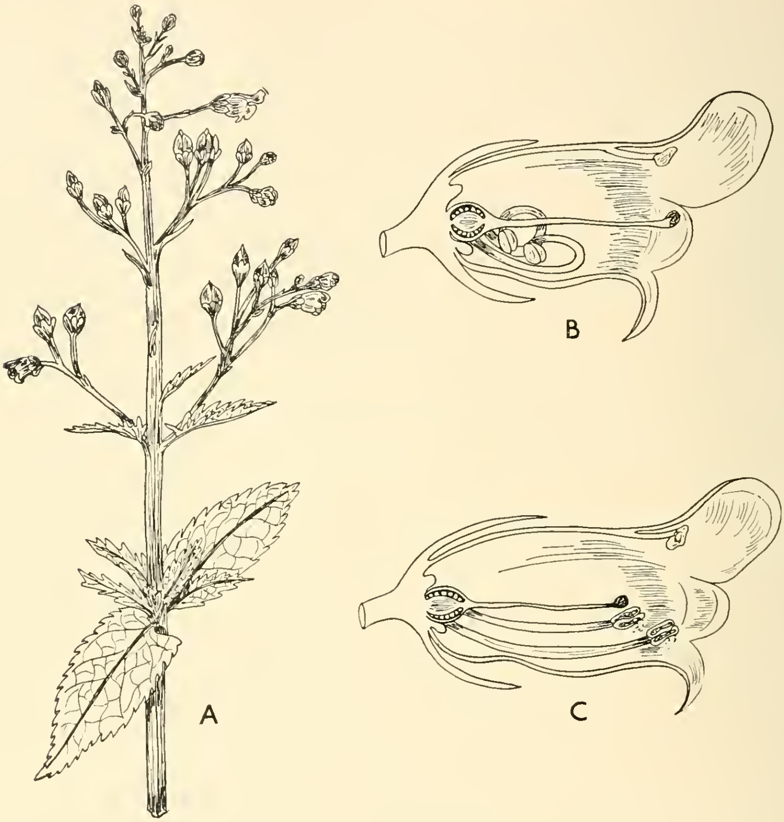


Fig. 1240.—*Scrophularia nodosa.* A, Flowering shoot. B, Flower in section. Early stage with stigma presented. C, Later stage with style withered and anthers presented.

pollen it may have on its head will be deposited on it. After about two days in this state, the style withdraws the stigmatic tip from the mouth of the flower and the filaments of the stamens straighten, bringing the anthers into the open mouth of the corolla. Here they dehisce and a wasp entering the flower at this stage will become liberally dusted on the head with pollen. Although the stigma moves away from the opening, it does not lose its receptive power, so that, if cross-pollination fails, it may be self-pollinated by pollen which falls from the anthers above it. Wasps, unlike bees, generally start with the young flowers at the top of an inflorescence and work downwards and hence the chances of crossing between different plants are increased. It has also been observed that, towards the end of the season, wasps cease to visit the flowers and at that time the remaining flowers may be visited by both Hive and Humble Bees.

The great genus *Ficus* has about 600 species distributed around the world in the warm zones and it appears to be pollinated everywhere by small chalcid wasps of several different genera. A single species of wasp, such as *Blastophaga brasiliensis*, may pollinate a number of Fig species. Others are limited to one plant species. Among the latter is *Blastophaga grossorum*, which pollinates the edible Fig of Southern Europe.

The Cultivated Fig, *Ficus carica*, is dependent upon this gall wasp for the production of seed, although edible fruits may be formed without pollination. These fruits are compound structures (syconia) composed of fleshy, pear-shaped inflorescence axes, which are hollow inside and open by a constricted apical pore surrounded by small scales (see Fig. 1404, p. 1543). Lining the inside are numerous unisexual flowers.

The Wild Fig produces three distinct types of "fruits" each year which differ both in the kind of flowers which they contain and the degree of fleshiness of the fruit.

1. *The Profichi.* In Italy, these fruits are produced during February. They contain male flowers which are formed chiefly around the apical pore and abortive female "gall flowers" which develop lower down, the proportion of male to female flowers being about 1 to 8. The "gall flower" has a rudimentary ovary, incapable of producing seed and a short style with an abortive stigma and an open canal leading into the ovary (Fig. 1241). It has no function other than its association with the wasps.

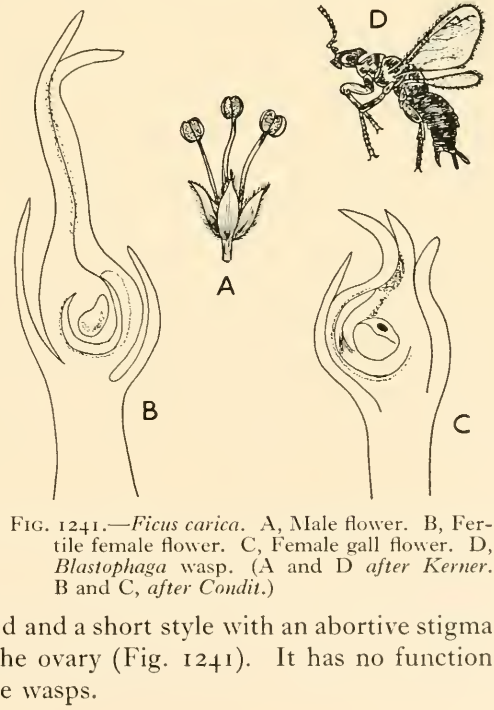


FIG. 1241.—*Ficus carica.* A, Male flower. B, Fertile female flower. C, Female gall flower. D, *Blastophaga* wasp. (A and D *after Kerner.* B and C, *after Condit.*)

2. *The Mammoni.* This type of fruit is formed at the end of May. Some contain fully developed female flowers with long stigmas and fertile ovaries. Others contain a mixture of fertile female flowers and " gall flowers " in varying proportions. Such fruits ripen at the end of September and are edible.

Although the wasps try to lay eggs in the fertile female flowers, the ovipositor cannot reach the ovary of the flower. The eggs are thus unsuitably placed and soon perish. The only effect of the visitors on the female flowers is, therefore, the deposition on the stigmas of pollen brought from the profichi.

3. *The Mamme.* This type develops during the summer and bears only " gall flowers " similar in structure to those found in the profichi. The fruits, are small and remain on the trees during the winter.

Thus we have three types of flowers, fertile male flowers which produce pollen, fertile female flowers capable of being pollinated, and infertile flowers whose function it is to nourish the grubs of the gall wasps which bring about pollination.

The Cultivated Fig derived from this wild species exists in two races. Firstly the Caprifig or Goat Fig, which never produces any edible fruits, and the Domestic Fig which does. Each race produces three types of flowers.

In early spring the Caprifig produces profichi which are invaded by gall wasps, who have passed the winter in the mamme. These wasps lay their eggs on the " gall flowers ", one egg being laid in each ovary. The egg hatches and the larva feeds on the tissues of the ovule and there undergoes its metamorphosis. The male wasps are produced first, they gnaw their way out of the ovary and move to " gall flowers " containing female wasps, pierce the ovary walls and fertilize the female wasps within. The male wasps then die without leaving the fruit. The female wasps escape from the ovaries through the holes made by the male wasps, crawl out of the syconium and in doing so become dusted with pollen from the male flowers which are developed around the opening.

The gravid females which have escaped from the profichi in June now enter the fruits which were formed in May. In the case of the Caprifig, these are the mammoni which, as we have seen, may contain a proportion of fertile female flowers. These are pollinated by the pollen carried from the male flowers of the profichi fruits while the " gall flowers " are used by the wasps to raise a further crop of grubs. In the case of the domestic race, the fruits are termed *Pedagnuoli*, and contain only fertile female flowers and these are pollinated but not galled. These fruits ripen into edible figs successively from August to December and form the main commercial crop.

A new generation of female wasps is produced in the mammoni, which escapes in September often without becoming dusted with pollen, for only a very few male flowers are found at the top of the fruit, and enter the third type of fruit, the mamme. In the Caprifig these contain only " gall flowers ", in which eggs are laid and the larvae pass the winter in the Figs which remain on the tree. These wasps after being fertilized, as described above, enter the profichi in the spring and the cycle is completed.

In the case of the Domestic Fig, the autumn fruits, termed the *Cimaruoli*, contain only fertile female flowers and these may become pollinated, in which case a crop of edible Figs will be produced in the winter.

From this complex arrangement of sexes we see that while the Caprifig bears male flowers and " gall flowers " the Domestic Fig bears only female flowers, that is the Domestic Fig is essentially female, while the Caprifig alone produces a small proportion of male flowers. Under wild conditions all revert to the Caprifig race.

In many districts it is believed that the Caprifig is required as a pollinator for the Domestic Fig and a few trees of it are grown in order that their flowering shoots may be cut and attached to the trees of the fruiting race. The process is called " caprification ". It is not a universal practice and seems to be merely traditional, for the development of the edible fruit does not demand it.

Although in the Caprifig the presence of the gall wasp is apparently essential for the production of fruits it is not necessary in the Domestic Fig which can produce succulent edible fruits in the absence of any pollination. No seed is set, however, as this requires pollination. The Domestic Fig is always raised from cuttings, so that the production of seed is unnecessary and caprification is probably superfluous.

(*f*) *Ichneumon Fly Flowers*

Though these insects visit many different flowers at times, there are very few flowers which can be regarded as exclusively pollinated by them. Indeed, very little is known about the importance of ichneumon flies as pollinators. The only genus which is generally credited with a pollination mechanism specially designed for these insects is *Listera*. *L. ovata*, the Twayblade, is a common British orchid and various observers have remarked upon the frequency of ichneumon flies around the plant. On the other hand, it is not equally clear that this Orchid is visited only by these flies and it is quite possible that it is visited by various other small flies and beetles, whose bodies are of a suitable shape to enter the narrow flowers. Indeed one beetle, *Grammoptera laevis*, has often been found bearing the pollinia on its head. Another Orchid which is usually considered to be pollinated by ichneumon flies is *Herminium alpinum*, which also has inconspicuous flowers, though once more it is possible that other small insects are sometimes responsible. The flowers are very small and are hidden among tufts of grass. None the less most of the flowers become pollinated and this cannot be brought about by self-pollination.

The common Twayblade, *Listera ovata* (Fig. 1242), is the best authenticated example, though it is very probable that *L. cordata* is pollinated in the same way.

Listera ovata occurs not uncommonly in woods, but its inflorescences are not conspicuous and it is often overlooked among the ground vegetation. There are three ovate sepals, which are somewhat infolded, while the corolla consists of two small narrow lateral petals and a long labellum, which hangs downwards and is deeply cleft. The whole of the perianth is greenish-yellow and the labellum has a bright green line down the centre in the position of the nectar groove. The rostellum is relatively large and leaf-like and at the slightest touch it expels mucilage, which appears as two white tenacious drops. The anther is situated behind the rostellum and dehisces while the flower is still in the bud. When it opens the pollinia are freely exposed. They lie on their backs with their apices converging towards the upper part of the rostellum, which at this stage arches over the stigmatic surface. The rostellum then moves slightly forward and draws the pollinia clear of the anther.

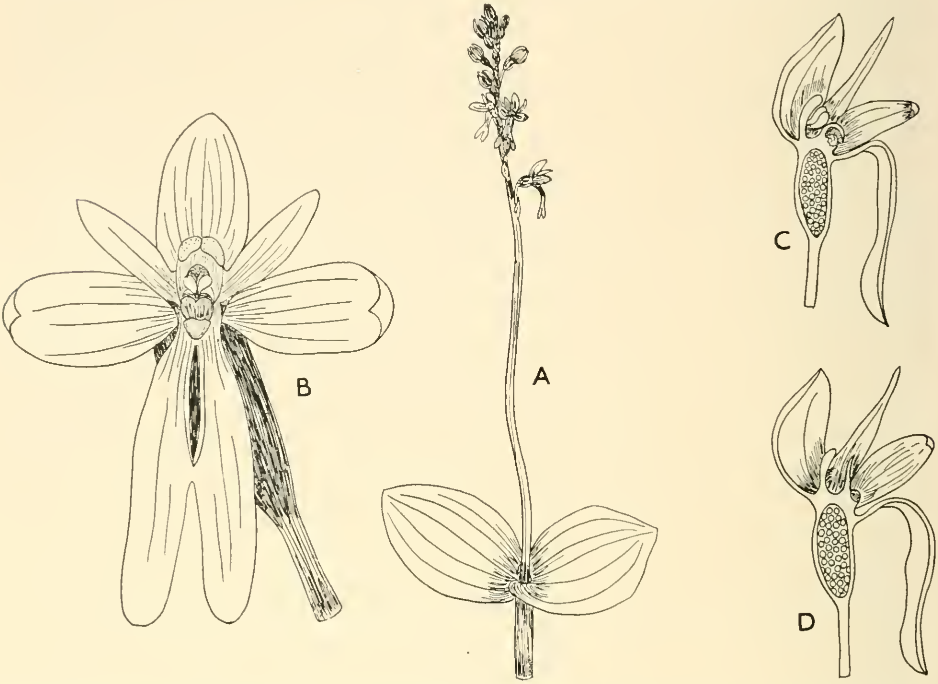


FIG. 1242.—*Listera ovata.* A, Flowering shoot. B, Front view of flower. C, Vertical section of flower with pollinia exposed above the downwardly curved rostellum. D, The same at later stage, the pollinia having been removed and the rostellum erected.

Ichneumon flies and other small insects use the labellum to alight upon and creep up it while they lick up the nectar secreted in the groove. When they reach the top of the groove they strike their heads against the rostellum, which immediately expels two drops of mucilage. These run together and adhere, both to the head of the insect and also to the tips of the pollinia, so that, when the insect flies away, it carries the pollinia with it. During this process the rostellum remains curved over the stigmatic surface so that self-pollination is prevented. Later, as the flower matures, the rostellum becomes more erect and the stigmatic surface is freely exposed. The surface becomes sticky and the nectar groove again becomes filled with nectar. If an insect, already bearing pollinia on its head, visits a flower in this stage, pollen will be deposited on the stigma as the fly reaches the top of the groove. Flowers on the same inflorescence can be found in various stages of development, but there appears to be appreciable cross-pollination between different inflorescences as well.

ii. *Lepidopterous Flowers*

Flowers visited by butterflies and moths are characterized by very long corolla tubes, such that the nectar can be reached only by insects with very long tongues. The length of this organ varies considerably in the different insect genera and some of the most efficient pollinators belong to those genera with the longest tongues, as for example the Hawk Moths and some of the larger butterflies. Occasionally, instead of long narrow corolla tubes, the nectar may be secreted in special pockets, as in the case of *Lilium martagon* (see also Fig. 1245, p. 1344). While a bee must collect steadily all the available nectar to store up for the use of its colony, a butterfly need only settle on a flower if it feels the need of food. Hence attraction may play a far more important part in the visits of these latter insects. Many of the flowers visited by butterflies are pink, red or violet in colour, but the total number regularly visited, as distinct from those settled on occasionally, is quite small. Müller, for example, was only able to record 33 true butterfly and moth flowers in the whole alpine flora. Moth flowers are in many respects quite different from butterfly flowers; many open only at dusk and rely upon night-flying moths for pollination. Such flowers are usually white or light in colour so that they are readily apparent in the dusk.

(*a*) *Butterfly Flowers*

Flowers which are regularly visited by butterflies are either red or violet in colour and as a rule the flowers stand erect, for pendulous flowers are rarely visited by them. For example, the orange-red *Lilium philadelphicum* has large, open, upright flowers and the perianth segments are contracted at their bases, leaving openings between them, so that rain-water drains away and does not collect in the base of the flower. The stamens and stigma project a little above the level of the perianth, while nectar is secreted in grooves formed on the perianth segments. The butterfly therefore can alight easily on the broad limb of the petal and run its tongue down the groove to the nectar. In contrast to this is *Lilium canadense*, in which the flower is pendulous, with broad overlapping perianth segments, which serve to throw the rain off the flowers. This flower is pollinated by bees, which alight on the stigma and crawl up the style to the nectar, which is secreted at the base of the flower. Such a flower would be quite unsuitable for butterflies, for it does not provide a suitable alighting platform for an insect of their shape. Moreover, while the anthers of *L. philadelphicum* are versatile and covered all over with pollen, those of *L. canadense* are fixed in one position.

It has been repeatedly pointed out that there is a marked correlation between the colour of the butterfly and the colour of the flower it normally visits. Bates observed this over and over again in the Amazon jungle and the same is true of a British species, the Brimstone butterfly, which is one of the visitors of *Primula acaulis*, whose flowers have precisely the same colour.

Another example of a butterfly flower is *Phlox paniculata*, a plant commonly cultivated in gardens (Fig. 1243). The flowers are produced in large panicles and are very conspicuous. Each flower has a tubular calyx made up of five fused sepals, enclosing a long corolla which is formed by the fusion of five petals into a tube about 20 mm. long. The distal limbs of the petals form a wide expanded surface on which the insect can settle. The five stamens are epipetalous, with short filaments, and alternate with the petals. The anthers block the entrance to the tube and open by longitudinal slits. The ovary lies at the bottom of the corolla tube and bears a long slender style. Nectar is secreted at the base of the ovary and is stored in the corolla tube. The flowers are protandrous and the anthers ripen almost as soon as the flowers open. A butterfly visiting the flower

FIG. 1243.—*Phlox paniculata*. A, Inflorescence. B, Vertical section of flower in early stage with anthers discharging pollen at the mouth of the floral tube. C, Later stage after the style has elongated to display the stigmas.

at this stage will settle on the corolla and, while thrusting its tongue into the flower, will receive pollen on its head. Later, as the flower matures, the style elongates till it reaches the level of the anthers, the three stigmatic surfaces diverge and in this stage will receive pollen from a visiting insect. Self-pollination may occur if the divergent stigmas pick up any remaining pollen, for they curve further backwards after opening out, though usually by that time no pollen is left in the flower. As a result of cultivation a number of different coloured varieties have been produced, but they are mainly pink, red or purple in colour, though white forms also occur.

(*b*) *Moth Flowers*

Flowers which are pollinated by moths are divisible into two types, those which are visited by day-flying moths, which are almost exclusively Hummingbird Hawk Moths, and those which are visited at dusk, which attract various other kinds of moths as well. Flowers belonging to the first type are often brightly coloured, as for example the flowers of *Lavandula*, while those of the second class are generally white. Both types usually emit a powerful scent and in the latter type the scent is most noticeable in the evening.

(*a*) *Flowers opening by day*. Among those moth flowers which open by day are *Lavandula*, *Lilium martagon*, *Lonicera* (Fig. 1244), and various species of Cacti, but the number is small compared to those which open at night,

FIG. 1244.—*Lonicera periclymenum*. Hawk Moth pollinating a flower, from which part of the corolla tube has been previously cut away to show the penetration of the long proboscis. (Electronic flash photograph by Father Webb, Ampleforth.)

which includes such genera as *Datura*, *Silene*, *Nicotiana*, *Saponaria* and *Oenothera*. In most instances the flowers have very long corollas and the stamens and stigma protrude well beyond the limits of the petals. The moths which visit these flowers do not, as a rule, settle on them, but hover in front of them like Humming Birds, darting their tongues deep into the corolla while remaining almost motionless in front of the flower.

Lilium martagon (Fig. 1245) may be cited as a striking example of the first group. The flowers are large and pendulous. The perianth consists of six large segments which are purple in colour and marked with deeper purple spots. These perianth segments curve backwards and on the adaxial surface of each there is a nectary about 15 mm. long. It consists of a groove which is closed by the folding together of its edges and by a thick growth of reddish hairs, thus producing a nectar-filled tube, the open end of which is only about a millimetre across. The six stamens have long stiff filaments and the anthers are versatile, dangle freely, and stand out well beyond the limits of the perianth. The style is a long stiff rod which projects a little beyond the anthers. A moth visiting the flower may alight on the perianth, or it may hover while it thrusts its tongue down one nectar groove after another. The flower is protogynous, so that in the early stage the stigma will receive

FIG. 1245.—*Lilium martagon.* Moth taking nectar from a petal pouch. The body and wings of the insect contact the versatile anthers. Note that the style and stigma are bent to one side so that in the post-staminate stage the stigma will contact a visiting moth. (*After Ross and Morin.*)

pollen from another flower. In the later stage the anthers split longitudinally so that the moth visiting the flower will now receive pollen on its wings. Automatic self-pollination is possible in the later stage of anthesis, because pollen from the mature anthers may fall on the stigma which hangs below them.

(*b*) *Flowers opening by night.* Among the flowers pollinated by night-flying moths, one of the best-known examples is *Nicotiana. N. affinis* is commonly cultivated and both red and white forms are known in gardens (Fig. 1246). The white flowers are readily pollinated by night-flying moths, but the red form is not so commonly visited since it is less visible at night. Both, however, emit a strong scent which is most highly developed in the evening. The five-parted tubular calyx is quite short, but the corolla tube is exceptionally long, sometimes 50 mm. or more. It terminates in five divergent limbs. There are five stamens which arise from the base of the corolla tube and have very long filaments and small rounded anthers. The ovary lies at the base of the corolla tube and bears a very long, slender style with a capitate

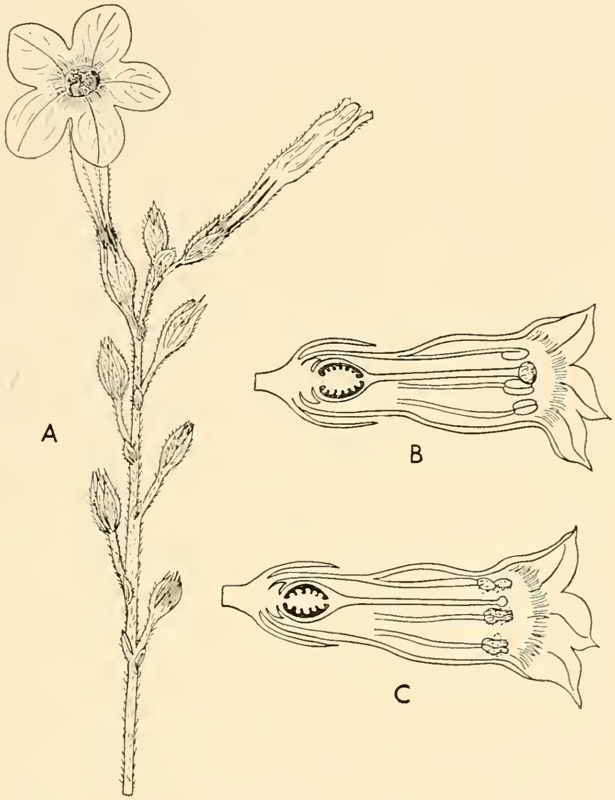


FIG. 1246.—*Nicotiana affinis.* A, Part of inflorescence. B, Young state with stigma presented at mouth of the floral tube. C, Later stage with stigma withdrawn and anthers presented.

stigma. When the flower first opens the stigma occupies the mouth of the corolla tube, while the anthers lie further down and are not yet mature. At this stage a moth will therefore pollinate the stigma if it has previously visited another flower. Later the anthers mature and pollen will be deposited on the tongue of an insect as it is thrust down the corolla tube. Pollen so collected will be deposited on the stigma of a younger flower as the moth seeks for the narrow opening to the nectar which collects in the base of the corolla tube.

A unique case of moth pollination is afforded by the *Yucca* and its pollinator the moth *Pronuba yuccasella*, which we have already described on p. 1263. So far as is known no other insect can effect pollination and indeed in those parts of the world where *Pronuba* does not occur, *Yucca* planted in gardens never sets seed.

iii. *Dipterous Flowers*

The Diptera are only feeble fliers and often effect pollination by crawling into flowers. Moreover in many cases it is doubtful if they obtain any nourishment from the flower and their reasons for visiting them may vary. Some are attracted by the carrion smell, which suggests dead meat, which they favour as a place to lay their eggs. Others visit the flowers for warmth or for protection from wind or rain. Others again are caught by some deceptive mechanism provided by the flower so that the animal can scarcely be said to be a willing visitor at all. Indeed, so diverse are the circumstances of fly pollination that it is more difficult to circumscribe this group than any of the previous ones. Six distinct types of mechanisms are recognized.

(*a*) *Nauseous Flowers*

The flowers which belong to this group usually have their nectar either completely exposed or only partly concealed and in this respect they show little specialization. In colour they are dull brown, purple or yellow, often spotted and generally suggestive of decaying meat, a feature which is emphasized by the nauseous odour which they emit. Such flowers are visited by carrion and dung flies, but they also attract many other insects. Further it must be remembered that flowers which emit odours not specially unpleasant to man may attract flies in the same way as the more nauseous odours do. It is therefore by no means easy to limit sharply the types which should be included in this section. For example, the flowers of Umbelliferae are generally fly-pollinated, for which their open form and the shallow layer of nectar they secrete are well suited. The flowers of many species have heavy aminoid odours attractive to flies, which sometimes frequent the plants in swarms, *e.g.*, *Smyrnium olusatrum*, but not all these odours could be classed as nauseous, nor is there usually the murky colouring which goes with truly nauseous odours.

Among the more common and simple types which belong to this class are various species of the genus *Saxifraga*. Müller, studying the alpine flora, found many species of this genus were pollinated by flies and we may refer particularly to one species *S. aizoides*, which he considers illustrates this type of flower very well.

Saxifraga aizoides occurs in the mountainous parts fo this country (Fig. 1247). It is a small rosette plant which bears loose panicles of yellow flowers, spotted with dull red. There is a five-parted calyx and five petals which open out quite flat to expose the ten stamens. The ovary is prolonged into a divergent pair of styles with small apical stigmas. The lower part of the ovary is spotted in a way similar to the petals. Nectar is secreted around the base of the ovary and is almost completely exposed. The flowers are protandrous; the outer stamens ripen first and there is a progressive ripening of one stamen after another till all ten stamens have discharged their pollen. Only after this do the stigmas mature. Cross-pollination is therefore almost inevitable, though in some districts the style appears to be receptive before pollen shedding is complete. Though sometimes visited by bees and small butterflies, the species is mainly pollinated by small flies, similar to the house fly, and also by ants and small beetles.

FIG. 1247.—*Saxifraga aizoides*. A, Flowering shoot. B, Young flower in section with connivent stamens discharging pollen. C, Later stage after anthers are shed. Ovary and stigmas fully developed.

Though this example may be cited as representative of temperate plants, by far the most striking examples are seen in the tropics. The most remarkable case is that of the flowers of the genus *Rafflesia*, especially *R. arnoldi*, which has a flower nearly a yard across and emits a most nauseous odour. It is said to be pollinated by carrion flies. An account of its features will be given under the family Rafflesiaceae (see p. 1707).

Among the other flowers which belong to this class are *Smilax herbacea*, *Trillium erectum* and *Calla palustris.* A peculiar case is that of *Cobaea scandens*, a rapidly growing climber often cultivated in gardens. It is a member of the Polemoniaceae. The large bell-shaped flowers at first emit a nauseous odour and are visited by carrion flies. Later this odour disappears and is replaced by sweet-smelling nectar. In this condition the flowers are sought after by butterflies.

(*b*) *Pitfall Flowers*

This term was used by Knuth to include various types of pollination mechanisms by which small flies are imprisoned. For one reason or another they find their way through a small opening in the floral organs and once inside they are trapped. Their prison may consist of a single flower or it may be an inflorescence and composed of large numbers of separate flowers. In either case the function of the fly is to be covered with pollen, which it brushes off on the stigma of the same or of another flower. Generally some part of the flower is chocolate brown in colour, a colour to which these small flies are attracted. What induces the insect to enter the flower is not always clear. Frequently it may be to obtain protection, for the temperature inside such structures as the spathe of *Arum maculatum* may be several degrees higher than that outside, so that warmth may at times be what these insects seek. Only very rarely is nectar secreted and few of these pitfall flowers reward the insects which visit them.

Pitfall flowers have probably been derived from nauseous ones and we may describe *Asarum europaeum* (Aristolochiaceae) as an intermediate type between the two (Fig. 1248). The plant is widely distributed and occurs occasionally in Britain, although not native. The flowers are inconspicuous and are borne in terminal inflorescences on creeping leafy shoots. Each flower is brownish on the outside and a dark, dirty purple within. It emits a strong odour likened to camphor. The ovary is inferior and above it rises a three-partite perianth with the lower halves of its segments joined to form an open cup. The perianth is lined with downward-pointing hairs. A short united style branches at the top into six arched segments, around and between which arise twelve stamens, whose long, pointed apices bend inwards to meet over the centre of the style. Small flies work their way down between the stamens and the arms of the style and find themselves there in a cage, escape laterally from which is prevented by the perianth hairs. There they stay until the anthers have shed the pollen, when the stamens bend outwards and the pollen-dusted flies are freed to go on to another flower. The flowers are protogynous, thus cross-pollination can only be ensured by flies which come from an older flower to a younger one.

This relatively simple example leads to the more elaborate mechanisms

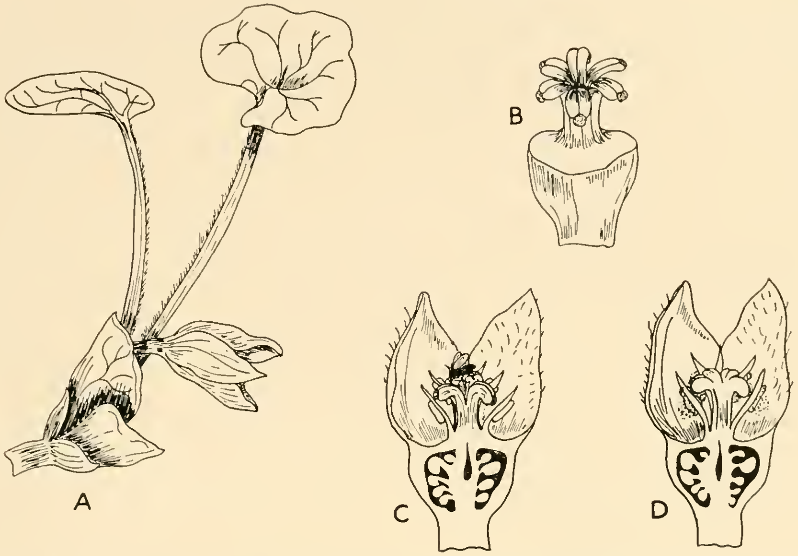


FIG. 1248.—*Asarum europaeum.* A, Shoot with flower and two foliage leaves. B, Gynoecium with divergent styles and terminal stigmas. C, Vertical section of flower in early stage with fly about to crawl down between the stylar arms. D, Later stage with anthers discharging. (*Partly after Le Maout and Decaisne.*)

found in other members of the Aristolochiaceae. Many pitfall and trap structures have been produced by various species of *Aristolochia*, with the result that the large, tubular flowers have become greatly modified and have earned the popular name of " Dutchman's Pipes ". These pollination mechanisms will be discussed under the description of the Family (see p. 1706).

Under the present heading can be included some of the most remarkable of the mechanisms in the Orchidaceae although they are not strictly dipterous flowers. Two well-known examples are those of *Cypripedium* and *Coryanthes.*

In *Cypripedium* the labellum forms a large pouch with an inturned edge, its proximal part being rolled into a tube surrounding the reproductive organs (Fig. 1249). The posterior stamen is here a large, sterile staminode, shaped like a shield, while the two lateral anthers of the inner whorl are

FIG. 1249.—*Cypripedium*, cultivated hybrid, showing frontal aspect of flower with large pouched labellum.

fertile and contain pollen mixed with a glutinous fluid. The stigma is convex and stands below the staminode, in the tube formed by the labellum. Its surface is not sticky, but is rough with papillae which can scrape the glutinous pollen from an insect. Flies and small bees (*Andrena*) enter the pouch and cannot crawl out of it directly, but have to go up the tubular part, where they meet, first the stigma, then the two fertile anthers. Thus they leave on the stigma any pollen they may be carrying and emerge at the base of the labellar tube smeared with fresh pollen.

The flowers of *Coryanthes* (Fig. 1250) are pendulous and the distal part of the labellum forms a large " bucket ", turned inwards adaxially. Two appendages at the base of the labellum hang over this bucket and secrete fluid in a steady flow of drops into the bucket, which may contain as much as 30 c.c. at a time. The fluid is only faintly sweet and is not the main attraction, for bees come to gnaw the tissue of the labellum itself. The bucket is provided with a spout turned towards the column and fitting closely to it, with the pollinia and stigmas immediately above the spout. The bees are small species of *Euglossa* and they come in such numbers that they jostle one another into the bucket. The first to fall in wallows his way through the water to the spout and in pushing his way out carries off the pollinia. Subsequent victims may bring pollen with them, which they leave on the stigma, since the same insect may be repeatedly immersed. Darwin remarked about this extraordinary performance that it "appeared utterly incredible !"

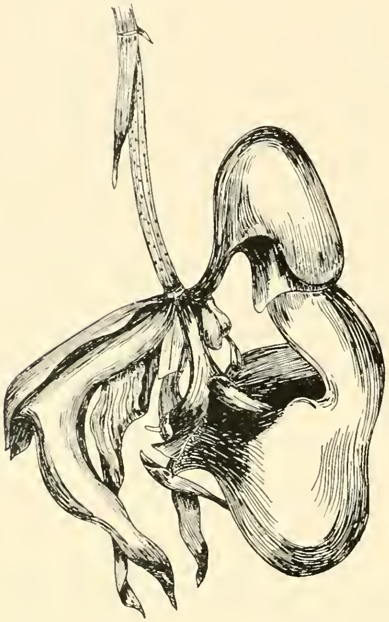


FIG. 1250.—*Coryanthes speciosa*. Pendulous flower with distal part of labellum forming large " bucket ". The exit spout is turned to the left. (*After Darwin.*)

(*c*) *Pitfall Inflorescences*

The type of pitfall mechanism developed in *Arum maculatum* is more elaborate and involves the trapping of the flies in a prison formed around an inflorescence. In this type the insects move from the region of the axis on which female flowers are produced, to one in which there are male flowers. Both their passage from the one to the other and their final escape are delayed by downward-projecting hairs which wither progressively, so that when they do finally escape the flies are completely smothered with pollen. Müller suggests that this climax type may have been evolved from forms like *Calla palustris* or *Lysichiton* in which the spathe surrounds, but does not enclose, the flowers, and the inflorescence axis is covered with flowers to the top and not prolonged as a sterile organ, the spadix. The pollination mechanism of *Arum maculatum* is one of the most remarkable in the plant kingdom and it will be described in detail under the Family Araceae (see p. 2017).

(*d*) *Pinchtrap Mechanisms*

The peculiar and highly specialized mechanisms included in this section are characteristic only of certain families or genera and in each case the process is quite different, although the result achieved may be similar. In general the insect is either forced by some obstruction to follow a particular route within a flower whereby it comes into contact with the anthers or stigma, or alternatively the whole anther may become attached to the body of the insect who, in visiting another flower, leaves the pollen on the stigma.

(*a*) *Clip mechanism.* The most important family so far as this mechanism is concerned is the Asclepiadaceae. Almost all the genera of the family exhibit some modification of the same basic arrangement. This is discussed in relation to the morphology of stamens (p. 1189) and again under the description of the family (p. 1883), and need only be briefly referred to here. There occur in the flowers a number of curious clips, each of which consists of a thin, hard plate, and bears two pollinia one from each of an adjacent pair of anthers. Owing to the shape of the clip, like the letter "c" (see Fig. 1796, p. 1884), it grips round the foot, proboscis or bristle of an insect visitor and is forcibly torn away when the insect leaves the flower. In this way the pollinia are removed and carried away by the insect. If the insect visits another flower of the same type a funnel-shaped cavity in the flower leading down to the stigmatic surface guides the pollinia into a position where they stick fast to the stigma and become severed from the clip. The clip remains attached to the insect but meanwhile another clip may become attached, and two more pollinia, from the second flower, are removed when the insect leaves it. The number of clips attached to an insect is therefore an index of the number of visits it has made to this kind of flower. From the fact that insects have been observed with not only a number of clips, but also a number of pollinia attached to them, it would appear that the mechanism is not entirely satisfactory and there is no certainty that the pollinia will inevitably reach the stigma when the insect visits another flower. Various kinds of insects, bees, butterflies and flies all visit species of *Asclepias*, for all can reach the nectar which the flowers offer.

Another asclepiad, the South American *Araujia albens*, sometimes cultivated for its white flowers, is pollinated at home by Humble Bees. In cultivation the flowers are visited by moths, which are trapped. The anthers have rigid wings and the moths get their probosces caught in the tapering slits between these wings and die as prisoners.

(*b*) *Orchid type.* The foregoing method of attaching the pollen in masses to the body of an insect visitor is similar in principle to that found in the Orchids. Here the insect is encouraged by the offer of nectar to thrust its head into the flower. In doing so it comes into contact with the rostellum and on withdrawing its head brings away attached to it two pollinia from the anther. For the details of the process see Chapter XXX, p. 2098.

The astonishing variety of mechanisms among Orchids may be learnt from Darwin's fascinating book, "On the Fertilization of Orchids by Insects". Some, as we have seen already (p. 1339), depart far from the *Orchis* type described under Orchidaceae in Chapter XXX. Some are definitely pinch-trap mechanisms, for example the Australasian *Pterostylis longifolia*, which has a sensitive labellum (Fig. 1251). The flower has the form of an upright hood with the petals and one sepal closely overlapping except for a narrow opening in front, through which the labellum protrudes. This has a distal portion like a tongue covered with long papillae and a proximal portion like a piece of watch spring. It responds to the lightest touch and when an insect alights on it the spring-like part folds up, lifting the distal part like a drawbridge and imprisoning the insect in the flower. Two large ear-pieces project from the sides of the column, forming a short tube which is the only avenue of escape. Any insect passing out that way is certain to remove the pollinia. There is no nectar and the flowers seem to be visited exclusively by Diptera.

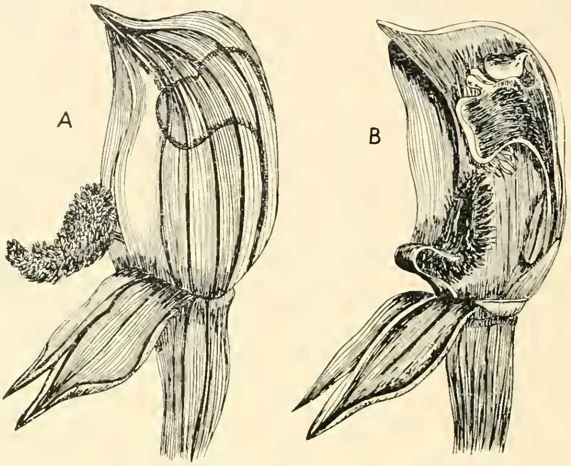


FIG. 1251.—*Pterostylis longifolia.* A, Side view of flower with the sensitive labellum protruding. B, Vertical section of flower showing labellum retracted and one of the side-pieces of the column, between which is the insect's only channel of escape. (*After Darwin.*)

The orchid genus *Catasetum* presents an extraordinary and probably unique case. The species are all dioecious and, while the male plants bear flowers which are easily distinguishable, as to species, the flowers on the female plants are not only quite different from the males, but may be quite similar to one another in distinct species, with the result that the taxonomy of the genus was for long in confusion. The male flowers possess an explosive mechanism of great interest, a feature which they share with some other orchid genera, such as *Dendrobium*, *Cynoches*, and *Mormodes.* In *Catasetum* (Fig. 1252), the column is large and rises above a basin-shaped labellum. At the top of the column is the anther and below it the rostellum.

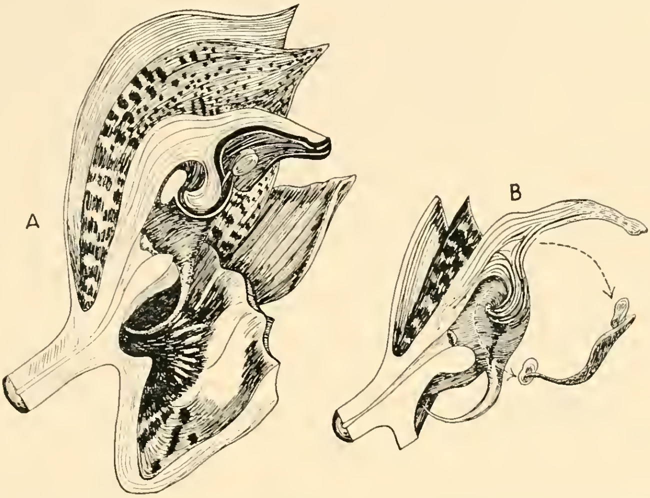


FIG. 1252. *Catasetum tridentatum.* A, Male flower in vertical section. B, Flower after stimulation showing pollinia with elastic band and viscid disc being discharged. See text. (*After Kerner.*)

Below this again the column is deeply hollowed and its edges are drawn out into two tail-like appendages which hang down into the labellum. Attached to the underside of the rostellum is the viscid disc, connected to the two pollinia by an elastic band which passes over the front of the rostellum. If one of the tails of the column is touched, however lightly, a stimulus is transmitted to the rostellum which leads to the liberation of the viscid disc. The elastic band thus freed, it straightens violently and shoots the disc forward, tears the pollinia out of the anther and projects the whole structure outwards with considerable force. The disc goes in front and if an insect is visiting a flower, the pollinia will naturally be firmly attached to it when the disc strikes its body.

(*c*) *Bristle mechanism.* A third type, to which reference may be made here, is found in the genus *Pinguicula.* In this genus there is a remarkable difference in the pollination mechanisms shown by the various species. *P. vulgaris* is pollinated by bees; *P. villosa* is probably pollinated by butterflies; *P. lusitanica* is self-pollinated, while in *P. alpina* there has been developed a trap mechanism quite unlike those described above.

Pinguicula alpina (Fig. 1253) is a mountain species with white flowers. The tubular corolla is bilabiate, the upper part being made up of two petals and the lower half of three. It is extended backwards below the calyx in the form of a spur. The two stamens and the ovary are inserted at the base of the corolla and lie below the upper lip. The stamen filaments are curved around the ovary and the small anthers are compressed and lie against the

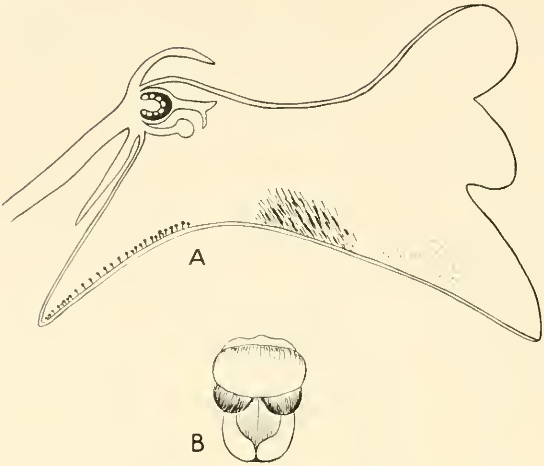


Fig. 1253.—*Pinguicula alpina.* A, Flower in longitudinal section. B, Stamens with anthers partly concealed by the lower lobe of stigma. (*After Schroeter.*)

style, arched over by the bifid stigma. The flower is devoid of nectar, but on the floor of the spur are a number of unicellular capitate glands, the heads of which contain a juicy substance attractive to flies. In the mouth of the spur is a bunch of bristles which project upwards and backwards into it. The remaining opening is large enough to allow a fly to climb over the bristles into the spur, but when it tries to withdraw it is opposed by the points of the bristles. This forces it to push upwards and it then comes into contact with the anthers and in this way becomes dusted with pollen. As it struggles outwards it turns up the lower flap of the stigma, preventing the pollen from coming into contact with the stigmatic surface, and thus escapes. The flowers are stongly protogynous so that if, after visiting an older flower, it enters a young one, it will, as it crawls down to the spur, touch the lower and larger flap of the stigma and deposit pollen upon it.

(*d*) *Explosive mechanism. Crucianella stylosa* is a member of the Rubiaceae, with the habit of a *Galium* and heads of pink flowers (Fig. 1254). Its honey scent attracts both Diptera and Hymenoptera, but the insects get a surprising welcome. The style elongates

Fig. 1254.—*Crucianella stylosa.* Inflorescence showing styles and stigmas extruded.

greatly while the flower is still in bud. The enlarged stigma is pushed up between the epipetalous anthers and carries with it the greater part of the pollen. It then presses hard against the dome formed by the closed petals. The style is now in a state of high compression and if the flower is touched the petals separate and the style springs out to about double its former length, striking the insect and forcibly scattering a cloud of pollen at the same time. Later, the receptive lobes of the stigma separate and are ready to take the pollen from subsequent visitors.

(*e*) *Deceptive Flowers*

This class is probably considerably larger than is appreciated at the present time, for the details of many pollination mechanisms remain to be studied. Flowers which are collectively referred to as deceptive agree in

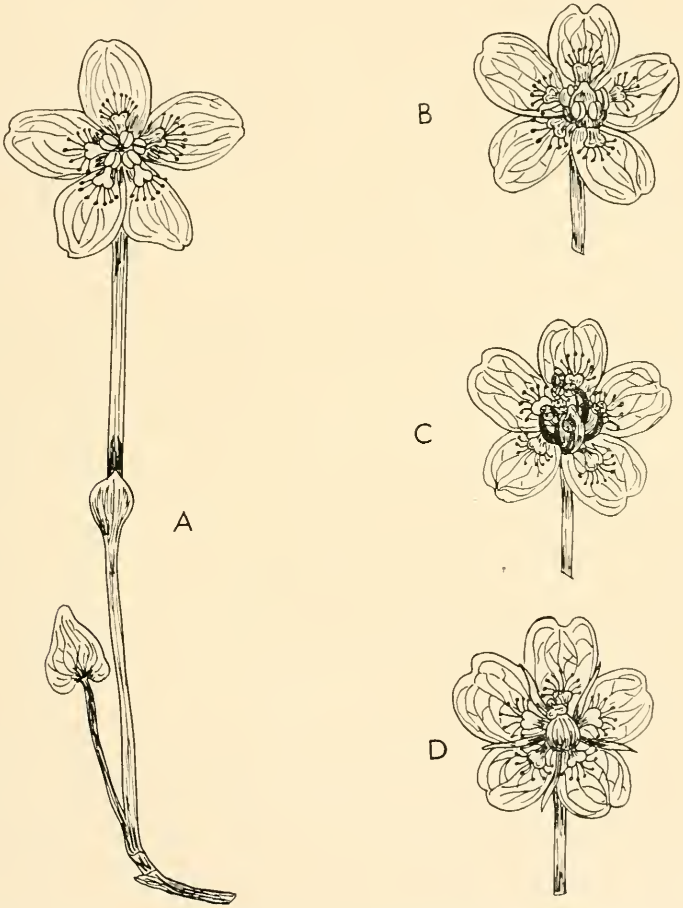


Fig. 1255.—*Parnassia palustris*. A, Flowering shoot. B, C and D, Successive stages of flower showing ripening of incurved stamens and finally, after shedding of the anthers, their outcurving to expose the ripened stigma.

appearing to offer a reward to the visitor though in reality the insect may obtain nothing in return for acting as a pollinator. Clearly it is only possible to determine whether a reward is actually given by a careful study of the flower and it is not surprising, therefore, that the well-known cases of this type of mechanism are ones in which the flower is peculiar in construction and has attracted careful study. The methods whereby insects are deluded may differ considerably and there is no general plan common to all.

(*a*) *Deceptive nectar flowers.* One of the most striking examples is *Parnassia palustris*, the Grass of Parnassus (Fig. 1255). It favours the acidic soils and is common in some parts of Britain. The flowers are produced singly and consist of a five-parted calyx and five large, whitish petals. Within the open cup formed by the petals are five fertile stamens which alternate with the petals, while opposite each petal, possibly representing an inner whorl of stamens, are five petaloid scales. Each scale consist of a basal portion, which terminates in a number of slender branches, arranged like the fingers of a hand, each ending in a bright yellow swelling. These swellings glisten and appear to be nectariferous glands, but they are perfectly dry and secrete nothing at all. In the centre is a superior ovary with a sessile stigma. When the flower opens the anthers are still unripe but their filaments soon elongate, one after another, so as to bring each anther in turn over the top of the immature stigma. After the pollen has been shed the anther bends outwards and is replaced by another. About five days later, when the last anther has moved away, the stigma unfolds and is placed in the position previously occupied by the anthers.

Only a small quantity of nectar is secreted at the base of the corolla, and is generally missed by less intelligent flies who concentrate their attention on licking the yellow pseudo-nectaries. Larger and more intelligent insects settle on top of the flower and turn round and round as they probe between the petals for the nectar. Hence in the early stage they will receive pollen on the lower part of their bodies, while this will be dusted off on the stigma of older flowers.

(*b*) *Deceptive nauseous flowers.* Another and quite different type of deception is found in the flowers of *Paris quadrifolia*, a member of the Liliaceae which is found in calcareous British woodlands (Fig. 1256). The offensive odour given out by these flowers suggests that they should belong to the Nauseous Flower group.

The flowers are yellowish-green in colour and consist of four lanceolate sepals, each about an inch long, inside which are four very narrow petals which often have a yellowish tint. Both the calyx and the corolla segments bend backwards over the stalk, while the eight stamens diverge upwards around the ovary. Each stamen consists of a fine green filament and an almost linear anther, the connectives being prolonged beyond the anther in a long fine process. The anthers open introrsely. The ovary is large and globose, purple in colour and somewhat shiny in its early stage. It is surmounted by a style with four or five divergent stigmas.

The flowers are protogynous and the stigmas are ripe as soon as the flower opens. No nectar is secreted, but an unpleasant smell is emitted and this, together with the purple colour of the ovary, attracts carrion flies, because presumably it suggests decomposing flesh to these insects. If they have previously visited another flower they will readily cover the stigmas with pollen. Later the anthers open and the pollen is very easily shaken off. Hence a fly visiting a flower in this state will probably touch the filament or the elongated connective thus scattering pollen on its body. The stigmas remain receptive until all the pollen has been shed so that, if insect visits should fail, and indeed insects rarely visit the flowers, self-pollination is possible either by wind or because of the movements of the stamens, which may converge towards the styles. Unisexual female flowers occur in which the stamens are devoid of anthers.

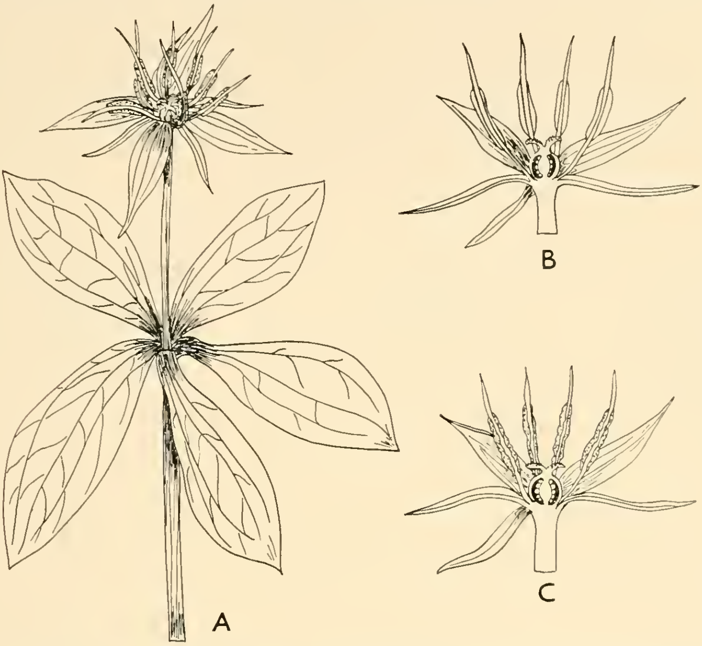


FIG. 1256.—*Paris quadrifolia.* A, Flowering shoot. B, Vertical section of flower in female state. C, The same, later state with anthers discharging pollen.

(*f*) *Hover Fly Flowers*

Most of the flowers which are pollinated by these insects are highly decorative and the colours are such that the centre of the flower is sharply distinguished from the surrounding petals. The mechanism is usually very delicate and suitable for a small, light insect which could not operate a more robust structure. Several genera have been observed to make use of Hover Flies as pollinators, but the best-known are *Circaea* and *Veronica*. Not all the species of *Veronica* appear to be pollinated by these flies, indeed, the type of visitors probably depends mainly upon the size of the flowers and their arrangement in the inflorescence. Those species in which the flowers are grouped in a solid spike, as for example, *V. spicata*, are probably visited mainly by bees and Hawk Moths. Those, like *V. chamaedrys*, in which the flowers are larger and open singly are more readily sought by flies. In all cases the structure of the flower is very similar, although there appears to be no uniformity as regards the order of the development in the parts of the flower. Some are protandrous, others protogynous or both types may be found, not only in different plants of the same species, but even among the flowers of a single inflorescence.

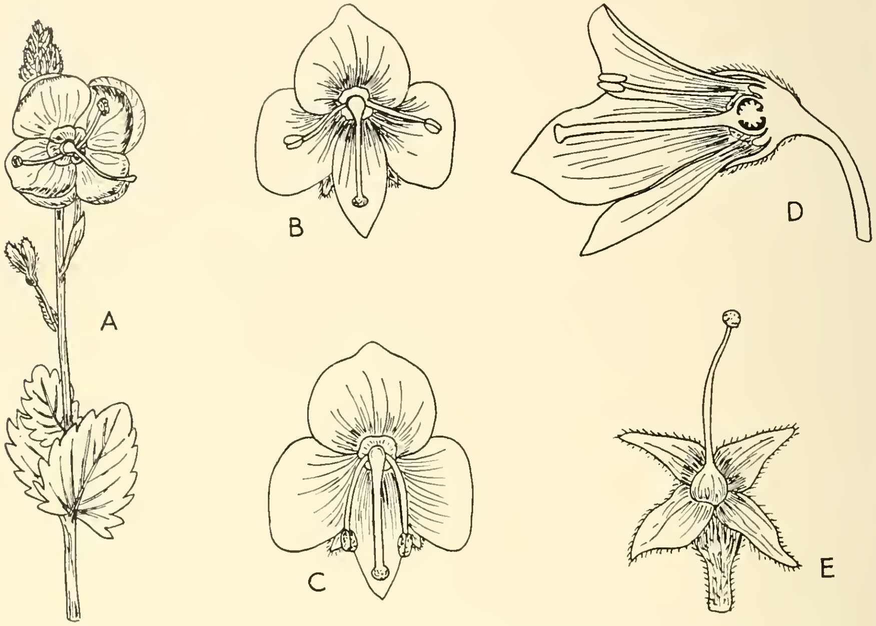


Fig. 1257.—*Veronica chamaedrys*. A, Flowering shoot. B, Front view of flower with the two divergent stamens. C, The same, later state with stamens drawn forward. D, Longitudinal section of flower. E, Flower after shedding of corolla with stamens.

The flowers of *Veronica chamaedrys* may be cited as an example of this class (Fig. 1257). This little Speedwell is common in hedgebanks all over Britain and its bright blue flowers make it very attractive and readily noticeable. The calyx is small and encloses the joined bases of four unequal petals. The posterior petal is double and it and the two lateral ones are large, while the anterior one is much narrower. The colour is not evenly distributed on the petals, which are bright blue at the margin shading almost to white in the centre and each petal is marked by branching lines of deeper blue. There are only two stamens, which have long filaments and rounded anthers and diverge widely across the flower. The ovary is superior and is prolonged into a long, slender style with a small stigma which stands over the anterior petal. Nectar is secreted at the base of the corolla tube and is protected by hairs. The corolla is rather flat compared with other species of the genus, but the two stamens stand out on either side of the flower while the style lies downwards and outwards from them. Automatic self-pollination is therefore impossible.

The pollination is simple. The lower petal provides a platform on which the fly settles and in so doing it comes into contact with the style and, if there is pollen on the ventral surface of the insect, pollination is ensured. In its effort to reach the nectar the insect grasps the filaments of the two stamens, drawing them towards it under its body, and thereby becomes dusted with pollen. The flowers only last one day and then the corolla is shed, together with the two stamens, by slipping over the style.

iv. *Flowers Pollinated by Small Insects*

Müller was responsible for the suggestion that a separate class of pollination should be made to include those flowers which are visited by tiny insects. These insects belong to various groups, but as far as pollination is concerned there is agreement in the fact that the floral parts are modified so that the anthers will come into contact with their tiny bodies. In most flowers these insects would be of no value, for they would pass around the stamens and style without touching the vital parts. Indeed, as we have seen, many flowers are specially formed to preclude their entry.

Observations have only been made on a small number of flowers which appear to belong to this group, though further research is likely to prove that more types rely upon these little insects than is recognized at present. The insects concerned include members of the Hymenoptera, Diptera, Coleoptera and possibly the Hemiptera and Thysanoptera as well.

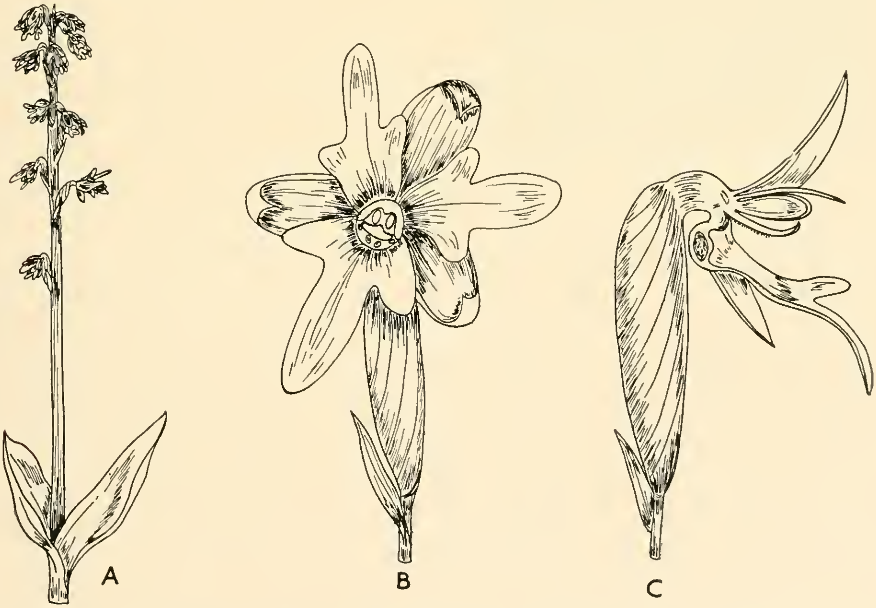


FIG. 1258.—*Herminium monorchis.* A, Inflorescence. B, Flower in front view. C, Longitudinal section.

We may instance one case which was studied by Müller, as an example. The flowers of *Herminium monorchis* are very small and greenish-white in colour, and emit an odour of honey (Figs. 1258 and 1259).

The three petals are much alike and form a tube, the labellum not being specially modified. There are two lateral stigmatic surfaces and above each is a disc, to the back of which are attached the caudicles of the pollinia belonging to the two fertile anthers. The discs are hard, but each has a hollow base which is viscid and into which any thin object slips. The insect visitors are small Hymenoptera, Diptera and Coleoptera, about 1 mm. long. The insect enters from the corner between the labellum and one of the upright petals. It can only get in its head and forelimbs and it is the latter which make contact with the discs and so become attached to the pollinia, which, if strong enough, the insect pulls out. This is followed, as usual, by the contraction of the caudicles and the pollinia are then ready to strike the stigmas of another flower.

Fig. 1259.—*Herminium monorchis*. Habit photograph. Box Hill, Surrey.

We have described a few of the almost infinitely varied means whereby pollination of flowers is ensured and cross-pollination favoured. A comparatively late comer in the field of Botany and strangely neglected, Floral Biology offers rich prizes of interest to those who have patience to study it for themselves. Darwin expressed his conviction that there was scarcely a single point of floral construction, however seemingly trivial, which did not have a meaning and a function that devoted study would reveal. However incomplete our knowledge of floral mechanism may be, records of the insect visitors are yet more imperfect. In many cases, even among common flowers, the identity of the pollinator rests upon a few isolated records, while in too many other cases it rests more on deductions from the shape of the flower than upon observations of the insects themselves in the act of pollination. When we contemplate the legions of the world's flowers it is easily grasped how very, very little we know about the inner life of even the more familiar among them. In the complex and beautiful interplay of structure and function at this critical point in the plant's life history, lie more problems of morphogenesis and organismal control than we can well imagine.

What will be our general impression if we survey what we know of pollination in different families, arranged in systematic order? If there is any value in our classifications they would give us at least an inkling of the drift of evolution. What has been the trend in the flower? Certainly an increasing economy of means may be deduced, coupled in many cases at least with increased sexual efficiency. If we postulate an ideal condition of sexual equality, with pollen grains and ovules equal in number and no wastage, then obviously it has nowhere been attained. Even in the Orchidaceae there are at least twenty pollen grains for every ovule. This apparent superfluity may, however, be a source of genetic advantage, since germinal selection is a very real force and it might well be a source of weakness to the species that the genome of all pollen grains alike should be perpetuated.

Alongside, however, of this trend towards increased efficiency, which is sufficiently obvious when extremes are contrasted, there goes another tendency, towards decreased fertility, shown by reduction in the numbers of sexual parts and more especially in the number of ovules. Here the Orchids are an outstanding exception, but putting them aside, the tendency towards uniovulate or pauciovulate carpels in the higher families is well marked. A balance may, of course, be maintained by the production of greater numbers of small flowers, but at how much greater an expense of material and with what a multiplication of the chances of failure. Sexual failure, indeed, is of widespread occurrence, even, once more, among the Orchids, with their wonderful pollination mechanisms. Its menace hangs over all the floral world and many species and even whole genera appear to have evaded the issue by relying exclusively, or almost exclusively, on self-pollination, with whatever genetic disadvantage it may entail. Other species which we have noted earlier (p. 1281) have gone further and have almost abandoned seed propagation in favour of vegetative propagation. We must not read too much into such observations, but they do carry a disturbing suggestion of a secular drift towards decreasing fertility, if not sterility.

One of the most remarkable ways in which the risks of pollination are avoided is the phenomenon of **cleistogamy**. By this is meant the production of flowers which never open and in which self-pollination is carried out within the closed bud, which then passes directly into fruit.

The list of genera in which **cleistogenes**, as these flowers are called, have been observed is a long one. Darwin named 67 genera, though unquestionably the list is far from complete. It includes the following: *Viola*, *Oxalis*, *Lamium*, *Ajuga*, *Salvia*, *Saxifraga*, *Scrophularia*, *Streptocarpus*, *Lycopus*, *Drosera*, *Subularia*, *Juncus*, *Commelina*, *Lathraea*, *Stellaria*, *Cardamine*, *Montia* and *Ononis*, to mention only the well-known genera. Further, it is widespread among grasses. Chase has recorded cleistogamous flowers in twenty grasses in the United States, including all the native species of *Triplasis*, *Danthonia* and *Cottea* and in *Muehlenbergia microsperma* and *Pappophorum wrightii*. Four South American species of *Danthonia* and one from New Zealand also produce them, as do *Stipa pennata* and *Stipa leuco-*

tricha. In Britain we have the case of *Triodia decumbens*, and it seems most probable that further search in the Gramineae would reveal many more.

In some of the above-mentioned examples, cleistogamy is more or less constitutional, but in others, and in a great number of tropical and subtropical species, it is ecological, that is to say that the presence or absence of cleistogenes is controlled by environmental factors. Among such factors are: submersion in water (*Elatine* and some *Ranunculus* species); prevalence of mist and high atmospheric moisture (*Liparis* in New Guinea); drought, in the case of species normally demanding high soil moisture (*Impatiens parviflora*); cold (*Specularia* and some montane species of *Viola* and *Thlaspi*); heat, if excessive (*Eranthemum*); shade (*Viola arvensis*, *V. sepincola* and *Linaria vulgaris*). Briefly the observations sum up to indicate factors unfavourable to the full development of the species in question, but not all species respond to such influences by cleistogamy. Unless there is a hereditable tendency to cleistogamy the majority of species merely fail to flower at all when conditions are bad.

The origin of cleistogamy is uncertain. According to Goebel's view, cleistogamous flowers correspond in structure to normal (chasmogamous) flowers of inhibited development, but endowed with the power of precocious pollination and therefore capable, in spite of their imperfect development, of forming seeds. This is contrary to Darwin's opinion, who held that cleistogamous flowers showed special modifications to ensure self-pollination. It is clear that they are not always ecologically conditioned, since they may be formed alongside of normal flowers on the same plants. Engler's observations on *Streptocarpus* led him to conclude that the inhibition of development in cleistogenes was the effect, not the cause, of their precocious self-pollination, which he attributed to inner causes which brought pollen and stigmas to functional maturity together at an early stage. In West African species of *Streptocarpus*, belonging to the section Caulescentes (Fig. 1260), some species produced only cleistogamous flowers, others had one or two chasmogamous but sterile flowers, as well. He further showed that in the many species of the genus which bear only chasmogamous flowers, self-pollination might occur.

Goebel's theory might apply in some cases where cleistogamy appears at a certain stage in the life history of the plant, but it can hardly apply to a species like *Salvia cleistogama*, where cleistogamy is a fixed specific character and no chasmogamous flowers are produced. In some South American species of *Plantago* cleistogamy shows a sex-linked inheritance. Some plants have only hermaphrodite, cleistogamous flowers, while other plants are wholly male. The hermaphrodite flowers, cleistogamously pollinated, give only cleistogamous offspring but if pollinated from male flowers the offspring are all male. Variations of nutrition had no effect on the condition.

Mather and Vines found two cleistogene plants among the offspring of a cross between *Antirrhinum majus* and *A. glutinosum*. These plants had distinct foliage and set good seed, the cleistogamy being heritable. Thus two species, one an obligatory cross-breeder and the other a facultative

Fig. 1260.—*Streptocarpus princeps.* A, Part of inflorescence with large, chasmogamous and small, cleistogamous flowers. B, Chasmogamous flower, cut longitudinally. C, Cleistogamous flower, cut longitudinally. D, Cleistogamous flower. (*After Engler.*)

cross-breeder, possessed between them all the genetical material for producing an obligatory inbreeding race.

The theory that cleistogenes are simply normal flowers inhibited in development does not hold good for most of the Gramineae cited above, for in them the cleistogenes are not part of the normal inflorescence, but are isolated flowers, produced in the axils of the lower leaf-sheaths on flowering shoots. They are produced after the maturity of the panicled spikelets and the seeds they form are longer and narrower than those of the chasmogamous flowers (Fig. 1261). It seems probable that they germinate *in situ*, being close to the ground, and that they are a regular means of propagation. *Stipa leucotricha* is an exception, however, for in addition to cleistogenes in the basal leaf-axils, cleistogenes are formed among the normal spikelets of the inflorescence, usually in its terminal portion, and their numbers are inversely correlated to the amount of soil moisture available, in other words cleistogamy is ecologically conditioned. *Leersia oryzoides*, on the other hand, is almost completely cleistogamous, under all conditions.

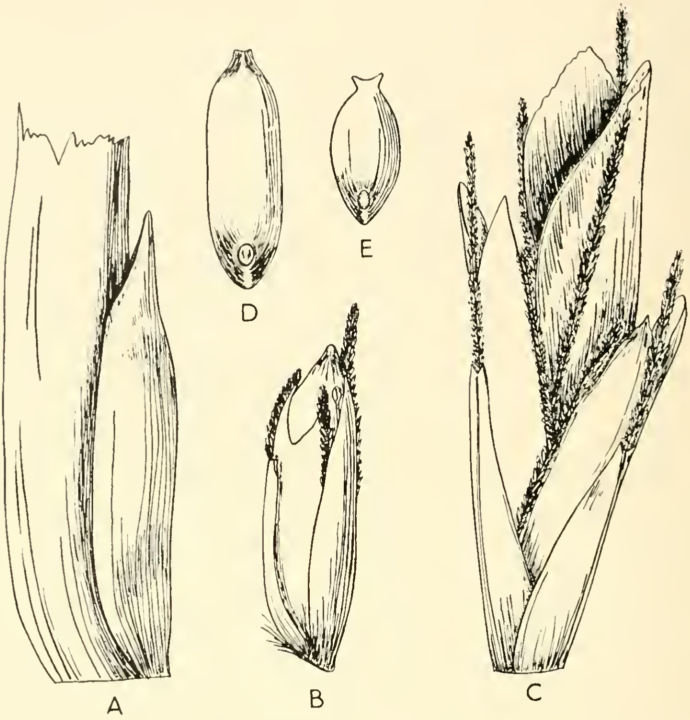


Fig. 1261.—*Triplasis purpurea*. A, Base of internode showing cleistogamous spikelet enclosed by prophyll. B, Cleistogamous spikelet. C, Spikelet from terminal panicle. D, Grain from cleistogamous spikelet. E, Grain from terminal panicle. (*After Chase.*)

Many Orchids are cleistogamous, some species entirely so, others partially. Some species normally chasmogamic have cleistogamic varieties and the distinction appears to be genetic and heritable. Thus local populations of a species may be wholly cleistogamic, others wholly chasmogamic. *Cephalanthera grandiflora* has its pollinia attached to the stigma by precociously formed pollen tubes and, left to itself, this may be enough to produce some seed, though much less than if pollination be normally carried out.

Cleistogene flowers are sometimes produced underground. Some species of *Commelina* produce such flowers on the rhizomes, the seeds ripening and germinating in place. A Brazilian species of *Cardamine*, *C. chenopodiifolia* (Fig. 1262), bears cleistogamous flowers while still in the seedling state, the axillary pedicels bending downwards and the flowers developing below ground among the roots. They show typically arrested development, the corolla, which is normally late in appearing, being absent. Chasmogamous flowers are produced later.

Fig. 1262.—*Cardamine chenopodiifolia.* A, Plant with underground cleistogamous flowers and chasmogamous flowers developing aerially. B, Siliqua from chasmogamous flower. C, Siliqua from cleistogamous flower. (*After Velenovsky.*)

By far the greater number of cleistogamic plants may be called facultative. They are of mixed type and bear both kinds of flowers, either as a regular feature or occasionally, when conditions determine it. Among the latter are the seasonal cleistogams, such as *Lamium amplexicaule* whose cleistogenes appear in the earliest spring, and *Oxalis acetosella* and *Viola odorata*, growing in shady places, which open their chasmogamous flowers in the spring, but later, when overgrown by other vegetation, bear only cleistogenes.

Exclusively cleistogamous species are much rarer. Two British plants in this category are the small and uncommon *Subularia aquatica* and *Polycarpon tetraphyllum. Leersia oryzoides* has also been named above and it may be pointed out that in this and other Grasses, no question of any lack of pollinating insects arises, since they are wind-pollinated in the chasmogamic state.

Certain facts seem to be incompatible with the idea of arrested development as the cause of cleistogamy. The wide difference between the two types of flower in the Grasses has already been remarked. Chase pointed out that the cleistogamous flowers were so different from the others that they would not, by themselves, be classified in the same tribe of Gramineae. In *Amphicarpa* (Papilionaceae) the chasmogamous fruits are falcate in shape, sparingly hairy and contain 2–3 seeds. The fruits of the subterranean cleistogenes are pyriform and one-seeded, while those of the aerial cleistogenes are densely hairy and 1–3 seeded. The anatomical structure of both kinds of fruit is different. In *Ononis alopecuroides*, the cleistogamous flowers are not reduced and show no marked difference in structure from the chasmogamous flowers. Moreover, the obvious fact that pollen and ovaries are precociously mature seems conclusively against the view that arrested development is the *cause* of cleistogamy, though arrested development of the later-formed structures may well be the *result* of it. More probably the fate of the flower is determined at the time of initiation in the inflorescence primordium, the change of physiological balance being perhaps dependent on a threshold reaction.

The cytology of cleistogamy has only been studied in detail in the classic case of *Viola* (Fig. 1263). In *V. odorata* var. *praecox* there are three types of flower, chasmogamous, semi-cleistogamous and cleistogamous. The first-named never set seed. In *Viola riviniana* there are the same three types, but the chasmogamous flowers occasionally form seed (Fig. 1264). In the anthers of all these types of flowers, two types of pollen grains are found: ovoid or tetrahedral grains, and round, ridged grains. The former only germinate if conveyed to the stigma, but the latter germinate in the anther of all three types of flower. While the pollen tubes remain inside the anthers of the chasmogamous flowers, in the cleistogamous flower they penetrate the reduced anther wall and grow out on to the stigma, while the tetrahedral grains degenerate. The semi-cleistogamous flowers show all stages of intermediacy as regard flower size, development of the spur and nectary, bending of the style towards the anthers and reduction of the anthers, but they behave like cleistogamic flowers in respect of their pollination. Such transitional forms are well known in other genera, *e.g.*, *Oxalis*, where flowers which are perfect in development, but of minute size, are pollinated cleistogamously. The actual details of the fertilization in cleistogamous *Viola* show nothing specially correlated with cleistogamy.

A final point in support of the belief that cleistogamy involves changes going deeper than simple arrest of development is to be found in the curiously neglected observation of Darwin's, that in trimorphic species of *Oxalis*, all three forms of flower occur in the cleistogamous as well as in the normal flowers. Although self-pollination of the chasmogamous flowers is almost totally sterile, yet the habitual self-pollination of the cleistogamous flowers is fully fertile.

FIG. 1263.—*Viola hirta.* Plant with cleistogamous flowers (a) and developed capsules (b). 1. Cleistogamous flower. p=petals, k=calyx, α=bracteole. 2. The same after removal of the calyx. (*After Velenovsky.*)

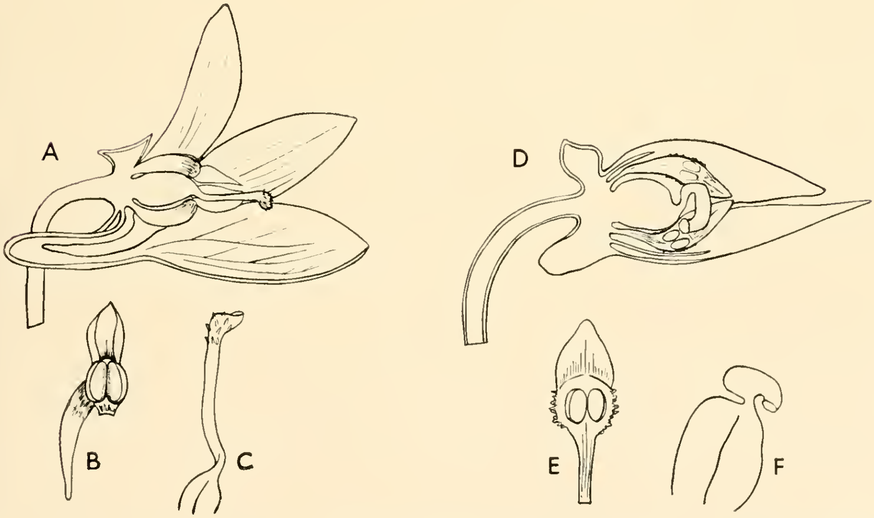


FIG. 1264.—*Viola riviniana.* A, Chasmogamous flower in section. B, Anterior stamen. C, Style. D, Cleistogamous flower. E, Anterior stamen. F, Style. (*After West.*)

Allied to cleistogamy is **cleistoflory**, a term applied to certain uncommon cases where flowers are pollinated in the bud, but by insects which bite or burrow their way into the closed flower. Small beetles penetrate the larger buds of *Magnolia* in this way and pollination has already been performed by the time the flower opens.

CHAPTER XXV

ANGIOSPERMAE: SEXUAL REPRODUCTION

The subject-matter of this chapter will be the development and structure of pollen grains and ovules; the gametophytic structures they produce; the phenomena of fertilization and the post-fertilization changes which ensue, including the growth of the embryo. The characters of fruits and seeds as matured structures and the germination of seeds will be dealt with in the following chapter.

POLLEN

The formation of the archesporium from the hypodermal layer of cells in the young anther has already been mentioned (p. 1197). The number of hypodermal cells which develops into archesporial cells is very variable. Sometimes the whole of the hypoderm in each lobe develops, more generally only a short, transverse row of cells is transformed into archesporium and in Malvaceae and in many of the Compositae there is only one such cell. Longitudinally, these groups of cells are extended for practically the whole length of the anther, except the rare cases where the anther is transversely septate and a longitudinal row of separate pollen-loculi is formed. In some of these cases, the archesporium in each of the loculi may be reduced to one cell, *e.g.*, in Mimosaceae.

The archesporial cells enlarge radially and divide parallel to the surface of the anther, to form an outer layer called the **primary parietal layer** and an inner layer which is the **primary sporogenous layer** (Fig. 1265). The cells of the primary parietal layer divide again, sometimes several times, forming radial files of cells of variable depth, which also divide anticlinally as the anther enlarges. There are usually from three to five layers formed, but the number is not constant, even in one anther. The innermost layer usually contributes to the tapetum, and the outermost layer forms part, or sometimes the whole, of the endothecium of the anther. The middle layers may become disorganized or may persist to form the remainder of the endothecium.

The primary sporogenous cells may be transformed directly into **pollen mother cells**, or they may divide once or several times before being so transformed.

The formation of the pollen mother cells is generally regarded as being the end of the sporophyte stage in this direction and it is often marked by a resting period. Many spring flowers are well advanced in development before the preceding winter begins and the anthers may be found to be in the mother cell stage by September or October. If the buds are formed

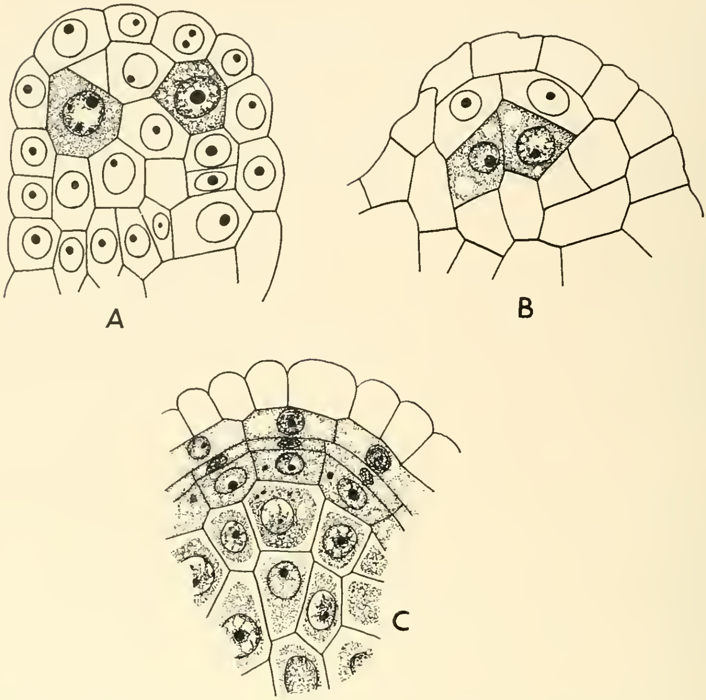


Fig. 1265.—*Rumex crispus.* A, Archesporial cells in young anther. B, Primary sporogenous and primary parietal cells. C, Pollen mother cells, tapetum and parietal layers developed. (*After Dudgeon.*)

below ground, as in plants with bulbs and corms, development may go on slowly during the winter, even when the soil is frozen, so that the pollen is mature before the spring growth begins, but in most cases the anthers appear to pass the winter in the mother cell condition. Of course this does not hold good for annuals and other summer-flowering plants, but even in them, although development is continuous, there is a short pause at the mother cell stage.

The development of the microsporangia in the anther is usually well in advance of the development of the megasporangia in the ovules or even in advance of the development of the ovules themselves. Indeed in *Quercus*, *Ulmus* and some Orchidaceae, the pollen is not only formed but liberated and pollination has taken place before the ovules are formed.

The division of the pollen mother cell is, of course, the reduction division, the special features of which we shall deal with in a future chapter (see also Volume I, p. 29) (Fig. 1266). At present we are concerned with the cells rather than with the chromosomes. Before division the walls of the mother cells increase in thickness, somewhat unequally at different points round the cell, and the thickened walls show concentric lamellation. In most Monocotyledons the middle lamellae between them dissolve and the cells separate and become rounded but this does not usually happen in

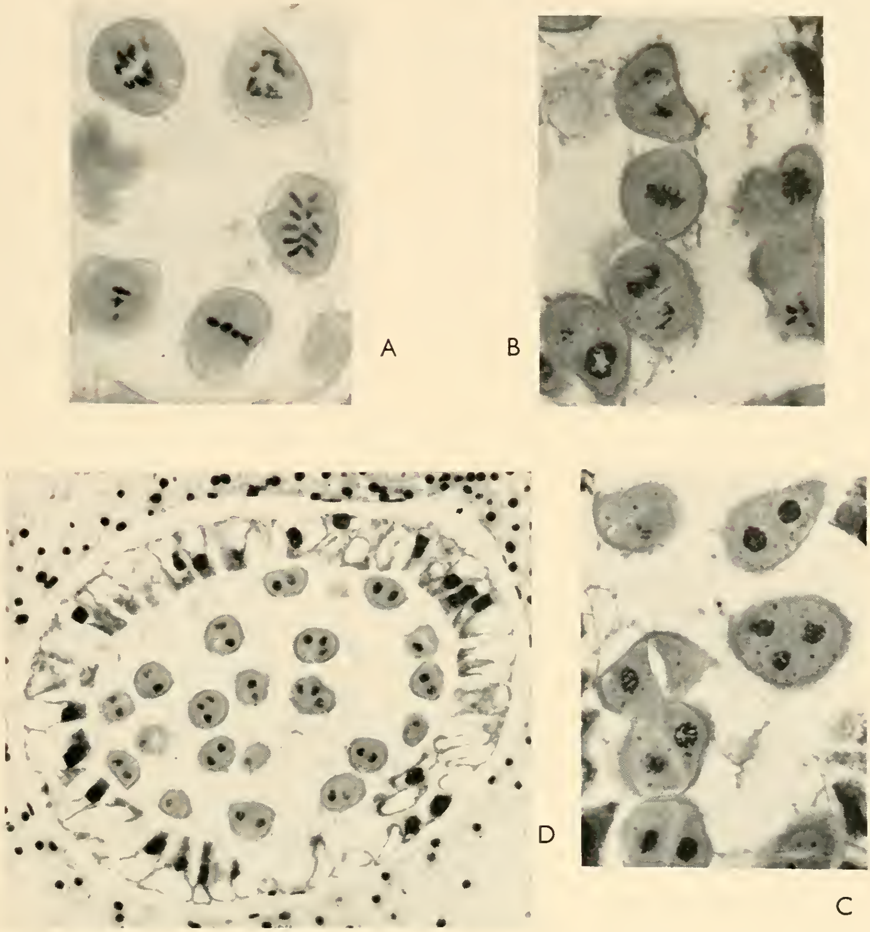


Fig. 1266.—*Lilium candidum.* Meiosis in the microspore mother cells. A, Early metaphase, metaphase and anaphase of meiosis I, showing lack of synchrony. B, Metaphase and early telophase of meiosis II. C, Telophase and internal wall formation at end of meiosis II. D, Transverse section of a loculus with cellular tapetum and tetrads mostly completed.

Dicotyledons. At the same time the anther enlarges markedly so that the mass of sporogenous cells is separated from the anther wall and the pollen loculus becomes visible as a space. When the mother cells divide, a tetrad group of haploid cells results, usually arranged in a tetrahedron but sometimes all in one plane (Orchidaceae). The difference depends upon whether the axis of the second meiotic division is at right angles to that of the first division (tetrahedral) or parallel to it (one plane). The mother cell wall remains, enveloping the tetrad, and becomes massive and mucilaginous, containing callose and pectose. Within this general wall is another wall, also mucilaginous, and containing callose and pectose, which surrounds each cell of the tetrad and constitutes the "special wall", or "special mother cell", as it is sometimes erroneously called. There is a thin, tri-radiate lamella between the special walls, separating the young pollen grains, and this lamella may survive the breakdown of the outer walls, both general and special, which finally liberates the grains at maturity.

Although the division of the mother cell normally produces a tetrad of microspores, some twenty-five to thirty species have been recorded in which supernumerary microspores occur. In *Fuchsia*, for example, Beer has observed numbers varying from five to fourteen in one mother cell. He shows that they arise from irregularities at the anaphase of the first meiotic division, some chromosomes lagging on the spindle and becoming separated from the main groups. These separate chromosomes usually form distinct nuclei and although they may contain as few as two or even a single chromosome, they undergo a second division along with the main groups. An interesting point is that these imperfect nuclei produce microspores which, except in point of size, are exactly like the normal grains both in structure and staining reactions. It is not known whether they are ever capable of functioning sexually.

In some families the wall of the pollen grain is very slightly thickened and remains undifferentiated; *e.g.*, Orchidaceae and Naiadaceae. The whole thickness of the wall of these grains takes part in forming the pollen tube. In the second group of cases the wall may thicken considerably and two layers are differentiated, an external coloured layer and an internal colourless layer, which are, however, continuous with one another and form only one wall; *e.g.*, *Allium*, *Cobaea*, *Senecio*. Here also the pollen tube is a direct prolongation of the whole wall thickness.

The great majority of pollen grains, however, have two distinct walls, the **extine** (or **exine**) and the **intine**, but the latter alone takes part in forming the tube.

The extine appears at first as a delicate new membrane, in contact with the special wall. Later, it thickens considerably and becomes differentiated into two layers, the **exo-extine** (Sexine of Erdtman or Perine of Kerner) and the **endo-extine** (Nexine of Erdtman). The exo-extine is thin, has a high refractive index and is difficult to see. Its outer surface is at first quite smooth and the growth of spines or other appendages is a later superficial development, only taking place after the endo-extine has developed, cutting off the exo-extine from contact with the internal protoplasm (Fig. 1267). The exo-extine envelops the whole grain, though in some cases it takes the form of a delicate reticulum rather than a continuous membrane. Over the pores or grooves of the grain, at which the pollen tube may appear, the exo-extine is cutinized.

The endo-extine is thick and uniform. It is cutinized throughout and is continuous, except below the pores, where it is perforated by pits or canals leading to the pores.

The extine of pollen grains and the walls of fungal spores contain a peculiar, highly polymerized, cyclic alcohol, called sporopollenin by Frey Wyssling. It is related to suberin and cutin but is more resistant than either.

There are two reactive end-groups in the molecule and by their means a spatial network is formed by esterification or ether linkages. Sporopollenin may be identical with the sporonine of Zetsche, which he found in *Lycopodium* spores and also in the pollen of some Coniferae and in *Corylus*. In *Pinus sylvestris* it makes up nearly 22 per cent. of the weight of the grain, but in *Corylus* only 7·3 per cent. It is of considerable practical interest as the preservation of pollen in peat and in older deposits seems to be chiefly due to membranes containing this substance.

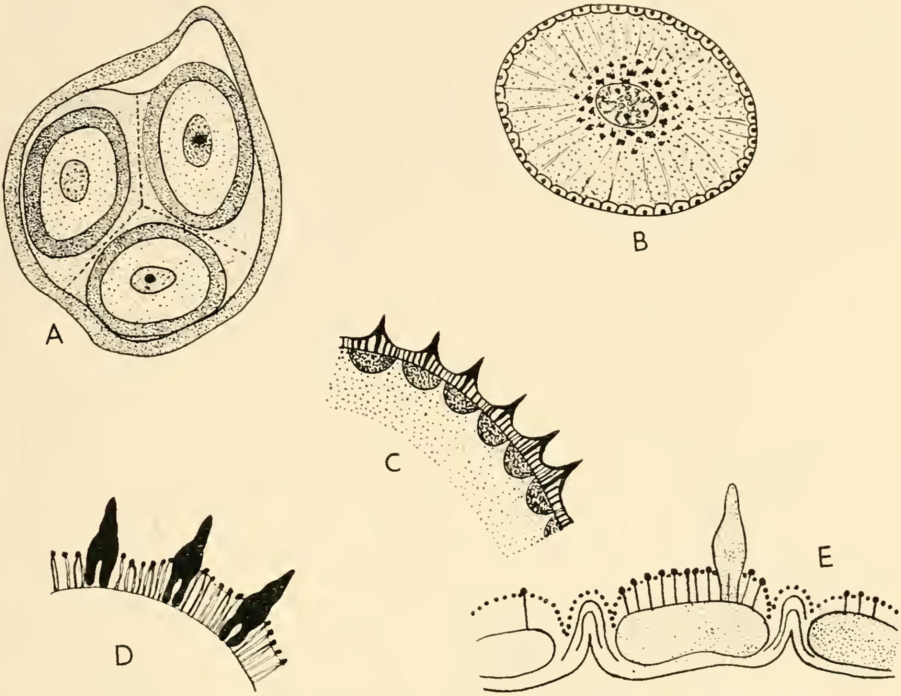


Fig. 1267.—*Ipomoea purpurea*. A, Young pollen grains with general and special walls. B, Young pollen grain liberated. C and D, Stages in exine development. E, Mature wall of grain, showing pila of exo-extine. (*After Beer.*)

The intine is variable in thickness, but it is always thicker under the pores, where it protrudes through the pits in the endo-extine and makes contact with the exo-extine. Only the innermost portion of the intine gives the reactions for cellulose; the outer portion gives reactions for pectin. Callose may also be present below the pores. The intine absorbs water readily and swells strongly, especially below the pores where its thickness is greatest. When this occurs it ruptures the exo-extine at the pores and protrudes.

While the layers of the grain wall are developing, the wall of the mother cell and the special walls are breaking down and becoming solvated. Their materials are amalgamated with the materials from the tapetum, which we shall describe shortly, and the young grains are left suspended in the resulting colloidal matrix, from which they absorb nutritive substances.

The pollen grains of *Carex* and some allied genera are singular in that they consist of the mother cell itself. The nucleus undergoes the ordinary meiotic divisions and then three of the four nuclei thus formed pass to the apex of the bluntly conical grain and there abort, disappearing into the intine. The wall of the pollen grain which develops is, therefore, the wall of the pollen mother cell.

Chemical analysis of mature pollen shows the following range of composition:

Protein	from	7·0–26·0%
Fats	from	0·9–14·5%
Carbohydrates	from	24·0–48%
Ash	from	0·9–5·4%
Water	from	7·0–16·0%

The protoplast of the grain in its earlier stages is only a hollow shell, with one large central vacuole. The nucleus increases in size and density and the cytoplasm gradually increases in bulk and finally occludes the vacuole, an event which marks the maturity of the grain. Mature grains contain large amounts of starch or in some species fatty material, probably absorbed from the tapetum.

Some stress has been laid on the difference between starchy and fatty pollen and it has been claimed that starchy pollen is commoner in cold latitudes. Systematic comparisons between plants in Lapland and in Germany do not seem to support this idea. In the worst seasons in Germany the number of species producing fatty pollen increased, though most starchy pollen species remain unchanged whatever the season. Starchy pollen species belong to several distinct ecological types and there is no apparent ecological relationship between them.

Many pollens lose their starch grains at anthesis. In others the grain is still starchy when shed and the starch is solvated in the pollen tubes, but at very unequal rates. There is usually a higher osmotic potential in the pollen tube than in the surrounding stylar cells and solvation of starch may promote this.

A curious variation is shown by *Lythrum salicaria*, where the green pollen in the heterostylous flowers is starchy and the yellow pollen is fatty. The former needs a higher sugar concentration for germination than the latter.

Some heterantherous flowers produce both " fodder pollen " with a high starch content, which is collected by bees, and fertilization pollen. In most species the former needs a higher concentration of sugar than the latter for germination, but in heterantherous species of *Cassia* the fodder pollen also requires the addition of diastase, which appears to call out internal formation of diastase. Otherwise the starch in the grain cannot be mobilized.

There are two main types of behaviour of the tapetum. One is the formation of a periplasmodium, the other is called by Goebel the " secretion type ". In both cases the cells of the inner parietal layers may take part, as well as the tapetum proper.

The periplasmodium is formed in three stages. The cell walls of the tapetum dissolve (Fig. 1268) and the protoplasmic contents of the cells separate from one another. They then grow out in strands of varying form, pass between the pollen grains, and only unite together when they reach the middle of the loculus. The amoeboid mass thus formed increases in bulk until the spaces of the loculus are almost or quite filled. *Lavatera* is exceptional in that the plasmodium concentrates around the grains and leaves large spaces of the loculus unfilled.

FIG. 1268.—*Commelina coelestis*. Formation of a plasmodial tapetum. Only one or two cell walls remain intact and the nuclei have become irregular in shape. (*From Tischler*, "*J. f. wiss. Bot.*" 55.)

The nuclei usually remain unchanged or somewhat enlarged, but in *Arabis* they disorganize. Total plasmodial formation is not always achieved, *e.g.*, *Knautia* and *Cobaea*, where the individual cell limits remain distinct.

The secretion type of behaviour does not start with the dissolution of the cell walls (Fig. 1269). Instead, the cells collapse and there is a gradual disappearance of their contents, the walls going last of all. Solution occurs much later than in the first type, sometimes not until the anther is practically ripe, and usually not before the pollen grains have reached the two-celled stage. Meanwhile the spaces between the grains are filled with a homogeneous colloidal material which can be stained and is presumably secreted by the disorganizing protoplasts of the tapetal cells. It is augmented by the dissolution of the mother cell walls.

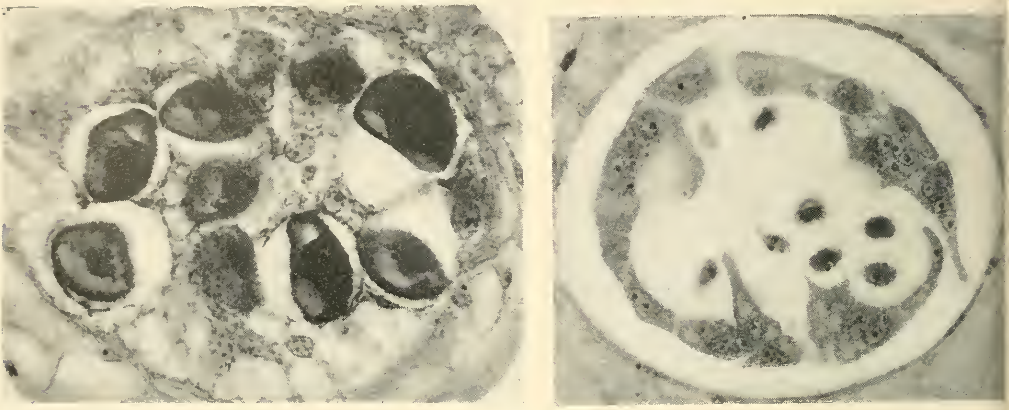


FIG. 1269.—*Lonicera coerulea.* Plasmodial tapetum. Right: the tapetal cells have lost their walls and are changing in shape. Left: completed plasmodium surrounding the pollen grains. (*From Jvel, "J. j. wiss. Bot."*, 56.)

The periplasmodial type, although it is found in the Pteridophyta (see under *Botrychium* in Volume I), is unknown in the Gymnosperms. It may be common throughout certain large systematic groups, *e.g.*, Rubiales, where it has been demonstrated in Rubiaceae, Caprifoliaceae, Valerianaceae and Dipsacaceae. On the other hand both types may occur in closely related genera. For example, *Cobaea* is periplasmodial and *Polemonium* is secretory; *Lonicera* is periplasmodial but *Viburnum* is secretory.

The chemical analyses previously quoted show that pollen grains are rich in carbohydrates and fats. Both these kinds of material may be stored in some quantity, the carbohydrates either as starch grains or sugars and the fats as droplets disseminated in the cytoplasm. In *Forsythia*, the flowers of which are heterostylous, it is a remarkable fact that the pollen grains, in the short-styled flowers only, contain 25 per cent. of lactose. This is the only recorded occurrence of this sugar in plants. Furthermore, it is formed in a male cell, whereas in animals the production of lactose is predominantly a female characteristic.

Protein deposits in crystalline form are also sometimes present, as for example conspicuously in the pollen grains and pollen tubes of Asclepiadaceae. Anthocyan colouring substances are not uncommon and many types of pollen are red or purple in consequence. The green pollen of *Lythrum* (see p. 1278) is not due to chlorophyll, which has not been recorded in pollen, although plastids are present, but to a mixture of a blue anthocyan with a yellow pigment. The former pigment turns red in contact with the acid secretion of the stigma. Some pollens contain aromatic substances which may affect the choice of pollen by collecting bees. The aromatic pollen of *Acorus* is sold in Iraq as a flavouring substance for cakes.

The external surfaces of pollen grains bear a great variety of markings, though a few are quite smooth, *e.g.*, some Gramineae. These are described as psilate, but they are rare except among Gymnosperms. The exo-extine or sexine is usually formed of *pila*, little processes like drumsticks, with a stalk, the *baculum* and a head, the *caput*. The capita are often confluent, forming a roof or *tegillum*, which may also be formed by a membrane covering the capita. The tegillum is often punctate with small holes. Spines, granules, warts and other forms of ornamentation may be produced superficially on the tegillum. Bladder-like expansions involve the separation of the pila from the nexine. Reticulations, striations and other patterns on the surface of the grain are due to special arrangements of the pila (Fig. 1270). These are all protrusions from the extine surface, but there may also be pits or a negative reticulation of grooves sunk in the wall.

Wodehouse has suggested a physical theory to account for at least some

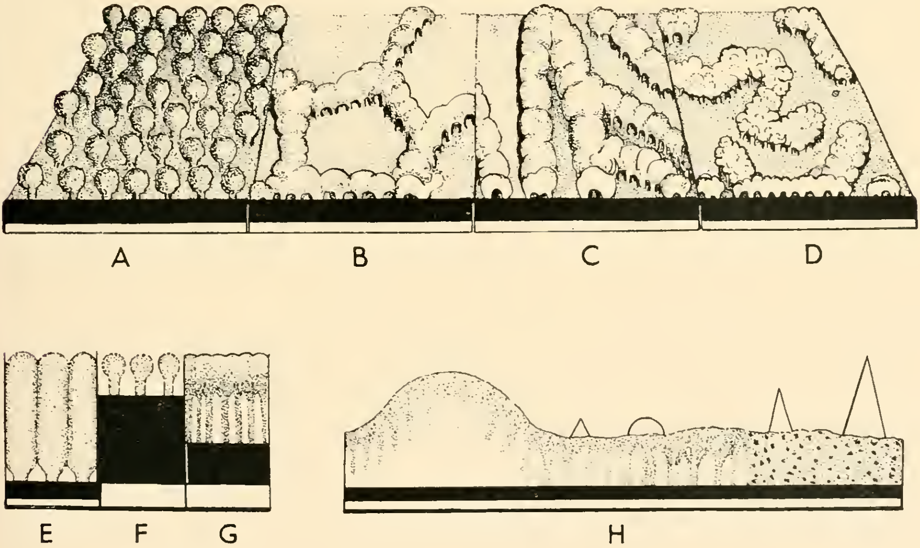


FIG. 1270.—Pollen sculpturing. A, Pilate. B, Reticulate. C, Striate. D, Ornate. E, Crassisexinous. F, Tenuisexinous. G, Tegillate. H (on left), Subsaccate; (on right), Tegillate, verrucous and spinose. (*After Erdtman.*)

of the sculpturing. He points out that sculptured grains have a fairly heavy coat of oil, which is absent from unsculptured grains. The extine is a deposit from the polyphasic colloid sol of the degenerating tapetal protoplasm. The developing grains absorb the aqueous phase of the sol but the oil is deposited as droplets on its surface. The droplets are separated from each other at first by the remaining part of the aqueous phase and they are free to adopt " least surface " configurations. Further deposition on the extine takes place only in ridges between the droplets, until the grain dries at maturity, when the droplets coalesce to form a continuous layer. The type of sculpturing deposited will depend upon the number, size and arrangement of the oil droplets.

The oily coating makes the pollen somewhat adhesive, hence it tends to cling to the anther, even after dehiscence, and will also cling easily to insects which brush against it. Furthermore the oily covering is a useful protection against wetting by rain. Wind-distributed pollens generally have no such covering and are dry or " dusty ", thus favouring easy dispersal.

Pollen forms have been made the subject of extensive study and an elaborate system of nomenclature has been devised by Potonié, Wodehouse, Erdtman and others, to enable pollen morphology to be accurately described. This is important from several points of view. Pollen may be used as evidence for the presence of species, both in existing vegetation and more especially in fossil deposits, where no other remains are available. The quantitative pollen-analysis of the younger geological beds has thrown a great deal of light on the history of the native vegetation in the countries where it has been exploited and its extension to older strata may well assist in building up a better picture of the early history of the Angiosperms. The closely related subject of spore-analysis has also proved of great value to geologists in the stratigraphy of Palaeozoic beds. Moreover the importance of pollens as respiratory allergens has given them a medical interest, in which accurate identification is equally necessary. Some of the results of the pollen-analysis of Quaternary beds will be given at the end of the chapter on Palaeobotany in Volume III.

Radial symmetry prevails among pollen grains and this is easily understandable, since the grains are free in the loculus from an early stage and are immersed in a fluid medium. Before the cutinization of the exo-extine they are moulded by surface tension and are only rarely affected by the pressure of surrounding cells. The pressure exerted in an isolated sphere by surface tension varies inversely with its radius: $P = 2\ T/R$, where T is the surface tension in dynes per $cm.^2$ and R is the radius. In very small spheres this pressure will obviously rise considerably and must have powerful effects. Oval-shaped grains are commoner in the Monocotyledons than in the Dicotyledons, but there is no constant distinction of form between the classes. In Monocotyledons the tetrad of grains is usually arranged in a single plane, while in Dicotyledons they are usually in a tetrahedron. Monocotyledonous grains are therefore typically boat-shaped, with bilateral symmetry about two planes, longitudinal and transverse. Dicotyledonous grains in a tetrahedron have each three surfaces of contact with their neighbours. Each contact area develops a median furrow which extends backwards to the distal end of the grain, crossing its equator at right angles. These furrows define the axis of the grain, extending from pole to pole. Once the grains have separated it is very rarely possible to distinguish one pole from the other, but their positions are clearly indicated by the convergence of the furrows. Monocotyledonous grains have typically only one furrow, along the " deck " of the " boat ", which corresponds to the distal side of the grain while they are still in tetrads. Dicotyledonous grains are typically three-furrowed. While these are useful distinctions, they are not, as we have said, absolute, for exceptions occur in both groups. For instance, compound grains, due to the failure of the spore tetrads to separate, are found in certain families and genera of both groups, *e.g.*, Epacridaceae, Juncaceae, *Drimys* (and other Winteraceae), *Drosera*, *Typha* and *Elodea*, while linear tetrads are formed in *Asclepias* and *Halophila*. Some exceptional forms of grains will be mentioned later.

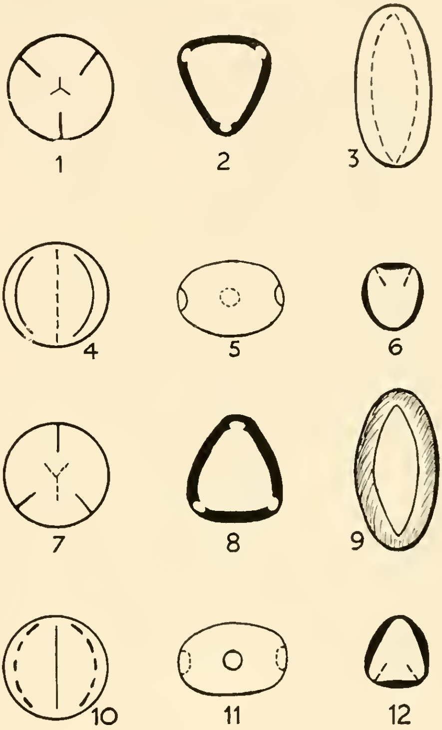


FIG. 1271.—Types of pollen furrowing. 1, Tricolpate pollen (*e.g.*, *Trapa*) with triradiate scar. 2, Three-pored pollen. 3, Monocolpate pollen. The lower figures show the above in different aspects. (*After Erdtman.*)

Erdtman distinguishes four kinds of " aperture " in pollen grains. These are not strictly speaking apertures, but are the places where the extine may eventually open for the protrusion of the pollen tube, or alternatively places where the extine is absent (Fig. 1271).

Sulcus. A longitudinal furrow confined to the distal half of the grain, crossing the polar axis at right angles.

Colpa. A meridional furrow crossing the equator at right angles and directed at each end to the poles of the grain (see above).

Ruga. A furrow which is not confined to the meridional region but placed irregularly on the grain surface.

Porus. A rounded aperture. If present in small numbers pori are confined to the equatorial region. There may be only one porus (monoporate) or many (polyporate, or if the pori are small, cribellate). In the latter case pori are not limited to the equator.

The typical dicotyledonous grain would therefore be described as tricolpate and the monocotyledonous grain as monocolpate. Exceptionally, larger numbers of colpae occur, up to thirty, corresponding to the number of the lines of contact between polyhedral grains. Acolpate grains, with no furrow, are also known.


FIG. 1272.—*Zostera marina.* Filamentous pollen grains.

One or more parallel, spiral furrows occur in a few quite unrelated plants, *e.g.*, *Eriocaulon*, *Mimulus*, *Thunbergia*, and in some species of *Berberis*.

The pollen grains of the submerged marine plant *Zostera* (Naiadaceae) are filamentous. The mother cells are elongate, the sporogenous cells from which they are formed having divided longitudinally. A minority divide transversely and they give rise to short cells which are sterile. The mother cells, which measure 5 × 60 microns, also divide longitudinally and produce a group of four cells which subsequently lengthen until they may reach 2 mm. This peculiarity is apparently associated with hydrophilous pollination (Fig. 1272).

The pollen of most wind-pollinated plants is smooth and dry, if such pollination is characteristic of the whole family, but in genera which are exceptional in this respect in their families, *e.g.*, *Artemisia* and *Ambrosia* in the Compositae, the pollen retains the family characteristics, though usually in a somewhat reduced form.

The outline of the grain, even in radially symmetrical types, shows great variation in the ratio of its principal axes to one another, ranging from perprolate grains, whose polar axis is more than twice as long as the equatorial diameter, to peroblate grains whose polar axis is less than half the equatorial diameter. The

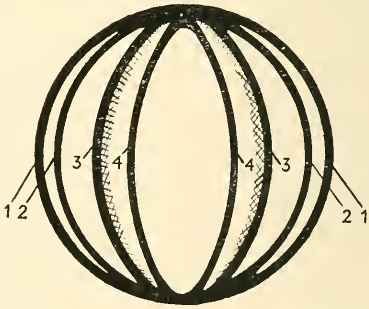


FIG. 1273.—Pollen shapes. 1, Spherical. 2, Subprolate. 3, Prolate. 4, Perprolate. (*After Erdtman.*)

intermediate forms are best described by means of the accompanying diagram, after Erdtman (Fig. 1273).

A special vocabulary of descriptive terms for various parts of the pollen grains has been devised, by means of which the grains can be described with something like the precision of a specific diagnosis. It is too detailed to be reproduced here, but those interested can find the terms defined in Erdtman's " Introduction to Pollen Analysis " or Faegri and Iversen's " Modern Pollen Analysis ". The description of grains with the necessary exactitude presents certain difficulties, for not only must the grain be viewed from several different angles in relation to its polar axis, but the appearance of the grains, whether in the fresh state or after they have been allowed to swell in contact with a watery mounting medium, is very different.

The sizes of pollen grains are as variable as their forms. Erdtman groups them as follows:

Perminuta	<10μ	Magna	50–100μ
Minuta	10–25μ	Permagna	100–200μ
Media	25–50μ	Gigantea	>200μ

Extreme sizes are rare. Among familiar plants the smallest pollens are those of *Myosotis alpestris* (2·5–3·5μ), *Echium vulgare* (10–14μ) and *Urtica urens* (14μ). At the other end of the scale are large grains such as those of *Cucurbita pepo* (230μ), *Mirabilis jalapa* (250μ) and *Elodea* (134μ). The largest grains are associated with a relatively small number in each pollen loculus. *Mirabilis* has only 32 grains per loculus, whereas in *Borago officinalis*, which has grains measuring only about 5μ, the number per loculus may be 60,000. The largest grains seem, as a rule, to be produced by ephemeral flowers which last only for a single day.

The systematic importance of pollen form should not be overrated despite the variety and intricacy of the grain structure. A wide classification based on pollen types would be artificial, but within limited circles of affinity the evidence they afford may often be very valuable. Most genera show a marked consistency of pollen form, though there are some striking exceptions. The generic identification of pollen is usually possible, but specific identification, with any reasonable certainty, is much less generally feasible. Exceptionally, we find pollen of two or more types even within a genus, but this has not been hitherto accepted as a sufficient ground for subdivision of the genera concerned. A good example is *Tulipa*, a genus with very constant floral characteristics, almost certainly a natural genus, but having monocolpate pollen in some species and tricolpate pollen in others. It is the only Monocotyledon with this latter type of grain. Again the genus *Crocus*, also a very natural group, has pollen either without any colpae or pori, or else with several, parallel, ring-like furrows. *Polygonum* grains have either a single median porus in each colpa or pori free on the surface, not in colpae.

In some families there are characteristic peculiarities which may be sufficiently constant for use in diagnosis. Thus Cucurbitaceae have all very large, echinulate grains, with pori closed by circular plugs of extine which are pushed outwards by the developing pollen tubes (Fig. 1274). The Betulaceae possess characteristic band-like thickenings of the extine, known as arci, which form sweeping curves from pore to pore. The submerged flowers of Naiadaceae and Ceratophyllaceae have smooth-walled grains with no extine. The Onagraceae (Oenotheraceae) have three prominent pores, each covered by an apsis or dome formed principally by the thickening of the intine. The grains are triangular in polar view and the pores occupy the angles (Fig. 1275). The Cyperaceae, already mentioned on p. 1369, have

Fig. 1274.—*Cucurbita pepo.* Section of a uninucleate pollen grain showing the plugged pori.

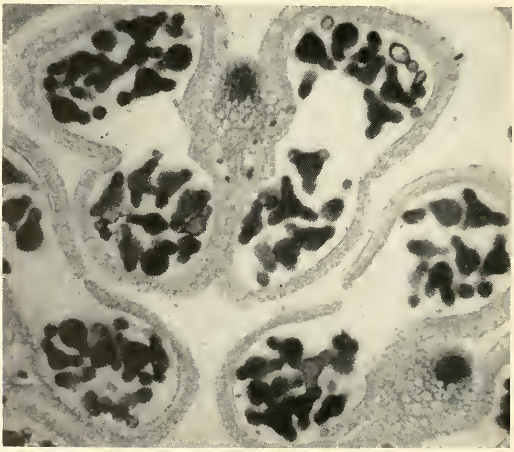


Fig. 1275.—*Oenothera biennis.* Transverse section of an anther showing the triangular grains with pores at the angles covered by domes.

tetrahedral, psilate grains with one prominent basal pore and three slit-like lateral pores. The Ericaceae are notable because the pollen remains permanently in tetrads, a peculiarity which they share only with a few other families, *e.g.*, Empetraceae. The grains are closely united in a tetrahedron, which may be almost spherical in outline (Fig. 1276). The extine is smooth or finely reticular and the three furrows of each grain are short, narrow and, in *Calluna*, poorly defined. The latter genus produces enormous quantities of pollen, which may be carried by the wind.

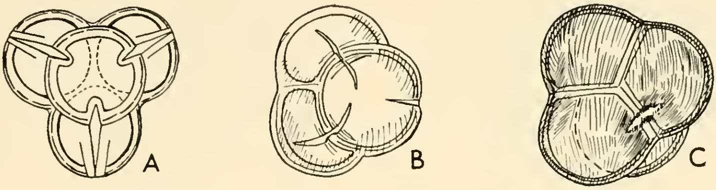


Fig. 1276.—Pollen grains united in permanent tetrads. A, *Empetrum nigrum*. B, *Andromeda polifolia*. C, *Kalmia latifolia*. (*After Erdtman.*)

On the other hand, some families are markedly heterogeneous in respect of their pollen. The Caryophyllaceae have, for the most part, cribellate grains, that is, grains with many pori, but *Spergula* and a few other genera have tricolpate grains. Apart from all others, however, are the Acanthaceae, which show an astonishing variety of pollen, almost every type being represented in the family, although the type in each genus is fairly constant. This is a family in which the pollen morphology may well call for systematic consideration.

Very little information is available about the effect of polyploidy on pollen morphology nor has the question of variation between local populations of the same species been much explored, though both of these avenues of research promise interesting results. (For variation in dimorphic flowers, see p. 1275.)

The permanent cohesion of grains into groups larger than tetrads is a conspicuous feature of certain families. The stamens of Mimosaceae have transversely septate pollen loculi in the anthers and each segment of the loculus may contain only a small number of grains. These grains are permanently united, in most species, into groups or massulae containing from 4 to 64 grains, the larger numbers involving all the grains in a single anther segment (Fig. 1277). Among the Orchidaceae there is considerable variation in this respect. *Cypripedium* has isolated grains, *Neottia* and *Listera* have grains united into tetrads. In *Orchis* the grains are closely united into massulae containing numerous grains, and in *Vanda* and many other Orchids all the grains in a loculus are united into one pollinium (Fig. 1278). The anther of *Orchis* has a relatively small number of primary sporogenous cells in each lobe, arranged in the arc of a circle. Each of these cells divides repeatedly and gives rise to a massula of grains, whose thin walls have no extine, except the grains on the outside, where there is an extine which

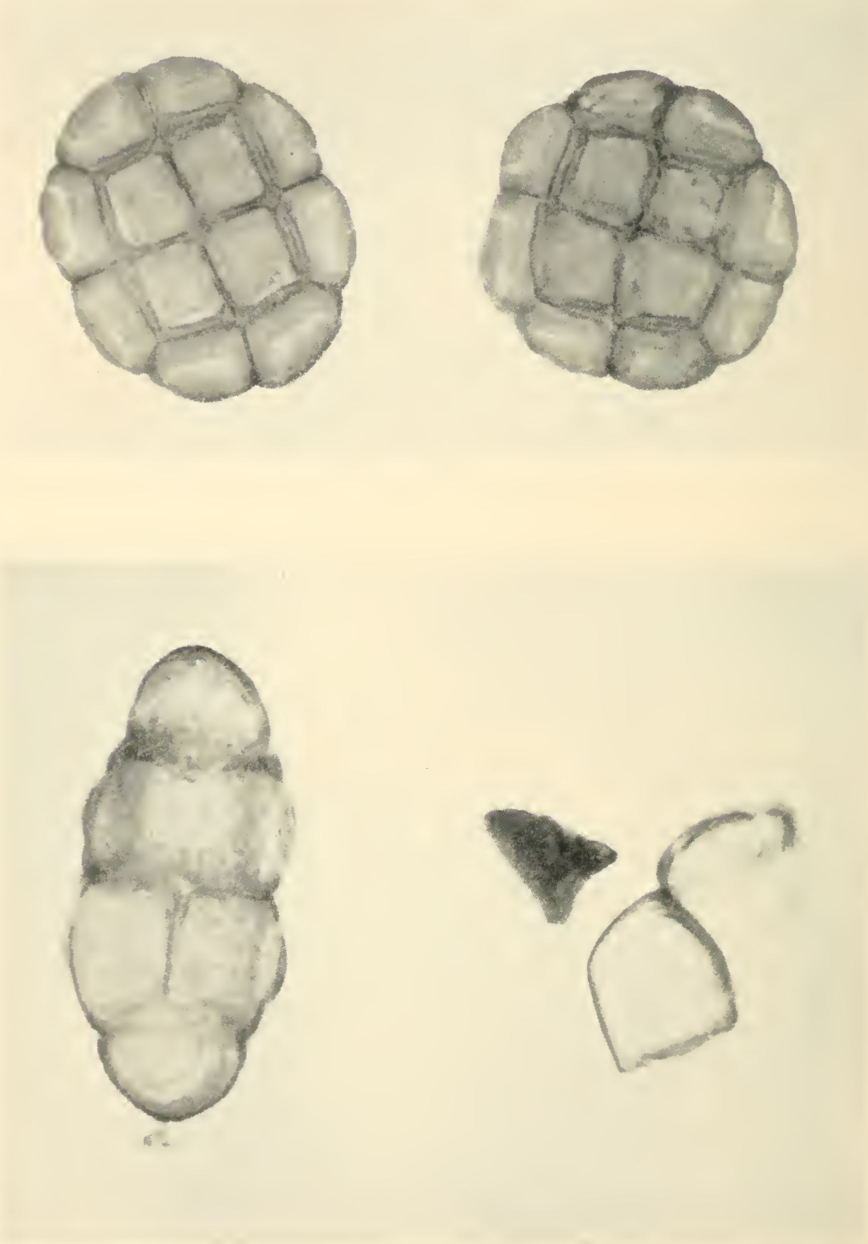


FIG. 1277.—*Acacia dealbata* (Mimosaceae). Compound pollen grains in face and profile view. Below right: component grains separated.

serves to separate each massula from its neighbours. All the massulae are loosely coherent and form a compound pollinium. The pollinia of Asclepiadaceae are similarly formed of coherent massulae.

Units of Organization in Pollen

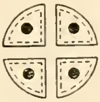
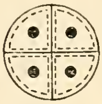
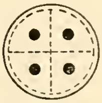
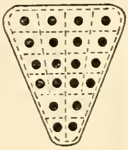
Synchronization Unit	*Orchidaceae*	*Other Angiosperms*
	Diandrae *Cephalanthera*	Normal
	*Epipactis*	Ericaceae Droseraceae
	*Listera* *Neottia*	*Anona* *Mitriostigma* Typhaceae *Fourcroya*
	Ophrydeae	Mimosaceae Asclepiadaceae

FIG. 1278.—Pollen organization in Orchidaceae. The dotted lines represent permeable walls, the continuous lines impermeable walls. The former permit synchronization of nuclear divisions. (*After Barber.*)

The cohesion of massulae in these families and the looser cohesion of single grains in many other cases is due to a mucilaginous substance called *viscin*, from its resemblance to the sticky "bird-lime" in the berries of *Viscum*. It is of complex but uncertain composition. Besides Orchidaceae it is found particularly in the Ericaceae and Onagraceae. When the anthers in a member of these families dehisce, the pollen trails out in ragged streamers which adhere to any object, even at the lightest touch. The anthers of Ericaceae open by pores and if the escaping pollen is touched the whole contents of the anther may be pulled out at once. Insects contacting the viscin will therefore carry off an abundance of pollen to the next flower visited.

Of systematic interest from the point of view of the relationships between Dicotyledons and Monocotyledons are the observations of Bailey and Nast on the pollen of Ranales (in Engler's sense). They showed that monocolpate pollen, which is common in Gymnosperms and Monocotyledons, is confined to certain Ranales and Piperales among the Dicotyledons. Most of the Ranalean families of tree habit, including the very primitive Winteraceae, have monocolpate pollen. The Ranunculaceae (with few exceptions), the Berberidaceae, Menispermaceae, and the homoxylous genera *Trochodendron* and *Tetracentron* are all tricolpate. The Nymphaeaceae, which according to one view, stand close to the Monocotyledons, are heterogeneous, Nymphaeoideae and Cabomboideae being monocolpate and Nelumbonoideae tricolpate.

At the time when the pollen grains separate from the tetrads in which they were formed, they are, for the most part, still uninucleate, but nuclear division soon follows. In the Ericaceae, of course, as the tetrads are permanent, mitosis takes place in that condition. The same is naturally true of composite pollens in Mimosaceae, Orchidaceae, etc. Some types in which the pollen eventually separates into single grains, however, regularly undergo the first mitosis before separation. Such are *Elodea*, *Salpiglossis sinuata* and members of the Juncaceae.

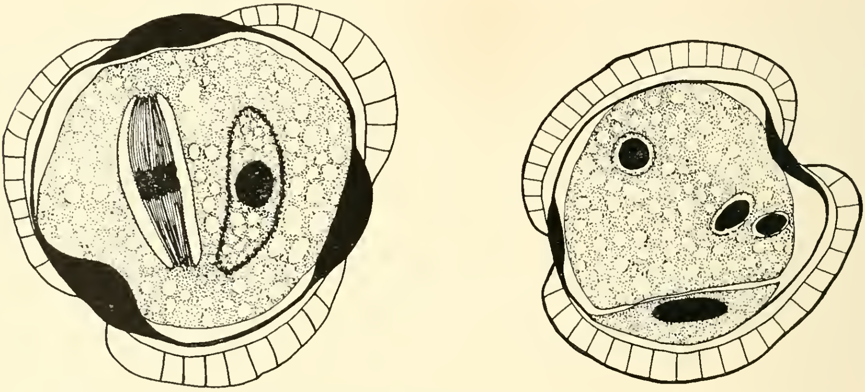


FIG. 1279.—*Cuscuta epithymum.* Left: pollen grain with generative nucleus in mitosis. Right: ripe three-nucleate grain with small prothallial (?) cell. (*After Fedortschuk.*)

A few isolated observations have been made of a preliminary division leading to the formation of a small cell at one side of the pollen grain, before the mitosis which gives rise to the generative nucleus (Fig. 1279). These cases, in *Cuscuta*, *Lilium*, *Eichhornia*, *Atriplex* and *Sparganium*, are too rare to be regarded as normal occurrences, but, if the facts are correct, the suggestion that this is a true prothallial cell, comparable with those normally formed in the pollen of Gymnosperms, is certainly very interesting.

There is not usually any long interval between the separation of the free microspores and the onset of mitosis, but in some spring-flowering species, where the floral organs are preformed in the late autumn, the grains may pass the winter in the uninucleate condition. Tropical plants have no resting period, but it tends to lengthen with increasing distance from the

Equator. Division may be simultaneous throughout the pollen loculus, particularly where the grains are united into massulae or pollinia, where the grains are not separated by cutinized walls (Fig. 1280), but frequently there is no accurate synchronization, though the differences in timing are not great.

FIG. 1280.—Pollinium of *Gymnadenia conopsea*, showing synchronization of nuclear divisions in all the component grains. (*After Barber.*)

Early in the development of the grain a vacuole appears in it, towards one end, which pushes the nucleus and the bulk of the cytoplasm towards the other end, but in some types (*Tradescantia*) a second vacuole appears at the cytoplasmic end and then nucleus and cytoplasm are held between the two vacuoles (Fig. 1281).

When mitosis occurs the angle of the nuclear spindle to the wall of the grain is constant in a species and even in whole genera. The position in which the generative cell is formed is determined by the position of the nuclear spindle, but in the majority of species it is cut off towards the pole which was innermost in the tetrad stage. The spindle is short and asymmetrical, being shorter and more pointed on the side of the generative nucleus, which leads to differences in the arrangement of the chromosomes at the two poles. The nuclear division is strictly equational, nevertheless the two nuclei formed are soon differentiated, one becoming the generative nucleus, from which the two male gametes will be formed, the other becoming the vegetative nucleus of the pollen grain, and later the "tube nucleus".

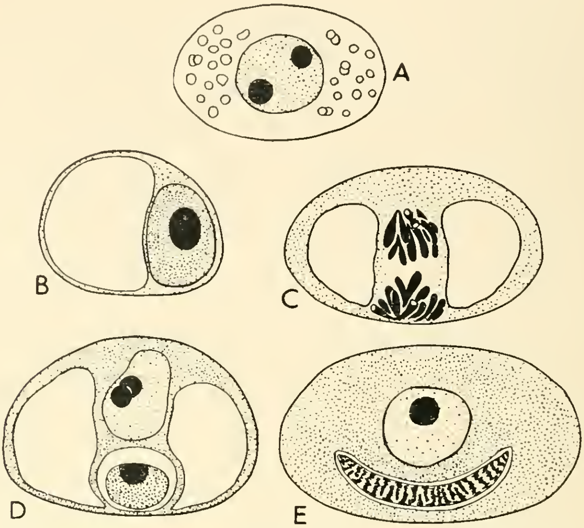


Fig. 1281.—*Tradescantia bracteata.* Successive stages in the first mitosis in the pollen grain. The density of stippling represents the distribution of protein and ribonucleic acid in the cytoplasm and of desoxyribonucleic acid in the nuclei. There is a high concentration of the latter in the generative nucleus as compared with the vegetative nucleus. (*After La Cour.*)

After mitosis the vegetative nucleus expands and loses much of its staining capacity. The generative nucleus, on the other hand, stains densely and is rich in desoxyribosenucleic acid (D.N.A.). In contrary fashion, the cytoplasm on the side of the vegetative cell gains in staining capacity and is rich in protein and in ribonucleic acid (R.N.A.). The cytoplasm surrounding the generative nucleus loses its staining capacity, having very little protein and no R.N.A. It would seem that this special cytoplasm is derived directly from the nuclear sap of the parent nucleus and is not invaded by R.N.A. from the general cytoplasm. These differences have been emphasized by La Cour as the key to the nuclear differentiation. The vegetative nucleus is supplied with materials which are factors for growth; the generative nucleus lies in a medium associated with mitosis, leading to its further division.

A delicate cell-wall is formed between the two nuclei, which is curved to cut off the generative nucleus in a small, lenticular cell against the wall of the grain. From this position it normally becomes free after a short time, and is then seen as a biconvex cell, surrounded by the cytoplasm of the vegetative cell. It is always smaller than the vegetative cell but its shape is variable, from spherical in some species to a long cigar-shape, the ends of which may almost encircle the vegetative nucleus. The grain is now mature; all vacuoles disappear and starch grains or oil drops accumulate (Fig. 1282).

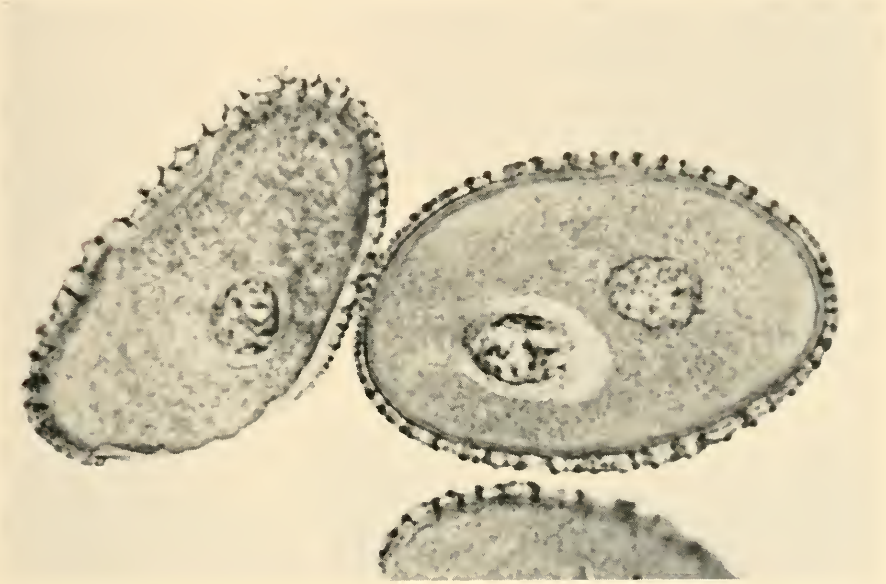


FIG. 1282.—*Lilium auratum.* Mature pollen grains showing vegetative nucleus and generative nucleus, the latter surrounded by hyaline cytoplasm. Note the pila of the sexine.

The vegetative nucleus does not normally divide again, though abnormal cases of from one to several divisions have been recorded. The generative nucleus may divide either before the pollen germinates or in the pollen tube. The latter is the commoner case but precocious division may occur even before the pollen is shed from the anther. Sometimes it occurs on the stigma, before the pollen tube begins to grow. At the other extreme, a case has been observed in *Euphorbia* in which division of the generative cell was postponed until the pollen tube had actually entered the embryo sac.

When division takes place in the pollen grain the nuclear division seems to follow the lines of a normal mitosis, a spindle being formed and the generative cell also dividing, either by a cross-wall or by constriction. Thus a three-celled grain results.

The process of division in the pollen tube will be described later when we speak of fertilization (p. 1442).

OVULES

The central feature in the structure of an ovule is the **nucellus**, which was called the nucleus in days before that name became appropriated to the central feature of the cell. It is a simple, rounded or oval mass of thin-walled parenchyma cells, which seldom show any differentiation. Within it is developed the **embryo sac**, which contains the **oosphere** or egg-cell, and around it there arise one or two coverings, called the **integuments**, which enclose it except for a minute opening over the apex, known as the **micropyle**. The ovule is generally attached to the placenta by a short stalk called the **funicle**.

The development of the nucellus on the placenta of the ovary begins with the elevation of a small protuberance on the placental surface. This has its origin in a certain number of sub-epidermal cells which divide repeatedly. This group of active cells lies usually in the hypodermal layer and in the case of certain very small ovules the origin may be traced to a single cell, *e.g.*, in *Monotropa* and the Orchidaceae. Exceptionally, cells of more than one layer in the placenta may be involved. The placental epidermis extends over the protuberance and accommodates itself to the increasing area by anticlinal cell divisions. The protuberance, which is at first more or less hemispherical, elongates rapidly and in doing so its basal region becomes distinguishable as a supporting stalk, which will be the funicle of the ovule.

At a very early stage, often before the appearance of the funicle, a hypodermal cell at the apex of the nucellus shows signs of differentiation, the cell and its nucleus enlarging and the cytoplasm becoming denser. This is the **archesporial cell**. In some species it may even be recognizable before nucellar development begins, but in any case its appearance is the first event of note in that development. While the archesporial cell itself is hypodermal it often appears to be the end-cell of an axile row in the nucellus (Fig. 1283).

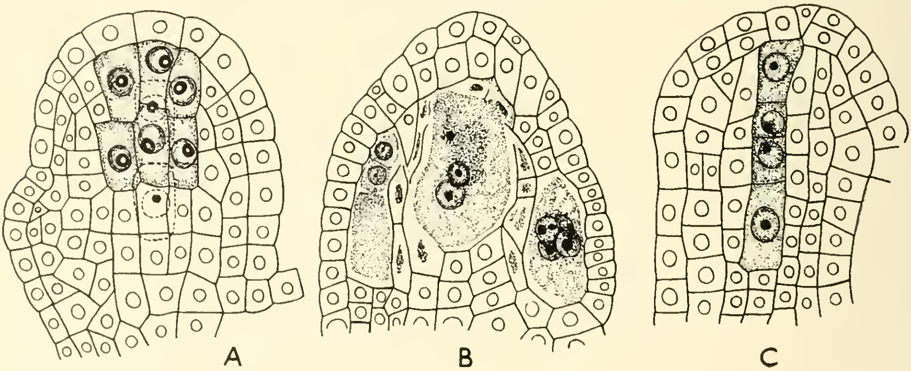


FIG. 1283.—*Ranunculus septentrionalis*. A, Nucellus with 8-celled archesporium. B, Three archesporial cells developing. C, *R. abortivus*. Row of four megaspore mother cells. (*After Coulter.*)

Whether the single archesporial cell is ever formed at a deeper level in the nucellus is not clear, but many cases are known in which there appears to be an archesporium of several or of many cells, among which some may have come from layers below the hypodermal layer. Pluricellular archesporia occur in many families of Dicotyledons, but only rare and occasional cases have been found in Monocotyledons (Liliaceae). In the former group the condition is most widespread in the Fagaceae, Salicaceae, Betulaceae, Corylaceae, Ranunculaceae and Rosaceae. As these families are all low in the evolutionary scale, it might appear that a pluricellular archesporium was a primitive feature among Angiosperms. Comparison with the microsporangium also suggests that this is so. Pluricellular archesporia are also found, however, in certain genera of advanced families such as Asclepiadaceae, Loranthaceae, Rubiaceae and Compositae, though in none of these sufficiently widespread to be reckoned a family characteristic, as in the first-mentioned families. It is not, in fact, certain in all these cases that the tissue concerned is the archesporium itself and not a mass of primary sporogenous cells derived from an archesporium. In *Casuarina*, for example, the number of archesporial cells is small but they give rise to a large group of sporogenous cells which occupies all the centre of the nucellus. These in their turn develop into very numerous potential megaspores, almost all of which are sterile.

To return to the development of the ovule, we see that no sooner has the archesporium appeared than the first or inner integument also appears, beginning in the form of a ring-like swelling around the nucellus. When the latter is large the integument arises at or near its base, but in some ovules with a small nucellus it may arise near the apex, or at least it makes its appearance there, as a distinct structure. The outer integument usually appears later and lower down than the inner, and generally develops more slowly (Fig. 1284).

There is much variation between families with regard to the presence of two integuments. The number is generally constant throughout a family, with few exceptions. Two integuments occur in most families of the Archichlamydeae and of the Monocotyledons. Exceptional families which are unitegminate are several of those grouped as "Amentiferae", *i.e.*, Betulaceae, Salicaceae, Myricaceae and Juglandaceae, also the Lauraceae, Cornaceae, Umbelliferae and some of the Ranunculaceae (*e.g.*, *Ranunculus* and *Anemone*) and Rosaceae. Exceptional unitegminate genera are also *Escallonia* and *Hippuris*. Among Monocotyledons, *Crinum* is reported to have no integuments at all.

One integument is characteristic of the Metachlamydeae, where it is usually massive. Exceptions which are bitegminate are the orders Primulales, Plumbaginales and Ebenales, all relatively primitive members of the Metachlamydeae.

It is the general opinion that the unitegminous condition has arisen from the bitegminous. The change may have happened in several evolutionary lines. It may have been brought about in two ways: either by coalescence or by abortion. The former has without doubt occurred in unitegminous Rosaceae, as Juel has shown, and this is probably true also of Betulaceae, Ranunculaceae and some Papilionaceae. Abortion of the inner integument is indicated in Salicaceae, where *Populus* species may possess a small and late-developing inner integument, while *Salix* has consistently only one.

FIG. 1284. *Hypericum androsaemum.* Young ovule, with nucellus and two integuments, curving to assume the anatropous position.

Complete absence of an integument is now only accepted for the Santalaceae (apart from the anomalous case of *Crinum*, mentioned above). Formerly a considerable number of families and genera were held to possess naked ovules, but it has been shown that earlier observers were deceived by appearances and that in these plants it is, in fact, the nucellus which has disappeared, and the single integument, enclosing the embryo sac, was mistaken for it. This does not apply to the Loranthaceae and Balanophoraceae (see p. 1386), in which there are not only no integuments, but the whole ovular structure has been reduced or suppressed.

Supernumerary coverings to the ovule are found in a few cases. A third integument or **aril** arises from the base of the ovule and overgrows the others but remains distinct from them. During the ripening of the seed it does not form part of the seed coat but develops as an outer, detached covering which usually has a distinctive colouring and texture. A different sort of outer covering is sometimes provided by an outgrowth from the lip of the outer integument, which turns backwards over the surface of the ovule, which it partially envelops. This type of outgrowth is called a **caruncle**.

During the development of the embryo sac, the integumental tissues may show partial dissolution or differentiation. The most noteworthy development is that of an ovular tapetum, or **endothelium**, formed by the innermost integumental cell-layer. This is characteristic of ovules in which the nucellus disorganizes, *i.e.*, principally in the Metachlamydeae, so that the tapetum immediately surrounds the embryo sac (Fig. 1285). The cells possess dense contents and large nuclei and are sometimes binucleate. They are often radially elongated and, in the Compositae, may be more than one-layered.

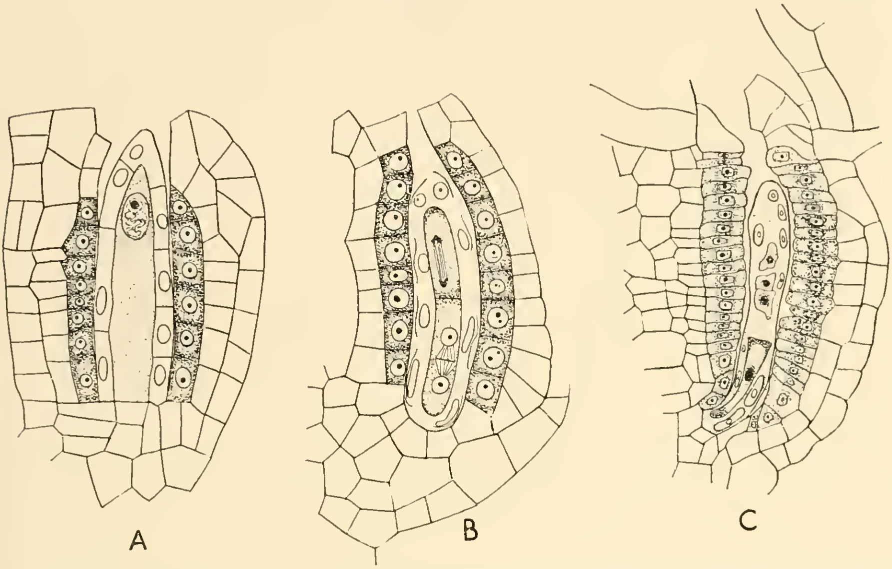


FIG. 1285.—*Calceolaria mexicana.* A, B, and C, Successive stages in the degeneration of the nucellus and development of integumentary endothelium in a tenuinucellate ovule. (*After Srinath.*)

The function of this tapetal layer has been much discussed. The cells have the characteristics of secretory cells and the most obvious suggestion is that they serve to nourish the embryo sac, as the anther tapetum nourishes the pollen grains. The chief difficulty in this opinion is the presence of a cuticle between the tapetum and the embryo sac. This has been demonstrated in a large number of Metachlamydeae, but it is not certain that it forms a continuous barrier. Srinath has indeed suggested that it is not a true cuticle but simply the remains of the nucellus. If there is no effective barrier, it is easy to suppose that the tapetum digests materials from the disorganizing middle layers of the integument and passes them on to the embryo sac. An alternative theory of its function is that it acts as a restraining layer, protecting the embryo sac from rupture during the growth of the endosperm, or else protecting it from loss of nutritive materials by exudation. This view does not seem to be well founded, but further inquiry is needed.

The use of the name tapetum for this layer is objectionable because the tissue is in no way homologous with the tapetum in the anther. The latter is derived from the archesporium, which, of course, is not true of these integumental cells in the ovule.

Little enough is known about the functions of the integuments in the early stages of the ovule. Chlorophyll occurs in the outer integument in several Monocotyledons (*Lilium*, *Gladiolus*, *Amaryllis*, *Nerine*) and stomata have also been found in a variety of genera (*Canna*, *Nelumbium*, *Nerine*, *Aquilegia*) and are probably to be found elsewhere. Deposits of starch are fairly common and storage seems to be increased at the beginning of endosperm formation. Buell has recorded in *Dianthus chinensis* that starch accumulates in the integuments around the micropyle and in the nucellus around the embryo sac and in a track up to the nucellar apex below the micropyle. After fertilization all this disappears and a secondary deposit appears at the base of the ovule, probably related to nutrition during endosperm formation.

Although the inner integument is in the closest contact with the nucellus, it is not united to it and is usually separated by a cuticle. Each ovule has normally three cuticles, one externally, secondly a double layer between the integuments and thirdly another double layer which belongs partly to the inner integument and partly to the nucellus, which usually has a delicate cuticle. Assuming that the cuticle is a relatively impermeable membrane, this implies that the embryo sac must draw its nourishment from the basal region of the ovule, rather than directly from the integuments. Only in certain families, such as the Rubiaceae, where the nucellus undergoes great reduction, is there an organic fusion between it and the inner integument.

The vascular supply to the ovule enters the funicle from the placenta and normally ends in the basal part of the ovule, the **chalaza**. It is sometimes an organized vascular bundle but often consists of little more than a procambial strand of elongated cells. Only rarely does the bundle continue into the integuments, but where it does it may branch into several strands, disposed around the ovule, as is the case in *Myrica* in which the integuments are almost completely free from the nucellus. Such integumentary bundles are frequent in the Gymnosperms and it has been maintained that their presence in Angiosperms is a primitive character. They do occur in certain families which have claims to be called primitive, *i.e.*, Ranunculaceae, Magnoliaceae, Betulaceae and Myricaceae, but they are also known in members of a number of truly advanced families, such as Cuscutaceae, Caprifoliaceae and Compositae, which largely discounts the idea of their phylogenetic significance (Fig. 1286).

The nucellus in most Archichlamydeae and Monocotyledons is a massive tissue, which persists into the ripening seed, where, in a few families such as the Piperaceae, it may even form a special nutrient tissue, the perisperm. Such a condition is called **crassinucellate**. On the other hand the

Metachlamydeae generally and a few Archichlamydeae have a very small nucellus, which may be no more than a single layer of cells around the embryo sac, and it may disintegrate and disappear at a rather early stage.

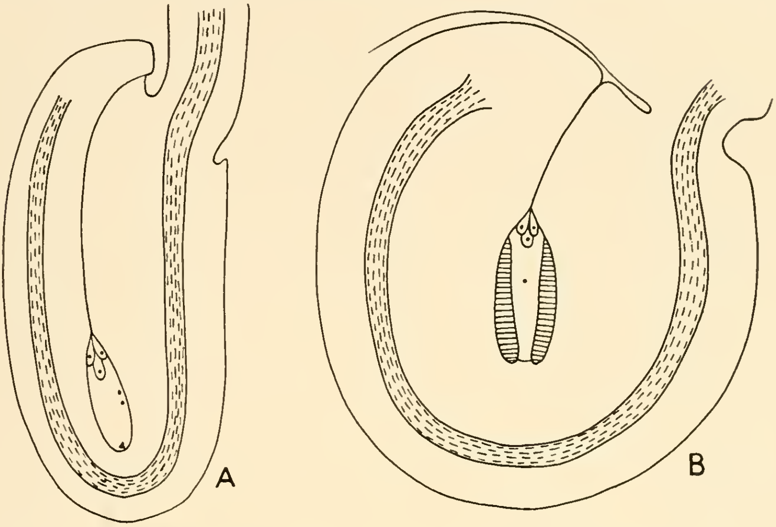


FIG. 1286.—A, *Menyanthes trifoliata*. B, *Fraxinus excelsior*. Funicular vascular bundles prolonged nearly to the micropyle. (*After Billings.*)

This condition is called **tenuinucellate**. The majority of crassinucellate ovules are bitegminous and the majority of tenuinucellate ovules are unitegminous. The crassinucellate type was called by Warming " eusporangiate " and the other type " leptosporangiate ". As these terms have a definite systematic significance in the Filicales, which is lacking here, they are best dropped, although morphologically they may be justifiable (see also p. 1395).

The tenuinucellate type may be regarded as reduced, and in some families reduction has proceeded to an extreme. Many of the plants which were formerly held to have naked ovules have been found, on closer examination, to have a single integument which had been mistaken for the nucellus, which has disappeared. For example, in the Rubiaceae a series of stages in the reduction of the nucellus can be traced, ending up with its suppression. In some genera of this family, *e.g.*, *Phyllis*, a tenuinucellate condition exists, the nucellus being partly sunk in the tissues at the base of the ovule and consisting only of a one-layered skin of cells over the archesporium. In *Bouvardia* the archesporium is still more deeply sunken and the nucellus is merely a cap of four or five cells over the top of it. In *Oldenlandia* the cap has been reduced to a single cell, while finally in *Houstonia* it has vanished altogether and the integument has closed over the archesporium, completely engulfing it.

In the parasitic families of Loranthaceae and Balanophoraceae, things have gone much further and the ovules themselves have been suppressed. As in the above case of the Rubiaceae, the work of Fagerlind has shown the way to an understanding of what happened. The genus *Thesium*, in the allied family of Santalaceae, has a free-central placenta bearing three pendent ovules, which are apparently naked nucelli, or, as Fagerlind considers, ovules with a single integument and an obsolescent nucellus of a few cells. In *Santalum*, the ovules are fused into one structure with the placenta (Fig. 1287). In most of the Loranthaceae the fusion of structure has gone further and the ovary is occupied by a massive upgrowth, the mamelon, embedded in which are the embryo sacs without any recognizable ovular coverings. In *Viscum*, the mamelon itself has been reduced and is united to the base of the ovary, the embryo sacs now appearing to be embedded in the latter (Fig. 1288). Finally, in the extreme case, *Balanophora*, the mamelon has been suppressed and the single embryo sac is now embedded in the swollen base of a cellular structure, which extends upwards into an elongated neck, the whole having a striking resemblance to an archegonium, except that there is no neck-canal. Goebel and Fagerlind regard this as a remarkably reduced carpel, the only vestige of the female flower. Comparative morphology supports this interpretation, although Lotsy and others have declared the structure to be a naked nucellus. In some other genera of the Balanophoraceae (*e.g.*, *Rhopalocnemis*) the male flowers retain a rudimentary perianth, which is wholly wanting in the female flowers, even though their ovarial structure has not been reduced as far as in *Balanophora*. It is therefore natural to expect the female flower in the latter to consist of the gynoecium only, without any perianth.

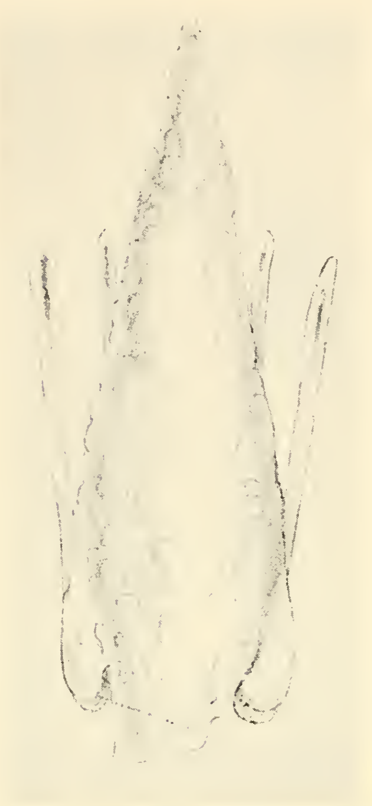


FIG. 1287.—*Santalum album*. The conical placenta with four emergent embryo sacs growing upwards. (*From Griffiths, "Trans. Linn. Soc."*, 1844.)

An approach to the condition in *Balanophora* is shown by *Tupeia*, one of the Loranthaceae endemic to New Zealand. There is no ovarial cavity and the archesporium lies at the base of a solid carpellary tissue, crowned by a style and a rudimentary perianth. There is no doubt that in this genus we have a reduced gynoecium and not an ovular structure.

As in some few cases, mentioned above, vascular strands enter the integuments and may even extend as far as the micropyle, so in some other plants there is a vascular supply in the nucellus itself. The condition is, however, rarer than vasculation of the integuments. In *Myrica* both types

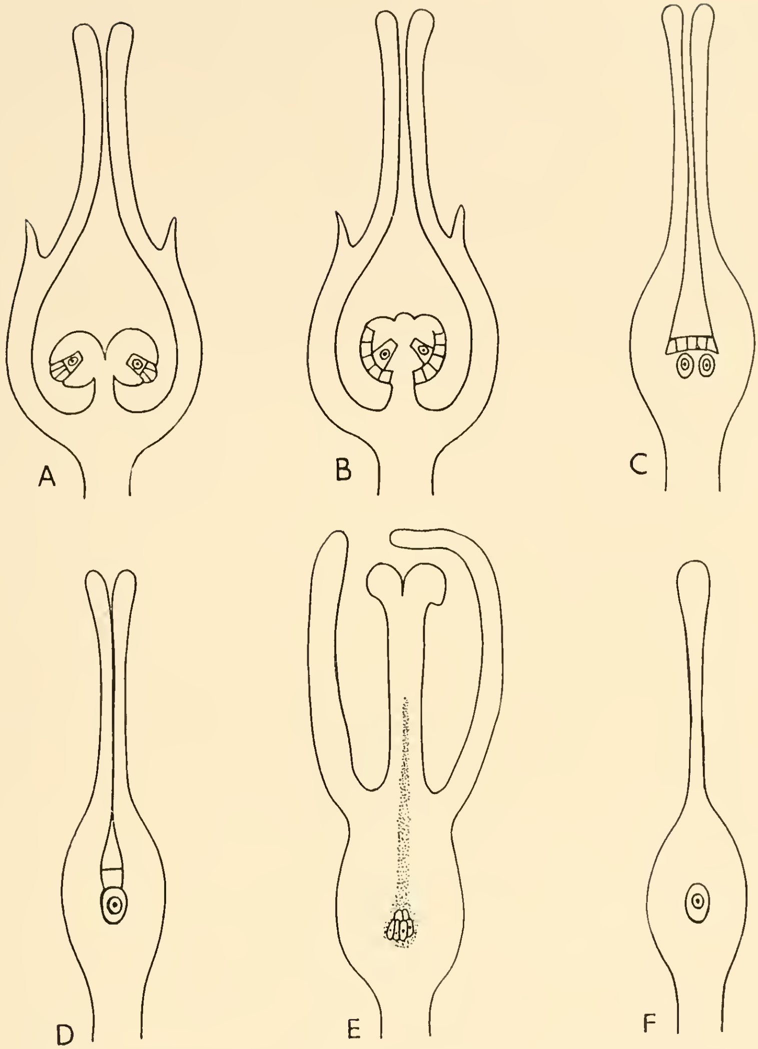


FIG. 1288.—Progressive reduction of the gynoecium in certain parasitic genera. A, *Thesium*. B, *Santalum*. C, *Viscum*. D, *Scurrula*. E, *Tupeia*. F, *Balanophora*. (*After Fagerlind*. E *after Smart*.)

of structure exist. Nucellus and integument are completely free from each other except at the base. In addition to the ring of bundles in the integument there is a central strand of elongated cells from the base of the nucellus up to the base of the embryo sac (Fig. 1289). There are no wall-thickenings and the strand has no connection with the true vascular tissue in the chalaza. One or two other isolated examples of similar axial strands of elongated cells in the nucellus have been recorded, *e.g.*, in *Butomus umbellatus* and in *Acacia baileyana*, where, however, the strand is connected, unlike that in *Myrica*, to the vascular bundle of the funicle.

The group of families formerly called the Amentiferae contains many examples of integumental vasculation, which as we mentioned above is regarded by some authors as a sign of their primitive status. Some also show nucellar vasculation. In *Carpinus* and *Castanea* true tracheids are found below the embryo sac, but there is no connection with the chalazal bundle. *Casuarina* has a chalazal strand which extends up in the nucellus to the base of the sporogenous tissue, some of the cells of which lignify and prolong the conducting tissue upwards. These plants are in many respects primitive, but nucellar vasculation also occurs, either regularly or sporadically, in some plants of quite advanced families, such as Asclepiadaceae, Capparidaceae, Euphorbiaceae and Agavaceae.

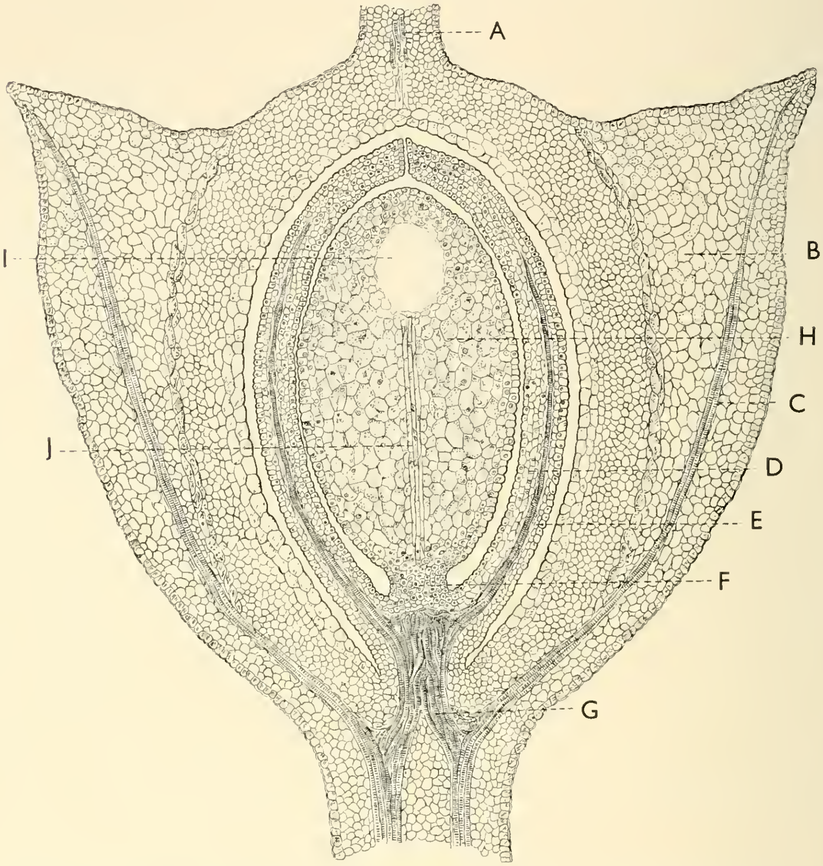


Fig. 1289.—*Myrica gale.* Longitudinal section of the fruit and contained ovule. A, Style. B, Adherent bract. C, Vascular bundle of bract. D, Integument. E, Vascular bundle of integument. F, Nucellar stalk. G, Main vascular supply. H, Nucellus. I, Embryo sac. J, Nucellar strand of conducting cells leading to embryo sac. (*From Kershaw, "Annals of Botany"*, 23.)

The micropyle, the apical opening which gives access to the nucellus, may be formed either by the inner integument only or more rarely by the outer integument only; most commonly it is bordered by both integuments, where two are present. In such cases the micropyle may have two distinguishable parts, the **exostome** and the **endostome**, which may be different in size and may sometimes not be in the same line, so that the whole passage is crooked. The two portions may even be at right angles, as in some Leguminosae. Extreme cases occur where the micropyle is completely closed by the contact of the integumental margins, or even obliterated, as in the Rubiacean genus *Houstonia* mentioned above, where only one massive integument is present. In a few species the tip of one of the integuments is extended into a tuft of filaments which grow up towards or into the stylar canal and form part of the conducting tissue for the pollen tubes. Examples are: *Isolepis gracilis* (Cyperaceae) where the filaments come from the outer integument, and *Myriocarpa longipes* (Urticaceae) where they come from the inner integument (see p. 1440). We have already referred (p. 1234) to the obturators which in some plants occlude the micropyle. They are usually outgrowths from the placenta or from the base of the stylar canal and they are in some respects the converse of the conducting filaments growing from the integument, as the obturator also functions as part of the conducting tissue system, linking the ovule and the stigma. Sometimes, as in *Grevillea*, the micropyle may be filled with a mucilaginous secretion, which comes partly from the integument and partly from the apex of the nucellus. This may perhaps facilitate penetration by the pollen tube.

There is no record of any endothelial layer lining the micropyle, even in species with massive integuments. The lining cells are apparently not specially modified.

The posture of the completed ovule presents a number of variations. The simplest of these is the straight position, the ovule standing upright from the placental surface with the funicle and the nucellus in the same straight line. This is the **orthotropous** position. It is relatively uncommon, the Polygonaceae providing the best known examples. The commonest form of ovule is that in which the funicle is lengthened and the whole body of the ovule is inverted through 180°, with the micropyle close to the placenta. The nucellus remains straight. This is the **anatropous** position (Fig. 1290).

There are so many variations of ovular posture that sharply defined classes cannot be separated, but in addition to the above the following types are sufficiently well-marked to have received names. (1) **Hemitropous**. The ovule is turned through 90° so that it makes a right angle with the funicle, which is attached to it at the middle of its long axis. The nucellus and embryo sac are straight. (2) **Campylotropous**. Like the last, but the apex of the ovule is bent over into the anatropous position. Nucellus and embryo sac are therefore bent through a right angle or more. (3) **Amphitropous**. Externally resembles the anatropous posture, but the inversion bending has taken place in the body of the ovule itself, the basal half remaining orthotropous and the apical half being anatropous. The nucellus and embryo sac are thus bent into a semi-circle. Within this semi-circle is enclosed a tissue which may be either of nucellar or of integumentary origin, which

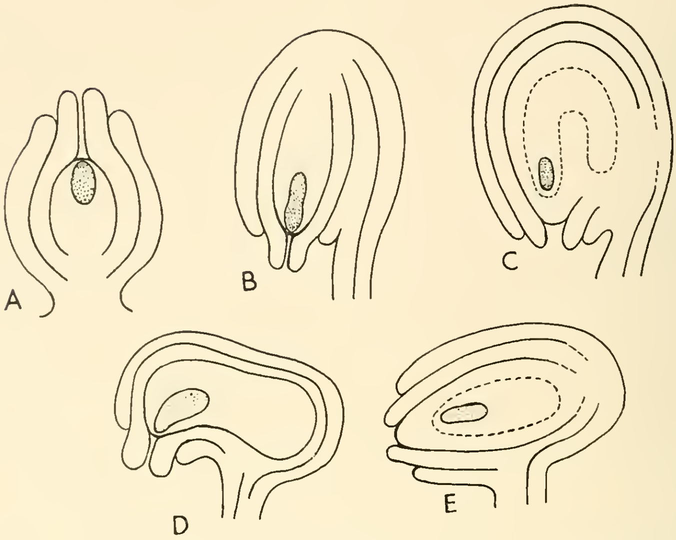


FIG. 1290.—Types of ovules. A, Orthotropous. B, Anatropous. C, Amphitropous. D, Campylotropous. E, Hemitropous. (*After Prantl.*)

sometimes persists into the ripe seed and stores food materials, constituting a perisperm, or which may later be compressed or destroyed. The amphitropous condition may, alternatively, arise from the hemitropous, both the micropylar and the chalazal ends of the ovule being bent downwards (*e.g.*, in *Atriplex*), like a saddle over the top of the funicle, which is then attached medianly between the arms of the semi-circular ovule.

One other curious ovular form deserves to be named. It occurs in some of the Plumbaginaceae and also in *Opuntia*, *Phyllocactus* and other Cactaceae. The funicle is exceptionally long and forms a complete circle around the ovule, which is free from it except for a small area of attachment at the end of the funicle. This has been called **circinotropous** (Fig. 1291).

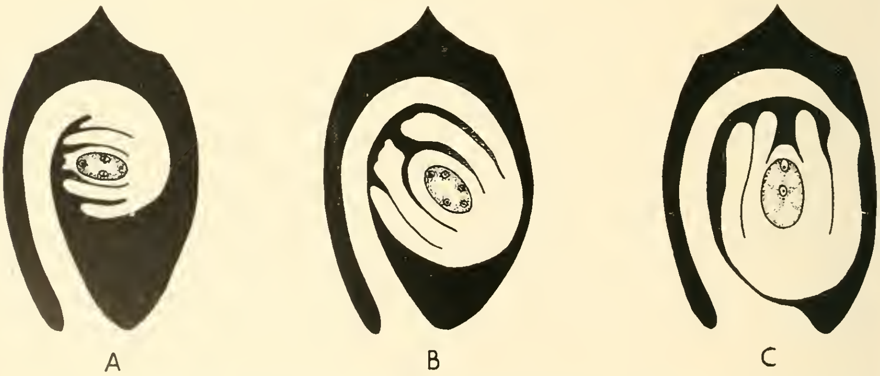


FIG. 1291.—*Plumbago capensis.* Three stages in the development of the circinotropous ovule. (*After Haupt.*)

Anatropous ovules have a ridge up one side, which is a continuation of the funicle and is generally called the **raphe**. This is customarily described as a union of the funicle with the outer integument, but the development of anatropous ovules shows that, in fact, no fusion takes place, but, on the contrary, the outer integument is suppressed on the side next to the funicle, only the tip, alongside the micropyle, sometimes appearing as a free structure. The bending over of the ovule is brought about by intercalary growth in the chalazal region.

The funicle is often very short and broad but examples of greatly elongated funicles, other than those just mentioned, are not common. Probably the best known are the long, flexible funicles of *Fraxinus*, and those of *Magnolia* by which the seeds remain suspended after the opening of the fruits. Members of the Combretaceae, moreover, have funicles which are generally long, sometimes interlaced or even fused together and furnished with knobbly outgrowths, providing, indeed, one of the family characters.

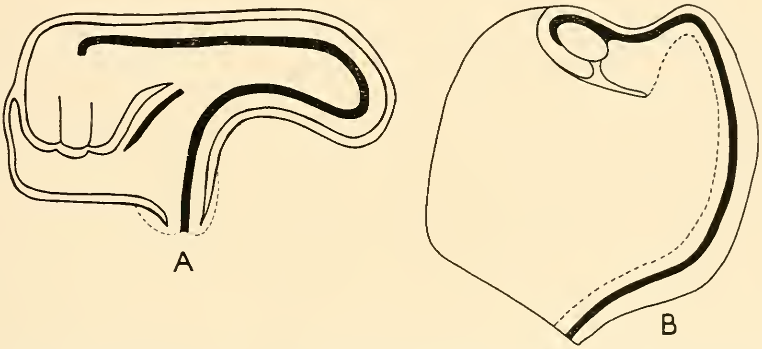


FIG. 1292.—*Juliania* sp. A, Young ovule in section. B, Mature ovule in section. The funicular " saucer " becomes massively enlarged. (*After Hemsley.*)

Very singular are the funicles in *Juliania* (Fig. 1292) and *Pistacia*. The resemblance which they show in this structure is striking because the two families of Julianiaceae and Anacardiaceae are not otherwise closely similar. The base of the funicle is short and broad. The upper part divides into two; one portion is long, folded sharply over on itself and bears the small, unitegminous ovule. The other portion forms a saucer, into which dips the ovular apex. Later it becomes immensely enlarged and fleshy and fills a large part of the seed.

Outgrowths of the funicle also occur not infrequently as arils, which in some cases completely envelop the ovule and provide a " third integument ", *e.g.*, in *Asphodelus*.

Where the ovule is attached, whether directly to the placenta or to the upper end of the funicle, an abscission layer forms later, by means of which the ripe seed is detached. This leaves a corky scar on the seed coat, known as the **hilum**, which is often large and distinctively coloured, especially in the Leguminosae, where the funicle may be very broad.

Apart from the position of the ovule on the funicle is the question of its position in relation to the ovary as a whole. The orthotropous ovule is nearly always basal, with its micropyle upwards, but anatropous ovules may occupy several alternative positions (Fig. 1293). If the raphe is on the side towards the ventral suture of the carpel it is said to be ventral. The ovule in this case faces outwards into the loculus. If the raphe is on the other side of the ovule, namely dorsal, the ovule faces inwards towards the placenta. If the micropyle is upwards the ovule is epitropous, if downwards it is hypotropous, and if directed horizontally it is pleurotropous. Basal ovules may be either orthotropous or anatropous but pendulous ovules, attached at the apex of the ovary, are invariably anatropous. In either case the raphe may be ventral or dorsal. These differences may sometimes be of systematic importance as family characters, but in a number of cases differences of position may be seen within a single ovary.

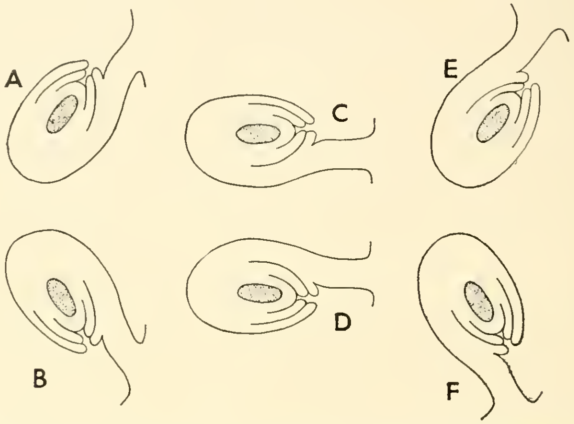


FIG. 1293.—Ovular positions. A, Ventral epitropous. B, Ventral hypotropous. C, Ventral pleurotropous. D, Dorsal pleurotropous. E, Dorsal epitropous. F, Dorsal hypotropous.

The order of development of ovules on the placenta follows one or other of three possible directions, as is generally the case with serial developments, *i.e.*, basipetal, basifugal or in both directions from the middle. There is no systematic significance in the direction. It is basipetal in Caryophyllaceae, Solanaceae and Berberidaceae, basifugal in Cruciferae, Rutaceae and Liliaceae and mixed in Passifloraceae, Rubiaceae and Amaryllidaceae, to cite only a few examples. Families are not always uniform in this matter and in the Papaveraceae it varies between different genera.

Certain features of structure in the basal, *i.e.*, the chalazal portion of the ovule require notice. Below the embryo sac, near the base of the nucellus, there is often a group of cells with lignified or suberized walls, which Van Tieghem called the **hypostase**. Although it is quite a prominent morphological feature in the ovules of some families, its function is doubtful. The cells are not always thick-walled; sometimes they are richly protoplasmic and resemble glandular cells; occasionally there are air-spaces among them. Van Tieghem believed that the hypostase limited the chalazal expansion of the embryo sac. Another suggestion is that the hypostase may produce a hormone required by the embryo sac. If this were so it is difficult to understand why it should not be universal.

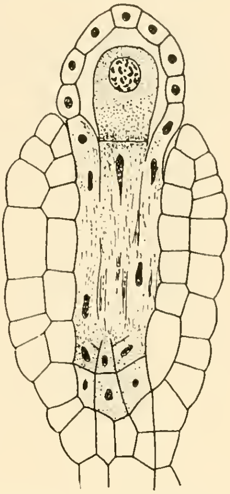


FIG. 1294.—*Mourera fluviatilis* (Podostemaceae). Young ovule in longitudinal section. Pseudo - embryo sac formed by the breakdown of the lower part of the nucellus. (*After Went.*)

A few plants belonging to widely separated families show a somewhat similar modification of the apical cells of the nucellus. Van Tieghem called this the **epistase**, but its nature also is unexplained. Both structures are well developed in the ovules of the Lentibulariaceae. There can be little doubt of their nutritive function in this family, as the cells are rich in protoplasm, and in some species they grow out into elongated haustoria which penetrate the nucellus around the fertilized embryo sac.

A singular phenomenon is seen in the ovules of many Podostemaceae. The outer integument develops first and envelops the nucellus, forming the micropyle. The inner integument develops later and only covers the lower portion of the nucellus. This lower portion breaks down into a space containing free nuclei and cytoplasm, called the pseudo-embryo sac, while the upper part of the nucellus, containing the true embryo sac, remains unaffected (Fig. 1294). This hollow suggests an analogy with the chalazal haustoria of many plants and is probably nutritive in function.

FIG. 1295. — *Cercidiphyllum japonicum.* Ovule in longitudinal section showing the large chalazal extension. (*After Swamy and Bailey.*)

The two genera *Trochodendron* and *Cercidiphyllum* have ovules of a peculiar pattern. According to Van Tieghem they develop laterally instead of terminally on the funicle and they have a sub-chalazal extension, which appears to be the funicle apex and into which the funicular bundle makes a hairpin bend, before ending below the nucellus (Fig. 1295).

Several other cases of remarkable chalazal developments are known. In *Bilbergia* (Bromeliaceae) there is a prolongation similar to the above but non-vascular, while in *Aechmea*, a member of the same family, the chalaza of the anatropous ovule is prolonged into a curly appendage which is twice as long as the ovule. *Narthecium* (Liliaceae) has anatropous ovules which are attached to the middle of a straight column, of which the lower part forms the funicle and the upper part is an outgrowth from the chalaza.

Such chalazal outgrowths are not uncommon in the Bromeliaceae. They are sometimes classified as arils and as they become flattened and membranous in the ripe seed, they aid its dispersal by wind.

The morphological interpretation of the ovule has long been a controversial question and it is clearly not one which can be considered only in relation to the Angiosperms, for the Gymnosperms and the Pteridosperms must also be taken into account.

Three opposed theories have long been in the field and each has obtained numerous supporters.

1. The Axial Theory. The nucellus is a bud, *i.e.*, a contracted axis, and the integuments are its lateral foliar appendages.
2. The Foliolar Theory. The ovule belongs to the category of phyllome. The nucellus is an emergence on the upper surface of a carpellary leaflet and the integuments are fused lateral lobes of the same segment of the megasporophyll.
3. The *Sui Generis* Theory. The ovule is an independent structure, borne either on axial or foliar organs, and the integuments are new formations.

The debate about these theories was formerly centred on the angiospermic ovule and the foliar nature of the carpel was accepted almost without question as a basis of argument. Thus, if the first theory were correct, then ovules, being buds, could not be borne directly on foliar carpels. As ovules are, in fact, often attached to carpels, it had to be maintained that the placenta was axial and that its fusion to the carpellary wall gave rise to the appearance of attachment to the carpels. If, on the other hand, the second theory were correct, then how could one account for basal ovules or those on free-central placentae, which appeared to be direct continuations of the floral receptacle? Moreover the second theory made the ovule a part of the carpel and this led its more extreme supporters to deny that the female reproductive organs of Gymnosperms and Pteridosperms are ovules, since without carpels, they could not be so. As Celakovsky said, " no ovule without a carpel ", an opinion indefensible at the present day.

The inconsistencies and the strained interpretations which resulted from the exclusive application of either theory led many morphologists to the conclusion that ovules might be of both kinds and the question whether in particular cases the ovules are cauline or foliar may still be found in textbooks in current use. The corollary, that this state of affairs might imply different lines of evolutionary descent for even closely related Angiosperms, did not obtrude itself.

Increasing knowledge of the Gymnosperms and, still more, of the Pteridosperms has led modern attempts to solve the problem away from the carpel altogether. It has directed attention to a much earlier and more primitive stage of evolution, and has given fresh meaning to the third or *sui generis* theory.

That the ovule includes a megasporangium may be taken as common ground, but there is obviously more to it than that. There is normally only one fertile megaspore, and we know that in *Lepidocarpon* and in *Selaginella apoda* a single megaspore may be enclosed by a megasporangium and fertilized *in situ.* The enclosing nucellus is therefore generally regarded as the megasporangium. Chadefaud has, however, made another suggestion. Going back to the Ferns, he points out that the leptosporangiate sorus bears a number of fertile trichomes (or telomes, as we would now say), but that in the eusporangiate sorus these telomes have been reduced to one and that one is sunk into the basal cushion, or soral placenta. The ovule, he argues, is a basisporangiate sorus, like that of the Eusporangiatae, and the nucellus is thus the equivalent of the soral placenta, sometimes with remnants of vascularization, and with one embedded sporangium.

This attractive idea, in spite of some difficulties, may be applied readily enough to crassinucellate ovules, but what of tenuinucellate ovules? Are they all the result of secondary reduction or are they truly " leptosporangiate ", as indeed Warming called them? If so, then we are back again at the same position as before regarding distinct lines of descent for nearly related Angiosperms. Following the principle of economy of hypothesis, the view that the nucellus is the megasporangium itself is to be preferred, at least for the present.

The integument surrounding the nucellus in Pteridosperms shows many signs of being a compound structure built up from a fusion of units. What these units may have been morphologically is far from clear. The original hypothesis of Benson was that they were sterilized megasporangia, forming the outer zone of a sorus, surrounding the single central sporangium which had remained fertile. On the other hand Chadefaud considers that the sorus was primitively amphisporangiate. In the male sori of Pteridosperms the central megasporangium is supposed to have disappeared and only the outer ring of microsporangia (sometimes fused together) remain. In the female sori the central megasporangium has developed and the integument represents a fused ring of sterilized microsporangia. A third possibility, suggested by *Yarravia* (see under Palaeobotany in Volume III), is that the megasporangium was terminal on a telome and that the units of the integument were a group of associated sterile telomes. There is little definite evidence, one way or the other, and the answer must await further discoveries.

The origin of the outer integument is even more puzzling. The cupule which surrounds the ovule in many Pteridosperms has been brought into consideration. It too shows indications of being formed of fused units, generally regarded as having been pinnae of the megasporophyll. It is not, however, a constant feature in Palaeozoic Pteridosperms, although the Mesozoic Pteridosperms appear to have been all cupulate. Again, the

Gymnosperms, with the exception of the Gnetales, have only one integument, and, except in Taxales, no cupules, unless the epimatium be interpreted as a vestigial cupule, or, more probably, the basal aril in *Ginkgo* and the basal disc in Bennettitales. Either, therefore, the majority of Gymnosperms are descended from non-cupulate Pteridosperms or they have lost their cupules, or alternatively the cupule has become united to the integument, forming the outer sarcotesta. Only in Gnetales and in the Angiosperms does the cupule appear to have remained as a second sheath around the ovule.

There are certainly difficulties in equating the outer integument with a cupule. For example, in *Sphaerostoma* the abscission of the seed took place above the cupule, leaving the latter attached to the plant, and this may have been the case in other types also. Further, the cupule in *Gnetopsis*, *Calathospermum* and in *Caytonia* enclosed a group of ovules and was therefore not an integument but an involucre. The first objection may be dismissed, since it refers only to a relatively primitive stage. The second also is not of serious weight, for these cases are exceptional and are not, in any case, involved in the direct ancestry of the Angiosperms, so far as we know. The further difficulty that many Angiosperms themselves have only one integument is not conclusive, for there is evidence in several cases that the unitegminous condition may result from the abortion of one of the two and we may reasonably consider the bitegminous condition as the original one.

There are a number of indications to be gleaned among the Pteridosperms, the Taxales and the Gnetales, which serve to confirm the idea that the cupule, like the seed-integument, is a compound structure and that it represents either a megasporophyll or a laminar portion of a megasporophyll. The homology of the cupule with the outer integument, although the evidence is far short of proof, remains, despite all difficulties, as the most probable solution to the question of its morphological nature. It must be realized, however, that its acceptance is bound to throw considerable doubt on the foliar character of the carpel. It must also cause speculation on whether the ancestors of the Angiosperms can have been related to the non-cupulate Cycads.

The Archesporium

The origin of the embryo sac can be traced to the archesporium, but the significance of this latter term is not quite precise, owing to many variations in ovular development. At a very early stage a sub-epidermal cell at the apex of the young ovule may become conspicuous by its size and the density of its contents and this is usually designated as the archesporial cell. This cell usually divides, cutting off a primary parietal cell and forming a primary sporogenous cell, from which the megaspore mother cell develops, either directly or after further division of the sporogenous cell. Such a sequence is closely parallel to that in the microsporangium and presents little difficulty.

All the hypodermal cells of the nucellus may, however, be potentially archesporial and two or more may develop equally, giving a multicellular archesporium, which again recalls the condition in the microsporangium. The number of cells involved is not always clear, for gradations may occur between obviously archesporial and unchanged nucellar cells. Multicellular archesporia are widespread in the Rosaceae, the Ranunculaceae (where the number of cells involved is very irregular) and in the " Amentiferae ". Isolated cases are found in many other families, but very rarely in Monocotyledons. Some of the cells composing these massive archesporia are probably not hypodermal, and this is almost certainly true of the large central mass of sporogenous cells which occurs in *Casuarina* and in certain species of *Carpinus*, *Quercus* and *Juglans*.

The massive archesporia of these genera might be interpreted as another of the primitive features of the Amentiferae, but single-celled archesporia are found in other genera of the same group, notably in *Betula* and *Alnus*.

Difficulties of interpretation arise in two opposite ways: either by the intercalation of a phase of development between the appearance of the apparent archesporial cell and the differentiation of the sporogenous cell; or by the suppression of one or more of the normal stages of development whereby the distinction of the various cells involved is lost.

The first condition is shown by *Arisaema* (Araceae) where the primary archesporial cell divides anticlinally into three or four cells, each of which behaves as an archesporial cell. Each cell, however, divides repeatedly and forms a row of cells, the apical cell of which again enlarges and functions as a sporogenous cell, turning indeed, owing to one of the puzzling suppressions which are frequent, directly into an embryo sac. What, in this case, is to be called the true archesporium?

There is a sequence of events, which may be regarded as normal or fundamental, on which we may try to base a judgment. An archesporial cell divides to cut off a parietal cell. The remaining cell then becomes the primary sporogenous cell, which is also the megaspore mother cell. This divides meiotically and produces four megaspores. So far there is a close parallelism with microspore formation, but in the megasporangium three of the potential megaspores abort and only one develops to form the embryo sac.

There are many departures from this sequence. No parietal cell may be cut off from the archesporial cell, whereby the differentiation of a distinct sporogenous cell is lost. This occurs most frequently in tenuinucellate ovules, while in crassinucellate species parietal cells are generally formed, though many exceptions are known in both cases. The archesporial cell itself may function as the megaspore mother cell, as we have just pointed out. It may also function, as may also the sporogenous cell where one is differentiated, as the embryo sac mother cell, making only one step from archesporium to embryo sac. Where the archesporium is multicellular there may, therefore, be a production of several megaspore mother cells, or of several embryo sacs. This multiplicity is usually only temporary and unity is generally established by the abortion of all but one of the supernumerary structures (see Fig. 1283).

So various are the processes of development in the ovule that one may doubt whether the term archesporium has any value in this connection. Schnarf gets over the difficulty by applying the term only to the megaspore mother cell, but this of course is quite different from its application in the microsporangium.

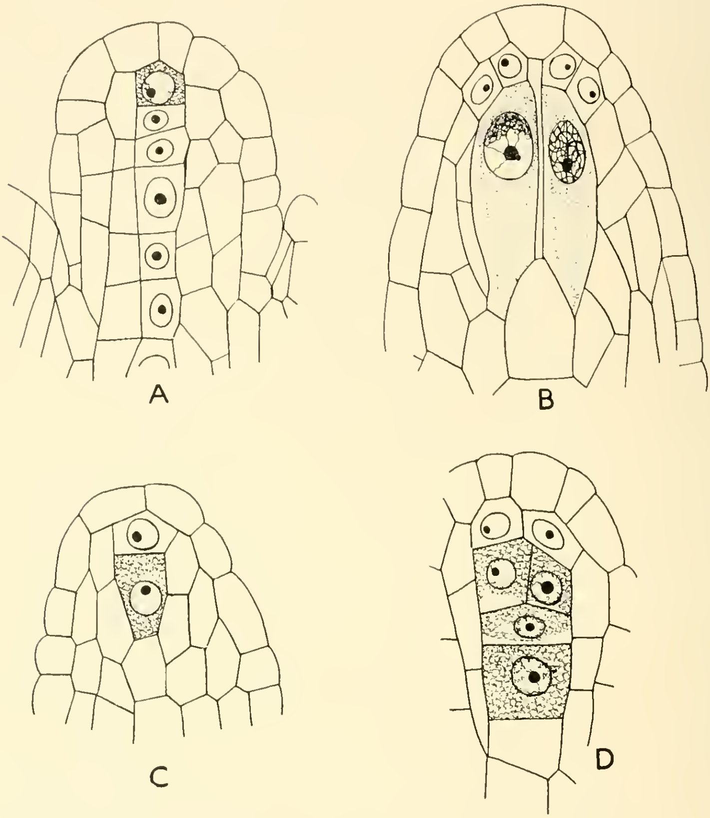


FIG. 1296.—*Rumex crispus.* A, Nucellus showing archesporial cell terminating an axial row. B, Two megaspore mother cells each with a pair of parietal cells. C, Mother cell with primary parietal cell. D, T-shaped group of megaspores, parietal cell divided anticlinally. (*After Dudgeon.*)

The parietal cell, when one is formed, becomes part of the tissue of the nucellus. It rarely remains undivided and its division may be anticlinal or periclinal or in both directions (Fig. 1296).

We have said that this happens commonly in crassinucellate species and indeed this multiplication of parietal cells is often, though not always, responsible for the crassinucellate condition, as the nucellar epidermis only occasionally divides periclinally, *e.g.*, in Rosaceae. In some species the parietal cells divide repeatedly, and strikingly regular files of cells may be built up between the epidermis and the archesporium, which thus comes to be deeply embedded in the midst of the nucellus. *Rosa* and *Alchemilla* are cases in point (Fig. 1297).

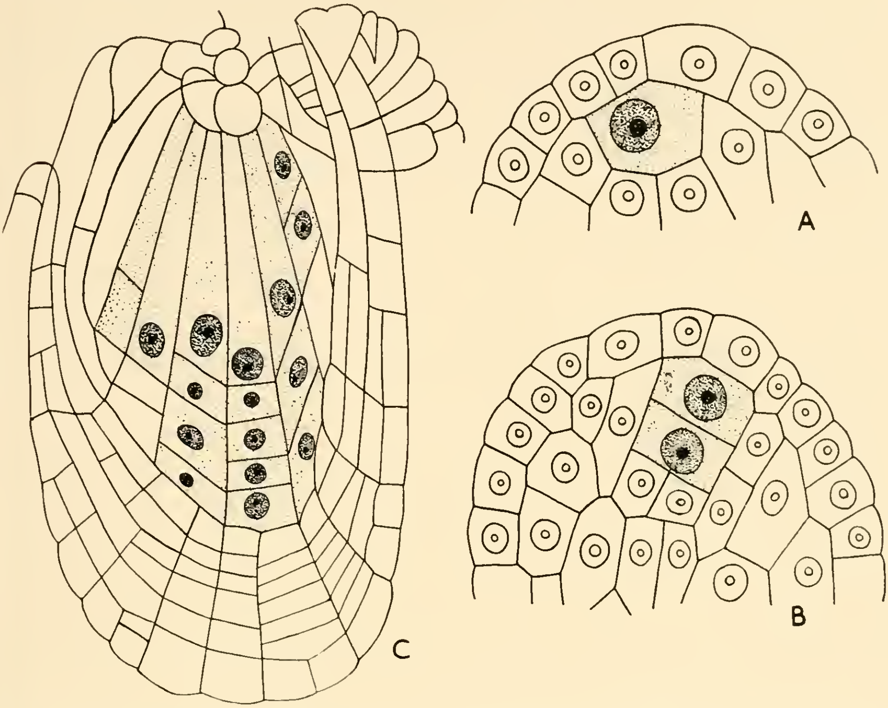


FIG. 1297.—*Salix glaucophylla.* A, Single archesporial cell. B, Archesporial cell divided into parietal cell and primary sporogenous cell. (*After Chamberlain.*) C, *Rosa livida.* Multicellular archesporium lying beneath several layers of parietal cells formed by the periclinal divisions of the primary parietal cell. The nucellar epidermis has also undergone several periclinal divisions. (*After Strasburger.*)

Generally the separation of parietal cell and sporogenous cell implies a functional differentiation, but instances are known in which the parietal cell or cells produce accessory embryo sacs. This is particularly the case in Malvaceae, in which most species have a rather massive development of parietal tissue, as a rule seven to twelve cells thick. Several of these cells may become accessory embryo sac mother cells, but only rarely is their development completed.

An attempt to reduce the varied conditions of archesporial development into a classified order has been made by Schnarf, who recognizes six types.

Type I. A number of sub-epidermal cells in the nucellus are differentiated as archesporium. Each cell divides periclinally into a short row of cells, the outer of which become parietal cells. The inner cells divide repeatedly to form a complex of sporogenous cells.

Type II. The first condition is as in Type I. Each archesporial cell divides once periclinally into a parietal and a primary sporogenous cell. The former may be further divided, the latter develops without division into a mother cell.

Type III. There is usually only a single sub-epidermal, archesporial cell, which divides once periclinally into a parietal cell and a sporogenous cell. The former undergoes further divisions, the latter becomes directly the mother cell.

Type IV. There is only a single sub-epidermal, archesporial cell. This divides periclinally into a parietal cell and a sporogenous cell. Both of these undergo further divisions. One of the innermost cells becomes the mother cell, though other, outer cells may show a tendency to develop into mother cells, which usually remain abortive.

Type V. There is only a single sub-epidermal, archesporial cell, which does not divide but passes directly into a mother cell.

Type VI. There is a complex of mother cells. Parietal cells are not formed. The complex of mother cells may arise from a single archesporial cell but this is uncertain.

The parietal cells may divide both periclinally and anticlinally, chiefly the former, up to three successive divisions. This produces quite a massive tissue, which naturally forces the sporogenous cells downwards, away from the surface. In the Rosaceae there is not only the formation of regular periclinal files of parietal cells but the epidermal cells also divide and add to the tissue complex (Fig. 1297). The greatest development is in the Malvaceae, where as a rule there are 7–12 rows of cells, and in *Althaea sulphurea* as many as 18 rows of cells separate the mother cell from the surface of the nucellus, all derived by the division of a primary parietal cell. (Type IV above.) In this family some of the accessory mother cells mentioned above, which usually remain abortive, may come from cells of the parietal complex. There is, therefore, not the clear-cut functional differentiation which normally accompanies the division of parietal from sporogenous cells. Similar occurrences have been observed in *Anthurium*, *Butomus* and *Ruppia*.

The parietal cell very rarely remains undivided; there are usually several rows of cells formed and their subsequent histories may be very different, but we never find among them the high degree of histological differentiation which is shown by the parietal layers in the anther.

It is scarcely possible to say definitely whether the development of a parietal tissue in the ovule is a primitive feature or not. The strongest argument in its favour is the almost universal absence of parietal cells in the Metachlamydeae, where it is associated with the tenuinucellate condition. Among Archichlamydeae the presence of parietal cells is inconstant, sometimes even within a single genus, and their suppression is unrelated to the size of the nucellus. It is noteworthy that they are absent from all the Ranunculaceae with the exception of *Helleborus* and *Thalictrum*, in which there is a single, undivided cell. Apart from this family, the evolutionary tendency seems to be towards suppression and, as the parietal tissue does not seem to have any important function in the ovule, this is reasonably to be expected.

A similar difficulty arises with regard to the pluricellular archesporium, which is sometimes regarded as a primitive character, in contrast with the usual unicellular type. Pluricellular archesporia occur regularly, or at least with some frequency, in families at all levels of advancement, *e.g.*, Cruciferae, Rosaceae, Papilionaceae, Cornaceae, Umbelliferae, Rubiaceae and Compositae, and one must reject the idea of a primitive character having been retained in all these cases. Furthermore, the later families in this list are tenuinucellate and have no parietal cells, two secondary characters that are incompatible with the retention of a primitive archesporium. The pluricellular archesporium cannot therefore be regarded as having a phylogenetic significance.

Although the term tapetum is sometimes applied to the parietal tissue, it does not undergo the same kind of changes which are shown by the tapetum in the anther. The term should be avoided, although it is morphologically justified, for the reason just stated and also because it has been applied to the " nutritive jacket " or endothelium around the enlarging embryo sac in many species, which is generally formed by the inner integument, as we have already described (p. 1383), and sometimes also from the nucellar epidermis. This may function as a tapetum but it is in no way homologous with that in the anther.

Some disintegration of cells around the embryo sac always occurs, but to a very variable extent. In some cases all the parietal tissue is involved and in many tenuinucellate ovules even the nucellar epidermis disappears by the time the embryo sac is mature. No general comparative study of these changes seems to have been made.

Megaspore Formation

The megaspore mother cell develops either directly from the primary sporogenous cell or, if the latter divides, or if there are several sporogenous cells, then normally one of them becomes the mother cell. At this point we reach the end of the life-history of the sporophyte, for the first division of the mother cell is the reduction division and the nuclei thereafter are haploid.

The procedure which is called " typical ", *i.e.* that which probably occurs in the majority of Angiosperms, consists of two successive divisions transversely to the long axis of the nucellus giving a row of four similar megaspores, of which the lowest, namely that nearest to the chalaza, generally develops into the embryo sac. Although a tetrad is usually formed there is much greater variability in megasporogenesis than in microsporogenesis. The extent of the variation in this procedure may be judged from the following details of conditions in the Araceae. In this family a distinct sporogenous cell is not formed, but it is represented by the primary archesporial cell. This, in different genera, may produce two megaspores of which the upper one develops; or four megaspores, of which either the top or bottom one may develop; or one megaspore which cuts off a parietal cell before developing into an embryo sac; or four megaspores in the transverse plane, of which one develops, cutting off a parietal cell beforehand; or, finally, no megaspore, the primary archesporial cell forming an embryo sac directly.

The first division is always transverse to the nucellus, forming a dyad of cells. This may end the process in some plants, two megaspores only being formed (*Allium*, *Commelina*), but this is rare. Three is a more common number, due to one of the first two cells failing to divide, although its nucleus may divide (*Yucca*, *Iris*, *Caltha*). All gradations are found between an undividing mother cell (*Lilium*, *Fritillaria*, *Piper*) and the regular group of four megaspores. Even double tetrads with eight spores have been found. There is no discernible relationship to the systematic status of the plant, nor any tendency towards suppression of megaspore development in more advanced families. Indeed the records of numbers found are of only minor interest, since the number and arrangement of the spores may vary in one species, or even, at different times, in one individual. An exception to this instability is provided by the Metachlamydeae in which the full complement of four spores is almost universal.

While the linear arrangement is most general, either the upper or lower dyad cell may divide longitudinally instead of transversely, yielding either T-shaped or ⊥-shaped groupings. The truly tetrahedral grouping has seldom been seen. It is reported as characteristic of *Fatsia japonica* (Araliaceae) but in other species it only occurs as an anomaly.

The general rule is that only one of the megaspores develops to form an embryo sac, the others disintegrating and being more or less completely resorbed. It is usually the chalazal member of the group which develops, whether for nutritional or other reasons is not clear. The exceptions to this are few. The micropylar spore generally develops in members of the Onagraceae and in some Compositae. In *Rosa* either the micropylar or the second spore may develop, while one or two genera are reported in which there is no fixed rule (*Gloriosa*, *Poa*). Lastly there are some peculiar cases (*e.g.*, *Galium*, *Sedum*, *Potentilla*) in which there is apparently a competition for nutriment between the four spores, accompanied by extensive outgrowths of haustoria, which seems to determine which spore shall form the embryo sac. Anomalous cases in which two or more spores develop towards embryo sacs are not uncommon. They seldom complete their development, as one usually prevails over the others.

The condition in *Casuarina* is highly peculiar and the only appearances at all like it are found in *Quercus*. In the former genus there are several hypodermal archesporial cells, which divide repeatedly to form longitudinal rows of cells, the upper members of which seem to be parietal, while a large number of the lower ones become sporogenous, providing a larger mass of this kind of cell than is to be found in any other plant. Treub estimated

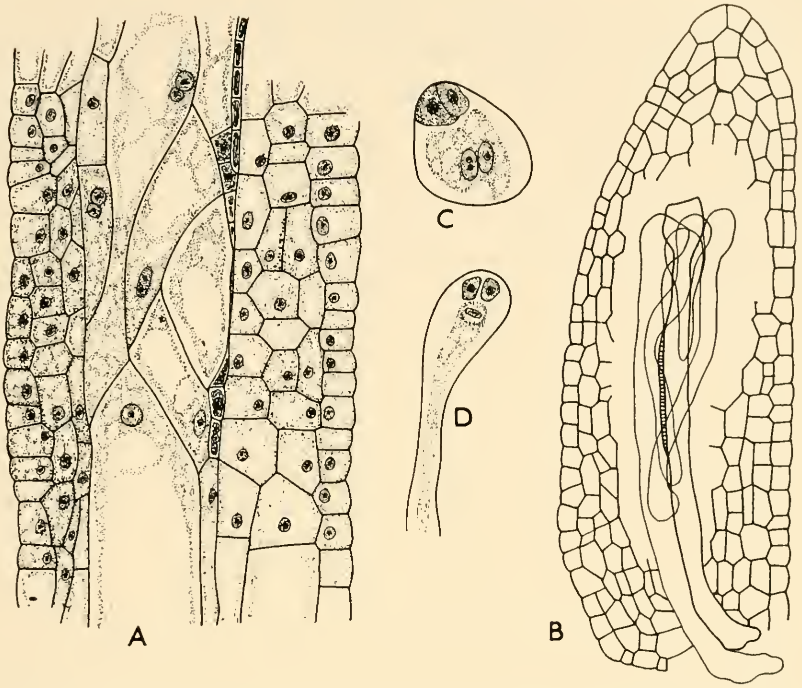


FIG. 1298.—*Casuarina suberosa.* A, Part of the nucellus in longitudinal section, showing the mass of sporogenous cells, many of which function as embryo sac mother cells. B, Elongation of the sporogenous cells into the chalaza. One has been transformed into a tracheid. C, Partial development in a non-functional sporogenous cell. D, Egg apparatus at the micropylar end of an elongated sporogenous cell, now an embryo sac. (*After Treub.*)

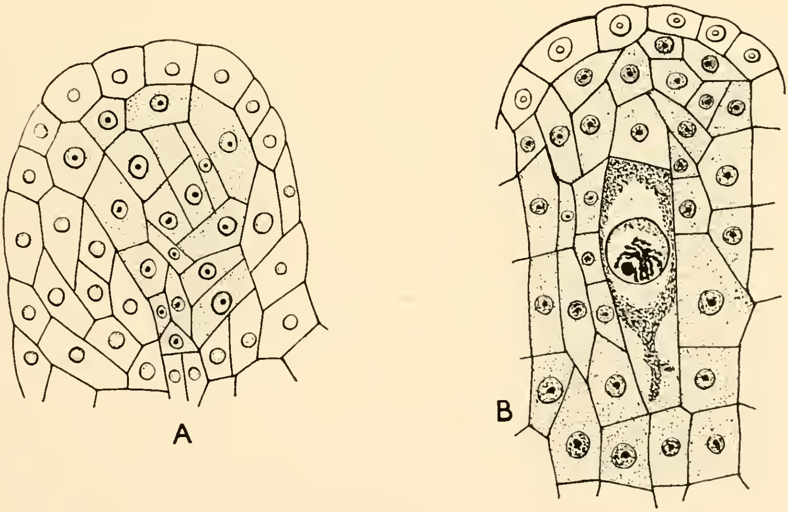


FIG. 1299.—*Quercus velutina.* A, Nucellus showing extent and position of the archesporial cells. B, Enlargement of an archesporial cell which develops directly into an 8-nuclear embryo sac. (*After Conrad.*)

the average number in *C. suberosa* to be about 300 (Fig. 1298). The lower limit of this mass is not sharply defined and some of the lowermost cells may be of chalazal origin. They sometimes assume the character of tracheids, forming a continuation of the end of the funicular vascular bundle. Only a limited number of the sporogenous cells undergo meiosis, some forming megaspore tetrads, and some, it appears, developing into embryo sacs. The rest remain sterile, become elongated and are eventually suppressed. A group of mature embryo sacs may be produced but generally only one is fertilized. In *Quercus*, the growing nucellus is occupied by a mass of between twenty and sixty archesporial cells (Fig. 1299). Several of these may begin development but usually only one, four or five cells deep, becomes a mother cell, the neighbouring cells disintegrating. The two meiotic divisions follow each other rapidly, without cell divisions, and a four-nucleate embryo sac results without the formation of separate megaspores. The mature embryo sac is of a normal eight-nucleate type and, by the time it is mature, all the nucellus, except at the base, has been resorbed and the synergidae push up into the micropyle.

The Development of the Embryo Sac

The angiospermic embryo sac is the product of the germination of a megaspore and is therefore the greatly reduced homologue of the female prothallus. Although ten different types are recognized, they are all variants of one basic pattern, a somewhat complex organization, which occurs with surprising regularity in all the main groups of the Angiosperms and constitutes one of the arguments in favour of their unity as an evolutionary class.

This basic pattern consists of an oval, thin-walled sac containing eight nuclei and, when mature, somewhat scanty cytoplasm. Three of the nuclei form a group at the micropylar end and are generally isolated by delicate surrounding pellicles. The median nucleus functions as the **oosphere** and gives rise to the embryo after fertilization. The two lateral nuclei were called the **synergidae** by Strasburger, a name which signifies their function as assistants or co-workers of the oosphere. These three are collectively called the **egg-apparatus**. At the chalazal end is another group of three nuclei, also generally surrounded by pellicles, which are called collectively the **antipodals**. They play no part in fertilization and sometimes disappear quickly. In other cases they may multiply or may become enlarged. They may have some glandular or nutritive function or they may be simply vestigial. Their status is uncertain.

In the centre of the sac, between the two other groups, is formed a pair of nuclei lying close together, usually called the **polar nuclei**. They lie free in the cytoplasm of the sac and sometimes unite before fertilization. In all cases they unite jointly with one of the two male generative nuclei from the pollen tube, an act known as **triple fusion**, the product of which is the **primary endosperm nucleus**. From this develops the endosperm, which, however, is sometimes abortive. Before the embryo sac is mature the eight nuclei are in two groups of four at opposite ends of the sac, and one nucleus from each group migrates to the centre to form the polar pair.

Embryo sacs are classified on two main characters. The first is the number of megaspores concerned in forming the embryo sac and the second is the number of nuclei in the mature sac.

As we have seen above, a complete tetrad of megaspores is formed in a very large number of species, probably in the majority. Only one of these may develop into an embryo sac, which is hence called a **monosporic sac**. In a minority of genera the sporogenous cell does not divide at all, but its nuclei divide and it enlarges directly into an embryo sac, which is called a **tetrasporic sac**.

Putting aside the considerable number of species in which anomalous numbers of nuclei may arise by irregularities in nuclear division or in other ways, which are not of great general interest, there are two main classes of embryo sacs with an exceptional number of nuclei, those with four and those with sixteen respectively. These constitute definite types with a certain constancy and may characterize whole genera or even whole families.

The ten types recognized on the basis of these considerations have been fully described by Maheshwari, from whose work the following account is taken. They have been named after the genera in which they were either first described or in which they are most characteristically shown (Fig. 1300).

1. *Monosporic, eight-nucleate sacs.* The *Polygonum* type. Four megaspores are formed, of which the lowest develops. Its nucleus divides thrice and the eight nuclei formed are arranged in the characteristic order. This is generally referred to as the " normal " type. The name of *Polygonum* has been attached to it because it was first described in *P. divaricatum* by Strasburger in 1879.

2. *Monosporic, four-nucleate sacs.* The *Oenothera* type. Four megaspores are formed of which the micropylar one normally develops, though occasionally the chalazal spore may also develop. The spore nucleus divides only twice and the four nuclei formed provide the oosphere, two synergidae and one polar nucleus. This type is only known in the Onagraceae and is characteristic of that family.

3. *Bisporic, eight-nucleate sacs.* The *Allium* type. The sporogenous cell divides only into two, a dyad. Either the lower (*Allium*) or the upper cell (*Scilla*) may develop. Its nucleus divides thrice and the eight embryo sac nuclei are normally arranged. This type is found sporadically in several monocotyledonous families, *e.g.*, Liliaceae, Amaryllidaceae and Orchidaceae, and is widespread in some others, *e.g.*, Alismaceae and Butomaceae. Among Dicotyledons it has only been found in members of certain aberrant families: Podostemaceae, Balanophoraceae and Loranthaceae.

4. *Tetrasporic, eight-nucleate sacs.* The *Adoxa* type. The nucleus of the sporogenous cell divides thrice, or to describe it in another way, the nucleus of the sporogenous cell divides twice to give four megaspore nuclei, without

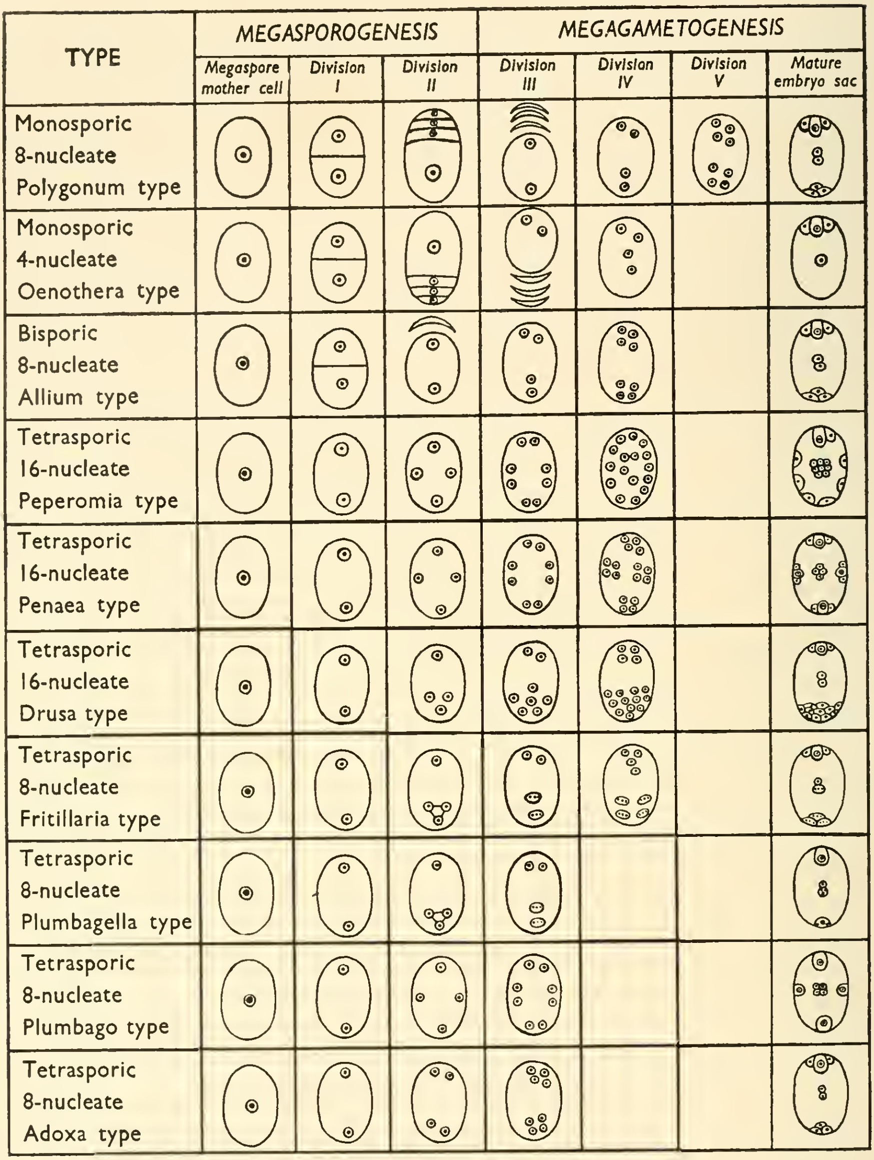


FIG. 1300.—Tabulated diagram of developmental stages of the principal embryo sac types. See text for details. (*After Maheshwari.*)

cell division, and these divide again once, to form eight nuclei which are normally arranged. This is the type to which the familiar embryo sac of *Lilium* was formerly supposed to belong. The true history in *Lilium* is more complex and conforms to the next type described. The present type is much less common. It is a regular feature only in *Adoxa* and *Sambucus* and occurs in some species of *Ulmus*, *Tulipa* and *Erythronium*.

5. *Tetrasporic, eight-nucleate sacs.* The *Fritillaria* type. This generic

name has been chosen to avoid confusion with what was previously known as the " Lilium type ", *i.e.*, the *Adoxa* type. The condition in *Lilium* and *Fritillaria* is, in fact, more complex. Four megaspore nuclei are formed in the sporogenous cell and these arrange themselves with three at the antipodal end and one at the micropylar end of the cell. The latter divides normally into two, but during division of the other three their groups of chromosomes are intermingled before separating, so that two *triploid* nuclei result. This provides a *second* four-nucleate stage, but very different from the first. All four nuclei now divide again to produce eight, four micropylar nuclei which are haploid and four antipodal nuclei which are triploid. The eight nuclei take up the normal arrangement and the two polar nuclei fuse to produce a tetraploid nucleus.

Finally, therefore, there are three haploid nuclei which form the oosphere and synergidae, three triploid nuclei which form the antipodals and one tetraploid polar nucleus. The latter after fertilization by a male gamete nucleus is naturally pentaploid and so are all the endosperm nuclei formed from it subsequently.

This curious type seems to be general throughout the Lilioideae and has been found in a number of other, quite unrelated genera, *e.g.*, *Piper*, *Cornus*, *Armeria*, *Statice* and *Gaillardia*.

6. *Tetrasporic, eight-nucleate sacs.* The *Plumbago* type. The four megaspore nuclei arrange themselves with one at each end of the cell and one at each side. They divide to make eight, arranged in pairs. One of the micropylar nuclei is cut off by a membrane and forms the oosphere. There are no synergidae. The other micropylar nucleus and one from each of the remaining pairs move to the centre of the sac and form a group of four polar nuclei which may fuse. The three remaining nuclei frequently disappear but they too may be cut off by membranes and give the appearance of accessory oospheres, one at the antipodal end and one at each side of the sac. This type is only known in the Plumbaginaceae.

7. *Tetrasporic, four-nucleate sacs.* The *Plumbagella* type. This resembles the *Fritillaria* type, but ends at the secondary four-nucleate stage. The four megaspore nuclei are arrayed as in *Fritillaria*. The three chalazal nuclei then fuse, giving a secondary two-nucleate stage. A further division yields two haploid and two triploid nuclei. One haploid nucleus forms the oosphere, with no synergidae; one triploid nucleus forms a single antipodal cell and the two others fuse to form a single tetraploid polar nucleus.

This type is known from only one species, *Plumbagella micrantha*, closely related to *Plumbago*, but it shows certain resemblances both to the *Fritillaria* and to the *Plumbago* types.

8. *Tetrasporic, sixteen-nucleate sacs.* The *Drusa* type. This type is characterized by the multiplication of antipodals. The four megaspore nuclei arrange themselves with one at the micropylar end and three at the chalazal end of the sac. This is followed by two successive phases of division, giving four micropylar nuclei and twelve antipodals. From each group one nucleus migrates to the centre to form the polar pair. Thus the

mature sac has the normal three nuclei at the micropylar end and eleven antipodals.

Drusa oppositifolia, the type species, is a member of the Umbelliferae, but the same conditions in the embryo sac have been found also in some species of *Rubia*, *Crucianella*, *Maianthemum*, *Chrysanthemum* and *Ulmus*, among others. Irregularities in number may occur through the failure of certain nuclei to divide.

9. *Tetrasporic, sixteen-nucleate sacs.* The *Penaea* type. The four megaspore nuclei undergo two successive divisions and the sixteen nuclei formed arrange themselves in four groups of four, one at each end of the sac and one at each side. One nucleus from each group moves to the centre, so that there are four polar nuclei. In this and some related cases where a number of polar nuclei exist, their fusion and fertilization produce a highly polyploid primary endosperm nucleus, which seems frequently to be associated with subsequent abortion of endosperm formation.

The remaining three nuclei in each group are isolated by membranes and form three groups like the normal micropylar group. Only the latter, however, seems to be functional in fertilization.

This type is found in a number of members of the small family Penaeaceae (Myrtales) and the same or closely similar conditions have been described from several of the Malpighiaceae and Euphorbiaceae.

10. *Tetrasporic, sixteen-nucleate sacs.* The *Peperomia* type. The four megaspore nuclei undergo two successive divisions and the sixteen resulting nuclei are at first distributed all over the sac. Generally two form the micropylar group, one as the oosphere and the other as one large synergid. Eight nuclei fuse in the centre of the sac, as polar nuclei, and the remaining six are cut off singly by membranes all round the chalazal part of the sac and may be regarded as antipodals. There are variations, however, even in the type species, *P. pellucida*, and more than one strain may exist in the species, for in some cases the sac is pear-shaped instead of spherical, and these sacs all seem to have two synergidae. In *P. hispidula* no fewer than fourteen of the sixteen nuclei are involved in fusion at the centre of the sac, and there are no antipodals.

Apart from *Peperomia* (Piperaceae), the same type of sac is only known in *Gunnera*, a peculiar genus of Haloragidaceae, with a southern distribution.

The telescoping of the two processes of sporogenesis and gametogenesis in the ovule has gone further than in the microsporangia of the anther, where spores are always formed as distinct structures, and it illustrates how far the reduction of the gametophyte has gone in Angiosperms. The end of one generation flows, as it were, directly into the beginning of the next and is marked by nothing but the nuclear change in meiosis. Among the Gnetales we may find approaches towards the same condition, but falling short of it, and, indeed, the only parallel is the remote one of *Fucus*.

Apospory as known in the Filicales is not a true parallel, since in this process there is no meiosis and certain somatic cells of the sporophyte develop directly into a diploid prothallus. Apospory of a similar kind is known to occur also in a few Angiosperms, *e.g.*, in certain species of *Hieracium* (*H. flagellare* and *H. aurantiacum*), also in *Malus*, *Crepis*, *Hypericum*, *Poa* and *Ranunculus*. In these cases although megaspores are formed, an embryo sac is produced from a neighbouring somatic cell of the nucellus, which may develop either in replacement of a normal sac, or side by side with it. The nuclei of these sacs are, of course, diploid.

There yet remains an ultimate step in reduction that, so far as we know, has not been taken, for it will be seen from the above descriptions that there is no case in which the four megaspore nuclei themselves, without any change or division, become the nuclear apparatus of the mature embryo sac. Perhaps this cannot be, but we do not know why.

The timing of ovular development is often out of step with that of the microspores, as we have previously mentioned. In some early-flowering species, such as *Corylus*, *Salix*, *Populus* and *Ulmus*, the ovules pass the winter in the form of nucellar primordia and development of archesporium only begins in spring, in some cases only after pollination. The latter is generally the case also among Orchids.

When there is any well-marked difference in the timing of development, the commoner condition is the ripening of the pollen grains before the ovules, *e.g.*, *Trillium*, *Populus*, *Tulipa*, etc. The opposite condition, that of the ovules developing in advance of the pollen, is rare, but a good example is *Empetrum*, where uninucleate pollen grains were observed to be formed at the beginning of August but division of the nucleus did not begin until the following spring. On the other hand the eight-nucleate embryo sacs were already complete early in August.

Structure of the Normal Embryo Sac

The embryo sac is a relatively large structure, limited by a thin cellulosic wall and containing at first eight nuclei of similar size and appearance as well as cytoplasm. The latter is mostly aggregated at the two poles of the sac, surrounding the two groups of four nuclei which are located there, while the central part of the sac contains a large vacuole containing sap with a low osmotic potential and with only a thin, peripheral layer of cytoplasm. When the fertilization stage is approached, this vacuole may become separated into several, while a secondary aggregation of cytoplasm forms around the two polar nuclei, which have then paired at, or near, the centre of the sac. The cytoplasm may also enclose a considerable number of starch grains, which disappear after fertilization. They are not included in the endosperm, even when this contains starch (Fig. 1301).

In crassinucellate ovules, the expansion of the embryo sac may be accompanied by the destruction and absorption of some of the inner layers of nucellar tissue, but its expansion is not otherwise restricted. In tenuinucellate sacs the entire nucellus may disappear, so that the wall of the sac becomes contiguous with the inner surface of the inner integument. This is generally cuticularized and may also be formed of a closely packed layer

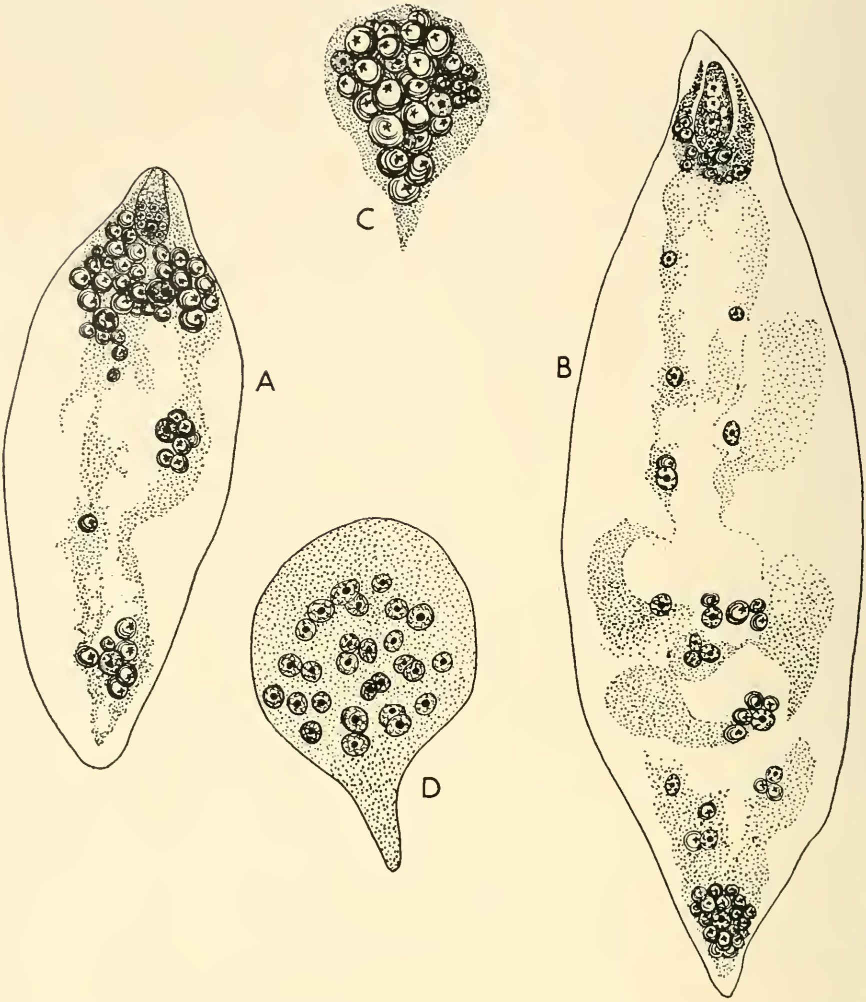


Fig. 1301.—*Hypericum mysorense.* A, Four-nuclear stage of endosperm development, showing starch grains surrounding nuclei. B, Sixteen-nuclear stage, with most of the starch around the chalazal nucleus. C, Chalazal coenocytic cyst with abundant starch. D, The same from nearly mature seed, showing the disappearance of starch. (*After Swamy.*)

of rectangular cells, which we have previously described as the ovular tapetum or endothelium. This has a restrictive action on the expansion of the sac, which remains narrowly cylindrical and only expands, if at all, at the micropylar and sometimes also at the chalazal ends, where it has grown beyond the cuticularized barrier layer. The epidermis of the nucellus is also generally cuticularized and this thin cuticle remains around the sac even after the nucellus has been destroyed. It is, however, usually dissolved at the micropylar end, so that it offers no barrier to penetration by the pollen tube.

It is an open question, though one of some importance, whether the nuclei of the embryo sac are qualitatively different, each having a predetermined part to play, or whether their fate is determined by the position they occupy in the sac. The details of embryo sac development have been followed in a very large number of plants, but they do not provide a sufficient answer to what is really a question of genetic constitution. Support for the first view may be found in the observation that the synergidae appear to be always sister cells and that the oosphere and the upper polar nucleus are also sisters. Similarly among the antipodals, though the question of differentiation does not usually arise, the two lower nuclei are sisters and the upper antipodal is the sister of the lower polar nucleus. Differences of size between the nuclei are not reliable as an index of differentiation, since this varies considerably during the maturation of the sac.

Once the eight nuclei have taken up their characteristic positions, cell formation follows, generally at both ends simultaneously, but where there is any difference it has always been observed that the antipodal cells are formed before the micropylar cells. On the mode of wall formation there are relatively few observations. In *Lilium martagon* and one or two other plants, spindle fibrils in the cytoplasm have been observed between the four micropylar nuclei, on which cell plates form between all four nuclei simultaneously, so that three complete cells are enclosed, while the polar nucleus is only partly enclosed, on the side towards the oosphere. The same process occurs in the antipodal group. This recalls the simultaneous wall formation between the nuclei of a nuclear endosperm (see p. 1453).

Cell wall formation is suppressed in some wild species of *Tulipa*. The eight nuclei remain free in the cytoplasm of the sac. The synergid and the oosphere nuclei have a distinct appearance but the others are indeterminate. This curious anomaly is probably derived from the *Fritillaria* type of embryo sac.

The Synergidae. The normal pair are usually apparently similar and equivalent. The name given them by Strasburger is generally justified in that they assist in fertilization, after which their usefulness seems to be over and they disappear. They may, indeed, disappear before fertilization, but this is exceptional. Their pointed upper ends are attached to the apex of the embryo sac and their rounded lower ends protrude into the space of the sac, reaching from one-fourth to one-third of its length (Fig. 1302). A few cases are known (*e.g.*, *Luffa*) where they are so much enlarged that they reach nearly to the base of the sac.

The walls of the synergidae contain cellulose, that is they are true cell walls. There is frequently a definite constriction of the wall, separating an upper and a lower part of each cell,* and above this the cells expand laterally,

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* The terms " upper " and " lower " have been used here throughout in accordance with the older usage, which regards the micropylar end of the ovule as its apex and therefore the point of reference in orientation. Moreover all illustrations of embryo sacs are drawn in this sense. The practice of some recent writers of using the terms in reverse, taking the orientation of the embryo for their guide, is to be deplored, as introducing confusion and as illogical when applied to structures before the embryo exists. It is no improvement; on the contrary.

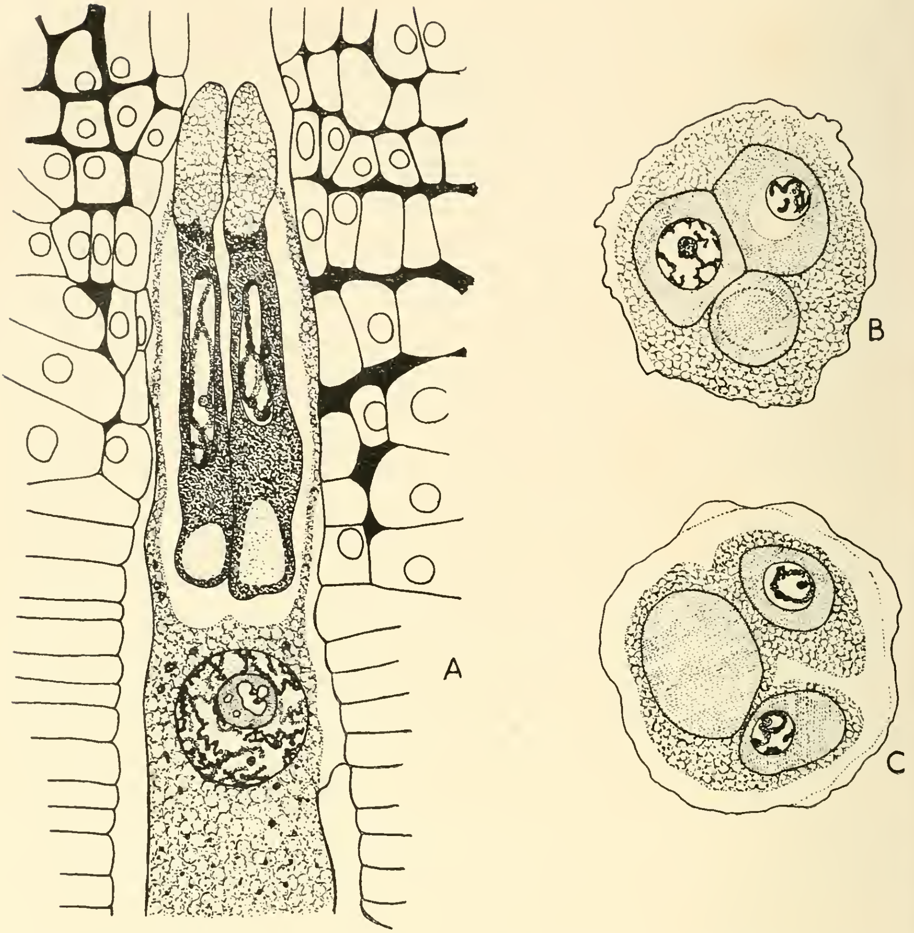

Fig. 1302.—*Impatiens glanduligera* (*I. roylei*). A, Micropylar end of embryo sac in longitudinal section. Synergidae fully developed. Below them the primary endosperm nucleus. The oosphere lies behind the synergidae. B and C, Transverse sections of the egg apparatus. The oosphere is to the left in each case. (*After Steffen.*)

at least in many plants, forming what are called " hooks " from their appearance in longitudinal section, but which are really " hoods ", since the expansion is all round the two cells (Fig. 1303). It is usually at this point that they make contact with the embryo sac wall and consequently it is here that the cytoplasmic lining of the sac terminates. The upper part of the cell wall is very often marked by a system of fine cellulose fibrils, called the " filiform apparatus", which is not always visible, though sometimes very conspicuous. The fibrils may be parallel or radiating from the apex or they may form a fine network or even a system of porose tubules (*Viola*) (Fig. 1304). The fibrils give some reactions of cellulose, but they are not soluble in cuprammonia.

This structure has been known since 1856 but its function is not yet

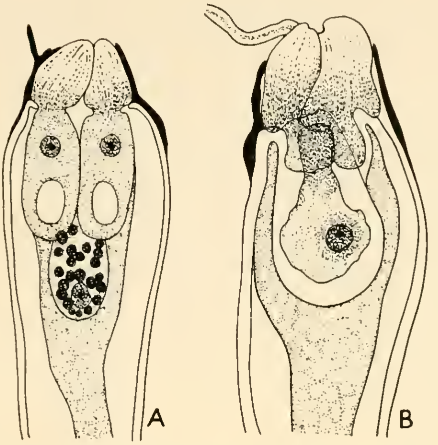

FIG. 1303.—" Hooked " synergidae. A, *Santalum*. B, *Daphne*. (*After Strasburger.*)

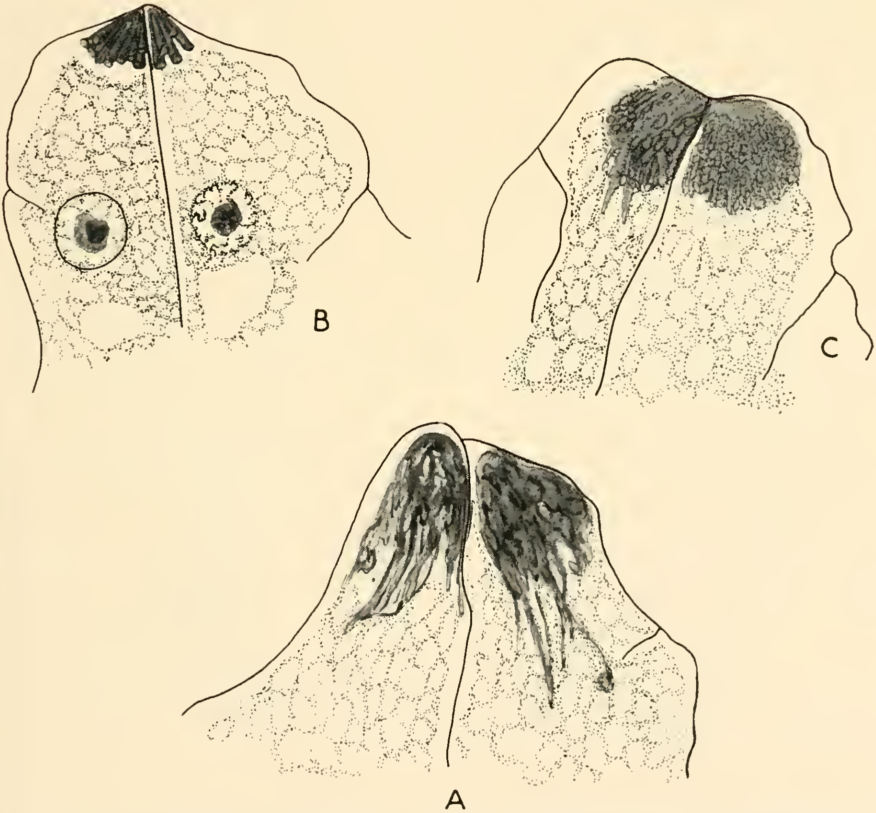

FIG. 1304.—*Viola riviniana*. Filiform apparatus in the synergidae. A, With stringy projections. B and C, With suggestions of tubular structure. (*After West.*)

understood. It may, however, protect the cell from bursting at the upper end during fertilization, as we shall see later. It may also have a secretory function in attracting the pollen tube, since the tube generally enters through it. It appears to be tough and durable as it often outlasts the disintegration of the rest of the cell. The lower, rounded end of each synergid contains a large vacuole, which also plays a part in fertilization.

In the Compositae and possibly in one or two related families, the synergidae break through the embryo sac wall and extend upwards into the micropyle. These plants being tenuinucellate, the nucellus has by this time disappeared, so that there is direct access from the sac to the micropyle. In one or two genera, such as *Calendula*, they even grow out of the micropyle into the ovarian cavity (Fig. 1305). It is not always possible to be certain

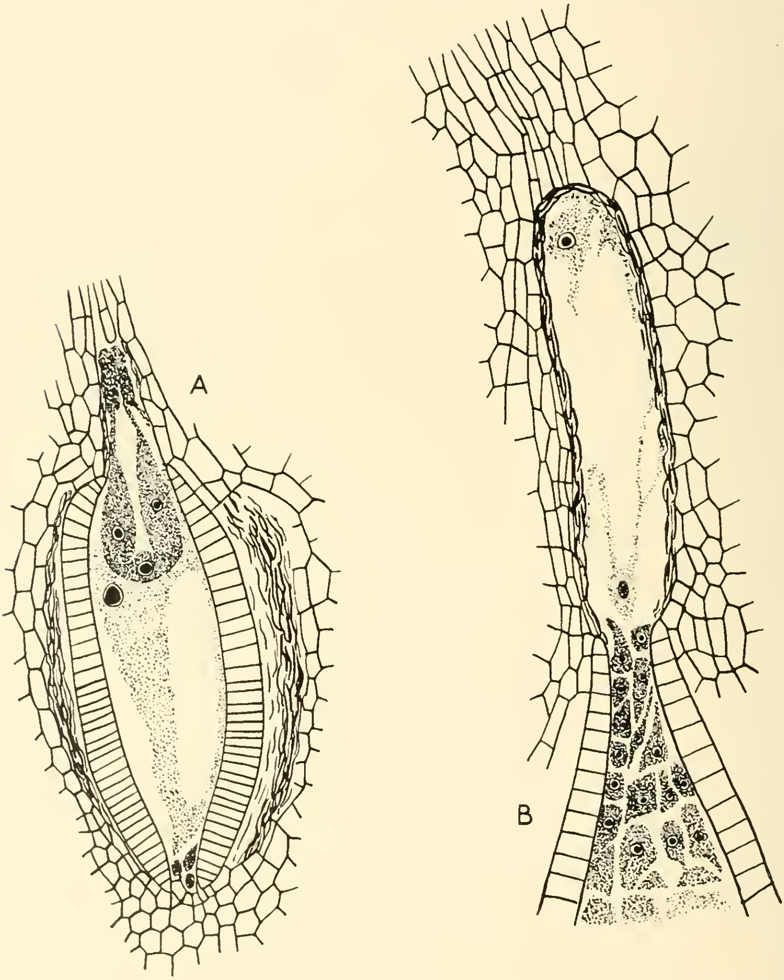

FIG. 1305.—*Calendula lusitanica.* A, Mature embryo sac with projecting synergidae. B, Later development of the micropylar haustorium with remains of the synergidae at the upper end. (*After Billings.*)

about these synergid haustoria or to distinguish them exactly from other cases in which the whole micropylar part of the embryo sac, including the oosphere, extends itself upwards into the micropyle, or from still other cases in which the haustorial cells are either endosperm cells or cells of the embryonal suspensor, which may develop in a similar manner and have very much the aspect of synergid cells, although naturally formed later and after the disappearance of the synergidae (Fig. 1306).

True synergid haustoria arise from the free apices of the embryo sacs in some Santalaceae (see below) and are often complexly branched.

The synergidae have generally a limited period of usefulness and break down after fertilization. They sometimes persist, however, the most remarkable case being that of *Trapella*, where they enlarge and remain active as haustoria even when the embryo is mature. (See Fig. 1315.)

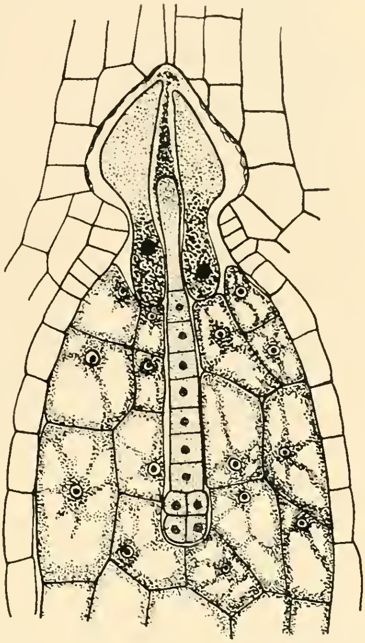

Fig. 1306.—*Lobelia cliffordiana*. Two uppermost endosperm cells projecting towards micropyle and simulating the appearance of the synergidae in *Calendula* (Fig. 1305 A). (*After Billings.*)

Micropylar outgrowths of the embryo sac itself, of a haustorial nature, are not uncommon. The classic case is that of *Torenia* (Scrophulariaceae), where the nucellus breaks down early and the upper part of the embryo sac protrudes through the micropyle and swells out like a balloon (Fig 1307 B). In the Utriculariaceae similar outgrowths are generally to be found. The ovules are unitegminous and anatropous. After the breakdown of the nucellus the embryo sac extends out of the wide micropyle and impinges upon an area of nutritive tissue at the base of the funicle, where it joins the placenta (Figs. 1307 and 1308). This tissue subsequently breaks down and after fertilization the haustorium is invaded by endospermal nuclei which enlarge and fuse, the haustorium wall separating it from the placenta breaks down and the cytoplasm and nuclei of both structures form a common mass, while the embryo is developing. A similar but smaller haustorium is also formed at the chalazal end, also in connection with a mass of nutritive cells (Fig. 1307 C).

In *Phaseolus* the upper portion of the embryo sac breaks through the nucellar tissue and occupies the micropyle, but does not extend beyond it. In *Galium lucidum* the whole sac appears to leave the ovule through the micropyle and " creeps " into the narrow space between the ovule and the ovary wall. This leads us to the extraordinary state of affairs in the Loranthaceae and Santalaceae in which no ovules are organized and the embryo

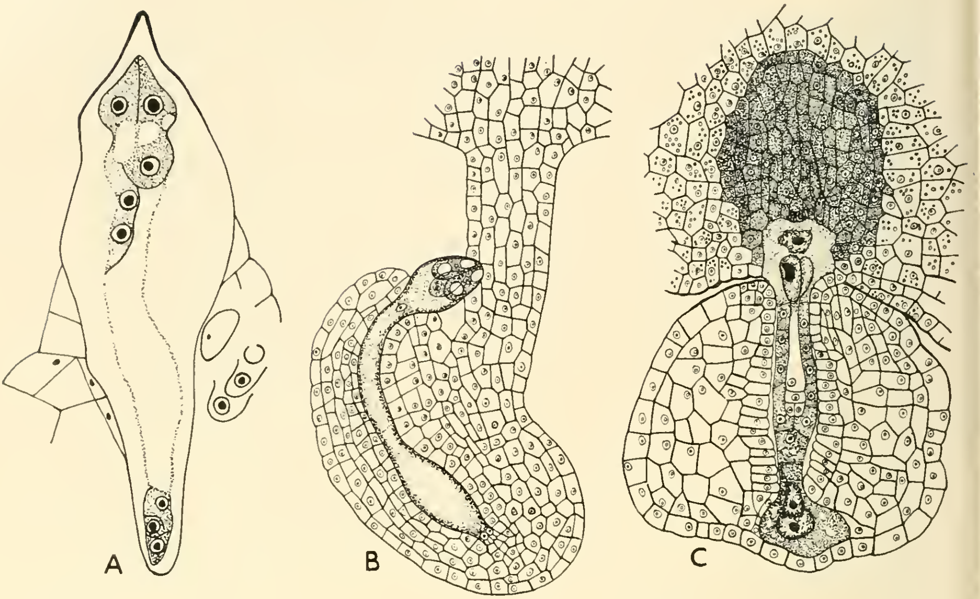

FIG. 1307.—Micropylar projection of embryo sacs. A, *Populus tremuloides.* B, *Torenia asiatica.* C, *Utricularia vulgaris* var. *americana.* Micropylar haustorium of embryo sac invading nutritive tissue of placenta. (B *after Engler.* C *after Wylie and Yocum.*)

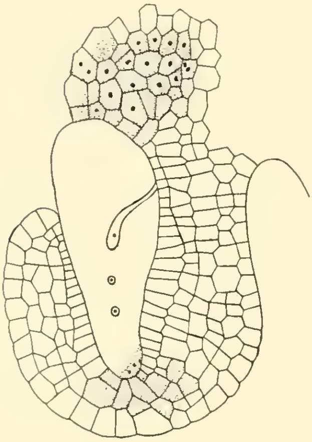

FIG. 1308.—*Utricularia stellaris.* Younger stage of the embryo sac development shown in Fig. 1307 C. (*After Goebel.*)

sacs are embedded either in the central placenta or in outgrowths from it which may be regarded as naked nucelli. The embryo sacs become immensely elongated, grow out into the ovarian cavity, follow up the surface of the placenta to its apex and from there, in some genera, continue up into the stylar canal, reaching even almost to the stigmas. They also extend somewhat in the chalazal direction, though this growth is limited by the resistance of the tissues (Fig. 1309).

As in all these cases the synergidae and the oosphere are carried forward by the growth of the embryo sac, fertilization must be promoted by an earlier meeting with the pollen tubes. One may recall, in this connection, the curious embryo sac tubes of *Welwitschia* (see Volume I, p. 776) which grow up through the massive nucellus to meet the descending pollen tubes.

The endospermal haustoria and the antipodal haustoria or caeca of the embryo sac are mostly post-fertilization structures and will be dealt with later in their proper sequence.

The Oosphere. The position of the oosphere is really lateral to the syner-

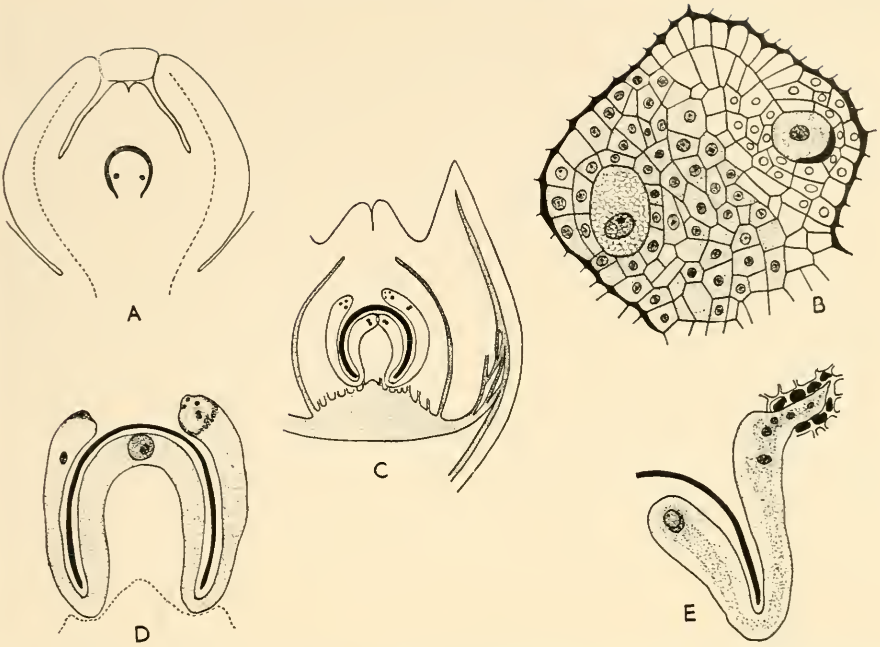

FIG. 1309.—*Dendrophthora gracile.* A, Longitudinal section of female flower with central "mamelon", containing two young embryo sacs. B, Mamelon enlarged showing two uninucleate embryo sacs. C, Flower in section showing mature embryo sacs growing upwards through carpellary tissue. Vascular tissue shaded and partly omitted. D, Fusion of lower ends of embryo sacs in the mamelon, forming one tube. E, Embryo sac showing three synergidae, oosphere and degenerating polar nuclei. (*After York.*)

gidae, but it descends below them as a rule, so that its lower end, containing the female generative nucleus, appears below the synergidae and gives the impression that the oosphere cell is attached to the base of the synergid cells. It has the shape of a rather stumpy pear, of which the obliquely flattened narrow end is attached to the embryo sac wall, lower than the attachments of the synergidae, and the inner surface forms common faces with both the latter cells.

The nature of the oosphere membrane is naturally of interest in connection with fertilization. Unfortunately these embryo sac cells have such thin membranes that it is not very easy to determine their nature. While cellulose and pectic substances have both been recognized in the synergid walls, there are various opinions about the wall of the oosphere, which, indeed, may not be of uniform nature. Cellulose has been recognized in its upper part, where it is in contact with the synergidae, but the lower, free, portion seems to have only a plasmatic membrane until after fertilization, when cellulose has been found to appear in it.

Apart from its nucleus, the possible presence of plastids or plastid rudiments in its cytoplasm is a matter of interest in the oosphere, which is obviously a focal point with regard to the permanence of plastids and their inheritance, which is sometimes matroclinous. Yet direct observations are very scarce, though one or two positive demonstrations have been claimed. Indirectly, the presence of starch grains both in the oosphere and in the cells of the young embryo may be accepted as evidence of the presence of starch-forming plastids, while in *Podophyllum* such plastids have been seen. Chondriosomes and chondriosome-like bodies have also been seen, but the usual cytological techniques applied to embryo sac study are not adapted to show cytoplasmic inclusions satisfactorily and further observations are required.

The oosphere nucleus at first is not markedly different from the synergid nuclei, or at most it may be distinguished in being somewhat larger. It has a larger nucleolus which it retains, and as the time of fertilization approaches, it begins to increase in volume. Nevertheless there is apparently always some differentiation of the oosphere nucleus from its neighbours. In the species of *Tulipa* investigated by Guignard there is no cell formation in the embryo sac but only eight free nuclei, of which two are smaller, placed at the micropylar end, and are apparently synergidae. Among the five remaining nuclei, however, the oosphere nucleus is always distinguishable from the others. No case of complete nuclear indifference is known.

The maturation of the oosphere nucleus is accompanied by a marked reduction in its stainability (Fig. 1310). This is most observable if the Feulgen stain for desoxyribose-nucleic acid is used. The chromatin first assumes a prophase-like appearance, then there is a progressive discharge of nucleic acid from the chromosomes, which take on a chromomeric structure. The chromomeres eventually all disappear except for particles which apparently correspond to chromocentres, although they are much smaller than usual. Finally these also may disappear with the exception of

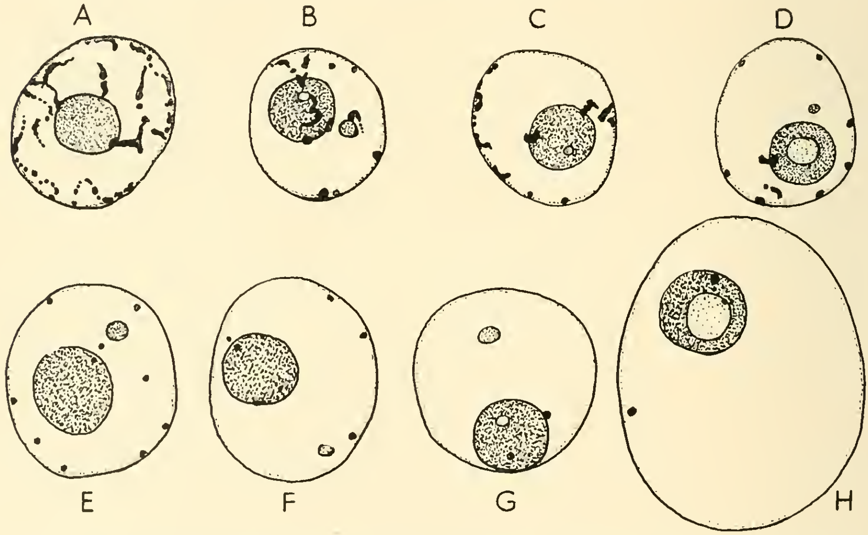

Fig. 1310.—*Impatiens glanduligera* (*I. roylei*). Maturation of the oosphere. Feulgen stain. Reduction of the chromatin threads to chromomeres and finally to two chromomeres at maturity (G). H, Mature nucleus unusually swollen. (*After Steffen.*)

one or two and the nucleus has then lost nearly all its chromatinicity. This condition persists until nuclear fusion occurs. There is no evidence of diffusion of the nucleic acid and what becomes of it is not known.

The Polar Nuclei. The fourth nucleus at each end of the embryo sac migrates towards the centre of the sac and together they form a contiguous pair. One of the pair may sometimes be larger than the other, but the difference does not seem to be significant, for in the great majority of cases they are indistinguishable. These nuclei unite, either before, during or after the entry of the pollen tube into the sac, and the product of their union is called, variously, the secondary embryo sac nucleus, the central nucleus or the primary endosperm nucleus, the last being perhaps the best description, since this nucleus and the cytoplasmic mass around it, which is the general cytoplasm of the embryo sac, may be regarded as the primordium of the endosperm.

This nuclear union is often delayed or suppressed, the latter in diploid, apomictic embryo sacs or in those cases where endosperm formation is itself suppressed. In the great majority of Angiosperms fusion of the polar nuclei takes place before fertilization (Fig. 1311).

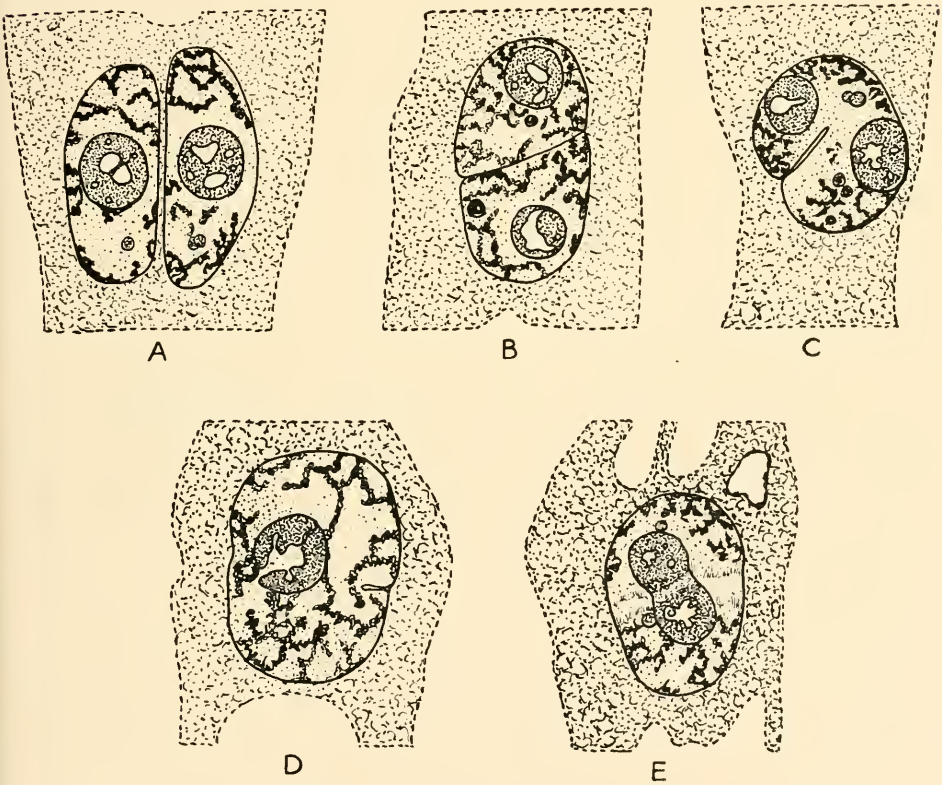

FIG. 1311.—*Impatiens glanduligera* (*I. roylei*). Successive stages in the fusion of the two polar nuclei. (*After Steffen.*)

Obviously what has just been said applies only to the normal condition where a pair of polar nuclei are formed, though this is true of the vast majority of cases. In four-nucleate sacs of the *Oenothera* type there is only one polar nucleus, which behaves as if it were the primary endosperm nucleus. In sixteen-nucleate sacs and even in some rare instances of eight-nucleate sacs (*Plumbago*) the number of nuclei combining to form the primary endosperm nucleus may be from three to fourteen, with a correspondingly high degree of polyploidy in the endosperm nucleus. In *Fritillaria* and other genera of its type (*e.g.*, *Lilium*) the lower polar nucleus, like the antipodals, is triploid and the primary endosperm nucleus before fertilization is thus tetraploid. Among the Balanophoraceae there are some types where the upper polar nucleus functions alone as the primary endosperm nucleus, while the lower polar nucleus combines with the three antipodals to form an evanescent structure.

If the two polar nuclei meet in the centre of the sac, then they subsequently move, or their fusion product moves, up to a position close beneath the oosphere, if not in actual contact with it. Beneath them there develops a single very large vacuole. When they remain in a central position, or if, as occasionally happens, they move downwards to the antipodal end, there is a thick cytoplasmic strand linking them to the oosphere. The antipodal position is quite uncommon and is always associated with the formation of cellular endosperm, where the first division wall traverses the embryo sac at its lower end.

The cytoplasm of the big cell, the endosperm primordium, frequently contains starch in notable amounts. This food reserve may have a double value, either in ensuring the continued life of the embryo sac under conditions where there is considerable delay in fertilization, from whatever natural cause this may arise, or alternatively in enabling the rapid development of the endosperm after fertilization. The starch reserve is used up in one way or the other and disappears after fertilization. It is not continuous with the reserves which appear in the endosperm cells at a later stage.

The Antipodals. Normally there are three antipodal cells, but as will have been seen from the descriptions already given of the various types of embryo sac (p. 1406) there are many exceptions; indeed, this is the most variable part of the embryo sac. Great differences exist in the size, the number, the nuclear condition, the durability and the fate of the antipodals. In tetranucleate sacs of the *Oenothera* type they are altogether absent. This is also the case in Podostemaceae and in individual cases in other families, *e.g.*, *Alchemilla.* Many other plants show, however, so rapid a degeneration and disappearance of the antipodals that the mature embryo sac may have none, even though they have previously been formed. Examples of such evanescent antipodals, which are usually small and insignificant, may be found in the following families, among others: Salicaceae, Potamogetonaceae, Caryophyllaceae, Hypericaceae, Aceraceae, Verbenaceae, Campanulaceae, Juncaceae. The condition is thus widespread and not limited to any particular class of Angiosperms.

Three antipodals is by far the most general number, although they may multiply secondarily. They are normally separated by delicate cell walls, which, although at first plasmatic, later become cellulosic. There are nevertheless a good number of cases where cell wall formation does not occur and the antipodal nuclei remain naked (Fig. 1312). This has been observed in particular species, as a more or less isolated phenomenon, in Cruciferae, Melastomaceae, Polygalaceae, Liliaceae and Orchidaceae. It is generally associated with rapid degeneration of the antipodals.

A reduction in number below three is usually associated with embryo sacs which are much narrowed at the chalazal end and hence may be interpreted as due to restricted development. Individual cases have been noted in Plumbaginaceae, Scrophulariaceae and especially among the Compositae, *e.g.*, *Helianthus*, *Bidens*, *Arnica*.

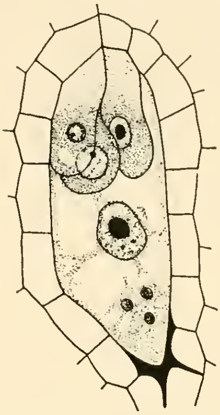

FIG. 1312.—*Thismia americana.* Embryo sac with free antipodal nuclei. (*After Pfeiffer.*)

Multicellular antipodal complexes are found in families scattered through the whole of the system, *e.g.*, Ranunculaceae (Fig. 1313 B), Papaveraceae, Umbelliferae, Gentianaceae, Compositae, Gramineae. In almost every case the condition is associated with exceptional development of the antipodals, either in respect of size, duration or unusually large nuclei. So far as embryo sacs of the normal type are concerned, it has been proved in many instances that the multiplication of the antipodals is a secondary procedure and that it starts from the normal three. This makes it unlikely that a multicellular antipodal complex is a primitive feature of the Angiosperms.

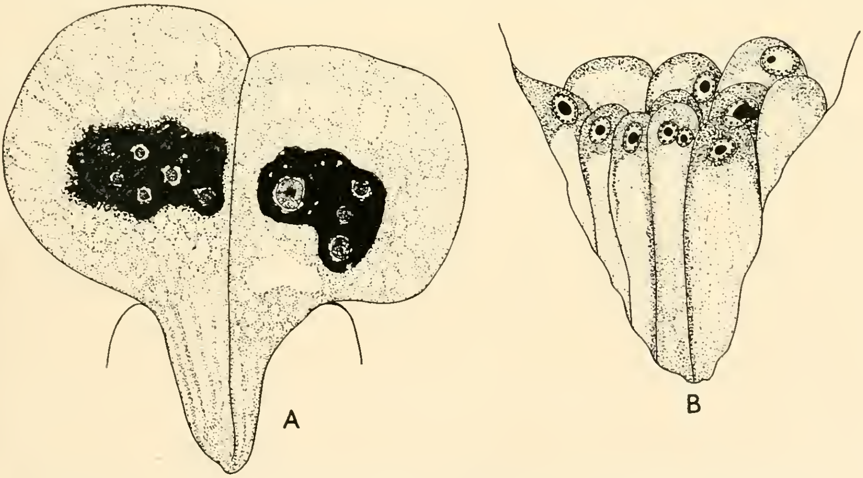

FIG. 1313. Unusual antipodal cells. A, *Clematis* sp. Two greatly enlarged antipodals with chalazal extensions showing filiform apparatus like synergidae. B, *Trautvetteria palmata.* Formation of a multicellular antipodal tissue. (*After Huss.*)

Both uninucleate and multinucleate cells may go to form the antipodal complex, sometimes both types in the same sac, and the cells may either form a compact chalazal tissue, as in some Gramineae and Gentianaceae, or simply an irregular mass, as in *Sparganium*. This genus shows multicellular development probably at its maximum, as more than 150 antipodal cells have been seen in one embryo sac. Multicellular antipodals are often associated with antipodal haustoria, as mentioned below.

Exceptional enlargement of the antipodal cells, without increase in number beyond three, has been observed in several genera of Iridaceae (*Crocus*, *Iris*, *Gladiolus*) and in a few other related Monocotyledons, *e.g.*, *Narcissus*, *Ornithogalum*, and *Commelina*.

In some of these and other cases the enlargement is downward and may be associated with invasion of the chalaza. In the Ranunculaceae, however, the enlargement takes place upwards, into the embryo sac itself, which the antipodal cells may largely occupy (Fig. 1313 A). Enlargement begins before fertilization but is often much greater afterwards and the big cells may persist, even into the ripe seed. *Hepatica* differs from other genera of the family in having a large group of antipodals, sometimes twenty-five cells, which enlarge greatly after fertilization and become multinucleate, as do also the three in *Caltha* and *Aquilegia*. There is evidence here of high metabolic activity on the part of the antipodals, which is probably connected with the nutrition of the embryo.

Multiplication of nuclei within antipodal cells has frequently been observed and also irregular fusions of nuclei in multinucleate cells. Nuclear division is generally, probably always, mitotic. Observations of amitosis are doubtful and are likely to be due to lobings and distortions of the nucleus, which is often large and irregular in shape, another feature associated with high metabolic activity, as in many secretory tissues.

The arrangement of the three antipodal cells is very variable, but that which simulates the micropylar group is the commonest, that is to say, two cells occupying the base of the sac with one above them. The reverse of this arrangement, likewise linear groupings, both longitudinal and transverse, also occur.

We may summarize the variations of the antipodal apparatus as follows:

1. Antipodals of free nuclei or separate cells, usually evanescent. (Some Orchidaceae, etc. See above.)
2. Antipodals of three evanescent cells which may disappear before fertilization. (Salicaceae, etc. See above.)
3. Antipodals of three relatively persistent cells, not remarkable for size or activity. (Many Metachlamydeae.)
4. Antipodals of three persistent cells which become markedly enlarged and active, especially after fertilization; sometimes multinucleate and sometimes persisting into the seed. (Many Ranunculaceae.)
5. Antipodals of an indefinite number of cells, forming a persistent complex, which grows and increases after fertilization and sometimes persists into the seed. (Compositae, Gramineae, etc.)

The question of the function of the antipodals is bound up with the more general question of the nutrition of the embryo sac. It will be remembered that the surface of the nucellus and the inner surface of the integuments are cuticularized, so that direct lateral passage of substances into the embryo sac is very restricted or non-existent. This alone seems to us sufficient reason for rejecting the name of " tapetum " as applied to the prominent mantle-layer or endothelium developed by the inner integument in most Metachlamydeae (see p. 1383). It is true that the growing embryo sac frequently destroys and perhaps absorbs the tissue of the nucellus and that it even encroaches on the inner integument in the same way. Nevertheless it is clear that the main supplies of water and food materials must come from the chalaza and enter the sac at the antipodal end.

In the chalaza, and often near the base of the embryo sac, is the end of the funicular vascular bundle. Between it and the embryo sac there are frequently formed specialized tissues, sometimes lignified and tracheidal, sometimes thin-walled and either starch-containing or mucilaginous, sometimes even broken down into mucilage-filled cavities. In Podostemaceae a very large lysigenous cavity is formed containing many free nuclei, which pushes the nucellus up above the inner micropyle, and is called the pseudo-embryo sac. In the chalaza also may be found the thick-walled mass of cells, called by Van Tieghem the hypostase (see p. 1392), which he considered to be a barrier to the growth of the embryo sac in this direction, but which is much more likely to be concerned with the passage of fluid both towards the growing embryo sac and also away from it during the ripening of the seed.

With these facts in mind it is not surprising to find that the antipodals often become aggressive and invade the chalaza as haustoria, which is quite in line with their supposed nutritive function. Similar aggressive outgrowths, both lateral and basal, may be formed by the embryo sac itself and it is noteworthy that these embryo sac haustoria are generally associated with a weakly developed antipodal apparatus. We are here dealing with haustoria formed before fertilization and we shall consider haustoria formed by the endosperm and the suspensor cells later (see pp. 1458 and 1471).

There is a clear distinction between these various types of haustoria but both antipodal and endospermal haustoria may be independently formed by the same sac, as in some Amentiferae. Some of the best developed antipodal haustoria are found among the Rubiaceae and the Compositae. Either the lowermost antipodal cell or sometimes all three may grow out into the chalaza, forming tubular or swollen expansions (caeca), while in the Compositae, where there may be numerous antipodals, they all take part in forming a long salient into the chalaza, (*e.g.*, *Senecio*). In *Aster novae-angliae* there is a large, multinucleate caecum (Fig. 1314) apparently formed from the lowermost antipodals, but it has been suggested that this caecum is really formed by the lower megaspores of the tetrad, which have persisted and taken on the appearance of antipodal cells. This recalls the

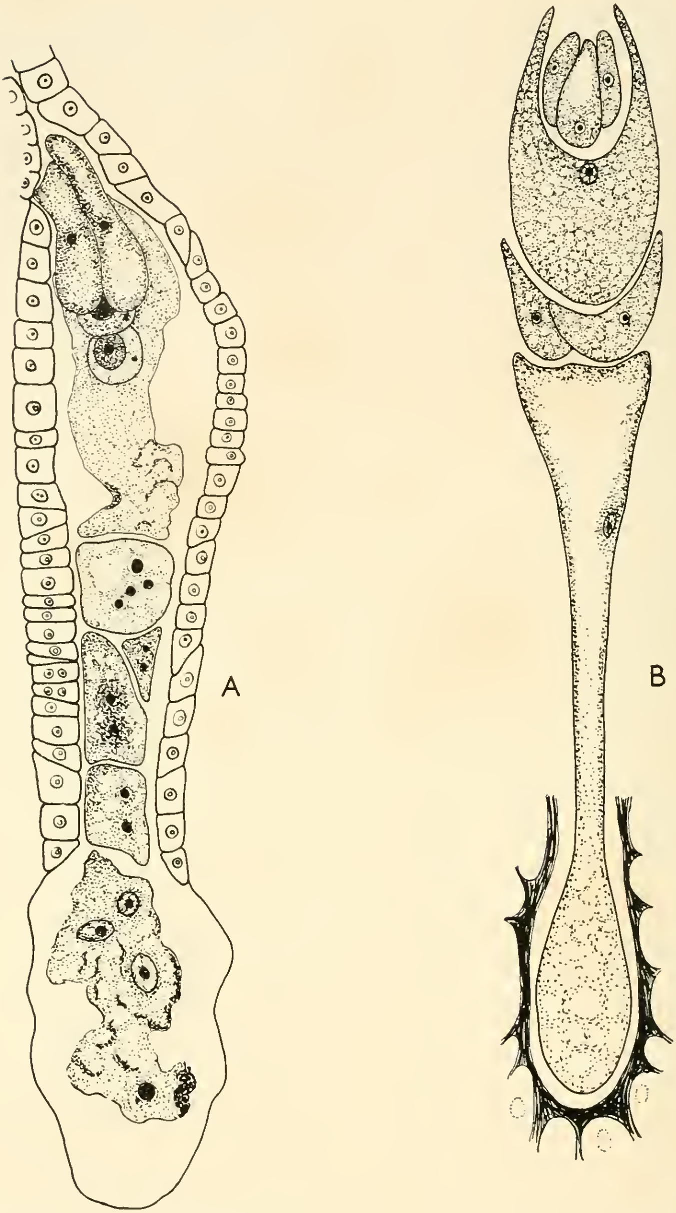

FIG. 1314.—Antipodal haustoria. A, *Aster novae-angliae*. Five multinucleate antipodals of which the lowest forms a haustorium in the chalazal tissue. (*After Chamberlain.*) B, *Sherardia arvensis*. Unicellular haustorium. (*After Lloyd.*)

case of *Trapella sinensis*, described by Oliver, where the lowest megaspore divides longitudinally and forms a long haustorium below the embryo sac (Fig. 1315).

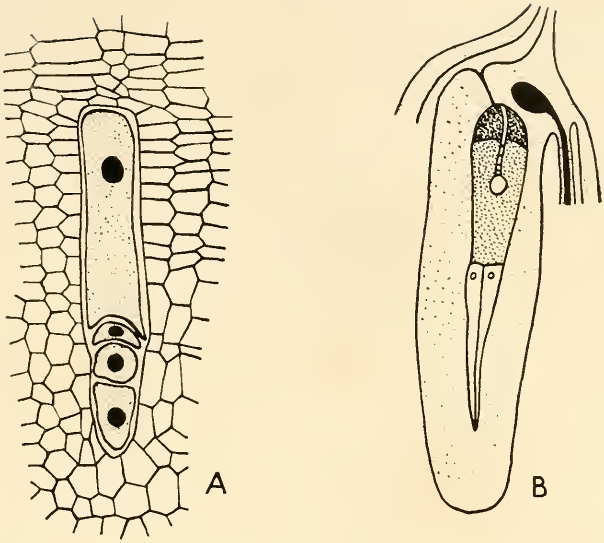

FIG. 1315.—*Trapella sinensis.* A, Young embryo sac with three undeveloped megaspores below. B, Later stage with young embryo in the sac. The lowest megaspore divided and forming a chalazal haustorium. The persistent synergidae shown above the embryo sac. (*After Oliver.*)

These latter cases are perhaps better classed with the " basal apparatus ", which Schürhoff described as being formed within the embryo sac, either by the concentration of a mass of cytoplasm and endosperm nuclei at the antipodal end or by the development of an aggressive basal cell, in endosperms of the Helobial type (see p.1453), which may divide or become multinucleate and sometimes forms a haustorium into the chalaza.

That all these types of structure are of similar physiological importance, which can hardly be other than nutritive, is shown by their mutual exclusion or vicarism. Thus in Ranunculaceae, etc, where the antipodals are markedly developed, there is no endospermal basal apparatus. Where the endospermal basal apparatus is most striking (Juncaceae, Helobiae, etc.), the antipodals are small and evanescent.

Haustorial outgrowths of the embryo sac itself, in the form of caeca or diverticula, are in a different category from those produced by the antipodal cells, for they may be formed at various parts of the embryo sac and they may, or may not, involve the antipodals, they may indeed be formed where no antipodals are present. A simple diverticulum is formed laterally from the embryo sac of *Agrostemma githago* and other members of the Caryophyllaceae. It may become nearly as large as the parent sac and penetrates the fleshy mass of tissue which is partly funicle and partly integument. The antipodals are evanescent and are not involved, but one of the two primary endosperm nuclei moves into the outgrowth, which persists as a remnant into the ripe seed, although containing very little endosperm. Similar lateral diverticula (Fig. 1316) are also characteristic of Boraginaceae and some other families.

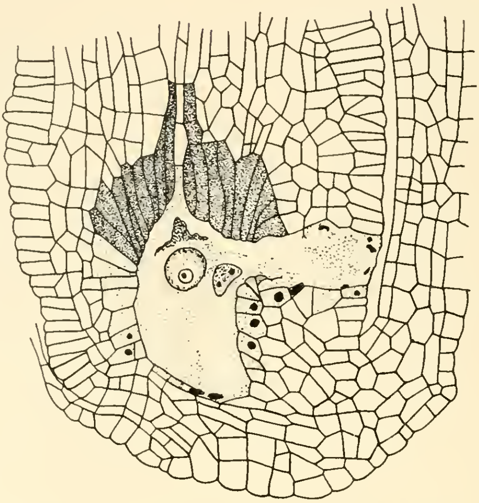

FIG. 1316.—*Fouquiera bourragei.* Mature five-nucleate embryo sac with lateral caecum. Epistase stippled, with median channel leading towards micropyle. (*After Johansen.*)

In *Stylidium* it is the micropylar end of the sac which forms a diverticulum. There is a prominent endothelium around the sac, and the latter spreads out over the upper end of this sheathing tissue and invades the integument on all sides, presenting the appearance of a pileus of which the rest of the embryo sac is the stipe.

A general downward extension of the embryo sac at the antipodal end occurs in a number of genera. In *Casuarina*, for example, it may begin to form as early as the binucleate stage of the embryo sac, and it penetrates the chalaza. Later, the primary endosperm nucleus and sometimes the antipodals may pass into it. A special peculiarity in this genus is that chalazal haustoria are formed not only by the embryo sac but also by the numerous sterile sporogenous cells, so that a remarkable complex of tubes is created.

In *Tropaeolum majus*, the sac grows downwards into the massive tissue of the chalaza, which it largely absorbs, forming a big caecum in which the embryo develops (see p. 1473 for the suspensor haustoria of *Tropaeolum*). The most exceptional chalazal outgrowths of the embryo sac, apart from those formed by the endosperm, are to be found in Loranthaceae and Santalaceae. We have already referred to the micropylar outgrowths of the embryo sac in these families. Their chalazal development is sometimes (*e.g.*, *Thesium*) almost as remarkable. The extreme case is that of the related genus *Myzodendron* (now placed in a separate family) where the chalazal growth of the embryo sac penetrates the placenta and extends down into the floral receptacle, where it ends in a swelling among the diverging vascular bundles of the floral axis (Fig. 1317). It is divided into uninucleate cells by transverse walls, though whether these cells should be reckoned part of the endosperm is not clear.

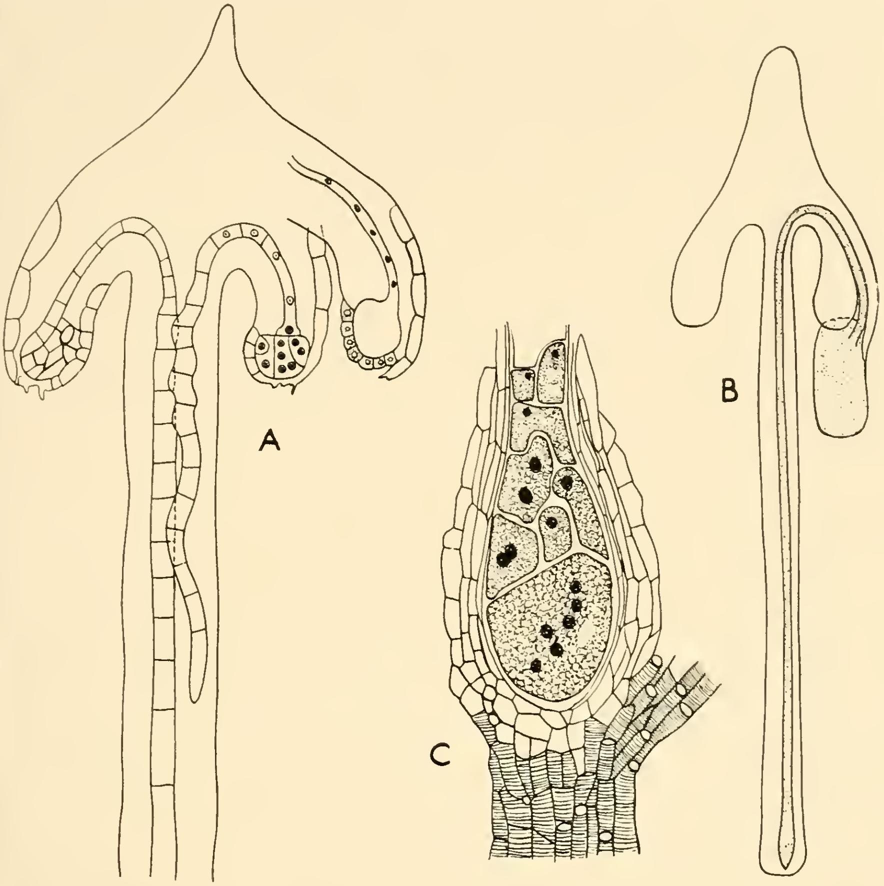

Fig. 1317.—*Myzodendron punctulatum.* A, Placenta of young fruit, flattened. Chalazal tubes from the embryo sacs penetrating the axis downwards. That on the right is still non-septate. B, Older stage showing the complete tube. C, Enlarged base of a tube in contact with the axial vascular tissue. (*After Johnson.*)

It is not always easy to draw a line between outgrowths of the embryo sac and the general swelling of the sac itself, which may encroach on the surrounding tissues, as happens in Gentianaceae, especially if the swelling is one-sided. The common factor in all these phenomena is that they involve aggressive invasion of other tissues and the absorption of their materials, a process called by Goebel " autoparasitism ". Though not confined to reproductive structures, it is nowhere else so conspicuous. Its extreme is reached in the ovules of *Symplocarpus foetidus* (Araceae), where the endosperm resorbs all the nucellus and integuments and is itself in turn resorbed by the embryo, which thus comes to lie naked within the pericarp of the fruit.

Interpretation of the Embryo Sac

The morphological interpretation of the embryo sac and its contained structures in the light of comparison with other groups of seed plants, has proved difficult. There are no really close comparisons possible with existing Gymnosperms, still less with the remoter Pteridosperms. At the same time the fundamental similarity which runs through all groups of the Angiosperms, combined with abundant variation in detail, reasonably suggests a considerable antiquity and is probably traceable to the still obscure origin and isolation of the Angiosperms as a class, in the late Mesozoic period.

Speculation has not unnaturally been stimulated by the absence of precise information and various schools of thought on the subject have found expression and supporters. The simplest view is the most non-committal, namely the acceptance of a general homology with the female gametophyte of the Gymnosperms, while rejecting any detailed comparison of components. This may be said to be Chamberlain's opinion, based on the belief that the Angiospermic embryo sac has become so specialized that its detailed homologies are obliterated.

A second view is that all the nuclei of the embryo sac are potentially, and were originally, gametes, and that their differentiation is secondary and peculiar to the Angiosperms, so that, again, no comparisons are possible. The idea that all the nuclei are potentially fertilizable invites an analogy, though scarcely a homology, with the condition in the young embryo sacs of *Welwitschia* and *Gnetum* and thus suggests a linkage between the Gnetales and the early Angiosperms. According to one interpretation (Lotsy), the micropylar cells are all gametic and equivalent to reduced archegonia, as in *Gnetum*, and the antipodals are comparable to the degenerating gametic nuclei in the same genus. Another view (Karsten) considers the antipodals as a remnant of the cellular prothallus at the base of the *Gnetum* embryo sac, and the polar nuclei as equivalent to free prothallus nuclei.

The Gnetalean theory in one form or another has found many supporters, partly no doubt because it harmonizes with theories of the Gnetalean origin of the Angiosperms, based on floral morphology and some vegetative similarities. That the Gnetales, especially *Gnetum*, do show close approaches to the Angiosperms, is undeniable, though the similarities may be due, as many think, to parallelism in evolution rather than to genetic connection. The embryo sac comparisons do not greatly strengthen the latter view. They draw into consideration, as intermediate stages, such sixteen-nucleate sacs as those of *Peperomia* and *Euphorbia*. It is attractive to suppose that these multinucleate sacs might be primitive and the eight-nucleate state a later reduction, but the idea is open to the very strong objection that these sacs are tetrasporic in origin, which it is wellnigh impossible to accept as a primitive condition.

The theory propounded by Strasburger in 1879 treated the antipodals, the polar nuclei and the synergidae as prothallial cells, remnants of the female prothallus of Gymnosperms. The oosphere alone represented the vestige of an archegonium. The impetus towards the formation of prothallus tissue was supposed to become exhausted, and only renewed after the stimulus of fertilization. In this view the formation of endosperm was looked upon as a continuation of the interrupted prothallus formation. This theory was put forward before the polyploidy of the endosperm cells was understood and it is certainly difficult to regard a tissue which is normally triploid, and may sometimes be highly polyploid, as being prothallial or in any way an extension of the haploid cells of the embryo sac. Even the antipodal cells in the *Fritillaria* type of embryo sac are triploid, which is equally against their being prothallus cells. This theory does not explain why the antipodal cells should be, in so many cases, arranged like a duplicate of the micropylar cell group, a point of some importance.

Schürhoff put forward a fourth theory in 1919. He considered that there is one archegonium, reduced to two cells, the oosphere and one of the synergidae, the synergid representing the ventral canal cell of the archegonium. The second synergid and the antipodals represent prothallial cells and the two polar nuclei are free prothallial nuclei. This initial prothallus formation is then completed by the growth of the endosperm, in the same way that Strasburger supposed. This hypothesis encounters the formidable difficulty that the synergidae are, at least in the vast majority of plants, sister nuclei and Schürhoff has not been able to produce any instance in which the oosphere and the synergid are sister nuclei, as they should be according to his theory. He rejects a derivation of the Angiosperms from Gymnosperms and considers that both have originated separately from archegoniate ancestors, which implies an independent evolution of the seed habit in each line.

In 1928 Schürhoff tried to meet the objections to his first theory by proposing a second, namely that one synergid is the ventral canal cell of the oosphere and the other is the ventral canal cell of the upper polar nucleus, the latter being a potential oosphere. There are thus two archegonia, of two cells apiece, and four chalazal prothallial cells. This again involves denying that the synergidae are sister cells, and the author argues that neither from the nuclear divisions nor from the cell wall formation can any proof be derived that they are. Equally, in this case, no proof can be forthcoming for his own view and we are left to balance probabilities.

The last theory we shall consider is that put forward by Porsch in 1907, which was anticipated in part by Marshall Ward, as long ago as 1880. He postulated that the embryo sac was a prothallus reduced to two fused archegonia, which have retained the essentials of archegonial structure, although the vegetative prothallus has disappeared. Analogies for this can be found in the male gametophytes of some Gymnosperms and even among Pteridophyta. Each polar group of four nuclei represents one archegonium, consisting of two neck cells, namely the synergidae, one oosphere, and one ventral canal cell, which has become the free polar nucleus. Thus the similar organization of the antipodals and the egg-apparatus is explained by their homology, although the antipodal archegonium is normally sterile.

This view is strengthened by various anomalous occurrences. For example, cases of reversed polarity are known, *e.g.*, in *Woodfordia* (Lythraceae) and *Ulmus americana* where the antipodals are organized as an egg-apparatus and the micropylar group have the appearance of antipodals. In *Balanophora indica* the embryo sac has a horseshoe form, with the oosphere group at one end and the antipodals at the other, in close proximity. According to Van Tieghem either group may be fertilized by the pollen tube. Fertilization of an antipodal cell by a male nucleus has also been seen in *Nigella arvensis* but there is no proof that such anomalous fertilization can produce a mature embryo. It is said that *Crinum* may have an egg-apparatus at both ends of the sac, and there are several observations of antipodal cells simulating synergids, even to the possession of a filiform apparatus. (See Fig. 1313A.)

The comparison of the egg-apparatus of an Angiosperm with a simple type of gymnospermic archegonium, like that of *Torreya*, is shown in Porsch's diagram here reproduced (Fig. 1318). The interpretation of the synergidae as neck cells, which was earlier supported by Guignard and by Treub, is argued by Porsch on the ground that in Gymnosperms (except in Gnetales) the archegonium is never reduced beyond four cells: two neck cells, the ventral cell or oosphere and the ventral canal cell, though the existence of the latter in *Torreya taxifolia* is doubtful, unless it is rapidly expelled from the oosphere. At least two neck cells are invariably formed. The alternatives to Porsch's view are that the synergidae are prothallial or that they are potential oospheres. The former suggestion we have already dealt with. Instances of the fertilization of synergid cells would be expected, if the latter suggestion were correct, and some have been recorded, but on the basis of embryos having been seen developing from these cells. These are almost certainly cases of the widespread phenomenon of polyembryony. Diploid, unreduced embryo sacs frequently occur, in which any, or several, of the nuclei may divide and produce embryos. Even in haploid sacs, haploid embryos may arise, but in none of these cases is there any fertilization involved in their formation. In fact, in view of the well-established cases in which it is known that the pollen tube enters and discharges its generative nuclei into and through a synergid, followed by normal fertilization of oosphere and endosperm nucleus, it is reasonable to conclude that synergid nuclei are not equivalent to egg-nuclei and are not fertilizable.

When we survey the various theories of the embryo sac outlined above, it is difficult to halt between the first and the last, which is open to fewer objections than the others. One item of evidence, not hitherto mentioned, may be cited from *Torreya*. Anomalous embryo sacs have been noticed in which two archegonia occur and, instead of lying side by side as in most Gymnosperms, they are situated at opposite ends of the sac, in just the position that Porsch believes them to be placed in the Angiosperms.

Berridge has criticized the Porsch theory on the ground of the improbability of the ventral canal nucleus exhibiting the activity and the sexual character shown by the upper polar nucleus in Angiosperms. She has put

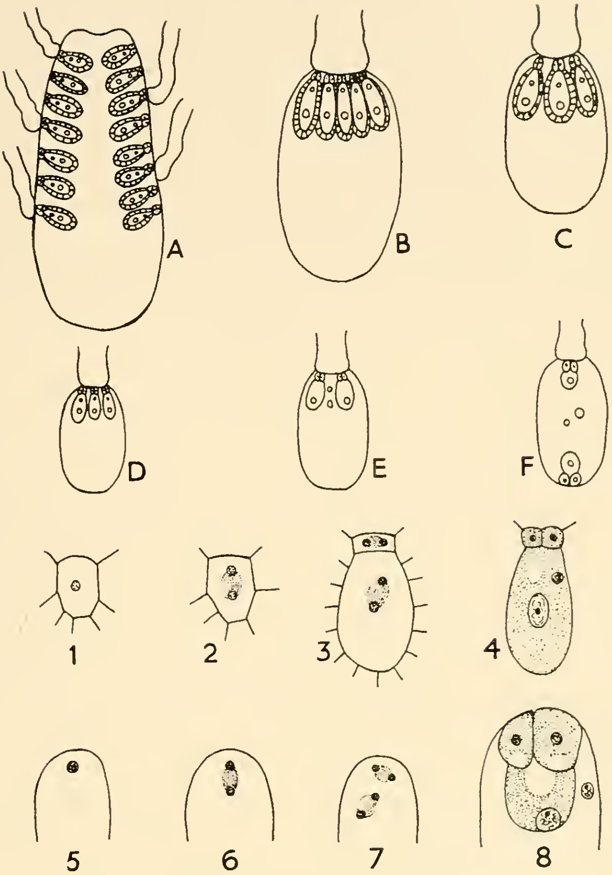

FIG. 1318.—A–F, Schematic derivation of the angiospermic embryo sac from the female prothallus of the Gymnosperms. A, *Sequoia* type. B, Cupressacean type. C, *Ephedra* type. D, Hypothetical type without archegonial jacket layers. E, Type reduced to two archegonia with two neck cells. Ventral canal nuclei separated from archegonia. F, Angiosperm type, with two archegonia at opposite ends of the sac. 1–4, Development of a gymnospermic archegonium. 5–8, Development of the angiospermic egg-apparatus, for comparison. (*After Porsch.*)

forward another theory, but as it chiefly concerns the origin of the endosperm, we will postpone its consideration until after we have dealt with fertilization. Against Berridge's objection may be urged the known cases in Gymnosperms in which the ventral canal nucleus is actually fertilized by the second male nucleus, *e.g.*, in *Abies*, *Thuja* and in two species of *Ephedra*. In some other genera the ventral canal cell divides and gives rise to a small mass of tissue, probably as a consequence of such fertilization.

Porsch's theory has also been attacked by Battaglia on the ground that variability in the formation and behaviour of the cells of the egg-apparatus precludes comparison with an archegonium. Further, he argues that the behaviour of the polar nuclei is inconsistent with anything known of the ventral canal cells in Gymnosperms. He denies the existence of any trace of an archegonium in the angiospermic embryo sac and suggests comparison with the embryo sac of *Gnetum*, in which also the archegonia have disappeared. This is not to suppose a derivation from the Gnetales but that there has been a parallel development in the evolution of the Angiosperms.

According to this view, gametogenesis is limited to the differentiation of one nucleus as the oosphere. The stages of development between spore formation and gametogenesis, involving, in the normal case, three nuclear divisions and culminating in wall formation after the last division, are regarded as somatic development and include vacuolation of the sac and polarization of its nuclei. Disporic development (*Scilla*) allows for the omission of one somatic division, while tetrasporic development (*Adoxa*) allows for the omission of two somatic divisions, to give finally a normal eight-nucleate sac.

Before leaving the subject of the embryo sac, some reference should be made to the question of whether the term " megaspore " is properly applied in the description of its development. The evolution of the seed plants from heterosporous ancestors has been so widely and for so long assumed that the expression of a doubt may occasion some surprise. Thomson in 1927 was the first to voice his scepticism and it has recently been revived by Doyle. Both base their views on comparative measurements of the male and female spores in Gymnosperms, which show that in the majority of cases the so-called microspore is actually the larger of the two, whereas in heterosporous Pteridophyta like *Selaginella* or *Marsilea*, the megaspores are very much larger. Doyle therefore questions the propriety of using the term megaspore among seed plants and substitutes "gynospore", a non-committal name.

It must be pointed out that under the conditions obtaining in the ovule it is necessary for purposes of comparison to fix somewhat arbitrarily on a certain stage, namely the beginning of vacuolization, when the female spore is taken to be mature and starting on the development of the prothallus. This may be justified, but when we regard conditions in the Pteridophyta we see there that the megaspore grows to its full size first and develops a prothallus afterwards, without further increase of size. If therefore measurements are made in the Gymnosperms taking for comparison the stage at which the prothallus has been formed, which is more nearly equivalent to the mature spore in *Selaginella*, then there is an equally great advantage of size in favour of the female spore. It is very desirable that further investigations of the question should be made among the Angiosperms.

FERTILIZATION

We now arrive at the crux of the whole elaborate process of sexual reproduction, which is the meeting and fusing of a male gamete nucleus and a female gamete nucleus. Owing to the seclusion and protection of the female structures in Angiosperms, first within the carpel and secondly within the ovule, contact between the gamete nuclei can only be established by means of that extraordinary structure, the pollen tube, which provides both a channel of entry and a protection for the male gamete from external dangers. Even the few peculiar instances where pollen grains gain access to the ovary through an open stylar canal or the nucellar pollination of *Rheum australe* (see p. 1284) are no exception, since the nucellus or the micropyle remains to be traversed by a pollen tube, as in Gymnosperms.

We have previously traced the development of the microspore or pollen grain up to the point of its liberation from the anther and we have dealt in Chapter XXIV with the adventures of its transference to the stigma.

Germination of the Pollen Grain

When liberated from the anther the grain may contain either two cells or three, that is to say that the generative cell may have already divided or it may not. The difference is not accidental, for it is constant for species and indeed often for whole families. Schürhoff has suggested that the two-nucleate condition is more primitive than the three-nucleate and that the latter condition prevails in the more advanced families. There is not enough information available to establish this conclusion, which obviously is phylogenetically important. Some at least of the pollen grains reported as two-nucleate were immature and we know from experiment that the balance between the conditions may be upset by artificial nutrition and other factors which may induce both types of grain in the same plant. Moreover in some two-nucleate grains the generative cell is already in mitotic prophase when the grain is shed. A survey of the records shows a rather irregular distribution of the two conditions among the families, so that the known facts scarcely seem to bear the weight that Schürhoff has placed on them, though the question deserves further investigation.

The content of the pollen grain is a true gametophyte, as is evidenced by the finding of both parental types of pollen grain in the anthers of the F_1 generation of certain hybrids. In other words the building of the grain is internally controlled by the haploid genotype. What comparisons we may draw with the male gametophytes of other phyla is, however, an open question. Reduction has gone too far to allow of more than a guess that the gametophyte in the pollen grain may represent a single antheridium. Otherwise an agnostic attitude is advisable.

The longevity of pollen or the time during which it retains its ability to germinate is a matter of importance to the plant breeder. It depends not only on the plant but on the prevailing conditions, of which humidity is the most important. Only a few species survive long in air of relative humidity 60 to 90 per cent. (*Hippuris* is an example) and most are longer lived in air of 30 per cent. humidity or less; many survive longest when desiccated over a drying agent. Some pollen, like that of *Hippuris*, is insensitive to changes of humidity, but most species have a definite optimum. Wetting followed by drying is very lethal. We may take a period of 30 to 40 days as an average for the survival of pollen in air, but there are some striking exceptions.

The longest-lived pollen recorded is that of *Pinus sylvestris*, which can survive for 279 days over sulphuric acid, but only about 70 days in free air. Holman records a small germination of *Typha* pollen after 336 days (conditions not stated) but only 56 per cent. germinated after 158 days. Other long-lived pollens are those of *Viola odorata* (235 days dry, but only 35 days in air), *Primula elatior* (179 days dry, 56 in air), and *Prunus padus* (181 days dry, 15 in air). The shortest lived is that of *Secale cereale*, which does not survive more than 12 hours under any conditions. Most other Gramineae have short-lived pollen. Longevity seems to be hereditarily determined rather than ecologically. Most spring flowering plants have pollen which is relatively insensitive and is long lived, though this is not an ecologically important feature in their case.

Pollen germination occurs under a much wider range of conditions than those suitable for the continued growth of the pollen tube. Pollen is very sensitive to moisture, which it rapidly absorbs, with swelling of the grain, but in pure water germination has scarcely time to begin before the grains burst. *Tradescantia* and *Impatiens* pollens are exceptional in their very rapid germination in pure water without bursting. Indeed 10 per cent. sucrose is enough to inhibit the germination of *Tradescantia*.

The fact that artificial germination of pollen is best carried out in sugar solutions, often of surprisingly high concentration, up to 60 per cent. in some cases, has given rise to the belief that the sugars secreted by the stigma have a nutritional value in promoting the germination of pollen. In most cases this does not seem to be true. The nature of the sugar does not seem to be of so much importance as its concentration and the conclusion is that its principal role is the osmotic control of swelling. There are a few exceptions where special sugars may be needed for heterotrophic nutrition. For example, the pollen of *Mussaenda* requires traces of fructose and that of *Cerastium* and some other Caryophyllaceae requires 20 to 30 per cent. of lactose for experimental germination. Dilute acids generally promote germination, the pollen of Ericaceae being especially stimulated by dilute malic acid.

When the grain has germinated the pollen tube penetrates the stigma, usually between the cells, but where there is an open stylar canal most of the tubes pass down it, keeping contact with its walls. The action of penetration does not seem to be chemotropically conditioned, under ordinary circumstances, but is primarily hydrotropic aided by negative aerotropism.

The stigmatic surface is generally papillose and the pollen grains are held between the papillae and germinate there. Germination usually occurs with extraordinary rapidity, in a few minutes in most cases. Jost records that five minutes after pollination, pollen tubes had already penetrated the stigmatic branches in *Secale*. The cells of the stigma have the appearance of secretory cells, dense cytoplasm and large nuclei, but they seem to be very loosely joined and are easily separated by maceration, even in water. It is between them, not into them, that the pollen tube penetrates (Fig.

1319). Accounts of the penetration of the papilla cells are ill-founded, though the young tubes may cling to them and even wind round them. On the other hand some stigmas have a continuous covering of cuticle and this the tubes perforate probably enzymatically, leaving round holes where they have gone through. Many stigmas are covered by a profuse secretion containing mucilage and oils, in which the pollen grains are bathed. This does not seem to be chemically important but rather to be a protection against desiccation.

FIG. 1319.—*Eschscholtzia californica.* Germination of pollen grains on the stigma, showing penetration of the pollen tubes into the stigmatic tissue.

Under most circumstances the conditions of germination on the stigma seem to be fairly uniform and pollen will readily germinate on the stigmas of plants which are systematically remote (*e.g.*, *Lathyrus* pollen on *Convallaria*). Recondite reactions can, however, be called out by hybrid pollination and intra-specific incompatibility or even by autogamy; reactions which are presumably in abeyance under usual conditions. These reactions resemble those of pathological immunity and they are of various degrees of intensity, from the death of pollen or stigma or both, to a mere slowing down of the rate of growth of the pollen tubes. These incompatibility reactions have great genetic importance, which we shall speak of in Volume III, but cannot go into further here.

An interesting example of such a reaction is seen in the following experiments. Pollen of the Peach variety " Elberta ", when germinated on artificial media, gives pollen tubes of two lengths. In 50 per cent. the mean length was $141 \cdot 75\mu$ and in 50 per cent. it was $2345 \cdot 58\mu$. The difference is factorial and is due to the presence of an inhibitor in the short-tube grains. The same thing is found in the Apple " Landsberger Renette ", but not in all trees. Crossings of this Apple were made with " Beauty of Boskoop " from trees with uniform pollen and from trees with heterogeneous pollen. The former gave successful fertilization, the latter were wholly sterile. This means that the 50 per cent. of grains giving long tubes were also inhibited on the stigma. They must also have contained an inhibitor, activated by interaction with the stigma, but inactive in culture.

In incompatible crosses the pollen tube growth is generally much slower than in fully compatible pollinations. Many tubes do not reach the ovary. The pollen may germinate normally and the effect becomes progressively evident thereafter. Pollen tubes become coiled and distorted. The inhibitor is extractable from the stigma and an extract inhibits pollen tube growth in cultures. There is a marked resemblance to an antigen-antibody reaction.

The Pollen Tube

The discovery of pollen tubes, or at least the recognition of what they are, is credited to Amici in 1823, in pollen of *Portulaca*. Certainly he was the first, in 1830, to trace the pollen tube of *Yucca gloriosa* from the stigma to the micropyle. The tube begins as a passive extension of the intine of the grain but it quickly acquires a terminal growth of its own. The tube is smooth-walled and cylindrical and the whole content of the pollen grain passes into it, including the nuclei, the vegetative nucleus, henceforth called the tube-nucleus, going first. The wall contains cellulose but the apex also contains pectins and seems to be differently constituted from the rest, judging by the ease with which it can be made to disgorge its contents in artificial culture and, of course, in the embryo sac. The final volume of a tube, in plants with long styles, may be many hundreds of times the volume of the original grain, but only a small portion of this is occupied by living matter. The protoplasm of the grain does not seem to increase noticeably in the tube and is all concentrated in the forward end. Behind it, at intervals, are formed callose plugs which cut off the older, empty part of the tube. When the ovule is reached there is, therefore, no longer any living connection with the pollen grain. The empty membrane does not last long and the older parts may have disappeared even before the end reaches the ovule. Such immense growth naturally requires nutrition. The tube generally contains starch grains, received from the grain, as well as plastid rudiments and other enclosures, but there seems little doubt that the tube takes up nutriment from the cells it contacts during growth in the style.

The rate of growth in pollen tubes is very variable. Rates varying from less than 1 mm. to 5 or 6 mm. per hour are recorded but these measurements were often in cultures and made without regard to temperature, which has a most marked effect. Thus in *Datura stramonium* at 11·1° C. the average rate of growth was 1·28 mm. per hour, while at the temperature optimum of 33·3° C., the rate was 5·86 mm. per hour, or four and a half times as great. In barley at 30–35° C., fertilization was accomplished in 20 mins. from the time of pollination, but at 5° C., 140 mins. was required. Grass pollen which has generally the shortest life also grows the fastest. Important and enormous variation also exists in the time elapsing between pollination and fertilization under natural conditions. Times of a few minutes are recorded for some Gramineae, while in Amentiferae, as in Coniferae, the time extends to months (*Betula*, one month; *Corylus*, four months; *Quercus velutina*, more than one year). The same is true of many Orchids, although in *Orchis* it is less (8–20 days). Periods between one and five days are fairly common. The time is not related to the length of the style; compare the times in Amentiferae, given above, with *Crocus*, 24 hours; *Iris*, 79 hours; and *Zea*, 25 hours, all plants with exceptionally long styles or stigmas.

The long delay between pollination and fertilization which is found in the most various families is a matter of some biological interest. In many cases it is due to the imperfect development of the ovule at the time of pollination. The pollen tube grows as far as the nucellus and there awaits the ripening of the ovule. In *Hamamelis* it gets only as far as the funicle and there it passes the winter, completing its work the following spring.

In the Orchidaceae not even the placentae are formed at the time of pollination, which apparently is a necessary stimulus for the completion of carpels and ovules.

Normally each pollen grain emits one pollen tube only, but multiple tubes arise in some pollen which is provided with numerous pori, especially in Malvaceae, Cucurbitaceae and Campanulaceae. The pollen nuclei enter one of the tubes formed and the others soon stop developing, but they may perhaps function temporarily as haustoria. This idea is supported by the not infrequent branching of the ends of pollen tubes to form haustoria in the ovule. Pollen tube haustoria are conspicuously shown in *Cucurbita pepo*. The nucellus in this plant has a long beak which fills the endostome and later becomes suberized. When the pollen tube meets this beak it enlarges into a broad vesicle from which spring a number of branches (Fig. 1320). One of these penetrates and partially destroys the nucellus and performs fertilization; the others then spread laterally into the integuments. The inner layer of the outer integument is made up of cells rich in starch and protoplasm and in this the pollen tubes ramify. Nourishment for the growing embryo and endosperm is thus conveyed through the vesicle and this continues until the seed is ripe. That there is a true haustorial function here rests on deduction and has not been proved. Similar bunches of branches on the nucellus occur in Malvaceae and Onagraceae, and over the embryo sac in *Betula*.

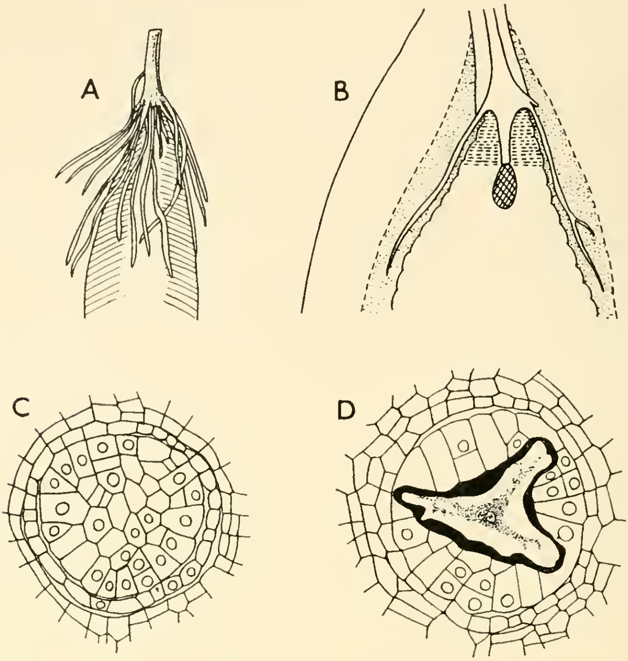

FIG. 1320.—A and B, *Cucurbita pepo*. Branching of the pollen tube at the nucellar apex, penetrating the inner integument. (*After Longo.*) C and D, *Cyclanthera explodens*. Transverse sections of the nucellar apex, before and after fertilization, showing pollen tube haustoria in the nucellus. (*After Kirkwood.*)

When the pollen tube has entered the stigma it may encounter the specialized conducting tissue which is found in many plants and assumes several forms (see p. 1233). Where there is a stylar canal, the conducting tissue may be represented only by its epidermal lining, which is rich in protoplasm and often papillose. There is thus an open canal and the pollen tubes grow on the surface of the conducting tissue. In other plants there may be a more massive conducting tissue, several cells thick, which may still leave an open canal, but which frequently fills the canal with a pectin jelly, derived from swollen cell membranes. The pollen tubes then grow through the jelly. Lastly there may be a solid style with an axial core of conducting tissue (Fig. 1321). There are also many solid styles which have no conducting tissue, notably those of the Grasses.

The conducting tissue is distinguishable by various features, singly or in combination, such as elongated cells, mucilaginous cell walls, richness in protoplasm, or the presence of sugars. We have seen previously that it is probably an upward extension of the placentae into the sterile stylar region of the carpel and it leads therefore downwards to the placentae. It is followed by the pollen tubes because it offers mechanically the path of least resistance and possibly also the best food supply. The tubes push their way between the cells, chiefly by mechanical pressure, though they may secrete a pectase which softens the middle lamellae. Only rarely do they penetrate into cells. Pollen tubes which follow a superficial course are called ectotropic and those which follow an intercellular course are called endotropic. The difference was at one time given some systematic importance, but it is too variable for this. The route followed is different in some closely allied genera and even (*e.g.*, *Cucurbita*) in species of the same genus. The particular direction followed seems to be physiologically determined and the differences argue in favour of a chemotactic influence on the direction of growth. What this may be is not definitely known but it has been found that most proteins are chemotactically positive for pollen tubes and only a few are negative. Among the sugars, glucose and sucrose are sometimes positive but not in all cases, while maltose is indifferent. The attractive substances may therefore be proteins and the importance of the sugars is more probably osmotic. The whole subject is very puzzling. What is the source of the attraction? If it is the placenta, why do the tubes leave the placenta and pass across an air-space to the micropyle, as they often do? If it is the embryo

FIG. 1321.—*Oenothera biennis.* Longitudinal section of style showing penetration by pollen tubes.

sac, why do pollen tubes penetrate ovules where the embryo sacs are abortive, as they may do, or even reach the ovary before ovules have been formed?

We are a long way from a full understanding of this important matter, but the answer will certainly not be a simple one. Perhaps we may conclude that the course of the tube in the style and as far as the placenta is mechanically determined and that towards the end of its course it comes within the influence of a chemotactic substance emanating either from the micropyle or from the synergidae or both, which completes the direction of its growth.

In the ovary the pollen tube may follow an aerial course to the micropyle, but rarely, if ever, over any considerable distance. In anatropous ovules the micropyle lies close to the surface of the placenta and the gap may be filled by mucilaginous secretions from the micropyle. In other cases the pollen tube usually creeps on the surfaces of the placenta, the funicle and the integument to reach the micropyle. A variety of special structures also exist to facilitate its course. The obturators which we have described on p. 1234 are structures of this kind, and the bunch of elongated cells which grow downwards from the base of the stylar canal in Thymelaeaceae, like hairs, directed towards the ovule, are similar in kind. Hairs from the placenta, hairs from the funicle, hairs from the integuments, may all be found helping to bridge the gap which must be crossed between the ovary wall and the micropyle. In a few species (*e.g.*, *Ixiolirion pallasii*, *Isolepis gracilis*, *Leucosyke capitellata*, *Myriocarpa longipes*, *Polygonum persicaria*, etc.) there is such a copious outgrowth of cell filaments from the micropyle, reaching up to, and into, the stylar canal, that one might almost call them ovular stigmas (Fig. 1322).

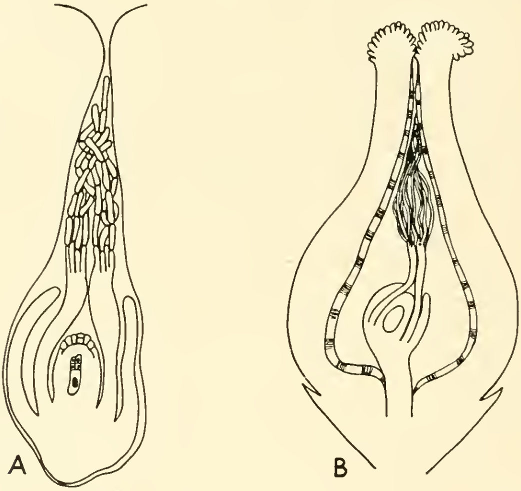

FIG. 1322.—Ovular "stigmas" formed by upgrowths from the micropylar endostome into the stylar canal. A, *Myriocarpa longipes*. B, *Leucosyke capitellata*. (*After Fagerlind.*)

Pollen tubes do not always, however, enter by the micropyle. This, which is the normal mode of entry, is called **porogamy**. When the micropyle is not used the method is called **aporogamy**. Under the latter heading are three variations: **basigamy** (**chalazogamy**) when the pollen tube enters through the funicle and the chalaza; **acrogamy**, when the pollen tube grows to the micropylar end of the sac but does not enter through the micropyle; and **mesogamy** when the pollen tube penetrates the ovule from the side.

Aporogamy may arise from other causes than the behaviour of the pollen tube; for instance in plants like *Torenia* where the embryo sac grows out of the ovule, or the opposite circumstance, where the micropyle is completely occluded (*Houstonia*, *Gunnera*, *Ficus carica*). These cases are acrogamous but not porogamous. Aporogamy can occur, however, even where there is an open micropyle, through the completely endotropic growth of the pollen tube, as in chalazogamy.

Chalazogamy was discovered by Treub in 1891 in *Casuarina*. The pollen tube enters the chalaza through the funicle, sends out in the chalaza many irregular branches and then makes its way upwards among the many elongated embryo sacs, the upper end of one of which it finally enters.

Similar behaviour has been discovered in a number of other plants, notably in the amentiferous genera *Betula*, *Corylus*, *Carpinus*, *Juglans*, *Carya*, *Pterocarya* and *Ostrya*, all members of the Betulaceae or Juglandaceae. The Fagaceae and Myricaceae are all porogamous. The limited distribution of chalazogamy in families held by some to be primitive gave rise to the belief, suggested by Navaschin, that it was the primitive type of fertilization. This idea, never very acceptable, has been countered by the discovery of occasional chalazogamy in a number of plants of other families not markedly primitive, *i.e.*, Anacardiaceae. Against Navaschin's theory, Murbeck has argued that it is not possible to draw a line between " true " chalazogamy and other cases, which are widespread, for example among Rosaceae, in which the pollen tube enters by the funicle but penetrates to the embryo sac by way of the integuments rather than through the apex of the nucellus. According to his view, chalazogamy is only a special case of completely endotropic growth of the pollen tube, which is intercellular throughout its length. This is a physiological peculiarity, found in many families and of no phylogenetic significance.

Mesogamy, if it is possible to distinguish it as a separate process, is exemplified by *Populus*. The pollen tube enters the ovule through the side of the integument nearest the placenta, curves round the channel of the micropyle and reaches the embryo sac through the nucellus.

The course of endotropic pollen tubes, especially in the ovular tissues, is very irregular, indeed erratic, and neighbouring tubes may sometimes be seen growing in opposite directions, which does not suggest any chemotactic control from the direction of the embryo sac.

The Male Gametes

The nature of the male gametes has been a subject of some controversy. The second division in the male gametophyte concerns only the generative cell. It is a mitotic, equational division and generally there seems to be no differentiation between the two nuclei formed, which are the actual male,

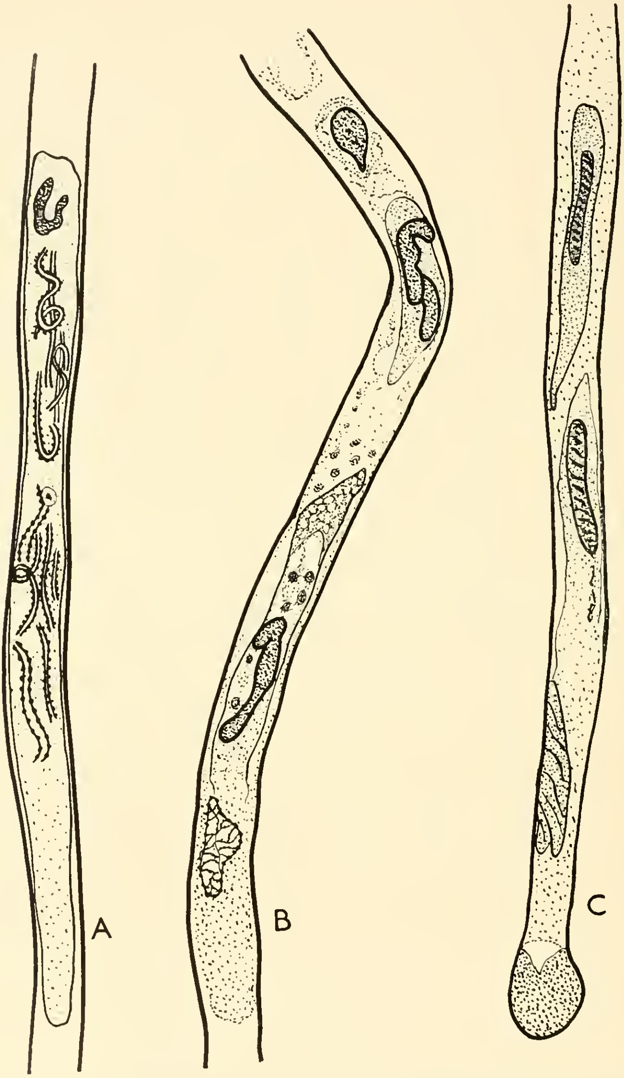

FIG. 1323.—*Lilium martagon.* A, Division of generative nucleus in the pollen tube. Twelve split chromosomes in the cell. *L. auratum.* B, Pollen tube from near base of style, showing irregular form of the generative nuclei. Tube nucleus below. C, Pollen tube nearing ovary. Generative cells, tube nucleus and swollen tip of tube. (*After Welsford.*)

fertilizing nuclei. This division may occur, as we have already seen, in the pollen grain, forming a trinucleate grain. Mitosis then seems to follow a normal course, with nothing peculiar about it. Division of the generative cell follows mitosis, either by means of a cell plate, or by constriction, or by a mixture of both processes. Two complete, uninucleate cells are thus formed, and in this condition they enter the pollen tube. The sperm cells, as we may now call them, often have long tails of finely vacuolated cytoplasm (Fig. 1323), and in the tube they may become drawn out to a remarkable length.

There are many other cases in which the division of the generative cell happens in the pollen tube and these divisions show peculiarities which have engaged much attention. For one thing they seldom show a visible spindle or metaphase plate and the chromosomal figures are distorted, apparently by the confined space in which division occurs (Fig. 1324). It is curious,

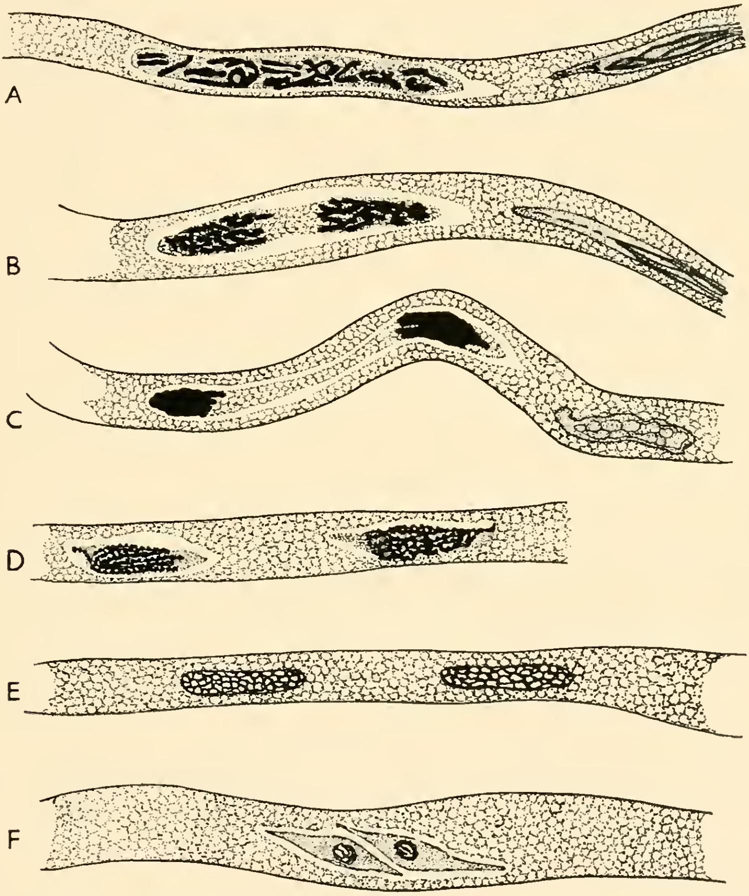

Fig. 1324.—*Convallaria majalis.* A–D, Metaphase, anaphase and telophase in division of the generative nucleus. E, Naked generative nuclei after division, in the protoplasm of the pollen tube. F, *Hemerocallis flava.* Generative cells each with its own cytoplasm. (*After Trankovsky.*)

however, to note that in *Zostera*, where the pollen grain itself is a tube about 2 mm. long and no thicker than a normal pollen tube, division appears to be quite regular. It is difficult to believe that there can be any fundamental difference between mitosis in the pollen grain and in the pollen tube, especially as the process may begin in the grain and be finished in the tube. The observed distinctions may be safely attributed to physical conditions, such as spatial restriction, and perhaps to the fact that the cytoplasm in the pollen tube is in a very active state of circulation.

There is no doubt that in some species spindle fibres cannot be seen in divisions in the tube, though they have been clearly demonstrated in others. The fact that colchicine interrupts chromosome movement in these divisions in the same way that it affects normal mitoses, argues in favour of the mechanism being the same, even when the spindle is not visible. A metaphase plate can be formed only when the tube is wide and the chromosomes are small. Otherwise only the essential of a plate is possible, namely the arrangement of the kinetochores in one plane, while the bodies of the chromosomes may lie in all directions.

Of much greater importance is the problem of the fate of the cytoplasm of the sperm cells and the question of whether it survives to take part in fertilization, for this may have a genetical significance. Most of the older observers thought that by the time the male nuclei entered the embryo sac they were naked and that their cytoplasm had disappeared. Modern observations have, however, tended generally to confirm the continued existence of cytoplasm, at least up to the anaphase in division of the generative nucleus. It has even been assigned a special importance at this stage as providing a stable enclosure for mitosis and preventing the disturbance of the chromosomes by cytoplasmic streaming in the tube. Many observations go further than this, and confirm that a zone, of somewhat modified cytoplasm, hyaline and structureless, which has been called the paragenoplast (Fig. 1325), continues to surround the sperm nuclei after division and indeed into the embryo sac.

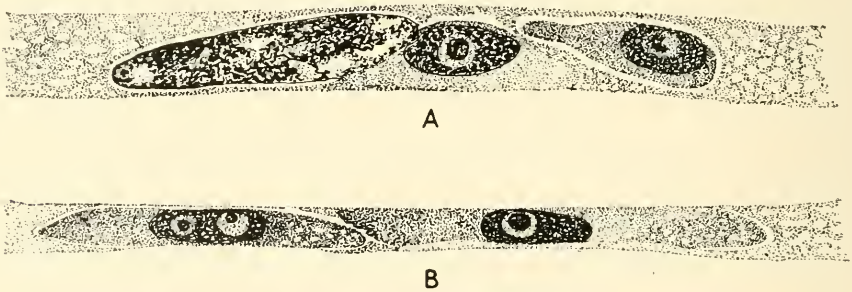

Fig. 1325.—*Vallisneria spiralis.* A and B, Portions of pollen tubes from the style showing complete generative cells and in A the tube nucleus to the left. (*After Wylie.*)

A number of descriptions refer to the sperm nuclei as " vermiform " and in some cases the chromatin does appear to be spiralized, while still in the tube. Comparisons with the spiral form of many free antherozoids have naturally been drawn, though whether the peculiarity of form has any connection with motility is uncertain, as it is not by any means universal. The movement of the sperm cells down the tube may be purely passive and attributable to cytoplasmic streaming but it has been pointed out that while the growth of the tube is continuous, the distance of the sperm cells from the end is variable, which suggests autonomous movement, perhaps by excretion pressure. They show no active movements comparable to those of antherozoids.

The tube nucleus may persist (Fig. 1326) and even enter the embryo sac, but it generally becomes amoeboid, may be greatly and irregularly elongated and has been described as fragmenting. It loses its affinity for basic stains whereas the sperm nuclei stain deeply.

FIG. 1326.—*Hyacinthus orientalis.* Pollen tube from a culture, showing swollen tip of tube, and the elongate tube nucleus followed by the two generative nuclei.

The Act of Fertilization

When the pollen tube reaches the embryo sac it penetrates its membrane. The latter is often, perhaps always, delicate and non-cellulosic at its upper pole, no more than a plasmatic membrane or a sheath of pectin. Accounts of subsequent events differ and there is no reason to suppose that they are necessarily of uniform character. Well-supported observations show that the tube may enter one of the synergid cells and there discharge its nuclei. This is followed by enlargement of the basal vacuole in the synergid cell, which then bursts, discharging its contents, including the pollen tube nuclei, into the embryo sac " with some vehemence " as Steffen says. The synergid is thus destroyed. This looks like a rather specialized discharge mechanism and it can only be set off once, since if a second pollen tube enters the other synergid, no reaction follows. Naturally nothing of the kind can occur where the synergids have not been formed or have already degenerated before fertilization and in many plants the pollen tube has been seen passing between existing synergids and penetrating more or less deeply into the embryo sac before discharging. The mechanism of discharge is still obscure, but it has been shown in pollen tube cultures that the end of the tube is very delicate and is easily ruptured. Occasionally terminal or sub-terminal openings in the wall of the tube have been seen. A noteworthy point is that the tube has never been seen to enter the oosphere, even when there are no synergids, although fertilization of the oosphere is the primary object of the whole process.

Quite frequently more than one pollen tube may enter the embryo sac. As many as twenty have been known to do so. Sometimes the accessory tubes do not open, but they may do so and discharge their sperm nuclei in various parts of the sac. Normally these superfluous nuclei simply degenerate and disappear, but this is not always so.

Two sperm nuclei may fertilize the oosphere giving rise to a triploid embryo. Fertilization of an antipodal cell has already been referrred to and fertilization of synergids has been inferred from the occurrence of supernumerary embryos, which may, however, have arisen apomictically. In *Myricaria* each polar nucleus has been observed to fuse separately with a male nucleus. Lastly, abnormal embryo sacs may contain more than one oosphere, each of which may be fertilized. All these processes are abnormalities and polyspermy, as it is called, is undoubtedly rare. When two sperm nuclei from different pollen tubes take part in fertilization they may be genetically different and give rise to anomalous inheritance. This is spoken of as heterofertilization.

The two normal sperm nuclei move from their point of liberation, one to the oosphere and one to the primary endosperm nucleus or to the pair of still unfused polar nuclei, as the case may be. This movement must take place very rapidly since intermediate stages are rarely to be seen in fixed material. They move in the cytoplasm of the embryo sac, but their movement seems to be active, not passively due to cytoplasmic movement. This is evidenced by the divergent paths taken by the two nuclei, which are normally close together at first, and by the fact that neither the tube nucleus, nor the remains of the synergid nucleus, if they are also extruded into the sac, show any movement of their own.

The union of the second male nucleus with the polar nuclei constitutes the **double fertilization** (Fig. 1327), which was established as a normal occurrence by Navaschin in 1898 and Guignard in 1899 (Fig. 1328). The actual union is also called **triple fusion** (Fig. 1329), from the three nuclei involved, though in some embryo sacs, the number of polar nuclei may be much more than two. The only parallel happening in other groups of plants is the occasional fertilization of the ventral canal nucleus in some Gymnosperms, which we have already referred to.

Although the oosphere is usually reached first by a male nucleus, their fusion takes longer than that of the second male nucleus with the primary endosperm nuclei, although the two processes appear to follow the same lines. There is very seldom any difference in appearance or size between the two male nuclei, but it has been fairly established, especially by the very careful observations of Steffen on *Impatiens glanduligera*, that the male nucleus going to the oosphere may retain its cytoplasmic sheath until fusion

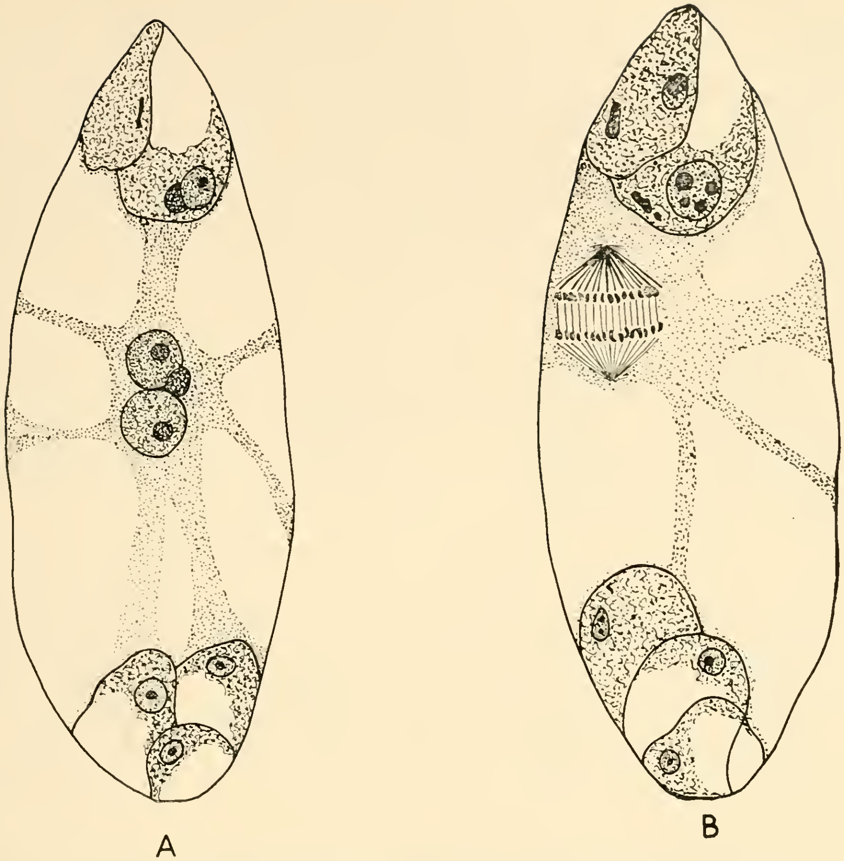

FIG. 1327.—Double fertilization in *Nicotiana.* (*After Guignard,* 1902.)

FIG. 1328.—Portrait of Leon Guignard.

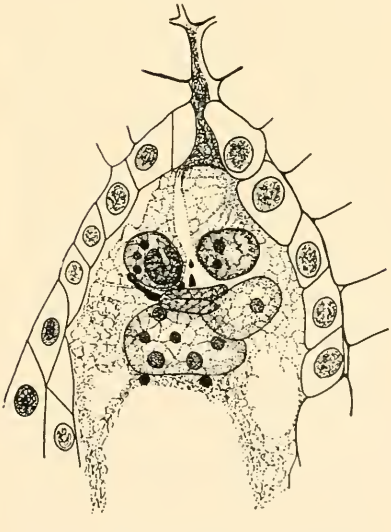

FIG. 1329. — *Lilium martagon.* Double fertilization showing triple fusion of two polar nuclei with one V-shaped male nucleus. (*After Blackman and Welsford.*)

takes place, whereas the second male nucleus may lose its cytoplasm on its way to the polar nuclei.

On entry into the embryo sac the male nuclei show various forms, spherical, elongate, curved or vermiform. Moreover they seem to change their shape very rapidly and they may lose their variable form and become more spherical as they approach the female nuclei (Fig. 1330).

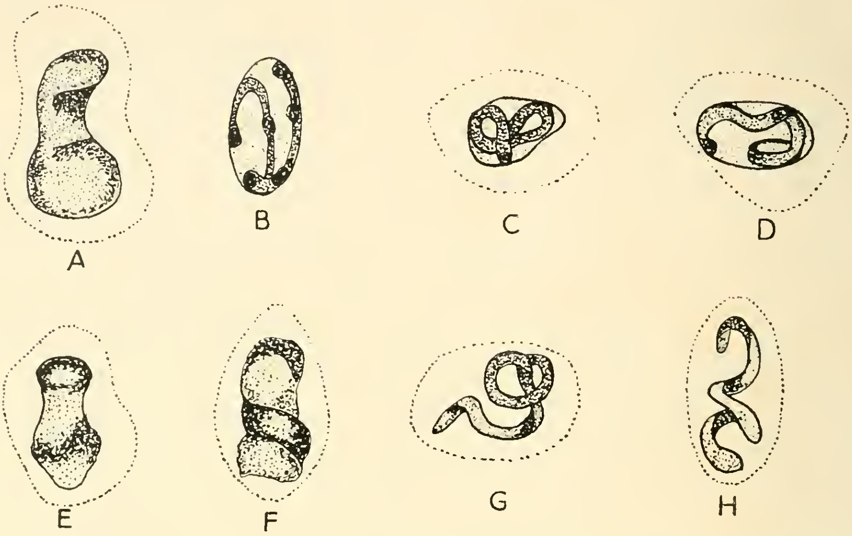

FIG. 1330.—*Impatiens glanduligera.* Male cells and nuclei in the embryo sac, showing changes in the conformation of the chromatin. A–D, Primary male nucleus. E–H, Secondary male nucleus. Feulgen stain. (*After Steffen.*)

Steffen claims that these appearances are those of the chromatin rather than of the nucleus as a whole and that a nuclear membrane may be seen surrounding the curved or spiral chromatin. As this membrane is exceedingly delicate and easily overlooked, the descriptions of the nuclei as being vermiform may be erroneous. On contact with the oosphere the male nucleus appears to " sink in " or be " immersed " in the oosphere, whose membrane, though very delicate, seems to be fairly firm. No aperture in the membrane has been seen and the nearest simile one can give is that of two oil drops fusing. The oosphere membrane, at least in its lower part, where entry usually occurs, is probably a weak thixotropic gel, which is reversibly solvated by contact with the male nucleus.

The many accounts of the process differ sharply on the question of whether male cytoplasm enters the oosphere, or not. There is too great a body of evidence each way to be easily dismissed, and genetical data support the belief that male cytoplasm sometimes takes part in fertilization and sometimes does not. When it does enter the oosphere it very rapidly ceases to be separately distinguishable.

The male nucleus then passes through the cytoplasm of the oosphere, presumably also by an autonomous movement. On contact with the female nucleus the male enlarges considerably and its content of nucleic acid diminishes, as in the oosphere nucleus, to such an extent that it gives hardly any stain with the Feulgen reagent. Nuclear fusion seems to be an amalgamation. There is no opening of the female nuclear membrane, nor has solution been observed (Fig. 1331). The nuclear membrane of the male has been seen after entry into the primary endosperm nucleus (Fig. 1332), though not in the oosphere. It must rapidly disappear, and the contents of the male nucleus disperse within the female. The sperm nucleus does not always possess a nucleolus, but at the time of fusion it appears, or reappears, at first as a minute granule, which rapidly enlarges, then moves towards and fuses with the female nucleolus. Nuclear fusion is a relatively slow process and may take several hours to complete from the time of first contact, but the data are very scanty.

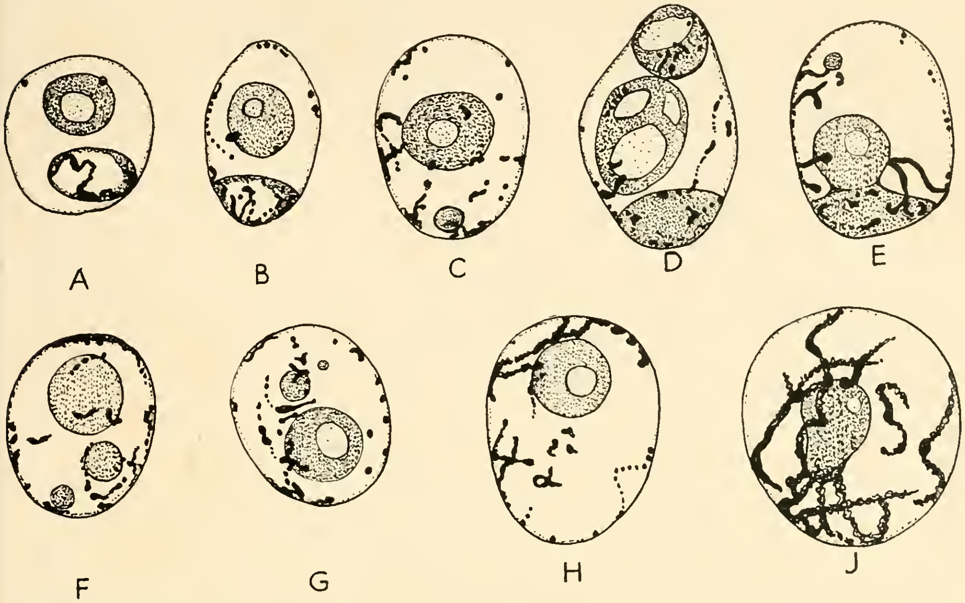

Fig. 1331.—*Impatiens glanduligera.* Entry of male nucleus into the female. A, Two nuclei in external contact. B, D and E, Solution of the contact membrane and entry of the male nucleus. C, F, G and J, Appearance of the male nucleolus and its union with that of the oosphere. B–J, Increasing chromatin content of the fertilized nucleus. J shows the prophase chromosomes of the first division of the zygote. D, A case of dispermy. (*After Steffen.*)

Immediately after fusion the nucleic acid content of the fusion nucleus rapidly increases and the structure of prophase chromosomes re-emerges, in other words, the fusion nucleus retraces the changes which took place during the maturation of the oosphere nucleus, and the duration of the process causes a certain delay before the first zygote division. In the endosperm cell the recovery process is quicker, hence it is usually the first to divide, in fact it may divide several times before the fertilization of the oosphere is completed. Some aberrations of the normal fertilization process will be discussed later under Apomixis. Here we may simply mention that dispermic fertilization of the oosphere sometimes occurs, but Steffen estimated it at only 0·3 per cent. of the examples he observed in *Impatiens glanduligera*.

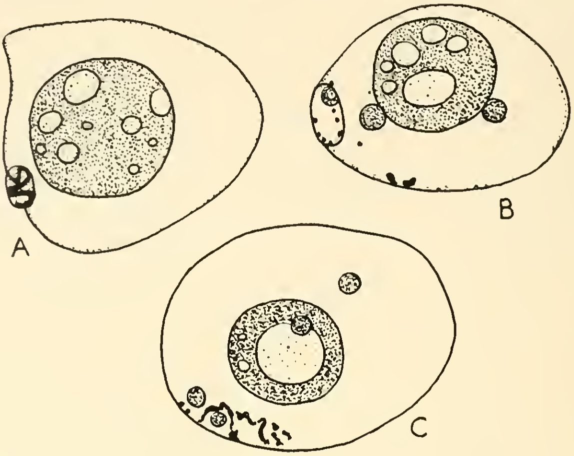

FIG. 1332.—*Impatiens glanduligera.* Entry of secondary male nucleus into the primary endosperm nucleus. A and B, Phases of entry. C, Nuclear membrane of male nucleus has disappeared and the chromatin is dispersing. B shows beginning of chromatin regeneration in the endosperm nucleus. (*After Steffen.*)

The uniting nuclei are generally said to be in the resting stage or else to show the appearance of early divisional prophase. If the essential feature of bi-parental inheritance is held to be the pairing of two sets of homologous chromosomes, then nuclear union cannot be considered complete until this has taken place, which cannot be until the first zygote division. Observations differ on whether two groups of chromosomes are still distinguishable in the early stages of this division, but it is at metaphase, at latest, that their intermingling must be completed.

In the primary endosperm nucleus separation of the chromosomes is maintained longer than in the fertilized oosphere. Distinct groups of chromosomes may still be evident at the second division, but it is not known how long this state persists. Tripolar spindles may be formed at the second division which are reduced to bipolar by the drawing in of the third arm.

The interesting question has often been raised, whether fertilization in the Angiosperms is entirely indiscriminate or whether such a thing as selective fertilization exists, either by a truly selective attraction between certain pollen tubes and certain ovules or else by competition. The latter must certainly be an element in some cases, where pollen tubes exhibit differential rates of growth. The genic composition of the pollen may control the rate of growth, as Buchholz has already shown in *Datura*. Some genes are lethal or semi-lethal to pollen tube growth and seem to affect the gametophytes only. Others have effects on the morphology of the progeny, where the characters appear as recessives.

On the other hand, in cases of weak self-incompatibility, it is the ovary or the ovules which seem to cause the differentiation between successful and unsuccessful pollen tubes. Darwin, and after him Bateson and Gregory, noted that in illegitimate unions in *Primula* approximately half the ovules are fertilized in all cases and the later writers suggested a differentiation between ovules as the cause.

Competition between pollen tubes seems to be indicated in experim nts with *Nicotiana tabacum*, where it has been shown that pollination with abundant pollen yields a relatively uniform F_1 generation, while if only a few pollen grains are used the offspring are more variable and aberrant types appear, which are suppressed by more liberal pollination. In the heterozygous *Oenothera berteriana* when self-pollinated, only heterozygous embryos are formed and the homozygotic combinations fail to appear. This has been attributed to preferential fertilization of ovules by pollen tubes which do not carry the same complex of genes. It is more likely to be due to a combination of lethals in the homozygotes.

The Interpretation of Double Fertilization

The significance of the fertilization of the endosperm nucleus has never been satisfactorily explained. Navaschin, its discoverer, looked upon it as a sexual act and considered the endosperm to be a misshapen twin of the regular embryo. Strasburger called it a vegetative fertilization and thought that the stimulus to development was the secret of its importance. This accorded with his idea of endosperm formation as a continuation of prothallus building. Schürhoff, on the other hand, denied all sexual character to the fusion, which to his mind is a purely nutritive act which he calls trophomixis.

The anomalous nature of endosperm as a polyploid tissue which is neither sporophyte nor gametophyte should not be overlooked. Moreover it is by means of this specialized tissue that the young sporophyte is nourished and there is no other provision for its nourishment. This is a unique situation in the plant world and it is not surprising, therefore, that unique circumstances should attend its origin. It is obviously important that the development of the nutritive tissue should be coupled as regards timing with the development of the embryo. Putting aside the deeper question of the nature of the sexual stimulus, the fact remains that union with the second male nucleus is the signal for development to begin and that without it the endosperm nucleus does not usually develop. Other, possibly chemical, stimuli to development must act in parthenogenetic embryo sacs, stimuli which in such cases affect both oosphere and endosperm development.

If we accept the Porsch theory of the embryo sac, *both* polar nuclei are the equivalents of ventral canal cells and are the sister cells of gametes, actual or potential. That, united together and combined with a male nucleus, they should show greater power of development than the comparatively slight development which follows when a ventral canal cell in a Gymnosperm is fertilized, might reasonably be expected.

A further consideration has been urged, both by Thomas and Nemec, namely that the incorporation of paternal genes in the primary endosperm nucleus makes it genetically related to the embryo and that for this reason the chemical nature of the nutritive substances provided by the endosperm may be more closely related to the requirements of the embryo than would otherwise be the case. Experiments on the transplantation of grass embryos into unrelated endosperms seems to bear this out.

As we mentioned earlier (p. 1430), Berridge dissented from the view that the polar nucleus was the equivalent of a ventral canal cell. She regarded the endosperm as an anomalous embryo and compared it with the apogamous embryos which she observed in *Ephedra*, which originate by the fusion of two archegonial jacket nuclei, to form a diploid nucleus which has the power of forming an embryo, if it escapes into the archegonial cell. These embryos only develop after fertilization has occurred and she suspected that there was an actual union of the diploid nucleus with a sperm nucleus before development. The jacket cells in *Ephedra* come from an initial cell which is closely related to the archegonium initial. As, in Berridge's view, the antipodals represent the lower prothallus tissue in Gnetales, the participation of one of their group in triple fusion could only have a nutritive significance.

The Endosperm

There are only two families of Angiosperms in which endosperm development is effectively absent, the Orchidaceae and the Podostemaceae. In the former the embryo remains a small undifferentiated mass of cells and its further development depends on mycorrhizal nutrition. In the latter the growing embryo is pushed down into the pseudo-embryo sac, below the true one, which apparently fulfils the nutritive function of the missing endosperm. Double fertilization has been shown to occur in Orchidaceae and it is not known why it produces no result. In all other families endosperm development begins, though in some of them it is only transient and the ripe seeds are non-endospermous.

Endosperm development does not seem to be affected by the triploid or polyploid status of its cells. There is, however, no immediate union of component chromosome groups. At the first, and even at some subsequent divisions, tripolar spindles are formed and the three chromosome groups remain distinct, though the tripolar spindle has sometimes been seen to pass over into a bipolar one. Certainly chromosome pairing is delayed, but when it takes place, if at all, is not known.

Although the endospermal fertilization is called triple fusion, the three nuclei do not always unite simultaneously. The following are the variations which have been observed in the order of events.

P_1 = upper polar nucleus; P_2 = lower polar nucleus; Sp. = sperm nucleus.

$(P_1+P_2)+Sp.$	This is the most frequent method, the polar nuclei uniting before union with the sperm nucleus.
$(P_1+P_2+Sp.)$	Observed in *Zea*, *Nicotiana*, *Fritillaria*, *Tulipa* and *Gagea*.
$(P_1+Sp.)+P_2$	Observed in *Monotropa*.
$(P_2+Sp.)+P_1$	Observed in *Adonis*, where the antipodal polar nucleus moves up to the egg-apparatus and unites with the sperm nucleus, then retreats. Both the two last procedures occur in *Lilium* and in *Nicotiana*.
$(P_1+Sp.)$	This happens in embryo sacs where there is no antipodal polar nucleus, *e.g.*, Oenotheraceae, *Helosis* and *Limnocharis*, and has also been noticed in *Adoxa*, and perhaps in *Lemna*, where direct fusion of the polar nuclei does not seem to occur, but they divide co-ordinately and fuse during this division.

Division of the endosperm nucleus usually precedes that of the oosphere and in many cases quite extensive formation of endosperm may take place before the first division of the oosphere. Every degree of precedence may be found in different plants, but it is rare for the oosphere to divide first, nor is simultaneous division at all common.

Since the days of Strasburger there have been two main types of endosperm development recognized, the **nuclear type** and the **cellular type**. A third type, of more restricted occurrence, is the **helobial type**, which is widespread among members of the order Helobiales and is found also in isolated cases in various families outside this order. One or two other anomalous types have been described, the distribution of which is not certainly known.

In the *nuclear type*, the first divisions of the endosperm nuclei are not accompanied by cell wall formation (Fig. 1333). The nuclei produced are free in the cytoplasm of the embryo sac and they may either remain free indefinitely or else wall formation occurs later, either progressively or more or less synchronously throughout the sac.

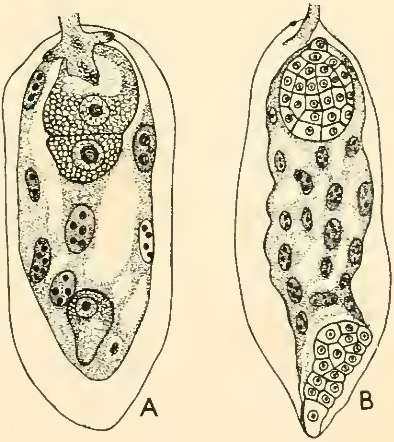

FIG. 1333.—*Ulmus americana*. Free-nuclear endosperm formation. A shows an antipodal oosphere. B shows an antipodal enbryo developing. (*After Shattuck.*)

The first few divisions are generally synchronous, as in most multinuclear cells, but this later gives way to irregularly distributed divisions, or to waves of division spreading from one point throughout the sac. Whether any cell plates are formed between the dividing nuclei is not yet clear, though the existence of such abortive divisions in the cytoplasm might indicate that the cellular type is the more primitive.

The number of successive divisions which take place depends on the size of the embryo sac, but as this is rapidly expanding at this time, the number may be considerable and in some cases several hundreds or even thousands (*Malva*, *Malus*) of free nuclei may be formed. On the other hand, in small sacs, wall formation may begin when there are no more than from four to sixteen nuclei.

The expansion of the embryo sac is accompanied by the enlargement of a central vacuole, which presses the cytoplasm out against the periphery, and in this thin layer of cytoplasm the multiplying nuclei are spaced out, roughly equidistant from each other. There may, however, be closer aggregation at the two poles, around the embryo or the suspensor, and at the antipodal end respectively. The latter nuclei may also become larger than the others. In some isolated cases, *e.g.*, *Musa* and *Hypericum*, some of the antipodal endosperm nuclei may be separated from the others by an enclosing membrane forming a multi-nucleate cyst (see Fig. 1301), which in *Hypericum* sends down a haustorial extension into the chalaza. Swamy has called this the **Hypericum type** of endosperm.

Wall formation generally begins at the periphery of the sac, cell plates growing inwards centripetally. How these originate is not altogether clear. They may start as granular deposits or as layers of minute vacuoles, and in many plants these are laid down on secondarily formed spindles. In a few cases, *e.g.*, *Asclepias*, they seem to start by the fission of the cytoplasm along certain lines. The areas between these walls are at first incompletely delimited, but later inner walls appear which accomplish the formation of a peripheral layer of cells.

Hegelmaier has distinguished the following varieties of wall formation in the endosperm.

1. A peripheral layer of cells is completed, as above described. These cells divide periclinally until the whole of the interior space is filled. A widely spread type.

2. A peripheral layer of centripetal walls appears and these prolong themselves until they meet in the middle of the sac, when division into cells follows (compare the process of " alveolation " in Gymnosperms). Occurs in some Cucurbitaceae, *Bocconia*, *Scabiosa* and *Euphorbia*.

3. Wall formation starts from the micropylar end and the chalazal end may remain undivided. Occurs in many plants, *e.g.*, *Cytisus*, *Polygonum*, *Rumex*, etc.

4. Endogenous type. The embryo sac is filled with cytoplasm and wall formation occurs simultaneously throughout. A rare type, known definitely in *Eranthis* and perhaps in *Tricyrtis*, *Vincetoxicum* and one or two other plants.

These types are useful descriptively but they do not cover the large number of variant and intermediate cases which are known.

The cells which are first formed may include several nuclei (Fig. 1334) or, on the other hand, the single nucleus included may divide and produce a multinucleate cell. In either case the nuclei later fuse, so that rarely is more than one left in each cell.

FIG. 1334.—*Helianthemum chamaecistus.* Cell formation in the endosperm. Several cells contain more than one nucleus.

Wall formation in nuclear endosperm may sometimes be suppressed and the nuclei remain free but the examples are not numerous and are scattered in different families as a specific peculiarity. Among well-known instances are: *Acer pseudoplatanus*, *Aesculus hippocastanum*, *Myricaria germanica* and *Limnanthes douglasii.* Further, it occurs in many Melastomaceae and in the tribe Viceae of Papilionaceae. All these are plants in which the development of the endosperm is incomplete and soon ceases, the ripe seeds being non-endospermic.

Peripheral endosperm formation does not always fill the whole sac and a central space containing fluid may be left, the most striking example being that of the Coconut, where the space is relatively enormous.

In the *cellular type* of endosperm formation there is no free-nuclear phase and wall formation starts with the first division (Fig. 1335). The arrangement of the cells formed is at first generally regular and constant. Irregular cell formation supervenes at later stages. Schnarf has recognized the following types, according to the direction of the first cell wall.

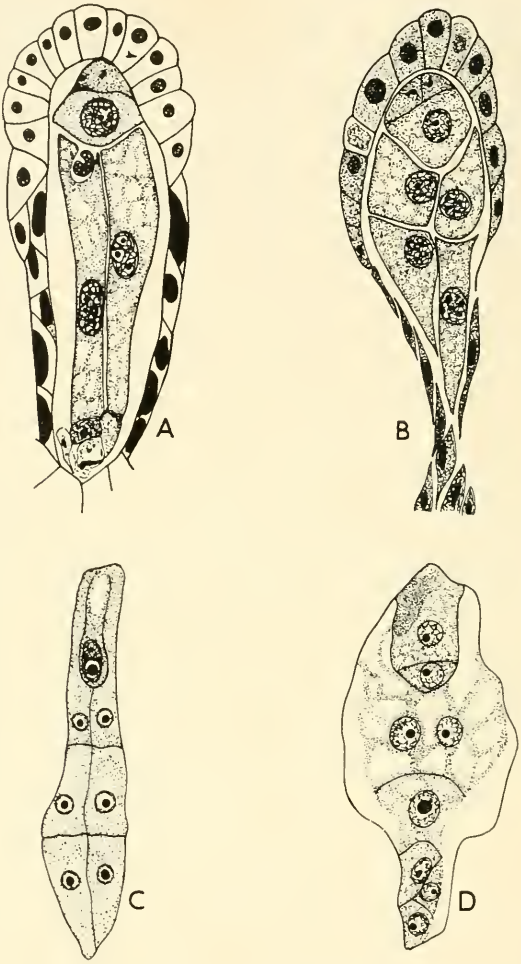

FIG. 1335.—A and B, *Adoxa moschatellina*. Cellular endosperm; two- and four-celled stages. C, Cellular endosperm in *Callitriche*. D, Helobial endosperm in *Butomus umbellatus* showing first transverse division. (A and B *after Lagerberg*. C *after Jorgensen*. D *after Holmgren*.)

1. The primary wall is longitudinal to the embryo sac. Examples are: *Adoxa*, *Centranthus* (sometimes) and a few Dipsacaceae. In *Lappula* (Boraginaceae) the first wall is vertical but does not reach beyond the micropylar end of the sac. Another vertical wall follows, at right angles to the first, and from these open " cells " nuclei pass down to the antipodal end

of the sac where they multiply freely. Cell formation is limited to the micropylar end. We thus see an interesting intermediate between the two main types of development.

2. The primary wall is transverse, but one or both of the daughter cells divide lengthways. Examples are: *Scutellaria* and *Verbascum*. In *Callitriche*, two transverse walls are formed and each of the three cells thus formed divides lengthways (Fig. 1335 C).

3. The primary wall is transverse, but one or both of the daughter cells divide transversely. Examples are: Ericaceae generally, and Annonaceae.

4. The primary wall is oblique. Example, *Myosotis arvensis*, where the two cells formed are of unequal size.

5. The direction of the primary wall is not constant. Examples are: many Valerianaceae, *Senecio* and *Gunnera*.

The *helobial type* of development begins with the formation of a transverse wall at the first division of the endosperm nucleus (Fig. 1335 D). This separates two portions of the embryo sac, a small antipodal portion and a much larger portion comprising the greater part of the embryo sac. In the small antipodal portion the nucleus may remain undivided, or at most it divides only a few times. Occasionally as many as sixty-four nuclei may be produced, *i.e.*, there are six divisions. Wall formation may also sometimes occur, so that a small mass or cushion of cells may underlie the main endosperm.

In the larger, micropylar segment of the embryo sac free nuclear multiplication takes place, as in the usual nuclear type of endosperm, followed by peripheral cell formation. The growth of this tissue usually crushes the antipodal development, which disorganizes and disappears.

In the Helobiales, the first division wall is transverse, but some Boraginaceae, *e.g.*, *Lycopsis*, show a modified helobial type in which an oblique wall is formed at the second division, cutting off a small lateral pouch in which only a few nuclei are formed, the main endosperm developing in the larger chamber of the sac.

We have already mentioned that endosperm development may cease at almost any stage, so that little or none may be visible in the ripe seed. Of this suppression, there are innumerable examples, including the Orchidaceae, in which there is generally no development at all, though in a few species one or two nuclear divisions take place. Even fully developed endosperm may, however, be absorbed and obliterated by the growing embryo, the food material so absorbed being usually stored in greatly enlarged cotyledons. This is characteristic of some large-seeded families such as the Fagaceae, Papilionaceae and Cucurbitaceae and it is also general among Compositae. In all these families the embryo finally fills the whole seed.

There are too many individual cases of peculiarity or anomaly in the formation of endosperm to be dealt with, except in a specialist monograph, but we may mention only the production of caeca or haustoria, which are prevalent in a variety of forms. Endospermal haustoria are of two kinds, micropylar and chalazal, though not infrequently, as in *Lobelia* and *Globularia*, both may be formed in the same ovule (Fig. 1336).

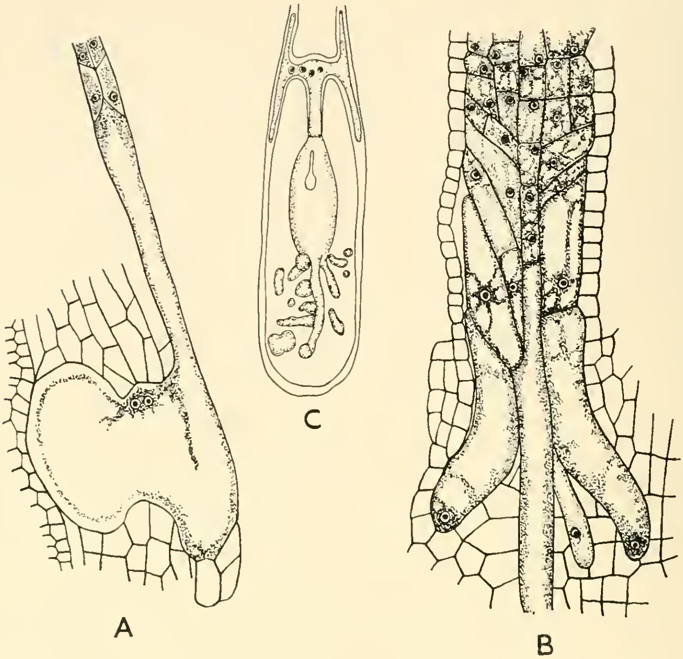

Fig. 1336.—*Globularia cordifolia*. A, Chalazal haustorium with a lateral caecum. B, Haustorial elongation of basal cells of the endosperm. C, Ovule in longitudinal section showing haustoria developed at both ends. (*After Billings.*)

Micropylar haustoria, though often extensive, are generally simple in organization. They mostly consist of unicellular outgrowths, in which, as they enlarge, free nuclear multiplication may take place, growing through the micropyle and branching freely in a mycelial manner over the surface of the ovule and the ovary wall or penetrating the tissue of the funicle or the placenta. In the Labiatae the haustorium begins as an enlargement of the apical end of the embryo sac, into which pass several endospermal nuclei. The sac thus formed may enlarge very considerably and throw out branches. Such is the case in *Galeopsis*, where a lateral outgrowth from the haustorial sac penetrates the integument and reaches upwards to the apex of the ovarial cavity.

Another type of micropylar haustorium is formed by groups of cells (Fig. 1337) from the micropylar portion of cellular endosperm, which enlarge upwards into the micropyle. *Veronica* (Fig. 1338) and *Lobelia* have such haustoria, composed often of a pair of enlarged cells which have been mistaken for large synergidae. Lateral outgrowths may be formed also in this type of haustorium, *e.g.*, in *Byblis* (Lentibulariaceae) where the lower

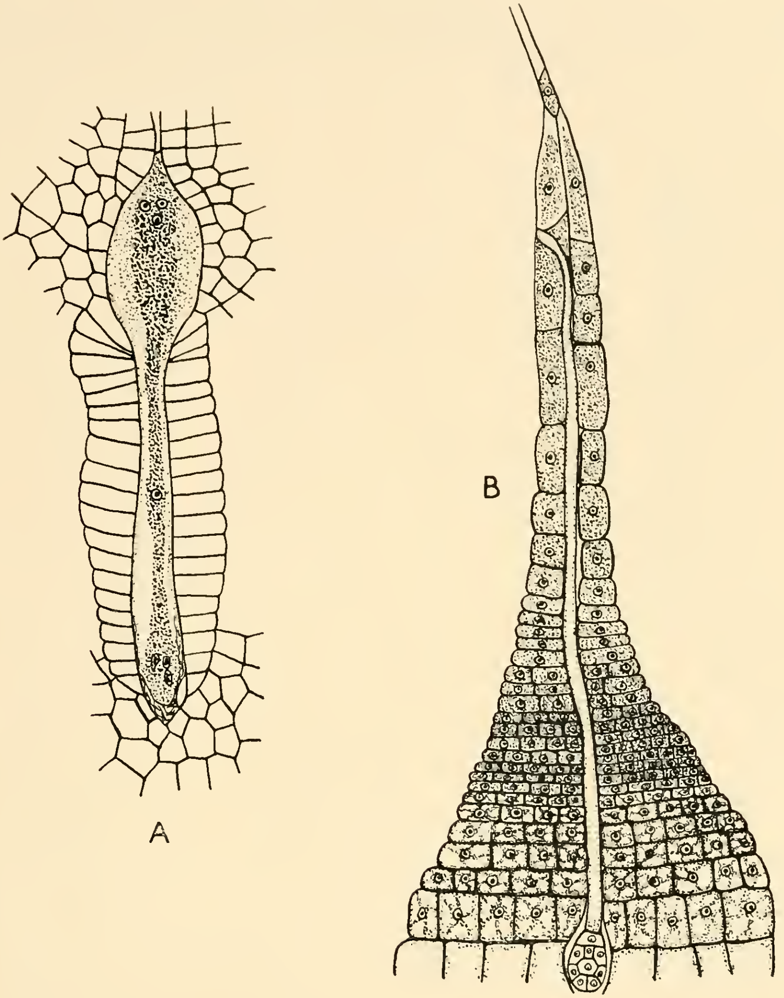

FIG. 1337.—*Myoporum serratum.* A, Mature embryo sac. B, Later stage showing massive micropylar haustorium formed of many cells belonging to the endosperm. (*After Billings.*)

part of the haustorium throws out numerous tubular branches into the tissue of the integuments.

The micropylar haustorium, in certain families, is cut off from the main endosperm at a certain stage of development by the ingrowth of the integument to form a conspicuous constriction called the isthmus. Examples are common in Labiatae, Scrophulariaceae and Bignoniaceae. In other cases a suberized separation layer may be formed.

The *chalazal haustoria* (Fig. 1339) are most frequently traceable to the antipodal segment which is cut off by the first transverse wall, in cellular endosperm formation. This cell may remain undivided and grow out into an irregular pouch or caecum (Fig. 1340), penetrating and destroying the chalazal tissue. The Scrophulariaceae usually develop haustoria at both

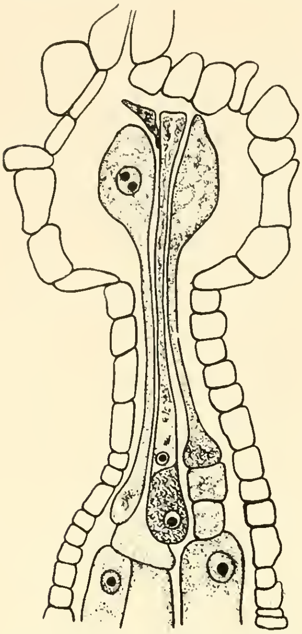

FIG. 1338.—*Veronica chamaedrys.* Micropylar haustorium formed of a pair of endosperm cells with the suspensor between them. (*After Gscheidle.*)

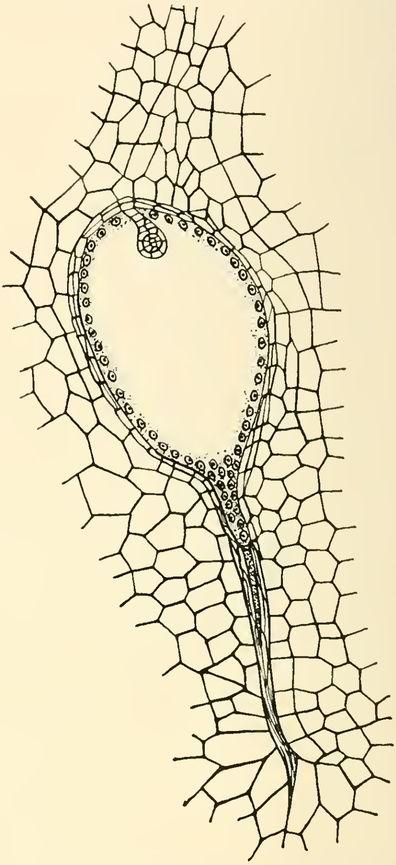

FIG. 1339.—*Leptosiphon androsace.* Basal haustorium invading chalazal tissue. (*After Billings.*)

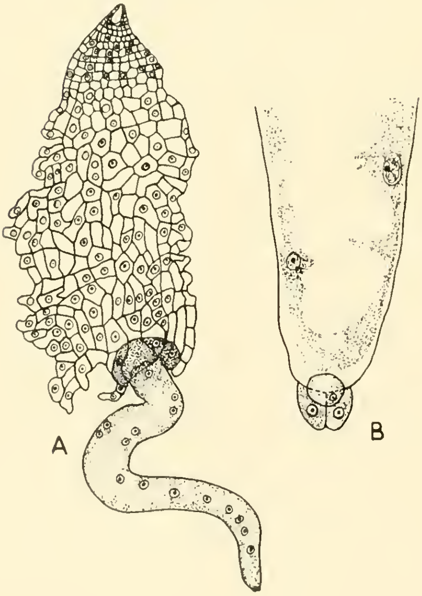

FIG. 1340.—*Grevillea robusta.* A, Vermiform caecum formed from lowest endosperm cell which remains undivided but becomes multinucleate. B, Lower end of caecum showing the three antipodals. (*After Kausik.*)

ends of the sac (Fig. 1341). In this family the primary division wall in the sac is transverse. The lower segment becomes the chalazal haustorium directly, the upper segment divides again, and of its two portions the upper develops the micropylar haustorium and the middle segment alone forms the main endosperm.

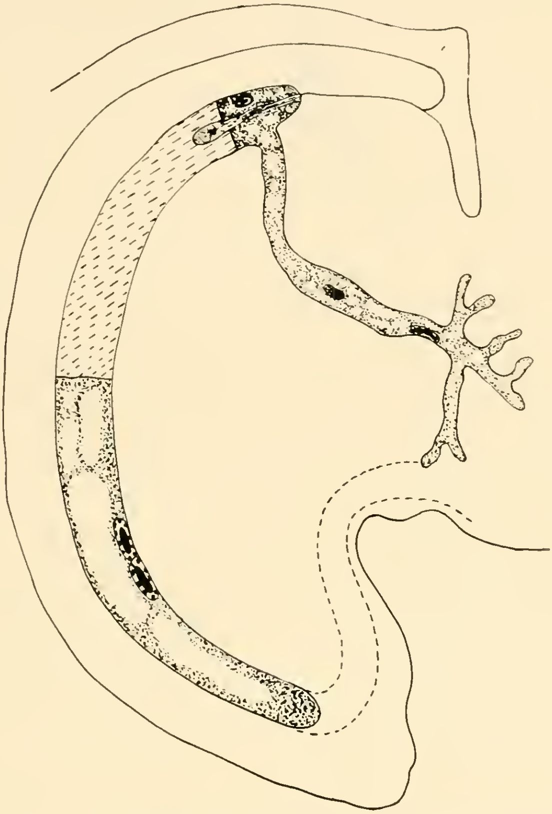

FIG. 1341.—*Rhinanthus major.* Well-developed haustoria at both micropylar and chalazal ends of the embryo sac. (*After Schmid.*)

A distinction must be drawn between truly haustorial outgrowths of the endosperm and chalazal enlargements or caeca of the embryo sac itself, the formation of which precedes endosperm development and which later become filled with endosperm which either invades the caecum or develops there.

In *Physostegia* (Labiatae) for example (Fig. 1342), a large chalazal tube is formed by the embryo sac, connected to the upper portion only by a narrow junction. The endosperm is cellular and fills the chalazal lobe, the main sac containing only a few cells. The chalazal lobe invades and destroys nearly all the tissue of the integuments and later absorbs the main sac as well. The embryo is pushed down by its suspensor into the chalazal endosperm which, in turn, is nearly all absorbed by it.

Reference should be made here to the occasional persistence of parts of the nucellus, especially its apical cap, during the ripening of the embryo. These cells may divide to form a tissue, called **perisperm**, which may be found, *e.g.*, in *Piper*, alongside of the embryo and forming part of the nutritive tissue in the seed. In the seeds of members of the Centrospermae the endosperm is reduced to a few layers of cells around the embryo, while the main mass of nutritive tissue is perisperm, formed on the concave side of the curved embryo.

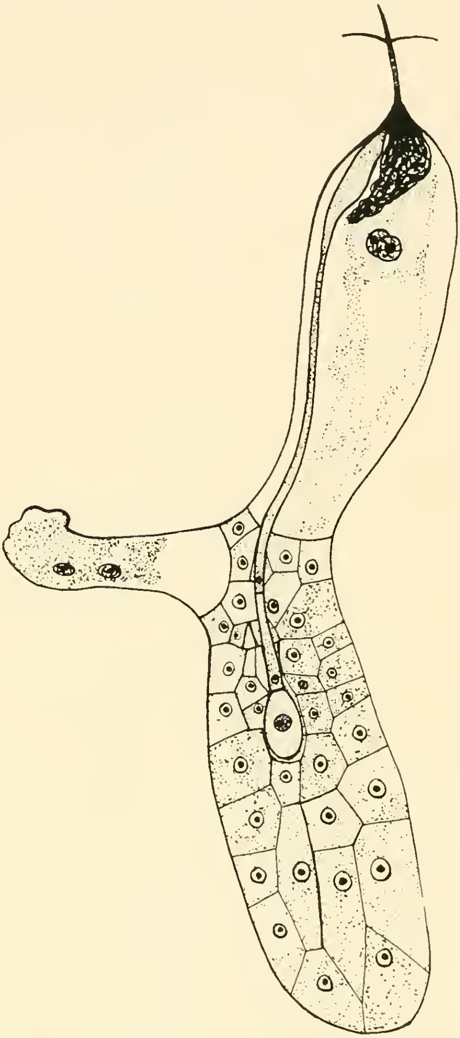

FIG. 1342.—*Physostegia virginiana.* Late stage of embryo sac with basal caecum filled with cellular endosperm but with none in the lateral caecum or the micropylar portion of the sac.

The cells of the mature endosperm are generally thin-walled and richly stored with reserve food materials. Of these, starch is the commonest, but oils, fats, proteins and "hemicellulose" are characteristic of certain genera and families. Mixed reserves, *e.g.*, oils and proteins, may occur, but starch and oil are always distinct and serve to distinguish seeds of different physiological types. Where starch and proteins are both stored they are usually in separate parts of the tissue, the protein-containing cells often forming a special "aleurone layer" on the periphery, a layer which may, however, have another importance as a source of hydrolytic enzymes during germination.

The deposits of hemicelluloses, or more properly polyuronides, cause great thickening of the cell walls, as in many Palmaceae, Iridaceae, etc. The walls of these thickened cells are penetrated by tubular pits and are often richly provided with protoplasmic connections.

The quantity of stored material is often so great that the other cellular contents may be disorganized or disappear, leaving nothing but a cellular framework holding the reserve materials and destined to complete solution at the time of germination.

Aggression by the endosperm on the integuments may lead to " rumination " or infolding of the two sets of tissues, which we shall refer to in the next chapter. It may go so far as to destroy the integuments completely, as in *Crinum*, where the outer layers of the endosperm become suberized and form a secondary covering layer to the seed.

The Development of the Embryo

Plant embryology long suffered neglect. The principal reason probably was that the earlier studies did not offer much prospect of contributions to the history of evolution parallel to those which had distinguished vertebrate embryology. Fifty years ago it was the habit of botanical lecturers to dismiss the angiospermic embryo as a relatively slight and simple structure, which had been so influenced and conditioned by its environment that it offered no indications of its phylogeny and was therefore (according to the ideas of the day) of little interest. The time has long gone by when it was possible to speak of a " typical " dicotyledonous or monocotyledonous embryo, for the great diversity revealed by extended embryological study has clearly shown that there is no such thing.

Embryology now embodies an immense amount of detailed comparative information and in the hands of a group of devoted investigators it has expanded into an important region of botanical knowledge. Into the details of the subject it is impossible to enter here. We must be content to indicate a few general principles. For a grand marshalling of the information we must refer readers in the first place to " Plant Embryology " by Dr. A. Johansen (Chronica Botanica Co., 1950) or to " Embryologie der Angiospermen " by Karl Schnarf (Borntraeger, 1927–9), or to the more concise review in " An Introduction to the Embryology of Angiosperms ", by P. Maheshwari (McGraw-Hill, 1950).

Johansen rejects consideration of the many ancillary aspects of embryo formation, such as the building of the female gametophyte, fertilization, the endosperm development and so on which we have been hitherto dealing with, and concentrates attention on the embryo itself, from various points of view; *i.e.*, its origin (embryogenesis), its architecture (embryotectonics), its destination and functions (embryogenergy) and lastly the laws of embryonic development (embryonomy). The second and the last of these aspects make up the core of the subject and they are sufficiently wide to warrant his extensive treatment. So great is the diversity in embryo building that Johansen does not separate Dicotyledons and Monocotyledons as distinct groups from the embryological point of view, for there is no general embryological distinction between them, at least in the important early stages.

The first practical scheme of classification of embryos into developmental types was made by Schnarf in 1928. He recognized five *Types* of development among Dicotyledons and named them after families in which each is the characteristic Type. This system was adopted with slight modification by Johansen, who has enlarged it by subdividing each main Type into a number of *Variations*, and has added a sixth Type.

This scheme of classification is a practical or working classification, in the sense that it is based upon comparison rather than arrived at through the application of fundamental laws of development. Such laws are too little understood yet to permit of their being used to contruct a workable classification, though it has been attempted by Souèges in the treatment of his own extensive observations.

His laws are as follows. 1. The Law of Origin. In any particular species the sequences of cell formation may be established in such a manner that the origin of the cells may be defined in exact terms by referring to the one or to the other termini of the sequence. 2. The Law of Numbers. The number of cells produced by different cell generations varies with the species and depends on the rapidity of the segmentation in the cells of the same generation. This law expresses the various rates of division of different cells of the young embryo. 3. The Law of Disposition. The cells are constituted by divisions in clearly determined directions and appear to occupy positions in accordance with the part they must play in development. 4. The Law of Destination. In any given species the cells of the young embryo give rise to clearly determined parts and always to the same parts of the embryonic body. 5. The Law of Parsimony. This is added by Johansen. It follows the law of economy in reasoning known to philosophers as "Occam's Razor" which runs thus: "Entities are not to be multiplied beyond necessity." It is a very pertinent limitation in such a subject.

The classification proposed by Souèges is little more than an outline. He recognizes four categories. 1. Fundamental types or archetypes. 2. Secondary or derivative types. 3. Superposed types. 4. Irregular types, which are not definable under the laws.

The archetypes are considered under two main divisions, first, those in which the whole zygote conforms to the development laws and secondly those in which it is only the apical cell of the two-celled embryo which conforms to the laws and the basal cell does not contribute to the development of the embryo. These divisions are further divided into series and sub-series. Six principal or megarchetypes are recognized in each division and the series or sub-series are divided into groups in accordance with the archetypes.

This scheme has all the inflexibility of a logical deduction and it could only be used by one who had the vast experience of Souèges himself, as it presupposes a complete understanding of the operation of the laws.

Souèges has also devised a scheme of embryological formulae for the concise description of development. It is based upon a system of lettering which denotes each of the significant cells or regions of the embryo and all their derivatives. Thus, in the two-celled embryo the basal cell is called *cb* and the apical cell *ca*. Although it is an essential tool for the specialist we shall not attempt to use it here.

The system proposed by Johansen recognized the following types:

1. The Piperad type. 2. The Onagrad Type. 3. The Asterad Type. 4. The Caryophyllad Type. 5. The Solanad Type. 6. The Chenopodiad Type.

The names are obviously derived from the names of the families in which the type is most characteristically shown. The only change from Schnarf's Types is the substitution of Onagraceae for Cruciferae in the second Type, since *Capsella*, which was the basis of the Cruciferae Type, has an embryonic development which so far from being generalized, as was once supposed, is limited to the Brassicae and forms one Variation in the Onagrad Type.

Before considering the characters of these Types, there are two general comments to be made. One is, that it is principally the pro-embryo that is in question and it is on the early cell-divisions that the Types are based. When exactly the pro-embryonic stage ends and the embryo " proper " begins is not very clear, though the general idea is plain. Schnarf gives the term a very restricted application, limiting it to structures before any divisions occur which begin the development of the embryo proper. This stage is generally reached with the first longitudinal division of the terminal cell, which is a precise limitation. Souèges uses the term in a broader sense and classes as pro-embryo all structures formed while the radial symmetry is retained. Embryo formation thus begins for him usually with the initiation of the cotyledons, when radial symmetry is lost. Most writers seem to have adopted the latter view.

The second comment is that the various embryonic types show surprisingly little systematic affiliation. Thus under the Onagrad Type are included Variations found in no fewer than nine unrelated families of Dicotyledons and two families of Monocotyledons. The other Types are almost equally miscellaneous. Even in the same families there is no uniformity. Onagraceae are, as a matter of fact, fairly uniform, but Solanaceae shows six Variations within the Type family itself. Nor are the smaller units, the Variations, always systematically homogeneous. In most cases they are limited to a single genus or species, but, for example, the *Myriophyllum* Variation of the Caryophyllad Type includes, besides *Myriophyllum* itself, *Portulaca*, *Pyrola*, and *Samolus*. This is not a criticism of the classification as such, but it does show that embryology has a limited value as a systematic criterion.

The following are the characteristics of the six embryological Types as defined by Johansen.

A. *Piperad Type.* The zygote divides by a longitudinal wall.

B. The zygote divides by a transverse wall.

  I. In the second cell-generation the terminal cell divides longitudinally.

    Onagrad Type. The basal cell contributes little or nothing to the building of the embryo.

Asterad Type. The basal cell contributes to the building of the embryo.

II. In the second cell-generation the terminal cell divides transversely.

a. The basal cell contributes little or nothing to the building of the embryo.

Caryophyllad Type. The basal cell becomes a large suspensor cell usually without division.

Solanad Type. The basal cell forms a suspensor of two or more cells.

b. *Chenopodiad Type.* The basal cell contributes to the building of the embryo.

The *Piperad Type* is based on *Peperomia* (Fig. 1343) rather than on *Piper*, about which little is known embryologically. The Type includes *Balanophora* and *Scabiosa*.

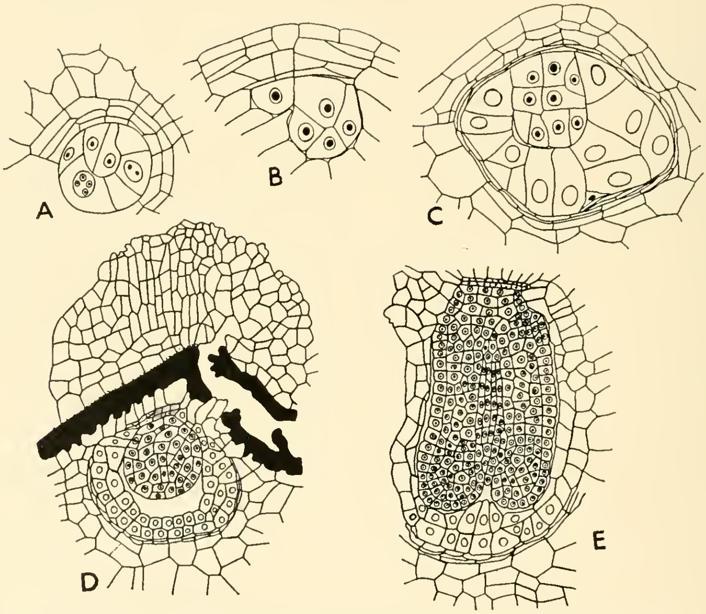

Fig. 1343.—*Peperomia pellucida.* Development of the embryo. A, Four-celled embryo surrounded by a few endosperm cells. B–E, Stages in embryo and endosperm development. (A *after Campbell, the rest after Johnson.*)

The *Onagrad Type* is fairly widespread and is more or less uniform in the Onagraceae. In this Type are also included: *Euphorbia*, *Capsella* (Fig. 1344), *Lythrum*, *Mentha*, *Veronica*, *Trifolium*, *Lilium*, and *Juncus*, as well as a number of other genera, each distinguished by some Variation.

The *Asterad Type* includes almost all the members of the Compositae which have been examined and the following well-known genera, as Variations: *Erodium*, *Polygonum*, *Urtica*, *Lamium*, *Oxalis* and *Poa* (Fig. 1345).

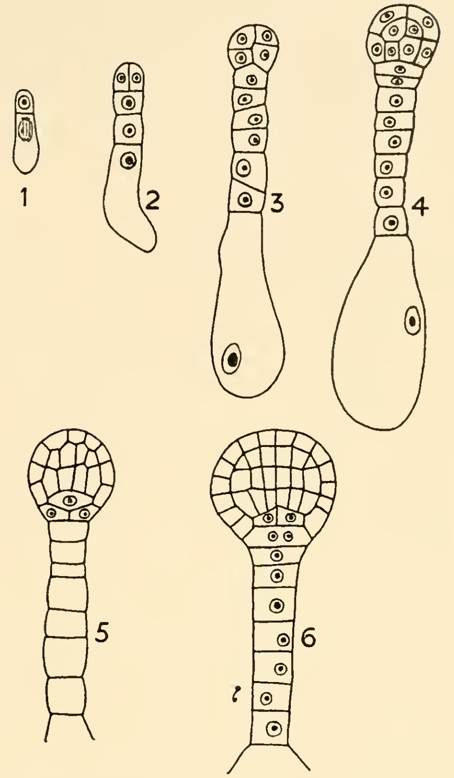

FIG. 1344.—*Capsella bursa-pastoris.* Development of the embryo (Onagrad Type). (*After Souèges.*)

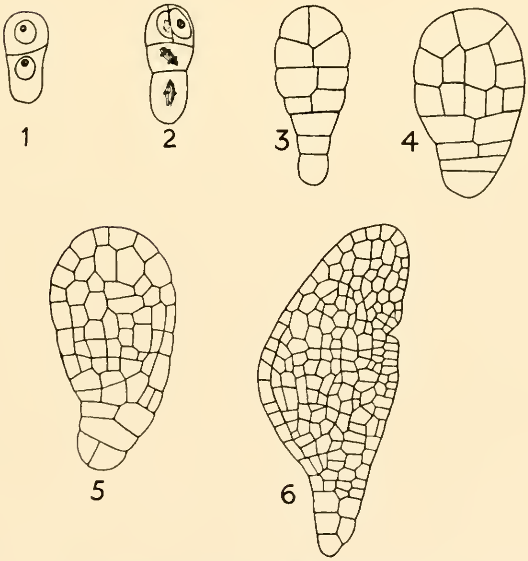

FIG. 1345.—*Poa annua.* Development of the embryo (Asterad Type). (*After Souèges.*)

The *Caryophyllad Type* includes both dicotyledonous and monocotyledonous genera. The Type was based on *Sagina* (Fig. 1346) but the same features, with Variations, are shared by: *Corydalis*, *Medicago*, *Myriophyllum*, *Drosera*, *Ruppia*, *Zannichellia* and *Sagittaria*, among others. As pointed out above, the *Myriophyllum* Variation is systematically heterogeneous.

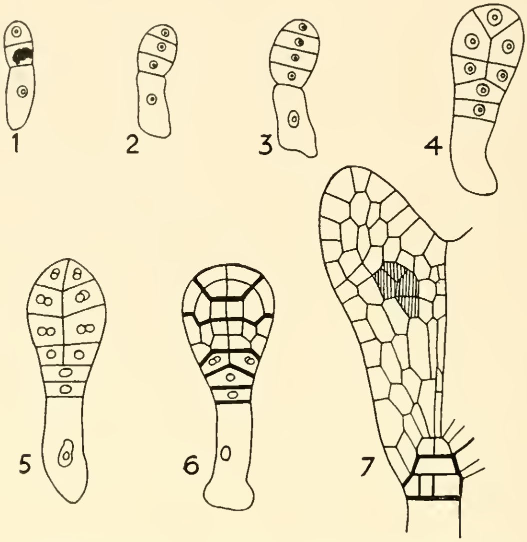

FIG. 1346.—*Sagina procumbens.* Development of the embryo (Caryophyllad Type). (*After Souèges.*)

The *Solanad Type* is distinguished by a linear tetrad of cells forming a constant stage of the pro-embryo, though in *Hydnora* the linear pro-embryo may become fifteen cells long. There are six Variations within the Type family, based respectively upon *Hyoscyamus*, *Datura* and *Nicotiana* (Fig. 1347), together with three Variations in the single genus *Physalis*. Apart from Solanaceae the Type includes *Papaver*, *Sherardia* and *Linum*.

The *Chenopodiad Type* is based on *Chenopodium* (Fig. 1347), with which *Beta* agrees in the main. The Type is not very common and the only other known genera which are included are *Myosotis* and *Polemonium*.

There can be no doubt that as investigation progresses these lists of genera (which are only those most widely known) will be greatly extended, but it is to be expected that many more anomalous or intermediate Variations will be discovered which may necessitate a revision of the system of classification. Moreover, it is by no means certain that Součge's Law of Destination holds good in all cases. There are some contrary observations. The techniques which make possible the cultivation of embryos *in vitro* have introduced the use of experimental methods, which have proved illuminating in Zoology. They should have interesting results among plants.

Many families in which the saprophytic or parasitic habits of life

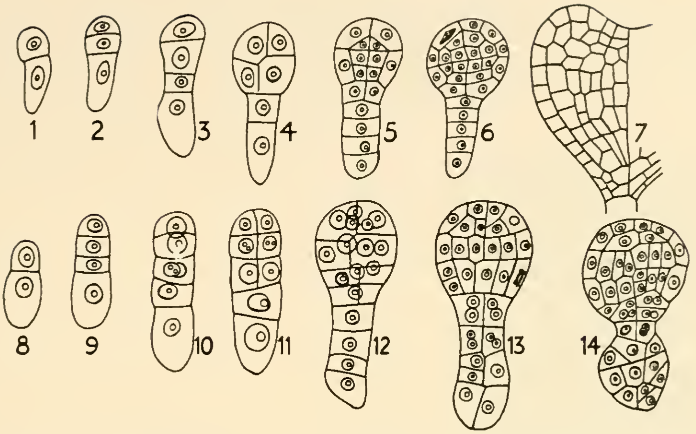

FIG. 1347.—*Nicotiana* sp. 1–7, Development of the embryo (Solanad Type). *Chenopodium bonus-henricus*. 8–14, Development of the embryo (Chenopodiad Type). (*All after Souèges.*)

including the mycorrhizal habit, are established, produce embryos which are incompletely differentiated in the seed and only develop fully after germination. Such are the Balanophoraceae, Rafflesiaceae, Pyrolaceae, Orobanchaceae and Orchidaceae. The pro-embryonic stages may be carried out normally but development is arrested, sometimes as early as the four- or five-cell stage, in other cases only after a multicellular body has been formed but without any differentiation of cotyledons and radicle or even of the primary cell-layers (Fig. 1348).

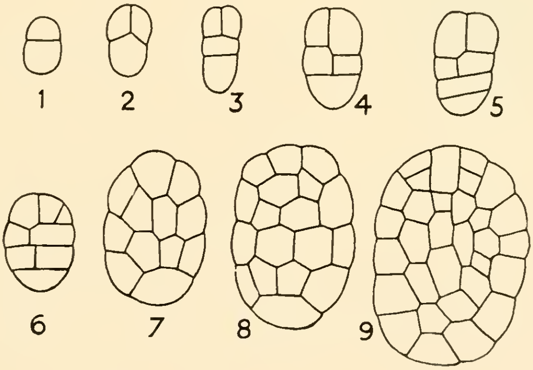

FIG. 1348.—*Epipactis palustris*. Development of the embryo up to the stage at which the seed is shed. (*After Treub.*)

In Orobanchaceae this arrested development is associated with a very tardy beginning of zygote division, when the endosperm is already well advanced, but in Orchidaceae the endosperm development is early arrested or suppressed. Although undifferentiated embryos are so constantly associated with heterotrophic nutrition, this is not so invariably. For example, they are also known in *Ranunculus ficaria* and in *Corydalis cava*, both autotrophic species, and in *Thismia americana*, which unlike other members of the Burmanniaceae is not saprophytic but which shares the family character of an embryo arrested at a very early stage. On the other hand the embryos of the parasitic Loranthaceae and Santalaceae, though in some respects anomalous, do not appear to be arrested.

FIG. 1349.—*Capsella bursa-pastoris*. Section of ovule with developing embryo, showing suspensor formed of a column of cells with a much enlarged basal cell.

The term **suspensor** is applied to the structures produced from the " basal " cell formed at the first division of the zygote, in other words the cell nearest to the micropyle. It may consist only of one much enlarged cell, as in embryos of the Caryophyllad Type, but more usually it consists of a row of cells, or even of a multicellular mass, forming a sort of pedestal to the embryo proper, and serving to attach it to the micropylar end of the embryo sac (Fig. 1349). It is a very variable organ, for it serves not only as an attachment for the embryo, a requirement that does not seem to be always necessary, but also, in many instances, for the conveyance of nutriment to the embryo. In many species the cells of the suspensor elongate in a manner which recalls the lengthy suspensors common among Gymnosperms, pushing the pro-embryo downwards into the midst of the endosperm. This is characteristic of the long narrow embryo sacs of the Sympetalae. The embryo in such cases is presumably capable of absorbing nourishment from the endosperm directly through its own surface and the function of the suspensor is purely mechanical. Such suspensors may either shrivel up when their function has been accomplished, or they may remain, as in *Trapa natans*, even to the maturity of the seed, being compressed by the growth of the embryo into a solid cap over the tip of the young radicle. Some of the longest known suspensors are found in members of the Loranthaceae, such as *Dendrophthoe*, where the embryo sacs penetrate far up the style. After fertilization the suspensors push the pro-embryos right down into the ovary, there to complete their development.

Elongated suspensors may also play a part in embryo nutrition. This is conspicuously so in the Papilionaceae (Fig. 1350), where the suspensor cells multiply and enlarge so that each cell may become larger than the entire embryo and, as in *Pisum*, extensively multinucleate. In *Phaseolus* and *Cytisus*, on the other hand, the cells remain uninucleate but multiply to form a considerable mass of tissue. The cells of these suspensors are rich in starch and there can be little doubt that they take part in the absorption of the endosperm.

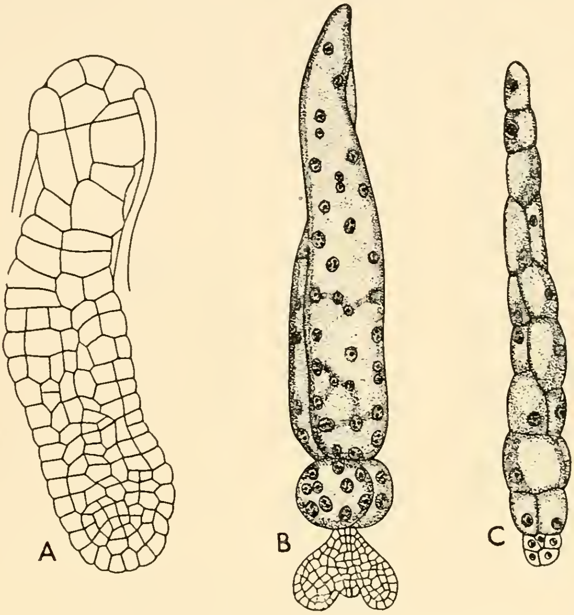

Fig. 1350.—Enlarged suspensors in Papilionaceae. A, *Phaseolus multiflorus*. Suspensor and embryo not clearly separable. B, *Orobus angustifolius*. C, *Cicer arietinum*. (*After Guignard.*)

The great majority of plants have relatively small suspensors, consisting of a short column of cells without any special differentiation and distinguished only from the meristematic cells of the embryo by their more mature, vacuolated aspect. Indeed in some massive suspensors, where the cells are small, *e.g.*, *Phaseolus*, there is no sharp division between the suspensor and the embryo, at least in early stages. That the purely supporting function of a suspensor is not indispensable is shown by the absence of any suspensor in most Araceae, in many Orchidaceae and in a variety of other unrelated genera.

The most remarkable suspensors are those which develop haustoria, either within the endosperm, or, frequently in association with poorly developed endosperm, outside the ovule. The simplest form of suspensor haustorium is the enlarged single cell which forms the suspensor in the Caryophyllad Type of embryo. This cell usually has a large and prominent nucleus and has been shown in some cases to contain aleurone grains as a food reserve. A similar enlargement of the lowermost cell of a columnar suspensor may also occur, as in *Capsella*, and may show aggression, encroaching on the tissues of the inner integument.

True haustorial outgrowths from suspensor cells were first noticed in certain Orchids, *e.g.*, *Phalaenopsis* and *Stanhopea*, and have since been found in several other families. One of the most remarkable developments among Orchids is found in *Herminium monorchis*. The extension in length of the suspensor pushes its basal end out through the micropyle. The cells thus exposed enlarge and send out numerous tubular haustoria which grow to a great length. Treub describes these filaments, coming from all the fertilized ovules, as forming an inextricable tangle involving the ovules and the funicles and smothering the placenta.

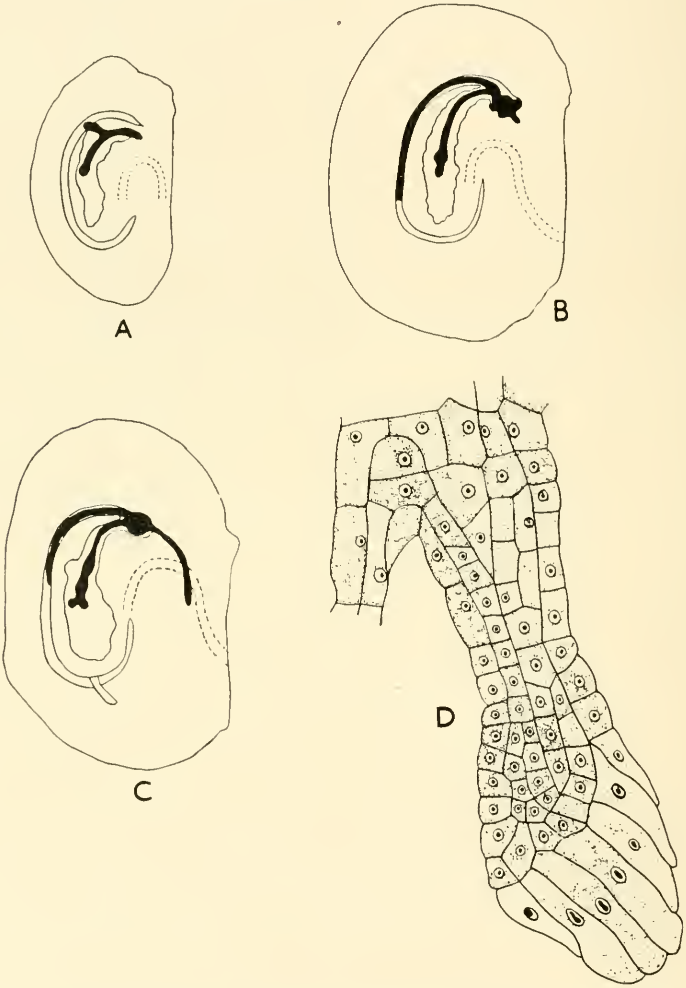

Fig. 1351.—*Tropaeolum majus*. Longitudinal sections of the carpel showing, in black, successive stages in the branching of the suspensor haustorium. A, In the ovule. B, In the carpellary cavity. C, In the funicle and placenta. D, Detail of apex of the haustorial branch in the carpellary cavity. (*After Walker.*)

The Rubiaceae, the Crassulaceae, and the Papaveraceae provide many examples of suspensor haustoria; but the case of *Tropaeolum majus* deserves more than a mention (Fig. 1351). The embryo sac penetrates the chalaza and forms a large chalazal sac in which the embryo, with its massive cotyledons, develops. From the base of the suspensor two haustoria arise. The first grows out through the micropyle and passes over the outside of the ovule, eventually penetrating the ovary wall. The second is directed into the funicle where it enters a cleft alongside of the funicle bundle and this it follows for some distance into the placenta.

Finally we would call attention to the case of *Sempervivum*, where haustorial processes are produced by the zygote before division or even by the oosphere before fertilization and reach an extensive development in the nucellus and integuments before embryo formation begins.

The occurrence of more than one embryo in a seed, a condition called **polyembryony,** has been known and remarked since pre-scientific times. Many of such cases owe their origin to apomixis and will be dealt with later. Two or more embryos may, however, arise in the same embryo sac as a result of fertilization and this is quite a distinct condition. It may originate in several ways (Fig. 1352). In some cases it arises from the division of the zygote itself but the number of known examples is not large. The first to be revealed was *Erythronium americanum* and similar conditions have later been found in *Tulipa gesneriana*, *Limnocharis emarginata*, *Vincetoxicum nigrum* and *V. officinale* and in *Habenaria platyphylla*. Whether it is of constant occurrence in all these species or not, is uncertain. The basal cell of the two-celled zygote divides repeatedly to form an irregular mass of cells called an "embryogenic mass", and several individual cells of this mass may produce embryos which are twins of the normal embryo. In *Habenaria* it is certain that only one of these embryos survives in the mature seed. In other species, twin embryos may occasionally survive.

True cleavage polyembryony, due to the splitting of the zygotic embryo into two or three at an early stage, has been recorded as an abnormality in several species, *e.g.*, *Empetrum nigrum*, but it occurs more regularly in some of the Orchids and in *Linum usitatissimum*. It is a rare phenomenon in Angiosperms. Budding of accessory embryos either from the primary embryo itself (*Eulophea* in Orchidaceae) or from suspensor cells (*Lobelia syphilitica*) is probably only an abnormality.

Secondly, accessory embryos may originate from other cells of the gametophyte in addition to the normal oosphere. Double oospheres have been recorded but their development is not known. More frequently, one or more synergidae may develop into embryos, either after fertilization by a second pollen tube, or without fertilization, as happens in *Linum usitatissimum*, where in certain strains a very small percentage of haploid-diploid twins occur. Other recorded instances are: *Poa alpina*, *Allium odorum*, *Iris sibirica* and *Lilium martagon* as well as several of the apomictic genera, *e.g.*, *Hieracium*.

The antipodals may occasionally also be fertilized and form accessory

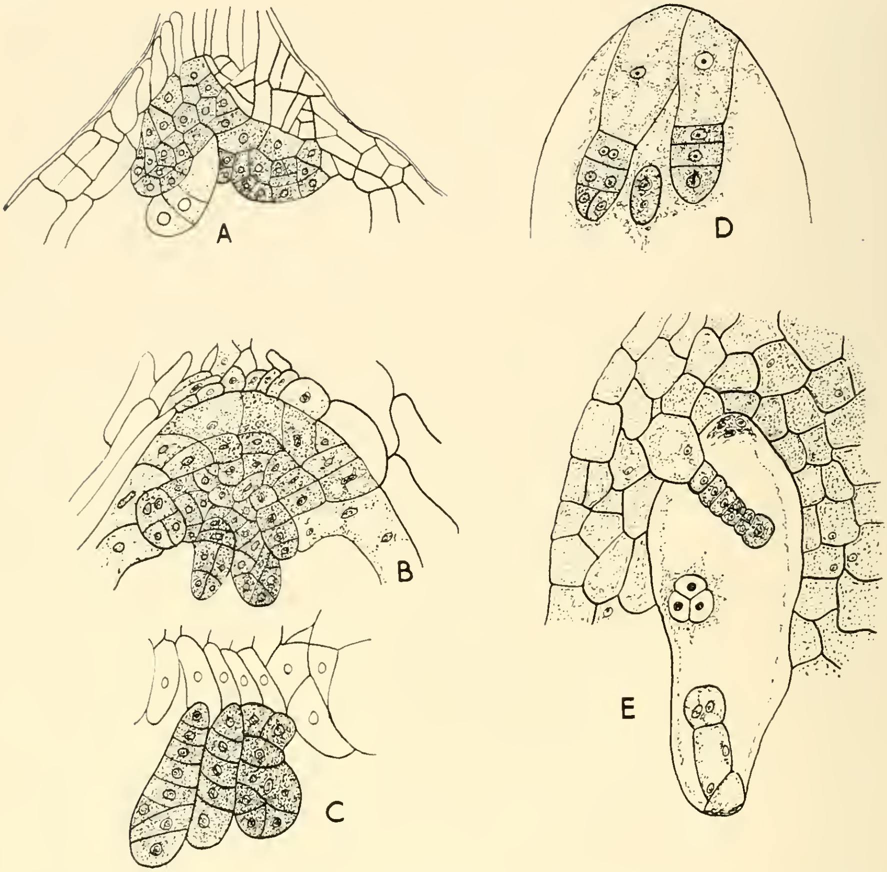

FIG. 1352.—Anomalous embryo formation. A, *Funkia* (*Hosta*) *ovata*. Weak embryo from the oosphere, two adventitious embryos growing from the nucellus. B, *Erythronium americanum*. "Embryogenic mass", arising from basal cell of the divided zygote, forming four embryos. C, *Allium odorum*. Three embryos derived from antipodal cells. D, *Naias major*. One embryo from the oosphere, the other from a synergid. E, *Alchemilla pastoralis*. One embryo from an unfertilized oosphere, another arising from the nucellus. (*From various sources.*)

embryos. This has been seen in *Allium odorum*, *Elatostema* (Urticaceae) and in *Ulmus*, where the antipodal cells resemble oospheres (see Fig. 1333). The subsequent fate of these embryos is not known, but their survival is improbable.

Doubling of the embryo sac in one nucellus occasionally happens, where the archesporium is multicellular and more than one cell develops into a mature sac (Fig. 1353). Instances have been previously cited. The development into embryo sacs of more than one megaspore of the normal tetrad is also not uncommon, *e.g.*, *Poa alpina*. Usually competition limits the further development of all but one of the sacs present and polyembryony of the seed has not been definitely traced to such an origin.

All other cases, where embryos arise adventitiously, *i.e.*, outside the embryo sac, we have classed with apomictic phenomena. A clear division is not always possible (*e.g.*, the development of unfertilized synergidae is really apomictic) and it is undesirable to try to classify cases of polyembryony into "true" and "false". Nevertheless embryos arising outside the embryo sac, that is from sporophyte cells, are clearly in a different category from those arising, in whatever way, from gametophytic cells, even when the sporophytic embryos invade the embryo sac and develop inside it.

The term **apomixis** in its widest sense covers all non-sexual methods of reproduction and therefore logically includes vegetative propagation and reproduction by non-sexual spores, etc, in Cryptogams. There is a good scientific sanction for this usage, since extensive vegetative reproduction is linked in many species with failure or abnormality of the sexual process. The older and narrower use of the term confines it to cases where a sexual mechanism exists but functions without sexual fertilization taking place, as the word itself, signifying "away from mingling", implies. It is in this sense that we use it here. If the wider concept of apomixis be adopted, the more restricted phenomena are called **agamospermy**, a term that may be criticized on the ground that it does not cover aposporic reproduction in Ferns, which is biologically similar.

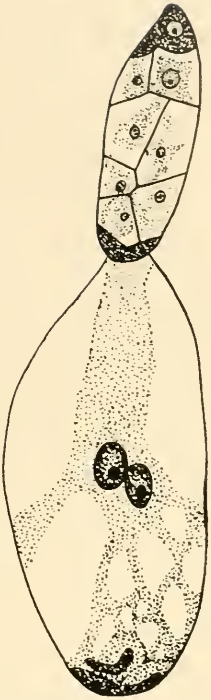

FIG. 1353.—*Nelumbo lutea.* Two embryo sacs in axillary order and with reversed orientation, the oosphere in the smaller sac being at the chalazal end. (*After M. T. Cook.*)

Several other terms are in use in this connection, which it is well to get clear.

Diplospory. A diploid embryo sac is formed directly from a megaspore mother cell, and an embryo is formed from the diploid oosphere without fertilization. Sometimes called somatic parthenogenesis or diplo-parthenogenesis.

Apospory. A diploid embryo sac is formed from a somatic cell, *e.g.* of the nucellus. Embryo development as above.

Parthenogenesis. A haploid oosphere is formed and develops an embryo without fertilization. (Diplo-parthenogenesis, if the oosphere is already diploid.)

Apogamy or *Apogamety.* One of the cells of a haploid or diploid gametophyte, apart from the oosphere, develops an embryo without fertilization.

Adventitious Embryony. Embryos are produced directly from somatic cells of the nucellus or integuments and develop usually within the embryo sac. This is really one form of vegetative reproduction and is closely linked to *Vivipary*, in which embryonic plants arise vegetatively from floral parts, often in replacement of the whole or part of the flower.

Pseudogamy. Certain apomictic plants (*e.g.*, species of *Rubus*) require pollination to enable them to produce embryos, although no fertilization takes place.

There are thus three ways in which agamospermy may occur: diplospory followed by diplo-parthenogenesis or apogamy; apospory followed by parthenogenesis or apogamy; and adventitious embryony.

The prevalence of apomixis, especially in certain genera, raises numerous points of theoretical importance, some of which we shall discuss in Volume III under Genetics. One of the first to occur is the question whether a diploid oosphere is to be reckoned as sporophytic or gametophytic, or, in other words, whether the haploid condition is the essential feature of a gametophyte. If the diploid oosphere is simply a special type of somatic cell, then its offspring should be the same as those arising from adventitious embryony, of which it is simply a special case. Winkler has shown that this is not so. The offspring of true adventitious embryos always exactly resemble the female parent but in dioecious species such as *Thalictrum fendleri*, the offspring of diploid oospheres comprise both male and female plants, while in *Bryonia dioica*, the offspring may be wholly male, as in parthenogenetic animals. Further, adventitious embryony is almost always accompanied by polyembryony, parthenogenesis never.

Strasburger showed that apomictic genera are characterized by high chromosome numbers, or as would now be said, they are polyploids. They also, as Ernst showed, behave in many ways like hybrids, although hybridity, apart from polyploidy, is not itself a cause of apomixis. In this connection the taxonomic aspects of apomixis are of the highest interest, especially from the point of view of the origin of species. It has long been known that some genera are taxonomically divisible into a great many units, differing only in minor characters but showing a high degree of constancy. These are called "micro-species", and they form polymorphic species complexes. At the beginning of the century it was shown by Juel and Murbeck that two of the species complexes, those of *Taraxacum* and *Hieracium*, were characterized by apomixis and investigation has shown that this is also true of other genera in which such species complexes exist. A number of important European genera are in this category : the two mentioned above and *Potentilla*, *Alchemilla*, *Sorbus*, *Crepis*, *Rubus*, *Rosa*, *Poa* and *Calamagrostis*, as well as others, while many more no doubt exist in other floras, *e.g.*, *Elatostema*.

In *Rubus*, as in some other genera, there are a few, original, diploid species which are fully sexual, but the greater number of the "species" are polyploid and apomictic. As in *Hieracium*, however, the apomictic species also produce some haploid, fertilizable embryo sacs. Cross-pollination therefore results in two kinds of offspring: purely matroclinous forms, which are pseudogamously produced from diploid oospheres, and also true sexual hybrids. The latter can subsequently perpetuate themselves apomictically and form new taxonomic units.

The great majority of apomicts produce their embryos in one way or another from diploid nuclei, *i.e.*, parthenogenesis is accompanied by apospory or diplospory. The occurrence of " true " parthenogenesis of a haploid oosphere, at least under natural conditions, is doubtful and the evidence rests largely on supposition. Direct observation has occasionally shown divisions in unfertilized oospheres, but there is no evidence that they proceed to form viable embryos. One of the most interesting experiments in this connection was the pollination of isolated female flowers of *Humulus lupulus* with pollen of *Urtica* and *Cannabis*. Embryos in young seeds were produced, though there was no evidence of fertilization and no endosperm was formed. The embryos, however, all died without germination. *Solanum nigrum* pollinated with *S. luteum* pollen has, however, produced about 20 per cent. of viable haploid offspring and haploid plants have also been raised in *Datura* and *Nicotiana* as a result of pollination with "foreign" pollen. In the case of *Solanum*, pseudogamy could be proved. Pseudogamous stimulation of haploid embryo development has also been proved in several Orchids but it is not known if these embryos can survive.

An apparently good case of haploid parthenogenesis has recently been described by Lindstrom and Ross. A tomato plant with twelve univalent chromosomes arose from a haploid oosphere. There was a high degree of microspore abortion but self-pollination gave a few diploid seedlings, which were fertile. Adventitious shoots arising from the callus of cuttings were frequently diploid, apparently due to the refusion of dividing nuclei in the callus cells. These shoots were, of course, completely homozygous.

The origin of diploid embryo sacs is a matter of some interest. They are formed either from a complete megaspore mother cell, or from a dyad cell after one division of the mother cell. The absence of chromosome reduction is accounted for by one of three distinct processes. (1) The first division of the nucleus in the megaspore mother cell is a somatic mitosis. (2) The first division resembles a first meiotic division (heterotypic) but the chromosomes at anaphase come together again to form a single, diploid restitution nucleus. (3) The first division is pseudo-homotypic with contracted chromosomes but there is no bivalent formation, no chiasmata, and the chromosomes split at metaphase. All three types may occur in the same species if the mother cell is directly transformed into an embryo sac. If the mother cell forms a dyad of cells of which one develops into an embryo sac, then its division follows patterns (2) and (3) only.

Apospory was first described by Rosenberg in *Hieracium flagellare*, in which a somatic cell near the normal spore-tetrad enlarges into a diploid embryo sac, either along with or in substitution for a normal haploid sac formed from a spore (Fig. 1354). Numerous other cases are known including the genera *Malus*, *Crepis*, *Hypericum*, *Poa* and *Ranunculus*. In

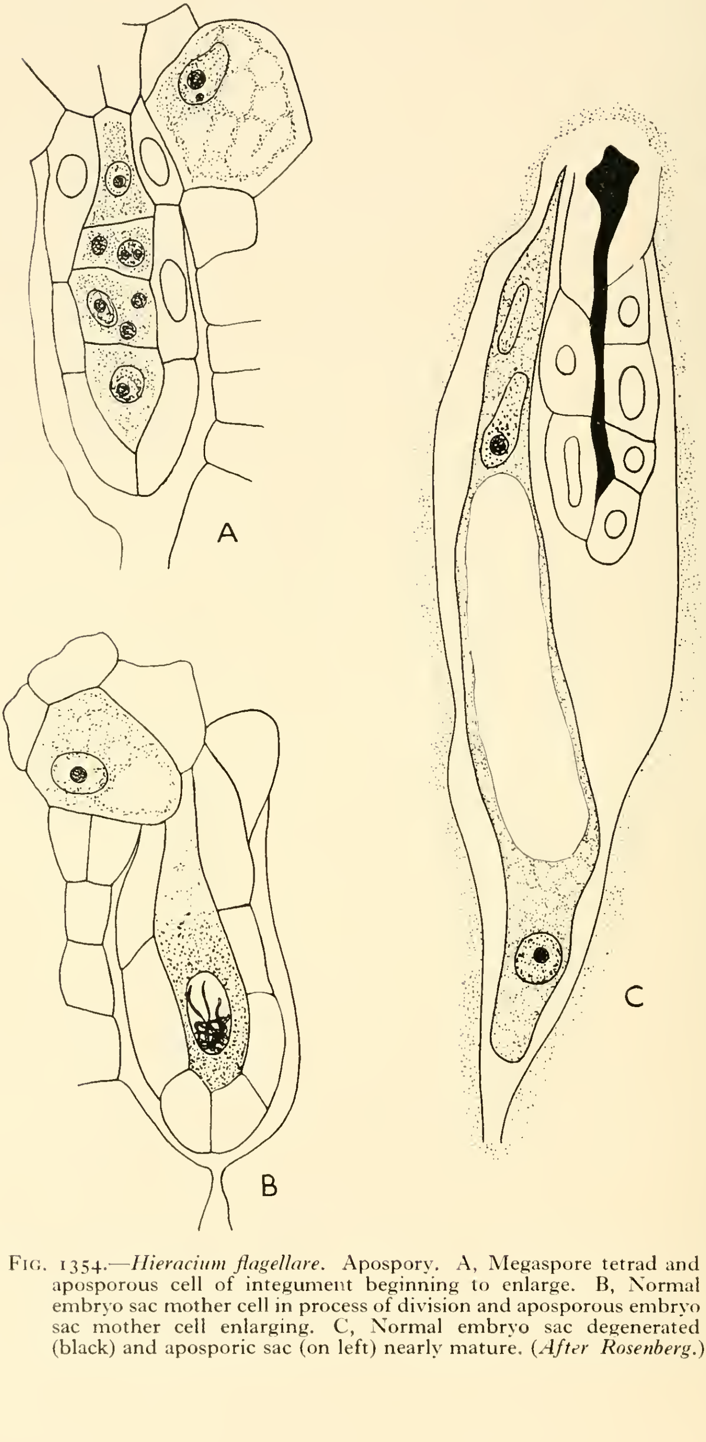

FIG. 1354.—*Hieracium flagellare*. Apospory. A, Megaspore tetrad and aposporous cell of integument beginning to enlarge. B, Normal embryo sac mother cell in process of division and aposporous embryo sac mother cell enlarging. C, Normal embryo sac degenerated (black) and aposporic sac (on left) nearly mature. (*After Rosenberg.*)

Alchemilla and *Potentilla*, where there is a multicellular archesporium, there may also be multiple embryo sacs which are not aposporic. A number of archesporial cells enlarge and become mother cells and may develop into embryo sacs either with or without meiosis. In spite of this there is seldom polyembryony.

The genus *Citrus* has long been known for the frequency of polyembryony in the ripe seeds. This is associated usually with the formation of adventitious embryos from nucellar cells around the embryo sac (Fig. 1355). Two or three embryos are commonly formed, but more than ten may occur in one seed, some of them very small. Competition eliminates some at early stages. Pollination seems to be necessary, even though, in some varieties, the pollen may be "foreign". A normally fertilized embryo is generally present and the fertilized oosphere may occasionally split to yield true twins. It is notable that the adventitious embryos are often clustered round the sexual embryo as if it provided a stimulus to their development. The formation of endosperm, following fertilization, seems to be essential if any of the embryos are to complete their development. Whether adventitious embryony is to be regarded simply as one method of vegetative propagation or not, raises difficult questions. In *Citrus*, at any rate, long continued propagation by cuttings leads to senility, while reproduction from adventitious embryos does not. The following genera may be added to *Citrus* as showing adventitious embryony conspicuously: *Mangifera*, *Opuntia*, *Euonymus*, *Ficus*, *Clusia*.

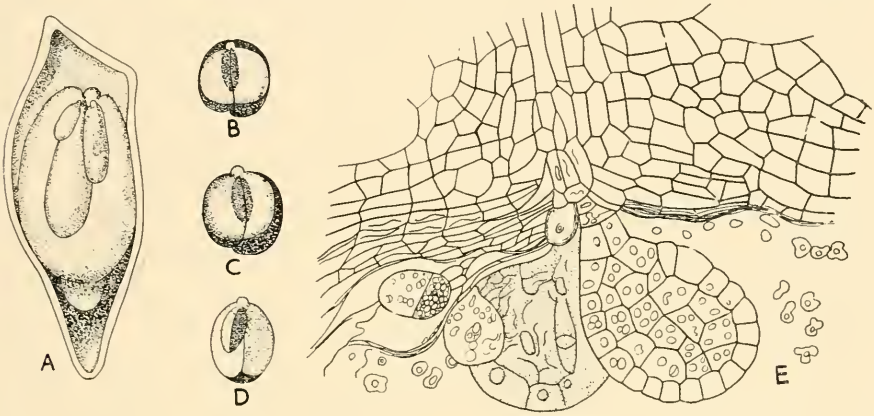

FIG. 1355.—*Citrus aurantium*. Polyembryony. A, Several embryos of different sizes in one seed. (*After Penzig.*) E, Embryo sac with normal embryo (right) and a group of adventitious nucellar embryos (left). (*After Strasburger.*) B to D, *Esenbeckia grandiflora*. Three embryos from one seed. (*After de Jussieu.*)

The causes of sexual sterility in Angiosperms are so varied that no simple theory of the origin of apomixis can be given. That it is closely related to polyploidy is well established. So is the perennial habit, to which vegetative means of propagation are related. Direct observation tends to confirm the conclusion that vegetative propagation and seed fertility are inversely related.

Yet although polyploidy is a concomitant of apomixis it does not necessarily determine it, since many polyploids are sexually fertile. It simply provides the genotypical background on which apomixis may arise. Apomixis signifies a departure from sexual crossing in the direction of vegetative means of dispersal and any hindrance to meiosis, climatic or otherwise, may influence the balance in this direction, turning sexual diploids into polyploids which are at least facultatively apomictic. The polyploid oosphere escapes fertilization by rapid division. The haploid oosphere has a relatively long resting period, which allows a necessary interval of time for the completion of the fertilization processes, but in parthenogenetic apomicts division of the oosphere may begin without any resting stage and developing embryos may be already present at anthesis.

The subjects of apomixis, polyploidy and vegetative propagation have important bearings on plant distribution and we shall revert to the subject in the next volume.

Fertilization has many consequences in the flower apart from the production of an embryo. Ovules grow into seeds, ovaries grow into fruits and vegetative parts are often involved in this development as means of protection or dispersal. Most of these phenomena will be touched upon in the next chapter. There is one phenomenon which is somewhat distinct from these, however, and that is the withering of the perianth. This is sometimes accelerated by pollination (Orchidaceae) and is sometimes independent of it (*e.g.*, *Cichorium*). Though the causation of flower withering has for long excited attention, it cannot be said that any clear explanation is yet forthcoming. It has been established that the fate of the perianth is decided before anthesis, except in flowers like the Orchids where the onset of moribundity dates from pollination. It is not due to starvation, since part of the carbohydrate content of the perianth usually remains unused. Low concentrations of cyanide, anaerobic conditions and low temperatures increase the lifetime of the perianth if applied immediately the flower opens. At later times their effect is quantitatively lessened. Oxidative processes, involving protein breakdown, are apparently inaugurated before anthesis and can be retarded but not reversed.

There is a marked export of Nitrogen, of carbohydrates and of minerals, including Phosphorus, Potassium and Magnesium, before withering. The CN-sensitive oxidation removes something that the flower has only in a limited amount and which is non-importable. The osmotic potential of the cells decreases markedly and at the onset of withering the petal cells are plasmolysed.

The protein breakdown is only the first link in the chain and it may be that there is a poisoning effect by some protein derivative shortly before final withering. On the other hand some flowers (*e.g.*, *Rosa*) abstrict their petals by the formation of an abscission layer before any external change is apparent.

CHAPTER XXVI

SEEDS, FRUITS AND SEEDLINGS

The two primary consequences of fertilization are the development of the embryo and of the endosperm but with these events there are linked a number of other developments which generally do not take place, or do not take place in the same way, unless a viable embryo is present. First in immediacy is the change of the ovule into a seed and secondly, though often contemporaneous, is the change of the ovary into a fruit. Along with these there often go changes in other floral parts: changes in the calyx, changes in the floral axis, even sometimes changes in the involucral bracts; which fit them to take part in the protection or dispersal of the fruits.

The mature seed is covered externally by a hard or leathery coat, the **testa**, which is the product of one or both of the integuments. Its colouring and surface texture are extremely variable in different plants but show a recognizable generic and even familial constancy. The position of the micropyle is often evidenced by a slight depression in the testa, but the most conspicuous mark externally is the scar left by the detachment of the funicle, known as the **hilum**, which is often coloured differently from the rest of the seed. Seeds of Papilionaceae usually have a very long hilum, sometimes extending nearly round the seed, due to the fact that the funicle, instead of merging into the raphe, is flattened and expanded at the top so that it clasps the seed along a wide arc of its circumference. In the case of anatropous seeds, the micropyle is at one end of the hilum and at the cther end, in the seeds of some families, is a small, elongated depression, surrounded by a ridge. This is the point traversed by the vascular bundle of the funicle, entering the raphe. It is important because it constitutes a break in the waterproof coverings of the seed and when it is present is the primary channel of rapid absorption of water before germination. In the majority of seeds the primary penetration of water is through the micropyle, but in some hard and resistant seeds there is no special channel of entry, and water can only penetrate if the testa is either softened or mechanically damaged.

The hilum may play a significant part in the loss of water from the ripening seeds. Evaporation is general from the testa until the water content drops to about 15 per cent., when the testa becomes impermeable. At a water content of about 25 per cent. a shrinkage cleft may open along the median line of the hilum and evaporation continues through this cleft until further shrinkage brings its edges together and finally seals the seed against further water loss.

Hairy coverings on the seed coat are not common, except in Malvaceae, but many seeds have long hairs attached to one end of the seed (*e.g.*, *Epilobium*, *Salix*, *Asclepias*) which aid in the dispersal of the seeds by wind. These outgrowths may be classed as arils. They arise sometimes around the micropyle (*Asclepias*) or from the chalaza (*Epilobium*). Exceptionally the testa may be soft, thick and fleshy or gelatinous, instead of hard. A good example of the former is the seed of *Magnolia*, and of the latter that of *Punica granatum*, the Pomegranate. Such seeds are usually dispersed by birds. Mucilage coatings will be dealt with later.

FIG. 1356.—*Odontoglossum* sp. Ripe seeds with loose, membranous testas and minute undifferentiated embryos.

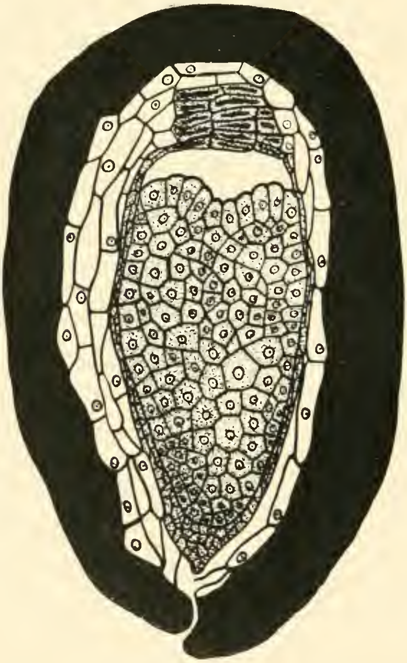

FIG. 1357.—*Vanilla planifolia*. Longitudinal section of mature seed. The outer integument remains intact, its outer layers becoming sclerotic and opaque. The inner integument is only a thin, crushed layer round the embryo. Note the prominent hypostase at the chalazal end. (*After Swamy.*)

The seeds of Orchids (Fig. 1356) (with the exception of those genera having fleshy fruits, such as *Vanilla* (Fig. 1357)) are exceptional in having a thin, papery and transparent testa, consisting of the epidermis of the outer integument, which forms a loose sack. The outer cell walls usually disappear, but the side and inner walls are cuticularized. The protection of the embryo is assisted by the development of a cuticle around the embryo itself.

Thin and papery testas are also characteristic of the solitary seeds of drupe fruits and other indehiscent fruits such as akenes, in which the protective function has been assumed by the stony endocarps or the pericarp as a whole. Likewise, in most Gramineae and Compositae the integuments do not develop into a testa but disappear, and the closely adherent pericarp forms the protection around the embryo and endosperm. Naturally ovules which have no integuments, such as those of the Santalaceae and

Loranthaceae, in which, indeed, there may be no proper ovules, cannot form true seeds, and the pericarp is, here also, the chief protective covering, though both embryo and endosperm may be cuticularized.

The external form of seeds depends on the size and form of the ovary. If they develop in a roomy loculus without overcrowding, they tend to be spherical, but narrow carpels or crowded ovules result in flattened or otherwise distorted seed forms, especially if the seeds are large. The size of seeds is also largely a resultant of their conditions of growth. In plants with very numerous seeds they are generally small (*Hypericum*, *Jasione*, *Digitalis*, *Orchis*); the less numerous seeds of Papilionaceae are large, while the largest seeds are usually solitary. The extreme in this direction is reached in the Palms, such as *Cocos*, and the gigantic seed of *Lodoicea*, which weighs up to 15 kilogrammes, is the largest of all.

The coloration of seeds is occasionally brilliant, either uniformly or in patterns. Whether this has any relation to dispersal by birds or other animals is, in most cases, doubtful. Information on this point is scanty and has been sometimes supplemented by imagination, but undoubtedly many highly coloured seeds are either inedible or are easily destroyed in the crops of birds or are digested by mammals.

Although a number of dimorphic fruits are known, very few plants have dimorphic seeds. A good example is *Plantago coronopus*, the capsules of which contain four large seeds, one in each loculus, and a single, small seed, of different shape, borne, in one loculus only, near the top of the central placenta. When the capsule dehisces the small seed is carried away with the detached lid of the capsule. The small seeds differ from the large seeds in their capacity for prolonged flotation, in the small amount of epidermal mucilage formed and in their delayed germination. These characters suggest a difference in biological function as well as in morphology.

Within the testa, the seed contains the embryo plant, generally in a dormant condition, and the endosperm tissue. In a number of seeds there is also a perisperm, a nutritive tissue formed by a development of the nucellus. If neither of these two tissues is present, the embryo, usually with enlarged cotyledons, fills the whole seed. The heavy thickening of the cell walls in the testa and the large quantity of solid food reserves deposited in the nutritive tissues imply that there is a relatively small water content and in many seeds it amounts to less than 10 per cent. of the whole weight.

The simple histological structure of the integuments in the young ovule presents a striking contrast to the complexities found in the ripened testa. Little change is visible until the development of the embryo is well advanced, but there may be a considerable amount of breakdown and absorption, which affects not only the nucellus but the inner portions of the inner integument. In some cases the whole of the inner integument and part of the outer integument as well may disappear. Thus the testa may be developed from only a part of the original integuments.

Where only one ovular integument is present it is generally absorbed in part, so that the testa only consists of the remainder of the tissues and the inner epidermis of the integument, *e.g.*, in Polemoniaceae and Plantaginaceae, is generally the thickened and most protective layer. In Linaceae, however, it is the outer epidermis of the nucellus which forms the protective layer, the integument being thin and weak.

In seeds produced by bitegminous ovules, the two integuments may remain separate and distinct, or they may become one tissue, or one or other of them may disappear in whole or in part. In the first case the inner testa, which is usually the thinner of the two, has been called the *tegmen*. The outer layers of the nucellus may also take part in forming the inner covering.

The histological structure of seed testas is immensely variable and is just as much an expression, though in a small compass, of specific and generic differences as any other part of the plant's structure. We must confine ourselves to one or two leading characteristics. There is usually an outer cuticle, which in some seeds may be replaced by, or combined with, a pectic or mucilaginous surface. There is also invariably at least one protective layer of highly thickened cells which may be formed from any layer of either integument. Sometimes there may be two or more thickened layers and the protection they afford is often supplemented by fatty cuticles, either between the integuments or on the inner side of the inner integument. Cutin, indeed, may appear in greater or less amount in the walls of all the cell layers. Commonly, there is also a layer, which may be several cells thick, of thin-walled cells which are filled with reserve food materials. This is called the *nutritive layer*. The food materials are consumed as the seed ripens and the cells finally collapse into a thin zone of tightly packed cell walls or disappear altogether.

The thickened protective layers, wherever formed, consist generally of the following cell types, either alone or combined: (*a*) cells which are either cubical or slightly elongated, with highly thickened and pitted walls; (*b*) elongated cells of the sclerenchyma type, often closely entwined, with their long axes lying tangentially, while in some families there may be two such fibre layers with the fibre axes crossing at right angles (*e.g.*, *Pyrus malus*); (*c*) cells in which the inner and side walls are highly thickened, but the outer walls are thin and cuticularized; (*d*) narrow cells which are greatly elongated radially, the walls of which are often relatively thin at the inner ends and thicken greatly towards the exterior. The last class of cells are called the Malpighian cells, after their discoverer. They appear polygonal when seen from the seed surface and form a marked palisade layer which is particularly characteristic of larger seeds with thick testas, in such families as the Papilionaceae, the Malvaceae, the Annonaceae and the Cannaceae (Fig. 1358). The palisade may represent the outer epidermis of the outer integument, but it is more usually the hypodermal layer and it may, in fact, be formed from various layers of either the outer or inner integuments. Such a protective layer, in which the cells may be as much as twenty times as long as broad, is an impressive structure and it has been the subject of a good deal of examination. The chief thickening material is secondary "cellulose" or more correctly polyuronide, but the outer caps of the cells and their lower ends may be suberized. The cells are generally closely packed, but in some seeds there are irregularities of diameter which produce narrow intercellular spaces, while in *Nelumbo* and in *Canna* the palisade is traversed by stomatal canals.

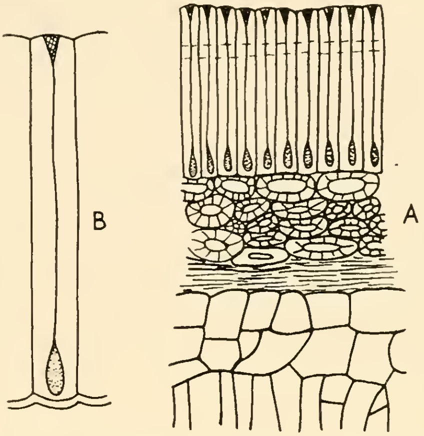

FIG. 1358.—*Canna indica.* A, Section through the testa showing the marked palisade layer, derived from the epidermis. The position of the " light line " is indicated by the dotted lines. Below is a zone of stone cells and the crushed remains of the inner integument, abutting on the endosperm. B, A single palisade cell showing the contracted cell lumen. (*After Humphrey.*)

Prominent in nearly every case is a narrow, almost colourless band, running tangentially through the whole palisade, near the top of the cells. This is called the " light line " or " light zone " and it has attracted much attention, based on the supposition that, like the Casparian band around endodermal cells, it constituted an impermeable, sealing belt around the palisade cells, which prevented the entry of water unless it were first ruptured. There seems to be little evidence for such an idea, for the zone does not appear to be chemically different from the rest of the cell wall, although in *Tilia* it is reported to be lignified. The most careful work indicates that it is only an optical effect, due either to a convex enlargement of the cell wall at that level, or to the refraction of light at a surface of contact between two transparent substances of different refractive index (the " Becke Line "). The latter certainly seems to be true in *Melilotus*, examined by Hambly, where the light line is formed at the junction between the suberized caps of the cells and the cellulosic body. This worker showed that when the microscope objective is raised the line appears to move towards the substance with the higher refractive index, as the Becke line does. This is probably not a universal explanation, for in

Malvaceae, where the palisade is formed by the inner integument, the light line may be very prominent, though there is practically no suberization.

Beneath the palisade layer there may be other sclerotic layers, sometimes of stone cells, sometimes of hour-glass-shaped cells, with big interspaces, forming an "arcade layer". These cells are called *osteosclereids* from their resemblance to knuckle bones. Dark-coloured tannin deposits commonly occur and there is often a pigmented layer, which may be a special layer of cells (*Linum*), or may consist of the caps of the Malpighian cells or of the walls of the outer epidermis. Where the chief protective layer is not superficial there may be one or more layers of relatively thin-walled cells external to it, including the outer epidermis, which is often large celled. In some families the outer epidermis constitutes a swelling-layer whose walls are thickened with mucilaginous material that swells readily in water, bursting the cells and forming an enclosing coat of mucilage around the seed. This substance is not chemically uniform. In most cases it consists of pectin, but in others it colours blue with iodine and is apparently an amyloid. One of the most familiar cases is that of Linseed (*Linum usitatissimum*), whose seeds, soaking in water, look like frog-spawn. Here the mucilage is amyloid, but in Cistaceae it is generally pectin, except in some species of *Helianthemum*. Perhaps the most striking examples are among the Polemoniaceae (*Gilia*, *Cobaea*, *Collomia*), where the thick slime layers on the epidermal walls include spiral or ring-like bands. Contact with water causes the amyloid material to swell enormously, bursting the tops off the cells and protruding in long columns, in which the unswollen spirals or rings are extended (Fig. 1359).

FIG. 1359.—*Collomia grandiflora*. Section of the testa after wetting showing the extruded spirals in the mucilage layer derived from the exploded epidermal cells.

We have already referred to certain plants (*e.g.*, *Crinum*) in which there is no testa and the endosperm forms the outer layer of the seed. Many other types have much reduced or else rudimentary testas, *e.g.*, *Veronica hederaefolia*, whose peculiar incurved seeds have only a single layer of very small cells covering the endosperm, and these soon disrupt, so that only their inner walls remain, which may however have a high protective quality. Similarly, many minute seeds have testas consisting only of a single cell layer, *e.g.*, Ericaceae. The bitegminous seeds of *Asparagus* depend chiefly on cuticle for their protective material (Fig. 1360). Fatty cuticles occur both between the integuments and on the inside of the inner integument. Twenty days after pollination shrinkage of the fleshy integuments sets in. The inner integument disappears so that the two cuticles come together. The parenchyma of the outer integument is completely flattened and finally only the outer epidermis, the crushed layer and the cuticles remain.

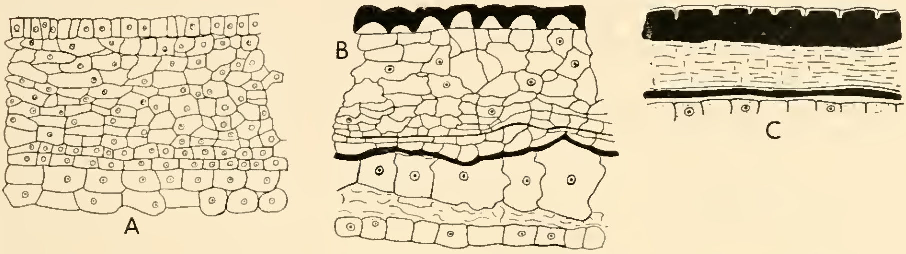

Fig. 1360.—*Asparagus officinalis.* Sections of the developing testa. A, 8 days after pollination. B, 20 days after pollination. C, Mature seed. (*After Robbins and Borthwick.*)

We have hitherto treated the testa as if it were unquestionably the product of the integuments of the ovule, with occasional participation by the nucellus or even the endosperm. There is evidence, however, that the chalaza may sometimes play an important part. We have pointed out, in the previous chapter, that the vascular bundle of the funicle usually ends in the chalaza, occasionally splaying out into a few short offshoots, but only in few cases entering the outer integument, or prolonging itself as far as the micropyle. Yet in many mature seeds integumental vascular bundles occur, both in the outer integument and, in Dipterocarpaceae, in the inner integument, or even in the perisperm, that is in tissue apparently of nucellar origin, although nucellar bundles are almost non-existent in Angiosperms. It is difficult to account for the presence of these bundles in the seed in any other way than by supposing that there has been a general extension of chalazal tissues towards the micropyle to form a more or less considerable portion of the testa. Indeed, in some cases, for example in *Canna*, *Ricinus* and *Eranthis*, the integumental portion of the testa seems to be limited to the region of the micropyle. The true condition in particular cases is difficult to judge, without developmental study, inasmuch as the tissue differentiation in the chalazal part of the testa is identical with that in the integumental portion, just as the differentiation in the raphe portion of the testa is the same as that in other portions, though the raphe properly belongs to the funicle rather than to the integuments. Upgrowth of the chalaza in this fashion has its parallels in the Gymnosperms and in the Pteridosperms and has therefore a long history behind it. It is no new thing in the Angiosperms but is something that might be expected. Very little information exists about it and developmental studies of seeds in such families as Nymphaeaceae, Magnoliaceae, Fagaceae, Euphorbiaceae or

Palmaceae, or others which are richly supplied with integumental bundles, are much to be desired.

Such a developmental study has been made by Corner in the Annonaceae. He showed that in this family the growth of the chalaza begins at an early stage of ovular development, the original body of the ovule, with free integuments, being carried away from the apex of the funicle and remaining in a rudimentary condition round the micropyle, while the chalaza forms the body of the ovule, its vascular bundle extending around the ovule in a hoop. In Annonaceae this extension of the chalaza is confined to the median plane, the integuments remaining free on the two flanks of the seed. A third, middle integument arises after fertilization as a further development from the chalaza. How far these conditions may be paralleled in other families is not known.

Imprisoned within its testa the embryo plant is an independent organization, cut off not only from external influences, but also from the parent plant (Fig. 1361). The formation of the corky covering of the hilum and the suberized layers in the chalaza, which cover the basal gaps in the integumental cuticles, antedate the actual separation of the seed from the placenta. Stress must be laid on the importance, as a protective layer, of the inner cuticle of the inner integument. The intermediate and outer cuticles may indeed also remain during ripening to contribute their protection, but they often disappear, while the inner cuticle almost invariably remains and frequently increases in thickness. There are only the rarest exceptions to this, *Aesculus* being the best known. This cuticle is highly impermeable to water and to gases and also to dissolved substances. It is a complete barrier to the entry of Bacteria or Fungi to the embryo. This applies even in species where a necessary mycorrhizal Fungus inhabits the seed coat. It never penetrates to the resting embryo, which only receives infection during germination. The whole of the complex outer coat may be rotted away or may be removed by maceration in strong chromic-sulphuric acid mixtures, and yet the inner cuticle will remain intact and the embryo unaffected. Such remarkable impenetrability enables us to understand how so many small seeds can be apparently sufficiently protected by the thinnest of cellular coverings and, on the other hand, how some seeds can survive drastic chemical

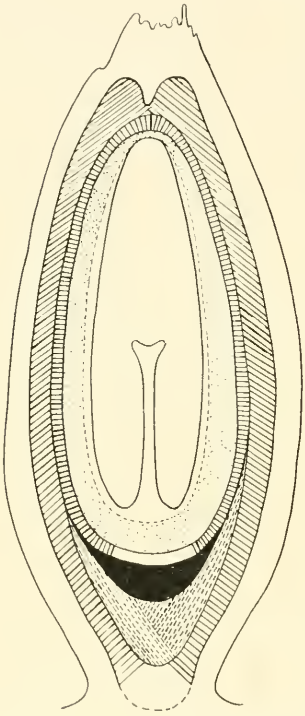

FIG. 1361.—*Urtica dioica.* Longitudinal section of akene with the single orthotropous seed. The embryo is straight and surrounded by endosperm. Note the large hypostase at the lower (chalazal) end. (*After Schmid.*)

treatment designed to soften the hard outer testa. It follows from these facts that the materials stored in the soft nutritive layer of the testa cannot be absorbed by the embryo and that they are therefore consumed by the outer tissues during the period of their differentiation. It is evidence of the importance of the inner cuticle that it is well developed in the seeds of water plants, whose vegetative organs may have little cuticular covering or none.

That some degree of mechanical protection is afforded by the testa is obvious from its structure, but it is often less than might be supposed. Great hardness of the testa may be compensated by lack of elasticity, so that the shell is easily broken. Even the hardest seeds may be broken up and digested by ruminant animals or in the crops of some birds and when the seed is softened and about to germinate the protection is least, just when the need for it might be supposed greatest. Moreover, seeds collected from the soil usually show more or less damage to the testa and some seeds germinate so rapidly in the soil that their testas never harden at all. Seeds such as those of many alpine plants must germinate thus, for they have no power of longevity and protection is scarcely required. On the other hand there does not seem to be any obvious correlation between great longevity and a particular testa structure.

The most extensive investigation of the anatomy of seeds is due to Martin (1946). He developed a classification based on the internal morphology of the seeds of 1,274 genera, representing two-thirds of the families. The criteria used were the relative sizes of embryo and storage tissues, the position of the embryo and its shape. There are five major divisions with twelve subdivisions, the latter depending chiefly on the form of the embryo (Fig. 1362).

The five major divisions are as follows:

1. *Basal.* Embryos relatively small and basal, in seeds that are usually medium to large but sometimes small. Examples: Magnoliaceae, Ranunculaceae, Papaveraceae, Nymphaeaceae, Juncaceae.
2. *Peripheral.* Embryos vary from small (in some Grasses and Sedges) to large or completely filling the seed, always contiguous to the testa, at least in part, and often curved. Endosperm starchy, lateral or central. Examples: Gramineae, Cyperaceae, Caryophyllaceae, Chenopodiaceae, Cactaceae, Polygonaceae.
3. *Axile.* Embryos vary from small to total (*i.e.*, completely filling the seed), central, straight, curved or coiled. Endosperm not starchy. Examples: Umbelliferae, Solanaceae, Liliaceae, Amaryllidaceae.
4. *Reduced.* Embryos usually minute, seeds small to minute, testa thin and delicate. Examples: Scrophulariaceae, Gentianaceae, Campanulaceae, Ericaceae, Orchidaceae.
5. *Foliate.* Embryos usually large, sometimes total, usually central, cotyledons expanded, seeds usually rather large. Examples:

Urticaceae, Cruciferae, Rosaceae, Malvaceae, Convolvulaceae, Fagaceae, Juglandaceae, Rubiaceae, Labiatae.

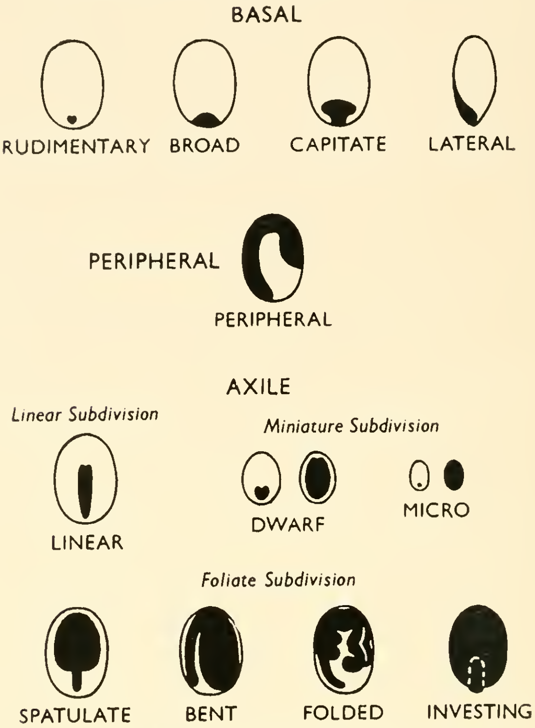

Fig. 1362.—Martin's twelve seed types in diagrammatic form. (*After Martin.*)

Martin traces certain lines of organizational advance among these types, considering the seeds as organisms in their own right, whose evolution may be viewed independently of the general evolutionary advance of the plants which produce them (Fig. 1363). Thus he considers that large seeds with small embryos are relatively primitive and that evolution has proceeded divergently towards quantity (of seed produced) on the one hand (Reduced Division) and towards quality on the other (Foliate Division). The high degree of insulation of the seed certainly justifies its treatment as a microcosm and its evolution along independent lines of advance has parallels among other organs of the vegetative plant.

The term **aril** is applied in its widest sense to all external outgrowths or "effigurations" of the seed, especially those which arise after fertilization (Fig. 1364). It is not easy to delimit exactly the application of the name. Logically it should include hairs, but in practice these are not usually treated as arils, not even the copious development of plumed hairs on the testa, which are of value in wind dispersal, although they are definitely arillar in nature. Nor are wing-like extensions of the testa usually included. The aril is therefore strictly something extra, something hypertrophic and dis-

FIG. 1363. — Number of genera in all seed types having endosperm (white blocks) and lacking endosperm (black blocks). Progression towards the non-endospermic condition is evident among genera of the higher seed types. (*After Martin.*)

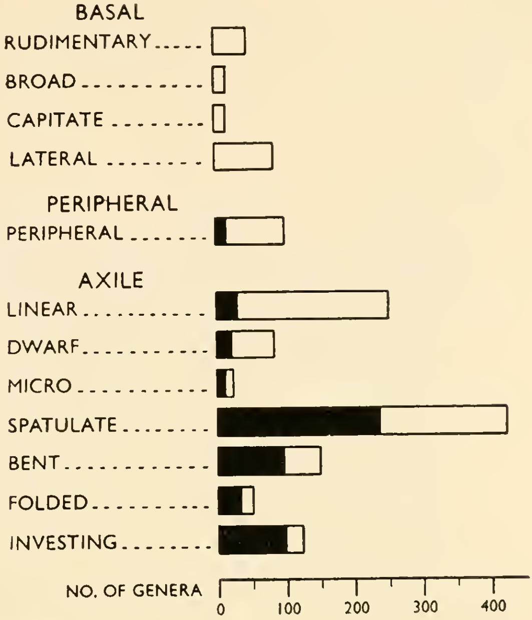

FIG. 1364.—*Celastrus orbiculatus.* Shoot with dehiscent capsules, revealing the seeds which are covered with fleshy scarlet arils.

FIG. 1365. — *Alectryon excelsus.* Sapindaceae. Section through a dehisced capsule from which emerges the single seed with its expanded, complex and edible aril. (*After Baillon.*)

tinct from all ordinary developments of the testa (Fig. 1365). At one time it was customary to restrict the application of the term to secondary structures arising from the funicle only and to call all others "false arils", but there is no sharp demarcation between them (Fig. 1366). The term **caruncle** is applicable only to knobby or wart-like arils, associated with the micropyle, while similar warts on the funicle or the hilum have been called by the name **strophiole**.

Fig. 1366.—*Euonymus planipes.* Red fleshy capsules opening to disclose the seeds which are covered by orange-coloured arils.

Arils occur on seeds of very many families, of all affinities. They take the form of knobs, horns, bands, ridges or, commonly, cupules, partly enclosing the seed. They are frequently of brilliant colours and contrast with the coloration of the testa, especially in tropical families. They are usually unhardened and frequently contain a store of oil. Occasionally they may serve to attract birds which carry away the seed, or, in smaller seeds, the attraction may be for ants, which are known to carry small arillate seeds like those of *Ulex*, *Chelidonium* and *Melampyrum* for considerable distances, eventually eating the oily caruncles, or elaiosomes as they are sometimes called. This mode of distribution is known as **myrmechory** (Fig. 1367). A good example of an aril which attracts birds is that of the familiar *Euonymus europaeus*, which covers the seed with an orange envelope contrasting strikingly with the red placentae. Arils may serve other purposes directly valuable. Those of *Nymphaea* enclose the seed in an air-filled sac which serves as a swim-bladder and keeps the seed afloat for a long time. The arils of *Myristica* and of some Marantaceae aid by their swelling in forcing open the dehiscent pericarps and may thereafter, when exposed, also attract birds by their bright colours. Whether the chalazal wings of the seeds of Bromeliaceae, which are wind-dispersed, should be called arils is doubtful. They originate before fertilization, but so do many of the arillar coverings which grow from the exostome lips at the micropyle (Euphorbiaceae). In some Papilionaceae (*e.g.*, *Sarothamnus scoparius*) there is an arillar swelling in the form of a cup, where the funicle joins the seed. This is supposed to assist in detaching the seed by constricting the funicle. The corky aril in *Caltha* keeps the seeds afloat in water and thus aids in dispersal.

FIG. 1367.—Seeds with oily caruncles which may act as attractions in aid of dispersal. Top: *Ricinus communis.* Bottom: *Ulex europaeus.*

A unique function is fulfilled by the aril in *Opuntia.* The seed is circinotropous, the funicle surrounding the ovule. From the funicle grow out two wing-like expansions which finally envelop the ovule completely, leaving only a narrow slit through which the pollen tube enters and, subsequently, the primary root emerges. This envelope hardens and forms the effective testa of the ripe seed, the integument being only a thin membrane.

Particularly well known is the aril of *Myristica fragrans*, the Nutmeg, cultivated as a spice in S.E. Asia. The ripe seed is about an inch long and is surrounded by an aril which grows from the funicle and extends towards the micropyle as a circle of fleshy fingers which anastomose in an irregular network (see Fig. 1471). When dry it turns golden orange and is rich in oil. The aril yields the spice called mace and it is used as well as the nutmeg seed. In the species of *Passiflora* which have edible fruits (*P. edulis* and *P.*

quadrangularis) there is also a fleshy upgrowth from the funicle which envelops the seed and grows beyond the micropyle. It forms part of the edible flesh of the fruit, in the same way that the soft outer testa does in *Punica*, the Pomegranate.

Many species of *Acacia* have extraordinarily long funicles, which are strikingly contorted and wind round the seeds (Fig. 1368). They become dry and brightly coloured and remain attached to the seeds when they are shed. They are not correctly described as arils but they are closely similar and probably have a similar attraction for birds to that of some arils.

FIG. 1368.—*Acacia melanoxylon.* Seeds surrounded by the orange arils which develop from the funicles. The seeds hang from the open pods.

We have previously mentioned that the **endosperm** in some ovules is arrested during the development of the embryo and may entirely disappear before the seed is ripe or may remain only as a thin membrane around the mature embryo. Only in a few plants, particularly some of the Orchids, is endosperm formation entirely suppressed, a reduction phenomenon which is in line with the imperfect and arrested development of the embryo in that family. Seeds in which the endosperm forms a visible mass are known as "albuminous", an archaic term, for the endosperm may often be wholly starchy. The endosperm is purely a reserve of nutriment for the embryo and shows no capacity for development or differentiation. Almost the only exception to this is in *Crinum* (Amaryllidaceae), where the endosperm develops a corky covering, supplying the place of the missing testa, and may also develop chlorophyll.

The presence or absence of endosperm has a certain systematic importance, since it may be a family characteristic. Thus, Umbelliferae and Rubiaceae have always a well-developed endosperm and Papilionaceae are almost entirely devoid of it, though there may be some remains around the radicle. In most families, however, it is at most a generic character.

Where endosperm is lacking, or only weakly developed, it may be replaced or reinforced by **perisperm**, a tissue which apparently is always derived from the nucellus. The latter usually disappears during seed ripening but in these cases it enlarges to form a reserve tissue which has the same character as true endosperm. Perisperm forms the principal storage tissue in seeds of Piperaceae and Zingiberaceae and in *Coffea* the hard substance of the seed, from which the beverage is made, is perisperm, the endosperm being no more than a papery membrane. Since the perisperm belongs to the tissues of the mother plant this is an important consideration to those engaged in coffee breeding.

Seeds of families belonging to the Caryophyllaceae and to the obsolete group of Curvembryae (Bentham and Hooker) which included Chenopodiaceae, Amarantaceae, Nyctaginaceae and Phytolaccaceae, have the common character of a curved embryo surrounding a mass of reserve tissue, which originates as a massive thickening of the nucellus on the concave side of the embryo sac and later of the embryo. This is a perisperm, but in members of the Butomaceae and Alismaceae, which also have curved or folded embryos, there are similar ingrowths which come from the funicles and these form no reserves and are generally obliterated in the ripe seeds.

The endosperm at first surrounds the very young embryo, but in many seeds with peripheral embryos, such as Gramineae, the endosperm on the outer side of the embryo disappears, so that the subsequent development is all unilateral. Not all cases of unilateral embryos arise in this way. In *Polygonum aviculare*, for example, the young embryo shows unilateral growth from an early stage and the embryo follows one of the angles of the triangular seed and adapts itself to its curvature.

The food reserves in the endosperm may be starch, oils or proteins or combinations of these with or without mineral crystals. The cell walls are sometimes amyloid and sometimes have thick secondary deposits of polyuronides (hemicelluloses), which undergo hydrolysis at germination like other reserve materials. Amyloid walls give a blue colour with iodine alone. They occur in *Tropaeolum*, Liliaceae, Amaryllidaceae, etc. The thick-walled endosperms in which the thickening material consists of deposits, sometimes massive, of hemicellulose, contain no starch and may be exceedingly hard, as is well seen in Palmae. The stone of the Date is one well-known example, another is the vegetable ivory formed by the endosperm of *Phytelephas macrocarpa*, a tropical American Palm, which is used principally for making buttons and collar studs (Fig. 1369). The combination of oil and starch together in the same cells is uncommon, though it occurs in *Ceratophyllum*, but it is not rare to find oil and starch both present in the endosperm, usually in inverse proportions.

Starch grains in endosperm are of the large storage type which is characteristic also of underground storage organs of the vegetative plant, though they are seldom as large. They may be rounded, or polygonal from mutual pressure when they are closely packed. As in other storage tissues the grains show concentric lamellation around a growth-centre or *hilum*, which may be central or excentric in the grain. Tightly packed grains may occupy the whole cell, to the almost complete exclusion of cytoplasm and nucleus, and they then give the endosperm a hard or bony consistency, as in the " flint " grains of *Zea mais*, while in " mealy " endosperms they are relatively isolated and rounded. The fine structure of starch grains will be dealt with under Physiology in Volume III.

FIG. 1369.—*Phytelephas macrocarpa.* Fruit in cross-section, showing the hard white endosperm which is used as " vegetable ivory".

Fatty oils may be present in the cells in the form of minute droplets, often to a large amount. Among the richest in oils are the various " nuts". For example, *Pinus koraiensis* (the Korean Pine), *Canarium* (Pili nuts) and *Carya pecan* all contain over 70 per cent. of oil on a dry-weight basis, and Walnut, *Macadamia* nuts, Brazil nuts and Coconut all have over 65 per cent. Most of the typically oily seeds are below these percentages, *e.g.*, Linseed, 36 per cent.; Groundnuts, 47 per cent., Sunflower, 41 per cent., Cottonseed, 33 per cent. Seeds which are characteristically starchy have often very low percentages of fats; *e.g.*, Wheat and Barley about 2 per cent.; Peas and Broad Beans, less than 1·5 per cent.

The term protein, as applied to reserves, covers also amides and free amino-acids, the former, especially asparagin, being often present in considerable amounts. Native proteins and amides may accompany starch in the cells, generally in granular form, or they may occupy a special layer of cells, normally on the periphery of the endosperm, as in the Wheat grain, known as the " aleurone layer", which is free from starch. Proteins frequently occur in crystalline form, and these crystals are conspicuous in some oily seeds, *e.g.*, *Bertholletia* and *Ricinus*, contained in the so-called " aleurone grains", throughout the reserve tissues. These grains are really minute vacuoles containing water-soluble globulins and including hexagonal or rhombohedral crystals of the protein, together with mineral crystals, either of calcium oxalate or, usually, of calcium-magnesium phosphate in the form of a spherical crystal called a " globoid". The aleurone grains rapidly swell and disintegrate in contact with water, the protein passing into solution.

The amount of protein present may be very considerable, and adds greatly to the food value of some cultivated seeds, though seed proteins are reckoned as only of second-class value in animal nutrition because they may not contain the appropriate amino-acids in suitable proportions. The Soya Bean comes nearest to milk and meat in the food-value of its proteins and the Groundnut and Cottonseed are nearly as good. The pulses stand high in order of protein content, the Garden Pea containing over 25 per cent. (dry weight), Broad Beans slightly more and Runner Beans somewhat less. Soya Beans contain 37 per cent., Groundnuts 30 per cent., and Cottonseed 39 per cent.

Besides the above-mentioned reserves many other substances are found in seeds, which may or may not act as reserves. Sugars occur in small percentages in the cereals, mainly as sucrose. Wheat and Barley contain 2 to 3 per cent. and Rye 6 to 7 per cent. The seed of the Sugar-maple (*Acer saccharum*) contains 6 to 7 per cent. of sugars and over 5 per cent. of other simple carbohydrates but no starch. Notable amounts of sugar occur in the seeds of the Pineapple and other Bromeliaceae, up to 13 per cent. of reducing sugars in some varieties. Tannins, resins, glucosides, mucilages, saponins and alkaloids may also be present, sometimes in considerable quantities.

A curious consequence of double fertilization, which was very puzzling before Navaschin's discovery, is that the endosperm may often show characters associated with the male parent. This was called **xenia**, in reference to the " foreign " influence supposedly at work. The effect is conspicuous in the grains of Maize, where the characteristics of the grains are largely due to the endosperm. The appearance of xenia depends upon whether the endosperm characters of the pollen parent are dominant over those in the ovule parent or not. If they are, the endosperms on the ovule parent will all follow the characters of the pollen parent. If they are recessive there will be no xenia effect apparent. The term *metaxenia* has been applied to a more remote effect of the pollen parent on the testa or the pericarp. Possibly this may be due to hormones diffusing from the embryo.

A peculiarity of certain families is the possession of what is known as *ruminate endosperm*, which refers to the invasion of the endosperm by infoldings of the outer tissues penetrating deeply and partially dividing up the endosperm by long, ingrowing processes. There may also be some reciprocal outgrowth of the endosperm itself. The character is found almost universally in the Annonaceae and in Myristicaceae, Araliaceae (Fig. 1370) and in many Palmae. In *Myristica* and in the Palms, it is the

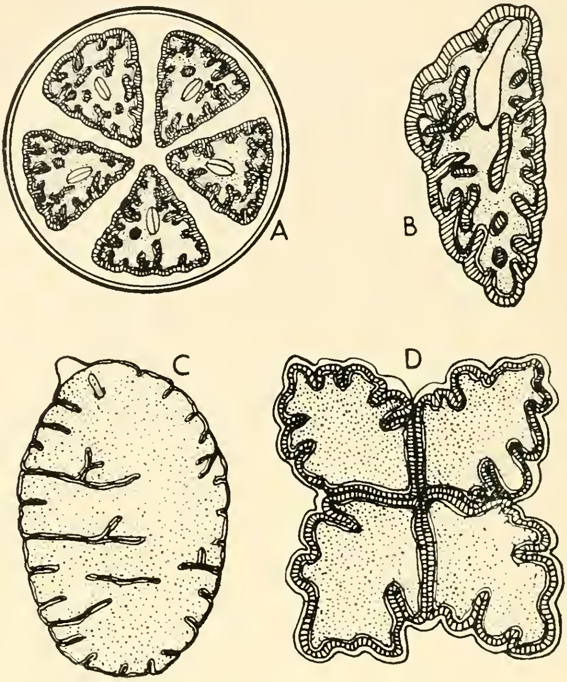

Fig. 1370.—Ruminate endosperms in members of the Araliaceae. A and B, *Hedera helix*. C, *Arthrophyllum diversifolium*. D, *Polyscias ornifolia*. (*After Harms*.)

nucellus which grows inwards, but this is not a true perisperm since it contains no reserves. In Annonaceae the infoldings are due to ingrowths of the integuments on the two flanks of the seed, where they are free (Fig. 1371). The seed coat is rigid in the plane of the funicle and in this plane there are no folds, but at the sides they appear in basipetal order (Fig. 1372). The effect is greatly to increase the surface of contact between endosperm and testa, which may be important in the movement of food reserves and of water during the maturation of the seed (Fig. 1373). The greater extent of surface may also have importance in the solution of these unusually massive reserve tissues at germination, since there is evidence that the peripheral layer of the endosperm may be the source of the hydrolytic enzymes which attack its reserves during germination. The single furrow in Grass seeds may be regarded as a simple form of rumination.

From the micropylar position of the oosphere in the embryo sac and the downward development of the embryo, it follows of necessity that the radicle of the mature embryo is directed towards the micropyle, from which, or in its neighbourhood, it eventually emerges, and that the plumule

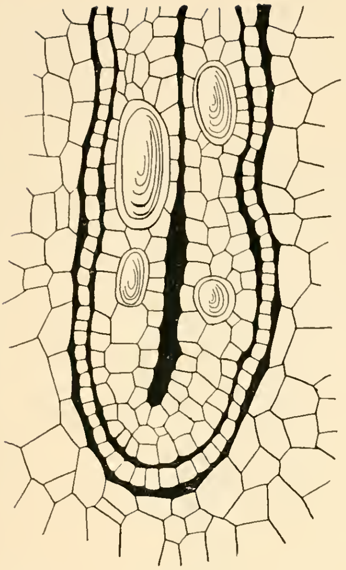

FIG. 1371.—*Anaxagorea javanica.* Annonaceae. Inner end of a ruminate fold of the integument, in contact with the endosperm. (*After Corner.*)

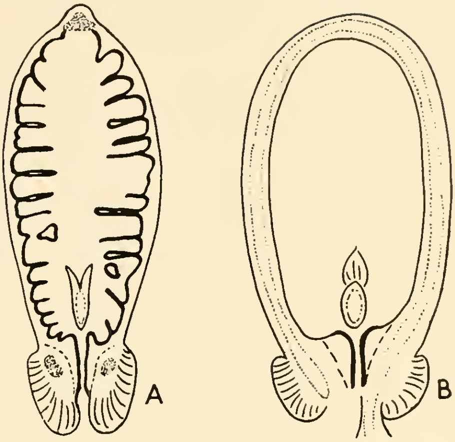

FIG. 1372.—*Annona squamosa.* A, Transmedian longitudinal section of the seed with the ruminate folds of the inner integument shown by the heavy line. B, Median section, at right angles to A, showing the absence of folding in this plane. The seed has a caruncle which is shown striped. (*After Corner.*)

(in Dicotyledons) is directed towards the chalaza. The simplest form and position of the embryo are straight and median but there are many complications. We have already referred to the lateral displacement of the embryo in many seeds and its causation. Curvature of the embryo is necessarily imposed where the embryo sac is curved, as in campylotropous and amphitropous ovules, but curved embryos may also arise in orthotropous ovules, as in the above-mentioned case of *Polygonum aviculare*, where the different angles of the seed coat appear to influence the growth of the embryo. In *P. fagopyrum* (*Fagopyrum esculentum*), on the other hand, all the angles are alike, and the embryo is not displaced but is median and complexly folded.

No doubt the shapes of seed and fruit do, mechanically or otherwise, influence the position of the embryo in many plants, as may be deduced

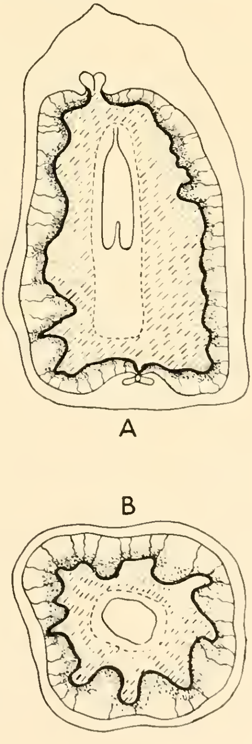

FIG. 1373.—*Verbascum montanum.* A, Longitudinal, and B, transverse sections of the seed, the folding of the inner integument shown by the heavy line. (*After Schmid.*)

from the fact that if very young embryos are removed from seeds where they normally become curved or otherwise distorted, and are cultivated in freedom, they remain straight. Conditions external to the fruit, for instance gravity, seem to have little to do with the growth of the embryo, whose symmetry and the relative degree of development of cotyledons and hypocotyl depend on internal and partly on hereditary factors (Fig. 1374). The Onion is a case in point, the embryo being curled in the form of a P, although entirely surrounded by uniform endosperm. Similarly the rolling up of the cotyledons of *Geranium* begins when the embryo is still quite small and free from any external pressure. The peculiar form of the embryo in *Restio*, a biconvex disc on top of the endosperm, is also difficult to attribute to mechanical controls.

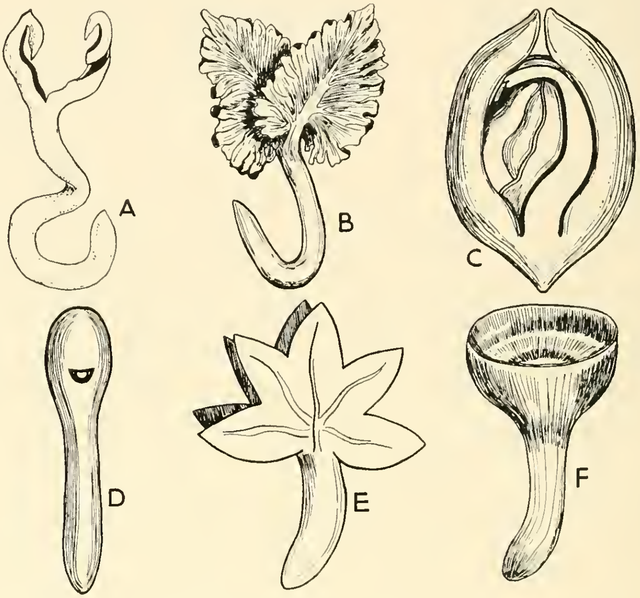

FIG. 1374.—Some unusual forms of embryos. A, *Capparis*. B, *Couroupita*. C, *Ceratophyllum*. D, *Astelia*. E, *Tilia*. F, *Myzodendron*. (*After Le Maout and Decaisne*.)

In the Cruciferae the embryos are bent double and their symmetry is an important taxonomic character in the separation of the genera. The chief cases are: 1, *incumbent*, the cotyledons straight and the radicle lying at the back of one of them (Fig. 1375); 2, *orthoplocous*, as above but the cotyledons conduplicate; 3, *spirolobous*, as above but the cotyledons folded once; 4, *diplocolobous*, as above but the cotyledons folded more than once; 5, *accumbent*, the cotyledons straight and the radicle lying against their edges.

The degree of development of the cotyledons in the seed is correlated with the extent of the reserve tissues. The smaller the amount of the latter, the larger, in general, are the cotyledons, which are themselves utilized as reserve stores. The limiting case is that of the absence of any endosperm with the cotyledons so much enlarged that they practically fill the seed, as we see in peas and beans. This enlargement may lead to complex folding of the two cotyledons, as in the seed of *Fagus*, or the condition in species of *Geranium*, where they are rolled together. The size of the containing seed is seemingly the controlling factor, the packing of the cotyledons being adapted to it, not vice versa. The paired cotyledons may be of unequal development, which modifies their packing pattern, or they may both be asymmetrical, which is associated with dorsiventrality of the embryo as a whole, the larger side of each cotyledon lying towards the dorsal or larger side of the embryonic axis. The behaviour of the cotyledons at germination, which we shall have something to say about later, is naturally related to their symmetry and position beforehand in the seed, which may be influenced by factors that have nothing to do with germination. For example, the convoluted cotyledons of the Walnut are related to the inner convolutions of the endocarp wall; broad or narrow cotyledons may be related to the shape of the embryo sac; divided cotyledons to their function in absorbing nutriment from the endosperm, as is beautifully seen in the ruminate endosperm of *Myristica*; or finally to differences of nutrition on different sides during the development of the embryo.

FIG. 1375.—*Capsella bursa-pastoris*. Longitudinal section of a seed showing the incumbent embryo.

While the cotyledons are the usual repositories of nutriment in the absence of endosperm, the hypocotyl sometimes takes their place. For example, in *Bertholletia excelsa*, the Brazil nut, and in some Guttiferae, the seed is filled by the immensely enlarged hypocotyl of the embryo (Fig. 1376), the cotyledons being scarcely visible as two minute, overlapping scales at one end and the radicle forming a mere point at the other. Indeed, in *Garcinia* the radicle is so reduced that the primary root soon aborts and is replaced by an adventitious root from the hypocotyl after germination. Similarly, in *Zostera*, *Ruppia* and some allied genera, the hypocotyl is enlarged into a big rectangular body, from the side of which the single cotyledon protrudes like a horn.

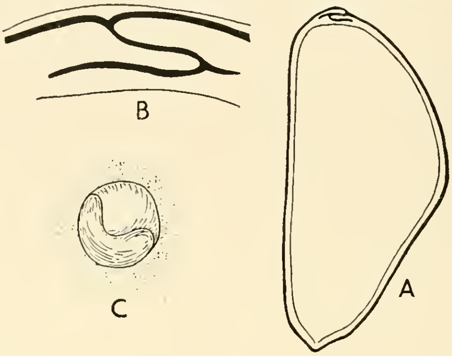

Fig. 1376.—*Bertholletia excelsa*. A, Longitudinal section of seed which is filled by the enlarged hypocotyl. The minute cotyledons are shown at the top. B, Enlargement of the folded cotyledons. C, Surface view of the cotyledons. (*After Goebel.*)

In Monocotyledons the single cotyledon may show the same division into blade and sheath which is characteristic of the foliage leaves. This is always the case in non-endospermic monocotyledonous seeds, *i.e.*, in Butomaceae and Alismaceae (Fig. 1377). These cotyledons emerge above ground as assimilatory organs, while in most endospermic seeds the whole cotyledon, or sometimes only its apex, is modified into a haustorium in the endosperm, as we shall describe in more detail later (p. 1574). In the embryology of Monocotyledons it is clear that the cotyledon is formed by the terminal segments and the hypocotyl and stem apex from the segments below. This would appear to indicate that the cotyledon is a terminal organ and the growing point lateral. The matter is, however, susceptible to argument and we shall recur to the question of the relationship of the monocotyledonous and dicotyledonous types when we are dealing with germination.

Seeds may present a normal external appearance and yet contain no embryo. This has been considered an uncommon occurrence, but recent work has shown that it is widespread in the Umbelliferae. The endosperm may be perfect but there is either no embryo or only an immature embryo which is incapable of germination. The percentage of such seeds varies between different genera and between different samples of seed, causing great irregularities in the germinable capacity. Out of 54 lots of Carrot seed, an average of 16 per cent. were embryoless, the maximum being 37 per cent.

FIG. 1377.—*Sagittaria sagittifolia.* Alismaceae. Section of the campylotropous ovule with embryo. The cotyledon is at the top, the growing point is seen at the right-hand side. The imperfect endosperm disappears as the seed matures.

In Parsley the average was 20 per cent., while in Fennel (*Foeniculum vulgare*) the average was 34 per cent., with the maximum at 58 per cent. There is no suggestion that this is the result of disease, but it has been shown that infestation by *Lygus* bugs raises the incidence of embryolessness and a similar infestation is known to affect adversely the pollination and seed setting in Alfalfa (*Medicago sativa*).

The culture of seed embryos excised at an early stage of development is a technique of recent growth which offers great practical benefits to the plant breeder, since embryos of certain types of hybrid which do not survive in the seed can be successfully reared into plants if cultivated artificially. Furthermore long periods of dormancy can be avoided.

There is a fundamental difference between the culture of mature embryos with storage cotyledons and that of minute, immature embryos. The former can often be developed successfully, if they have been allowed a full period of after-ripening, on a purely inorganic growth medium solidified with agar. The latter are heterotrophic and must receive organic nourishment in addition to the mineral requirements. Sucrose has generally been found to be the best carbon source, closely followed by maltose. As sources of nitrogen, amino-acids and amides are essentially important. Artificial mixtures of amino-acids and the natural mixture in casein hydrolysate have been used with good effect, but some, at least, of the acids included in these mixtures are unsuitable and have an adverse effect although their action may be antagonized by other acids present. With Orchid embryos, arginine alone supported good growth, but in *Datura* no incomplete mixture or single amino-acid equalled the effect of casein hydrolysate or the complete mixture of its constituent acids. Experiments with *Capsella* showed that the amide glutamine gave better growth than a complete amino-acid mixture of equivalent nitrogen content. Asparagine was ineffective with *Capsella* though it is abundant in seedlings of *Lupinus* and *Pisum*, as glutamine is in *Brassica*. Evidently species differ in regard to their amide requirements.

Early workers on embryo culture, having discovered deficiencies in their media, took refuge in the addition of " natural " fluids, especially coconut milk, which proved very successful with some species but not with others. The effect was attributed to an " embryo factor " in the milk, but later work has shown that it is not essential and probably owes its efficiency to its amino-acid content rather than to any hormone. Auxin does not seem to be essential but has a small positive effect in low concentrations.

The type of growth in cultured embryos often follows a different pattern from that in normal development and there is some evidence that this can be modified by variations in the osmotic potential of the medium.

The culture of pro-embryos has not yet been accomplished. Possibly physiological gradients or as yet unknown substances are influential in the earliest stages.

The **dormancy** of seeds is a physiological condition to which we shall return in the next volume of this work, but it has very important biological aspects. Dormancy may be due to a variety of causes, such as extra hard coats; or the need for a period of internal chemical change, known as after-ripening; or the lack of oxygen; or the presence of inhibitory substances, or to other reasons. It is often associated with a low water content in the seed but some seeds will remain dormant even when lying in a moist medium, like the soil, and fully imbibed with water. However it arises, dormancy can often be of value to the plant in passing through unfavourable seasons and in allowing time for wide dispersal of the seed.

The seeds of the principal crop plants have usually only a short period of obligate dormancy, for strains with prolonged dormancy are a nuisance to the cultivator and have been eliminated by human selection through the ages. Some indeed have no dormancy at all and will sprout in damp conditions even before they have been shed. Even in these highly selected strains of seed, however, variations occur with hard coats, which may only germinate after considerable delay.

Many seeds will undergo the period of after-ripening successfully in the dry state, but there are others which can do so in the moist state and a considerable number must be held in the moist state as they cannot tolerate drying. In all these cases the term dormancy properly applies to that period, which may be short or long, during which the seed is incapable of germination under natural conditions, and ends when the seed becomes germinable, which, again under natural conditions, usually means that germination takes place. Thus true or obligate dormancy should be distinguished from induced dormancy due to the absence of the necessary conditions for germination.

The seeds of wild plants are very variable in their periods of dormancy. Even seeds from the same ovary may behave very differently and their germination times be spread over a period of several years. This variability is chiefly advantageous in uncertain climates and it is noteworthy that tropical seeds usually have short dormancies. When one considers that in general the seeds of wild plants fall into the soil, it is perhaps surprising that so many seeds will ripen in dry storage, but it must be remembered that moisture does not necessarily enter the seed. Seeds capable of prolonged dormancy in the soil usually have impermeable coats and do not absorb water or become germinable until the testa has either been mechanically injured or else has sufficiently rotted to become permeable. Even where this is not the case the seed may have special requirements, such as a period of low temperature or exposure to light, which are needed to render it germinable. The need for a period of exposure to low temperature is often the reason why some seeds, called "two-year seeds", will not germinate until the second spring after their maturation. Exposure to low temperature is sometimes also needed to overcome *epicotyl dormancy*, which occurs in some plants after germination has begun and a root has started to grow. No shoot is produced until the seedling has been chilled for two or three months. This curious condition has been observed especially in seeds of *Lilium*, *Paeonia* and *Viburnum*.

Both high and low temperatures may sometimes be required, as in *Cotoneaster*, the former to promote decay of the testa and the latter to allow after-ripening.

Dormant seeds are present in most soils to a surprising extent and may remain viable for very long periods. At Rothamsted Experimental Station there is a field known as Broadbalk which has grown wheat every year since 1843. In 1925 a system of sectional fallowing was adopted to reduce the weeds. Samples of the soil were placed under greenhouse conditions and carefully observed for seed germination. The weed-seed population in 1925 was actually 300 million per acre. Most of the seeds present were germinable and their seedlings appeared during the first three months, but others were still resistant and seedlings kept appearing at intervals during fourteen subsequent years. Seeds of the Poppy have a remarkably long dormancy and therefore accumulate in the soil year after year. Even after two years, in the above experiment, only about half of the Poppies had germinated. Grass seeds, on the other hand, have mostly only a short period of obligate dormancy.

Periodicity in germination is characteristic of many weeds, the majority germinating in autumn, after the summer heat (winter annuals), and a minority in the spring (summer annuals). Even in a heated greenhouse periodicity is maintained although, in this case, there is a larger germination in the spring months than under exposure to seasonal changes of temperature.

Dormancy must be distinguished from longevity, which means the period during which seeds can survive induced dormancy, under certain conditions, and remain viable, that is to say capable of germination. Ewart distinguished three main classes of seeds in this respect: *microbiotic*, those with a longevity not exceeding three years; *mesobiotic*, those which survive more than three but not more than fifteen years; and *macrobiotic*, those which survive from fifteen to a hundred years or more. Such a classification requires, however, a knowledge of the optimum conditions for survival, which we only have in a few cases.

There are many stories of seeds apparently surviving for fabulous periods. The most famous of these, the legendary mummy wheat from ancient Egyptian tombs, is revived from time to time but has never stood the test of investigation. True mummy wheat looks sound externally, but the embryo has gone and only the starchy endosperm remains. The oldest viable seeds known with certainty are those of the Lotus, *Nelumbo nucifera*, which were found by Ohga embedded in peat on the site of an ancient lake in Manchuria. When the coats were filed through, they gave 100 per cent. germination. Measurements of the radio-active carbon content have shown these seeds to be between 800 and 1,250 years old. They have exceedingly hard, impervious coats, which must be broken or decayed before the seed can germinate. Most of the seeds found had partly decayed coats and probably all would eventually germinate if not too deeply buried.

We have already drawn attention to the very long survival of many seeds of weeds in soil, a fact which is familiar to gardeners and excavators. The Poppies which blazed across the shell-torn land of Flanders in the First World War have been immortalized in remembrance, but the Snowdrops which covered the trenches around Sebastopol in the Crimean War were an earlier instance which has been forgotten. Tiny seeds like these soon wash down deep into the soil, where they may rest for unknown periods until some disturbance restores them to the air.

Storage in soil is often more favourable to survival than dry storage, but dry seeds can also survive for remarkable periods. Seeds of *Nelumbo* had been in store in the British Museum for 150 years and hard-coated seeds of *Albizzia julibrissin* for 149 years in the herbarium, when they astonished the keepers by germinating after having been wetted during the London "blitz" in 1941. Becquerel tested old seeds stored in the National Museum in Paris in 1900 and again in 1934. They were nearly all seeds of Leguminosae and they showed life periods varying from 55 to 158 years. All these seeds are hard-coated and Becquerel attributed their longevity to the very low moisture content (2 to 5 per cent.) and absence of oxygen inside the testas.

Experiments with buried seeds of common American weeds were begun by Beal in Michigan in 1879. The seeds were mixed with sand in uncorked bottles, which were buried neck downwards to keep out water. The first germination test was in 1884, when eleven out of twenty-one species germinated. At the test in 1940, after sixty years, only three species were found to have survived: *Oenothera biennis*, *Rumex crispus*, and *Verbascum blattaria*, but the last named still showed a 68 per cent. germination. It is planned to extend the tests to a period of 160 years.

Most of the species in these tests plainly fall into the mesobiotic class and many of the commonly cultivated plants are also in this class. If curves are drawn to show the drop in percentage germination against time, it is seen that there is usually a fairly rapid loss of vitality in the first five years, but the curves flatten out slowly and after fifteen to twenty years there may be a few resistant seeds still alive in any batch.

Microbiotic seeds are often intolerant of drying in the air. Seeds of some Grasses, Oaks, Beech, Sugar-maple, Poplars and Willows, *Citrus* species, and *Hevea brasiliensis* are all in this category. The seeds of many alpine plants likewise have no obligate periods of dormancy and germinate immediately after shedding, a feature which is reputed to be correlated with the very short growing season they experience. This deduction is somewhat weakened by the fact that the same character is shown by a number of common weeds.

Most of these seeds are not killed by drying as such, but apparently by concomitant oxidations, since they can be dried even to exceptionally low moisture contents, provided this is done at a low temperature, preferably in the absence of oxygen. In this condition they will retain their vitality for much longer than the normal periods, *e.g.*, in *Salix* for nearly a year. Possibly at higher temperatures bacterial growth may assist their deterioration.

Dispersal of Seeds. The dormancy of seeds makes them particularly fit to be agents of dispersal as well as of reproduction. Every seed is a new life and every seed which is of biparental origin is a new whole, with new potentialities. The survival of the species is best ensured by dispersing the seeds to as many different localities as possible. In this way new genotypes may find the conditions with which they best accord and develop into new ecotypes. At the same time some degree of isolation will favour their survival by lessening the chances of back-crossing with the parent plant. Unrestricted competition between seedlings around the parent plant would also greatly increase the mortality, with the loss of potentially valuable genotypes. It would, in fact, have effects somewhat similar to those of autogamy in tending to stereotype the race.

Lastly there is the very important consideration that a dense local population of a single species is much more vulnerable to epidemic attacks of insects or parasitic fungi. Long-lived seeds are often heavy and devoid of any means of dispersal. Instead of being distributed in space the offspring are distributed in time.

The means whereby the dispersal of seeds is favoured are closely similar, in general principles, to those which apply in the case of fruits, and the same agencies, mechanical projection, wind, water and animals, are employed.

Mechanical Dispersal. First in consideration come the methods of dispersal by mechanical means. Here the seeds play a passive part and the fruits provide the means of projection. Among dry fruits there are two principal means; either by the release of a spring or by compression.

In the first category come the legume fruits of many Papilionaceae, in which the two valves, in drying, set up a considerable strain, due to the shrinkage of two superposed layers of crossed fibres, which is violently released when the valves eventually separate. Each valve twists spirally and throws out the attached seeds with some violence. A similar method is found in species of *Cardamine*. The fruit is a siliqua and the two halves,

FIG. 1378.—*Geranium pratense.* Mature fruit in which all five carpels have sprung upwards. The central column is formed of the inner portions of the five styles and the stigmas may be seen above.

first becoming detached at the base, roll up instantaneously towards the apex, tearing off the seeds and jerking them outwards. In *Geranium* a third spring-mechanism is seen (Fig. 1378). In this genus the five one-seeded carpels have long, beak-like prolongations, each of which is a hollow style, firmly united to the others and terminating in one of the five stigmas. The wall of each style contains a heavy strand of sclerenchyma and an outer layer of soft tissue, the drying of which causes a contractile strain that eventually tears away the wall of the ovary from the central placenta. The wall of the style, now released, coils upwards violently, shooting out the seed from the ovary with an action rather like underhand bowling.

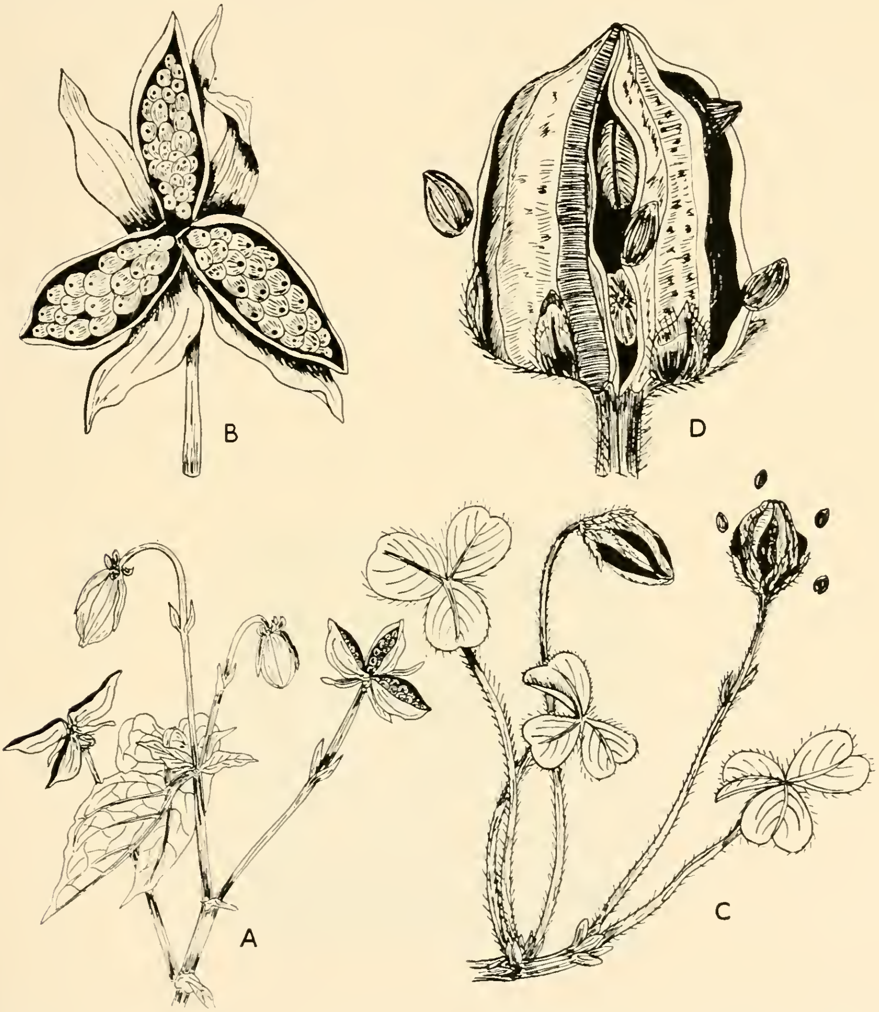

FIG. 1379.—*Viola riviniana.* A, Fruiting shoot. B, The separated carpel segments with the seeds ready for expulsion. *Oxalis acetosella.* C, Fruiting shoot. D, Dehiscent capsule with expelled seeds. In this case the outer integument of the seed is under strain. It splits and rolls back suddenly, ejecting the seed in its inner coat. (*After Kerner and Oliver.*)

A number of species of *Viola* disperse their seeds by a squeezing operation, which is fundamentally similar to methods found in many other genera (Fig. 1379). The ripe capsules are triangular in section and open into three boat-shaped portions or carpels, whose walls are composed of successive layers of thin-walled cells, long curved sclerenchyma and broad, thickened cells. These layers dry unequally and cause the contraction of the sides, which press upon the hard, polished seeds and eventually force them off their attachments and eject them, much in the way that a cherry stone can be shot from between the fingers. By this means *V. canina* and *V. riviniana* can reach distances up to 15 ft., though the average flight is about 10 ft. Each carpel segment of the capsule is emptied of seeds in turn, the seed nearest the apex going first and the basal ones last.

Claytonia (Portulacaceae) has also a squeezing mechanism. Here the capsule also opens into three segments, exposing three seeds arranged triangularly. The seeds are slightly tuberculate, which affords some resistance to the pressure of the carpels as they shrink inwards on drying. When this resistance is overcome the seeds fly off, sometimes in succession, sometimes all together.

A combination of splitting and sudden twisting of the carpels or of their woody endocarps is also responsible for seed dispersal in the families of Acanthaceae and Euphorbiaceae, in which the seeds are usually large and heavy. Further examples are *Alstroemeria*, *Dictamnus*, and *Streptocarpus*.

The woody capsules in *Acanthus* are two-valved and contain 2 to 4 flat seeds, each attached by a funicle which is curved and becomes woody and is called a retinaculum. When the valves suddenly separate, the retinacula spring up and straighten, shooting out the seeds to a distance of 20 to 25 ft.

FIG. 1380.—*Hevea brasiliensis*. Rubber tree. Carpel splitting and ejecting the one large seed.

The trimerous capsules of the Euphorbiaceae have an endocarp of fibrous cells, which are straight when moist but curved when dry. The fruit dries at maturity and the curvature of the fibres causes the carpels to snap apart. In *Hevea* each carpel then opens loculicidally, the two halves separating suddenly, with a twist, which ejects the single large seed. The seeds of *Hevea* are an inch long but they fly as much as 40 yds. from big trees, partly burying themselves in soft ground (Fig. 1380).

Two examples of explosive soft fruits are well known and very striking. One is *Impatiens*, species of which are known as Balsams. They are large herbs usually growing near water. The five carpels are joined into a cylindrical fruit, swollen at its upper end, where the seeds are. Tension is set up by a lining layer of large turgid cells and when the fruits are ripe any slight disturbance causes the carpels to break apart and roll up inwards, throwing off the seed in all directions. The seeds often fall into the water and are further distributed by floating, though they are only ejected to a few yards distance (Fig. 1381).

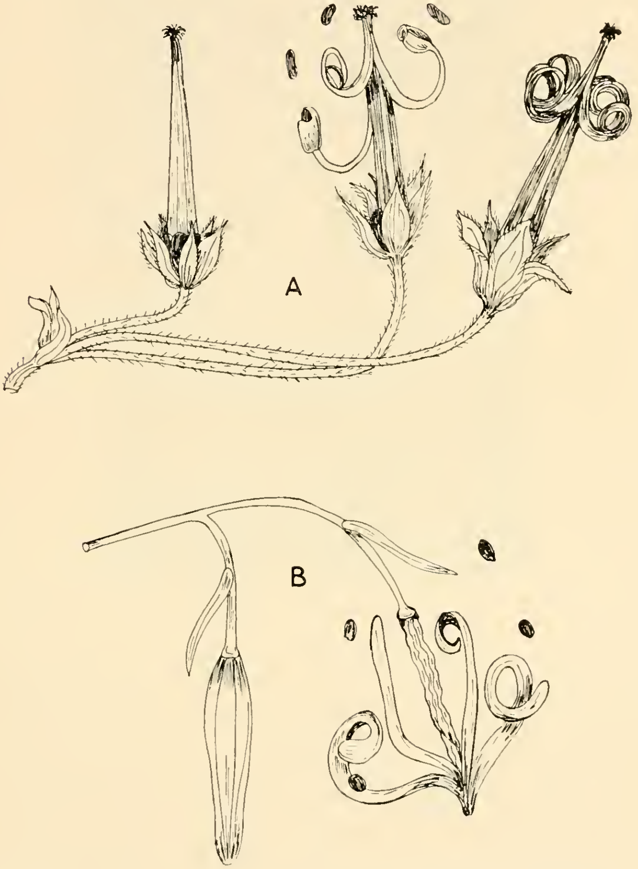

Fig. 1381.—A, *Geranium palustre*. Ejection of seeds. (See also Fig. 1378.) B, *Impatiens noli-tangere*. Mechanical ejection of seeds. See in text. (*After Kerner and Oliver.*)

The second example is *Ecballium elaterium*, the Squirting Cucumber (Fig. 1382), a member of the Cucurbitaceae with oblong, green fruits about 2 inches long. It is native to the Mediterranean area but it is to be found in many warmer parts of the world, usually in dry places, climbing or spreading prostrate on the ground. The end of the pedicel forms a plug in the base of the fruit, the connection between them breaking down as the fruit ripens. Inside the fruit is a number of oval, flattish seeds, surrounded by mucilaginous fluid. In the wall of the fruit is a layer of highly osmotic cells which are under compression. A slight touch loosens the connection with the pedicel and the fruit jerks off, the compressed cells expand and the seeds and the sticky fluid are shot out of the basal opening with great force, flying as much as 20 ft. away (Fig. 1383). Indeed it is a feature of many of these mechanical methods of seed expulsion that the seeds are adhesive and so are capable of being additionally dispersed by animal carriage.

Fig. 1382.—*Ecballium elaterium.* Shoot with ripe fruits, about natural size.

Wind Dispersal (Anemochory). Wind is undoubtedly the most general agent of dispersal both of seeds and fruits. It is not essential that the seed should possess obvious accessories for wind dispersal, such as wings or plumes, for strong winds are capable of blowing even heavy seeds for considerable distances while they are dropping from the plant, or even of rolling them along while they lie on the ground. This leaves out of account exceptional occurrences like whirlwinds, which are capable of lifting and carrying quite large and bulky objects, though such storms are common enough in some climates to be important for seed dispersal. The normal storms of autumn are quite capable of carrying plant debris, including seeds, for distances of several miles.

FIG. 1383.—*Ecballium elaterium.* Ejection of seeds from a detached fruit. See in text. (*After Kerner and Oliver.*)

Among mountains, and in the desert, wind effects are magnified and their importance increased. The only outstanding exception to the general influence of wind is the undergrowth of tropical rain forests, into which none but the most violent winds can penetrate, and the absence there of plants with winged or plumed seeds is notable. Even the Grasses seem unable to enter the forest from outside, and their seeds as well as others are stopped by the dense marginal growth of the forest shrubs.

Wind dispersal seems to be less effective across the sea than overland, and plants with winged seeds or fruits are reputed to be absent from islands which are more than 25 miles distant from the nearest land. Only a few plumed seeds, and minute " dust " seeds, have reached remote islands which were not originally joined to a continent. The last-named category of dust seeds, *i.e.*, very minute seeds, are those most widely dispersed by wind, and in some cases, such as that of the three Polynesian Orchids which have reached Hawaii, they are known to travel for hundreds of miles either over land or sea. Grains of quartz weighing up to 0·003 mgm. have been collected in dust 600 miles from land. Seeds of low specific gravity and of larger relative surface could probably travel as far, even if they weighed ten times as much.

The reason for the relative ineffectiveness of wind over the sea is probably that the wind moves in waves rather than as a continuous current. On land a seed or fruit may therefore be dropped and picked up again, time after time, but this cannot happen so easily over water.

Wind dispersal means, as a rule, wide dispersal. Ridley has pointed out that an annual plant with a plumed seed (*e.g.*, *Senecio vulgaris*) capable of travelling 25 miles in a year, could girdle the earth in 1,000 years, an insignificant fraction of the life-span of a species.

Space will not allow more than a mention of a few types of seeds which are wind-dispersed. Dust-seeds form the smallest and lightest group of seeds. In addition to their minute size and light weight, they often have the advantage of having a flattened, wing-like testa (*Rhododendron* spp.), or one drawn out terminally into long extensions (*Buddleia*, *Nepenthes*) which have somewhat the same effect as wings.

The family of the Orchidaceae are the most notable for the possession of dust-seeds, some weighing as little as 0·004 mgm., which are produced in tens of thousands or even millions per plant. They are conveyed by wind all over the world but the difficulties attending their establishment, and the immense mortality, are vividly illustrated by Darwin's calculation that if all the seeds of one plant of *Orchis maculata* were to germinate and grow to maturity, the great-grandchildren would suffice to cover the whole land surface of the globe.

Such masses of small seeds present a problem analogous to that of the large mass of spores in the spore capsules of Hepaticae, in that they are difficult to break up in the first place. The Hepaticae make use of elater cells. A number of Orchids have achieved an analogous remedy in the shape of long, hygroscopic hairs which grow from the placentae among the seeds. These by their twisting movements separate the seeds from one another, in a manner quite similar to the action of the elaters in Hepaticae.

Many seeds which are not furnished with any structural peculiarity aiding wind dispersal may nevertheless be blown for considerable distances by reason of their very light weight. Salisbury has made extensive measurements of seed weights among plants of the British flora. In his published tables he groups species according to the types of vegetation in which they occur. Among 98 species of herbs from open, unshaded habitats, the average weight, including both seeds and small fruits, was only 1·3 mgm.; ranging from *Sagina apetala*, 0·0075 mgm. and *Limosella aquatica*, 0·009 mgm. to *Elymus arenarius*, 8·9 mgm. The average weight of the " seeds " of thirteen species of common meadow grasses was only 0·8 mgm. Although a good deal bigger than the " dust " category of seeds, objects as light as these would easily be carried about by strong winds.

The subjoined table, after Salisbury and Fisher, shows how the mode of the variation curve of seed weight rises steadily from herbs of open habitats to trees.

Summary of the Data of Weights of all Types of Propagules

The class intervals are arranged in ascending order from 1 to 24. The upper limit of each class is twice that of the upper limit of the preceding class. (Class 3—0·00000381 gm. to 0·00000763 gm. Class 24—8 to 16 gm.) Salisbury and Fisher, 1942.

Class	*Open Habitats*	*Short Turf*	*Meadow*	*Scrub*	*Woodland Herbs*	*Shrubs*	*Trees*
24							1
23							1
22							2
21						1	
20						1	
19							2
18						1	**3**
17						2	**3**
16					4	**5**	1
15	1	1		3	3	2	3
14	3	3	3	4	7	**5**	1
13	2	1		**9**	**10**	4	1
12	7	7		**9**	4	1	
11	10	**10**	4	8	3	2	1
10	15	**10**			4		
9	**17**	4	1	6			
8	**18**	9		2	1		1
7	8	1		9			
6	4	1					
5	6	2					
4	6	1					
3	1	1					
Totals	98	51	8	50	36	24	20

The wings of seeds may be terminal either at one or both ends, like those on *Pinus* seeds, or else surround the seeds (Fig. 1384), like the wing of a samara fruit, such as that of *Ulmus*. They are of all sizes, according to the size of the fruit and seed, but the largest are those of the Cucurbitaceae and Bignoniaceae. In *Zanonia macrocarpa*, a tropical cucurbitaceous climber, the flat seed is surrounded by a fine membranous wing with two lateral expansions, up to 10 cm. in diameter, which is the largest known. The seeds float horizontally in the air like an aerofoil and describe elegant spirals as they slowly descend, looking like large butterflies.

Winged seeds are almost confined to woody plants. A few herbs, *e.g.*, *Spergularia*, have small wing-like frills around the seed and many Iridaceae, Apocynaceae and Cruciferae have thin, flat, light seeds, which are blown about for short distances, even without wings. *Linaria vulgaris*, which is

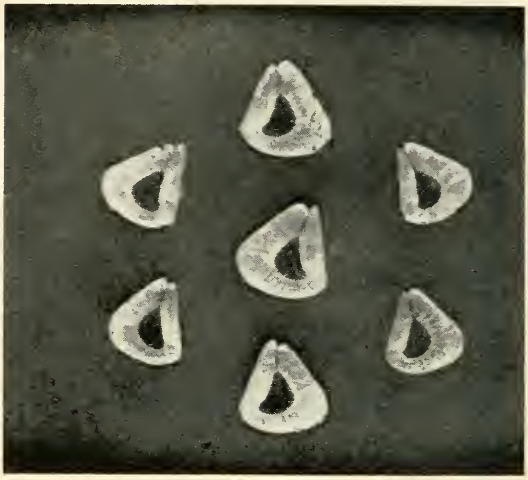

Fig. 1384.—*Lilium (Cardiocrinum) giganteum.* Seeds with surrounding wings.

the most abundant species of its genus, at least in Britain, has also winged seeds, and so have some of the taller Gentians and Lilies and the tall *Eremurus*, but they are exceptional (Fig. 1385).

Fig. 1385.—*Eremurus bungei.* Seeds with unilateral wings, which are both right and left handed with respect to the flat side of the seed.

The wings, in all the above examples, are expansions of the testa. *Clivia*, a member of the Amaryllidaceae, is exceptional in that the wing, although attached to the seed, is an outgrowth of the placenta. The seeds are rather large and heavy so that it is not likely to be very effective as a means of dispersal.

Plumed seeds are far commoner than winged seeds and are to be found in all groups of Angiosperms. They are generally small and are always contained in capsule fruits, usually elongate and dehiscing slowly, as in *Epilobium*, so that the seeds are released in a long succession (Fig. 1386). The two families in which plumed seeds are most frequent are the Apo-

FIG. 1386.—*Epilobium montanum.* Long capsules splitting open to release the plumed seeds.

FIG. 1387. — *Strophanthus speciosus.* Apocynaceae. Fruit dehiscing to release seeds with very long plumes.

cynaceae and the Asclepiadaceae, especially the latter, in which the plumes reach their most impressive development, being sometimes several inches long (Fig. 1387). One genus, *Calotropis*, is widely cultivated in the tropics for these seed plumes, which are used for stuffing pillows, and *Asclepias curassavica*, much cultivated for its flowers, has also naturalized itself widely by its plumed seeds.

The plumes are generally from one end of the seed and may be reckoned as arils, but in *Tillandsia* (Bromeliaceae), a genus of epiphytes in tropical America, the plumes are produced from the long straight funicles. The surface of the funicle and the testa develops parallel ribs of elongated, thickened cells, and these ribs eventually separate off, as long " hairs," which remain attached only at the base of the funicle to form a long plume.

Woolly seeds are not to be distinguished from plumed seeds, except that the hairs grow as a rule all over the testa. The Salicaceae, *Salix* and *Populus*, are well known for the woolly fluff in which the seeds are borne. On a windy day the fluff may be seen streaming away on the leeward side of a Willow tree in extraordinary quantity. It is produced even by unfertilized ovules and, at least in *Populus*, is therefore frequently seedless, the trees being unisexual. The other important family here is the Malvaceae in which four important genera have large capsules full of small, woolly seeds. These are *Bombax*, *Ochroma*, *Eriodendron* and *Gossypium*. The latter is the Cotton plant and the seed-hairs need no description, while *Eriodendron anfractuosum* produces hairs which form the Kapok of commerce. *Ochroma lagopus* is the Balsa tree.

There are two other aspects of the wind dispersal of seeds which do not depend on any special modification of the seed itself. One is the shaking of small seeds out of open capsules by the force of the wind swaying the plant. This has sometimes been called the "censer mechanism". It depends for its effectiveness on the dehiscence of the capsules at or near the top, so that the seeds do not naturally fall out, but require a sharp jerk to dislodge them. The classic example is the capsule of *Papaver* on its long, springy pedicel, but *Digitalis*, *Campanula*, *Verbascum* and *Oenothera* are equally good instances and many more could be cited, for it is a common method among tall herbs. A curious feature related to this method is seen in *Campanula*. The capsules of *C. rapunculus* are held upright and the small apertures of dehiscence are at the top, as also in *Antirrhinum*, but in *C. rapunculoides* the capsules are pendent and the openings in this case are at the morphological base of the capsule, which is here the upper end. Most seeds dispersed in this way are small and as they are only discharged in high winds they can also be carried several yards by the wind itself.

The second case is that of "tumble weeds". The whole plant dies when the seeds are ripe and is readily blown off the ground and rolled along, dropping the seeds as it goes. This is a peculiarity of plants growing on open plains or prairies, where it is most effective. The tumble weeds of the North American prairies, *Sisymbrium altissimum* (Cruciferae) and *Salsola kali* (Chenopodiaceae), the "Russian Thistle", although both introduced plants, have become widespread and noxious weeds through this habit. In some species it is not the whole plant but only the infructescence which is detached and blown away. Several of the Clovers (*Trifolium globosum* and *T. subterraneum*) are thus distributed and the method is not uncommon among grasses. A famous example in the latter family is *Spinifex squarrosus*, together with some other species of this seashore grass, which range all over S.E. Asia and Australasia. The female spikelets form a round head, with greatly elongated bracts ending in spines (Fig. 1388). When this head breaks off it rolls on the tips of the spines and travels at a surprising speed, dropping seeds as it goes. It is so light that it can also float and drift on water. The light panicles of several other dry-land grasses are rolled about in a similar way after being detached from the plant. Clumps of thistle-down may also be borne or rolled by the wind for great distances over both sea and land, but the fruits do not often remain for long attached to them.

One of the so-called "Rose of Jericho" plants is the little annual Crucifer, *Anastatica hierochuntica*, which rolls up its branches into a ball when the seeds are ripe and the plant dries up. The mass of fruit-bearing branches is blown about by the wind, but in this plant the branches spread out when it lands on a wet place and it is only then that the capsules open and the seeds are dropped.

FIG. 1388.—*Spinifex squarrosus.* Female inflorescence which is detached from the plant and rolls before the wind on the tips of the long awns. About one-fifth natural size.

Animal Dispersal (Zoochory). Distribution of seeds by animals occurs in three ways. First, by animals feeding on fruits and swallowing the seeds, which resist digestion and are passed with the excreta, uninjured and sometimes actually more germinable than before. Secondly, by seeds or fruits sticking to the outside of the animal, either by adhesive mucilage or by means of hooks or spines. Sometimes small plants may be carried about entire in this way. Thirdly, by seeds or small fruits being picked up by the feet of an animal trampling in muddy soil. The wading birds are of particular importance in this last method.

Of all the groups of animals the birds are the most active in seed dispersal, because of the fruit-eating habits of so many of them and because of the long distances they travel. They are the only animals capable of carrying seeds far across the sea and they are responsible for many plants reaching oceanic islands. The mammals come next in importance. Insects, especially ants, are active transporters over short distances, while reptiles, fish and molluscs may occasionally contribute their services.

Seeds with hard testas are often very slow to germinate and there is evidence that in some cases the hard covering is softened and germination accelerated by passing through an animal's body. Seeds enclosed in fleshy fruits, such as drupes or berries, or the fruit of the Fig and Strawberry, which are commonly swallowed by birds, are those which seem to be most improved by internal passage, germinating more rapidly and strongly than without such treatment. In some instances this is possibly only due to the removal of the flesh of the fruit, which seems to have an inhibiting action on germination, since even the cleaned seeds germinate better than those sown with the fruit flesh still adherent.

Herbivorous animals, browsing on herbaceous plants, swallow large numbers of dry seeds and fruits, but their food is normally so thoroughly masticated that only a few of these seeds escape destruction. Nevertheless even cereal grains, such as Oats, do pass through safely, and germinating in the excreta produce well-nourished seedlings. Nitrophilous species like *Urtica dioica* and *Polygonum aviculare* are generally dispersed in sheep droppings and are to be found abundantly wherever sheep congregate.

Seeds of many species of *Acacia* are difficult to germinate and are greatly improved in this respect by passage either through goats or elephants, which readily eat the pods. Elephants are great travellers and as they eat many kinds of fruits, their excreta often abound in germinable seeds. The Indian elephant eats fruits of *Mimusops* and *Dillenia* and also the elephant grass, *Themeda gigantea*, as well as Mangoes, Rice and other cultivated plants when it can get them. The African elephant eats *Acacia* pods, *Tamarindus*, *Adansonia*, many species of *Grewia*, and above all the fruits of *Borassus aethiopum*, the Palmyra Palm, the seeds of which, though extremely large, are passed unharmed and germinate in the droppings.

Storage of seeds or fruits by Squirrels and Chipmunks is another means of dispersal, as the hoards are sometimes forgotten and may germinate where they have been hidden. Birds may scatter seeds without swallowing them, by pecking and shaking the soft parts of the fruit, as they do with Rose fruits, or the seeding catkins of *Betula*, which are worried by the tits while eating the fruits and many winged akenes are thus launched on the air, though many are also eaten and destroyed.

In the same manner as the insects are attracted by the colours of flowers, so birds are attracted by the colours of fruits, and, as in flowers, bright colours are often combined, making them more conspicuous by contrast. Frequently it is an aril which is coloured; shiny black seeds being

FIG. 1389.—*Clerodendron trichotomum*. Verbenaceae. Dark blue berries surrounded by the red, fleshy sepals.

combined with a scarlet, orange or white aril, but more often it is the carpels which provide the contrasting colour as, for instance, the scarlet carpels and black seeds of *Sterculia*, or else the persistent calyx, as in *Clerodendron fargesii*, a well-known garden shrub with blue berries surrounded by a red, fleshy calyx (Fig. 1389). In other species the contrast may be between ripe and unripe fruits, as in *Viburnum lantana*, whose unripe fruits are scarlet, while the ripe ones, which alone are eaten, are black. *Sorbus vilmoriniana* has umbels of fruits, those unripe being red and the ripe ones white. In *Momordica charantia*, the wild Pumpkin, there are three colours: the fruit which is reddish, the seeds which are black and the arils which are orange. Shades of red are the commonest colours in fruits and they are well adapted to show up clearly against the green foliage. The colour patterns on the seed-coats of some species of *Phaseolus*, *Lathyrus* and *Ricinus* do not seem to be attractions to birds, as the seeds are mechanically dispersed, and it has been suggested that they serve rather to conceal the seeds, as they lie on the ground, from the eyes of rodents and other small seed-eating animals.

External adhesion is brought about by gummy secretions or by hooked hairs or bristles. The latter are much more characteristic of fruits than of seeds and will be described later. Seeds provided with hooked hairs are decidedly rare, almost the only example being in *Barclaya*, a small member of the Nymphaeaceae, which seems to be dispersed by wild pigs in Malaya.

Carriage of seeds in mud is very common, especially those of marsh or water plants, which are picked up on the feet of wading or running birds. Charles Darwin was the first to investigate this means of dispersal and he raised many plants from specimens of such mud cakes on birds' feet, especially species of *Juncus*, *Carex*, *Polygonum*, and aquatic Gramineae. Small plants like *Lemna* or portions of *Elodea* may also be thus transported and they will withstand exposure to the air for long enough to be carried by ducks for long distances. Not only birds, but hooved animals, human boots and cart-wheels may carry seed-bearing mud about with them. Small floating seeds may also be picked up on the feathers of swimming birds.

Water Dispersal. Dispersal by water includes both fresh water and sea water. The latter has been made the subject of extensive studies, especially by Darwin and by Guppy, because of its importance in the colonization of distant islands.

Almost any seed that is light enough to be wind-dispersed may also be water-borne and many larger seeds which will float are carried by rivers. The only requirement for long-distance transport is a sufficiently impermeable testa to withstand immersion for a not too prolonged journey. Many seeds that are primarily distributed by wind are also capable of floating if they fall into water. Even some seeds which do not float will germinate beneath water, and the seedlings rise to the top and are carried off. Apart altogether from moving bodies of open water, a factor of very widespread influence is rain-wash in the soil. Vast numbers of seeds and fruits are moved thus every year, especially on sloping ground, while others are buried in the soil, where they may long remain dormant, a form of distribution in time rather than space. Mountain streams may also move seeds mechanically without reference to their ability to float, in the same way that they move stones and rocks, by mere force. It is a common experience to find alpine species growing by streams far below their usual level on the mountains, having been carried down either as seeds or as portions of plants.

Enormous quantities of seeds and fruits are carried in the drift floating on rivers, including many which are non-floating by themselves. From a patch of drift in an American river, McAtee isolated 2,490 seeds, many of them non-buoyant, as well as tubers of *Cyperus*.

Millions of seeds must yearly be carried down to the sea by rivers and the vast majority lost. It is therefore important for a fresh-water plant that it should not float for too long a time. Two or three days is usually sufficient to allow adequate dispersal.

For successful dispersal by sea a much longer period of buoyancy is desirable and, furthermore, the seedlings must be resistant to salt water as they will have to establish themselves on beaches or estuaries. Some maritime plants get carried by the tide a long way inland on big estuaries but they will always be within the reach of water which is at least brackish. It follows that sea dispersal is practically confined to shore-living species. The chief exceptions are those seeds which may be transported on floating logs. They may come from inland forests, but the seeds must be impermeable to salt water if they are to survive the journey and the odds against their successful establishment at the end of it are considerable.

The number of species which are dispersed by the sea is not large and they are mostly to be found in S.E. Asia and Polynesia, where the many islands offer suitable stepping stones in dispersal. Ocean currents move over vast distances, it is true, but many of them are of little value for dispersal, inasmuch as they either lead to destinations where the climate is completely different from that at their source, or else they touch no land on their way, so that seeds die on the journey. If the salt water penetrates a seed while it is still floating it either dies or it germinates. In either case it is lost. A well-known example of the first difficulty is afforded by the N. Atlantic drift, which carries seeds from tropical America and the West Indies to the shores of N.W. Europe. Seeds of *Entada*, *Mucuna*, and *Ipomoea* may survive this journey of at least a year's duration, but naturally they are quite unable to grow on the cold shores where they come to land.

Many sea-borne species must have commenced their wanderings during the Tertiary period when the disposition of land and sea was very different from that of the present day, so that their distribution can only be understood on the basis of sea drift across regions which are now land. Thus there are a number of such plants common to the shores on both coasts of tropical America which probably passed across the isthmus of Panama in the Pliocene period, when it was submerged.

Among the routes of successful migration by sea are the following: (1) Australia and Malaya to Polynesia; (2) Malaya across the Indian Ocean to E. Africa; (3) Western America to Polynesia; (4) South America to Africa and thence to southern Asia; (5) Around the Arctic Sea. All but the last of these routes are inter-tropical.

Sea dispersal has been going on for such a long time that many littoral plants have become virtually pan-tropical or pan-arctic and it is now a matter of great difficulty to say whence they originated. Only in cases where they happen to have a number of close systematic relations in one area can it be concluded that they probably belong to the area thus indicated.

Of prime importance in deciding the success of sea migrations is the quality of the land on which the seeds are eventually thrown. Plants of estuarine muds, for example, will stand no chance of establishment on coral islands, nor will rock or sand plants be any more successful on a low-lying and swampy coast. Great numbers of drifting seeds must be wasted for these reasons, nevertheless a few species have reached wide distribution by this means. Such littoral plants must generally have been the first arrivals on new land, since before their establishment there would be little inducement for birds, bringing other species, to visit the area. With few exceptions the littoral species with wide distributions belong to large genera with many inland species, but whether they were the progenitors of the inland species or specialized derivatives from the latter is a matter for speculation.

A few living seedlings, like those of the " viviparous " Rhizophoraceae which are dropped from the trees into the tidal mud of the mangrove swamps, are floated away by sea currents and are dispersed like seeds, except that they cannot survive as long as most seeds and are more liable to be eaten or destroyed. Nevertheless *Rhizophora mucronata* ranges all round the Indian Ocean and into Polynesia, evidence of considerable success in flotation.

The influence of ice as an agent of dispersal should not be overlooked. Icebergs which break off from the foot of a land glacier often bear a load of stones and soil, in which many seeds may be included, and the wide dispersal of many Arctic plants must be largely due to this means of transport. The ice may also drift southwards, especially in the Atlantic, and Darwin considered that the large number of European plants occurring in the Azores might well be due to ice transport during or after the glacial period.

There is a wealth of observations recorded touching the fascinating subject of seed dispersal and those who wish to read further should consult H. N. Ridley's " Dispersal of Plants Throughout the World " and H. R. Guppy's " Studies on Seeds and Fruits " and " A Naturalist in the Pacific ", to which we ourselves are indebted for many of the foregoing particulars.

We have occasionally referred to the productivity of plants in respect of seeds in certain special cases. Productivity of seeds is, however, only one factor, it needs to be considered in the light of germinability and capacity for establishment to give a truer picture of the reproductive capacity of species. For the world as a whole there is all too little information available on these points, vital though they are to any proper appreciation of the life and survival of plant species. For the British Flora, Salisbury has made a most valuable contribution in his book entitled " The Reproductive Capacity of Plants". Much of his information is too detailed for citation but some of his general conclusions may be quoted. If the variation of weight among seeds of a species be plotted for several different types of habitat, it is found that the mode of the curve always corresponds to a higher value the more shaded the conditions with which the developing seedling has to contend. The main exceptions to this rule are parasites and saprophytes and plants of mycorrhizal habit. The conclusion drawn from these observations is that the capacity to colonize in the face of competition, that is into advanced communities, is associated with increased amounts of food reserve in the seeds. As polyploids tend to have heavier seeds than diploids they may be specially important in ecologically advanced plant communities.

Seeds derived from parent plants of very different degrees of vigour show no significant difference in viability or in the vigour of the seedlings. The main effect of poor conditions is to reduce the amount of seed formed but not to affect its quality. It would appear that among ecologically comparable species, the specific reproductive capacity is an important determining factor with regard to frequency and abundance. On the other hand, the reproductive capacity has little relation to the respective risks of mortality and it appears that the seed output is usually high enough to be well above the minimum safety limit.

The lowest seed outputs are characteristic of the herbaceous shade plants of woodland undergrowth, the difficulties of the conditions experienced being met by increased seed weight and the development of vegetative propagation. The highest seed outputs characterize those plants, the " opportunists", which grow in habitats only intermittently available, such as clearings in woods. The biological success of a species appears to be directly related to its reproductive capacity.

FRUITS

The definition of a fruit presents certain difficulties. It is customary to say that it is the product of the ripening of the gynoecium of the flower, not, be it noted, of the ovary only, for styles and stigmas may both play a part in fruit formation. This is the strict, or as one may say, the " botanical " idea of a fruit, but there are many instances in which other organs contribute to the formation of the fruit, such as the calyx, the floral receptacle, the flower pedicel or even the inflorescence axis. These or other organs may develop simultaneously with the development of the gynoecium and become so much an integral part of the ripened fruit that it is practically impossible to separate their contribution to the structure from that of the gynoecium itself. The usual botanical custom is to distinguish these compound structures as "false fruits", a term which is open to objection, since they are no more false fruits than an akene is a false seed, or any other plant structure in which cohesion of different organs has occurred. Moreover the false fruits fulfil exactly the same biological functions as the fruits which consist only of gynoecial tissues. All the parts concerned contribute to the same end of protecting, nourishing and ultimately of dispersing the contained seeds. These false fruits are however of such various construction that it is not easy to include them in a classification of fruits, except as a special class, so we shall consider them apart, though with the reservation that the custom is not logically defensible and, in the case of berries in particular, a matter only of convention.

It is generally said that the fruit, considered simply as a structure enclosing the seeds, is peculiar to the Angiosperms and that it arises after fertilization, yet neither statement is wholly correct. The berry of *Juniperus* encloses its seeds more effectively than does the open ovary of *Reseda*, while in *Jeffersonia* and *Leontice* among the Berberidaceae, the ovules burst out of the carpels and complete their ripening unenclosed. Furthermore, fruits may develop to perfect formation without any fertile seed being formed, the phenomenon known as **parthenocarpy**.

Under this general title several different conditions are included. In the first place there is a *natural* or *autonomous parthenocarpy*, which implies the development of the complete fruit without pollination. The most outstanding example of this is the Banana (Fig. 1390). The basal flowers

FIG. 1390.—A "hand" of young Bananas formed from the parthenocarpic female flowers at the base of the inflorescence. The remains of the perianths and the massive styles and stigmas are attached to the fruits.

of the cluster, which alone produce the fruit, are pistillate and are unpollinated, whereas the upper flowers, which contain stamens, do not form usable fruit. Other fruits which are naturally parthenocarpic include several seedless varieties of the Orange (*e.g.*, Navel and Valencia Oranges), seedless varieties of Cucumber, of the Persimmon (*Diospyrus virginiana*) and some seedless Grapes such as Black Corinth and Thompson Seedless. The Apple and the Pear will sometimes form fruits without pollination if the trees are vigorous and pollination is wholly prevented. In the Fig, the variety Kadota and other Californian varieties are completely parthenocarpic, while the Calimyrna, a Smyrna Fig, is non-parthenocarpic. Tomato fruits may sometimes be produced without pollination but they are quite small.

The second condition is that in which pollination provides the stimulus to fruit formation but without fertilization or the production of seed. The leading case here is the Pineapple, which in cultivation is normally self-pollniated, but is self-incompatible. Seed formation is therefore a rarity but it occurs if plants are artificially cross-pollinated. The wild plant seems to be self-fertile and self-fertile mutants have occurred in cultivation, but offer no commercial advantage. Seedless parthenocarpic fruits are also formed by many self-incompatible Pears after self-pollination. The seedless Pears are smaller than the normal fruits at the carpel end, but they contain more sugar. The Peach also produces parthenocarpic fruits after incompatible pollination, but the fruits are much smaller than normal and ripen more slowly.

Lastly there is the condition of *induced parthenocarpy* which comprehends all the cases where sterile fruits result from artificial treatment. Various procedures have this effect. Foreign pollen may be used, which stimulates fruit development though it has no power of fertilization. Some examples of success by this method have been recorded among the Solanaceae and Cucurbitaceae and in the Grape. Aqueous extracts of pollen, even of foreign pollen, injected into the ovary have sometimes resulted in fruit growth in Solanaceae.

Most of the experiments have been in the use of growth-promoting substances of the hetero-auxin class. Parthenocarpic fruiting in Tomato can be very successfully induced by spraying the flowers with alpha-naphthaleneacetic acid, and in Calimyrna Figs by para-chlorophenoxyacetic acid or gamma (indole 3) n-butyric acid. Most of the fruits so produced, in Tomato, Strawberry, *Lilium regale* and others, do not differ in size or external appearance from the normal fruits, although they are seedless, but in the Calimyrna Figs the fruit is somewhat compressed longitudinally. In the Kadota Figs fruits may be rendered fertile by artificial pollination although they are naturally parthenocarpic, and the fruits differ markedly from each other. The pollinated fruit is greenish, ribbed and has a dull surface but it has a richer or sweeter flavour than the normal parthenocarpic fruits which are yellow, smooth and shiny.

Although it would seem that naturally parthenocarpic ovaries contain sufficient growth-promoting substance to prevent the formation of an abscission layer in the pedicel and thus permit fruit development to go on without pollination or other stimulation, such fruits may also be aided in development by growth-substances applied artificially. The two seedless grapes mentioned above, if treated in flower or in the young fruiting stage with beta-naphthoxy-propionic acid yield considerably bigger fruits.

It is known that pollens contain growth-promoting substances and we may conclude that in normal fruit production the first stimulus to fruit formation comes from this source. Several of the above examples do suggest, however, that developing seeds also exercise an influence upon fruit development, which may be a continuing influence, necessary for the growth of the fruit to its full size and character. Indeed it has frequently been remarked that if one carpel of a syncarpous fruit is sterile that part of the fruit is under-developed compared with the rest.

Nearly all the cases of parthenocarpy which we have mentioned refer to fleshy fruits, but dry fruits may also be parthenocarpic, *e.g.*, in *Acer Hesperis*, *Pisum*, *Nicotiana* and *Papaver*.

The extent of the development which takes place in the ovary during fruit formation is extremely variable. In some species there is little enlargement and there is no new cell formation. In others there may be relatively enormous growth, as in Cucurbitaceae, so that it is difficult to recognize in the mature fruit, weighing thirty or forty pounds, the product of the tiny ovary of the flower. Such growth is accompanied by great multiplication as well as enlargement of cells. From being only a few cells in thickness, the fruit wall may come to possess forty or fifty layers of cells.

The time taken for fruit development is likewise very variable, though there is a general proportionality between size and ripening period. Many herbs, especially weeds of open ground, mature their fruits in one or two weeks and may therefore pass through several generations in one growing season. The great majority of plants take several months, but are within the limits of a single year. The large fruits of some Palms take at least a full year and the great *Coco de mer* of the Seychelles, *Lodoicea*, may take ten years. Many Orchid fruits are also slow to ripen and may take two years or more. They are often massive and contain millions of seeds, so that the accumulation of the necessary quantity of food materials may be the retarding factor.

The ripened ovary wall becomes the coat of the fruit and is then called the **pericarp**. The classification of true, ovarial fruits, depends in the first place on the consistency of the pericarp, which may be either dry or fleshy, and secondarily on whether the fruit wall does or does not open to release the seeds.

I. Dry Fruits

1. *Indehiscent Dry Fruits.* The pericarp does not open and the fruit with the seed is shed from the plant as a unit (Fig. 1391).

(*a*) *Akene* or *Achene.* The product of a single, uniovulate carpel, the pericarp being papery, leathery or woody. Examples: *Ranunculus*, *Alisma*.

(*b*) *Nut* (Nux). A single-seeded indehiscent fruit arising from a pluricarpellary ovary, by abortion of all but one developing ovule. Examples: *Valerianella*, *Tilia*.

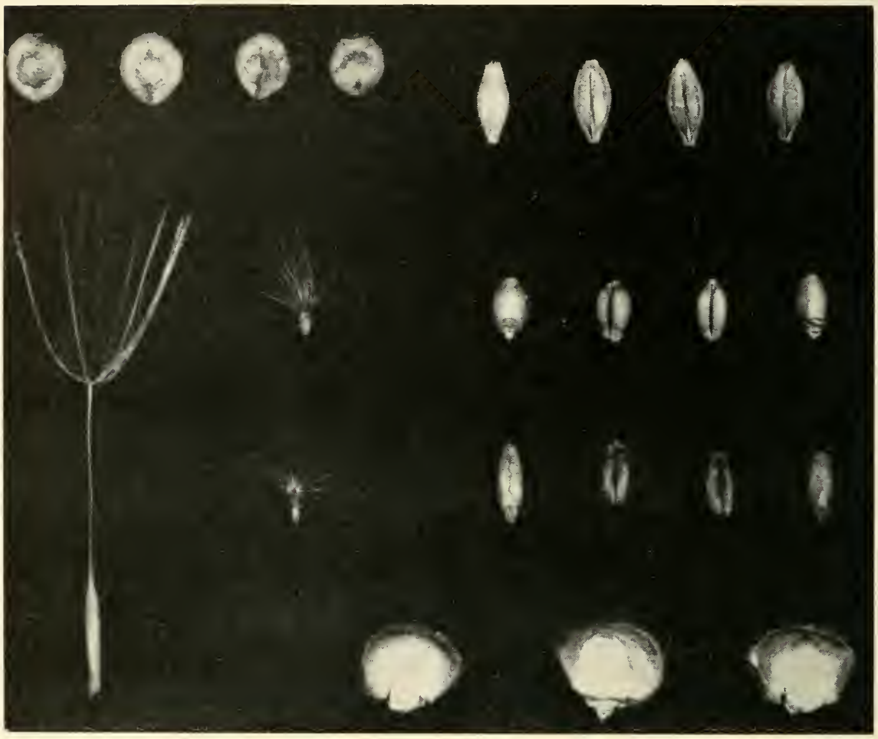

FIG. 1391.—Group of akenal fruits, including, from the top left hand downwards: *Atriplex*, *Hordeum*, *Tragopogon*, *Carduus*, *Triticum*, *Avena*, *Zea*.

(*c*) *Cypsela*. An akene formed from an inferior ovary. It is thus sheathed with other floral tissues in addition to the ovary wall and is strictly a " false fruit". Example: Compositae.

(*d*) *Caryopsis*. An akene in which the pericarp and the testa are indissolubly united. Examples: Gramineae, with the exception of Bambuseae in which the pericarp is distinct from the testa.

(*e*) *Samara*. A winged akene. Examples: *Fraxinus*, *Ulmus*.

The term Nut is unsatisfactory in that it is applied in a sense very different from that of ordinary usage. The fruits of *Corylus* and *Quercus* arise from inferior ovaries and although they correspond otherwise to the definition of a nut, they are distinguished by the term *Glans*. Certain other fruits, popularly called "nuts", *e.g.*, Walnut, Almond, Coconut, are the endocarps of fleshy fruits (see below), enclosing single seeds.

The name *Carcerulus* has also been applied to indehiscent fruits formed from a superior, pluricarpellary ovary and containing one or more seeds. It is not entirely distinguishable from the term nut, but can be applied to some of the Cruciferae in which the fruit does not dehisce, *e.g.*, *Bunias* and *Crambe*, and to some rare types of indehiscent capsules.

True akenes may sometimes be enclosed by external structures without thereby falling into the category of false fruits. For example, in the Nyctaginaceae the akenes are enclosed by the indurated base of the perianth, and in *Carex* the akene is enclosed in a sac, called the utriculus or perigynium, which is an undivided, sheathing bracteole.

While the akene may be regarded as the simplest type of fruit and the one in which usually the amount of alteration of the tissues during ripening is least, there are signs that in some cases its simplicity is not primary but secondary and that it has been reduced from a many-seeded type of fruit. Abortive or vestigial ovules persist in some cases, notably in *Anemone*, either with or without vascular supply bundles. Among Rosaceae and Ranunculaceae a series of forms may be selected which illustrate the possibility of reduction leading from a multiovulate, three-trace carpel, to a uniovulate, single-trace carpel; the greatest degree of reduction being shown by *Ranunculus*. Reference back to what we have previously said about peltate and semi-peltate carpels (see p. 1215) will show that there are, however, reasons for thinking that some uniovulate carpels with median ovules belong to a different development pattern from the multiovulate types with marginal placentation and are primitively uniovulate.

2. *Schizocarpic Fruits*. These are products of plurilocular ovaries which at maturity separate into their component carpels, each of which is an akene, indehiscent and one-seeded. The component parts are called *mericarps*, or sometimes cocci. True schizocarps are found in the Umbelliferae and in some of the Malvaceae (*Malva*, *Lavatera*) (Fig. 1392). As the former are from inferior and the latter from superior ovaries, they provide another instance of the illogical nature of the separation of "false" fruits. In Umbelliferae the fruit is called a *cremocarp* (Fig. 1393). It is bicarpellary and the two carpels, after separation, remain for some time suspended from a forked prolongation of the floral axis called the *carpophore*. The bicarpellary fruits of *Acer* are also cremocarps, each mericarp being a winged samara. In the Labiatae (Lamiaceae) the ovary is also bicarpellary, but at maturity the carpels separate into four one-seeded units, with hard walls, which are called *nutlets* (nuculi or cocci), each of the carpels being subdivided by a false septum which develops secondarily from the true septum.

The schizocarps provide a link between indehiscent and dehiscent fruits,

FIG. 1392.—*Althaea rosea.* Hollyhock. Schizocarpic fruit breaking up into a ring of mericarps.

for they include a sub-type which is dehiscent, called the *regma.* In these cases, the mericarps when they separate from the central axis, open along the ventral suture and expel the contained seed, sometimes with violence. Good examples are afforded by *Geranium* (see p. 1508), *Dictamnus* and some *Euphorbias.*

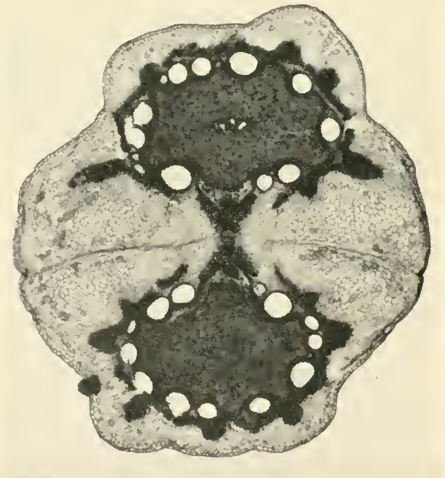

FIG. 1393.—*Oenanthe crocata.* Umbelliferae. Transverse section through the cremocarp with one seed in each mericarp.

3. *Dehiscent Dry Fruits.* The ripe fruit dehisces to release the seeds, usually several, often many in each carpel.
   (*a*) Fruits formed of a single free carpel.
      (i) *Follicle.* A pod-like fruit which splits down one side, generally the ventral side, and occasionally down part of the other side. Examples: *Aconitum*, *Delphinium*.

Among the follicles should be mentioned the remarkable woody fruits of some Proteaceae, in which the fruit wall becomes extremely thick and hard. Only one fruit is formed by each flower, which splits open to release two flattened and delicately winged seeds. Examples: *Banksia*, *Xylomelum*, the Woody Pear of Australia, *Hakea* and *Grevillea*. In some genera of the family the fruit is indehiscent and one-seeded. The single follicles in this family are unusual. Follicles are generally formed in groups from the clustered carpels in apocarpic flowers.

      (ii) *Legume.* Like the follicle, this is the product of a single free carpel. It is also many-seeded, but it differs in opening down the full length of both the ventral and dorsal sutures, so that the fruit separates into two halves or valves, with seeds attached alternately to the margin in each half. When separating the valves usually twist rapidly, causing the detachment of the seeds. The tension which results in the sudden dehiscence and twisting is due to the differential shrinkage of the soft outer tissues and an inner sclerotic layer of the carpel wall, as the fruit dries in ripening.

This is the simple legume as it is found in the majority of the Papilionaceae (Fig. 1394), but there are several variants. In the big genera *Astragalus* and *Oxytropis* the united ventral margins grow inwards and form a longitudinal septum dividing the seeds into two ranks. The valves in the fruit of *Carmichaelia* have thickened margins, from which they are detached and fall, the margin remaining like a frame with the seeds attached.

A frequent form of legume is that called a *lomentum* in which the valves are constricted between the seeds and break across transversely when ripe, each one-seeded portion falling off as an indehiscent, or sometimes dehiscent (*Entada*), unit. Example: *Onobrychis.* Lomentaceous fruits are very common in the Mimosaceae and in many species the thickened margin of the flattened legumes forms a frame, as above, from which the lateral walls drop away separately. The legumes of some of the species of the tropical genus *Cassia*, *e.g.*, *C. fistula*, are of astonishing length, up to three feet in some cases. They are blackish, hard, and cylindrical and are provided internally with numerous cross-septa, dividing the fruit into one-seeded portions, which however do not separate like lomenta. These cylindrical fruits are indehiscent and only break up by decay or damage. Other species of *Cassia* have long, flat pods which dehisce longitudinally.

A further variation of legume structure is seen in the spirally wound legumes which are familiar in *Medicago*, different species of which show all variants between one partial turn and several complete turns of the spiral. In *M. arabica* the margins of the fruit are furnished with long spines, pointing in different directions, which form an adhesion mechanism aiding dispersal by animals. *Prosopis pubescens*, the Screw Bean of the southern United States, has fruits wound into a long, tight spiral of many turns. The pod is fleshy and is eaten by animals which distribute the seeds in their excreta, as is the case with many other legume fruits.

Fig. 1394.—*Arachis hypogaea.* Ground Nut. One of the subterranean legumes opened to show the two seeds. One cotyledon of the upper seed has been removed to show the embryonic plantlet. The point of attachment of the fruit is below.

(*b*) *Syncarpous Fruits.* The product of two or more concrescent carpels.

(i) *Siliqua.* A pod-like fruit formed of two carpels.* It is generally regarded as a special type of the next class, the capsules, but it has several points of distinction. The form of the siliqua may be either long or short, cylindrical as in *Hesperis* (Fig. 1395), or flattened as in *Lunaria* (Honesty). When it is as broad as its length, or broader, it is called a *silicula* (*Capsella*, *Thlaspi*). It may be flattened in either direction, that is either in the plane of the carpel walls (*Lunaria*) in which case the carpels themselves are broad and flat, or at right angles to this plane (*Capsella*), when the carpels are narrow, but deeply pouched. In *Camelina* the siliqua is globose. Most siliquas contain a number of seeds, but a few have only one seed in each carpel (*Iberis*, *Biscutella*) or only a single seed (*Isatis*).

Fig. 1395.—*Hesperis matronalis.* Dame's Rocket. Long siliquas, constricted between the seeds.

The suture at the carpel edges marks the position of the placentae and forms a thick rib which surrounds the fruit. From the suture on each side of the fruit there grows inwards a longitudinal membrane and the two membranes meet and overlap, forming a false septum and dividing the

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* Kerner and some other subsequent authors, especially Saunders, have maintained that there are really four carpels involved. The two outer carpels being sterile and forming the valves, while the marginal ribs represent two inner, reduced but fertile carpels.

loculus of the carpel into two, with two rows of seeds on each side. When ripe the carpel walls separate from the suture rib, beginning at the base, and detach themselves upwards, finally falling off. The rib now forms a frame to the exposed septum, the whole being called the *replum*, to which the seeds remain attached. The seeds are often round and have no other means of dispersal than rain-wash (see also *Cardamine*, p. 1508), but in *Lunaria* and some other genera, the seeds are quite flat and can be blown by the wind for short distances. Often the fruits do not dehisce until they have been shed and in some forms (*Iberis*, *Thlaspi*, *Biscutella*) the carpels are winged and the whole fruit is blown about before the seeds are dropped. The Woad plant, *Isatis tinctoria*, has one-seeded, indehiscent siliquas, which are in fact samaras, and are similarly wind-dispersed. Other genera having indehiscent siliquas are *Bunias*, *Myagrum*, *Crambe* and *Zilla*.

Where wind dispersal occurs, the fruiting pedicels lengthen considerably, holding the fruits well out from the stem and fully exposed. The whole infrutescence may be detached either before or after dehiscence of the fruits, and the papery membranes of the replums then act as sails and the infrutescence is blown about like a tumble-weed, shedding its seeds broadcast.

Siliquas in all varieties are the characteristic fruits of the Cruciferae and occur also in a few of the Papaveraceae.

> (ii) *Capsule.* A many-seeded dry fruit composed of two or more carpels, which dehisces in various ways to release the seeds. In general the dehiscence starts at the apex and the separated portions or *valves* do not become detached.

This is a very wide category and includes fruits of the most diverse forms. They are classified according to the mode of dehiscence (Fig. 1396).

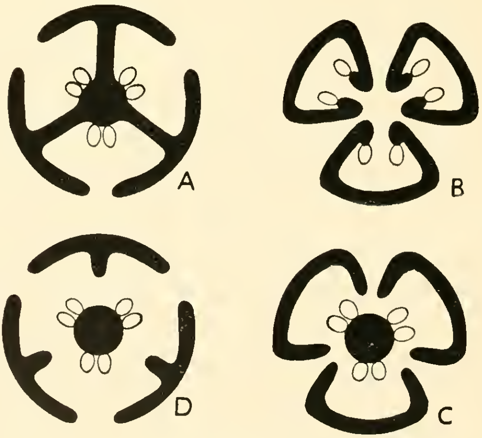

FIG. 1396.—Diagrams of capsular dehiscence. A and D, Loculicidal. B and C, Septicidal.

In septate fruits there are three patterns of longitudinal dehiscence. *Loculicidal:* The carpels may split down their dorsal sutures, thus opening directly into each loculus. *Septicidal:* the splits separate the carpels entirely from each other, thus dividing each septum into two. *Septifragal:* the carpels split opposite the outer end of each septum, the outer walls being detached and the septa remaining attached to the central axis.

All but a minority of capsules dehisce by one or other of these methods. The exceptional cases may be mostly classified under the three following types. *Porose:* the carpel walls open by means of small localized openings, where the tissues split apart. A common example of this is the capsule of the Poppy, whose outer wall shrinks in drying and separates from the stigma-bearing cap of the fruit, leaving a gap all round under the edge of the cap. The gap is divided into pores by the outer edges of the false septa, which are exposed by the opening. The seeds are scattered by the shaking of the capsule on its long stalk in the wind. *Circumscissile:* the line of dehiscence girdles the capsule transversely, detaching a lid. This is not common but is seen in *Plantago*, *Anagallis* and *Hyoscyamus*, all well-known plants. *Valvate:* the capsule opens at the top by the separation of the tips of the carpels, which bend outwards, exposing the interior. The fruits of the Caryophyllaceae are valvate in many genera.

When a capsule is unilocular the mode of dehiscence is naturally somewhat modified, as there are no septa. In such types the carpels usually separate at their edges, which is most nearly analogous to septifragal dehiscence. The circumscissile capsule of *Anagallis* (see above) is an exception.

Capsules which dehisce longitudinally mostly separate into as many segments as there are carpels, but occasionally there are supernumerary splits. For instance, the capsule of *Datura* consists of two carpels but the capsule wall splits into four valves. The dehiscence is truly septifragal but each carpel splits secondarily along its midrib, opposite the false septum formed by the placentae (Fig. 1397).

Dehiscence of fruits is generally brought about by the shrinkage of the pericarp in drying but in the fruits with stony endocarps to be described later, it is the swelling of the contained seeds as they take up water which forces open the hard shell around them.

If some akenes can be regarded as reduced follicles, others may equally be looked upon as reduced capsules. This is the case with the Nut where reduction has, by definition, occurred. The inferior nut or glans of *Corylus* arises from a bicarpellary ovary of which one only is fertile. The septum adheres to the inside of the pericarp, except for its central strand, which remains, attached to the ripe seed, as a woody cord at the top of which is attached the shrivelled ovule of the infertile carpel (Fig. 1398). The samara of *Fraxinus* has the same structure except for the wing, the plane of which is perpendicular to the septum. The samara of *Ulmus* is a parallel case, though one carpel is sterile from the beginning. The cremocarps also may be classed as reduced bicarpellary capsules, in their case

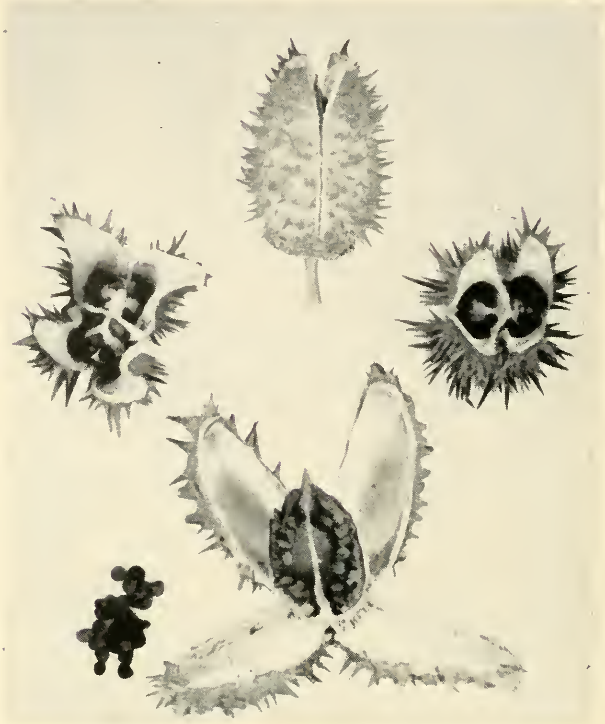

FIG. 1397.—*Datura stramonium.* A bicarpellary capsule which splits secondarily into four valves.

FIG. 1398.—*Corylus avellana.* Hazel Nut. Glans cut open to show the one ripe seed, to the top of which is attached the shrivelled remains of the infertile ovule.

with septicidal dehiscence, separating two uniovulate portions which are closed and are therefore akenes, just as the separated portions of the septicidal fruits, which contain several seeds and do open, are follicles. Capsule and follicle are, in fact, fundamental types among the dry fruits and the rest, except for some akenes, can all be derived from the one or the other.

Dehiscence in capsule fruits is primarily due to the strains set up by unequal shrinkage of the cell-layers in the pericarp as the fruit dries towards maturity. Drying is assisted by blockage of the water supply, due to thickenings in the pedicel, and furthered by evaporation from the fruit itself and from any attached floral organs, *e.g.*, sepals, which may remain. The lines of dehiscence are predetermined by lines of weakness formed of thin-walled cells in the pericarp, either at the sutures or along the median line of the carpels. Circumscissile dehiscence is also determined by a mechanically weak zone, due either to the alignment, or the size or the state of thickening of the cells, or their meristematic condition, or by a combination of these factors. A typical case is that of *Portulaca oleracea*, where dehiscence takes place along a zone of thin-walled cells, lying between two zones of sclerenchyma. In *Anagallis*, *Sesuvium* and some others the thin-walled layer remains meristematic.

II. **Fleshy Fruits**

Manifold in appearance as these are, their classification is relatively simple, for they fall into two main types only, neither of which is truly dehiscent, though partial splitting may occur.

1. *Berries.* Here the pericarp is usually massive, soft, juicy and short-lived. It is formed of three distinct layers. Outermost comes the skin or *epicarp*, which generally colours conspicuously when ripe. Within this is the comparatively thick flesh, or *mesocarp*, and innermost is the membranous *endocarp*. The whole encloses the seeds, which are rarely solitary (*Myristica*, *Phoenix*), and may be numerous. The berries of *Actaea* (Ranunculaceae), *Arum* and *Berberis* are formed from a single carpel; *Atropa*, many other Solanaceae and *Vitis* have berries of two carpels; *Convallaria* and *Asparagus*, berries of three carpels; in *Actinidia* (Chinese Gooseberry) of many carpels. The pericarp is sometimes relatively thin, though soft, as in *Galium*, forming a transition to the capsule. Indeed the berry differs from the capsule principally by its soft pericarp and there are some types which might be considered as belonging to either category, *e.g.*, *Capsicum*, *Podophyllum* (Fig. 1399), *Lardizabala*. The berry of *Myristica*, although unicarpellary, dehisces to expose the single seed.

It might be logical but it would be a *reductio ad absurdum* to separate the berries formed from inferior ovaries as "false fruits", most of them being perfectly typical berries. In this category we have *Coffea*, two carpels; *Sambucus*, three carpels; *Hedera*, five carpels and *Ribes* (Gooseberry) with two carpels but unilocular and with two parietal placentae. Here as in the similar case of *Punica*, the pulp mostly consists of the mucilaginous testas of the seeds. The development of the fleshy consistency of the pericarp frequently leads to the suppression of septa and the abortion of some of the seeds, so that the structure of the mature berry may be difficult to discern.

FIG. 1399.—*Podophyllum emodi*. Fleshy capsule.

Berries assume many forms, some of them very different from that familiarly pictured in our minds by the name. The Banana, for example, falls into this class and so do the Cucumber and the Melon. These are all from inferior ovaries and like the Gooseberry are unilocular, the two latter with parietal placentae. They have received the special name of *pepo*. The Orange has also been given the special name of *hesperidium* (Fig. 1400). Its epicarp is thin and aromatic, the mesocarp soft and pithy and the thin endocarp of the individual carpels bears numerous trichomes which become large and pulpy and form the flesh of the fruit, surrounding the seeds, which are borne on axile placentae.

2. *Drupes*. These are fleshy fruits which are distinguished from berries by the hard, stony endocarp which encloses the seed or seeds. Simple drupes like the Cherry arise from a single carpel. Several of the most familiar fruits, the Plum, Peach, Apricot and Almond, all members of the Rosaceae, resemble the Cherry in being unicarpellary. The endocarp thickens considerably in ripening, at the expense of the mesocarp, and forms the stone of

FIG. 1400.—*Citrus aurantium.* Orange. Transverse section of a young hesperidium fruit. The pulpy hairs are just beginning to develop.

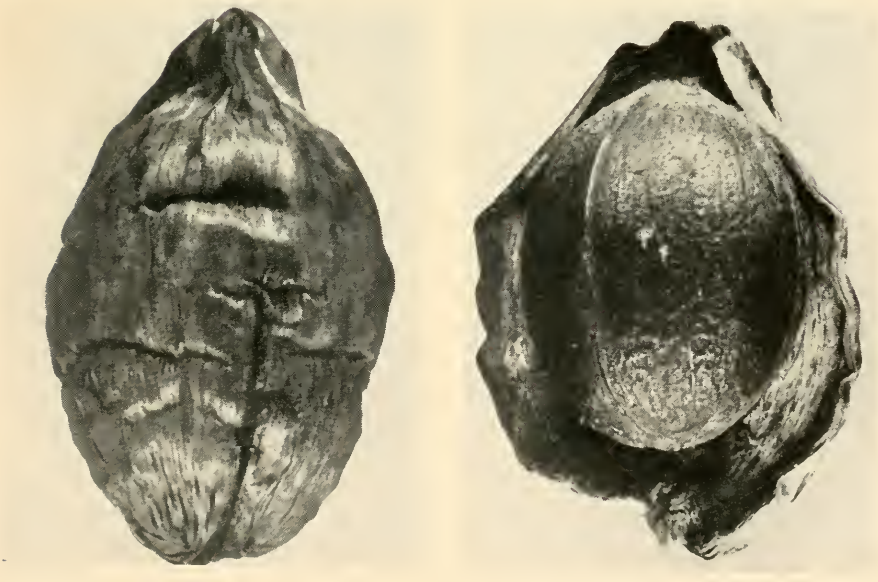

FIG. 1401.—*Cocos nucifera.* Coconut. Left: the complete fruit with leathery epicarp. Right: the fruit opened to show the fibrous mesocarp surrounding the woody endocarp which is the " nut " as commonly understood.

the fruit. Normally it encloses only one seed, which has a thin, papery testa, the endocarp giving all the protection needed. The only drupes which possess more than one stone, with rare exceptions (*Ilex aquifolium*), are those formed from inferior ovaries, which are classed among the pseudocarps, the stones being, in fact, akene fruits. In the fruits mentioned above, the mesocarp is soft and edible, except in the Almond, itself the endocarp, where the rather hard, green mesocarp splits open to reveal the stone. Some of these hard stones present difficulties at germination, which we shall touch upon later. The mesocarp may contain an abundance of fibrous tissue and in such cases the soft parts may disappear at maturity, leaving a purely fibrous mesocarp. Drupe fruits are common among the Palms, and many of them are of this fibrous type, notably the Coconut (Fig. 1404). The "nut" here is the seed covered by the endocarp, which is enclosed in a massive fibrous mesocarp and this in turn by a leathery epicarp, the whole fruit being about twice the size of the nut. The resistance of the Coconut to salt water is chiefly shown by the complete fruit, which can float unharmed for a considerable time, while the nut itself soon decays in the sea. The fibre is the *coir* or coconut fibre of commerce. Another Palm with a fibrous mesocarp is *Nipa*, which, like *Cocos*, grows close to the sea, often in brackish swamps.

III. **Pseudocarps** or " False Fruits "

The examples of the class of fruits, generally distinguished by this title, are only a few of the most striking. Many others equally eligible for inclusion are, as we have seen above, neglected because they present no prominent difference from other related types. The strict criterion is that a pseudocarp includes structures other than the gynoecium, but, as we have already argued, all the structures in a fruit, of whatever origin, are integrated to form a biological unit, even if it is not morphologically homogeneous.

The first examples in this class are the Apple and the Pear, which come from inferior ovaries. The five central carpels have thin cartilaginous walls, enclosing the seeds. The external flesh must necessarily include other floral tissue, which may be interpretable as either a hollowed floral receptacle or a sheath of concrescent sepal, petal and stamen bases. This question we have already gone into (see p. 1219). It is probable, however, that the cartilaginous wall is really an endocarp and that some part of the outer flesh is truly mesocarp. Indeed a cleavage may sometimes develop medianly in the flesh, separating an outer portion and an inner, five-lobed portion, which lends support to this view. These fruits and related types, like the Quince, are called *pomes* (Fig. 1402).

The Rose fruit or " hip " is somewhat similar to the pomes except that the surrounding tissue is not united to the enclosed carpels, a cluster

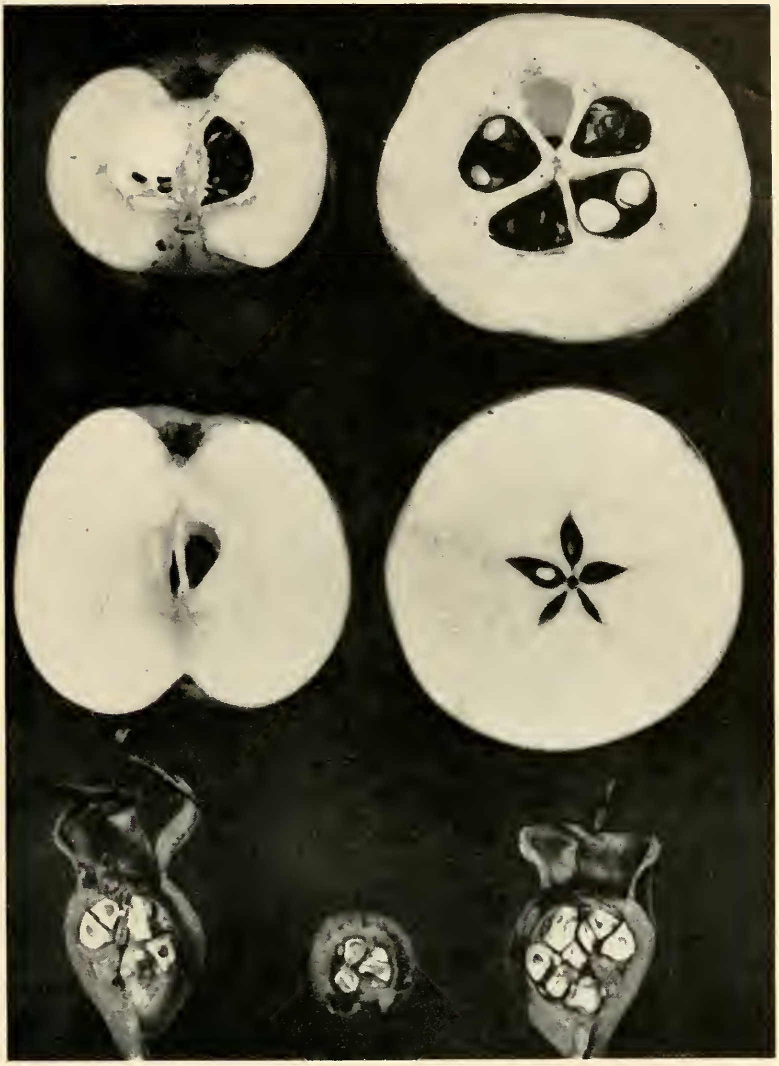

FIG. 1402.—Various pseudocarps. Above: pome of the Quince, *Cydonia vulgaris*. Middle: pome of Apple, *Pyrus malus*. Below: Hip of *Rosa*. See in text.

of free akenes. In *Crataegus* the soft external tissue encloses a group of hard objects, like a drupe with several stones. This is in fact a drupe of several carpels and the stony walls are endocarps. It is analogous to a small Apple with hardened, instead of cartilaginous, carpel walls. The Medlar (*Mespilus*) also has several stones, which are free from the outer flesh, not united to it as in *Crataegus*. The stones in these latter fruits are called *pyrenes*.

One may note that all these fruits belong to the Rosaceae which seems to be rich in pseudocarps. Another example, from the same family but of a different type, is *Fragaria* (Strawberry), the fruits of which are minute, hard akenes, set on the surface of the much enlarged and highly coloured receptacle which forms the popular idea of the fruit.

From the Anacardiaceae comes another receptacular fruit, *Anacardium occidentale*, where the kidney-shaped true fruit is drupe-like and contains one big seed enclosed in an oily pericarp. It is not this, however, but the receptacle which is most conspicuous, for it swells up to the proportions of a lemon, underneath the drupe which it supports. (See Fig. 1693.)

Several familiar pseudocarps are made up of an entire inflorescence, in which the individual flowers are united to and by the swollen tissues of the axis. Among these is the Pineapple, which is formed from an intercalary spike of flowers (Fig. 1403). Although the flowers are sterile in the cultivated form of the plant, the fruit develops by the hypertrophy of the axis, which envelops the remains of the flowers and all but the tips of the floral bracts. The flesh of the fruit is therefore wholly due to vegetative growth. The Mulberry (*Morus*) on a smaller scale is also an inflorescence fruit, formed of a close aggregate of small drupes united to a swollen axis and to each other by the persistent calyces, which become succulent and provide the flesh of the fruit.

FIG. 1403.—*Ananas sativus.* Pineapple. Longitudinal section of the fleshy inflorescence axis, in the surface of which the sterile flowers and their bracts are embedded. The axis proliferates above into secondary vegetative growth.

Lastly there is the Fig (*Ficus carica*) which belongs to the same family as the Mulberry, the Moraceae. One genus of Moraceae, *Dorstenia*, has its flowers set upon the upper surface of a flat, expanded axis, while in *Ficus* the axis has been not only expanded but curved upwards into a hollow flask with a tiny orifice, on the inner surface of which are set the numerous small flowers. This peculiar structure is called a *syconus* (Fig. 1404). The pollination and the sex relationships of the flowers of *Ficus* have already been described (p. 1327). The genus is a very large one with a world-wide distribution in hot countries, but the syconus fruit is its constant characteristic. Similar but much less well-known syconus fruits are found in the Monimiaceae.

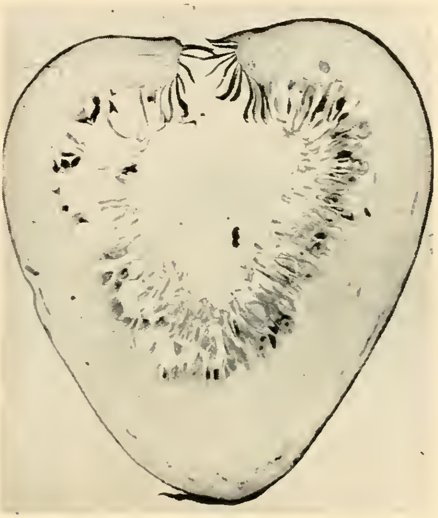

Fig. 1404.—*Ficus carica*. Fig. Longitudinal section of a young syconus showing the interior layer of flowers, with a cluster of sterile flowers round the orifice.

When the carpels of an apocarpous flower ripen separately they form an *etaerio*, which is the collective name for the group. Thus there may be in Ranunculaceae an etaerio of akenes or an etaerio of follicles. If, however, during ripening they become so closely crowded that they form a coherent structure the product is called an *aggregate fruit*. Examples of such aggregates are provided by the Raspberry and the Blackberry, both species of the genus *Rubus* (see Fig. 1514). The various cultivated species of the genus *Annona* also form aggregate fruits, *i.e.*, Custard Apple, Sweet Sop, Sour Sop, etc. *Magnolia* and *Cornus* provide other well-known examples (Fig. 1405). The individual portions of the *Rubus* fruit are drupes or *drupels* (diminutive) but in *Annona* the individual fruits are completely fused into a fleshy mass and have no separate existence, though by analogy they may be described as one-seeded berries.

The term *collective fruit* is applicable to compound fruits made up of the consolidated fruits of the flowers of an inflorescence, with the exception of those, like the Mulberry, the Pineapple and the Fig, which involve other parts besides the actual fruits. Such are, for example, the fruits of *Monstera* *deliciosa* (see Fig. 1952) and of many other Araceae such as *Acorus*; of the Bread Fruit (*Artocarpus incisa*) (see Fig. 1627) and of the related Jack Fruit (*A. integrifolia*), all well known in the tropics. The foregoing are all fleshy, but the woody fruits of *Pandanus* are also collective. In spite of their hard exterior the *Pandanus* fruits are pulpy inside and are individually berries. There are not many examples of collective fruits among familiar temperate genera. *Casuarina* (see Fig. 1653) and *Liquidambar* both have collective fruits of united capsules and *Lonicera* has inferior berries which fuse in pairs, sometimes at quite an early stage of development.

Fig. 1405.—Aggregate fruits of *Magnolia acuminata* (above) and of *Annona cherimolia* (below).

We have described in an earlier chapter (see p. 1354) certain plants which produce differently shaped fruits from their cleistogamic and chasmogamic flowers. Some plants, for unknown reasons, produce fruits of more than one kind on the same individual, without cleistogamy, though examples are not common. This is known as **heterocarpy**. For instance a small Crucifer on Juan Fernandez, *Heterocarpus fernandesianus*, closely resembles *Cardamine chenopodiifolia* in its two kinds of siliquas (see p. 1355), although they are both above ground. Those cases in which fruits of two kinds are borne respectively above and below ground have been called **amphicarpy**.

The best-known cases of heterocarpy are undoubtedly among the Compositae, where the cypselas formed by the ray-florets and the disc-florets respectively are sometimes very different in appearance. The genera *Calendula* and *Dimorphotheca* provide striking examples. In

Calendula the disc fruits are strongly curved and the convex side is edged with small knobs, while the ray fruits are much larger and expanded into a pair of fringed wings, besides having a dorsal row of spiny processes. In *Dimorphotheca* the ray fruits are practically straight, tapered downwards and slightly roughened. The disc fruits are broad and flattened, with wing-like expansions, and are smooth (see Fig. 1182). They germinate quicker than do the ray fruits. A common British plant, *Leontodon leysseri* (*L. hirtus*), has a still more marked difference between the fruits of the disc- and the ray-florets, the former being thickest at the top, with a pappus of small scales, and the latter tapering to the top and having a large, plumed pappus.

All these cases indicate a different dispersal for the two types of fruit, since the winged or flattened fruits are certainly more easily transported by wind than the others, though whether a double dispersal, near and far, is a biological advantage to the plants requires proof. There are many other Compositae with similarly heterocarpous fruits in which there is no difference in their possibilities of dispersal, as in *Bidens radiatus*, where both disc and ray fruits have clinging hooks for animal dispersal, though the former are nearly twice the length of the latter.

Dimorphic fruits (cypselas) also occur in *Xanthium*, the Cocklebur, a genus of Compositae. There are two fruits in each involucre. The uppermost is the smaller of the two and is convex outwards, the lower fruit is convex inwards. The latter germinates in the first season, the smaller fruit does not germinate until the second or a subsequent season.

Atriplex hortensis (Chenopodiaceae) is often grown as a vegetable. There are two, sometimes three forms of fruit, one which is vertically flattened and held between two large, thin bracts, the fruit being sometimes yellow and sometimes brown. The other is black, is horizontally flattened and has no bracts, but has adherent remains of the perianth, the latter being absent from the fruits enclosed between bracts. At first sight it would be supposed that the bracts are agents of wind dispersal, but this may not be so, for these fruits remain adherent to the plant, while the black fruits are readily shed. If there may be no difference in dispersal here, there is also none discernible in *Valerianella*, where the terminal fruit of the cyme is several times as large as the lateral fruits, though otherwise similar, or in *Polygonum*, in which several species produce both three-angled and two-angled fruits indiscriminately, which are otherwise identical.

Under the name of **heteromericarpy** are included certain cases, particularly in the Umbelliferae, where one part of a fruit differs from the rest. The outermost flowers in the umbels are often markedly exotrophic, that is, they are better developed on the outer side than on the inner side, and the same holds good for the fruits. In *Torilis nodosa* the outer mericarps of the outer flowers are larger and are furnished with hooked trichomes, which are effective in animal dispersal. On the inwardly directed mericarp the trichomes are small and not hooked, while on the fruits of the inner flowers of the umbel they are absent. Where one side of a bilateral structure is more developed than the other, the difference is often designated by plus and minus. Thus in the fruit of *Antirrhinum majus* the lower carpel of the bicarpellary fruit is always "plus", the upper, smaller carpel is "minus".

Heterocarpy is almost always associated with some constant difference in the positions of the two kinds of fruit on the plant, which suggests differences of nutrition as a possible explanation. There are, however, some exceptions, one being a climbing member of the Euphorbiaceae, *Tragia volubilis* from Brazil. The fruits are axillary and borne singly on long pedicels. Most are the typical trimerous capsules of the family, but some fruits are unicarpellary and one-seeded, the two sides of the carpel growing out into long horns and the ventral suture being extended into a third, shorter horn. Both types of fruit are produced indiscriminately in the leaf-axils. The horned fruits are indehiscent and are probably dispersed by animals, while the tricarpellary fruits dehisce in the usual way.

It will have been gathered from some of the foregoing observations that some parts of the flower other than the gynoecium are affected by post-fertilization developments. Some of these later floral developments function for the protection of the fruit, others for its dispersal, sometimes both are aided. The calyx is an organ which is often affected in this way, not only persisting as the fruit ripens but changing its appearance and sometimes its size. A familiar example is the Bladder Cherry, *Physalis alkekengi*, the synsepalous calyx of which is transformed into a thin, orange-coloured balloon (see Fig. 1130) about an inch and a half across, entirely enclosing the berry fruit. Similar, but uncoloured calyx envelopes (Fig. 1406) occur also in other Solanaceae. Some members of the Convolvulaceae have enveloping calyces in which the sepals become fleshy and excrete water internally, the so-called "water calyces", the fruit developing in a water bath. This doubtless helps to protect the young fruit from desiccation, but whether it is of any survival value is not known.

FIG. 1406.—*Hyoscyamus niger*. Henbane. Infrutescence showing the enlarged, persistent calyces which conceal the small capsule fruits.

The swollen sepals in the fruit of

Morus we have already mentioned, and quite a considerable number of other cases of sepal hypertrophy could be added. One of the most striking is that of *Dillenia retusa*, in which the calyx becomes exceedingly fleshy and the sepals, tightly wrapped around the capsule, create a ball as big as a coconut. The fruit itself has little fleshy tissue and this is augmented by the fleshy and edible sepal tissues, while in most other genera of the Dilleniaceae the fruit itself is fleshy. The petals as well as the sepals may be brought into play to enclose the fruit, as in some species of *Cotyledon* (Crassulaceae), where the corolla tube shrinks at the end of the anthesis and closes around the carpels. We may here refer once more to the hardened envelope around the fruit which is formed by the base of the corolla in *Mirabilis* and other Nyctaginaceae.

These examples are primarily protective arrangements, but other cases show assistance in dispersal. The most obvious instances are those Compositae, *Valeriana*, etc., in which the calyx has become a plumose attachment or *pappus*, which is an important aid to wind dispersal. The styles may also become hairy and act as plumes, though they may perhaps be regarded as legitimately part of the fruit (*Clematis*). An example where the calyx assists animal dispersal is that of *Clerodendron fargesi*, which has blue berries, set off and made more conspicuous to fruit-eating birds by the fleshy, red sepals which surround the fruits. The leaves fall before the fruits are ripe and they are thus left conspicuous on the tree. Failing bird dispersal the sepals act as rather primitive wings and the fruits may be blown for over twenty yards (see Fig. 1389).

Bracts are frequently retained and used either for the protection or for the dispersal of the fruits, or both. The involucral bracts in some of the Compositae, *e.g.*, *Arctium*, *Carlina*, not only form protective, spiny *chevaux-de-frise* around the fruits but may be hooked or barbed for clinging to clothing or hair. The bracts in *Carpinus*, on the other hand, develop into wings. The pedicel may also share the development of the fruit or may sometimes exceed it. *Anacardium occidentale*, already referred to, is one such case, where the swollen pedicel greatly exceeds the size of the fruit itself. Another example is that of *Laportea*, the stinging tree of Queensland, a member of the Urticaceae (Fig. 1407). The short pedicel becomes greatly swollen, pushing the single akene to one side, where it is covered by a persistent and fleshy perianth segment. The swollen "berry" is an attraction to birds and aids dispersal.

There have been suggestions that some features of the fruit and of other post-fertilization developments may be influenced by the nature of the pollen which caused fertilization. This is an extension of the idea of Xenia, already referred to in connection with endosperm, and is called *Metaxenia*. The effect, if it is a genuine effect, can scarcely be direct, but must operate through the developing embryo and endosperm, whose hormonal activity may be supposed to be affected by their genetic constitution. The number of fertile seeds formed, and still more, the absence of fertile seeds, certainly have an effect upon the character of the fruit which is, of course, traceable in the long run to pollination. An insufficient amount of evidence is available for detailed discussion.

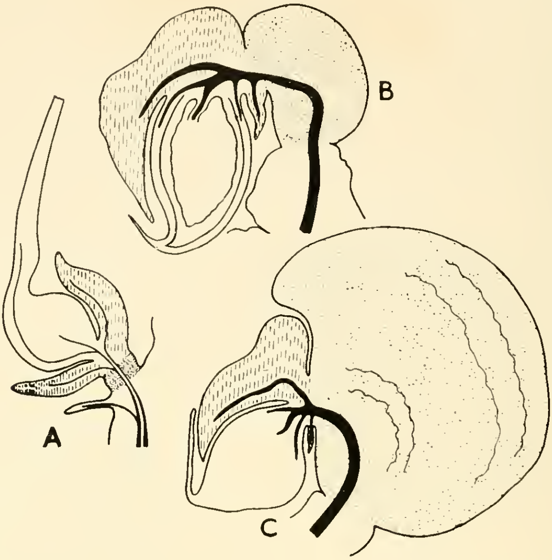

FIG. 1407.—*Laportea moroides*. A, Female flower. B, After fertilization. Pedicel and upper perianth segment swelling. C, Later stage. The cell arrangement in the swollen pedicel indicated by wavy lines. Pedicel stippled. Perianth segments hatched. (*After Goebel.*)

Fruit Dispersal. The dispersal of fruits follows much the same lines as the dispersal of seeds already described, except that mechanisms assisting dispersal are produced by carpellary or other structures, not by the testa. One might imagine that in dehiscent fruits the onus of dispersal would naturally fall upon the liberated seeds and that therefore fruit dispersal as such would be limited to akenes, but this is not entirely so, although true up to a point, for there are fruits in which dehiscence is delayed and the fruit is dispersed by one means or another, especially by animals, before the seeds are shed. It is true, however, that many-seeded fruits which are furnished with special means of fruit dispersal are generally indehiscent. When one considers the circumstances of dispersal and the great advantages of numbers and of lightness, it seems reasonable to suppose that dispersal of seeds is more likely to reach high efficiency and that fruit dispersal is a second-best.

Wind Dispersal. There are a very large number of wind-dispersed fruits of the akene type, in which either flat expansions or wings or plumes are employed to catch the wind. Not all fruits with such forms are normally wind-distributed, one exception being *Begonia*. Its capsules have three conspicuous wings at the angles but they dehisce and release a horde of minute seeds without becoming detached.

Fruits which become inflated like bladders are in a special category, for while they may be dispersed by wind, if they are detached without dehiscence, they also float easily and may often be carried about by rivers. Two familiar garden shrubs, *Colutea* and *Staphylea*, are in this group. Several genera of Leguminosae produce swollen, parchment pods, which normally dehisce on the plant and only occasionally may be dispersed as fruits.

Wind dispersal of fruits, as of seeds, is usually associated with the production of either wings or plumes. Prominent among the types of wing formation are those in which the wings are outgrowths of the pericarp. They are usually one-seeded, indehiscent fruits, known as *samaras*, and are either akenes or reduced follicles or legumes. Many examples can be cited without going outside the British flora: *Ulmus*, *Fraxinus* (Fig. 1408) and *Acer*, all with one wing, but in the latter genus with the winged akenes cohering in pairs, so that the familiar "keys" of the Sycamore have two symmetrical wings; *Betula*, *Isatis* and *Heracleum* with the edges of the pericarp extended into two wings, as well as several two-winged siliculas of Cruciferae, *e.g.*, *Thlaspi* and *Lepidium*. There are a great number of similar fruits in other parts of the world and the method seems to furnish efficient dispersal (Figs. 1409 and 1410). The very light winged akenes of *Betula* probably fly for hundreds of yards, but heavier fruits may not make more than six to ten yards in falling from the tree, and only travel further along the ground if the wind is strong or gusty. An interesting variant is found in some plants, the wing being twisted so that the fruit rotates in falling, which delays its descent and allows time for considerably greater travel, up to 100

FIG. 1408.—*Fraxinus excelsior*. Ash. Bunches of winged fruits or " keys ".

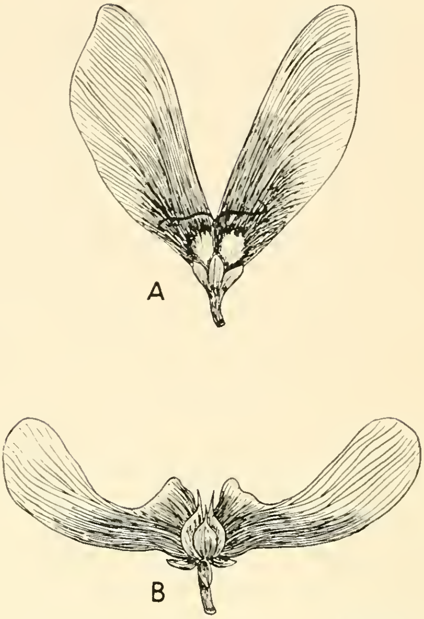

Fig. 1409.—Winged fruits in Malpighiaceae. A, *Acridocarpus zanzibaricus.* B, *Heteropteris laurifolia.* (*After Niedenzu.*)

Fig. 1410.—*Combretum apiculatum.* Cluster of winged fruits.

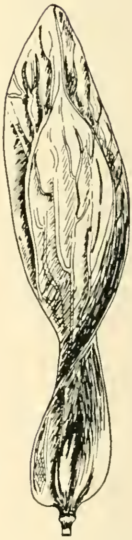

Fig. 1411.—*Koompassia malaccensis.* One-seeded legume flattened to form a spiral wing. (*After Ridley.*)

yards. This may be seen in *Koompassia* (Fig. 1411), a large leguminous tree of Malaya, whose fruit is a reduced one-seeded legume, which is flattened and twisted. Another leguminous tree with flattened one-seeded fruits is *Pterocarpus*, also Malayan (Fig. 1412). In both the above it is the whole pericarp which forms the wing. The

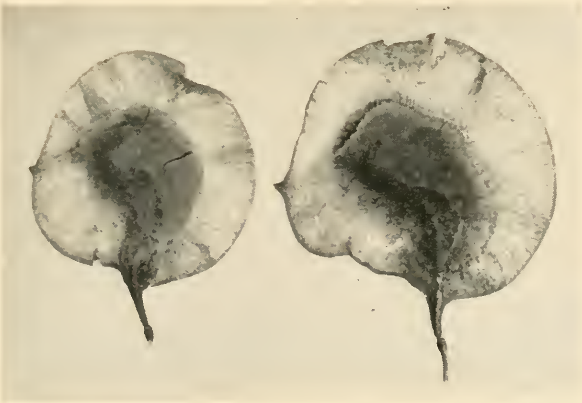

FIG. 1412.—*Pterocarpus indicus.* One-seeded legume with broad marginal wing.

Sterculiaceae likewise often have winged fruits which are singular in being dehiscent, the separated carpels acting as wings, to which the seeds remain adherent during flight, *e.g.*, *Firmiana* (Fig. 1413).

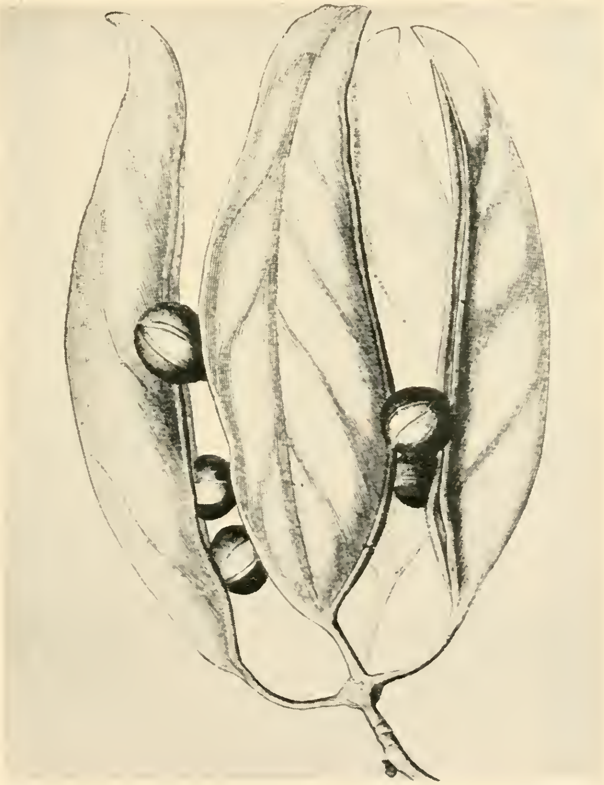

FIG. 1413.—*Firmiana platanifolia.* Sterculiaceae. Dehiscent capsule of which the carpels form wings. *(After Schumann.)*

Perianth members, usually sepals but occasionally petals, may be retained as wings in the fruiting stage and often develop considerably in size. The most striking and one of the best known examples of sepal wings is provided by the family of large Asiatic timber trees, the Dipterocarpaceae (Fig. 1414). The fruits are generally one-seeded by reduction and are large, the nut being from half an inch to two and a half inches long, and quite heavy. Two, three or all five of the sepals, in different genera, may develop into long narrow wings, upwards of six inches long in some species, and set obliquely so that they impart rotation to the falling fruit and delay its descent. Some of these trees reach an immense height, upwards of 180 ft., and they do not fruit until they are well grown and about 30 years old, so that the fruits have good clearance in falling. Yet Ridley has shown that the fruits generally do not travel more than 40 yards and that 100 yards is about the extreme range in high winds. At this rate the species *Dipterocarpus grandiflorus*, which ranges from Malaya to the Philippines (Fig. 1414), would have taken at least one and a half million years to travel the whole distance and probably double this period. Lighter fruits will naturally travel further than this but there seems much evidence that the spreading of large trees is a slow process under any conditions.


FIG. 1414.—*Dipterocarpus grandiflorus*. Fruit with two large sepaline wings. (*After Ridley*.)

A persistent and inflated calyx is sometimes effective in aiding distribution of herbaceous plants; as in *Trifolium fragiferum* and *Anthyllis vulneraria*, where the legume fruits are small and are enclosed in a papery calyx hood. The fruits of *Rumex* are also enclosed by expanded sepals which, in some species, act as wings for wind carriage, *e.g.*, *Rumex acetosa*, *R. crispus*, but in others each sepal is provided with a corky boss on the midrib, which can only be understood as a float for water or sea dispersal.

Petals which function as organs of flight are less common but can be seen in many Ericaceae, especially species of *Erica*, where the capsules dehisce inside the dry, papery corolla tube, which is detached and blown away with its load of seed. *Calluna* behaves in similar fashion, but the sepals as well as the petals take part. The withered corolla remains attached to the fruits in some species of *Trifolium*, such as *T. repens*, and is detached and blown away with the fruit.

Bracts, either singly or conjoined into involucres, quite commonly form wings. Three common plants in the British Flora illustrate this function well. In *Tilia*, the Lime Tree, the bract is partially adnate to the pedicel, its upper part only being free. The pedicel is detached with the bract and the group of small, hard fruits, as a unit. The weight of the fruits causes the structure to fall with the fruit lowermost and the bract makes it rotate rapidly. The wind may also carry it further along the ground after falling and the fruits are detached as it goes. The common Hop, *Humulus lupulus*, bears a catkin of minute akenes, each with a large papery bract. In the Hornbeam, *Carpinus betulus*, the fruits are also borne in a loose catkin and each nut is subtended by a large, leafy and three-lobed bract to which it is firmly attached. These also rotate in falling and are readily carried for forty or fifty yards or more.

The habit of spinning in the air seems to offer the advantage of delaying the fall of the fruit. It is beautifully seen in *Congea*, a verbenaceous climber of southern Asia, in which each cluster of small flowers is surrounded by four spreading, pink bracts. When detached each cluster spins like a propeller in descending.

Bracts united in an involucre, or rather an involucel, surround each flower of *Scabiosa* and expand into a papery cup when the fruit is ripening. In some species of the genus this is large enough to act as a parachute for the fruit, sometimes aided by the sepals, which may be plumed or may bear hooked hairs for attachment to animals. The latter is probably the more

FIG. 1415.—*Paliurus spina-christi.* A, Mature winged fruits. B, Inflorescence. C, Fruit in section. D, Flower. (*After Marzocca and Marthi.*)

important method of distribution in our native species. It should be noted that the very similar parachute cup in *Armeria* is formed by the sepals.

Many of the Gramineae drop their caryopses enveloped in the glumes or they may abstrict whole spikelets as units of dispersal. Definite layers of abstriction tissue are formed, the cells of which either break or separate easily from one another, causing abstriction. This may occur above the empty glume (Agrosteae), the fruit remaining encased by the flowering glume and the palea; or, the spikelet may fall as a whole (Paniceae) with both glumes; or, if the spikelets form a spike (Hordeae), the rachis of the latter may disarticulate, separating into joints each with one spikelet. Whichever method is used, the attachment of the glumes increases the chances of wind carriage. The frequent occurrence of grass plants on walls at some height above ground shows that the method is successful.

A curious case of wing formation is shown by *Paliurus* (Fig. 1415), in which it is the enlarged disc of the flower which forms a parachute for wind dispersal.

FIG. 1416.—*Clematis vitalba.* Fruiting shoot showing the long, persistent styles which are becoming plumose.

Plume formation displays the same kind of variation that is shown by wing formation and the two often occur together, supplementing one another. The style itself is often beset with long silky hairs which form a plume, as in *Clematis* (Fig. 1416) and some species of *Anemone*, where the hairs grow greatly in length as the akenes ripen. Some other species of *Anemone* of tall habit have hairs on the carpel itself, which form little woolly plumes around the minute akenes and are effective over fairly short ranges (Fig. 1417). Grass fruits are not only distributed with the aid of the glumes but also form plumes of hairs, either attached to the glume itself or coming from the rachilla below the glume and growing much longer than the latter. Good examples of plumed grasses are *Phragmites*, *Saccharum*, *Calamagrostis*, all with small fruits. In *Stipa* it is the long awn which bears the plumes and, in addition, the awn is twisted at the base and serves for seed burial by its hygroscopic movements. Plumes of axial hairs also surround the fruit in *Platanus* and *Typha*. Their hygroscopic movements prise apart the massed akenes and then act as parachutes.

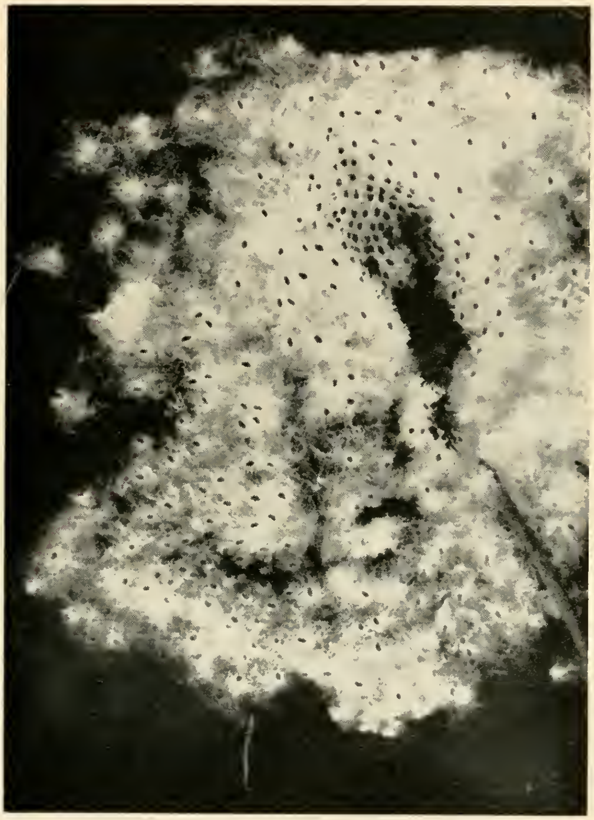

FIG. 1417.—*Anemone japonica.* Mass of akenes from a single flower, each surrounded with fluffy plumes.

More common and important than the above are the cases of sepaline plumes, so characteristic of the Compositae and found in divers other families. The cypsela of Composites is an inferior fruit and thus the calyx stands on top of it. In some genera there is only the merest trace of sepals, or none, but in a vast number of genera the calyx takes the form of a silky mass of hairs, the *pappus*, which provides a parachute for each fruit. Other families in which the fruit may have a pappus, often indistinguishable from that in Compositae, are Valerianaceae, Amarantaceae and Proteaceae.

Among Compositae the pappus takes all sorts of forms, from a few simple hairs or a ring of wing-like scales in *Ursinia*, to a most complex structure in *Taraxacum* and *Tragopogon* (Fig. 1418), in which the base of the calyx elongates into a fine tube, the top of which is set with thickly-branched radiating ribs, like an umbrella. The pappus of *Tragopogon* is one of the most complex and the ribs are even adjustable by hygroscopic pulvini (Fig. 1419). The pappus is an extremely effective means of dispersal, especially if the fruits are light, and by its aid they can be carried by the

Fig. 1418.—*Tragopogon pratensis*. Fruiting capitulum. Each fruit bears a parachute-like pappus.

wind for great distances over land. Over sea they are not so effective and most of the pappose-fruited genera on oceanic islands have probably been

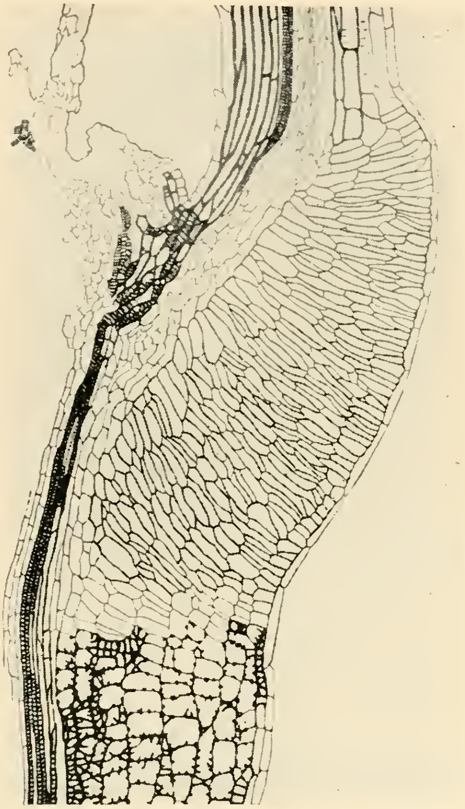

FIG. 1419.—*Tragopogon pratensis.* Longitudinal section of the base of one of the rays of the pappus, showing the pulvinus-like tissue which causes the hygroscopic folding and unfolding of the rays. (*After Hirsch.*)

carried there by birds or by man. If the pappus-borne fruit comes to earth, it may be held by the friction of small prickles which are turned upwards so that they catch easily if the cypsela is dragged along the ground. These grapnels are well seen in *Taraxacum*, while *Senecio* is furnished with sticky slime glands which serve the same purpose of attaching the fruit to the ground after it has once fallen there. The pappus may then blow away and leave the fruit. Quite a large proportion of those seen blowing in the spring airs have dropped their cypselas and are travelling light.

Water Dispersal. The flotation of whole fruits by water most frequently concerns indehiscent fruits. Some dehiscent fruits can float for some time and dehisce in the water, the seeds, when released, either sinking or continuing to float by themselves. As we pointed out in the case of seed dispersed by rivers, the property of eventually sinking is almost as important as that of floating, if the fruits are not to be carried out to sea. Flotation for a few hours may be quite sufficient. Fleshy fruits such as berries are often floatable but their seeds are more generally dispersed by birds.

Devices which increase the power of flotation are not numerous and are on the whole simple. Bracts which persist as coverings for the fruit, even after it has been shed, as in the Grasses, are often useful in this respect, especially if they are unwettable and enclose air around the fruit, which increases buoyancy. Many of the common waterside grasses, *Glyceria*, *Oryza*, *Phalaris*, etc., are dispersed in this way. Especially remarkable is the peculiar grass *Coix*, which has unisexual spikelets, the female, which produces only one seed, being enclosed in a large, white, bony bract which makes an excellent float. The perigynial sac in *Carex* is also a valuable float for the small, light fruits. The pericarp is, however, the usual flotation agent and in many fruits it contains air-spaces or has tissues formed of dry, dilated cells which give at least temporary buoyancy, until they decay or water penetrates the air-spaces and the fruit sinks. Akenes of the aquatic *Ranunculus*, *Sagittaria*, *Potamogeton* and *Alisma* all float by such means.

Some of the widest dispersal by flotation has taken place in the sea and in this connection the Coconut deserves the first mention. According to Ridley's view *Cocos nucifera* is not an Old World tree but may have originated on the west coast of tropical America. Apart from its carriage by man, its present wide dispersal, especially in the Pacific and Indian Ocean areas, seems to have been chiefly due to sea flotation. The tree commonly grows on or close to beaches and there is no doubt that the fruits do roll down the beach to within reach of the tide and get carried away. It is only in its complete state, with the leathery epicarp and fibrous mesocarp intact, that it is capable of surviving for long in sea water. The stripped " nut " itself rots in the sea in a few weeks. Similar hard coverings are also formed on the fruits of two other tropical sea-coast trees, *Barringtonia* and *Nipa*, which are dispersed by ocean currents. Only sea-coast plants like these would readily establish themselves in places where they were drifted up. This explains why the Coco-de-mer, *Lodoicea*, although it was for long known only by its floating fruits, has not established itself beyond the Seychelles. It is an inland plant and its huge nuts only reach the sea by being carried down by flooded rivers.

Coconuts sometimes reach European coasts in the Gulf Stream drift and there is an amusing story that a sacred relic which was for centuries venerated at Skalholt in Iceland as the skull of St. Thorlac, eventually proved to be no more than a far-wandering coconut.

Several species of Mangrove trees are generally dispersed by sea, especially *Cerbera adollam* (Fig. 1420) and *Heritiera littoralis* (Fig. 1421), whose fruits may be found plentifully on beaches throughout tropical Asia. The former has a pulpy outer coat which quickly decays, but the fibrous inner covering permits the fruit to float for months. The latter has a light fibrous coat and there is an internal air-space, both features increasing buoyancy. Another Mangrove tree, *Aegiceras majus*, is dispersed by its seedlings, which germinate quickly in the sea and then float about for some time. So also do the viviparous seedlings of *Rhizophora*, to be described later. A number of investigators, among whom may be mentioned Darwin, Guppy and Schimper, have experimented on the length of time during

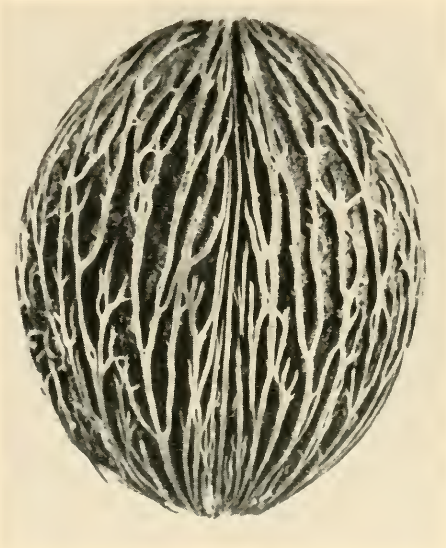

FIG. 1420.—*Cerbera adollam*. Apocynaceae. Fruit with fibrous, corky mesocarp surrounding the hard endocarp.

FIG. 1421.—*Heritiera littoralis*. Sterculiaceae. Floating fruit.

which seeds and fruits will float. Their results are not always consistent and it is evident that there must be a good deal of natural variation in this respect and that probably a great many fruits sink quickly and are lost.

Dispersal by sea is not by any means confined to trees. Seashore plants in all parts of the world may be carried by sea currents to fresh shores. Among north temperate species we may mention especially: *Crambe maritima*, *Cakile maritima*, *Lathyrus maritimus*, *Honckenya peploides*, *Crithmum maritimum*, *Calystegia soldanella*, *Euphorbia paralias*, and *Spartina townsendii*. Common seashore species of warm climates which are dispersed by sea include the following, some of which are trees or shrubs and some herbaceous: *Calophyllum inophyllum*, *Hibiscus tiliaceus*, *Carapa moluccensis*, *Canavalia rosea*, *Erythrina*, *Mucuna*, *Entada* and *Cassia* (various species), *Terminalia catappa*, *Barringtonia racemosa*, *Heritiera littoralis*, *Pemphis acidula*, *Sesuvium portulacastrum*, *Selliera radicans*, *Scaevola koenigii*, *Ipomoea pes-caprae*, *Pandanus fascicularis*, *Remirea maritima*, *Fimbristylis spathacea* and *Thuarea sarmentosa*. This list includes only the species with wide distributions and excludes most of the Mangrove species (which we have mentioned before and will deal with again later) and a few which have been specially mentioned above. In some of these species it is the fruit which floats and in some it is the seed, but we have thought it best to keep them together as they form a natural biological group.

The last-named species, *Thuarea sarmentosa*, deserves a word of special description for its peculiarity. It is a grass of sea sands, with a short spike of flowers borne on a very broad rachis. The upper flowers are male and the one female spikelet is at the base of the rachis. The latter folds over the female spikelet as the seed ripens and then becomes thick and hard, forming an excellently protected floating body. It is principally found on islands in the Indian and Pacific oceans.

Animal Dispersal. The dispersal of fruits by animals is chiefly external. When fruits are eaten by birds or animals it is usually the seeds which are scattered or excreted and we have already referred to this method of dispersal in dealing with seeds. An exception to this statement must be made in the case of small, hard fruits, mostly of herbaceous plants, which are regularly swallowed by cattle in large numbers while browsing and are excreted, like many seeds, unharmed. Among common genera thus dispersed are: *Ranunculus*, *Galium*, *Leontodon*, *Urtica*, *Atriplex*, *Chenopodium*, *Polygonum*, *Rumex* and of course the caryopses of many pasture Grasses. For some of these genera such a mode of dispersal is of primary importance, for others, *e.g.*, *Leontodon* and *Galium*, it is only secondary to dispersal by other means.

It has frequently been suggested that certain seeds, like those of *Ricinus*, are dispersed by birds because of their resemblance to beetles, which would attract insectivorous birds. We have already seen that there is reason to doubt this, but another case of mimicry which may have an analogous effect is that of the fruit of *Biserrula pelecynus*, whose legumes resemble centipedes and may be picked up in error by foraging birds (Fig. 1422). Direct proof of this is, however, lacking.

Further examples of this apparent mimicry may be seen in the indehiscent legumes of *Scorpiurus*, of which *S. subvillosa* resembles a centipede and *S. vermiculata* a caterpillar. The seeds of *Abrus precatorius* and of *Jatropha* spp. have also a rather striking likeness to beetles.

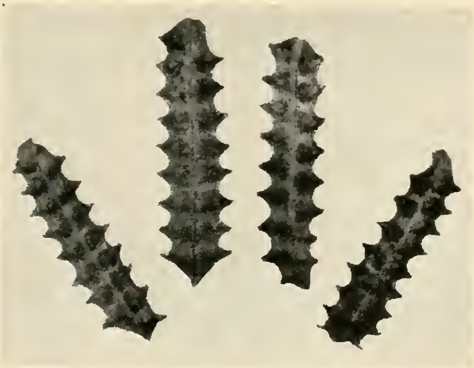

FIG. 1422.—*Biserrula pelecynus*. Legumes mimicking centipedes.

Attachment externally to animals is usually ensured by prickly or hooked hairs or by stickiness. Hairs and bristles may be a means of protection rather than of dispersal, especially in the unripe condition of the fruit, when it is desirable that the seeds should be protected from disturbance. Bristles on the outside of dehiscent capsules serve such an end, for when they dehisce the seeds are ripe and are then fully exposed. The fruits of many Mimosaceae, likewise, are spiny around the septum, but the unprotected valves drop or are picked out of this prickly framework when they are ripe. The same prickles which protect the unripe fruit may, however, assist its dispersal when ripe, as in some species of *Medicago* (*M. turbinata*, *M. arabica*), where the margin of the spirally curved legume is furnished with two rows of crossed prickles which easily catch in a woolly covering.

The prickles are commonly hardened hairs, often with hooked tips, as in *Galium aparine* and *Myosotis arvensis*. They may be produced on the pericarp, as in the former example, or on the persistent calyx as in the latter, the enclosed fruit being smooth. In *Agrimonia* the prickles are formed on the outside of the perigynous receptacle which encloses the two ripe akenes like a calyx. The list of other plants whose fruits are attached to animals or to clothes by such hooked hairs is a long one, but examples need not be multiplied beyond a few common genera: *Daucus*, *Caucalis*, *Xanthium*, *Urtica*, *Cynoglossum* and *Circaea* (Fig. 1423).

Hooked or viscid hairs are not always confined to the fruit parts but may be formed on leaves or branches as well and in some plants whole

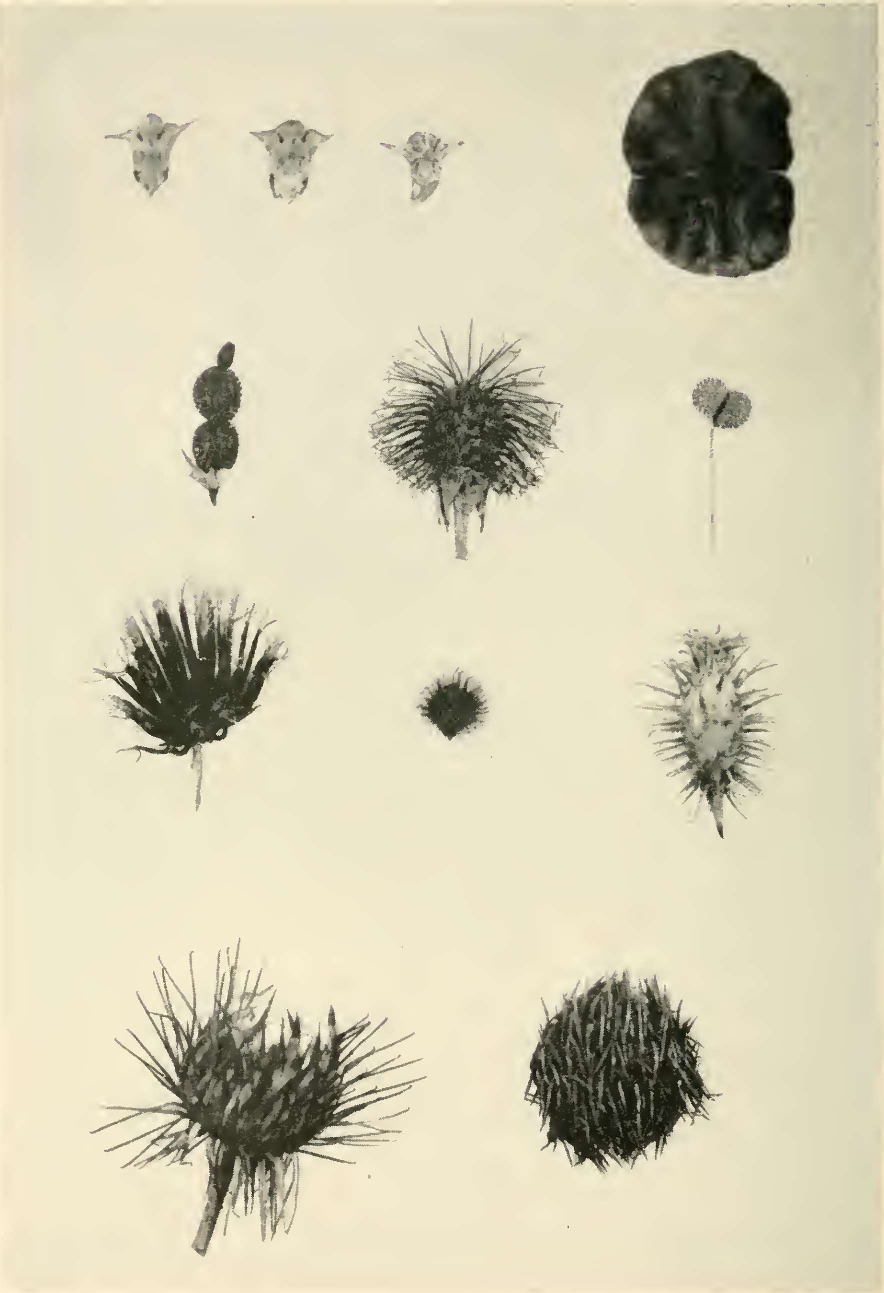

Fig. 1423.—Group of fruits provided with hooks or spines which attach them to animals. Top row: *Emex australis* (see next figure), *Pretrea zanguebarica.* (Flat fruit with two spines which scarcely show in the figure.) Second row: *Desmodium* sp., *Geum urbanum, Galium aparine.* Third row: *Bidens tripartita, Sanicula europaea, Xanthium spinosum.* Bottom row: *Arctium nemorosum, Medicago arabica.*

twigs and shoots, with fruits attached, may be carried about by animals or birds, as for example in *Galium aparine*, and *Cerastium tetrandrum*. The same thing is observed in other parts of the world, and *Opuntia* in Australia, *Forskohlea* in the Mediterranean region and *Pemphis acidula* on oceanic islands (*e.g.*, Cocos-Keeling) are easily disarticulated and carried about in this way.

Sometimes plant organs may provide means of attachment instead of hairs. The styles in some species of *Geum* (*G. urbanum*, *G. rivale*) are persistent and are sharply deflexed below the stigma. The hook so formed becomes woody and sharp after the stigma and upper portion of the style have been detached, and provides a very effective attachment. The arctic and montane species of *Geum* have long plumed styles like those of *Clematis* and are wind-distributed, which may be associated with the absence of large mammals in their environments. Many species of *Ranunculus* also have sharply curved, though short styles (*R. acris*, *R. bulbosus*) which often attach the akenes to woolly clothes. The genus *Bidens* takes its name and owes its dispersal to the two (sometimes three or four) calyx segments which constitute the pappus and take the form of stiff spines with barbed, reflexed bristles by means of which the fruits are pulled off and transported. The widespread southern genus *Acaena* (Rosaceae) is similarly equipped, the sepals either ending in sharp points or bearing hooked spikes which are persistently adherent. The inner sepals of *Rumex* are persistent and in some species are furnished with sharp spiny edges by means of which the fruits adhere to animals. Another genus of Polygonaceae, *Emex* (Fig. 1424), has also spiny sepals, but only one spine on each of the three persistent sepals. They are hard and sharp, but are not

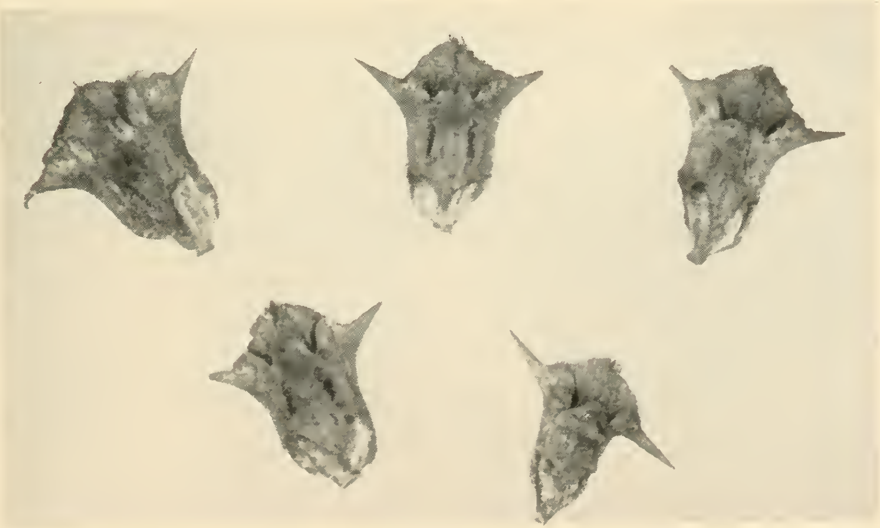

FIG. 1424.—*Emex australis* (Polygonaceae). Spines on three of the persistent perianth leaves.

hooked, and the fruits lie on the ground always with one spine erect. This pierces the feet of animals or gets between their toes, or it may be picked up by rubber tyres. In all these ways it gets transported, though it often causes great suffering to the animals, for which reason it is called the Devil Thorn in South Africa. Such a method recalls *Tribulus*, a member of Zygophyllaceae, in which each of the five carpels of the fruit bears two divergent spines which stick out all round so that some of them are erect however the fruit lies. They also pierce the feet of animals and cause much trouble through being thus carried off. In this case the spines are direct outgrowths of the pericarp, not of the sepals. (See also below, p. 1565, under Pedaliaceae.)

An instance where spiny bracts assist in dispersal is given by the genus *Arctium*, the Burdock, in which each member of the involucre surrounding the capitulum becomes hardened and ends in a hook. Their efficiency in promoting distribution needs no remark to anyone who knows the English countryside. A curious example of the use of a stem structure as a means of adherence is that of *Uncinia*, which is a southern hemisphere relative of *Carex*, with only one species (*U. microglochin*) in the north. The rachilla of the spikelet, which is abortive in *Carex*, is here prolonged into a sterile outgrowth, ending in a hook, which protrudes from the perigynium and very readily catches in fur, feathers or wool.

Many grass fruits are dispersed by animals to which they adhere by means of hairs on the glumes or of barbs on the awns or simply by the penetration of the awns into clothing. The number of Grasses which can be transported in this way is familiar to every country rambler, in fact most of the common grasses are concerned in it, especially *Bromus sterilis*, *Bromus racemosus*, *Festuca*, *Holcus*, *Hordeum*, *Poa*, *Helictotrichon* (*Avena*), *Alopecurus*, *Trisetum* and *Arrhenatherum*. In other parts of the world the dispersal of grasses in this way is equally common and is shown by such widespread genera as *Tragus*, *Eriochloa*, *Cenchrus*, *Themeda*, *Stipa*, *Oplismenus* and many others. One that requires a special mention is *Heteropogon contortus*, a well-known pest of grazing animals in many parts of the world (Fig. 1425). The spikelet bears an awn several inches long, the lower part spirally twisted, as in some species of *Stipa*. At the base is a tuft of sharp, stiff, upright hairs. The spiral portion twists and untwists hygroscopically and drives the sharp-pointed base, with its grapnel hairs, into the wool and

FIG. 1425.—*Heteropogon contortus*. Mass of the long-awned fruits which have twisted themselves together.

skin or into the mouth of the animal, penetrating sometimes deeply into the body and causing death.

One family which is signalized by its hooked fruits, found in almost all the genera, is the Pedaliaceae, in which the hooks reach their most formidable development. In *Pedalium* there are five on each fruit, small but strong and acting like the spines of *Tribulus.* In *Sesamum* the two carpels end in two sharp points, developed from the styles, and in *Martynia* these have become very large, woody hooks, while in *Proboscidea* they are lengthened to several inches, exceeding the length of the capsule and curved and pointed like fish-hooks (Fig. 1426). The fruit lies on the ground with these horns upwards and if an animal steps on it the fruit tips up and the horns clasp the fetlock. It is almost impossible for the animal to scrape it off and it works its way upwards as the animal walks. Sheep on trek, or deer, may carry the fruits along with them for great distances, dropping seeds as they go. In *Harpagophytum* there is a different development (Fig. 1427). Here the flat fruit has four wings which are modified into an armoury of claws each about an inch long and provided with numerous strong hooks, which attach themselves irremovably to any part of an animal which is unfortunate enough to touch them. It is a South African plant, like *Proboscidea*, and like it is a curse of stock animals.

Fig. 1426.—*Proboscidea fragrans* (Pedaliaceae). The "Mule Grab", with long recurved hooks. South Africa.

Fig. 1427.—*Harpagophytum prostratum.* Fruit with hooks. S. Africa. See in text.

There are three points of general importance which may be noted in connection with the numerous devices of adherence to animals. The first is that in their simplest forms some of them seem to have been directed to adherence to the soil rather than to animals. The second is that another

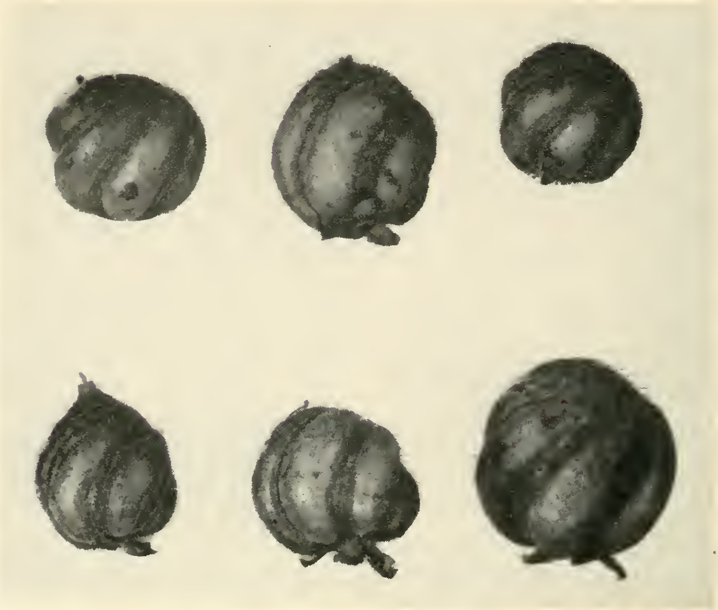

FIG. 1428.—*Siegesbeckia orientalis.* Fruiting capitula covered with intensely adhesive bracts.

line of evolution has developed them from devices for wind dispersal. Indeed many of the typically wind-dispersed pappus fruits are also able to cling to animals as an alternative means of transport and the change over to this mode of dispersal involved relatively little alteration of structure. The third point is that geographically the greatest number of adhesion devices are found in open, grassy country, where herds of wild ungulates roamed in former ages, and where man has now substituted his grazing stocks. Relatively few are in forest or desert plants.

Simple adhesion either by means of sticky secretions or simply by wetting is a further important means of dispersal. Among the former we may mention *Siegesbeckia orientalis*, a small Composite with sheathing bracts covered with glands of so adhesive a nature that the seed-bearing capitulum can be picked up off the ground merely by touching it with the point of a needle (Figs. 1428 and 1429).

Sticky calyces are found in *Verbena officinalis* (Vervain) and in the genus *Plumbago.* Both are readily adhesive to long hairs and to clothes.

FIG. 1429.—*Siegesbeckia orientalis.* Capitulum being picked up by a single strand of the adhesive matter.

The genus *Pisonia* (Nyctaginaceae) consists of trees and shrubs which are found in all warm regions, usually near the seashore and frequently on oceanic islands. The one-seeded fruits are covered by the intensely sticky perianth tube which adheres firmly to birds' feathers. So glutinous are the fruits that they sometimes trap smaller birds, who cannot disentangle themselves. Even large birds such as Herons and Boobies can be seriously troubled by them though it is chiefly by their agency that the plants are distributed.

The classic case of a sticky fruit is that of *Viscum album*, the Mistletoe, whose berries are eaten by Thrushes. The glutinous pulp, with its contained seeds, sticks to the bird's beak and is carried away. The thrush then strops its beak on the bark of another tree, to clean off the mess, and in so doing plants the seeds in crevices of the bark where they later germinate.

Simple adhesion in wet mud, without any special device, to the feet and fur of animals and birds, or to the boots and wheels of mankind, is quite common and affects a great many plants, especially those which grow in wet places. Wading birds are very important in this kind of dispersal and sea birds undoubtedly carry many seeds in this way to distant islands. Nearly all the plants concerned are small herbs, trailers or scramblers which may be trodden on, or else semi-aquatic plants among which water birds may swim or wade, or animals like the Moose or the Water Buffalo or Wild Boar may trample and wallow. In Pleistocene days when great herds of grazing animals, Deer, Reindeer, Bison, etc., roamed the northern countries, transport and distribution of plants by their means must have taken place on a great scale.

Charles Darwin was the first to draw attention to the feet of birds as a means of dispersal. From a ball of mud from the leg of a partridge he raised twelve Monocotyledons and seventy-two Dicotyledons, of three different species. Marsh birds fly direct from one marsh to another and by their agency many, perhaps the majority, of marsh plants are carried from place to place, even to very isolated spots. In this way plants are frequently noticed appearing around ponds where they were previously unknown, although the nearest locality for the species may be many miles away. One of the authors has seen *Damasonium alisma* appear thus suddenly by a much-frequented pond in Berkshire, though the plant had been unknown in the county for over a century.

The wheels of farm carts and muddy boots also act as carriers. One may often see cart tracks filled with such plants as *Radiola linoides*, *Juncus bufonius*, *Montia verna* or *Tillaea muscosa*, affording evidence of dispersal by a combination of adhesion and rain wash.

Dispersal by internal carriage is generally associated with fruits which are pulpy and attractively coloured and flavoured, so that they are eaten by birds or other animals. Occasionally it may be an aril or some part of the flower, such as the calyx or the receptacle which provides the attraction (Fig. 1430). The seeds or endocarps are hard and indigestible and they are voided uninjured, or even softened and rendered more apt for germination.

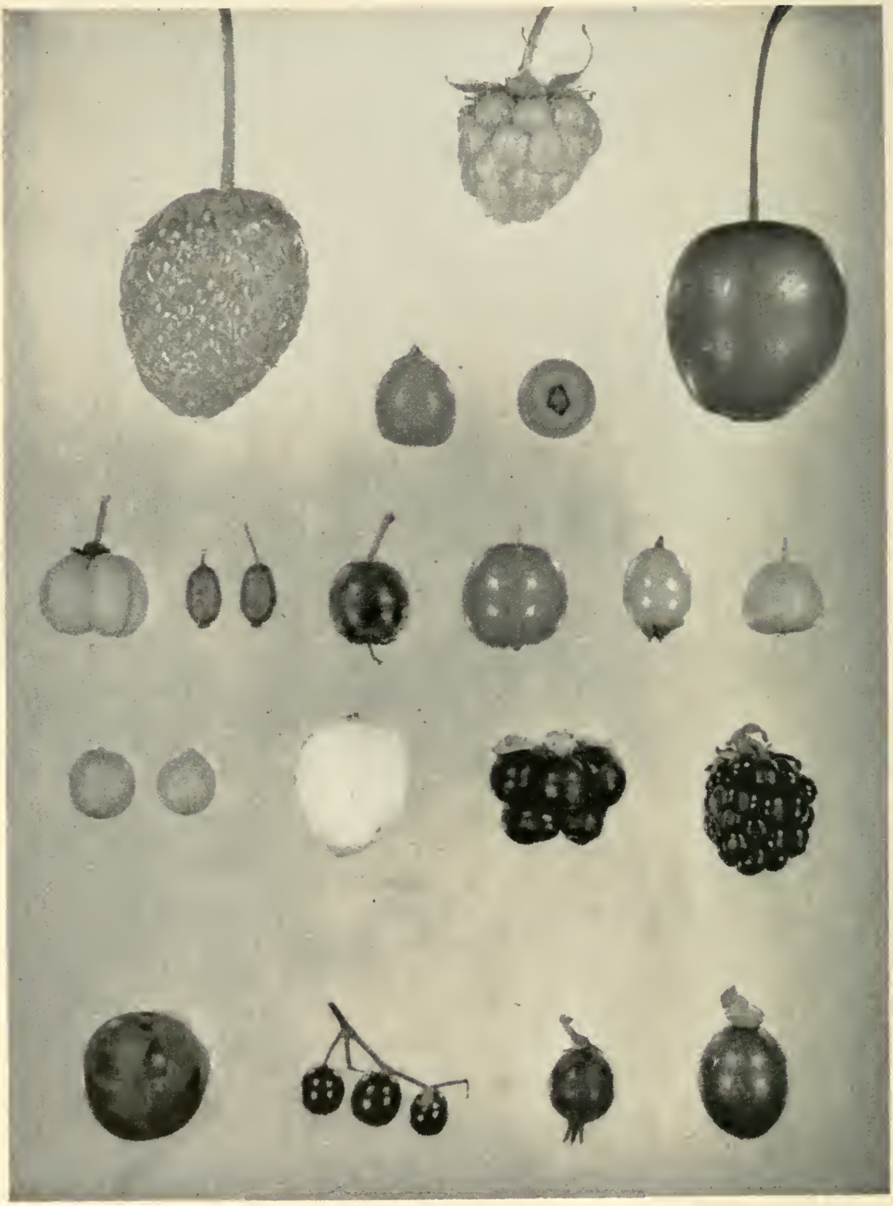

Fig. 1430.—Fruits and pseudocarps attractive to birds. Including, from above downwards: Raspberry, Strawberry, Cherry, Yew (in which the aril round the seed provides the attraction), *Euonymus*, *Crataegus*, *Tamus*, *Ribes*, *Symphoricarpus*, Dewberry, Blackberry, *Solanum*.

Where the hard part is large, as in Cherry, it may not be swallowed but simply flung away by pecking birds.

This means of transport is very effective over relatively short distances, but in migrant birds the digestive tract may be almost entirely emptied during flight and there is therefore only a small chance of seeds being thus carried to remote places.

Mechanical Dispersal. Concerning the mechanical dispersal of fruits as distinct from seeds, which we have already dealt with, there is not much to say. The relatively few examples apply to akenes, which are dispersed like seeds mostly by the resilience of elastic tissues. The fruits of *Polygonum virginianum* are thus shot off with considerable force, when the hardened style is struck, by the elastic elongation of the pith cells in the pedicel, which are held in compression by the abscission layer below the fruit. When this is broken the pith elongates and shoots the fruit off as from a catapult.

Dorstenia is a genus of Urticaceae, consisting of small herbs with a wide distribution in the tropics generally. The inflorescence axis is a flat expanse covered with minute flowers which form akenes. The pericarp is hard around the top of the akene but fleshy on two sides of the lower part, forming a sort of nut-cracker holding the hard part in its jaws. As the fleshy portions dry and shrink, the hard part breaks away and is shot out by pressure. Two other members of the same family, *Pilea* and *Elatostema*, have also an explosive mechanism, which closely resembles that by which the pollen is dispersed (see p. 1291). There are three staminodes, strongly bent inwards with their ends lodged beneath the carpel. As the latter ripens the staminodes grow bigger and exert a lifting force on the akene, a force which is released when the akene becomes detached. The staminodes spring up and the akene is shot out to a distance of several metres. *Circaea alpina* is reported to have an explosive projection mechanism for its fruits, but its nature still needs investigation.

The boring awns of some Grasses and of *Erodium* may be mentioned here, though they are not strictly organs of dispersal, but rather the opposite, organs which help to fix the small fruits in the ground where they have fallen. The principle is the same in all, namely that the awn (or in *Erodium* the style) is divided into two zones, the lower of which is spirally twisted while the upper is straight and bent at right angles to the first. The fruit comes to rest with the akene pointing obliquely downwards. Changes of humidity cause the spiral to twist and untwist, while the top of the awn is held in place by pressure against the ground. The movement of the spiral portion thus twists the akene round, first one way, then the other, like a bradawl, boring it into the soil. The akenes are always provided with stiff hairs pointing upwards, which act as barbs and prevent the akene from being withdrawn but offer no hindrance to its downward movement.

These plants bury their fruits after they have been dispersed, but there is a considerable class of plants which bury their fruits themselves, without dispersal, by means of movements of the pedicels. The phenomenon is called **carpotropy** and it may be differentiated as *geocarpy* or *hydrocarpy* respectively, according to the place of growth.

There are numerous examples both among familiar and unfamiliar plants. Among the first we note *Arachis hypogaea*, the Ground Nut, already described (p. 1140), in which the " gynophore " elongates while the legume is still small, thrusting it downwards into the soil alongside the roots, where it ripens. Although always called the gynophore, the long carpotropic stalk in *Arachis* is really the elongated base of the ovary itself, which is quite sessile and has no gynophore in the proper sense of the word, which implies a true floral internode.

A comparable and very interesting case is that of *Trifolium subterraneum*, where the pedicels bend geotropically after fertilization and thrust the heads of flowers below ground. Only the lowest flowers of the inflorescence are, however, fertile, the rest are sterile and so imperfect that, while the lower ones have some calyx lobes spreading like the flukes of an anchor, the uppermost are merely stumps crowded into a head. These sterile flowers have been regarded both as anchors and as organs of absorption; which they really are, is not clear. In *Arachis* those fruits which fail to bury themselves do not generally develop, but the *Trifolium* species does develop some aerial fruits as well as those underground. It is notable that the former are hard-shelled and delayed in germination, while the latter are soft-shelled and germinate the same season. This differentiation is probably the chief biological advantage of the habit to the species.

Several other Papilionaceae have the geocarpic habit, among them the cultivated *Voandezia subterranea*, the Bambarra Groundnut. The plant is stoloniferous and the flowering branches grow downwards from the stolons, the flowers being produced underground. The pedicels lengthen and carry them up to the surface before pollination, then contract and draw them down again to ripen the one-seeded fruits.

In contrast to the foregoing it is often the pedicel of the individual flower which becomes geocarpic after fertilization. *Linaria cymbalaria* grows on walls and rocks and holds its flowers outwards and well exposed until they are pollinated. The phototropic reaction of the pedicels is then reversed and they turn inwards, pushing the young fruits into cracks and crevices, where they ripen and where the seeds are shed. The various species of *Cyclamen* show a very curious action, for the pedicels not only become geotropic but coil themselves into tight spirals by whose pressure the fruits are forced against the soil. They are too large to be buried directly but they are soon covered by the action of rain on the soil (Fig. 1431).

An example of hydrocarpy is given by *Eichhornia speciosa*, the Water Hyacinth, whose inflorescence axis bends by the curvature of a thickened, pulvinar region and plunges the fertilized flowers below water to ripen the fruits (Fig. 1432).

Amphicarpy is a term applied especially to plants which have subterranean cleistogamous flowers and aerial chasmogamous flowers, pro-

FIG. 1431.—*Cyclamen neapolitanum.* An example of carpotropy. The flower stalks coil up as the fruit ripens and press it against the soil.

ducing two different forms of fruit. There are many such species, of which the already cited *Cardamine chenopodiifolia* (p. 1355) may stand as a type.

FIG. 1432.—*Eichhornia speciosa.* The flower stalks bend at a pulvinus and plunge the ripening fruits below the water.

GERMINATION AND SEEDLINGS

The primary fact in the process of germination is the swelling of the seed by the absorption of water. The content of water rises from the 5–10 per cent., which is characteristic of air-dry seeds, to 30–50 per cent. or more in some cases. There is great variability in the amount of water absorbed, not only as between different species but also in the same species under varying conditions, *e.g.*, temperature, oxygen supply, etc. Starchy seeds generally absorb more than seeds with a high protein content, though they may absorb it more slowly, and most seeds absorb less when immersed than when there is a free supply of air. An exception to this is the seed of *Oryza*, which is a water plant. Indeed there is evidence of an ecological differentiation in regard to water absorption, seeds of dry environments generally germinating at a lower water content than those accustomed to mesophytic or hydrophytic conditions. As the seed is not a homogeneous structure, the rate of water uptake depends on the differing powers of imbibition of the testa, the endosperm and the embryo respectively and it may be irregular and slow. Some of the water absorption by the endosperm and embryo is osmotic, since it has been shown that in the dormant condition the cells of these structures are plasmolysed, but become turgid before germination.

We have seen previously that the testas of many seeds are almost completely impermeable and that water uptake and germination may be indefinitely delayed until the testa has been broken or has decayed. Even with free penetration of water it may be upwards of 48 hours before the seed becomes fully imbibed. This absorption of water is accompanied by considerable imbibitional swelling, which may burst the testa and, as we shall see hereafter, may also cause the bursting of hard fruit shells in which the seeds are enclosed. It is the necessary first condition for germination.

A point which is important is that many seeds absorb water more readily at low temperatures and some indeed, *e.g.*, *Papaver rhoeas*, will not germinate at temperatures above 15° C. This inhibits the germination of the seeds during the summer, which restricts this species to one generation a year, although the vegetative period is relatively short.

We have already referred, in the earlier part of this chapter, to some of the conditions of delayed germination and to the very complex nature of the seed coats. Many testas contain cell layers, or cell walls of a single layer, which produce amyloid or mucilage with strong affinities for water, which is readily absorbed, while others have no such substances and may offer the greatest resistance to penetration. To the latter class belong many of the seeds formed in berries, which, bathed as they are by nutritive, albeit somewhat concentrated juices, would otherwise tend to germinate in the fruit, to their detriment. Chemical inhibitions also play a part in restraining germination in many cases, especially in fleshy fruits.

It is not our intention to enter now into the problems of the physiology of germination, which will be reserved for the section on the physiology of growth in Volume III.

As the absorption of water proceeds, the solution of the reserve foods in the endosperm or embryo begins (Fig. 1433). Many endosperms are very hard in the dry state, and contribute to the mechanical protection of the embryo, but even the hardest soften considerably as the starch or protein reserves become fully imbibed. The starch-free endosperms, in which the cell walls are highly thickened with "reserve cellulose", swell very strongly and the cells lose their outlines and the tissue becomes slimy and semi-liquid, as in *Trigonella*, *Lotus* and many other Papilionaceae.

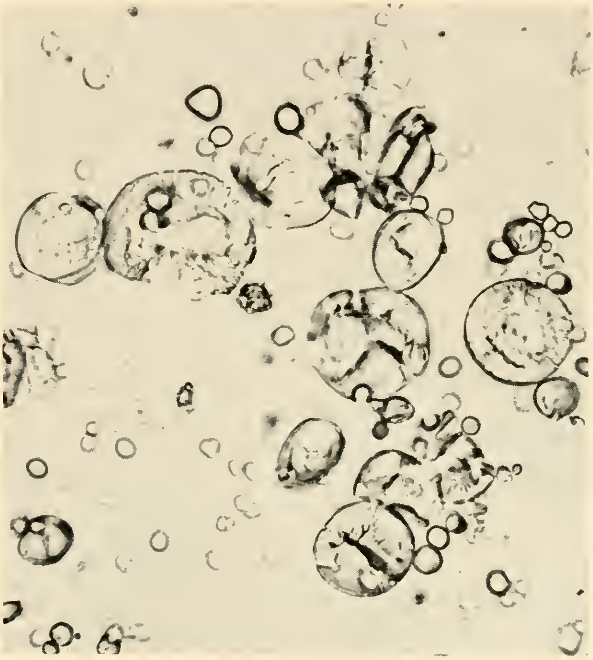

FIG. 1433.—Grains of starch from a germinating Wheat grain, showing the process of digestion.

The embryo, before dormancy, may absorb and destroy the inner endosperm which is in immediate contact with it, only the outer endosperm being left intact, but the swelling of both endosperm and embryo tissues after imbibition brings the two structures into intimate and pressing contact, which facilitates the transfer of materials from one to the other. The seeds of the Grasses and some other plants, *e.g.*, *Fagopyrum*, have a cambium-like layer on the periphery of the endosperm, which remains active until the maturity of the seed, cutting off, internally, layers of starchy cells. This activity ceases at maturity, but the cambium cells then divide anticlinally into short, square cells, which become filled with solid protein. This is the so-called *aleurone layer*, which is prominent in many of the cereals. An analogous cambium forms the protecting suberized layer around the endosperm of the naked seed of *Crinum*, already mentioned.

Where the whole of the reserve material is contained in the tissues of the embryo, germination is generally quicker than in seeds with endosperm, probably because the food substances are more directly available. Where the embryo is entirely surrounded by the endosperm, the surface layer of the embryo acts primarily as an absorptive layer and is only later differentiated into an epidermis or a piliferous layer, that is to say it retains the character of embryonic protoderm until the endosperm is exhausted. The lateral or curved embryos in some seeds may only be in contact with the endosperm at certain places, for example at the abaxial side of one cotyledon. The protoderm retains its undifferentiated nature only at these places, whereas the other cotyledonary surfaces develop epidermis and stomata immediately. Later on the absorptive surface also differentiates into typical epidermis.

Specialized absorbing organs are found in some Monocotyledons. A simple form is shown by seedlings of the *Allium* type, where the cotyledon is withdrawn from the seed coat during germination, and becomes a green leaf, but the tip remains embedded in the endosperm within the seed and continues the absorption of food substances until it finally withers and falls off (Fig. 1434). The protoderm in these absorptive parts never becomes permanently differentiated, and the

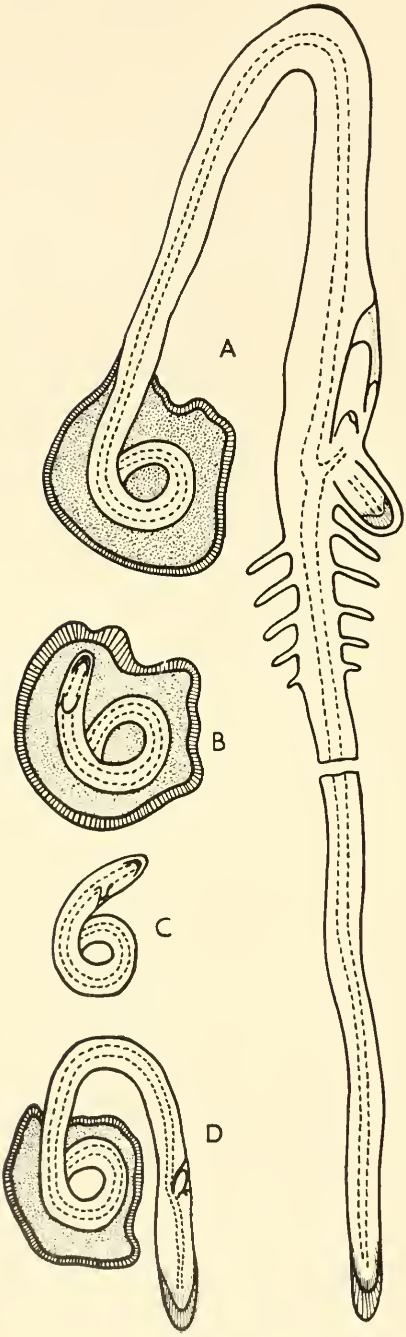

Fig. 1434.—*Allium cepa*. Onion. Germination. A, Seedling with the tip of the cotyledon embedded in the endosperm in the seed. B, Section of the seed before germination, showing the coiled embryo. C, The embryo freed from the seed. D, Emergence of the radicle as the first stage of germination. (*After Sachs.*)

absorptive tip is often swollen and tuberous, or else is drawn out into an attachment clearly differentiated from the leaf-like portion of the cotyledon, as in *Tradescantia*, *Crocus* and many other types (Fig. 1435). It thus forms a distinct organ of absorption or *haustorium*. This differentiation of a suctorial portion of the cotyledon is important in the interpretation of the Grass embryo, as we shall see later.

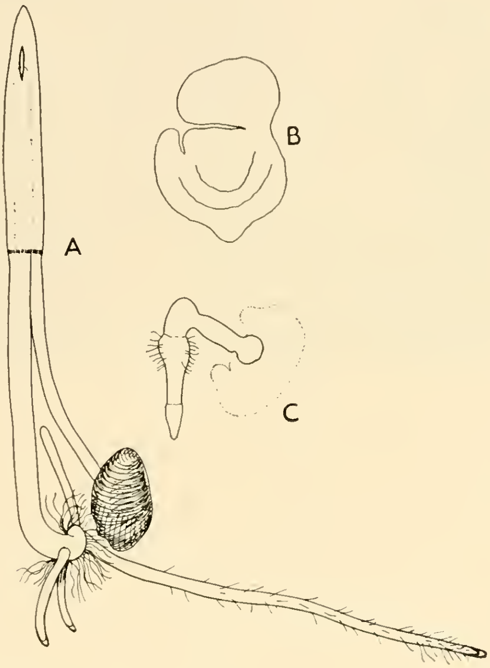

Fig. 1435.—*Tradescantia virginica*. A, Seedling. The coleoptile forms the apex, showing the slit from which the first leaf emerges. The tip of the cotyledon is still embedded in the seed, while the "middle piece" of the cotyledon is joined to the base of the coleoptile and partly fused to the hypocotyl. B, Embryo extracted from the seed. The cotyledon is on top. C, Early stage in germination showing the haustorial tip of the cotyledon in the endosperm. (*After Goebel.*)

The lateral scutellum in Gramineae acts as a haustorium (Fig. 1436). Its dorsal surface abuts on the endosperm and during germination the cells of its protoderm elongate and separate from each other, closely resembling root hairs. Like the latter they have very thin walls and are rich in protoplasm. When the endosperm is exhausted, these absorptive cells collapse.

The most remarkable haustoria are formed in the seeds of the Palms. In principle they are similar to the others, being specialized portions of the cotyledon, but they reach an immense development. In *Phoenix dactylifera*, the Date Palm, the resting embryo is very small and is laterally placed in the hard endosperm (Fig. 1437). At germination the tip of the cotyledon

FIG. 1436.—Section of a germinating Wheat grain. The embryo is on the left, the scutellum in the middle and the endosperm on the right. Digestion of the endosperm is proceeding from the surface of the scutellum.

enlarges to a mushroom-shaped mass which invades and destroys all the endosperm. It is connected by a stalk or *middle piece* to the sheathing base of the cotyledon, which surrounds the plumule in the developing plantlet outside the seed. In *Cocos nucifera* the endosperm is hollow and the haustorium enlarges to fill the entire space. It is a mass of soft white tissue as big as an apple, contacting the endosperm all round its surface and remaining active and absorbent for several years, as is commonly the case in the Palm family (Fig. 1438). The middle piece is very long, 40–50 cm., so that the seed and the embryo are far apart. Indeed in some Palms, the middle piece has been known to rise above ground, bearing the seed with it, at some distance from the rest of the young plant.

The two Palm genera *Nipa* and *Phytelephas* differ markedly from all other Palms in that the haustorium is formed from the primary root. The cotyledon consists only of a short sheath and the root enlarges to fill the big hollow space in the middle of the endosperm. The result of this peculiarity is that it is the plumule, not the radicle, which emerges first from the pericarp in which the seed is enclosed (Fig. 1439). Adventitious roots spring from the cotyledonary axil and bend downwards into the ground like stilts. The state of affairs in *Nipa* is connected with the usual Palm type, and indeed with the Grass type, by certain other Palms (*Thrinax*, *Oncosperma*) in which the primary radicle, though external to the seed, forms no root hairs and is quickly replaced by endogenous adventitious roots from the short hypocotyl.

In many seeds and fruits there exist special structures concerned with germination of which only a few can be mentioned. The seeds of some monocotyledonous families have an opening in the testa, over the place at which the radicle will emerge, which is closed by a hard plug against which the radicle pushes at germination. These are found in the Zingiberaceae, Marantaceae and Musaceae, the plug being formed by an aril. Similar " seed-lids " occur in the Commelinaceae, Potamogetonaceae, and Lemnaceae. Among Dicotyledons, the genus *Sorbus* also has a kind of " lid " opposite the radicle, which the latter carries with it, on germination, as a temporary root cap.

Hill investigated the mode of germination in a number of cases where the seeds remain enclosed in a stony endocarp, which is often very hard.

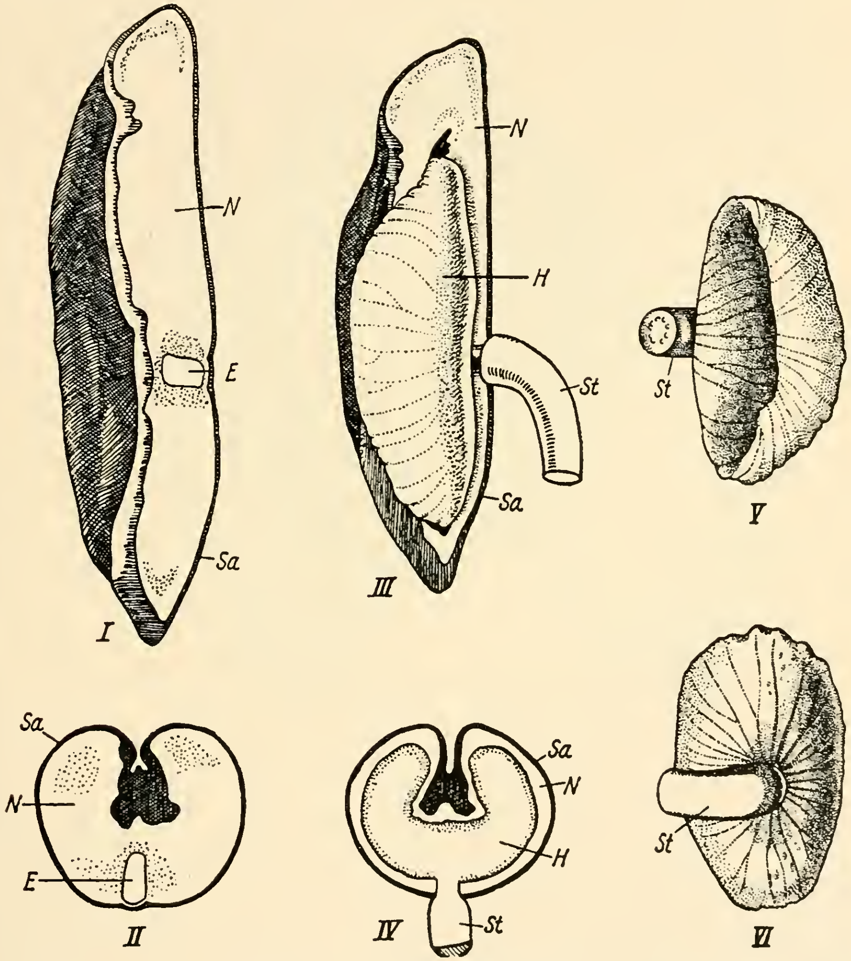

FIG. 1437.—*Phoenix dactylifera.* Date Palm. Germination. I. Seed in longitudinal section. II. Seed in transverse section (E=embryo). III. Germinating seed in longitudinal section showing the great development of the haustorial cotyledon. IV. The same in transverse section. V and VI. Two aspects of the embryo. (*From Troll, "Vergleichende Morphologie der höheren Pflanzen".*)

The testas of such seeds are usually papery and the endocarp is the true protective structure. Among the simplest devices are those in which the endocarp splits into two halves, as in *Prunus* (single carpel) or *Juglans* (two carpels). In these cases a definite plane of cleavage is formed beforehand and the shell is forced open by the swelling seed inside. In *Cocos* there is no special opening, but one of the three round depressions at one end of the shell is unlignified and through this the seedling forces its way out. A more advanced device is the provision of a special portion of the endocarp, a kind of shutter or fenestra (Fig. 1440) which is readily pushed open from inside like a valve, *e.g.*, *Nyssa* (one seeded), *Cornus* (two seeded) and *Tectona* (four seeded). A further device is that of an aperture closed by a stony plug which is pushed off by the seedling, *e.g.*, *Sclerocarya* (Anacardiaceae) (Fig. 1441). *Pleiogynium*, another genus of the same family, has up to twelve seeds in each fruit and has a stony mesocarp in addition to the

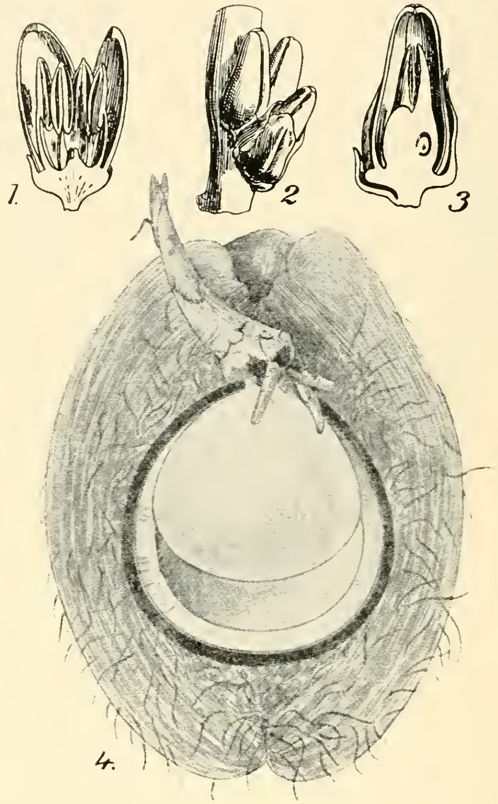

Fig. 1438.—*Cocos nucifera*. 1, 2 and 3. Male and female flowers. 4. Germinating fruit. The cotyledonary haustorium has enlarged to fill nearly all the hollow space surrounded by the layer of endosperm. (*After Baillon. From Lotsy, "Vorträge Über Botanische Stammesgeschichte".*)

endocarp. The former has oval-shaped windows exposing the endocarp over each seed and a cap of the endocarp is pushed off by the radicle. In this fruit, as in some others, the number of seedlings obliged to germinate

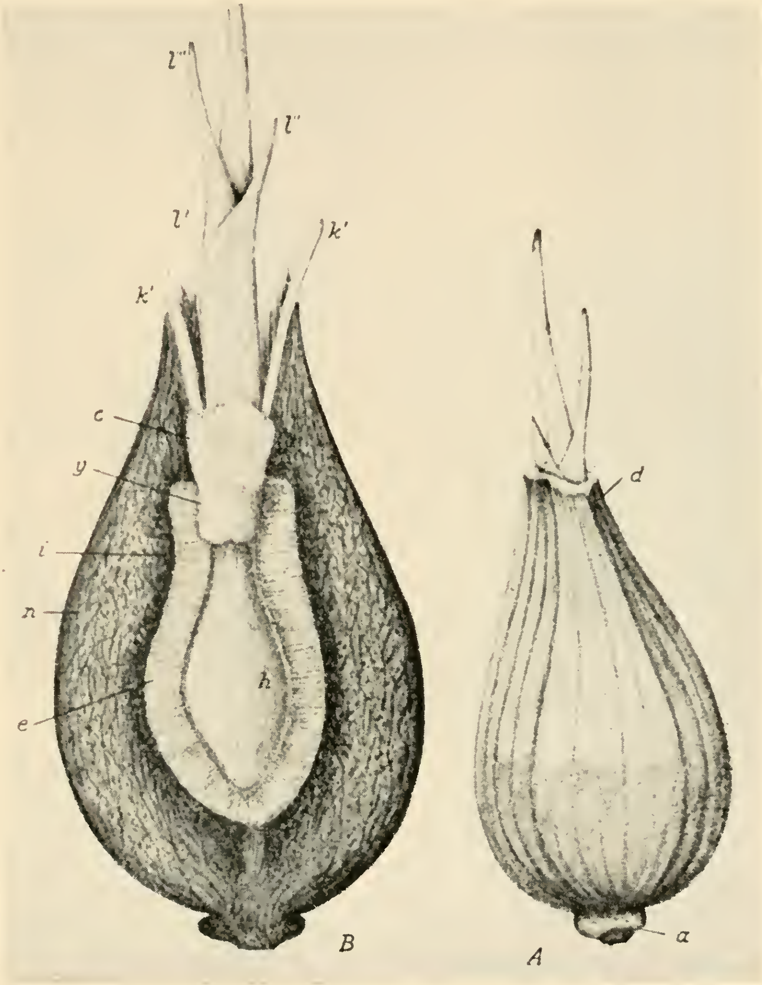

FIG. 1439.—*Nipa fruticans*. A, Germinating fruit. B, The same in section. (c = cotyledon. h = haustorial radicle.) (*After Velenovsky.*)

close together results in severe competition, so that only one usually survives. The extreme case of this germinal competition is that of *Bertholletia excelsa*, the Brazil nut, in which a hard fruit like a small cannon-ball holds a number of seeds. The only opening is at the base, which is covered and closed by the woody calyx. The seeds germinate in the fruit and there is a keen struggle for survival, as only one can successfully occupy the "escape hatch" and establish itself outside. Such methods look wasteful but they may have an evolutionary value.

Quite different from the above and interesting because found in *Vicia faba*, is the clamp structure described by Orr. The radicle lies in a pocket of the testa, close to, but above the micropyle. On each side of this pocket there is a dark, raised patch, and the surfaces fit very closely against opposite sides of the base of the radicle, the surfaces of both structures being papillate. It is suggested that these are clamps holding the expanding radicle at germination and preventing it from exercising a back-pressure which might rupture the hypocotyl. Experiment shows that this is a real danger. Similar preventions may exist in other seeds.

Fig. 1440.—*Davidia involucrata*. Cornaceae. Germination of the stony fruit. The germinating seeds push off longitudinal valves or shutters in the pericarp.

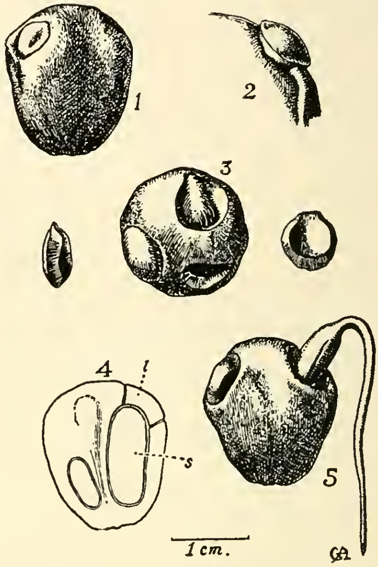

Fig. 1441.—*Sclerocarya caffra*. Germination of the tricarpellary stony fruit. The fenestra in the stony pericarp are closed by plugs which are pushed out by the radicles of the germinating seeds within. (*From Hill, "Annals of Botany"*.)

The **cotyledons** of seedlings, appendages of the embryo before germination, have always been the subjects of remark on account of their variety of form and the marked differences which often exist between them and the foliage leaves. In spite of all their modifications there can be little doubt that they are, in fact, leaves, but in many cases, leaves with a repressed development. Some would see in them types of the primitive foliage of their species, and the intermediate stages which are often present, between the cotyledonary form and that of the mature foliage, as recapitulatory phases of a phylogenetic sequence. The fact that in many species, *e.g.*, in *Statice*, *Lysimachia* and many Rubiaceae, there is little or no difference between the cotyledons and the foliage leaves, lends support, however, to the view that in other cases the cotyledons have been secondarily modified by restriction. There are, nevertheless, important differences which in the view of some, isolate them from the category of leaves; namely that their origin in the embryo is different from that of all subsequent leaves, their vascular connection with the axis may be quite different and they generally have no axillary buds. As however the same line of argument can be applied to the hypocotyledonary stem and to the primary root, we might as well conclude on the same grounds that the embryo is not a plant.

The almost infinite variation of cotyledons (see Lubbock, " On Seedlings", 1892, *passim*) can be in general related to their variety of functions. (1) They protect the apical bud both in the embryo and after germination. (2) When they are raised above ground they become photosynthetic and assist the independent establishment of the seedling. In some tuberous plants, *e.g.*, *Eranthis*, the cotyledon is the only leaf produced in the first year. (3) They are frequently used as storage organs for reserves of food and may be greatly thickened for this function. (4) They may act as haustoria for the absorption of endospermal reserves, as we have described. (5) They may act as boring organs in rising to the surface of the soil. (6) In some Monocotyledons the middle piece is positively geotropic and functions in pushing the seedlings down into the soil.

Perhaps the most important distinction is between cotyledons which are raised above the soil and become green (**epigeal**) and those which remain below ground, usually in the seed testa (**hypogeal**). This serves to differentiate two main types of germination. Hypogeal cotyledons are either haustorial or else they themselves, in non-endospermic seeds, contain the main reserves of food. In the latter case they are often greatly thickened, the tissue consisting largely of somewhat thick-walled parenchyma filled with reserve materials. Nevertheless they have stomata and do not always remain underground. The cotyledons in the non-endospermic seeds of Cruciferae and some Papilionaceae, although storage organs, are epigeal and become green and photosynthetic, serving a double function. This change is usually, though not invariably, delayed until the reserve materials in the cotyledons have been used up.

The two kinds of behaviour, though physiologically important, have no systematic significance and the one must be readily changeable into the other, as is shown by the fact that closely related species of the same genus may differ in their cotyledonary behaviour. Thus *Phaseolus multiflorus* and *Mercurialis annua* are hypogeal, while *P. vulgaris* and *M. perennis* are epigeal.

Most cotyledons are short lived. They are seldom abscissed and usually wither after a few weeks. When they persist they are poorly placed for assimilation, at the base of the stem, and can be of little importance. They increase in size during germination but they generally remain small relative to the foliage leaves. This seems to be correlated with the development of the plumular bud, for if this is removed the cotyledons continue to grow in size and in *Streptocarpus*, where the apical bud is naturally suppressed, the one surviving cotyledon may grow to be 30 cm. long (see p. 1596).

Cotyledons are usually simple in outline, even in plants with compound leaves, which may be attributed to the growth restriction we have referred to. The existence of this restriction is best shown in those cases where it is only temporary. The Onagraceae provide many examples of this. *Clarkia* (Fig. 1442), *Fuchsia*, and some species of *Oenothera* have cotyledons which are at first short, broad and sessile. Intercalary growth follows germination, the cotyledons elongate and the new, basal portions have many of the characters of the foliage leaves, differing from the original cotyledons in outline, venation and often in hairiness. The junction of the two portions is marked by a constriction. The later growth also develops a petiole. In these species it is evident that the cotyledonary restriction has disappeared.

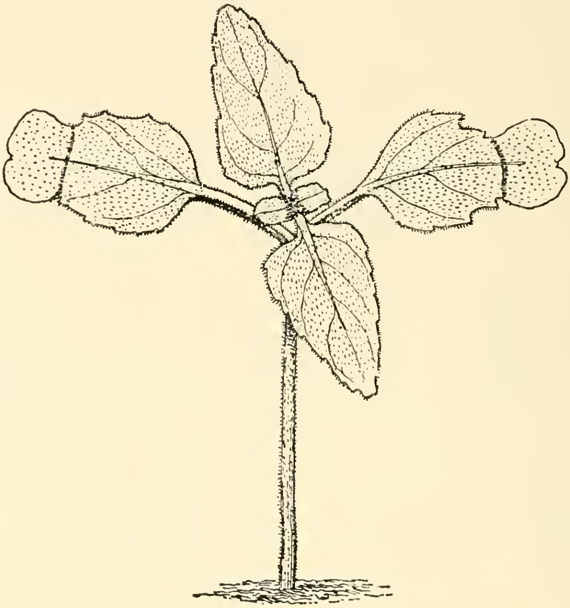

FIG. 1442.—*Clarkia integripetala.* The two cotyledons, right and left, show marked intercalary growth, the added portions at the base being quite different from the original apical portions. (*From Lubbock, "A Contribution to our Knowledge of Seedlings", Vol. I.*)

How far the cotyledonary characters, especially the growth restriction, can be attributed to conditions in the embryo sac and the seed, is a matter not fully explored. The shape of the cotyledons in *Juglans* is obviously moulded on the wall of the pericarp, but in *Geranium* the rolling together of the cotyledons begins in the embryo sac and is not apparently due to external conditions. The inequality of the cotyledons, which is often seen in curved embryos, may be due to their relative positions in the seed affecting them both mechanically and nutritionally.

The absorptive function of the cotyledons in endospermic seeds may also influence their form, as is well seen in *Myristica*. The endosperm in these large seeds is ruminate and the cotyledons during germination become markedly lobed, the lobes growing into the corresponding lobes of the endosperm. The same absorptive function has obviously influenced the cotyledons of endospermic Monocotyledons, notably in Grasses.

Cotyledons practically never have stipules. The seedling of *Fagopyrum* is unique in that the cotyledonary node bears an ochreal sheath surrounding the plumule, though it is absent from other polygonaceous seedlings. The ochrea here is common to the two cotyledons. In other genera connate union of the cotyledons is not uncommon, the bases being united into a sheath around the plumule. Petiolate cotyledons, *e.g.*, *Psidium* (Guava), may also be united by the edges of the petioles, so forming an elongated tube. Fusion of cotyledons will be dealt with later.

Because one or two familiar seedlings like those of *Vicia faba* have buds in the cotyledonary axils, it is not generally realized that this is actually an uncommon condition outside the Papilionaceae and that in most cases of their occurrence their further development is inhibited by the growth of the plumule. There are cotyledonary buds in *Linum* and they form the normal renewal shoots of perennial species of that genus in the second year. In *Galium* there are serial buds, three or four in the axil of each cotyledon, and these develop freely and form part of the normal branch system.

Inequality of the cotyledons may develop inside the seed or it may appear during germination. The seeds of *Peperomia* show interesting stages in the evolution of heterocotyly due to the specialization of one cotyledon as a haustorium while the other remains epigeal.

Almost invariably the two cotyledons arise oppositely at one node, below which is the primitive axis or **hypocotyl** and above which is the **epicotyl** arising from the plumular bud. Only rarely is there an internode, or **mesocotyl**, between the cotyledons. The hypocotyl varies greatly in length. In big dicotyledonous seedlings (*Ricinus*, *Helianthus*) it may be a foot in length. In a great many Monocotyledons it is very short and not infrequently tuberous. Tuberosity of the hypocotyl is common also in Cruciferae, Ranunculaceae and some Monocotyledons. In Cruciferae it forms the greater part of the "roots" of Turnip and Radish (Fig. 1443). At the lower end the hypocotyl passes directly downwards into the **primary radicle**. The point of junction, the *collet* of French anatomists, is usually distinguishable, but in the tuberous forms mentioned above, the external transition is often gradual and difficult to locate exactly. The hypocotyl is part of the stem, although a specialized part, and has normally the structure, epidermis and colouring of a stem, but the level of anatomical transition, the junction between stem structure and root structure, is not always at the *collet*. In some cases the transition takes place at intermediate levels in the hypocotyl, with no change in external appearance and, on the contrary, it sometimes occurs below the *collet*, the stem anatomy persisting downwards some way into the radicle. Normally the hypocotyl does not produce any outgrowths but exceptionally it produces endogenous adventitious roots (see the account of the Podostemaceae, below). In *Cinnamomum* the dwarf hypocotyl produces even the primary radicle endogenously, an almost unique case in the Dicotyledons, though found commonly in the higher Monocotyledons. Adventitious buds are not uncommon on the hypocotyl of *Euphorbia lathyrus*.

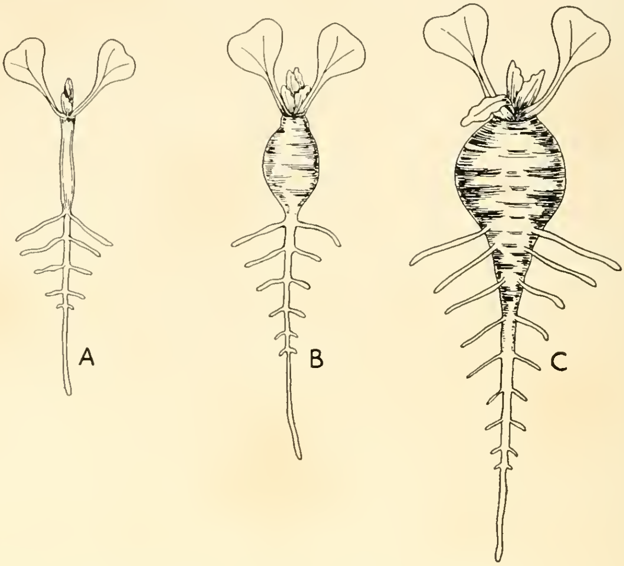

FIG. 1443.—*Raphanus sativus*. Radish. Development of the swollen hypocotyl. (*After Troll.*)

There are a number of departures from the usual paired cotyledons in Dicotyledons. Several genera regularly produce more than two, for example *Bruguiera* (Rhizophoraceae) has four, and *Persoonia* (Proteaceae) three or four. *Eranthis* frequently has three. Splitting of the cotyledons (**schizocotyly**) occurs in varying degrees as an anomaly in many seedlings of different families, all stages between simple emargination and complete fission being found. Everything points to the two-cotyledonary state as primitive and to the supplementary cotyledons being formed by the splitting of one or of both of them. Hill and de Fraine considered that this is true also of the polycotylous seedlings of Coniferales. The opposite condition or **syncotyly** occurs in a great number of dicotyledonous seedlings and like schizocotyly it occurs in all degrees of completeness. In endospermic seeds the union is generally symmetrical, by both edges, forming a cotyledonary tube, while in non-endospermic seeds (*i.e.*, with storage cotyledons) the union is generally lateral, by one edge only, the differences being due to space and symmetry relationships within the seeds. A number of genera, especially in Ranunculaceae, have normally only one cotyledon and are therefore classed as pseudo-monocotyledonous. We shall discuss them later in relation to the origin of the Monocotyledons as a class.

In many seedlings the first epicotyledonary leaves show at once the character of the mature foliage. Examples are: *Paeonia*, *Hepatica*, *Hedera*, *Ampelopsis*, and *Salix*. In many others there is a gradual transition from simpler forms towards the mature form, as may also be seen in some buds of trees. This is especially the case where the mature leaves are compound, as in *Robinia* and *Glycine* and in many other cases, especially in Rosaceae, *e.g.*, *Rosa*, *Fragaria* and *Potentilla*, the last named often showing a particularly striking series of stages. The stool-shoots which arise from the base of the trunk or the roots of many trees show a similar series of stages in leaf development. In many Pyrolaceae, Lauraceae and Annonaceae the first few leaves are much reduced and scale-like and the mature leaf form appears suddenly at the fifth or sixth node. In Monocotyledons there may be a similar gradual appearance of full leaf development, the first leaves often having a well-formed sheath, but little or no leaf blade. The differences are, however, not so marked as in Dicotyledons. The question arises whether this is a true recapitulation of an evolutionary series or not. The probabilities are against it and it seems more likely that it is due to an upward extension of the growth restriction which is evident in the cotyledons.

We may now consider shortly how we may arrange the various seedling conditions we have referred to, in a tabular order, as a classification of types of germination.

Dicotyledons

Epigeal: Endospermic: Polygonaceae, Plantaginaceae, *Ricinus* (Fig. 1444) and many others.
Non-endospermic: Cruciferae, Lamiaceae, etc., *Phaseolus vulgaris* (Fig. 1445).

Hypogeal: Endospermic: Annonaceae, *Hevea*.
Non-endospermic: Fagaceae, etc., *Phaseolus multiflorus*, (Fig. 1446), *Tropaeolum*.

Monocotyledons

Epigeal: Endospermic: Liliaceae, Butomaceae.
Non-endospermic: Alismaceae.

Hypogeal: Endospermic: Palmae, Gramineae (Fig. 1447).
Non-endospermic: *Aponogeton* only.

The case of *Aponogeton* deserves notice for its singularity. The cotyledon is a fleshy cone filling the seed. The latter floats and the embryo drops out of it and germinates on the mud below water (Fig. 1448).

The question of the evolutionary origin of the Monocotyledons has often been debated on the ground of seedling structure. Since John Ray first distinguished the two classes of Angiosperms on the number of their cotyledons, this difference has tended to assume too great an importance in theoretical arguments, since it is only one among several important structural distinctions.

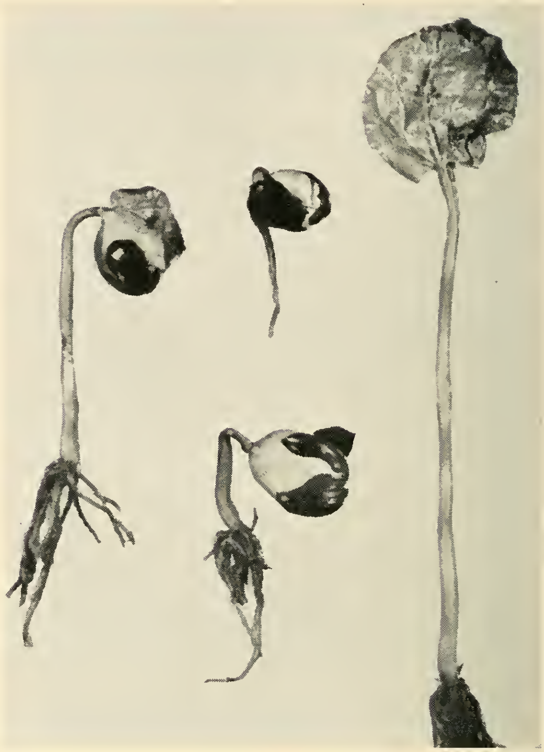

FIG. 1444.—*Ricinus communis.* Germination: dicotyledon, epigeal, endospermic.

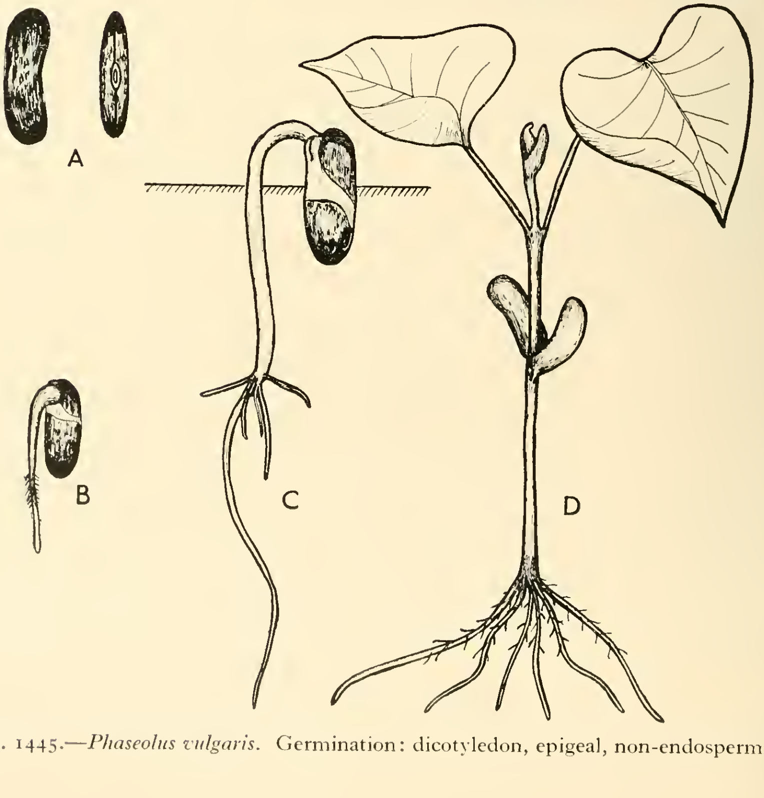

FIG. 1445.—*Phaseolus vulgaris.* Germination: dicotyledon, epigeal, non-endospermic.

FIG. 1446.—*Phaseolus multiflorus*. Germination: dicotyledon, hypogeal, non-endospermic.

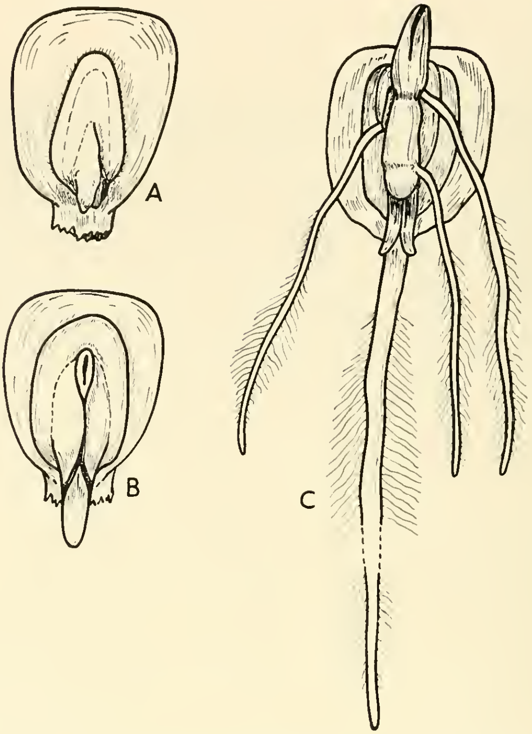

FIG. 1447.—*Zea mais.* Germination: monocotyledon, hypogeal, endospermic.

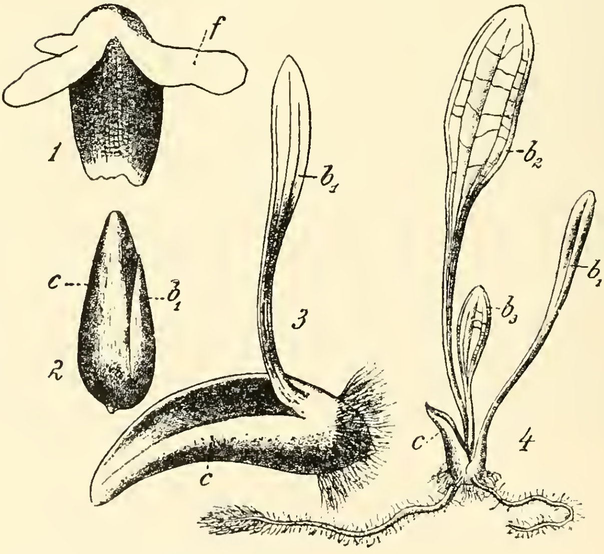

FIG. 1448.—*Aponogeton distachyum.* Germination: monocotyledon, hypogeal, non-endospermic. 1, The empty fruit. 2, The embryo. 3 and 4, Young seedlings. c is the cotyledon in each case. (*From Wettstein, "Handbuch der Systematischen Botanik".*)

While it is interesting to compare the monocotyledonous embryo with the dicotyledonous and to try to find common terms between them, we should do so with Goebel's remark in mind, that the origin of monocotyledony is by no means the same thing as the origin of Monocotyledons.

To begin with it has been very generally accepted in recent years that the Monocotyledons are a derivative class, though the older morphologists thought otherwise. They appear rather later than the Dicotyledons in the geological record and some structural characters, like the absence of secondary thickening, the adventitious root system, and the prevalence of the geophilous habit, seem to indicate secondary specialization. Their characteristics serve to isolate them from the Gymnosperms, with which, on the other hand, the Dicotyledons have much in common. Acceptable evidence, no doubt, but not conclusive. If we regard the Monocotyledons as a single, monophyletic class, we may still think of them either as evolved parallel with the Dicotyledons or else as an offshoot of the latter. We may also, on the contrary, prefer to regard them, with Lotsy, as comprising two groups, evolved independently; one, including Araceae and Palmaceae, arising from the Piperales, and the other, including Helobiae and Liliaceae, arising from the Ranales.

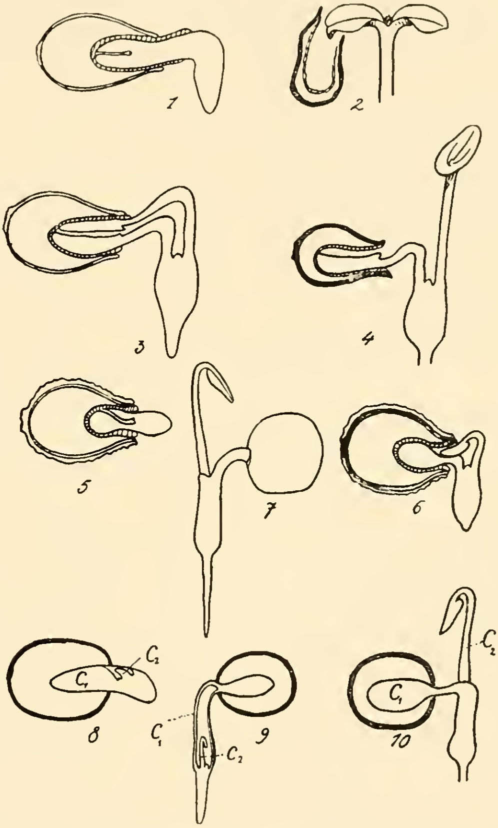

Fig. 1449.—Heterocotyly as the origin of the monocotyledonary condition. Hill's interpretation. 1 and 2, *Peperomia pellucida*. 3 and 4, *P. peruviana*. 5 and 6, *P. parvifolia*. One cotyledon has been reduced to a haustorium. 7, *Arisaema dracontium*. Araceae. Germination for comparison with the above. 8, 9 and 10, Germination of typical monocotyledons. C_1 and C_2 are the two cotyledons.

If the Monocotyledons have in fact arisen from Dicotyledon ancestors then, so far as the seedling character is concerned, there are at least two possibilities. Either the single cotyledon represents a fusion of two, as Miss Sargent believed, or else the single cotyledon is the survivor of an original pair, the other member having either disappeared or been altered out of recognition. The latter view was maintained by A. W. Hill on the basis of a comparison of seedlings in *Peperomia* (Fig. 1449). His argument was that a single cotyledon had been modified into a haustorium and was therefore the only one of importance in the embryo. The appearance of the second cotyledon was post-embryonic, and it was, in fact, the organ usually called the first leaf. This is as much as to to say that Monocotyledons are not monocotyledonous but only extremely heterocotylous. Lotsy believed this to be true of the Araceae and he therefore accepted their relationship to *Peperomia*, but it is much more difficult to apply the argument to the Helobiae, which are more understandable on Miss Sargent's view, and he accepted their derivation from Ranales.

The striking fact is that in the Ranales there are a number of genera which have monocotyledonous or pseudo-monocotyledonous seedlings, and others which display further monocotyledonous characters, such as closed vascular bundles, scattered bundles in the stem and absence of secondary thickening, as well as trimerous flowers, failure of the primary root, sheathing petioles, a geophilous habit and the absence of vessels in the secondary wood (which is also true of those Monocotyledons which are thickened by means of a secondary cambium).

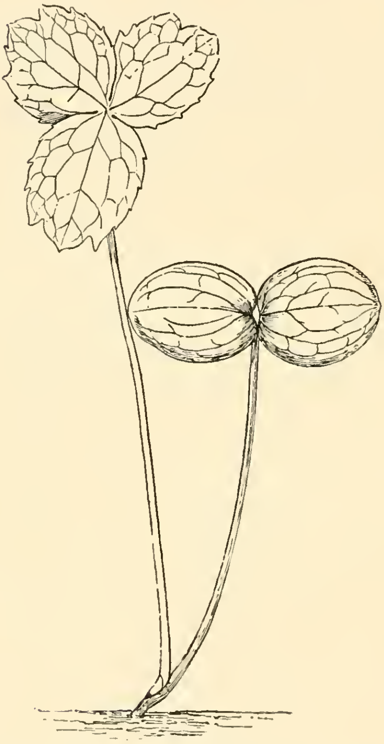

FIG. 1450.—*Podophyllum emodi.* Pseudo-monocotyledonous germination. See in text. (*From Lubbock, "A Contribution to our Knowledge of Seedlings".*)

The pseudo-monocotyledonous seedlings form an interesting group, with examples both in Ranunculaceae and Berberidaceae, *e.g.*, *Ficaria verna*, *Ranunculus illyricus* and *Podophyllum emodi*, though we are obliged to add that isolated cases occur in other families, *e.g.*, Papaveraceae, Celastraceae and Umbelliferae, where they can have no phylogenetic connection with Monocotyledons. *Podophyllum emodi* affords a good type of the others mentioned (Fig. 1450). The two cotyledons are united on one petiole, with a sheathing base. There is no hypocotyl and the plumule emerges from a slit at one side of the base of the cotyledonary stalk and stands opposite to the combined "cotyledon", as in Monocotyledons. In some other species (*Delphinium nudicaule* and *Chelidonium majus*) the union of cotyledons is practically complete and in *Bunium bulbocastanum* and *Corydalis solida* there is definitely only a single cotyledon. There is, however, a double vascular supply in the petiole and by analogy with this, Miss Sargent relied on the presence of a double vascular bundle in the cotyledon of Monocotyledons with no midrib, as evidence of its double nature. The first foliage leaf always has a midrib, usually with lateral bundles as well, while a midrib is always present in the cotyledons of Dicotyledons. The genus *Nelumbo* (Nymphaeaceae) has been for long a subject of interest because the cotyledons arise in the embryo as a single ring around the apex, the ring becoming two-lobed later. Is this evidence of the origin of two cotyledons by the division of a primordial one, or is it, as seems more probable, simply a congenital union of two? It would violate all probability to remove this and other pseudo-monocotyledons from the families to which they plainly belong and transfer them to a place among the Monocotyledons. Much more readily will we accept the idea that one cotyledon may arise from the fusion of two.

The lack of normal secondary thickening among Monocotyledons is, in quite another direction, evidence of their derivative status, since temporary bundle cambia have been found in the seedlings of a number of genera: *Yucca*, *Typha*, *Fritillaria*, *Zea* and *Musa*, among others. Some additions are made to the vascular elements from these cambia for a short time, but the cambium is subsequently distorted and lost.

We have referred above to two possibilities regarding the relationship of the one cotyledon to the two, assuming that the two conditions are indeed related. Mrs. Arber has presented a third possibility. It is difficult to do justice in a few lines to her thesis, which is fully and elegantly argued in her book, "Monocotyledons". She dismisses the argument for the double nature of the single cotyledon from its double vascular supply by pointing out that recent research has shown that the midrib of each cotyledon in Dicotyledons is also very often a double structure. This, she argues, arises from the nature of its vascular supply, which comes from the primary root, instead of, as in epicotyledonary leaves, from the stem. The primary root is usually either diarch or tetrarch and the " double bundle " of the cotyledon is equated to one pole of the root structure, a xylem between two phloems, with some additions to the xylem and its separation into two portions, very often associated with the disappearance of the protoxylem. She emphasizes that the cotyledons, despite their special name, are essentially the first leaves and concludes that, as the growth rhythm in Monocotyledons is such as to produce only one leaf, with a sheathing base, at each node, there is no need to assume that the cotyledonary node would be different, or that vestiges of a second cotyledon need be there in any shape or form.

We see the monocotyledonous seedling at its simplest in *Naias* (Fig. 1451). The embryo is spindle-shaped, the upper half being the cotyledon and the lower half the hypocotyl. The plumule is entirely enclosed by the base of the cotyledon. There is no endosperm, so there is no haustorial modification of the cotyledon, which forms a straight green leaf. The development of the primary radicle comes after germination, but it is preceded by a collar of root hairs, markings its base, a feature which is repeated in many other seedlings. Seedlings of the Alismaceae, Juncaginaceae

(*Triglochin*) and many Liliaceae are of almost equal simplicity, though the hypocotyl is sometimes lacking and the tip of the cotyledon remains for

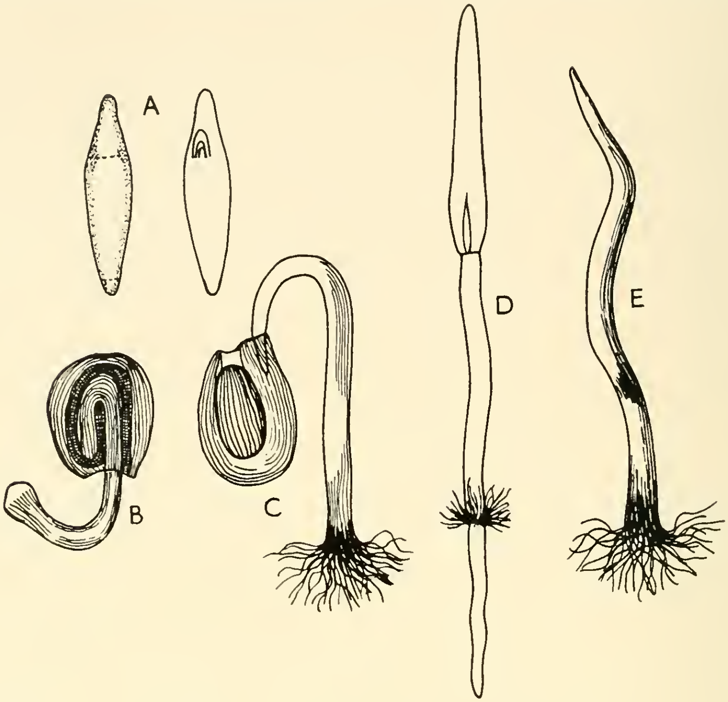

FIG. 1451.—*Naias major*. A, Seedling whole and in section. *Alisma plantago-aquatica*. B to E, Stages of germination, the cotyledon being simple, erect and epigeal. (*After Velenovsky*.)

some time in the endosperm, the cotyledon being, however, erect and carrying the seed up with it. The evolution of the haustorium can be traced through a series of types (Fig. 1452), beginning with forms like *Allium*, where it is scarcely differentiated and is simply the deflexed apex of the cotyledon, passing to a stage like that in *Iris* where the haustorium in the seed is united to the apex of the cotyledon by an elongated middle piece; next to a stage where the middle piece is laterally attached to the cotyledon (*Crocus*) and finally, as in *Tradescantia*, to the attachment of the middle piece to the base of the cotyledon. This leads us to the embryo of the Gramineae, the most highly specialized and the most difficult to interpret.

Its principal characters are shown in the section of the embryo of *Zea mais*, Fig. 1453.

They may be briefly enumerated as follows: the haustorial *scutellum*, embedded in the caryopsis and frequently bearing a small ventral scale attached to its upper portion; the *epiblast*, a small scale opposite the scutellum; the *coleoptile*, a sheath, sometimes colourless, enclosing the well-developed plumular leaves; the *coleorhiza*, a sheath surrounding the rudiment of the primary root.

It would take too long to review the various theories which have been propounded to try to bring the Grass embryo into line with other Monocotyledons, and it has been adequately done elsewhere.* We shall content ourselves with indicating certain probabilities.

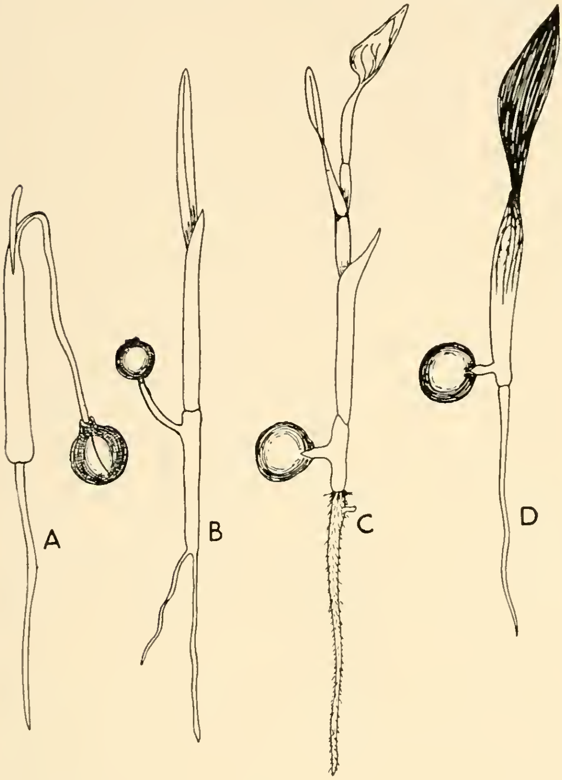

Fig. 1452.—Examples illustrating the apparent change in the position of the cotyledonary middle piece. A, *Nolina longifolia.* Attached to the apex of the cotyledonary sheath. B, *Crocus vernus.* Descended to the base of the sheath and now attached to the hypocotyl. The sheath remains as a coleoptile. C, *Smilax aspera.* Descending on the hypocotyl. D, *Gloriosa superba.* Descended almost to the base of the hypocotyl, the portion of which above its point of junction now being the mesocotyl. (*After Velenovsky.*)

Fig. 1453.—*Zea mais.* Longitudinal section of an entire grain with the embryo, which shows a coleoptile, a coleorhiza and the laterally attached cotyledonary scutellum.

It should be noticed that in progressing from the apical attachment of the haustorial portion of the cotyledon towards a basal attachment, as described above, we have also been advancing from epigeal to hypogeal germination. With the cotyledon underground the need for rapid plumular development becomes more pressing and we find a correspondingly greater development of the plumule before germination. Thirdly, in more advanced Monocotyledons the leaves have not only a sheathing base but also a ligule, which must be taken into account.

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* See a good short statement by Boyd in "Trans. Bot. Soc. Edinburgh", Vol. 30, 1931.

It will not have escaped notice that the sheathing part of the cotyledon has not altered its nature with the descent to its base of the attachment of the middle piece. Although now above the point of attachment to the seed it is still the sheathing base of the cotyledon. Indeed it is probably wrong to speak of the *descent* of the point of attachment. Rather has the cotyledonary sheath developed upwards, assuming negative geotropism and a new function as a boring organ for the hypogeal plumule. Such an upgrowth can be followed ontogenetically in *Tradescantia.* In this genus we also see the beginning of a further process, namely the union of the cotyledonary middle piece with the hypocotyl, a union which has become complete in *Carex* and *Cyperus* and is also found in some of the Grasses. This compound axis is a new structure and it is called the *mesocotyl.*

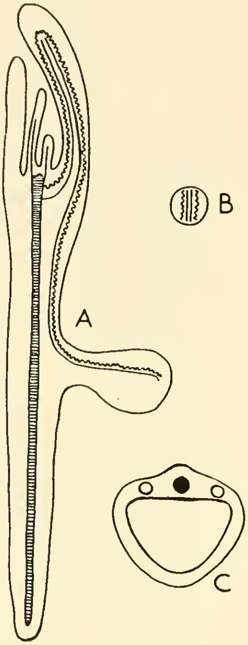

Fig. 1454.—Diagram of the vasculation in the seedling of a *Carex.* A, Longitudinal section. The haustorial portion of the cotyledon is attached to the side of the hypocotyl but its vascular strand descends from the tip of the cotyledonary sheath or coleoptile. B, The double bundle in the sheath. C, Section of the sheath, the double bundle shown in black.

The vascular bundle from the haustorium enters the mesocotyl but remains distinct and only joins the vascular system of the hypocotyl at the base of the plumule, where it divides to supply two bundles to the cotyledonary sheath. In *Carex* it does not unite until it has travelled up into the sheath and down again (Fig. 1454). The cotyledonary ligule was presumably originally a ring, but it seems most probable that it is now represented only by the epiblast. No Grass has retained a complete ligular ring, but *Oryza* shows an approach to it.

We may now suggest homologies for these various structures in a tentative way, based on the foregoing considerations. The scutellum represents the haustorial part of the cotyledon. So much is generally agreed. The middle piece has been united to the hypocotyl to form the mesocotyl. The coleoptile is the basal sheath of the cotyledon, now advanced upwards in accordance with its new function as protector and leader of the plumule. It is not possible to interpret it as the first plumular leaf, as has been attempted, because it should then be opposite the cotyledon, whereas it stands on the same side as the scutellum, with its adaxial side, as marked by the slit opening through which the plumule emerges, facing away from the scutellum. In *Cyperus* this is more obvious than in most Grasses. The epiblast may be the remains of the cotyledonary ligule. In some grasses, *e.g.*, *Zizania aquatica*, Wild Rice, the epiblast is remarkably long and well developed and it may be that it has survived through fulfilling a useful protective purpose (Fig. 1455). The coleorhiza is simply the base of the hypocotyl from which the primary root, if present, or else the first adventitious roots emerge endogenously. An endogenous primary root occurs in the dicotyledonous *Cinnamomum*, with, likewise, a coleorhiza.

There are many anomalous seedling structures and we can mention only a few of the most striking. In a few twining plants the twining habit appears in the seedling, which grows very rapidly, with very long internodes. An example of this is *Physostigma venenosum*, the Ordeal Bean. A similar growth is seen in the climbing parasite *Cuscuta*, whose seedling consists only of a colourless filament, bearing a few minute scales and no trace of cotyledons, which acts as a "seeker", growing freely and unattached along the ground until it encounters a host plant, around which it immediately entwines itself. The primary radicle is functionless and soon aborts. Absence of the cotyledons is characteristic of several parasitic families, whose peculiar germination methods will be treated in Volume IV.

If the Grasses have the most advanced seedlings among Monocotyledons, the Orchidaceae surely have the simplest,

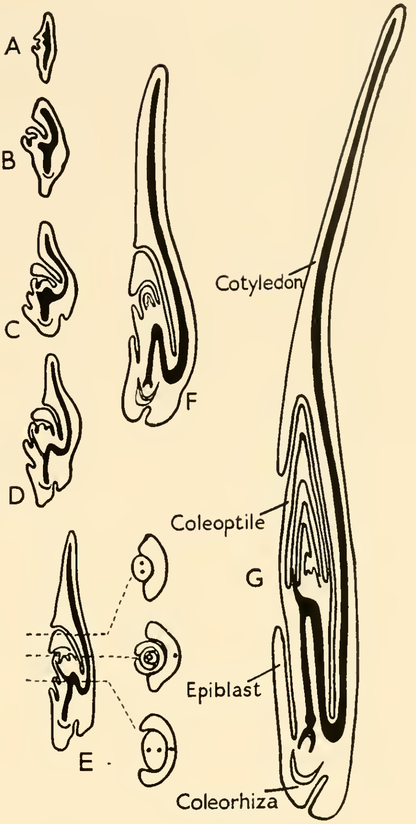

FIG. 1455.—*Zizania aquatica.* Stages in the development of the embryo to illustrate the morphology of the graminean embryo. The vascular strands in black. Note that the cotyledonary trace originates at the base of the coleoptile and travels downwards in the mesocotyl before entering the cotyledon. (*After La Rue, Avery and George.*)

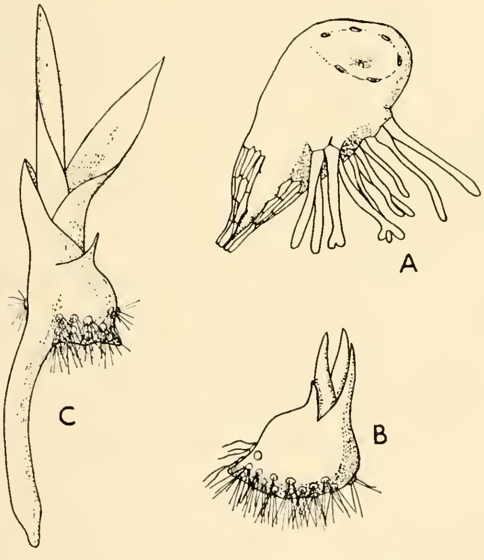

FIG. 1456.—*Odontoglossum* sp. A, Tuberous hypocotyl with rhizoids. B, First appearance of the plumule. C, The first root appearing. (*After Burgeff.*)

for the embryo at germination is still quite undifferentiated. It merely increases in size into a minute green tuber, which gets no further unless it is invaded by the right mycorrhizal fungus, when it develops a growing point and produces the first small leaves (Fig. 1456).

Several cases are known of seedlings in which the plumule is abortive. Some genera of the Papilionaceae have no vestige of a plumule, even its vascular traces having disappeared. The cotyledons in these plants (*Scorpiurus*, *Securigera*, *Tetragonolobus*) have serial buds in their axils and the whole epicotyledonary structure arises from these buds.

A very striking and well-known case is that of *Streptocarpus* (Gesneraceae). The features are not quite the same in all species but the general outline is as follows. The freshly germinated seedling has two equal, or sometimes unequally sized cotyledons, with a minute plumule between them. One cotyledon then begins to grow rapidly, while the other cotyledon and the plumule remain unchanged. The growing cotyledon acquires the size and appearance of a large foliage leaf and is, in fact, the only leaf usually produced by the plant. Its thickened petiole forms a prolongation of the hypocotyl, pushing aside the other cotyledon and the plumule, which abort and disappear. In some species even the primary root also disappears and the hypocotyl takes its place and forms adventitious branch roots. At the base of the cotyledonary lamina there now arises an exogenous bud, which grows into the main stalk of a cymose inflorescence. In the axil of this stalk there arise, serially, secondary and tertiary inflorescence buds. It is argued that their presence proves that the original inflorescence bud is not adventitious but is an axillary bud of the cotyledon, carried upwards by the vigorous growth of its petiole.

We have remarked above upon peculiarities in the seedlings of parasitic plants and the same remark applies to some insectivores. In some species of *Pinguicula* there is only one cotyledon and the primary root is abortive, but it is in *Utricularia* that modification is most profound. No comprehensive account of the genus is here possible as nearly every species has its own peculiarities. Plasticity of organs reaches an extreme in this genus where leaves, shoots and, in some related genera, roots alter their character and substitute for one another in bewildering fashion.

The embryo is undifferentiated at first and never produces roots. The minute, green tuber forms two cotyledons in some species. One of these may remain leaf-like and the other develop into the main axis, or both may remain small and the axis be formed from a third leaf, the plumule being abortive in all cases. In *Utricularia vulgaris*, there seems to be no cotyledons, their place being taken by a whorl of unequal, green spikes, one or more of which grow out into the long axes which bear the insect-catching bladders.

The rootlessness here is probably associated rather with the aquatic than the insectivorous habit, since some other floating aquatics, *e.g.*, *Ceratophyllum*, are also rootless.

The morphological oddities of the Podostemaceae as well as their unique habitat in tropical waterfalls and their peculiar distribution, have long made them famous among botanists. Some genera have adopted a thalloid habit which makes their vegetative parts scarcely distinguishable from lichens or algae. Others closely resemble Jungermanniaceae. Willis first observed the germination stages in Ceylon. What he then observed is probably common to most Asiatic and African species, though the story of the American species may be different. The young embryo has two cotyledons but no radicle and attaches itself to the rock by the stumpy hypocotyl. The further development of the plant is wholly due to adventitious roots springing from the hypocotyl, which rapidly elongate and flatten themselves on the rock surface, to which they become attached by exogenous lateral outgrowths called haptera. These roots are green and assimilatory and often spread into thalloid expansions. From their upper sides endogenous buds arise in acropetal order, from which leafy and flowering shoots arise, the latter during the dry season when the water level is low. We shall have another occasion to deal more fully with the family under Bionomics in Volume IV.

Lastly we would mention a unique occurrence in some species of *Oxalis*, especially *O. hirta*. Here the interior of the stele in the primary radicle separates from the endodermis, which with the cortex forms a tube. By collapse of the central tissues of the stele, the plumule is drawn down through this tube, below the soil level, where, in a protective pocket of root tissues, it develops into a bulb.

Vivipary is a word that is used in more than one sense. It may be applied to the precocious germination of seeds within the fruit, the young seedlings being dropped on the ground in a vegetative state, or it may be applied to the special case of vegetative reproduction in which the flowers are replaced by detachable bulbils or buds. In the latter case the young plant is merely an offshoot of the parental sporophyte. The first case is the only true vivipary and if we exclude the second there is no need for the special term of biotechnosis which has been coined for precocious germination. Instances of precocious germination are frequently noticed in certain plants growing in damp situations and such events are probably ecologically conditioned, like the precocious germination of spores which may occur under similar circumstances in Bryophyta and Pteridophyta. Many observations of precocious germination have been made on plants in greenhouses and it seems to be only a casual phenomenon in such circumstances.

The Mangrove trees are in a different category, for some of the predominant trees in these swamp forests, *e.g. Rhizophora*, *Bruguiera* and *Ceriops*, always produce their seedlings in this way and drop them into the tidal mud on which they grow (Fig. 1457). *Rhizophora* is particularly striking, as the seedling may reach a length of 50 cm. before dropping and hang on the tree like fruit. The single seed germinates in the capsule and the radicle emerges from the micropyle and then forces open an operculum at the top of the fruit, emerging into the open air, where it continues to grow and thicken, especially at its lower end. The cotyledons are completely united to each other, forming a tube around the plumule. Their inner ends remain embedded as haustoria in the endosperm, but when this is exhausted an abscission layer at the base of the tube allows the radicle to drop away from them, taking the plumule with it. If the tide is low their weight thrusts the seedlings upright into the mud, where they continue

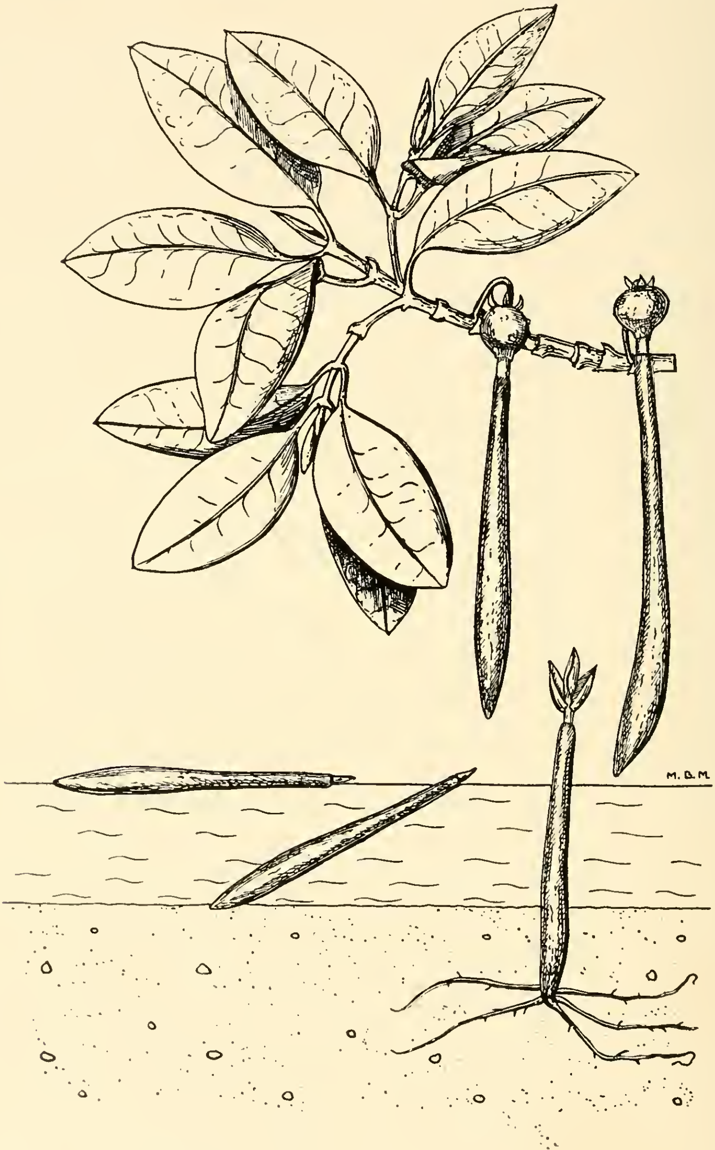

FIG. 1457.—*Rhizophora conjugata.* Branch with fruits and pendent seedlings. Below, seedlings floating and one rooted. (*From Ridley, "The Dispersal of Plants throughout the World".*)

to grow, but if they fall into the water they may float out to sea and travel great distances without losing their vitality.

Another well-known case of vivipary is that of *Cryptocoryne ciliata*, a small Aroid which grows in the brackish *Nipa* swamps of S.E. Asia. This is a case of vivipary within the seed, for the seeds are shed and float in the water as also do the embryos when liberated. The plumule forms a cluster of about a score of primary leaves, enclosing two or three leaves of the mature form (Fig. 1458). This emerges from the inner integument, only the haustorial cotyledon remaining behind. The outer integument is gradually absorbed and its remaining outer layer distended by the plantlet within. The hypocotyl becomes tuberous and finally the embryo breaks away from the cotyledon, bursts the integument and falls out, opening into a leaf rosette and forming roots as it floats.

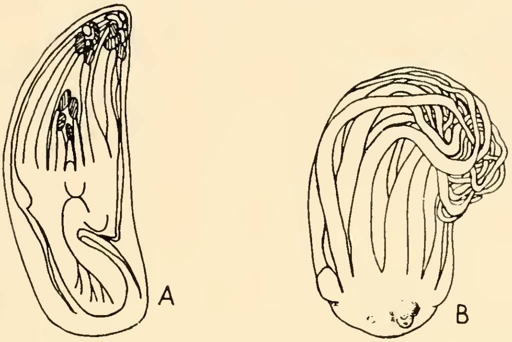

FIG. 1458.—*Cryptocoryne ciliata.* A, Section of an immature seed. The swollen cotyledon, below, fills the embryo sac. The plumule is already fully developed. B, Older embryo detached from the cotyledon, the scar of which lies beside the rudiment of the first root. (*After Goebel.*)

The unique morphological nature of the hypocotyl, in which stem and root appear to meet and mingle, has long made it an object of interest. After Naegeli pointed out, in 1858, the characteristic difference in the arrangement of the vascular tissues in the stem and in the root, the interest began to centre upon what was regarded as a kind of puzzle, namely how the two systems were joined up. The nature of the change and the **transition level** at which it occurred were sought and Van Tieghem in 1871 essayed to give precision to the study by defining three types of transitional change. His descriptions treat the bundles topographically from below upwards, the root structure being viewed as transforming itself into that of the stem.

Type 1. The phloem bundles of the root run straight up into the hypocotyl. The xylem bundles at the transition level increase in size and divide radially. The halves diverge to right and left respectively and turn through 180° C. so that their exterior point (the protoxylem) is now directed inwards. Each half attaches itself to one of the phloem bundles to form a duplex, collateral bundle. There are thus in the hypocotyl as many bundles as there were phloem bundles in the root.

Type 2. The phloem bundles divide, like the xylem bundles, and the halves separate and place themselves facing the halves of the xylem bundles. There are thus twice as many bundles in the hypocotyl as there are phloems in the root and the medullary rays are narrower than in Type 1.

Type 3. Both xylem and phloem bundles divide, but the xylem bundles remain in place, turning round, as before, and it is the phloem halves which move across to unite with the xylem halves.

Normally the transition level lies at the *collet* and the change is passed through in a short vertical distance, but intercalary growth either above or below may cause an apparent displacement either up or down from this level, though the external *collet* does not move.

Actual sections of seedlings often show inconsistencies with Van Tieghem's simple, one might say geometrical, schemes. One outstanding discrepancy is that as the xylem halves separate there is often seen a median protoxylem group which is not attached to either of them. Van Tieghem evidently thought of the hypocotyl above the transition level as equivalent to an epicotyledonary internode, but things are not quite so simple. Before the epicotyl is reached, the cotyledonary node is passed through and the cotyledonary traces are of a special type, which has a marked effect on the vascular structure from which the traces come. So concerned have been the later workers with the cotyledonary traces that one might imagine the epicotyl to be non-vascular for all they say about it. Miss Thomas laid stress on the fact that the cotyledonary midrib is either V-shaped in section or composed of two divergent halves, in either case with a common protoxylem between them in the endarch position. It is really a triad rather than a dyad structure, for this protoxylem is the independent protoxylem which we saw between the xylem halves at the transition level. As the node is approached from below, two of the phloem-xylem bundles in the hypocotyl come together and unite to the intermediate protoxylem to form the midrib of the cotyledon. There are also lateral bundles in the cotyledon and these also may sometimes originate well down the hypocotyledonary stele.

Chauveaud performed a service by pointing out, in this connection, that it is not actually the vascular bundles which "move" or "turn", an impossible feat, but the positions in which differentiation is taking place. Instead of vessels or sieve tubes continuing upwards in a vertical line, the locus of differentiation moves by degrees in one direction or another so that the succeeding elements are displaced relative to the earlier ones, thus bringing about the appearance of bundle movement. He considers the change from alternate vascular tissues to the superposed arrangement to be a repetition of a phylogenetic change. The root shows the primitive arrangement, which changes to the later disposition at higher levels, the earlier stages being then omitted, so that in the epicotyl only the superposed arrangement is produced.

We would like to close by pointing out that the discussion of seedling anatomy well illustrates the value of de Candolle's principle, that the structure of every organ should be interpreted as emerging from the organ which bears it and never as entering into that organ. How many confusions might have been avoided had this always been done!

CHAPTER XXVII

THE FAMILIES OF THE ANGIOSPERMAE

INTRODUCTION

The Angiospermae of today are represented by plants showing the greatest possible diversity of form. They occur wherever life is possible between the equator and the poles, on land, in water and even in the sea. Many occur as epiphytes and some as parasites. They range in size from minute floating forms such as *Wolffia arrhiza*, to giant trees such as the *Eucalyptus* of Australia. Many are dispersed over entire continents while others are restricted to local areas or to small islands, and explorers have shown that even small differences of habitat may be sufficient to cause one species to be replaced by another.

Since the delimitation of species is often a matter of opinion, the total number of species of Angiosperms cannot be accurately estimated but a conservative reckoning would place it between 100,000 and 150,000.

Out of this vast assemblage we shall select a few families for detailed study, choosing those which are most characteristic of the British Flora. Since however to study the British Flora alone would give a very imperfect impression of the Angiosperms as a whole, we shall briefly refer to a wider range of families under their respective orders and mention some of their more interesting features.

It must be borne in mind that in the study of flowering plants the subject should be considered as a whole and that the systematic treatment of the group cannot be entirely divorced from the wider aspects of ecology, bionomics, geographical distribution and economic importance. In addition, the activities of the horticulturist in breeding, crossing and selection have materially altered the appearance of many plants. The wild Asparagus found on the rocky coast of our western seaboard, for example, bears little resemblance to the succulent shoots which are sold in the greengrocer's shop.

The Angiospermae are divided into two series: Dicotyledones and Monocotyledones, each of which is further subdivided into Orders and Families. The following classification indicates the system of treatment which will be followed in this book. A comparison of this system with that adopted by various authorities will show certain differences. It would clearly have been simple to follow any one of the accepted treatments, but unfortunately they all differ markedly from one another, and all are open to criticism in some respects.

In general it may be said that while the present sequence of treatment is intended to indicate a phylogeny from the more primitive to the more advanced, there has been a definite attempt to keep families together in large orders rather than to split them into many smaller ones. In this way considerable space has been saved and the classification becomes easier for students' use. At the same time Bentham's group of Apetalae has been rejected in favour of the more modern view that the apetalous families are reduced derivatives from various other families. We have however retained the Ranales in their traditionally primitive position, in opposition to Engler's treatment of them, and have placed the Monocotyledones after the Dicotyledones. This is in conformity with Hutchinson's recent view. The present treatment however differs from his in that we do not separate the orders into two lines, namely those predominantly herbaceous, starting with the Ranales, and those predominantly woody, beginning with the Magnoliales, nor do we follow him entirely in his separation of many smaller orders.

It is obvious that in a linear series it is impossible to indicate a true phylogeny and the horizontal lines across the following list of Orders and Families are intended only to indicate boundaries between different cycles of affinity. The order following such a line may be regarded as being an offshoot from one of the orders, but not necessarily from the last, of a previous block.

Despite this method of treatment the families of the Angiospermae occupy a considerable section of this volume, which may be taken to indicate their great importance in the study of Botany. For convenience the two groups of the Dicotyledones, *i.e.*, Archichlamydeae and Metachlamydeae, and the Monocotyledones will be treated in separate chapters.

OUTLINE CLASSIFICATION OF THE ANGIOSPERMAE

I. DICOTYLEDONES

A. ARCHICHLAMYDEAE

1. **Ranales***	**Ranunculaceae,** Nymphaeaceae, Berberidaceae, Magnoliaceae, Annonaceae, Myristicaceae, Lauraceae, Calycanthaceae, Ceratophyllaceae.
2. **Rhoeadales**	Capparidaceae, **Papaveraceae,** Resedaceae, **Cruciferae.**
3. **Rosales**	Pittosporaceae, Hamamelidaceae, Platanaceae, **Rosaceae.**
4. **Saxifragales**	Crassulaceae, Cephalotaceae, **Saxifragaceae,** Podostemaceae.
5. **Leguminosae**	Caesalpiniaceae, Mimosaceae, **Papilionaceae.**

6. **Parietales**	Cistaceae, Bixaceae, Tamaricaceae, **Violaceae,** Passifloraceae, Caricaceae.
7. *Cucurbitales*	Cucurbitaceae, Begoniaceae.
8. *Guttiferales*	Theaceae, Guttiferae, Dipterocarpaceae.
9. *Cactales*	Cactaceae.

* Those Orders and Families printed in heavy type are considered in detail: the others are treated more superficially.

10.	**Aristolochiales**	Aristolochiaceae, Rafflesiaceae, Hydnoraceae.
11.	**Sarraceniales**	Sarraceniaceae, Nepenthaceae, Droseraceae.

12.	**Centrospermae**	Amarantaceae, Phytolaccaceae, Portulacaceae, **Chenopodiaceae**, Aizoaceae, Nyctaginaceae, **Caryophyllaceae**.
13.	**Proteales**	Proteaceae.
14.	**Polygonales**	Polygonaceae.
15.	*Piperales*	Piperaceae.
16.	**Urticales**	Ulmaceae, Urticaceae, Moraceae, Cannabinaceae, Eucommiaceae.

17.	**Salicales**	**Salicaceae**.
18.	*Garryales*	Garryaceae.
19.	*Myricales*	Myricaceae.
20.	**Fagales**	Fagaceae, **Betulaceae**.
21.	*Casuarinales*	Casuarinaceae.

22.	**Myrtiflorae**	Thymelaeaceae, Lythraceae, Punicaceae, Halorrhagidaceae, **Onagraceae**, Callitrichaceae, Lecythidaceae, Rhizophoraceae, Combretaceae, Myrtaceae, Melastomaceae.
23.	**Malvales**	Tiliaceae, Bombacaceae, Sterculiaceae, **Malvaceae**.
24.	**Sapindales**	Anacardiaceae, Sapindaceae, Aceraceae, Hippocastanaceae, Celastraceae, Aquifoliaceae, Staphyleaceae, Empetraceae.
25.	*Santalales*	Loranthaceae, Santalaceae, Balanophoraceae.
26.	*Rhamnales*	Rhamnaceae, Vitaceae.
27.	**Geraniales**	Linaceae, Oxalidaceae, Tropaeolaceae, **Geraniaceae**, Balsaminaceae, Erythroxylaceae, Malpighiaceae, Zygophyllaceae.
28.	*Rutales*	Rutaceae, Meliaceae.
29.	**Euphorbiales**	**Euphorbiaceae**.
30.	*Juglandales*	Juglandaceae.
31.	**Umbelliflorae**	Araliaceae, Cornaceae, **Umbelliferae**.

B. **METACHLAMYDEAE**

1.	**Ericales**	Pyrolaceae, **Ericaceae**, Epacridaceae.
2.	**Ebenales**	Sapotaceae, Ebenaceae, Styracaceae, Symplocaceae.
3.	**Primulales**	**Primulaceae**.
4.	**Oleales**	**Oleaceae**, Loganiaceae, Gentianaceae, Apocynaceae, Asclepiadaceae.
5.	*Plantaginales*	Plantaginaceae.
6.	*Campanulales*	Campanulaceae.

7. **Boraginales**	Boraginaceae.
8. *Plumbaginales*	Plumbaginaceae.
9. **Solanales**	**Solanaceae**, Convolvulaceae.
10. **Personales**	**Scrophulariaceae**, Orobanchaceae, Lentibulariaceae, Gesneriaceae, Bignoniaceae, Acanthaceae.
11. **Lamiales**	Verbenaceae, **Labiatae**.
12. **Rubiales**	Rubiaceae, Caprifoliaceae.
13. **Asterales**	Adoxaceae, Valerianaceae, Dipsacaceae, **Compositae**.

II. MONOCOTYLEDONES

1. **Helobiae**	Butomaceae, Naiadaceae, Potamogetonaceae, Aponogetonaceae, Hydrocharitaceae, **Alismaceae**.
2. **Farinosae**	Commelinaceae, Eriocaulonaceae, Bromeliaceae.
3. *Zingiberales*	Musaceae, Zingiberaceae, Cannaceae, Marantaceae.
4. **Liliales**	**Liliaceae**, Trilliaceae, Pontederiaceae, Smilaceae, Ruscaceae.
5. **Alstroemeriales**	Alstroemeriaceae, Philesiaceae.
6. **Arales**	**Araceae**, Lemnaceae.
7. **Typhales**	Typhaceae, Sparganiaceae.
8. **Amaryllidales**	**Amaryllidaceae**.
9. **Iridales**	**Iridaceae**.
10. **Dioscoreales**	Dioscoreaceae.
11. **Agavales**	Agavaceae.
12. **Palmales**	**Palmaceae**.
13. **Pandanales**	Pandanaceae.
14. **Glumiflorae**	Juncaceae, Cyperaceae, **Gramineae**.
15. **Microspermae**	Burmanniaceae, **Orchidaceae**.

CHAPTER XXVIII

THE DICOTYLEDONES: ARCHICHLAMYDEAE

DICOTYLEDONES

The Dicotyledones are Angiospermae in which the embryo on germination possesses two cotyledons. These may be retained within the seed coat at germination (**hypogeal**), or they may grow out and become green (**epigeal**). The primary root of the seedling generally persists and becomes the main root of a branched root system in the mature plant. The leaves are normally petiolate and net-veined. The flowers may be either pentamerous, tetramerous or dimerous, but are rarely trimerous. They may be polypetalous, gamopetalous or apetalous. The carpels may be free or united. The vascular bundles of the stem are generally arranged in a ring, around a pith. A cambium is normally present, which frequently builds up a woody stem.

The Dicotyledones are a larger group than the Monocotyledones, with about 90,000 species. They may be trees, shrubs or herbs and they include the more primitive groups of the Angiosperms. Many are of great economic importance, for they supply, among many other materials, all the hardwoods of commerce, most of the fruits and vegetables, as well as many of the spices and Materia Medica. We shall consider this aspect more fully in Volume IV.

The Dicotyledones are divided into two classes: the Archichlamydeae and the Metachlamydeae.

ARCHICHLAMYDEAE

The Archichlamydeae are Dicotyledones in which the perianth may be formed of sepals only, but if petals are present they are seldom united. A perianth may be sometimes completely absent. In the primitive families, the floral parts may be spirally arranged, wholly or in part, and the carpels may be free.

The Archichlamydeae as here defined include both the Benthamian groups of the Polypetalae with free petals and the Monochlamydeae with a simple perianth, but it must be borne in mind that in thus separating off from the group those families in which gamopetaly is characteristic it is not suggested that gamopetaly is entirely absent in the Archichlamydeae. It is an attempt rather to indicate a general tendency. In fact we must recognize that in the evolution of the Dicotyledons both divergence and convergence have played a part, and it would be unwise to assume that all the genera at present included in a family are necessarily monophyletic, that is to say in one line of descent. Two evolutionary series may have converged along similar lines till they became associated in the same family, as is possibly the case in the Rosaceae.

RANALES

The Ranales are Archichlamydeae in which the number of the floral parts is generally indefinite and the carpels are free and either superior or rarely immersed in the receptacle. The embryo is minute and embedded in a fleshy endosperm. The flowers are usually hypogynous or rarely perigynous, hermaphrodite, and with the parts arranged spirally, cyclically or spiro-cyclically.

The leaves are often large, are usually arranged alternately, rarely opposite, and very rarely possess stipules. The vascular bundles in the stem are sometimes scattered, as in Monocotyledons.

The systematic position of the Ranales has been a subject of much controversy. That they are relatively primitive is generally accepted but whether they are to be considered as the most primitive group of the Dicotyledons depends upon the attitude adopted regarding the systematic position of those Monochlamydeae which are devoid of petals and whose flowers are pollinated by wind. This latter group was considered by Bentham and Hooker to be a reduced series derived from more elaborate ancestral types. On the other hand Engler and Prantl placed them first, as the most primitive Dicotyledons, on a supposed similarity between their floral structure and that of the Gymnosperms.

In the arrangement adopted here the Ranales are represented as the most primitive group. This is supported by the free carpels, the indefinite number of the floral parts and the fact that they may be spirally inserted on the receptacle. It has been decided however not to follow Hutchinson who splits the order into two distinct parts, retaining the Ranales for the herbaceous types and making a new order, the Magnoliales, for the arborescent forms.

The Ranales as treated here include a number of important and well-known families of which we may mention the following: Nymphaeaceae, Ranunculaceae, Berberidaceae, Magnoliaceae, Annonaceae, Myristicaceae, Lauraceae, Calycanthaceae and Ceratophyllaceae. Of these we shall consider only the Ranunculaceae in detail (page 1619). The order as a whole is well represented as fossils in Tertiary Rocks and appears to have been very widely distributed at an early period.

The **Nymphaeaceae,** or Water Lily Family, include a number of aquatic herbaceous plants which are widely distributed in tropical and north temperate regions, and many are cultivated in this country. The family includes eight genera and about sixty species. In *Nymphaea* the flowers are variously interpreted but most authors consider that the four outermost segments represent a calyx. There are four outer and four inner petals, within which are eight series of spirally arranged segments, which show a gradual transition from petals to stamens. These segments and the very numerous stamens are inserted on the side of the gynoecium, which has from ten to twenty loculi, each containing many ovules scattered over the carpellary surface. The fruit ripens under water and there dehisces and the seeds float to the surface where they separate and float but later sink when decay of their arils liberates the entrapped air. There is a large perisperm around the endosperm except in *Nelumbium* where both are absent. The yellow Water Lily, *Nuphar*, has smaller flowers, which smell of brandy. The gynoecium is not enclosed by the receptacle and forms a globular fruit which bursts to release the seeds. (*Nelumbium* fruit, see p. 1139.)

The Victoria Water Lily (*Victoria regia*) (see Vol. I, Fig. 942) is a native of Brazil and Guiana. Its floating leaves may measure as much as 6 ft. across, and are sufficiently buoyant to support the weight of a child. In spite of its great size the plant is cultivated as an annual. The Egyptian Lotus (*Nelumbium speciosum*) (Fig. 1459) was regarded by the early Egyptians as sacred to Isis and is still venerated in many parts of the East (Fig. 1460). Many species of the genus *Nymphaea* (Figs. 1461 and 1462) are grown in ponds and are extremely beautiful. As a result of hybridization white, pink, yellow and red-flowered forms have been produced. *N. lotus*, *N. zanzibarensis* and others with blue flowers can only be grown in this country in heated tanks. *Nymphaea alba* and *Nuphar lutea* occur wild in Britain.

FIG. 1459.—*Nelumbium speciosum*. (*After Baillon.*)

The family is divided into two sub-families, Cabomboideae and Nymphaeoideae. To the former belongs the genus *Cabomba* with six species occurring in the warmer parts of America. The submerged leaves

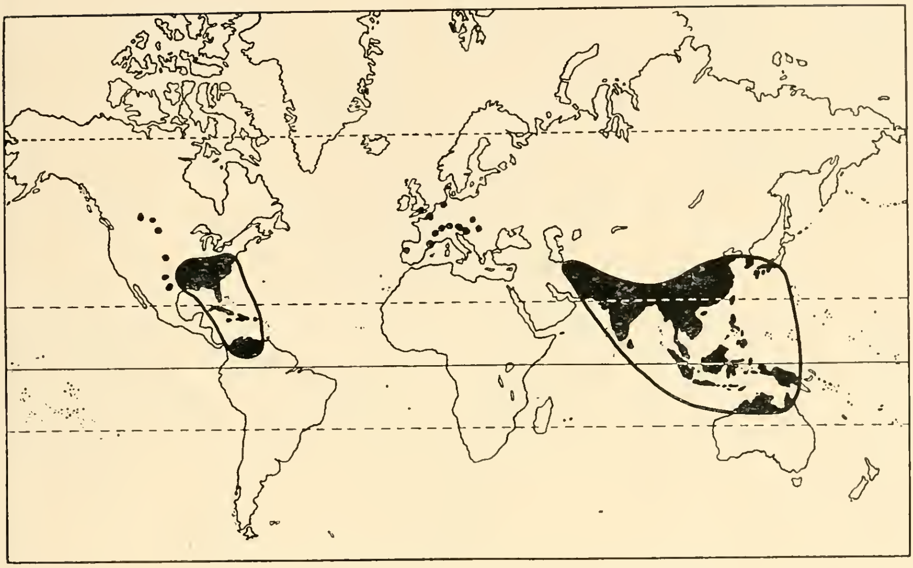

FIG. 1460.—*Nelumbium.* Geographical distribution.

FIG. 1461.—*Nymphaea alba.* White Water Lily.

FIG. 1462.—*Nymphaea alba.* Flower in vertical section. (*After Caspary* in *Engler-Prantl.*)

(Fig. 1463) are dissected but the floating leaves are circular, the latter being produced only at the flowering season. In the latter sub-family there are no submerged leaves for all grow up to the surface during the growing period and all are entire. It is to this sub-family that all the Water Lilies belong.

The **Berberidaceae,** or Barberry Family, comprise a small number of genera most of which are deciduous shrubs. There are about 200 species in north temperate regions. They are either shrubs or perennial herbs. The flowers are hermaphrodite and are produced in racemes. The perianth may consist of four whorls of three segments each, which are followed by two whorls each of three stamens. The anthers are introrse and open by two valves. There is a single carpel with one or numerous ovules. The fruit is a berry. The chief genus is *Berberis*, with 190 species, of which *B. vulgaris* (Barberry) is wild in Britain. The pollination mechanism is unusual and worthy of special reference. The inner surface of the base of each stamen is sensitive to contact and the stamens at rest stand out, away from the ovary. Nectar is secreted at the base of the two inner whorls of perianth segments. An insect searching for this nectar, on touching the stamens causes them to spring inwards, violently shaking their pollen on to its head. In this position the pollen will come into contact with the stigma when the next flower is visited. Many species are cultivated on account of their bright yellow flowers and red berries. Some are evergreen such as *B. aquifolium*, with pinnate leaves, now often separated in the genus *Mahonia* (Fig. 1464), others are deciduous and provided with leaf spines which represent the

Fig. 1463.—*Cabomba aquatica.* A, Habit, with peltate floating leaves and dissected submerged leaves. B, Floral diagram. C, Fruits. (*After Baillon.*)

Fig. 1464.—*Berberis* (*Mahonia*) *japonica.* Inflorescence.

Fig. 1465.—*Epimedium alpinum.* Raceme of flowers.

leaves on the long shoots. They are often trifid and in their axils arise short shoots bearing normal leaves.

The common Barberry was largely exterminated in Britain during the eighteenth century, following the discovery that it was the alternate host of the Stem Rust of Wheat, *Puccinia graminis*, and the extermination of the host plant is now being strenuously attempted in the Wheat Belt of North America.

The genus *Epimedium* (Fig. 1465) with dimerous flowers, also has an interesting pollination mechanism. The flowers are protogynous and the nectar is concealed. The anthers dehisce by valves (Fig. 1466) which come together above the already mature stigma. They cannot, however, pollinate it because, at this stage, the flowers, which are borne in a raceme, are pendulous. Nectar is secreted in four shoe-shaped nectaries, together

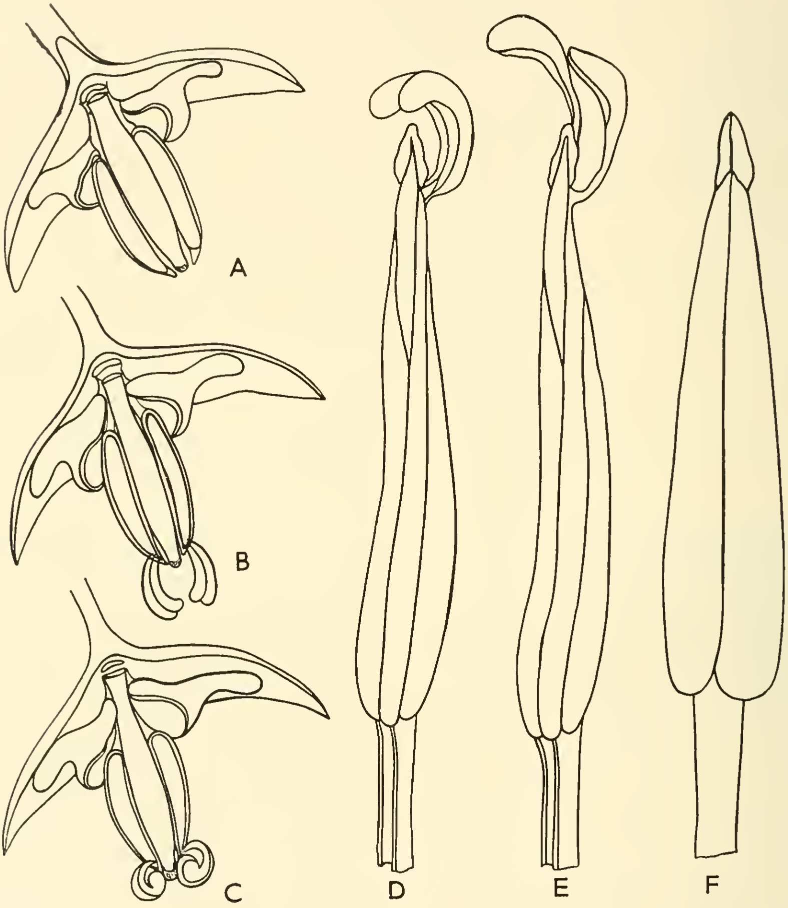

Fig. 1466.—*Epimedium*, pollination. A – C. Longitudinal sections of the flower showing the nectaries and the valvate dehiscence of the anthers. D – F. Dehiscence of a single anther, enlarged. (Stages from right to left.)

making up a corona, which is yellow in colour. Bees searching for the nectar come into contact with the stigma first, since it projects; meanwhile, during the sucking of the nectar, the lower surface of the insect is dusted with pollen. Species of *Epimedium* flower early in the year when insect visits are infrequent but self-pollination is possible if cross-pollination fails because, as the flowers mature, they become erect and in this position pollen may fall directly on the stigma. Automatic self-pollination may also occur by the elongation of the style, so that the stigmatic surface comes into direct contact with the anthers.

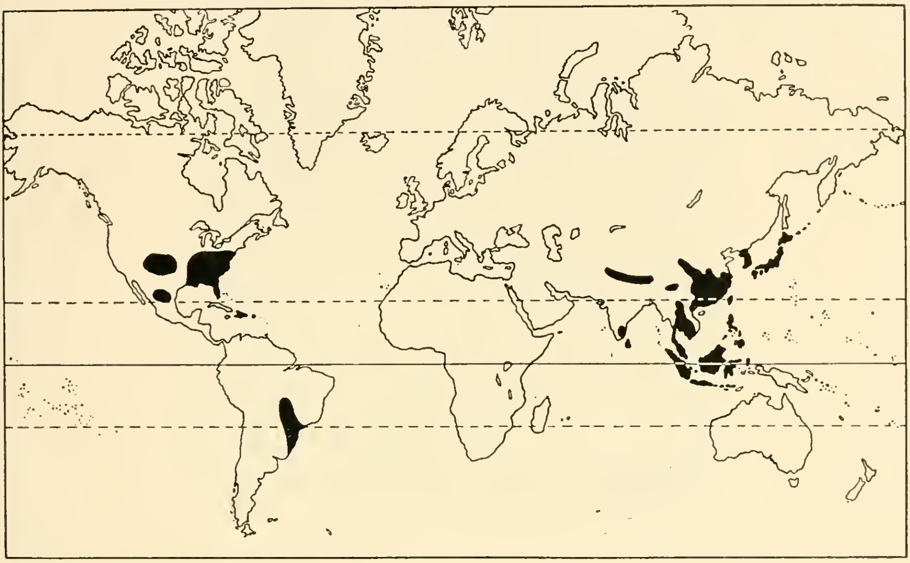

FIG. 1467.—Geographical distribution of the genus *Magnolia*.

The **Magnoliaceae** are a family of considerable interest not only from a horticultural standpoint but also because of the primitive features displayed by many of the species. Hutchinson considers that the Magnoliaceae may represent the ancestal type of Angiosperm, thereby reviving the earlier suggestions of Hallier, while Arber and others have suggested a relationship between the Bennettitales and the Magnoliaceae.

There are nine genera and about seventy species which are distributed mainly in tropical and subtropical parts of the northern hemisphere (Fig. 1467). The plants are mostly trees or shrubs, though a few are climbers. Anatomically the wood shows a number of primitive characters and in some genera, *e.g.* *Drimys*, can be compared with that of the Gymnospermae. (See Vol. I p. 904.) Oil passages occur in the parenchyma. In the genus *Magnolia* large stipules are developed which form a covering over each of the young leaves and are shed as the leaves expand. The flowers are terminal or axillary, usually solitary and often of large size. In *Magnolia* the perianth is cyclic, though it is spiral in the other genera. The androecium and gynoecium are spiral in all genera. The number of stamens is large and the carpels are numerous. The fruit is a follicle, a berry or a samara. In *Magnolia* the individual seeds hang suspended by the unrolled spiral vessels of the funicle when the follicle splits open. These seeds have bright red or orange testas and are therefore highly decorative.

The more important genera besides *Magnolia* are *Drimys*, *Liriodendron*, *Illicium*, *Schizandra* and *Kadsura*. The genus *Magnolia* is important mainly on account of its horticultural value. There are some sixty species, which are found in two areas, the one in tropical North America and the other in south-eastern Asia and Japan. They are mostly trees with large white or pink flowers (Fig. 1468) which fall into two groups, those in which the number of perianth segments is large, giving a smaller star-like flower about 3 inches across, and those in which the number of petals is few but the flowers are very large, up to 12 inches or more in diameter. Many species flower early in the spring before the foliage and are therefore of great decorative value. A large number of hybrids are known, the identity of which is a matter of doubt, and the recognition of the species is a matter of great difficulty. The perianth is cyclic in two whorls of three. The number of perianth segments in other genera varies but is usually four or five. The stamens and carpels are very numerous and always spirally arranged on an elongated central axis. *M. acuminata*, the Cucumber Tree, so called because the green fruits resemble a cucumber, is used for timber especially in the United States. Some like *M. grandiflora* are evergreens and are often cultivated in this country as wall shrubs. Others, such as *M. denudata*, are deciduous and are often grown as specimen trees. Many of the species however have not yet been introduced into cultivation owing to the very short period during which the seeds remain viable.


FIG. 1468.—*Magnolia lennei* (hybrid). Flower.

The genus *Liriodendron* contains the single species *L. tulipifera*, the Tulip Tree, which is often cultivated in parks. It is a native of North

America where the trees often reach a large size. The flowers are greenish-yellow in colour (Fig. 1469) and the fruit is an etaerio of samaras not unlike a pine-cone in appearance. The timber is sold commercially under the name of canary whitewood.

FIG. 1469.—*Liriodendron tulipifera.* Tulip Tree. Flower.

The genera *Drimys* and *Illicium* are now separated by Hutchinson in the family Winteraceae. The former genus contains twenty species which are widely distributed in South America and in Borneo southwards to New Zealand. *D. winteri* is often grown as a decorative shrub on account of its clusters of white flowers. The bark is used medicinally. *Illicium* contains the same number of species but is restricted to the Atlantic coastal zone of North America and to south-eastern China: *I. verum*, which grows in China, is the source of star anise. Commercial star anise is the fruit and is used medicinally and in liqueurs. The separation of these genera from the Magnoliaceae is based mainly upon the gradual transition from sepaloid to petaloid structures exhibited by the perianth in *Illicium* and the distinct sepals and petals found in *Drimys*.

The two genera *Schizandra* and *Kadsura* are climbers. In the former genus seven species are recognized in the warmer parts of North America and Asia, while in the latter there are eight species restricted to China and Japan. In *Kadsura* the flowers are unisexual. This genus is also distinctive in having no stipules. Finally we may mention the genus *Zygogynum*, with fused carpels, which contains only three species all restricted to New Caledonia.

The primitive nature of the Magnoliaceae is well shown by the spiral arrangement of the floral parts and in various anatomical features. The remarkable geographical distribution of the family, which at the present day is entirely absent from Europe, Africa and to a large extent Australasia, has been interpreted as evidence of the antiquity of the family. This is further supported by the evidence of leaves, attributed to *Magnolia* and *Liriodendron*, found in the Tertiary beds of both Europe and Greenland, which suggests that at one time the group was probably distributed all over the northern hemisphere, whence, as in the case of *Drimys*, it spread southwards.

The **Annonaceae** are essentially tropical in distribution. They are a large family with eighty genera and over 800 species, consisting of trees or shrubs, mostly occurring in the Old World. Oil passages are present in the stems. The flowers are regular and hermaphrodite, with three whorls of three perianth segments, the outer two being sepaloid. The stamens and carpels are numerous and spirally inserted, each of the latter containing numerous anatropous ovules. The endosperm of the seeds is bulky and is ruminate, that is to say it is penetrated by extensive folds of the inner testa. This condition is one of the distinguishing marks of the family. The fruit is either an aggregation of berries or a pseudocarp in which the receptacle as well is involved (Fig. 1470). The chief interest in the family lies in these fruits, which, though they contain large seeds, are in many cases sweet and succulent, and in consequence are largely cultivated in tropical countries. Among the better known of these we may mention the Cherimoya (*Annona cherimolia*), Custard or Sugar Apple (*A. squamosa*), Soursop (*A. muricata*), Bullock's Heart (*A. reticulata*), and Ilama (*A. diversifolia*). Recent analysis shows that these fruits contain about 18 per cent. of sugar.

FIG. 1470.—*Annona cherimolia*. Aggregate fruit. (By courtesy of the Florida Field Experimentation Station.)

The **Myristicaceae** are a small tropical family allied to the Annonaceae. They are mostly trees or woody shrubs with large, simple, entire leaves. The flowers are mostly dioecious. *Myristica fragrans* (Fig. 1471), a native of the Moluccas, is now widely cultivated since both the seed, the nutmeg, and the fleshy aril, mace, are used as spices.

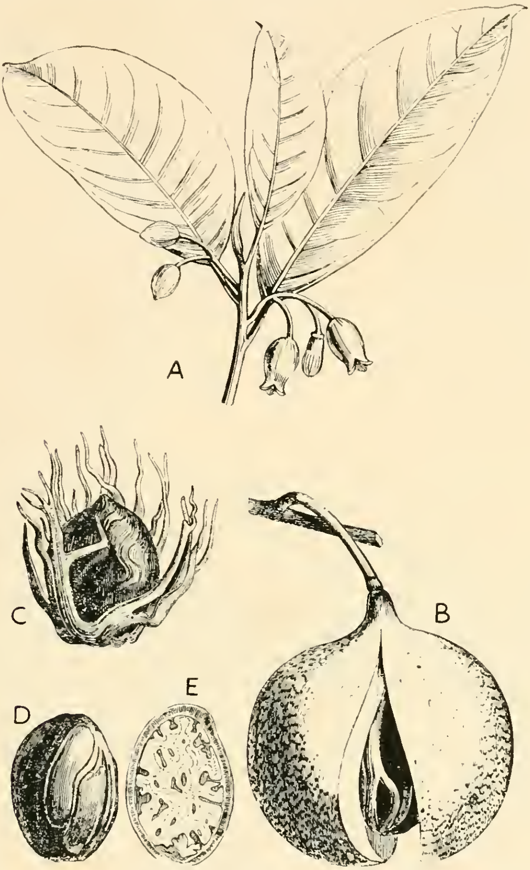

FIG. 1471.—*Myristica fragrans.* A, Flowers. B, Fruit dehiscing and exposing seed. C, Seed with aril. D, Seed externally. E, Seed in section showing ruminate endosperm. (B *after Baillon. The rest after Le Maout and Decaisne.*)

The **Lauraceae** include a large assemblage of some 1,000 species which are common as forest trees of both tropical and subtropical Asia, Africa and America. There are apparently two main centres of distribution, the one in south-eastern Asia whence the family ranges westwards through Africa to the Canary Islands and also to south China and Japan and southwards to Australia, and a second in Brazil whence a few species extend into North America as far as Canada. The only European species is the Bay, or true Laurel (*Laurus nobilis*), whose leaves are used in flavouring. In ancient times wreaths of Laurel were used to crown victors and the statues of the gods, hence the name Laurel from the Latin *laus*—praise.

A number of other species possess economic and medicinal properties, chiefly on account of the volatile oils which are contained in parenchymatous oil glands. Among the more important of these we may mention *Cinnamomum zeylanicum* and *C. camphora* which yield cinnamon and camphor respectively. *Persea gratissima* is widely cultivated as a tropical fruit under the name of the Alligator or Avocado Pear. It is a native of tropical America Many of the trees yield valuable timber; for example the Greenheart wood of Demerara is produced by *Nectandra rodiaei*, while *Sassafras officinale* yields a scented wood used in the preparation of a medicinal oil.

The **Calycanthaceae** are a small family with two genera, *Calycanthus* and *Chimonanthus*. The former includes three very widely distributed species which are shrubs with opposite simple leaves and terminal acyclic flowers. The perianth is composed of an indefinite number of spirally arranged segments showing a gradual transition from sepals to petals. There are from five to thirty stamens and an indefinite number of free carpels enclosed in the hollow axis of the receptacle (Fig. 1472). Each carpel encloses two anatropous ovules. *Calycanthus floridus* (Carolina Allspice) is a commonly cultivated shrub. *Chimonanthus fragrans* (Winter Sweet) is also a cultivated garden shrub whose flowers appear in early spring (Fig. 1473).

FIG. 1472.—*Calycanthus floridus.* Hollow receptacular fruit.

FIG. 1473.—*Chimonanthus fragrans.* Flowers on a leafless branch in early spring.

The **Ceratophyllaceae** have only one genus, *Ceratophyllum*, with three species, of which two, *C. demersum* and *C. submersum* (Hornwort), are found in Britain. They are rootless water plants with submerged leaves (Fig. 1224), which are propagated vegetatively by fragmentation following the decay of the older parts of the parent plant. The flowers (Fig. 1474) are monoecious, the anthers breaking off and floating up through the water, liberating the pollen, which has the same specific gravity as the water. The perianth segments and stamens are numerous but the female flowers have only one carpel. The leaves are borne in whorls and are much divided. They are obviously highly specialized plants whose systematic position is uncertain. Eichler placed them in the Urticales.

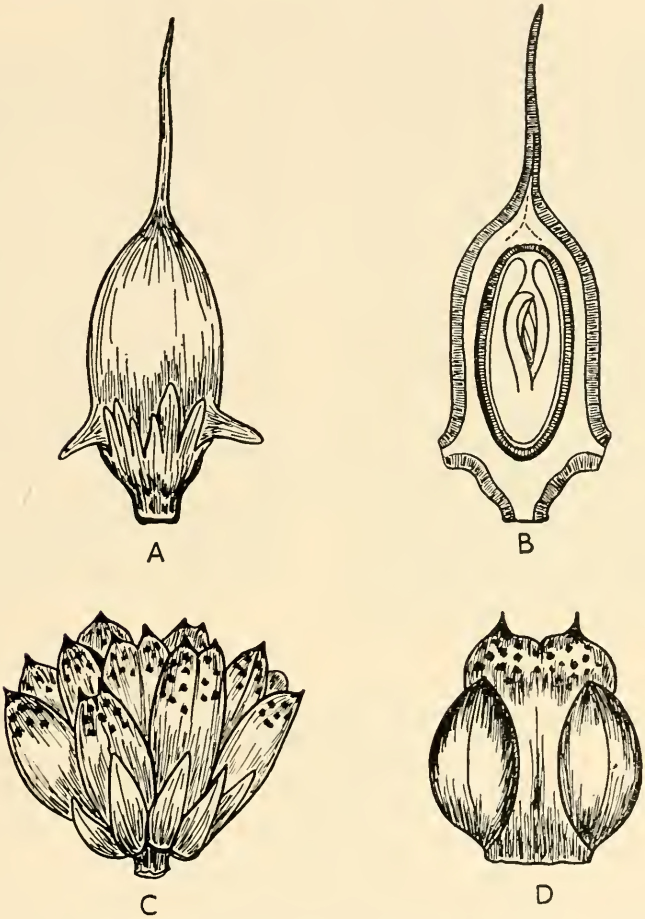

FIG. 1474.—*Ceratophyllum demersum.* A, Female flower with mature gynoecium. B, Section of fruit with embryo in seed. C, Male flower. D, Single stamen. (*After Le Maout and Decaisne.*)

Ranunculaceae

The family includes many common British plants, among which are *Ranunculus* (Buttercup), *Caltha* (Marsh Marigold) (Fig. 1475), *Clematis* (Traveller's Joy), *Helleborus* (Christmas Rose), *Anemone* (*e.g.*, Wood

Anemone), *Thalictrum* (Meadow Rue), *Paeonia* (Peony), *Trollius* (Globe Flower), *Adonis* (Pheasant's Eye), *Aquilegia* (Columbine), *Delphinium* (Larkspur), and *Aconitum* (Monkshood).

FIG. 1475.—*Caltha palustris.* Flowering shoot and a single flower in face view.

The plants, with the exception of the genus *Clematis*, are herbaceous with alternate or radical leaves. The plants generally perennate by sympodial rhizomes, the primary root being lost and replaced by adventitious roots, the latter often becoming tuberous, *e.g.*, *Aconitum* and *Ranunculus ficaria* (Fig. 1476) (Lesser Celandine). A few species are annuals.

The **flowers** are often solitary and terminal (*e.g.*, *Anemone*) (Fig. 1477) but where an inflorescence is produced it is in most cases cymose. Racemose inflorescences are seen in *Aconitum* and *Delphinium*. The flower is hermaphrodite, the parts being wholly or partly spiral in arrangement (Fig. 1478). The symmetry is usually actinomorphic, or rarely zygomorphic as in *Aconitum* and *Delphinium*.

The **perianth** often shows no distinction of calyx and corolla, but is usually simple and petaloid, and is often associated with nectar-secreting structures of various forms, which are considered to be usually modified petals, though in some genera they are developed in association with sepals, stamens or carpels.

The **androecium** is hypogynous, the stamens being free and generally indefinite in number. The anthers are basifixed and extrorse, with two loculi.

The **gynoecium** is apocarpous. The carpels are usually numerous or more rarely reduced to one. The ovules are either numerous or reduced to one, anatropous, with either one or two integuments.

Fig. 1476.—*Ranunculus ficaria* (*Ficaria verna*). Flower in face view.

The **fruit** is usually either an etaerio of akenes or follicles, more rarely a berry. The akenes sometimes possess long persistent feathery styles which assist their distribution by wind (*e.g.*, *Clematis* and *Anemone*). The seeds of *Helleborus* are distributed by ants which are attracted by the

Fig. 1477.—*Anemone japonica.*—Flower in face view.

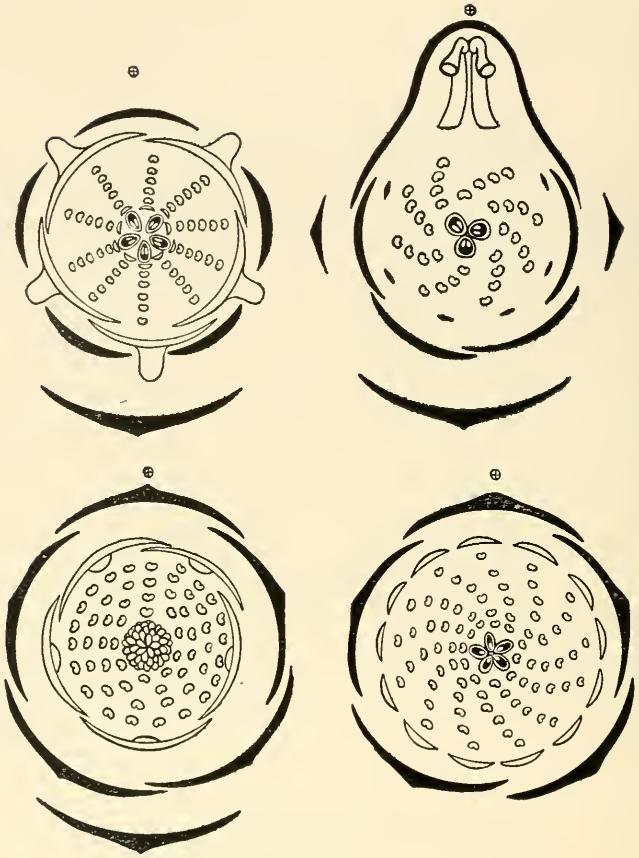

FIG. 1478.—Ranunculaceae. Floral diagrams. Top left, *Aquilegia*. Top right, *Aconitum*. Bottom left, *Ranunculus*. Bottom right, *Helleborus*. (*After Eichler*.)

oil-containing swellings on the raphe. The fruits of some species of *Ranunculus* are hooked and are distributed by animals and birds. The seed contains copious oily endosperm with a very small embryo, which only develops after dispersal in *R. ficaria* and *Eranthis*.

Pollination is effected either by insects or by wind. The flowers are usually protandrous, but those of *Thalictrum* and *Helleborus* are protogynous, while those of *Anemone* and *Trollius* are homogamous. *Thalictrum* is wind-pollinated but most of the other genera rely on insects for pollination.

The family contains forty genera and about 700 species, which are distributed in north temperate regions and are well represented in Britain. The plants are mostly terrestrial perennial herbs, but in *Paeonia* and *Clematis* they may be shrubby or in the latter genus scrambling climbers with clasping petioles. Tendrils are developed in *C. aphylla* in which the whole leaf becomes modified and carbon assimilation is limited to the stem cortex. Some species of *Ranunculus* are aquatic, in which case the leaves may be heterophyllous; finely dissected leaves being developed below the water. The petiole is usually broadened downwards into a sheath which may be elongated into a pair of lateral, stipular lobes.

The Ranunculaceae do not show any important anatomical peculiarities, except in a few species. In *Clematis* the stem anatomy, particularly in the climbing species, shows a separation of the secondary wood by wide medullary rays similar to those in *Aristolochia.* Several circles of vascular bundles occur in the stems of *Cimicifuga* and *Thalictrum* while medullary bundles occur in *Anemone japonica* giving it the appearance of a Monocotyledon. Hutchinson considers that there is a close relationship between this family and the Alismaceae.

The Ranunculaceae are classified as follows:

I. **Helleboroideae**

The ovules are numerous and the fruit is either a follicle, berry or capsule. The flowers are usually in racemes, or in cymes or solitary. Nectaries are present. *Helleborus*, *Nigella*, *Eranthis*, *Actaea*, *Caltha*, *Trollius*, *Aquilegia*, *Delphinium*, *Aconitum.*

II. **Paeonioideae**

The ovules are few in number and the fruit usually a follicle. The flowers are usually solitary and nectaries are absent. *Paeonia.*

III. **Anemonoideae**

There is a single ovule and the fruit is an achene. *Anemone*, *Clematis*, *Ranunculus*, *Thalictrum*, *Myosurus*, *Adonis.*

In the more primitive forms of the Helleboroideae, such as *Helleborus* (Fig. 1479) and *Caltha*, the perianth is spiral and is continued from the spiral arrangement of the foliage leaves. In *Nigella* the five perianth leaves are generally followed by eight well-developed nectaries and an eight-rowed superimposed androecium. The five to twelve carpels are often more or less united. The zygomorphic *Delphinium* and *Aconitum* are based upon a *Nigella*-like plan. The stamens and carpels are spirally arranged and show none of the zygomorphic character of the sepals and petals.

In *Helleborus foetidus* (Fig. 1480) the flowers are protogynous and insects are attracted by the large sepals. When the sepals first open they remain in a ring about 1 cm. across, through which the stigmas protrude. The nectar is concealed in tubular nectaries, derived from petals, developed between the stamens and the sepals, so that any large insect must brush against the stigmas in its entry into the flower. Later when the carpels have been fertilized the filaments of the stamens elongate in centripetal order until the extrorsely dehiscing anthers completely fill the flower, which opens to a diameter of about 2 cm. Insects now visiting the flower will be liberally dusted with pollen before they can reach the nectar. Damage to the flowers by rain is prevented by their pendulous position. The visitors are chiefly bees.

FIG. 1479.—*Helleborus niger.* Christmas Rose. Flower.

In *H. viridis* the pollination mechanism is similar but the flowers open more widely and the insects visiting the young flower, before the filaments have elongated, must hang on to the styles in order to suck the nectar.

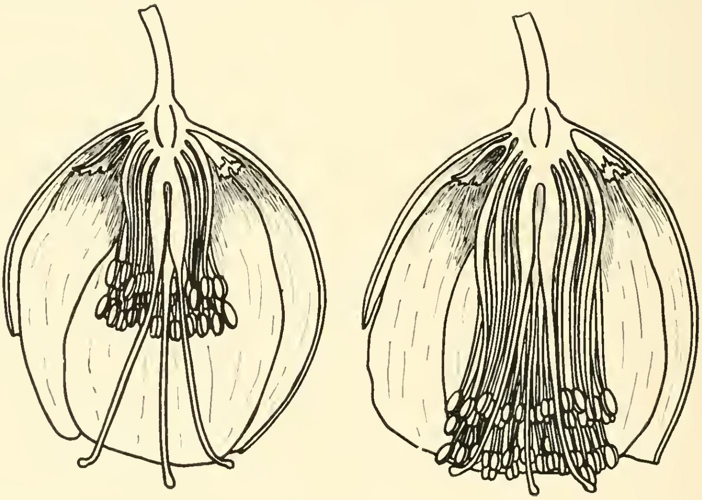

FIG. 1480.—*Helleborus foetidus.* Flower in vertical section showing the protogynous protrusion of the stigmas and the subsequent elongation of the stamens.

In *Aquilegia vulgaris* (Fig. 1481) the nectar is secreted at the base of the petal spurs. These spurs are funnel-shaped and readily accommodate the head of a humble bee. Since the flowers are pendulous, rain does not reach the nectar and the insect is forced to hang on to the spur with its fore-legs and to the stamens and carpels with its two hind pairs. In so doing, in young flowers, the lower surface of the abdomen comes into contact with the anthers, while in older flowers this same region touches the spreading stigmas which now project among the stamens. Should insect pollination fail, the styles grow downwards into the middle of the stamens and ultimately reach a lower level than the anthers.

FIG. 1481.—*Aquilegia vulgaris.* Flower in section showing the petaloid nectary spurs.

In *Delphinium elatum* (Fig. 1482) the flowers are protandrous, nectar being secreted at the base of one or of both spurs belonging to the two upper petals. It can only be reached by the long proboscis of the humble bee. The sepals serve to attract the insect. There are several bundles of

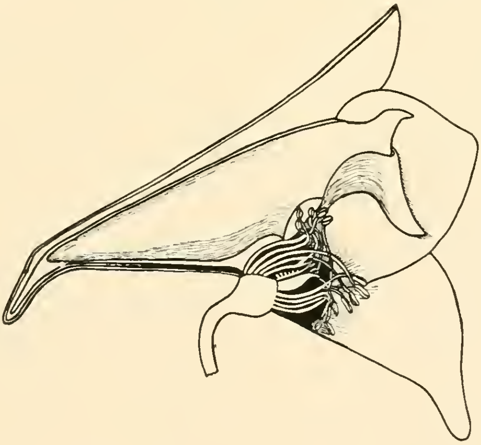

FIG. 1482.—*Delphinium elatum.* Flower in section showing empty anthers directed downwards.

erect, yellow hairs, which serve as nectar guides, on the front surfaces of the two lower petals. The stamens in the immature condition are directed downwards but become erect as their anthers dehisce, thus ensuring that the head of the bee will come into contact with them. After they have discharged their pollen they bend down again and make way for the styles, which now turn upwards, presenting newly matured stigmas to the head of a visiting insect.

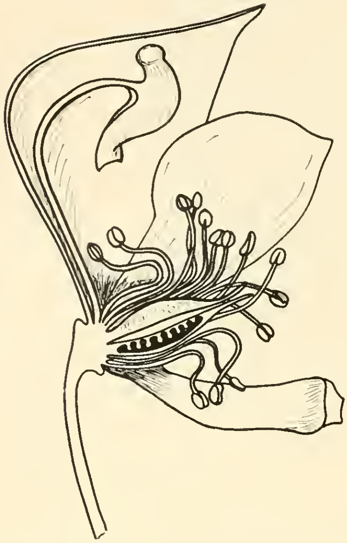

FIG. 1483.—*Aconitum napellus*. Flower in section showing one of the two petal nectaries under the hood formed by the posterior sepal.

In *Aconitum napellus* (Fig. 1483) the flowers are protandrous. The large sepals are brightly coloured and in conjunction with the smaller petals attract humble bees. The two upper petals are converted into long-stalked, hood-shaped nectaries which are covered by the upper sepal. It has been shown that each species of *Aconitum* has its own particular species of humble bee and moreover that the shape of the flower exactly fits a medium-sized female bee. So close is this relationship that species of *Aconitum* are entirely dependent for their survival on certain species of humble bee and it is interesting to note that the distribution of the plant genus closely follows that of its insect pollinator (Fig. 1484).

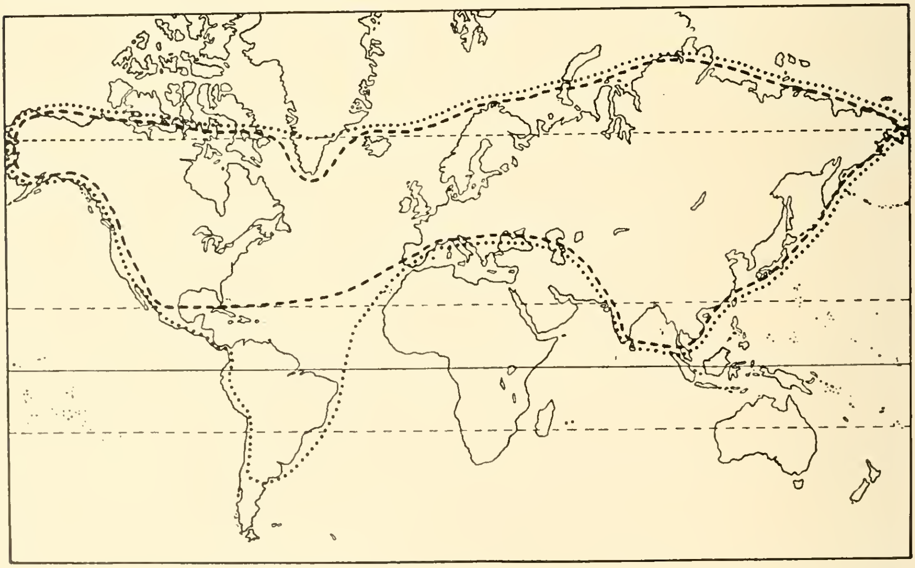

FIG. 1484.—Map of the distribution of the genera *Aconitum* and *Bombus*, plant and pollinator. Interrupted line, *Aconitum*; dotted line, *Bombus*. (*After Kronfeld, from Knuth.*)

In *A. napellus* the three smaller, lower sepals together with the lower petals serve as an alighting platform for the bee and at the same time form a protective investment for the stamens and carpels. The numerous stamens become erect as the anthers mature, so that pollen must be dusted on the lower surface of the insect. The stamens then wither and the carpels, now freed from their staminal investment, occupy the entrance to the flower and receive pollen from a visiting bee.

FIG. 1485.—*Paeonia delavayi.*

The genus *Paeonia* (Fig. 1485) comprises some fifteen species most of which are native to temperate Asia, Europe and the Mediterranean region. One species is found wild in California. They are mostly herbs or shrubs with divided leaves and very large, solitary, showy flowers. In the fleshy outer integument the ovule of *Paeonia* resembles the Berberidaceae. No nectar is secreted, but it has been recorded that *P. moutan* is visited by beetles which lick the base of the carpels. The flowers may be visited by insects for their pollen.

We may recognize several sections of the Anemonoideae. The first, comprising *Anemone*, consists of herbaceous, rarely shrubby plants usually with palmate leaves and with a whorl of three bracts forming an involucre for the flower. The flowers are usually solitary, with five, six or more perianth parts. True petals are absent and there are numerous stamens and carpels. There is a single pendulous ovule. In *A. pulsatilla* (Fig. 1486) the carpels are crowned with long hairy styles. Above the single fertile ovule there are a number of abortive ovules which indicate that the uniovulate

FIG. 1486.—*Anemone pulsatilla.*

FIG. 1487.—*Thalictrum flavum.* Meadow Rue. Inflorescences showing the numerous brightly coloured stamens.

condition in this section has been reached by reduction from a follicle. In the second section is the genus *Clematis*, which is separated from the other genera by the valvate aestivation of its four or more petaloid sepals. The plants are generally woody climbers with opposite, simple or compound leaves, sometimes with sensitive petioles which function as tendrils. The stamens and carpels are numerous. The third section includes the genera *Myosurus* and *Adonis*, in which the single ovule is pendulous, and *Ranunculus* in which it is erect. The flowers usually have five green sepals and five or more coloured petals, generally with a nectary at the base of each. The stamens and carpels are numerous and spirally arranged. They are mostly herbs of small size and some are annuals. Others are aquatic and some, like *Ranunculus repens*, form runners.

In the genus *Thalictrum* the plants have tripartite leaves and numerous small flowers borne in panicles or corymbs. The perianth consists of four or five small greenish segments which soon fall off leaving a mass of stamens which are often brightly coloured (Fig. 1487). The fruit is either an etaerio of akenes or may be reduced to a single akene. The genus is essentially a north temperate one, occurring widely in the north of Europe, Asia and America (Fig. 1488).

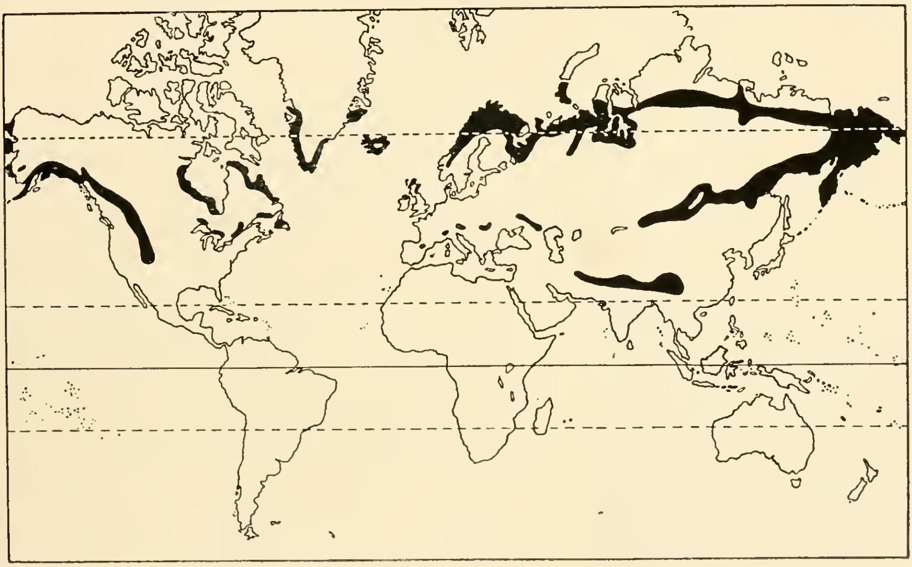

Fig. 1488.—Geographical distribution of *Thalictrum*. (*After Hutchinson*.)

In *Ranunculus* (Fig. 1489) the flowers are usually protandrous. Insects are attracted to the flowers by the yellow petals. At the base of each petal is a nectar pit formed by the prolongation of a membranous scale. On dehiscence the anthers are inclined towards the petals thus preventing pollen falling on the styles. Later the stamens fall off leaving the stigmas

FIG. 1489.—*Ranunculus acris.* Field Buttercup.

exposed. Only large, nectar-collecting insects come into contact with the stigmas, effecting both cross- and self-pollination with equal ease.

RHOEADALES

The Rhoeadales are Archichlamydeae in which the plants are mostly herbaceous, with scattered, entire or more or less divided alternate leaves without stipules. The flowers are cyclic, hypogynous or rarely perigynous and hermaphrodite, with free sepals, petals and stamens. They are usually actinomorphic, more rarely zygomorphic. The stamens may be definite or indefinite in number and are occasionally united into two bundles. The carpels are united into an ovary which may be one-chambered, with numerous ovules on parietal placentas, or the ovary may be bilocular as a result of the development of a septum between the placentas. This latter structure is termed a false septum because it is incomplete and is not produced as an ingrowth of the ventral edges of the carpels but is a new structure arising late in the development of the ovary. The stigmas instead of arising on the median plane of each carpel are often placed immediately above the placentas, when they are said to be commissural. The seeds are usually small, often curved, generally with a well-developed endosperm and small embryos.

The species are found mainly in north temperate regions. Included in this order are the Papaveraceae and Cruciferae which we shall consider in detail subsequently, and also the Capparidaceae and Resedaceae.

The **Capparidaceae**, which are separated by Hutchinson as a distinct order, are either herbaceous or woody plants mainly occurring in the tropics. The chief feature which separates them from the rest of the Rhoeadales is the absence, or at least very scanty development, of endosperm. A few are cultivated in gardens, while the flower buds of *Capparis spinosa*

Fig. 1490.—*Capparis spinosa.* (*After Baillon.*)

(Fig. 1490) provide capers. The plant is of Mediterranean origin. A remarkable feature of the Capparidaceae is the frequent development of a gynophore, a prolongation of the floral axis which carries the gynoecium upwards to a position above all the other parts of the flower, where it stands isolated on a long column.

The **Resedaceae**, which are sometimes included in the Parietales, are annual or perennial herbs, with zygomorphic flowers. The flowers are small, the receptacle being enlarged on the posterior side, where the petals and stamens are bigger than on the anterior side. The ovary is generally compound but unilocular and remains open at the top. The seeds do not possess any endosperm. They are

Fig. 1491.—*Reseda lutea.* Wild Mignonette.

mainly Mediterranean plants, though two species of *Reseda* (Fig. 1491) are found in the British Isles. Some, such as Mignonette (*Reseda odorata*) are cultivated in gardens.

Papaveraceae

The family is a small one but includes several British genera, among which we may mention *Papaver* (Poppy); *Meconopsis*, which occurs chiefly in America and eastern Asia, but is represented in this country by the rare *M. cambrica* (Welsh Poppy); *Glaucium* (Horned Poppy); *Chelidonium* (Celandine); *Corydalis* (Holewort); and *Fumaria* (Fumitory). *Eschscholtzia* (Californian Poppy) and *Dicentra* (Bleeding Heart) are commonly grown in gardens.

The **plants** are generally herbaceous or shrubby (*e.g.*, *Romneya*) or in the case of *Bocconia* may become a small tree. The leaves are alternate, rarely entire but more often lobed or deeply dissected. A laticiferous system is often well developed. Some are annuals but many are perennial.

The **flowers** (Fig. 1492) are usually large, solitary or in cymose inflorescences. Usually they are actinomorphic, but are consistently zygomorphic in *Corydalis*, *Dicentra* and *Fumaria*, with the result that these genera are by some writers included in a separate family. The genus *Hypecoum*, however, connects the two families together and little is gained by this separation.

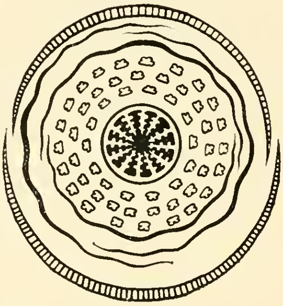

Fig. 1492.—*Papaver rhoeas*. Floral diagram. (After *Eichler*.)

The **sepals** are usually two in number, occasionally three, and fall off at an early stage in development.

The **petals** are usually four, more rarely six, eight or twelve, regularly alternating in two whorls. They are imbricate and often much crumpled in the bud. When expanded they are large and usually brightly coloured, falling off very soon after expansion. Petals are absent in *Bocconia* and *Macleaya*.

The **androecium** is hypogynous. The stamens are indefinite in number, except in the zygomorphic types, usually in two, three, four or six alternating whorls. The anthers are bilocular and the split is longitudinal.

The **gynoecium** consists of from two to many carpels. The ovary is usually unilocular with a number of placentas equal to that of the carpels, forming a series of radial plates, arising from the ovary wall and almost meeting in the centre. A false septum may be developed in the unilocular ovary to produce a bilocular appearance. The ovules are anatropous or campylotropous. The stigmas are opposite or alternate with the placentas.

The **fruit** is a capsule opening either by valves or pores; it is rarely indehiscent.

The **seeds** are small, spherical, or ovoid and often minutely warted or reticulate; occasionally they are arillate. The embryo is minute with an oily endosperm.

The family includes twenty-eight genera with about 600 species, which occur chiefly in northern temperate regions. The chief anatomical features of the family are the absence of subsidiary cells accompanying the stomatal guard cells and also the occurrence of simple perforations in the vessels. The wood parenchyma has simple pits. Secretory canals producing white or yellow latex are widely distributed. The classification of the Papaveraceae is simple:

I. Papaveroideae

The petals are not spurred: the number of stamens is indefinite and the number of carpels varies from two to indefinite. *Eschscholtzia*, *Chelidonium*, *Glaucium*, *Papaver*, *Meconopsis*, *Argemone*, *Platystemon*, *Bocconia*, *Macleaya*.

II. Hypecoideae

The petals are not spurred: the stamens are four in number and the gynoecium is composed of two carpels. *Hypecoum*, *Pteridophyllum*.

III. Fumarioideae

The petals are spurred and there are two branched stamens, each with three members. *Dicentra*, *Corydalis*, *Fumaria*.

The section Papaveroideae includes the regular actinomorphic types in which the petals are usually large and conspicuous. Many species exude a milky or yellowish juice. The largest genus is *Papaver* (Fig. 1493) which contains about 110 species. They are found in central and southern Europe and in temperate Asia, but *Papaver nudicaule*, the Iceland Poppy, grows as far as the polar circle in both hemispheres as well as in the mountainous regions of central Asia and in Colorado. Many poppies are annual weeds, but some are perennial. They contain an elaborate laticiferous system often accompanying the phloem. This latex may contain various alkaloids and *P. somniferum*, the Opium Poppy (Fig. 1494), is largely cultivated in India and the Far East for the opium which is extracted from the latex of the unripe fruits.

The genus *Meconopsis* (Fig. 1495) occurs mainly in southern and eastern Asia and is cultivated in this country, particularly *M. betonicifolia* on account of its bright blue flowers. Other species have yellow flowers. The genus differs from *Papaver* in the presence of a distinct style, on which the four- or

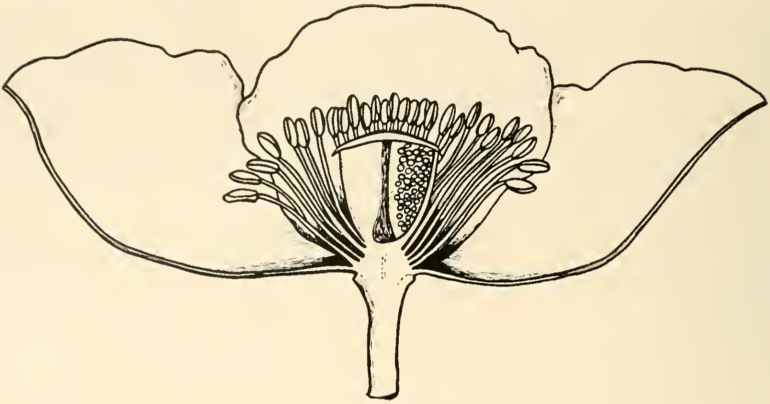

FIG. 1493.—*Papaver rhoeas.* Vertical section of flower.

FIG. 1494.—*Papaver somniferum.* Flower.

six-rayed stigma is borne. Closely allied to *Meconopsis* is *Argemone*, an American genus which includes the Mexican Thistle, *A. mexicana*, which is widely naturalized in the Old World.

The genus *Glaucium* is interesting chiefly because of the long curved pod (Fig. 1496), formed from two carpels. This pod becomes two-chambered as the result of the development of a false septum uniting the two parietal placentas. When ripe it dehisces by two valves. In structure and appearance it recalls the fruits of the Cruciferae and suggests a link with this family. The Yellow Horned Poppy of our sea coasts is the only British

FIG. 1495.—*Meconopsis cambrica*. Flower.

FIG. 1496. — *Glaucium flavum*. Siliqua-like fruits, showing basipetal dehiscence.

representative of the genus, which is chiefly found in the Mediterranean region. There is also one Chinese species.

In contrast to the fruit of *Glaucium*, that of *Chelidonium* has no septum, although it also is formed from two carpels. The seeds are distributed by ants. This genus is represented by the single species *Chelidonium majus* (Great Celandine) which is distributed from Europe to Japan including Britain, where it is only doubtfully native. Among the American genera we may mention *Eschscholtzia* and *Platystemon*, the latter being particularly interesting because it is considered to show a close relationship with the Ranales. This is indicated in the multilocular ovary which is formed from many carpels which are laterally united only in the basal region.

The genera *Bocconia* and *Macleaya*, which are natives of America and the West Indies, and of China and Japan respectively, are interesting because of the absence of any corolla and the aggregation of the flowers into compound racemes. There are five species of *Bocconia*; one is a small annual, three are medium-sized perennial herbs and one is a small tree, an unusual diversity of form for a single small genus. *B. cordata*, the Plume Poppy, is often cultivated in gardens.

The flowers of the Papaveroideae are slightly protogynous or rarely protandrous. The bright colour of the petals is sometimes enhanced by the colour of the stamens. Nectar is rarely produced and insects visit the flowers mostly to collect pollen. In *Papaver* and *Eschscholtzia* the flowers are visited chiefly by flies, while in *Glaucium* and *Chelidonium* bees occasionally visit the flowers on account of their bright yellow colour.

The Hypecoideae is a small sub-family containing two genera, *Hypecoum* and *Pteridophyllum*. The flowers are dimerous and actinomorphic. The stamens are four in number and developed opposite the petals. The fruit is a long pod or lomentum derived from a bicarpellary gynoecium. Later in life it becomes divided up by transverse septa into one-seeded portions. The plants are mostly perennial herbs with pinnately divided leaves and are devoid of any laticiferous system. *Hypecoum* contains some twelve species which range through Europe to central Asia and China. *Pteridophyllum* is represented by a single Japanese species.

In *H. procumbens* the pollen is shed in the bud into pockets on the inner surface of the inner petals, which close up before the stigma develops. The stigma only opens when it has grown above the level of the pollen pockets. When an insect visits the flower, the pockets open and dust it all over with pollen.

The members of the Fumarioideae are distinguished by the marked difference in appearance of the two whorls of petals; also by the spurs which are developed at the base of one or two of the inner petals and by the two tripartite stamens. There is no laticiferous system but oil-containing sacs may be present. The plants are mostly small herbs, though some climb with the aid of their thin, slender stems and much divided leaves. Unlike most of the Papaveroideae, the flowers are small and are borne in terminal racemes and they are insect pollinated. In *Dicentra* (Fig. 1497), *Corydalis* and *Fumaria* the flowers are interesting as examples of a rare type of zygomorphy in which the plane of symmetry is transverse and vertical to the central axis. In *Corydalis* the fruit is a many-seeded, bivalved capsule, while in *Fumaria* it is an indehiscent, one-seeded nut. Many species of

FIG. 1497.—*Dicentra formosa*. Flowering shoot.

Corydalis are myrmecochorous, the seeds being attractive to ants. Some of the species of both genera are peculiar in having only a single cotyledon, a condition which, it has been suggested, may be associated with the development of a fleshy tuber or rhizome.

The pollination mechanism is quite distinct from that in either of the other sub-families. The flowers are zygomorphic and are pollinated by bees. The nectar is secreted in spurs or pouches formed from the petals; there being two nectaries in *Dicentra* but only one in *Corydalis* and *Fumaria*. The two inner petals are fused at the top to form a hood-like sheath which encloses the stamens and stigmas. The bee presses down the hood when seeking nectar, but it springs back to its original position when the pressure is removed. In the younger flowers the bees become dusted with pollen and later transfer it to older flowers. The bee in visiting each flower of an inflorescence from below upwards will, therefore, effect pollination mainly from one inflorescence to another.

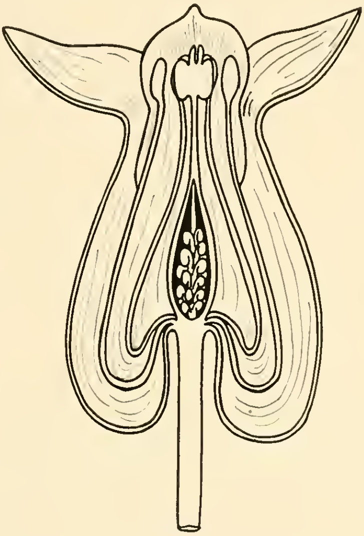

Fig. 1498.—*Dicentra spectabilis*. Longitudinal section of flower.

In *Dicentra spectabilis* (Fig. 1498) the petals and stamens form grooves, at the base of which lies the nectar. So elaborate is this system of grooves that only two native bees are able to reach the nectar and they alone normally perform pollination.

In *Corydalis* (Fig. 1499) one of the two outer petals is prolonged backwards into a spur containing nectar. The two inner, lateral petals are fused at their tips and cohere at their bases with the two outer petals, thus forming a hood which encloses the anthers and stigma. Long-tongued bees in search of the nectar must insert their probosces between the hood and the upper spurred petal and in doing so they press down the hood, with the

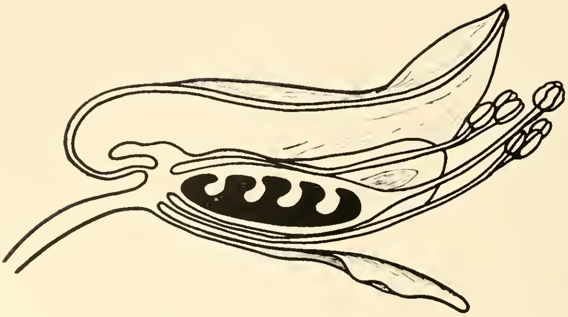

FIG. 1499.—*Corydalis lutea.* Longitudinal section of flower to illustrate the description of pollination in the text.

result that, in young flowers, their under surface is dusted with pollen, which has been shed on to the stigma, and transfer it to the stigmas of older flowers which have already lost their pollen. When the weight of the insect is removed the hood springs up by its elasticity and again covers the stigma. The pollination mechanism in *Fumaria* (Fig. 1500) is essentially similar to that in *Corydalis*, but the flowers are usually smaller and owing to their late flowering it seems likely that self-pollination is more common. This is emphasized by the fact that viable seed is often set in very wet weather.

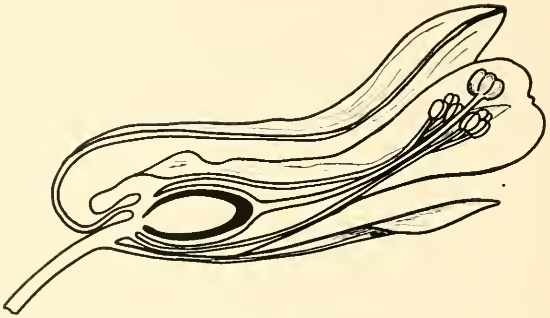

FIG. 1500.—*Fumaria* sp. Longitudinal section of flower to illustrate pollination. See in text.

Cruciferae (Brassicaceae)

Included in this family are a large number of important vegetable crops as well as many well-known garden and wild flowers. Probably the most important is the wild Cabbage, *Brassica oleracea*, from which all the vegetables known as "Greens" have been developed. Among these we may mention the Cabbage, Brussels Sprout, Cauliflower, Broccoli, Kohlrabi, Kale or Borecole and Savoy, all of which are varieties derived from the above species. Other species of the same genus have also contributed to the vegetable crops: *Brassica rapa* has given rise to the Turnip and *B.*

napus to the Swede; *Brassica* (*Sinapis*) *alba* is White Mustard and *B. nigra* is Black Mustard.

Turning to other genera of economic importance we may mention: *Lepidium sativum* (Cress), *Cochlearia armoracia* (Horseradish), *Raphanus sativus* (Radish), *Crambe maritima* (Seakale) and *Nasturtium officinale* (Watercress).

FIG. 1501.—*Cheiranthus cheiri.* The Wallflower.

Common garden plants include: *Matthiola* (Stocks); *Cheiranthus* (Wallflower) (Fig. 1501); *Hesperis* (Dames' Rocket) (Fig. 1502); *Alyssum* (Sweet Alyssum); *Aubrietia*; *Iberis* (Candytuft); *Lunaria* (Honesty); and *Arabis* (Rock Cress).

FIG. 1502.—*Hesperis matronalis.* Dames' Rocket.

Many are common weeds, such as *Capsella bursa-pastoris* (Shepherd's Purse); *Brassica arvensis* (Charlock); *Cardamine hirsuta* (Hairy Bitter Cress);

Cardamine pratensis (Milkmaids); *Erophila verna* (Vernal Whitlow Grass); *Thlapsi arvense* (Penny Cress) and many others.

The **plants** are generally herbaceous, rarely woody, and many are annuals with a life cycle of only a few weeks. The leaves are alternate and are normally beset with simple or branched hairs, the forms of which have been employed in the systematic arrangement of the genera. The plants may form storage organs, especially in biennials such as the Turnip or Swede.

The **inflorescence** is generally racemose and often a corymb. Bracts or bracteoles are so rare that their absence is regarded as a family character.

The **flowers** (Fig. 1503) are hermaphrodite and actinomorphic, occasionally somewhat zygomorphic; polypetalous and hypogynous, with the parts arranged either in twos or fours.

Fig. 1503.—Cruciferae. Floral diagram.

The **calyx** is polysepalous and consists of four sepals which are arranged in two whorls, the lateral, inner sepals being frequently pouched at the base.

The **corolla** is polypetalous and cruciform; composed usually of one whorl of four petals which are often differentiated into a narrow claw and a broad, expanded limb.

The **androecium** is composed of six hypogynous stamens which are arranged in two whorls, the inner being composed of the four longer stamens while the outer whorl consists of two short lateral ones (Fig. 1504). Nectaries are developed as small green glands at the base of the two short stamens. Here the nectar accumulates as well as in the pouches formed by the lateral sepals.

The **gynoecium** is bicarpellary and syncarpous. The ovary is superior and bilocular as a result of the development of a false septum which arises from the parietal placentas. The ovules are generally numerous, anatropous or campylotropous. The stigmas are generally commissural.

The **fruit** is either a siliqua or silicula or a lomentum and this feature is often used as a basis of classification. (See also below, p. 1642.)

The **seed** is almost devoid of endosperm and the testa is often mucilaginous. The embryo is generally bent, in some genera in the plane of the cotyledons and in others at right angles to this plane. This difference has also been used in classification. The family is a large one, comprising about 220 genera and over 1,900 species. They are found mainly in north temperate regions of both the New and Old Worlds, some extending their range northwards into the sub-arctic.

FIG. 1504.—*Erysimum perofskianum.* Longitudinal section of flower.

The chief anatomical feature is the presence of characteristic secretory cells which contain myrosin.* The stomata are peculiar in that the guard cells are surrounded by three subsidiary cells, of which one is smaller than the other two. The vessels have simple perforations and there is rarely any medullary ray parenchyma. Epidermal hairs are frequent and very variable in form. Some are multicellular and dendroid and the form of these hairs may be used as a basis of classification.

There have been a number of attempts to split up this large family into natural units but it must be admitted that each of them is largely artificial. The uniformity of the floral structure makes the discrimination of groups or even of genera a difficult matter. Linnaeus made use of the shape of the fruit as his basis of separation. This view was extended by de Candolle and later adopted by Hooker in his "Student's Flora". Pomel drew attention to the arrangement of the cotyledons while in the seed, and to the early development of the radicle, and used this character as the basis of his classification, thereafter using the fruit character to split up his three main groups still further. Prantl in the "Pflanzenfamilien" depended mainly on the presence or absence and the branched or unbranched

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* Myrosin is an enzyme which accompanies the sulphur containing-glucosides in Cruciferae and hydrolyses them to glucose and various isothiocyanates (mustard oils).

character of the hairs. In this way he separated two main groups, which were further divided by the development of the style, and these groups again were further separated on the number of nectaries, the shape of the fruit and the character of the cells of the septum. Bayer based his classification upon the distribution of the nectaries as the basic character while Schweidler made use of the distribution of myrosin cells in the tissues in his method of classification.

Clearly no obvious system of subdivision can be adduced under the circumstances and it is simply a matter of personal choice which set of characters is regarded as most suitable for this purpose. While it is probably true that Prantl's system makes use of the greatest number of characters and might therefore be said to be the most natural, the system is unsatisfactory because it employs as its foundation a character which modern research has proved to be subject to change under environmental conditions. Hence we can no longer regard the presence or absence of hairs as a diagnostic character. There seems little to justify the preference of any one of the other systems, and we shall therefore fall back on the original Linnaean system, with the elaborations employed by Hooker. The following summarizes these views so far as the British genera are concerned:

I. **Brassicoideae**

Pods elongated, dehiscing throughout their length, not compressed at right angles to the septum.

1. *Arabideae.* Flowers white, yellow or lilac. Seeds uniseriate, occasionally biseriate. Radicle accumbent. *Matthiola*, *Cheiranthus*, *Nasturtium*, *Barbarea*, *Arabis*, *Cardamine*, *Dentaria.*
2. *Sisymbrieae.* Flowers white, yellow or violet. Seeds usually uniseriate. Radicle incumbent. *Sisymbrium*, *Erysimum*, *Hesperis.*
3. *Brassiceae.* Flowers yellow. Seeds uniseriate or biseriate, radicle incumbent, longitudinally folded or very concave. *Brassica*, *Diplotaxis.*

II. **Alyssinoideae**

Pods short, dehiscing throughout their length, not compressed at right angles to the septum. Flowers white or yellow.

1. *Alysseae.* Seeds biseriate, radicle accumbent. *Draba*, *Erophila*, *Alyssum*, *Cochlearia.*
2. *Camelineae.* Seeds biseriate, radicle incumbent. *Camelina*, *Subularia.*

III. **Lepidinoideae**

Pods short, dehiscing throughout their length, much compressed at right angles to the septum which is hence very narrow.

1. *Lepidieae.* Cotyledons straight, incurved or longitudinally folded, radicle incumbent. Flowers white. *Capsella*, *Senebiera*, *Lepidium.*

2. *Thlaspideae.* Cotyledons straight, radicle accumbent. Pods on horizontal pedicels. Flowers white. *Thlaspi*, *Iberis*, *Teesdalia*, *Hutchinsia.*

IV. **Raphanoideae**

Pods indehiscent or with very short valves which cover a few of the seeds only.

1. *Isatideae.* Pods indehiscent, one-seeded and one-celled. *Isatis.*
2. *Cakileae.* Pods transversely two-jointed, the lower joint indehiscent and seedless, or two-valved, and two or more seeded. The upper joint one- or two-celled. *Crambe*, *Cakile.*
3. *Raphaneae.* Pods elongated, one-celled and many-seeded or indehiscent or jointed, the one-celled joints being indehiscent. *Raphanus.*

It should be explained that in the above classification the term "radicle accumbent" implies that the embryo is so folded that the radicle lies against the edges of the two cotyledons. "Radicle incumbent" means that the radicle lies against the back of one of the cotyledons. (See also p. 1500.)

It is impossible in the space at our disposal to do more than touch upon some of the more interesting features of this large family. Mention has already been made of the swollen storage organs which are developed by some of the biennial genera such as the Turnip and the Swede. In such plants the primary root and hypocotyl enlarge steadily during the first year's growth, storing up reserves as they are made during that summer. In the autumn most of the radical leaves die away and the root remains in the soil. The following spring growth begins again, but this year only a flowering shoot is formed. This may grow to a considerable size using up the food reserves of the previous year to supply the seeds as they are formed. It may be noted that the leaves produced on the inflorescence are small as compared with the radical leaves of the previous year. In the Radish, a similar swollen hypocotyl region develops early in the life of the plant and the inflorescence is produced during the first year. Special methods of vegetative propagation are found in certain species. Bulbils are formed in the axils of the leaves of *Dentaria bulbifera* and on the leaves themselves in *Cardamine pratensis.*

The flowers are remarkably constant so far as the six stamens are concerned. These are arranged in two whorls; the outer consisting of a pair of lateral stamens with shorter filaments and an inner group of four stamens with longer filaments. These latter may remain more or less united even in the adult flower. This tetradynamous character of the flower was first observed by John Ray, and recorded in his "Historia Plantarum" (1686–1704) and was subsequently selected as a diagnostic character of one of his classes. Thus the limits of the Cruciferae today differ but little from Linnaeus' original description.

The morphological interpretation of the flower is uncertain. The two perianth whorls are probably truly tetramerous. The androecium, on the other hand, may consist of two dimerous whorls, the inner pair having split congenitally into four. This is borne out by the appearance of their rudiments during development.

It is true that slight variations from the typical flower are found in certain genera. Thus the petals may be reduced or even absent in such genera as *Nasturtium*, *Lepidium* and *Coronopus*. Two of the outer petals of the marginal flowers of the corymb may be enlarged, giving the flower a zygomorphic form, as in *Iberis* and *Teesdalia*. There is an increase in the number of stamens to sixteen in the genus *Megacarpaea*, while the two lateral stamens are often missing in *Cardamine hirsuta*.

The fruit (Fig. 1505) is a capsular pod, which dehisces usually by two valves which separate from *below* in an upward direction leaving the seeds attached to the framework of the septum, which is formed by the placentas. The whole structure is termed the **replum**. In the majority of species the pod is elongate and is termed a **siliqua** or, when it is broad and not much longer than it is wide, it may be referred to as a **silicula**. In the former, the placentas alternate and the seeds lie in a single row in each loculus. In the silicula they are generally formed in two rows. In certain genera the siliqua, before maturity, becomes divided into one-seeded parts by transverse septa, thus in *Cakile* the siliqua consists of two one-seeded segments, while in *Crambe*, though two segments are formed, the lower one is barren and forms a continuation of the stalk. Only in *Raphanus* is a true lomentum of many one-seeded segments normally formed. On the other hand in-

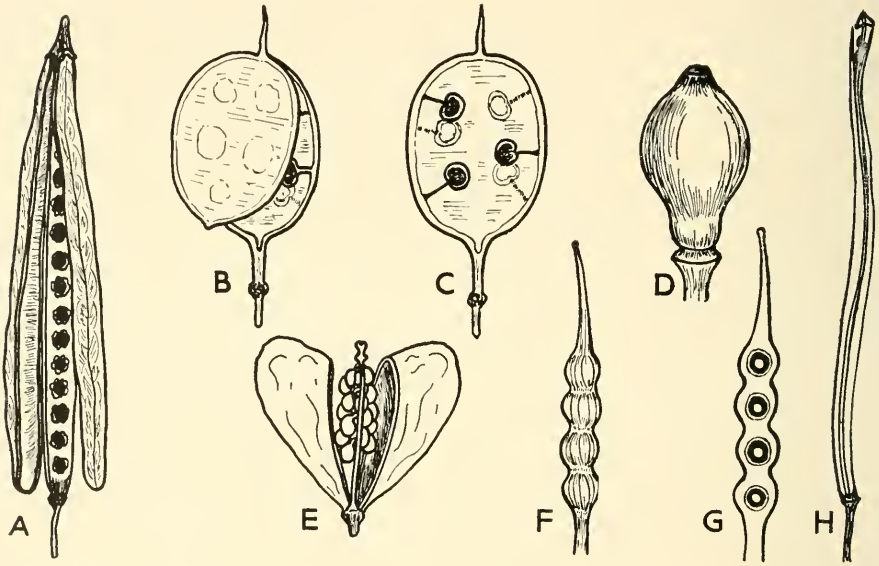


FIG. 1505.—Types of cruciferous fruits. A, *Cheiranthus*. B and C, *Lunaria*. D, *Crambe*. E, *Capsella*. F, *Raphanus* (lomentate siliqua). G, the same in longitudinal section. H, *Nasturtium*.

dehiscent, one-seeded pods are formed in *Isatis tinctoria* (Woad) which still grows wild along the cliffs bounding the River Severn.

In some genera the pod may be laterally compressed, and as a result the septum becomes very broad, as is seen in *Lunaria rediviva* (Honesty). Alternatively the pod may be flattened from back to front, when the septum remains very narrow. This is well seen in *Capsella bursa-pastoris* (Shepherd's Purse).

Mention may be made of the genus *Morisia*, which contains one species, a native of Corsica and Sardinia. In this annual herb the peduncle bends down after flowering, and buries the closed pod in the ground close to its roots. Another interesting case of a specialized distribution mechanism is exhibited by *Anastatica hierochuntica*, the Rose of Jericho, a native of the eastern Mediterranean. While the seeds are ripening in the dry season, the leaves fall off and the branches fold inwards, reducing the plant to a ball enclosing the fruits. The whole plant, which is an annual, now becomes free from the soil and is blown about until it reaches a wet spot or the rainy season begins, when the branches uncurl and the seeds are liberated.

All the Cruciferae are entomophilous and most of them are homogamous. The inflorescence which may begin as a corymb becomes, by elongation, a raceme and renders the flowers fairly conspicuous. However the flowers of many species are not sufficiently noticeable to ensure regular insect visits and we find that all the Cruciferae are capable of automatic self-pollination.

The calyx is apparently designed not only to protect the developing flower but later holds the petals together in a tube, at the bottom of which lie the nectaries. Despite the general similarity in structure of the floral parts there are considerable differences in the number and position of the nectaries, not only in relation to the stamens and the stigma, but also in the mode of storing and concealing the nectar. (See p. 1244.)

Velenovsky, who has made a detailed study of over 170 species, found that nectaries were invariably present. From this analysis Velenovsky suggests that it would be possible to classify the Cruciferae on the basis of the position and form of the nectaries. Since the nectaries are presumably essential in pollination they must obviously be important in the evolution of the flower, and therefore of the family.

ROSALES

The Rosales are Archichlamydeae in which the flowers are mostly actinomorphic and cyclic or spirocyclic. Both sepals and petals may be present or one or both may be missing. When present they are free and imbricate or valvate in the bud. The stamens may be the same as, or a multiple of, the number of the petals; they may be perigynous or epigynous or less commonly hypogynous. The ovary similarly may be either superior or inferior. The ovules are axile or parietal and there may be one or many in each loculus. The seeds may or may not have endosperm and the embryo is usually minute.

Many are trees or shrubs, a few are climbers, while at the same time there are a large number of herbaceous forms.

The Rosales as conceived by Engler was a very large and rather indefinite order containing some twenty families, between many of which there are few points of similarity. Hutchinson has attempted to circumscribe the group by splitting up the old Englerian order into a number of distinct orders, which has in some ways simplified matters. On the other hand his treatment has necessitated the rearrangement of a number of genera into new or different families. Thus, for example, he would remove some of the genera of the Saxifragaceae, redistributing them among three families and placing them in a new order along with certain other Englerian families of the Rosales. The method of treatment adopted here is a combination of Hutchinson's method with that of Engler's.

Three orders are recognized. Firstly, the Rosales, which include the Pittosporaceae, placed in the Pittosporales by Hutchinson; the Hamamelidaceae and Platanaceae, grouped by Hutchinson in the Hamamelidales, and the Rosaceae. Secondly the Saxifragales, which include the Crassulaceae, Cephalotaceae, Saxifragaceae and Podostemaceae. Thirdly the Leguminosae which are separated into Mimosaceae, Caesalpiniaceae and Papilionaceae. The diagnosis at the head of the section therefore applies to the Rosales as here treated. We shall consider the Rosaceae in detail, but must first refer briefly to the more outstanding features of other families belonging to the order, which are given in the above list.

The **Pittosporaceae** are mostly trees or shrubs, though many are climbers. The leaves are simple, evergreen, alternate or whorled, and are devoid of stipules. The flowers are pentamerous, the gynoecium consisting of two carpels. The seeds are mostly immersed in a viscid pulp and often remain sticky for a long time even when dry. The family is a small one containing some nine genera and about 200 species which are, with the exception of *Pittosporum*, confined to Australia. *Pittosporum* which contains about seventy species is common in the tropics and sub-tropics and several species are with some difficulty cultivated out of doors in Britain. The bright evergreen foliage is much used in winter house decorations. The timber is used for high-class furniture in Australia. *Billardeira*, with nine Australian species, is sometimes cultivated in greenhouses. It is an evergreen climber with coloured fruits.

The **Hamamelidaceae** are trees or shrubs with alternate leaves and paired stipules, which are normally persistent and sometimes large. The floral parts are in fours and the calyx tube is adnate to the bicarpellary ovary. It is quite a small family with only fifty species grouped in eighteen genera, but a number of them are well known either on account of their timber or because their flowers, which are produced early in the year before the leaves, make them desirable shrubs for early spring decoration.

Among the most important of these are *Corylopsis* (Fig. 1506), *Fothergilla*, and the Witch Hazels, which are species of the genus *Hamamelis* (Fig. 1507).

Species of *Liquidambar* produce important resins as well as being valuable timber trees. *L. orientalis* which grows in Asia Minor produces Storax which is a fragrant balsam, while *L. styraciflua* of North America provides the satin walnut wood of commerce. *Altingia excelsa* of Java and south-western China is also a fine timber tree.

FIG. 1506.—*Corylopsis pauciflora*. Racemes of pale yellow flowers.

FIG. 1507.—*Hamamelis mollis*. Flowers tetramerous with long golden petals.

The family **Platanaceae** is small, containing the single genus *Platanus*, which includes about half a dozen species. *P. orientalis* is the common Plane Tree, which is much planted in the cities, where it thrives exceptionally well, possibly on account of its bark, which scales off every year leaving a smooth surface. The axillary buds develop enclosed in the bases of the petioles, which thus protect them during early development. The wood is of some value, but that of the North American Sycamore, *P. occidentalis*, is superior and is of considerable economic importance. In the Platanaceae the flowers are monoecious, hanging in pendulous heads, which are anemophilous (Fig. 1508). The ovules are orthotropous and the one to eight carpels each produce an achene which is surrounded by a tuft of long hairs. The species so frequently planted in London streets is *P. acerifolia*, the London Plane, which is a hybrid of the two species mentioned above.

In Cretaceous and Tertiary times the genus appears to have been widespread in Europe, northern Asia and North America.

FIG. 1508.—*Platanus orientalis.* Above, clusters of female flowers and, below, of male flowers.

Rosaceae

The Rosaceae are one of the most important families of the Archichlamydeae, for not only does the family embrace a very large number of genera and species, but so many of them are of economic importance that a very considerable proportion of the fruit trade depends upon species belonging to the family. Many are so well known by their popular names, such as the apple, the pear or the plum, that they need no description. Others are less well known and we may begin by listing some of the most important.

In the genus *Prunus* (Fig. 1509): *P. spinosa* (Sloe or Blackthorn), *P. avium* (Wild Cherry), *P. cerasus* (Cherry), *P. padus* (Bird Cherry), *P. persica* (Peach), *P. armenaica* (Apricot), *P. amygdalus* (Almond), and *P. domestica* (Plum) may be mentioned, the first four and the last occurring wild in Britain.

In the genus *Rubus: R. idaeus* (Raspberry), *R. fruticosus* (a group name including the many forms of Blackberry), *R. saxatilis* (Stone Bramble) and *R. chamaemorus* (Cloudberry) are all well known.

FIG. 1509.—*Prunus armenaica.*
Apricot.

In the genus *Pyrus* we may mention *P. communis* (Pear), *P. malus* (Fig. 1510) (Apple), *P. aucuparia* (Rowan or Mountain Ash), *P. torminalis* (Wild Service), *P. aria* (White Beam), and in the allied genera *Crataegus*

FIG. 1510.—*Pyrus malus* var. *lemoinei* (*Malus lemoinei*) with dark red flowers.

monogyna (Hawthorn), *Mespilus germanica* (Medlar), and *Cydonia vulgaris* (Quince).

Certain other common members are well known among British wild flowers. *Rosa canina* (another general name embracing all the Dog Roses), and *R. rubiginosa* (Sweet Briar), *Fragaria vesca* (Wild Strawberry), *Potentilla anserina* (Silverweed), *P. erecta* (Tormentil), and *P. sterilis* (Barren Strawberry). Then there are the species of *Geum*: *G. rivale* (Water Avens) and *G. urbanum* (Wood Avens), *Agrimonia eupatorium* (Common Agrimony), *Filipendula ulmaria* (Meadowsweet) and many others.

When we turn to garden plants the number of common or well-known genera is far too great even to catalogue. Genera such as *Cotoneaster* and *Spiraea* comprise dozens of species and far larger numbers of varieties. Many have been grown for ornament and at least two bigeneric graft hybrids between species of *Crataegus* and *Mespilus* have been successfully cultivated (see Volume IV).

With such a varied assemblage of forms it is obvious that the limits of the family may be a matter of dispute, and while some retain them all together in a single large family, others would prefer to separate them on relatively minor points.

The **plants** may be either herbs, shrubs or trees, woody types predominating. The leaves are alternate, simple or compound and usually stipulate. Various types of vegetative propagation by means of runners or suckers are common.

The **inflorescence** may be either racemose or cymose or occasionally the flowers may be solitary.

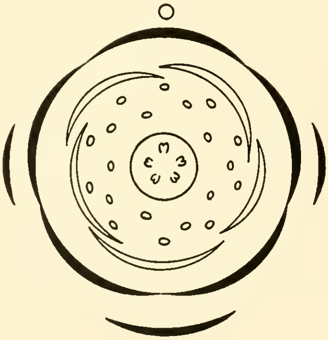


Fig. 1511.—Floral diagram of *Pyrus malus*. Rosaceae.

The **flowers** (Fig. 1511) are usually hermaphrodite, regular and usually pentamerous or more rarely tetramerous. They are generally perigynous and sometimes epigynous (Fig. 1512).

The **calyx** is sometimes gamosepalous, composed of five or occasionally four sepals. Sometimes there is an epicalyx, produced by the fusion of sepal stipules in pairs below the true sepals, as in *Fragaria*.

The **corolla** is polypetalous, consisting of five petals which are often brightly coloured and of large size; white, red or yellow being the predominant colours. These petals are imbricated in the bud. Petals may be absent in certain genera, *e.g.*, *Alchemilla.*

FIG. 1512.—*Pyrus malus.* Longitudinal section of flower.

The **androecium** is made up of stamens which are in number either a simple multiple of the perianth parts or indefinite. They are free, the anthers being small and bilocular. They split longitudinally.

The **gynoecium** may consist of from one to many carpels which may be free or adnate to the receptacle. The ovary is usually apocarpous and each carpel contains either one or two anatropous ovules.

The **fruit** may be either dry or succulent; in the latter case usually a drupe, or occasionally a pseudocarp. Alternatively it may be a cluster or etaerio of small akenes, follicles or drupes.

The **seeds** are almost always non-endospermic and the embryo possesses planoconvex, fleshy cotyledons which on germination are epigeal.

The family is world-wide in distribution, though its main centre appears to be in the north temperate regions. There are some 2,000 species which are grouped in 100 genera.

Anatomically there are certain features which are more or less characteristic of the family or at least of the woody members. The cork cambium in one sub-family is epidermal while in another it is hypodermal. The primary cortex normally has a collenchymatous hypodermis and crystal sacs occur in the cortical parenchyma. Stone cells are usually absent from the primary and secondary cortex. The medullary rays are broad in the sub-families Rosoideae and Prunoideae but narrow in the Pomoideae. Pear wood is one of the smoothest and finest-grained woods known. It is selected for making mathematical rules and drawing instruments and is a favourite with wood carvers. In the Prunoideae gum is often produced by the disorganization of the wood, probably due to bacterial infection. Prickles and other hard epidermal outgrowths are common in certain genera (*Rosa*, *Rubus*), and branch thorns are produced commonly in others (*Crataegus*).

The subdivision of the Rosaceae as proposed by Focke in the " Pflanzenfamilien " is somewhat elaborate but in following it out carefully we may find a method of separating what, at first sight, appear to be closely similar genera.

I. **Spiraeoideae**

In this sub-family there are from one to twelve, usually two to five carpels, which are arranged in a whorl, being neither on special carpophores nor sunk in a receptacle. Each carpel contains two or more ovules and the fruit is usually dehiscent, frequently being a follicle. The flowers have a pentamerous calyx and corolla. The stamens vary from ten to indefinite. The plants are usually shrubs, devoid of thorns or prickles, with simple or compound exstipulate leaves. This sub-family is considered to be most closely related to the Saxifragaceae. It is divided as follows:

1. *Spiraeeae.* The fruit is a follicle and the seeds are not winged. *Spiraea* (Fig. 1513).

FIG. 1513.—*Spiraea japonica.* Inflorescence.

2. *Quillajeae.* The fruit is a follicle but the seeds are provided with wings. *Quillaja*, *Lindleya*.
3. *Holodisceae.* The fruit is an akene. *Holodiscus.*

II. **Pomoideae**

In this sub-family the floral axis forms a deep cup with the carpels more or less completely united to its inner wall, and with each other. The carpels are usually five in number and each contains two to five ovules. The fruit is a pseudocarp called a **pome**. Certain genera, *e.g.*, *Crataegus*, have woody carpels enclosed in the soft receptacle tissue, each carpel being called a **pyrene**. The flowers have a pentamerous calyx and corolla and the stamens number twenty or more. The plants are mostly trees or shrubs with simple or pinnate stipulate leaves.

1. *Pomarieae*. The only tribe. *Pyrus*, *Mespilus*, *Crataegus*, *Cotoneaster*, *Eriobotrya*, *Amelanchier*.

III. **Rosoideae**

In this sub-family the carpels are either situated on a swollen receptacle or enclosed within a receptacular cup. Each carpel contains one or two ovules and the fruit is indehiscent and one-seeded. Occasionally there is only one carpel, borne on a carpophore. The flowers are usually pentamerous, though double or semi-double flowers are common, caused by the transformation of the outer stamens into petals. The leaves are very variable in form. The plants may be trees or shrubs but many are herbaceous. It is the largest of the sub-families.

1. *Kerrieae*. The stipules are distinct and the axis does not contribute to the formation of the fruit. The stamens are indefinite and each tapers from a broad base. The carpels are few in number and whorled. *Kerria*, *Rhodotypos*, *Aruncus*.
2. *Potentilleae*. The carpels are generally numerous and are developed on a large rounded or convex development of the central receptacle, which is surrounded by a distinct receptacular ring, forming a saucer around the central receptacle. This tribe is usually further subdivided on the structure of the fruit.
    - (*a*) *Rubinae*. The fruit is an etaerio or cluster of small drupes. There is no epicalyx. *Rubus* (Fig. 1514).
    - (*b*) *Potentillinae*. The fruit is an akene, the seed is pendulous and an epicalyx is present. *Fragaria*, *Potentilla*, *Sibbaldia*.
    - (*c*) *Dryadinae*. The fruit is an akene, the seed is erect. *Geum*, *Dryas*.
3. *Cercocarpeae*. The receptacle is more or less tubular, with a single carpel. The leaves are slightly stipulate. *Adenostoma*, *Purshia*.
4. *Ulmarieae*. The receptacle is flat or slightly concave. The stamens have narrow bases to the filaments and the ten carpels ripen into one-seeded, indehiscent fruits. *Ulmaria*.
5. *Sanguisorbeae*. The persistent, urn-shaped receptacles enclose the carpels, which are never numerous and often are reduced to two. The receptacle, together with the fruits, often becomes hard and almost woody. The number of stamens is very variable, but it may be reduced, even to one. Many of the

FIG. 1514.—*Rubus.* Right, flowers of *R. odoratus.* Left, fruits of *R. fruticosus,* the Blackberry.

fruits are dispersed by birds and other animals, due to the barbed trichomes which they possess, and possibly as a result of this the tribe is very widely distributed. *Alchemilla*, *Poterium* (Fig. 1515), *Agrimonia*, *Acaena*, *Brayera*.

FIG. 1515.—*Poterium polygamum.* Inflorescence with male flowers at base, hermaphrodite flowers in middle and female flowers at top.

6. *Roseae.* The receptacle is urn-shaped and encloses numerous carpels. It becomes fleshy and bright-coloured and contributes to the formation of the fruit. The plants are mostly shrubs with compound stipulate leaves. *Rosa.*

IV. **Neuradoideae**

This sub-family contains only two small genera, which are desert-loving herbs with yellow flowers. The five to ten carpels are united with each other and also with the receptacle, which enlarges and forms a dry covering around the fruit.

1. *Neuradeae.* The only tribe. *Neurada*, *Grielum.*

V. **Prunoideae**

This sub-family is characterized by the solitary carpel, with a terminal style and a pair of pendulous ovules. The fruit is a one-seeded drupe. The flowers are regular and pentamerous. The stamens may be ten, twenty or more in number. The seed or kernel has a papery testa and contains two large cotyledons. There is no endosperm. The plants are mostly trees or large shrubs with simple undivided leaves, and small stipules; many are evergreen.

1. *Pruneae.* The only tribe. *Prunus*, *Nuttallia.*

VI. **Chrysobalanoideae**

This sub-family differs from the last in that the style is basal and the ovules are ascending. The flowers frequently show signs of zygomorphy and the plants are mostly tropical evergreen trees or shrubs whose chief centre of distribution is South America. This sub-family is held to show a connecting link between the Prunoideae and the Leguminosae.

1. *Chrysobalaninae.* The flowers are nearly regular. *Chrysobalanus*, *Parinarium.*
2. *Hirtellinae.* The flowers are definitely zygomorphic. *Hirtella*, *Acioa.*

Space will not allow us to consider all these genera separately nor to consider each of the tribes in detail. We may however review those pollination mechanisms which are most typical of the family as a whole.

The Rosaceae show a wide range of pollination mechanisms, from anemophily to very specialized flowers suitable for pollination only by particular kinds of insects. Some flowers, as for example those of *Alchemilla*, are insignificant and unattractive while in others the flowers are large and conspicuous like those of most species of *Rosa*. The form of the inflorescence is very varied even within the same genus. Many flowers secrete nectar from an annular ridge on the surface of the receptacle but the quantity varies greatly. In some species of *Rubus* for example the quantity is large while, at the other extreme, in *Potentilla* it forms a scarcely perceptible film.

The common genera fall naturally into the following classes in regard to their pollination mechanism.

1. Anemophilous.
   Poterium.
2. Entomophilous: pollen flowers, devoid of nectar.
   Rosa, Ulmaria, Aruncus, Kerria.
3. Entomophilous with exposed nectar.
   Alchemilla, Sibbaldia, Amelanchier.
4. Entomophilous with partly concealed nectar.
   Prunus, Geum, Potentilla, Spiraea, Crataegus.
5. Entomophilous with concealed nectar, pollinated chiefly by hive bees.
   Rubus, Fragaria.

In species of the genus *Rosa* the flowers are homogamous and often fragrant, with large, brightly coloured petals but devoid of nectar. When the flower opens the stamens curve outwards and an insect will alight on the apices of the carpels which occupy the centre of the flower. These visits are primarily for the purpose of collecting the abundant pollen but in the process cross-pollination is made possible. Should insect visits fail, automatic self-pollination generally occurs by pollen falling directly into the stigmas, for the quantity of pollen produced is very great. In *Alchemilla* (Fig. 1516), the flowers are small and apetalous and the nectar is secreted by a fleshy ring on the rim of the receptacle cup. As a rule the flowers are either protandrous or protogynous. Automatic pollination is therefore rendered difficult. Moreover in many flowers in which the stigma develops normally the stamens are greatly reduced and their filaments remain much shorter than the style. Most of the species are apomictic.

Fig. 1516.—*Alchemilla vulgaris.* Flowers in longitudinal section, showing marked protandry.

A more specialized condition is found in the genus *Spiraea* (Fig. 1517). In *S. sorbifolia*, a Siberian species often grown in gardens, the flowers are large and fragrant. These flowers are protogynous and even in the bud the stigmas are provided with receptive papillae and project beyond the stamens, which are bent towards one another. When the flower opens the stamens gradually become erect and dehisce successively from the outside inwards.

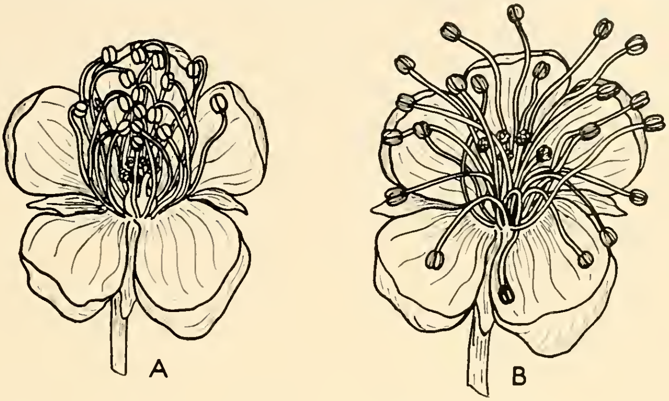


FIG. 1517.—*Spiraea* sp. Pollination. See text.

Insects are attracted to the flowers by nectar which is secreted in abundance by an annular, orange-yellow thickening on the inner wall of the concave receptacle, internal to the insertion of the stamens. At the beginning of anthesis, therefore, insects perform cross-pollination whereas later they may perform self-pollination, since the stigmas remain receptive until the innermost anthers have dehisced. Finally automatic pollination may occur.

The most specialized condition is found in the genus *Rubus*. The flowers (Fig. 1518) are either pink or white in colour and when the buds

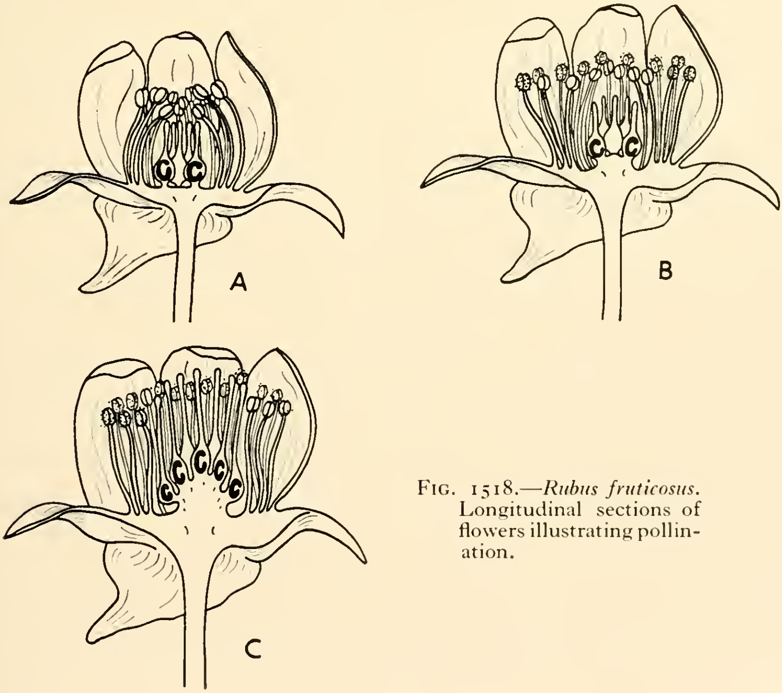


FIG. 1518.—*Rubus fruticosus*. Longitudinal sections of flowers illustrating pollination.

open the stamens diverge so widely that even short-tongued insects can thrust their heads between the filaments and the carpels to obtain the nectar, which is secreted by a ring at the base of the flower. The outermost anthers dehisce first and turn their valves outwards while the stigmas mature at the same time. At this stage, therefore, most insect visitors perform cross-pollination, and the flower is pollinated before all the anthers are ripe. Automatic self-pollination very rarely occurs and then only towards the end, when the innermost anthers dehisce. Because of the amount of nectar secreted insect visitors are very numerous and self-pollination normally only occurs in very bad weather.

In contrast to these examples we have the species *Poterium sanguisorba* in which the flowers are nectarless. The inflorescence is a close spike, composed of female flowers at the top, followed below by hermaphrodite ones and finally at the base by male flowers. The female flowers have conspicuous red, bushy stigmas. The hermaphrodite flowers are usually homogamous but this varies in individual plants. The anthers are yellow and pendulous with long reddish filaments and in most inflorescences the male flowers greatly outnumber the female, while hermaphrodite flowers may be scattered among the unisexual ones. Hover flies occasionally visit the flowers in a profitless search for nectar, but, on the whole, the plants rely on the wind for pollination. Although mechanisms to ensure cross-pollination are so marked a feature of the family, it should be noted that in certain genera, particularly *Rosa*, *Rubus*, *Crataegus* and *Alchemilla*, there is very frequent apogamy, many embryos being developed without fertilization, so that they carry only the maternal characters. This peculiarity, continued with frequent inter-specific crossing, has resulted in the production in these genera of large numbers of very closely related " species " whose taxonomic status is often doubtful. More will be said about this subject in Volume III.

Another interesting point bearing on cross-pollination is the prevalence of self-sterility, especially in the genera *Pyrus*, *Prunus* and *Fragaria*. This affects some of the most important cultivated fruits, and must be taken seriously into account by the cultivator who finds that a self-sterile variety grown by itself will yield no fruit and must be cross-pollinated by the introduction of other suitable varieties as pollinators.

Before bringing our account of the Rosaceae to a close we must refer briefly to certain species of economic importance whose fruits, in warmer climates, take the place of the temperate Apples, Pears and Cherries.

The Prune (*Prunus domestica* var. *Juliana*) is cultivated mainly in the warmer parts of Europe and particularly in the Mediterranean region. It is a variety of the wild Plum. Those grown in France are dried in large quantities and form an important commodity for export. The Balkans also at one time exported prunes. Luther Burbank, experimenting on breeding new varieties of plants, produced a stoneless Prune in which the seed was replaced by a jelly. This form does not appear to have been economically exploited. More typically subtropical is the Loquat (*Eriobotrya japonica*), the fruit of which resembles an Apple. It is a small tree about 20 ft. in height with lanceolate leaves. The flowers are white and fragrant. The fruits are borne in clusters, each being rather pear-shaped, from 1 to 3 in. in length, pale yellow or orange in colour. The skin resembles that of a Peach but the flesh is firm, juicy and rather acid in taste. The fruit is a berry and contains some four or five seeds. It is grown commercially in the warmer parts of the United States and China.

Chrysobalanus icaco, sometimes called the Coco Plum, is not a fruit of great value though it is extensively grown in tropical America. The tree is somewhat similar in form to the Loquat and bears plum-like fruits about 1·5 in. in length. The skin is thin, the flesh is white and insipid and adheres to the large oblong seed.

The bark of *Quillaja saponaria*, the soap tree of Chile, yields a lather with water and is still used for native laundry work.

Finally we may mention the dried female flowers of *Brayera anthelmintica* which are known as Koso and are used in Abyssinia as a cure for tape worms.

LEGUMINOSAE

The Leguminosae are Archichlamydeae in which the flowers are either actinomorphic or zygomorphic. The petals are usually free or sometimes partly united. The stamens may be five in number but are often numerous, free, monadelphous or diadelphous. The carpels are solitary and the ovary superior. The fruit is a legume and the seeds are devoid of endosperm. The plants may be trees, shrubs or herbs with simple, pinnate or bipinnate leaves. Stipules are often present.

The order as here defined requires some explanation. Formerly the Leguminosae were regarded as a single family placed within the Rosales. The marked tendency to zygomorphy, however, separates it rather sharply from the latter order. Moreoever, it is clearly composed of three distinct series of forms which are most conveniently considered as separate families. Here, therefore, we shall follow Hutchinson and recognize the Leguminosae as an order containing the families Caesalpiniaceae, Mimosaceae and Papilionaceae. We shall refer briefly to the first two and consider the Papilionaceae in detail.

The **Caesalpiniaceae** are a rather small family which is distinguished by its zygomorphic flowers, with the imbrication of the corolla ascending, in contrast to the Papilionaceae in which it is descending. It includes a number of important plants of which we may mention the following: The genus *Cassia* is the source of the drug senna. Alexandrian senna is produced by *C. acutifolia*, Italian senna by *C. obovata* and Arabian senna by *C. angustifolia*. Purging Cassia is obtained from *C. fistula*. In each case the leaves or the pods are dried in the sun and it is in that form that the drug is imported (Fig. 1519). *Erythrophleum guineense* is the Red Water Tree of Sierra Leone. From it is derived the poisonous Sassy bark which is used by the natives for trial by ordeal. *Tamarindus indica*, the Tamarind, is a valuable tropical tree not only on account of its fruits but also on account of its beauty. It is indigenous to Africa, but has for long been widely cultivated in the tropics. It is widely used as an ingredient in pickles and chutneys. *Haematoxylon campechianum* is a native of Central America and the West Indies. The young foliage is red and thorns develop in the leaf axils. The heart wood contains the substance haematoxylin and is used in dyeing under the name of Logwood. We may also mention *Hymenaea courbaril*, the Locust Wood; *Copaifera publiflora*, Purple Heart Wood; *Poinciana regia*, Flamboyant Tree, which is often cultivated in warm countries because of its magnificently striking red blossom. The Bird of Paradise Flower, *Caesalpinia gilliesii*, is also grown all over the subtropics for its yellow and crimson flowers.

FIG. 1519.—*Cassia acutifolia*. Fruits (Senna pods).

In *Cercis siliquastrum* (Fig. 1520) the flowers are typically papilionaceous with a zygomorphic corolla, the lower anterior petals forming a large pair enclosing the essential organs, while the posterior pair are reflexed and

FIG. 1520.—*Cercis siliquastrum*. Judas Tree. Flowers arising from one of the older branches.

wing-like, with the odd petal erect. In *Cassia* all five petals are spreading and more or less equal. *Cercis siliquastrum* is the only species of the genus which is at all commonly cultivated in this country where it is easily recognized by the purple-red flowers, which appear on the tree before the leaves. It is known as the Judas Tree because it is said that Judas Iscariot hanged himself on one. There are five species, distributed in north temperate regions. None of the other genera is commonly cultivated in Britain.

The **Mimosaceae** are characterized by minute, actinomorphic flowers, in close clusters, with long coloured stamens (Fig. 1521), and by thin bipinnate leaves. They occur in the tropics and subtropics, often in dry or semi-desert regions. The most important genus is *Acacia*, which includes some 550 species which are known under the general name of Wattles, especially in Australia, where some 300 of the species occur. Many species do not develop their pinnate leaves during the early stages of seedling development and the petioles become phyllodes. In many species stipules develop as large spines. In the Central American *A. sphaerocephala* these are inhabited by ants, which bore in and remove the entire internal tissue. Extra floral nectaries are developed on which the ants feed. If the tree is harmed the ants rush out to protect it.

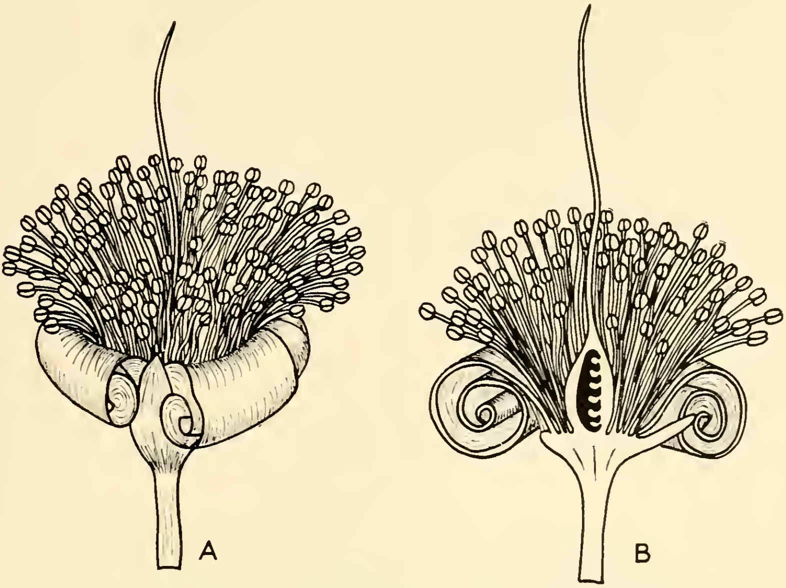


Fig. 1521.—*Acacia* sp. A, Flower. B, Longitudinal section.

Many species of *Acacia* are of economic importance. *A. senegal*, which occurs in the Sudan, yields the best Gum Arabic, which is exuded from the branches during dry desert winds. *A. catechu* is a native of the East Indies. It yields catechu or cutch which is employed in tanning and is prepared by digesting the wood in hot water. Several species produce barks which are used in tanning; that of *A. decurrens*, an Australian tree known as the Black

Wattle, is considered the best. Many species produce valuable timbers, particularly *A. melanoxylon*, the Australian Blackwood. The flowers (Fig. 1522) are often very sweetly scented and are used in perfumery, for example *A. farnesiana* which provides the "Cassia" flowers.

FIG. 1522.—*Acacia neriifolia.* Globose inflorescences.

Another genus deserves mention. *Entada scandens* is a common tropical American climber whose seeds (Fig. 1523), known as Nicker Beans, are sometimes carried to Europe and the shores of Britain by the Gulf Stream, whence the name Sea Bean is also given to it.

FIG. 1523.—*Entada scandens.* Lomentate pod breaking into one-seeded portions. Below, seeds.

Among important timber trees we may mention *Xylia dolabriformis*, the Ironwood of India; *Pithecolobium saman*, the Rain Tree, which incidentally shows nyctinastic movements of the leaves; *Lysiloma sabicu*, and *Prosopis* *juliflora*, the Mesquite Tree of the Central American savannahs, the branches of which are used for fodder. *Albizzia moluccana* is frequently used as a shade tree in young tea plantations on account of its very rapid growth, reaching 10 ft. in a year.

Finally we may mention the genus *Mimosa* itself, which is a large tropical and subtropical genus with about 400 species, most of which occur in America in contrast to the Australian Acacias. They are mainly herbs or small shrubs which are frequently beset with stipular spines. The best-known example is the pan-tropical *Mimosa pudica*, called the Sensitive Plant on account of the movement of its leaves when disturbed (see Volume III).

Papilionaceae (Viciaceae)

The Papilionaceae are a very large family which includes those plants which are sometimes referred to as the Pulses or, in common parlance, the Peas and Beans. These plants are biologically remarkable in that they possess the power of utilizing atmospheric nitrogen, through the agency of the bacteria which occur in nodules in their roots (see Volume I). In consequence they are of first-rate importance in agriculture. Not only are the seeds rich in food reserves and therefore valuable for food, but at the same time the aerial parts are useful as cattle fodder. After these have been cut and gathered, the roots left behind liberate nitrates as they decay and so improve the soil.

In temperate climates these leguminous plants are generally grown as part of a crop rotation, immediately preceding cereals such as Wheat, or other crops with a high nitrogen demand. In Britain the Red Clover is usually included in the four-year rotation; roots, Barley, Clover, Wheat. In tropical countries leguminous crops frequently serve an additional function. Due to the intensity of the sun, bare ground loses water from the surface very rapidly and freshly planted crops would very probably die before they could establish themselves. It is customary, therefore, to plant what is termed a Cover Crop, generally a legume, which covers the ground around the young plants and helps to protect them. In some instances a further cover crop of quick-growing trees, such as the leguminous *Erythrina*, may also be planted to serve the same purpose. As the crop develops the leguminous cover crop is cut and mulched, whereby the plants of the economic crop receive additional nourishment. If this economic crop consists of perennials, as for example Coffee or Bananas, a tree cover crop will be planted and eventually cut down, when the Bananas are sufficiently grown. On the other hand a herbaceous cover crop may be planted time after time to cover the ground and prevent not only loss of water but also the encroachment of weeds which might eventually stifle the main crop.

Among species which are either wild or commonly grown, we may mention the Garden Pea (*Pisum*) (Fig. 1524), the Beans (*Vicia* and *Phaseolus*), the Vetches and Alfalfa (*Vicia*), the Clovers (*Trifolium*), Lucerne (*Medicago sativa*), and Sainfoin (*Onobrychis*). A number of common shrubs

FIG. 1524.—*Pisum sativum.* The Edible Pea. Typical papilionaceous flower.

also belong to this family, among which we may mention Gorse (*Ulex*), Broom (*Cytisus*) (Fig. 1525), Petty Whin (*Genista*), which are native to Britain, and *Wistaria*, *Laburnum*, *Lupinus* (Lupin), *Robinia* (False Acacia), *Spartium* (Spanish Broom), *Indigofera* (Indigo), and *Desmodium*, which are commonly cultivated. One of the most extensively cultivated members of this family is *Arachis hypogaea*, the Ground Nut or Pea-nut, which is grown in all warm regions of the world, both for the sake of its edible seeds and for the oil expressed from them. This oil is used on a large scale for making margarine. Many species are well-known field plants, as for

FIG. 1525.—*Cytisus.* Hybrid Johnston's Crimson. Flowering shoot.

example, *Ononis spinosa* (Rest Harrow), *Lotus corniculatus* (Bird's-foot Trefoil), *Anthyllis vulneraria* (Lady's Fingers), *Astragalus glycyphyllos* (Milk Vetch), *Hippocrepis comosa* (Horseshoe Vetch), *Lathyrus pratensis* (Meadow Vetchling), and *Melilotus arvensis* (Melilot).

To the number of ornamental plants cultivated in gardens and greenhouses the Papilionaceae contribute very considerably. Some have been mentioned above, among the others we may cite especially *Galega*, *Baptisia*, *Erinacea*, *Sophora*, *Coronilla* and *Colutea*.

Mention may also be made of two genera from which important insecticides have been marketed recently. The first is the genus *Derris*. *D. elliptica* and *D. trifoliata* are climbing plants living in the jungle undergrowth of India and Malaya. From the roots, which are referred to as Tuba Roots, is obtained the derris powder of commerce. The second genus is *Lonchocarpus*. From the species *L. nicou* which is locally common in South America has been prepared a similar insecticide. In this case however the material is made from the bark. The poisonous properties of both have been known locally for a long time, for the natives use them to poison arrow heads. The insecticidal property in both is due to an active ingredient known as rotenone.

The members of the Papilionaceae may be trees, shrubs or herbs, with either simple or compound leaves, the latter not infrequently having one or more leaflets modified as tendrils. Stipules are usually present and may be either large and leaf-like, as in *Pisum* and *Lathyrus*, contributing largely to the assimilating area, or small and reduced, or even modified into spines, as in *Robinia*.

The **inflorescence** is always racemose. It is commonly a simple raceme, sometimes a panicle or a spike consisting of but few flowers.

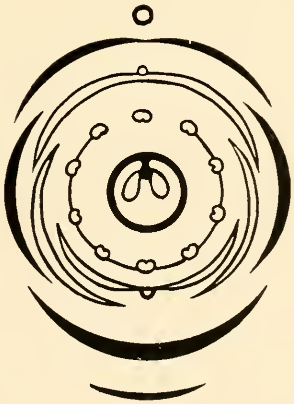


Fig. 1526.—Floral diagram of *Vicia faba* (Papilionaceae).

The **flowers** (Fig. 1526) are hermaphrodite, hypogynous or perigynous and zygomorphic, and are often of considerable size and brightly coloured.

The **calyx** is gamosepalous and five-toothed or sometimes bilabiate, caused by a partial split of the tube into a two- and a three-toothed part.

The **corolla** is polypetalous, composed of five petals which are regularly imbricated in a characteristic descending manner in the bud (Fig. 1527). These petals are all dissimilar and have received separate names. The adaxial petal is large and forms the *standard* or **vexillum**; the two lateral ones form the *wings* or **alae** and lie more or less parallel to each other, while the two lower petals which lie internal to the wings and are united by their lower margins, form the *keel* or **carina**.

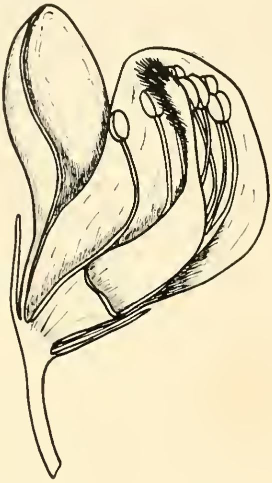


FIG. 1527.—*Pisum sativum.* Longitudinal section of flower showing arrangement of corolla parts in relation to the sex organs

The **androecium** consists of ten stamens which may be all free or either monadelphous, as in *Cytisus*, or diadelphous, as in *Lathyrus*, where the posterior stamen is free. The anthers mostly open lengthwise.

The **gynoecium** is monocarpellary and the ovary superior and unilocular. The ovules are indefinite in number, anatropous or campylotropous, alternating in two rows, with marginal placentation.

The **fruit** is usually a legume or more rarely a lomentum.

The **seed** is large and non-endospermic, the embryo consisting of two large hemispherical or flattened cotyledons, with a generally superior or ventrally placed radicle.

The family is the second largest of the Dicotyledons and contains about 500 genera and over 11,000 species. It forms a very characteristic and natural group with world-wide distribution. There are few anatomical features which are characteristic of the whole family. Internal secretory systems of various kinds are generally present. Anomalous stem structure is associated with liana types and consists mainly of the development of phloem tissue in the secondary wood, *e.g.*, *Phaseolus*, or the development of successive rings of vascular bundles as in *Wistaria*. On account of its very large size the classification of the Papilionaceae is necessarily somewhat complicated. The following therefore is an outline of the main points.

I. **Sophoroideae**

The flowers have ten stamens which are all free, the leaves are compound and are pinnately arranged. *Sophora*, *Myroxylon*.

II. **Podalyrioideae**

The flowers have ten stamens all of which are free. The leaves however are either simple or palmate. *Podalyria*, *Anagyris*, *Baptisia*.

III. **Genistoideae**

The stamens are ten in number and generally monadelphous. The plants are usually shrubs or occasionally herbs with simple or pinnate compound leaves and entire leaflets.

1. *Liparieae.* Leaves simple exstipulate, posterior stamen free, or rarely (in uniovulate genera) connate with the others. Seeds with a caruncle (p. 1670). *Priestleya*, *Liparia*.
2. *Bossiaeae.* Leaves simple, often stipulate. Stamens united into a tube which is split above. Seeds with a caruncle. *Bossiaea*, *Hovea*.
3. *Crotalarieae.* All stamens united into a tube which is split above. Seeds without a caruncle. *Crotalaria*, *Lotononis*, *Aspalanthus*.
4. *Spartieae.* All stamens united into a closed tube. Seeds without a caruncle. *Lupinus*, *Spartium*, *Genista*, *Laburnum*.
5. *Cytisieae.* All stamens united into a closed tube. Seeds with a caruncle. *Ulex*, *Cytisus*, *Hypocalyptus*.

IV. **Trifolioideae**

The stamens are ten in number and either diadelphous or more rarely monadelphous. The plants are herbs or rarely shrubs, with pinnately or occasionally palmately trifoliate leaves, the veins generally ending in teeth at the leaf margin. *Ononis*, *Trigonella*, *Medicago*, *Melilotus*, *Trifolium*.

V. **Lotoideae**

The stamens are ten in number and either diadelphous or monadelphous. The plants are herbs or undershrubs with pinnately trifoliate or multifoliate leaves with entire leaflets. *Lotus*, *Anthyllis*, *Hosackia*.

VI. **Galegoideae**

The stamens are ten in number and usually diadelphous. The plants are herbs, erect shrubs or, more rarely, trees or climbing shrubs with pinnate leaves, and generally entire leaflets.

1. *Psoralieae.* Shrubs or herbs with leaves glandular-punctate. Inflorescences racemes or spikes, terminal or axillary. Legume small, indehiscent, usually one-seeded. *Amorpha*, *Dalea*.
2. *Indigofereae.* Shrubs or herbs, often hairy. Inflorescences axillary racemes or spikes. Anther connectives with apical appendages. Legume two-valved. *Cyanopsis*, *Indigofera*.

3. *Brogniartieae.* Erect shrubs. Pedicels paired in the axils or arranged in terminal racemes. Seeds with caruncle. Radicle of embryo straight. *Harpalyce*, *Brogniartia.*
4. *Tephrosieae.* Habit various. Inflorescences variable. Legume two-valved. *Galega*, *Tephrosia*, *Millettia.*
5. *Robinieae.* Habit various. Inflorescences axillary racemes or fasciculate at the older nodes. Posterior stamen often free. Legume two-valved, usually flat. *Robinia*, *Biserrula*, *Carmichaelia.*
6. *Coluteae.* Shrubs or herbs. Inflorescences racemose, axillary. Standard petal usually flat or reflexed. Posterior stamen free. Style bearded. Legume inflated and opening only at the apex. *Lessertia*, *Colutea.*
7. *Astragaleae.* Shrubs or herbs. Inflorescences all axillary. Flowers racemose or solitary. Standard petal erect, usually narrow. Posterior stamen free. Style without beard. Legume usually inflated, longitudinally septate. *Astragalus*, *Oxytropis*, *Glycyrrhiza.*

VII. **Hedysaroideae**

The stamens are ten in number and usually diadelphous. They are characterized by the fruit, which is a lomentum and not a legume.

1. *Coronilleae.* Shrubs or herbs. Leaves pinnate, rarely simple. Inflorescenes axillary, umbellate. Posterior stamen free. Stamen filaments dilated upwards. *Ornithopus*, *Coronilla*, *Hippocrepis.*
2. *Euhedysareae.* Herbs or sub-shrubs. Leaves pinnate, rarely with one leaflet. Stipules often dry and membranous. Inflorescences axillary, racemose. Petals often withering but persistent. Wing petal very short. Carina obliquely truncate at apex. Posterior stamen usually free. Filaments not dilated. *Hedysarum*, *Onobrychis.*
3. *Aeschynomeneae.* Shrubs or herbs. Leaves pinnate, pinnae usually indefinite. Flowers in axillary racemes of few flowers. Alae usually transversely folded. Stamens all united or united into two groups. Posterior stamen rarely free. *Aeschynomene*, *Smithia.*
4. *Adesmieae.* Shrubs or herbs. Leaves pinnate, pinnae indefinite. Flowers in terminal racemes. Stamens all free. *Patagonium*, *Adesmia.*
5. *Stylosantheae.* Woody herbs, often gummy. Leaves with few pinnae. Flowers in capitate terminal spikes or axillary. Stamens all united in a closed tube. Anthers alternately basifixed and versatile. *Stylosanthes*, *Arachis.*
6. *Desmodieae.* Herbs or woody climbers. Leaves pinnate, with three pinnae, terminal leaflet with two stipellae. Flowers usually in pairs on rachis, racemes terminal or axillary. Standard petal narrowed at the base, wing petals united to the keel near the

base. Posterior stamen free or united at the base only. *Desmodium*, *Lespedeza.*

VIII. **Vicioideae**

The flowers have ten stamens which are always diadelphous. The plants are herbs with imparipinnate leaves, the rachis ending either in a tendril or a short prolongation representing a modified terminal leaflet. *Vicia*, *Lathyrus*, *Pisum*, *Lens*, *Abrus*, *Cicer.*

IX. **Phaseoloideae**

There are ten stamens which are diadelphous. The plants are usually climbing herbs or more rarely erect shrubs, or occasionally trees. The leaves are pinnate, generally trifoliate, leaflets usually with stipellae.

1. *Glycineae.* Standard petal sometimes with minute basal appendages. Posterior stamen free or united at the base only. *Glycine*, *Kennedya.*
2. *Erythrineae.* Inflorescences of interrupted racemes. Flowers large. Standard petal sometimes the largest, sometimes shorter than the carina. Posterior stamen free or united at the base only. Bracts usually shed early. *Erythrina*, *Apios*, *Mucuna.*
3. *Galactieae.* Inflorescences of interrupted racemes or broad panicles. Bracts dropping very early. Calyx usually four-lobed, the two posterior united into one. Posterior stamen free. *Spatholobus*, *Galactia.*
4. *Diocleae.* Inflorescences of interrupted racemes. Bracts shed very early. Calyx usually four-lobed or sometimes two-lipped. Posterior stamen free to the base, the others united into a closed tube. *Camptosema*, *Dioclea*, *Pueraria.*
5. *Euphaseoleae.* Inflorescences of interrupted racemes. Bracts shed very early. Carina often long-beaked or spiral. Posterior stamen free. Style bearded above on the interior face. *Physostigma*, *Phaseolus*, *Dolichos.*
6. *Cajaneae.* Inflorescences in continuous racemes or subumbellate. Bracts falling very early. Bracteoles absent. Posterior stamen free. *Dunbaria*, *Cantharospermum*, *Rhynchosia*, *Cajanus.*

X. **Dalbergioideae**

There are ten stamens which may be monadelphous or diadelphous. The plants are trees or shrubs or occasionally climbers. The leaves are pinnate with from five to many pairs of leaflets. The pod is indehiscent and is sometimes a drupe.

1. *Pterocarpeae.* Leaves with alternate pinnae or rarely solitary. Seeds often transversely attached. *Dalbergia*, *Machaerium*, *Pterocarpus.*
2. *Lonchocarpeae.* Leaves with opposite pinnae. Seeds often transversely attached. *Lonchocarpus*, *Derris.*
3. *Geoffraeae.* Keel petals free. Legume drupaceous or swollen. Seeds one, pendulous. *Andira*, *Coumarouna.*

In such a vast assemblage of genera as are included in the Papilionaceae it is obviously impossible to do more than touch quite briefly upon a few of the more outstanding. In the Sophoroideae the more important genera, *Sophora* and *Ormosia*, are widely distributed throughout the tropics, though the sub-family also includes a number of small or monotypic genera mostly restricted to the warmer parts of America. Species of *Sophora* are cultivated in the warmer parts of Britain, where their large yellow flowers make them desirable shrubs. The wood is very hard. *S. japonica* is the source of the dye which was used for the Imperial yellow of China.

The sub-family Podalyrioideae contains some forty genera, the great majority of which are restricted to Australia; two genera occur in South Africa, the remainder in temperate Asia and North America. They are of little economic or cultural importance.

The third sub-family, Genistoideae, contains a number of important genera, several of which occur wild in Britain. Species of *Crotalaria* and more particularly *C. juncea* and *C. retusa* are large annual plants which are cultivated for the fibres which are obtained by maceration of the stem. These fibres form the Sunn Hemp or Madras Hemp which is exported from India as a cheap substitute for European Hemp. *Crotalaria* is a large genus of some 350 species which is widely distributed in the tropics and subtropics.

The genus *Lupinus*, from which the garden Lupins (*L. polyphyllus*) have been bred, is principally American, with about 150 species. The fruit is explosive, the two valves of the legume twisting spirally to eject the seeds. In some countries, species of *Lupinus*, chiefly *L. luteus*, are grown as a field crop like clover, the stems being used as fodder and the seeds as an article of food in south Europe.

Laburnum, a tree, with three species, and *Cytisus*, a shrub, with forty species, are both natives of southern Europe. In the latter genus the leaves are reduced or scaly and assimilation is performed by the green stems. The fruit explodes as in *Lupinus*. The first "graft hybrid", one between the Common Laburnum (*L. anagyroides*) and the purple Broom (*Cytisus purpureus*), was produced by J. L. Adam in his nursery at Vitry near Paris in 1825. This was a graft of the Broom on Laburnum which produced shoots of an intermediate type. Older trees showed branches not only of the hybrid but of both parents as well. These graft hybrids are termed **chimaeras**, because there seems to be a mixture of the tissues of both parents, rather than a genetic fusion. On microscopic examination it is often found that the outer tissues are characteristic of one parent, which seem to form a covering over the inner tissues which are characteristic of the other parent. We shall refer again to graft hybrids in Volume III.

In the genera *Ulex* (Gorse) and *Cytisus* (Broom) the seeds possess at one end, near the hilum, an orange-coloured appendage which is termed a **caruncle** or **elaeiosome**. It is rich in oil which is apparently attractive to ants, which carry off the seeds, thereby assisting in their distribution. The pollination mechanism in this sub-family is explosive. There are minor differences in the mechanism in various genera but we may describe that of *Genista* as typical (Fig. 1528).

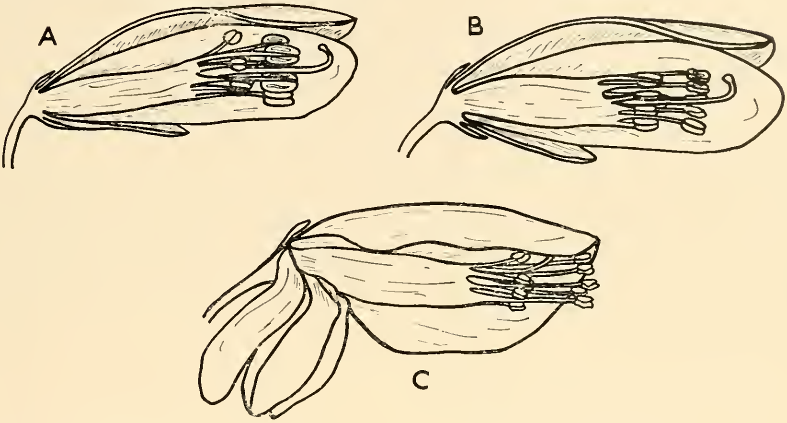


FIG. 1528.—*Genista anglica.* Longitudinal sections of flowers illustrating pollination.

The yellow flowers are arranged in racemes and are devoid of nectar and of nectar guides. The two pentamerous whorls of stamens and the projecting style are closely surrounded by the keel. While still in the bud the four upper stamens of the outer whorl dehisce and their pollen is pushed towards the lips of the keel by the elongation of the five inner stamens. The filaments then wither. As soon as the standard expands the remaining six stamens discharge their pollen so that now the upper part of the keel encloses all the pollen and the lower part of the style. The style together with the staminal tube makes a compressed spring exerting upward pressure, while the claws of the keel petals and the interlocking alae form a second spring which presses downwards. These two springs operate against one another and the parts remain in equilibrium until the upper edges of the keel petals are separated. The wing petals interlock with angular projections from the two keel petals and it follows that when a bee settles on the flower with the legs on the wing petals and thrusts its head under the standard, the wing petals are pressed down and slip off the keel while the two keel petals open out and release the style and stamens. This sudden movement presses the pollen on to the lower surface of the insect, which is also touched by the style simultaneously. If the insect has previously visited another flower, cross-pollination occurs. If cross-pollination is not effected, self-pollination is ensured as the insect backs out of the flower, since the stigma will be dusted with the pollen that the insect has received on its ventral surface. This explosive mechanism can apparently be brought into action only by the application of external pressure.

In the Trifolioideae, a small sub-family of only six genera, five occur in Britain. One of these, the genus *Ononis*, is essentially a Mediterranean one. It contains about seventy species. *Trigonella*, with the same number of species, has spread from the Mediterranean northwards into central Europe, though several species occur in other parts of the world. The genus *Medicago* is more widely distributed. There are about fifty species occurring in Europe, Asia and North Africa. *M. sativa* (Lucerne) is an eastern Mediterranean plant which is extensively cultivated, particularly in America, as a fodder crop. It is interesting to note that for successful growth in new areas the seeds must be inoculated with the appropriate strain of nodule bacteria. *Melilotus*, with twenty species, occurs in temperate and subtropical parts of the Old World. Finally there is the large genus *Trifolium* with about 290 species, which occur chiefly in the north temperate zone, though a few species are found in more southern mountainous regions. Several species are cultivated, of which *Trifolium pratense* var. *sativum* and *T. incarnatum* are the most important. In Britain *T. repens* is very valuable as a source of nectar for hive bees.

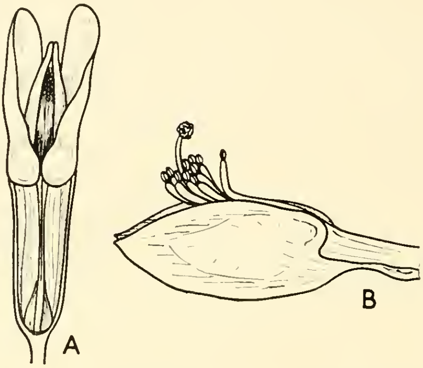


FIG. 1529.—*Trifolium repens.* A, Flower from above after removal of calyx and standard petal. B, *T. pratense.* Carina of flower after depressal showing emergence of stamens and stigma. (*After Knuth.*)

As will be gathered, these flowers (Fig. 1529) possess nectar and the pollination mechanism is relatively simple. The nectar is secreted on the inner side of the base of the staminal tube. Since the calyx tube is short, even short-tongued insects can reach the nectar. The wing petals are partly fused with those of the keel and the whole moves upwards and forwards together, but the depression is facilitated by very slender claws which are fused for the most part to the staminal tube. The closing of the flower is brought about by the claws of the standard, which grasp the other petals as well as the stamens, and by their elasticity guide them back into place when the pressure exerted by the visiting insect is removed. To reach the nectar the insect must thrust its head below the standard and owing to the small size of the keel it has only the wing petals to support it. These, together with the keel, are consequently depressed and the stamens and stigma protrude from the keel. Since the stigma projects well beyond the anthers, it touches the insect first and consequently cross-pollination is made sure. Only bees are able to work the mechanism successfully. This species is apparently entirely self-sterile and in the absence of insect visits no viable seed is produced.

The Lotoideae are also quite a small sub-family of eight genera. *Lotus* itself has about fifteen species mostly in temperate Europe and Asia. *Anthyllis* with thirty species occurs in Europe, North Africa and Asia, while *Hosackia* with thirty species is found in western North America.

The pollination mechanism in *Lotus* is somewhat different from those so far described and is based upon a pumping system. In *Lotus corniculatus* (Fig. 1530) nectar is secreted as usual at the base of the stamen tube. The wing petals possess deep depressions near the base of the limb, which fit into corresponding pits in the upper ends of the keel. Immediately behind this point the wing petals are fused together so that when a suitable insect visits the flower the wings and keel are simultaneously depressed. In the bud the ten anthers discharge their pollen into the tip of the keel and then shrivel up. As the flower grows the filaments of the five outer stamens elongate, and their ends thicken and shut off the tip of the keel forming a pollen chamber. This conceals the stigma and there is a slit along its upper margin. When the keel is depressed the filaments are thrust further into the keel and push out pollen through the slit. As pressure continues the stigma is also protruded so that either cross-pollination or self-pollination may take place. The latter however is ineffective because the stigmatic surface must be rubbed before it is receptive and this can only happen when it is touched by a visiting insect.

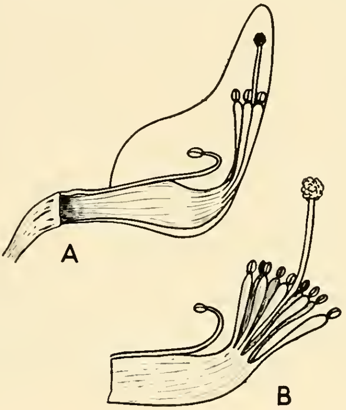


Fig. 1530.—*Lotus corniculatus.* A, Flower from the side after removal of one wing petal. B, Androecium and style in position immediately after removal of the pollen. (*After Knuth.*)

When we pass to the next sub-family, the Galegoideae, we find a much larger assemblage of nearly seventy genera, arranged in a number of distinct tribes. Several of the genera are important. *Indigofera* is a large tropical genus with about 350 species. *I. leptostachya*, *I. tinctoria* (Fig. 1531) and others are the source of the indigo dyes. The plants are cut just before flowering and are soaked in water producing a yellow solution, which, on exposure to the air, oxidizes and precipitates insoluble indigo. Another very important genus is *Astragalus*, one of the largest in the world. It contains some 1,600 species, the majority of which inhabit the north temperate regions of the Old World, almost all in dry continental areas. About 200 species are found in North America, but none is found in Australia. Many of the species are thorny, the thorns being produced by the petiole or mid-rib which hardens when the lamina disappears. Several possess gums which are used commercially. *A. gummifer* is the source of Gum Tragacanth which is obtained by wounding the stem.

FIG. 1531.—*Indigofera tinctoria.* Flowering shoot.

Several genera are grown in gardens. *Robinia*, with six North American species, is the Locust or False Acacia. The leaflets move upwards in hot air and the base of the petiole forms a cup over the developing axillary buds. *Colutea* with twelve species occurs from southern Europe to the Himalayas. *C. arborescens* is the Bladder Senna. Its leaves have the same properties as Senna (*Cassia*) and are used as an adulterant. The pods are inflated and burst on pressure. *Glycyrrhiza* is a small tropical genus, important because *G. glabra* is the source of Spanish liquorice which is extracted from the rhizome and exported chiefly from Iraq. The species *Carmichaelia australis* is sometimes grown in gardens. It is interesting because it is characteristically xeromorphic, the stems being converted into cladodes without any green leaves. There are some twenty species which are restricted to New Zealand and Lord Howe Island. *Biserrula pelecinus* (Fig. 1532) produces pods which superficially resemble caterpillars and are said to be picked up by birds in mistake, whereby the seeds are distributed.

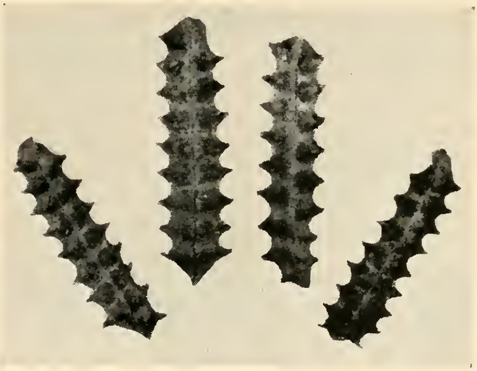


FIG. 1532.—*Biserrula pelecinus.* Legumes resembling caterpillars.

The sub-family Hedysaroideae is also a large one, containing nearly fifty genera, the majority of which are either tropical or subtropical plants. A few occur in the Mediterranean region, temperate Asia and South America. One of the most important genera is *Arachis*, of which there are ten South American species. *A. hypogaea* is the Ground Nut or Pea-nut, which is now widely cultivated in the warmer parts of the world, especially in West and East Africa. The seeds are edible and when pressed yield one of the oils which are used for the manufacture of margarine. The plant is interesting in that the flowers after fertilization bend downwards, and, by the elongation of the flower stalk, the young pod is thrust underground where it ripens.

Coronilla varia exhibits a pollination mechanism not unlike that in *Lotus corniculatus*. The nectar is usually secreted on the outer surface of the calyx although in some flowers it may be absent. All ten stamens are concerned in pushing the pollen forward into the keel; moreover the pollen grains are joined together in threads. The keel is not easily depressed. Bees settling on the flower push about among the petals for the nectar and effect cross-pollination. It is doubtful if self-pollination can take place.

The Vicioideae are a small and remarkably uniform sub-family comprising only six genera and about 150 species. Two of these, *Vicia* and *Lathyrus*, are common in this country. *Pisum*, with six species, is a native of the Mediterranean and western Asia, and *Lens*, also with six species, is similarly distributed. All the genera are of great economic importance, as for example the Broad Bean, *Vicia faba*; the Garden Pea, *Pisum sativum* and *Lens esculenta*, largely cultivated in southern Europe and sold as the Lentil. *Cicer arietinum* is the Chick Pea which is used for food in southern Europe and India. The genus *Abrus* contains six tropical species, of which

A. precatorius has hard, red seeds with black tips which are often manufactured into necklaces. In India they are used as weights. The roots yield Indian liquorice.

In this sub-family the pollination is again somewhat different and depends upon a brush mechanism. In *Vicia cracca* (Fig. 1533) the wing petals are united to the keel at two places. When a bee visits the flower it settles on the wings and since these are firmly united with the keel they act as the arms of a lever and cause its depression. When the flowers have reached about half their full size the anthers dehisce. They closely surround the style, the upper part of which is beset with upwardly projecting, dense, fine hairs. Thus the stigma and the hairs become liberally dusted with pollen. When a bee visits the flower, pollen adheres to its underside and the stigma is, at the same time, rendered sticky and receptive by the brushing of its papillate surface.

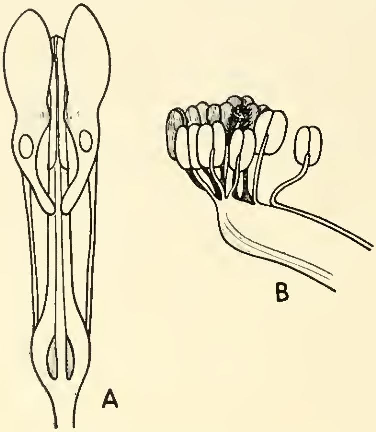


Fig. 1533.—*Vicia cracca.* A, Flower from above after removal of standard and calyx. *Vicia sepium.* B, Androecium and style in position in the unopened flower. (*After Knuth.*)

In many species of this genus there are extra-floral nectaries. These are dark-coloured spots situated on the underside of the stipules. They only secrete nectar in sunny weather. The secretion is sought after by ants, which may perhaps protect the plants against caterpillar attacks.

The genus *Lathyrus* is a large and important one. There are over 100 species. *Lathyrus odoratus* is the species from which the garden Sweet Peas have orginated. *L. latifolius* is the Everlasting Pea. Several species are of economic importance. *L. sativus* and *L. cicera* are used as fodder, while *L. macrorrhizus* has tuberous roots which may be eaten like potatoes. Morphologically the genus is interesting because of the large green stipules, which in *L. aphaca* are the only assimilating organs. The lamina of the leaf is converted into a tendril, while the petiole may become flattened into a phyllode, as in *L. nissolia.*

The Phaseoloideae are another large sub-family, comprising some fifty genera which are widely distributed in the tropics and warmer parts of the world. The most important genus is *Phaseolus* with 160 species, mostly in tropical regions; *P. multiflorus* (Scarlet Runner) and *P. vulgaris* (Kidney or French Bean) are both South American in origin and were originally cultivated for their flowers. Another extremely important species is *Glycine soja* which provides the Soya Bean of commerce (Fig. 1534). Not only is the bean itself used for food but the pressed seeds provide an oil which after fractional distillation can be used, not only for nourishment, but also as an illuminant. The flour is used as cattle cake and the foliage as fodder. A fermented mash of the seed provides the aromatic "Soy" which is the base of Worcester sauce. Another tropical genus which is extensively cultivated is *Dolichos*. *D. lablab* is grown for its edible seeds, while *D. biflorus* is used for feeding horses and cattle, particularly in India. A number of genera are grown as ornamental flowers, for example *Kennedya*. The genus *Physostigma* includes two African species, of which the poisonous *P. venenosum* is the Calabar Bean, which is used in various ordeal ceremonies.

FIG. 1534.—*Glycine soja*. Soya Bean. Shoot with pods.

The pollination mechanism in this sub-family may be exemplified by *Phaseolus* (Fig. 1535). The flowers yield nectar and the anthers closely surround the style and shed their pollen on to it, but the stigma is never dusted. There are two nectar passages and the filament of the single free stamen broadens out forwards so that it closes completely the staminal tube. Insects can only obtain nectar legitimately by alighting on the left wing petal and thrusting their probosces under the opening on the right side of the tip of the keel. Only large humble bees can do this. When the keel is depressed the style springs out. It is a coiled brush-like structure and it is pushed out of the opening in the keel. The free stamen retains its position but the other nine are depressed. Since the proboscis of the insect touches the stigma before the pollen, cross-pollination is regularly effected and unvisited flowers remain sterile.

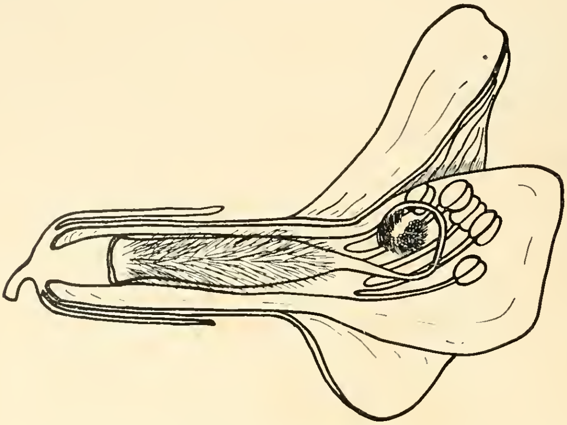


FIG. 1535.—*Phaseolus multiflorus.* Flower in longitudinal section.

The final sub-family is the Dalbergioideae, which contains twenty-seven genera. They are mostly trees or shrubs and many of them produce woods of economic importance. *Pterocarpus santalinus* yields red Sandalwood, *P. marsupium*, Bastard Teak, *Dalbergia nigra*, Rosewood, *D. melanoxylon*, Blackwood, and *D. latifolia*, East Indian Rosewood. Many are lianas, climbing by short lateral shoots which are sensitive to contact, as in *D. variabilis.* They are mostly tropical plants occurring especially in Africa and southern Asia. There are no British representatives.

From the above account it may be noted that the pollination mechanisms are distinct in each of the sub-families. The following scheme in which some common genera are grouped according to the mechanisms employed serves to bring out this point more clearly.

1. *Simple valvular arrangement.* Stamen and stigma project from the keel as long as the pressure of the insect continues and then return to their former positions. Such flowers allow a number of effective visits.

(*a*) Nectar present. *E.g.*, *Melilotus*, *Trifolium*, *Galega*, *Onobrychis*, *Astragalus*, *Oxytropis*, *Phaca*, *Ornithopus*, *Hedysarum.*

(*b*) Enclosed sap reached by boring. *E.g.*, some species of *Cytisus.*

2. *Explosive arrangement.* Stamens and stigma suddenly spring out of the keel. Such flowers allow of only one effective visit.

(*a*) Nectar present. *E.g.*, *Medicago.*
(*b*) Nectar absent.
  (i) Ventral surface of the bee comes into contact with the pollen and the stigma. *E.g.*, *Genista*, *Ulex.*
  (ii) The bee is struck on the back by the pollen and by the stigma. *E.g.*, *Sarothamnus.*

3. *Pump arrangement.* The thickened ends of the filament press out the pollen in successive portions from the tip of the keel. Several insect visits are necessary for pollination.

(*a*) Nectar present. *E.g.*, *Lotus*, *Anthyllis*, *Hippocrepis.*
(*b*) Nectar absent. *E.g.*, *Ononis*, *Lupinus*, *Coronilla.*

4. *Brush arrangement.* A brush of hairs on the style sweeps the pollen out of the tip of the keel. Repeated insect visits are usually necessary for pollination.

(*a*) The tip of the style is straight. *E.g.*, *Lathyrus* (Fig. 1536), *Pisum*, *Vicia*, *Lens*, *Robinia.*
(*b*) The tip of the style is coiled. *E.g.*, *Phaseolus.*

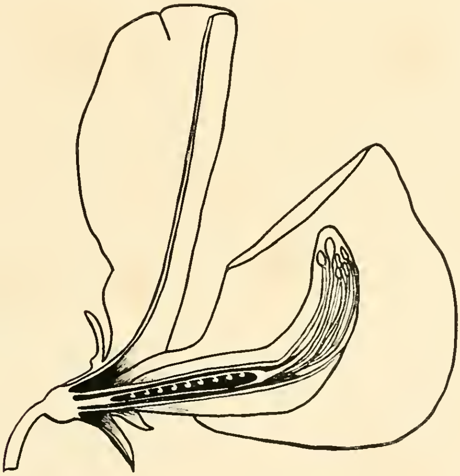


FIG. 1536.—*Lathyrus odoratus.* Flower in longitudinal section.

SAXIFRAGALES

It has already been explained why it is considered desirable to separate the Saxifragales from the Rosales. Under the present treatment the Saxifragales are regarded as including only the four families: Crassulaceae, Cephalotaceae, Saxifragaceae and Podostemaceae. The Saxifragales may be defined as Archichlamydeae in which the plants are typically herbaceous, with flowers which are actinomorphic and more or less perigynous, though a few are epigynous. A corolla is present and the stamens are definite in

FIG. 1537.—*Kalanchoë (Crassula) flammea.* Flowering shoot.

number and free. The ovary is either apocarpous or syncarpous and the ovules are generally numerous with axile placentation. The seeds usually possess copious endosperm and the embryo is straight.

We shall consider the Saxifragaceae in detail below, but before doing so we must say something about the important family Crassulaceae and refer more briefly to the Cephalotaceae and Podostemaceae.

The **Crassulaceae** are a large family containing some twenty-five genera and about 1,450 species, a number of which occur in Britain. They are mostly perennial plants living in dry situations, especially in South Africa. The plants are usually xerophytes, generally showing succulent characters, with fleshy leaves and sometimes with contracted stems. Many exhibit vigorous vegetative propagation by means of rhizomes or offsets. Some, such as *Crassula* (Fig. 1537), form bulbils, others, such as *Bryophyllum*, produce new plants from buds borne on the leaves. The anatomy of the leaves usually shows a large development of parenchyma and a small development of vascular tissue. Mucilage cells are generally present.

The flowers are usually borne on long fleshy stems, the inflorescence being a cincinnus, as in *Echeveria* (Fig. 1538). The flowers are usually hermaphrodite, actinomorphic and very regular in construction, the number of parts varying from three to thirty. The family is exceptional in having the petals more or less united into a corolla tube in certain genera, *e.g.*, *Bryophyllum*, *Cotyledon*, *Rochea*, etc., a feature which is rare in the Archichlamydeae. There are usually twice as many

FIG. 1538.—*Echeveria elegans.* Inflorescence.

stamens as petals. The carpels are generally united at their bases and nectaries are usually present. Each carpel contains numerous ovules. The fruit is often an etaerio of follicles and contains many very small seeds. These seeds are usually devoid of endosperm. Pollination is often effected by flies, the flowers being mostly protandrous. Many of the plants are cultivated and are commonly planted in dry walls and rock gardens. *Sempervivum* (Fig. 1539) is called the House Leek, because one species, *S. tectorum*, was once commonly planted on cottage roofs as a protection against "thunderbolts". The plants are amazingly tenacious of life and will grow even in a herbarium press. Some fifty species are known from southern Europe and the Himalayas. *Cotyledon umbilicus* (Pennywort) is common on old walls in the western parts of Britain, and the same is true of a number of species of *Sedum* (Fig. 1540) of which *S. acre* (Biting Stonecrop) is the most common in dry and exposed places.

FIG. 1539.—*Sempervivum tectorum*. House Leek. Flowering plant with many rosettes growing over a rock.

The family **Cephalotaceae** is monotypic, the only species being

FIG. 1540.—*Sedum* (*Rhodiola*) *rosea*. Flowering shoot.

The flowers are apetalous but the calyx consists of six coloured lobes which are united at the base. There are twelve stamens which are perigynous and inserted at the top of the calyx tube. There are six carpels which form a polycarpellary gynoecium, each with one, or rarely two, basal, erect ovules. The fruit is an etaerio of follicles, which is surrounded by the accrescent calyx, covered outside by dense hairs.

The fourth family, the **Podostemaceae**, includes a number of very remarkable though very reduced aquatic plants. Some twenty-two genera are recognized and include about 100 species. They are all of them tropical but the family is widely distributed. The anatomical modifications in these

Cephalotus follicularis which is found only in marshes in Western Australia (Fig. 1541). It is a remarkable insectivorous plant, whose leaves are developed into pitchers. These pitchers resemble in structure those of *Nepenthes* but are only produced by some of the leaves. The lower leaves of the rosette form pitchers while the upper leaves are flat, elliptical and entire. Only the latter assimilate carbon dioxide.

FIG. 1541.—*Cephalotus follicularis*. Habit of the flowering plant. (*After Robt. Brown.*)

plants have proceeded so far that it is very difficult to recognize the original organs from which the structures have been produced, and in the vegetative state many of them might be mistaken for Thallophytes (Fig. 1542). The minute seeds on germination give rise to an axis which is devoid of any primary root. From this primary axis is budded off endogenously a creeping thallus which is more or less root-like. Its form and mode of growth vary greatly in different genera. In *Podostemon* it is more or less filamentous, creeping over rocks to which it is attached by exogenously developed haptera. Secondary shoots arise endogenously from the thallus and may produce minute leaves, and subsequently the flowers. These flowers are hermaphrodite, achlamydeous and enclosed in a spathe. There is a variable number of stamens and a bicarpellary gynoecium with two loculi and numerous ovules with axile placentation. The plants live only in very fast running water and grow submerged on rocks in rivers. Naturally in such very greatly specialized plants the systematic position is subject to dispute and the inclusion of them in the Saxifragales is tentative. Hutchinson relegates them to a separate order, Podostemales.

FIG. 1542.—*Mourera weddeliana.* A large representative of the Podostemaceae. (*After Baillon.*)

Although the family is widespread in the tropics, the individual species have often a very restricted distribution and many occur only in a single locality. They provide an interesting problem in evolution.

Saxifragaceae

The family is a large one, containing a number of well-known genera, of which four are native to Britain. They are *Saxifraga*, *Chrysosplenium*, *Parnassia* and *Ribes*. Species of *Saxifraga* are typical of alpine districts, though *S. granulata* (Meadow Saxifrage) and *S. tridactylites* are lowland plants. *Chrysosplenium oppositifolium* (Golden Saxifrage) grows in wet ditches. *Parnassia palustris* (Grass of Parnassus) grows in wet grassland, frequently coastal. The genus *Ribes* includes several species which are cultivated on account of their fruits. *R. uva-crispa* is the Gooseberry, *R. rubrum* is the Red Currant and *R. nigrum* the Black Currant. The genus *Ribes* is sometimes placed in a separate family, the Grossulariaceae, on account of its woody habit and inferior ovary.

The family is widely represented in gardens. Many species of *Saxifraga* have been introduced as rock plants and the genus is among the most important to the rock gardener. Many cultivated shrubs also belong to this family among which we may cite *Ribes sanguineum* (Flowering Currant), *Hydrangea* and *Philadelphus* (Mock Orange) as examples.

The limits of the family vary considerably in the view of different authorities, Hutchinson, for example, excluding Currants, Hydrangeas and Escallonias as separate families and grouping them in the Rosales. We shall not adopt this separation here but take the older and broader view which includes them as separate tribes of the Saxifragaceae.

The **plants** are mostly herbs or small shrubs with usually alternate leaves and generally small or moderate-sized flowers which are arranged in complex inflorescences.

The **inflorescence** may be either racemose or cymose, though occasionally solitary flowers occur.

The **flowers** (Fig. 1543) are hermaphrodite, usually actinomorphic and show a transition from hypogyny through perigyny to epigyny.

The **calyx** is composed of five or rarely four sepals, which may be free or united together into a tube.

The **corolla** is composed of five or occasionally four petals, which are imbricated in the bud. In *Chrysosplenium* the corolla is wanting.

The **androecium** is composed of ten, or rarely eight, stamens, which are obdiplostemonous. They may be borne on a prolongation of the receptacle above the tip of the ovary, forming a marginal ring.

The **gynoecium** is composed of from two to five carpels, often two; and the ovary may be either unilocular or multilocular. The swollen marginal placentas bear several rows of anatropous ovules (Fig. 1544). The ovules frequently possess only one integument.

The **fruit** is either a capsule or a berry and contains many small seeds with a copious supply of endosperm. The embryo is minute.

The family is most characteristic of temperate and arctic regions. Many of the species are cosmopolitan, while others are restricted to certain mountain ranges. There are some ninety genera and 750 species. There are few general anatomical features though a tendency to form scalariform perforations in the vessel walls is of frequent occurrence. Hydathodes on the leaves and chalk glands connected with them occur in some genera, especially *Saxifraga*, where they distinguish certain sub-genera known as the "Crusted Saxifrages". The family is subdivided as follows:

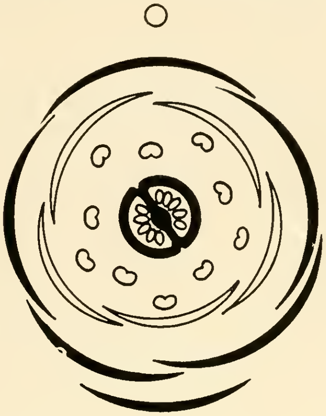


FIG. 1543.—Floral diagram of *Saxifraga granulata* (Saxifragaceae). (*After Eichler.*)

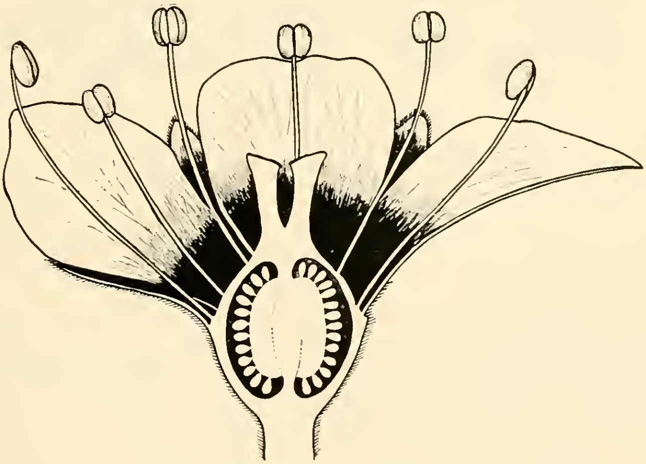


FIG. 1544.—*Saxifraga granulata*. Longitudinal section of flower.

I. Saxifragoideae

Herbs of varying habit, leaves alternate, flowers pentamerous or tetramerous. Gynoecium bicarpellary, either hypogynous or epigynous, with one or two loculi. *Saxifraga* (Fig. 1545), *Tellima*, *Chrysosplenium*, *Parnassia*, *Heuchera*, *Astilbe*.

FIG. 1545.—*Saxifraga longifolia.* Cambridge University Botanic Garden.

II. Francoideae

Perennial herbs with radical leaves and flowers in spikes or racemes on naked scapes. Flowers tetramerous. Gynoecium with four loculi. *Francoa, Tetilla.*

III. Hydrangeoideae

Shrubs with generally opposite leaves. Flowers usually pentamerous with epigynous stamens and a gynoecium with three to five loculi. *Deutzia* (Fig. 1546), *Hydrangea, Philadelphus.*

IV. Pterostemonoideae

Shrubs with alternate stipulate leaves. Flowers pentamerous, androecium of ten stamens. Gynoecium with five loculi, with four to six ovules on axile placentas. *Pterostemon.*

V. Escallonioideae

Trees or shrubs with simple alternate leathery leaves. Stamens of equal number to the petals. Gynoecium either superior or inferior, ovules indefinite in number. *Brexia, Escallonia, Phyllonoma, Polyosma, Itea.*

VI. Ribesoideae

Shrubs with alternate simple leaves and flowers borne in racemes. The gynoecium is inferior and unilocular with two parietal placentas. The fruit is a berry. *Ribes*.

FIG. 1546.—*Deutzia scabra*. Flowering shoot.

VII. Baueroideae

Shrubs with opposite trifoliate leaves and simple axillary flowers. The ovary is semi-inferior with two parietal placentas. The fruit a loculicidal capsule. *Bauera*.

The Saxifragoideae are the largest and most important of the sub-families and contain some thirty genera and 600 species. Many species are American in origin, occurring especially in the Andes. Certain genera are widely distributed, as for example *Astilbe*, which occurs both in eastern Asia and also in North America.

The pollination mechanism is typically entomophilous and we will consider in detail the mechanism in the genus *Saxifraga*. This genus is the largest, containing at least 325 species which are distributed on the mountains of the Arctic and north temperate regions and also in the Andes. In colour the flowers may be white, yellow or spotted with pink. The nectar is almost always fully exposed and secreted on the outer walls of the ovary. In this position it can be reached by short-tongued insects among which flies predominate. Owing to the large number of visitors self-pollination is almost if not entirely impossible, and is made more difficult on account of a more or less pronounced dichogamy. Most of the species are protandrous although a few are protogynous. In this latter type the flowers are considerably smaller in the first or female condition than in the second or male stage. After the stigma has shrivelled, the flowers increase to twice the original diameter so that visits paid by insects will be most probably in the order most advantageous for cross-pollination.

In *S. granulata* the white flowers (Fig. 1547) are markedly protandrous, with nectaries situated on the upper side of the ovary. The calyx holds the petals so closely together that they form a tube in the base of which the nectar is protected from the rain. When the flowers first open the anthers are unripe and the filaments short. Then two of them elongate and assume oblique positions so that their anthers, which have dehisced meanwhile, lie immediately over the style. When these anthers have shed their pollen they bend back towards the petals and two or three others take their place. Pollen is shed over a period of about three days during which time the styles with their immature stigmas lie close together. Only after all the pollen has been shed do the styles elongate and the stigmas diverge so as to occupy the position previously taken up by the anthers (Fig. 1548). Beetles

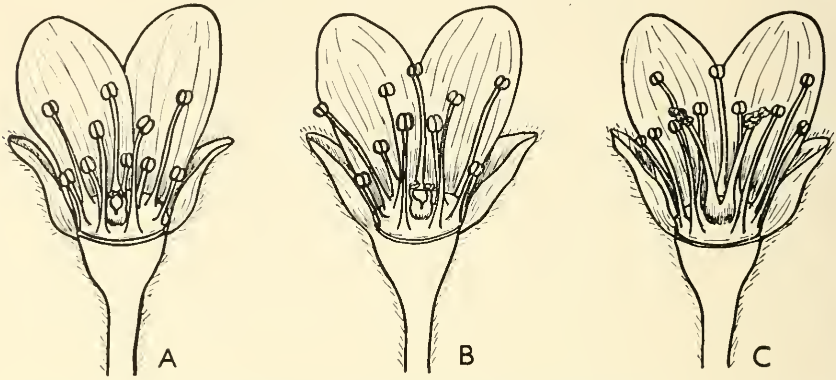


Fig. 1547.—*Saxifraga granulata.* Longitudinal sections of flower at successive stages of development, showing protandry. (*After Knuth.*)

Fig. 1548.—*Saxifraga burseriana.* Flower in female stage with stigmas exserted.

and flies as well as short-tongued bees have all been observed to pollinate this flower.

The genus *Tellima*, with seven species occurring in North-western America, is noteworthy because the flowers are zygomorphic. This is brought about by the great development of two petals to form wing-like projections. The flowers are pollinated by butterflies and bees. The genus *Chrysosplenium* with some sixty species is represented in Britain by *C. oppositifolium* and *C. alternifolium.* The flowers are tetramerous and apetalous but are surrounded by yellowish bracts. The ovary is unilocular with two parietal placentas and a deeply sunk receptacle. The flowers are protogynous and are visited by small insects.

The genus *Parnassia* occupies a rather anomalous position. It is characterized by a conspicuous whorl of branched staminodes tipped with false nectaries and by the ovary, which is unilocular with three or four parietal placentas which become axile at the base of the ovary. Some authorities have therefore placed it in the Droseraceae, but others consider it inadmissible in that family and prefer to regard it as a somewhat anomalous member of the Saxifragaceae.

The members of the next two sub-families, Francoideae and Hydrangeoideae, are largely cultivated in gardens. *Francoa* and *Tetilla* come from Chile, while the members of the Hydrangeoideae are found in North America and eastern Asia. *Philadelphus coronarius*, correctly known as Mock Orange (Fig. 1549), is also referred to by gardeners as " Syringa", a fact which causes confusion, for *Syringa vulgaris* is the botanical name of

FIG. 1549.—*Philadelphus coronarius.* Flowers.

the Lilac, a member of the Oleaceae. *Carpentaria californica*, with large, white flowers, is like *Philadelphus* but has a superior ovary (Fig. 1550). Also belonging to this sub-family is the genus *Hydrangea*, several species of which are grown in gardens. The flowers are produced in cymose corymbs in which, in most cultivated forms, the flowers, or at least the outer ones, are neuter and possess large petaloid calyces, giving the inflorescences a very conspicuous appearance.

Fig. 1550.—*Carpentaria californica*. Flowers.

In the Escallonioideae the best-known genus is *Escallonia*, with about sixty species, several of which are cultivated. They show a marked tolerance to sea spray and are frequently planted in coastal districts to form evergreen hedges. The genus is a South American one, found chiefly in the Andes and the drier parts of southern Brazil. *Phyllonoma*, with one species, occurs from Mexico to Columbia. *Polyosma*, with thirty species, occurs in Australia and south-eastern Asia, while *Itea*, with six species, occurs in eastern Asia and also in North America. Several species are cultivated, particularly *I. ilicifolia* (Fig. 1551) with evergreen spiny leaves.

The genus *Ribes* contains about 140 species, many of which are common in North America (Fig. 1552). The fact that members of this genus form one of the hosts of the White Pine Blister Rust has led to wholesale destruction of the genus in the United States and Canada. We have already referred to three species which are cultivated under the names of the

FIG. 1551.—*Itea ilicifolia.* Inflorescence.

Gooseberry and Black and Red Currants. The White Currant which is cultivated only in more specialized fruit collections is similar to the Red Currant but is considered by many superior in taste. The Flowering Currants which are planted in gardens are principally *R. aureum* and *R. sanguineum*, both of North American origin.

The flowers show certain interesting points in connection with their pollination mechanism and since this is so important in the setting of the fruit, we must refer to it briefly (Fig. 1553).

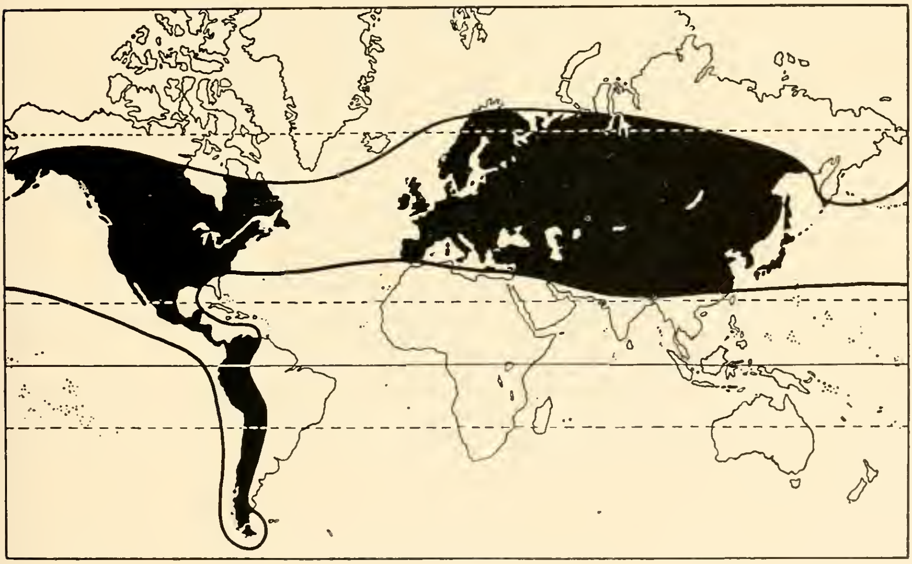


FIG. 1552.—*Ribes*, distribution.

The flowers are mostly pink or yellowish-green in colour and are usually associated together in pendulous racemes. The nectar may be free or concealed and is secreted by an epigynous disc. In *R. alpinum* the nectar is secreted in a shallow depression of the receptacle and is accessible to very short-tongued insects. In *R. rubrum* the depression is much deeper and only the bottom is covered by nectar. It is pollinated by bees. In *R. uva-crispa* the flowers, unlike those of *R. rubrum*, are somewhat narrow and the opening is protected by stiff hairs which project from the edges of the receptacle and the style. Such flowers can be pollinated by bees but not by flies. In *R. nigrum* the bells are deeper, being almost spherical and pendulous, and are better adapted for bee pollination than *R. rubrum.* In *R. sanguineum* the flowers are tubular and erect in position. Long-tongued bees can reach the nectar, but in *R. aureum* the tubes are considerably longer, *i.e.*, 11 mm. as against 5 mm., and consequently the nectar can only be reached by lepidopterous insects.

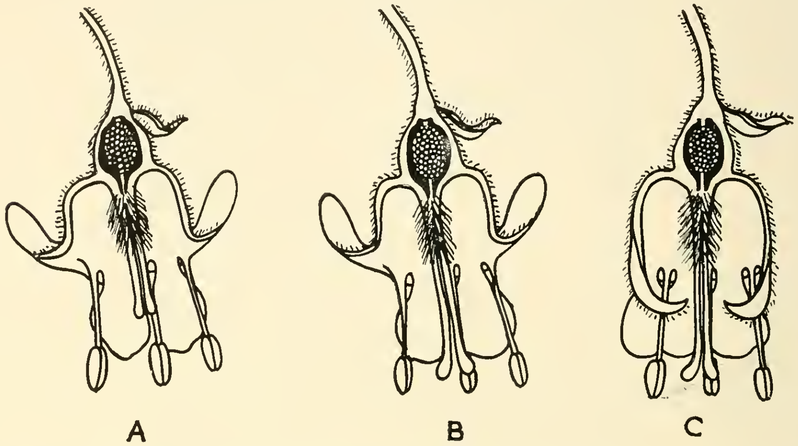


FIG. 1553.—*Ribes uva-crispa.* Successive stages of anthesis, showing at B the secondary exsertion of the stigmas and at C the infolding of the calyx at the close of anthesis. (*After Knuth.*)

Turning finally to the last sub-family, we have the single genus *Bauera*, with three species in eastern Australia and Tasmania. *B. rubioides* is the state flower of New South Wales.

As has already been pointed out, Hutchinson and others elevate several of these sub-families to the rank of families. The group however is probably united and we have preferred to keep them together.

PARIETALES

The Parietales are Archichlamydeae in which the flowers are actinomorphic or zygomorphic and generally monoecious with a separate pentamerous calyx and corolla. There may be five stamens or a multiple of that number. The ovary consists of three united carpels and may be superior or may be more or less sunk into the floral axis. There are numerous ovules arranged on parietal placentas. These ovules possess two integuments, except in one family, the Loasaceae, in which there is only one. The seeds usually have endosperm. The plants are either woody or herbaceous and possess either opposite or alternate leaves often provided with stipules.

As originally conceived by Engler this order was a large one embracing several groups, the relationships of which are far from obvious. Hutchinson has therefore divided the Parietales into a number of separate orders and redistributed these in his system of classification. Thus he includes the families Cistaceae, Bixaceae, Frankeniaceae and Flacourtiaceae together in the order Bixales. The Tamaricaceae are placed alone in the Tamaricales, the Violaceae in the Violales, the Loasaceae in the Loasales and the Passifloraceae in the Passiflorales. Finally two families are included in other Englerian orders, the Caricaceae in the Cucurbitales and the Elatinaceae in the Centrospermae (Caryophyllales). We need not discuss here the details upon which these views are based, since only a single family, the Violaceae, will be considered in detail in this book. We should however note some of the characteristics of certain of the more important families which are embraced in the Parietales as originally defined.

The **Cistaceae** are small herbaceous or shrubby plants, some of which are strongly calcicole while others are calcifuge. Among the more important members are *Cistus* (Fig. 1554) and *Helianthemum* (Rock Rose), one species of the latter occurring commonly in this country while three more are very local. It is interesting to note that a mycorrhizal fungus has been demonstrated in the roots of a number of species, which also appears to be present in the gelatinous wall of the seed. These plants inhabit dry, sunny situations and it may be that the mycelium assists in the early development of the seedling.

Fig. 1554.—*Cistus ladaniferus.* The flowers are two to three inches in diameter.

Members of the **Bixaceae** are all tropical. *Bixa orellana* is a native of America, but is cultivated throughout the tropics for its seeds, which have a fleshy red seed coat containing a colouring matter known commercially as Annatto or Oilean and used in colouring processes. It is orange in colour and is frequently employed in producing a bright yellow colour in butter and cheese.

The small family **Tamaricaceae**, of about 100 species, lives chiefly in the desert and steppes of central Asia and round the shores of the Mediterranean. One species, *Tamarix gallica* (Fig. 1555), is a doubtful native of Britain and other species are often cultivated in gardens.

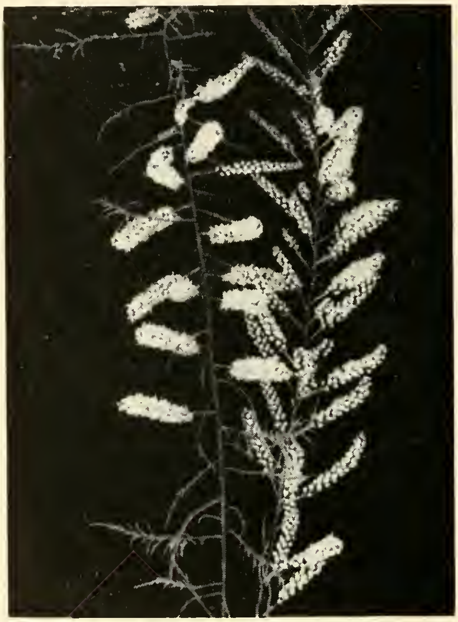


Fig. 1555.—*Tcmarix gallica.* Inflorescences.

The **Passifloraceae** are a small family of some twelve genera and 580 species. The flowers are very beautiful and so remarkable in appearance that many species are cultivated. The family is widespread in the warmer temperate regions, particularly in America. The plants are mostly climbers, which obtain their support from tendrils in the leaf axils. Pollination is by the aid of insects and humming-birds. The large flowers have five petaloid sepals and five petals. Within the perianth is a corona of long, blue filaments. There is a long gynandrophore bearing five stamens and a terminal ovary with three long-stalked stigmas. The name of "Passion Flower" was given because it symbolizes the instruments of Christ's Passion. The gynandrophore is the scourging post, the corona is the crown of thorns, the stamens are the five wounds and the stigmas the three nails

FIG. 1556.—*Passiflora coerulea.* Flower in face view.

of the Crucifixion. *Passiflora coerulea* (Fig. 1556) with blue flowers is doubtfully hardy in this country, while species of *Tacsonia* (Fig. 1557) with red or crimson flowers are grown in greenhouses. *P. quadrangularis* is cultivated in many parts of the tropics on account of its large edible berries. It is known as the Granadilla. *P. edulis* produces the Passion Fruit.

FIG. 1557.—*Tacsonia van-volxemii.* Pendent flower in side view.

The **Cariceae** are important only on account of *Carica papaya*, the Papaya or Pawpaw, which is widely cultivated throughout the tropics for its fruit. The plant is a small tree with a stout stem and large palmate leaves. It is remarkable for the fact that it is generally unbranched, a feature uncommon in Dicotyledons but frequent in Monocotyledons, *e.g.*, Palms (Fig. 1558). The tissues are permeated with a laticiferous system containing the powerful proteolytic enzyme, papain, which can attack human skin. The fruit is large, varying from 6 in. to 20 in. in length, and weighs up to 20 lb. The skin is smooth and encloses orange-coloured flesh and numerous black, parietal seeds. In fact it resembles in general appearance a melon. It contains about 10 per cent. of invert sugar, sucrose being almost entirely absent.

FIG. 1558.—*Carica papaya*. The Pawpaw. Fruiting tree. Photograph supplied by courtesy of the South African Railways and Harbours Department.

Violaceae

This is a small family with fifteen genera and some 800 species. *Viola* (Fig. 1559) is the only British genus. It has been subjected to very critical study, with the result that many species and varieties have been described. Without going into minor differences we may mention the following well-known species: *V. odorata*, the Sweet Violet; *V. canina*, the Dog

Violet; *V. sylvestris*, the Wood Violet; *V. palustris*, the Marsh Violet, and *V. tricolor*, the Heartsease or Pansy. Many cultivated varieties have been produced and are employed as bedding plants under the names of Viola (Fig. 1560) and Pansy.

FIG. 1559.—*Viola gracilis.* Flower in face view.

FIG. 1560.—*Viola.* Garden form.

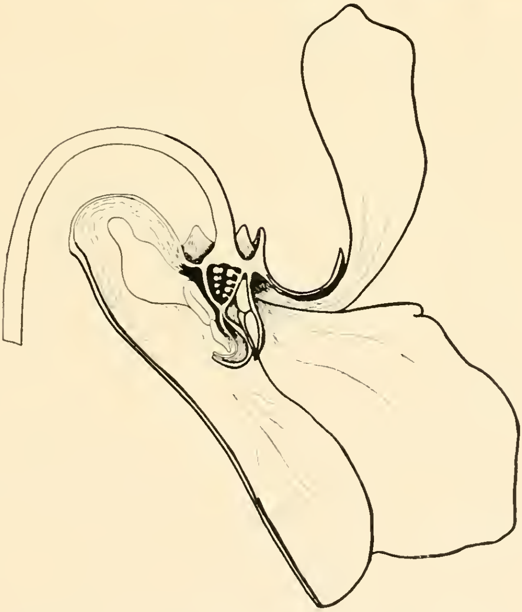


FIG. 1561.—*Viola odorata.* Longitudinal section of flower showing spurred petal. (*After James and Clapham.*)

The **plants** are annual or perennial herbs in temperate regions, but in the tropics some genera are shrubs or even small trees, or occasionally shrubby climbers. The leaves are alternate or rarely opposite and are usually simple and spathulate. Stipules are developed which may be either small or large and leaf-like.

The **flowers** spring from the axils of bracts and the pedicel bears two bracteoles. In many of the genera the flowers are actinomorphic, the zygomorphic character of *Viola* (Fig. 1561) being somewhat exceptional. It is caused by the enlargement of the anterior petal which becomes spurred. The flowers are hermaphrodite, or rarely polygamous. Cleistogamic flowers are often produced in *Viola* and produce a greater amount of seed than the open flowers normally do.

The **perianth** (Fig. 1562) consists of five persistent sepals and five petals, which may be of unequal size, in which case the anterior becomes larger.

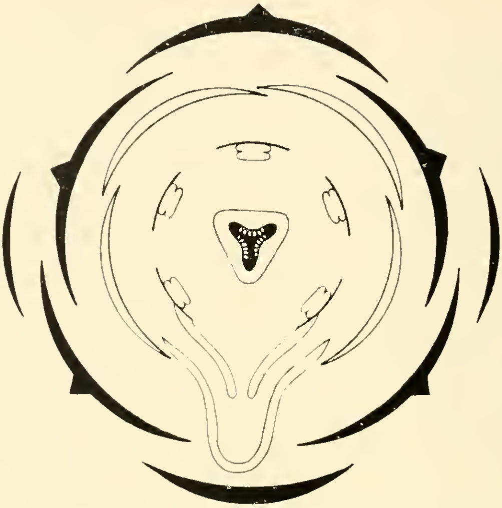


FIG. 1562.—Floral diagram of *Viola*. Violaceae.

The **androecium** consists of five stamens which are hypogynous. The anthers are erect and converge to form a ring around the style. These anthers are introrse with longitudinal openings and apical appendages. The two anterior stamens are often spurred at the base.

The **gynoecium** is unilocular, composed of three to five carpels, and the ovules are arranged on parietal placentas. These ovules are numerous and anatropous. The style is short and the stigma is often hooded.

The **fruit** is a capsule, splitting elastically and loculicidally into three boat-shaped valves. These on drying close along the mid-line and in so doing eject the smooth seeds with considerable force, sufficient to throw them several yards. In *Hymenanthera* and a few other genera the fruit is a berry.

The **seed** is small, the testa being hard and shiny. Many species have an oil body or elaiosome on the seed, which attracts ants, and myremecochory is characteristic. In climbing genera, such as *Agatea*, which is found in New Caledonia and Fiji, and *Anchieta*, native of tropical South America, the seeds are winged.

Cleistogamic flowers are commonly produced in the genus *Viola* (see p. 1356) and others. These cleistogamic flowers have been subject to considerable study and are worthy of some reference. In species such as *V. canina*, *V. odorata* and *V. sylvestris*, which produce flowers early in the year, insect visits are rare and little seed is set. Later in the season the cleistogamic flowers appear. They never open and the seeds are produced entirely by self-pollination. In *V. canina* the flower looks like a bud, the sepals remain closed and five minute petals are produced. The two anterior stamens possess anthers with a little pollen, the posterior three have no anthers. The anthers remain closely appressed to the stigma and the pollen grains germinate in their anthers and the pollen tubes burrow through the anther wall into the stigma. In *V. odorata* the cleistogamic flowers are similar in structure but all five stamens bear anthers.

In the genus *Viola* (Fig. 1563) the open flowers are adapted for pollination by insects, predominantly bees, although a few species with long spurs rely upon butterflies and moths, while some, like *V. biflora*, are pollinated by Diptera. The flowers are brightly coloured, yellow, violet and blue predominating. The lower petal is spurred and the anthers of each of the lower stamens possess a nectar-secreting process which projects backwards into the spur of the corolla where the nectar is stored. The connective of each of the five stamens is produced into a membranous appendage and as these overlap laterally and clasp the style underneath the stigma, they form a conical chamber into which the dry pollen falls when the anthers dehisce. The stigma projects beyond this cone and closes the entrance to the flower. An insect probing for the nectar must therefore first touch the stigma and then raise it up so as to open the anther cone from which the pollen falls on to the upper surface of its proboscis. Since the visitor normally thrusts its proboscis only once into each flower it must regularly effect cross-pollination. Failing an insect visit the flower remains infertile. (For further details of pollination in *Viola* see p. 1237.)

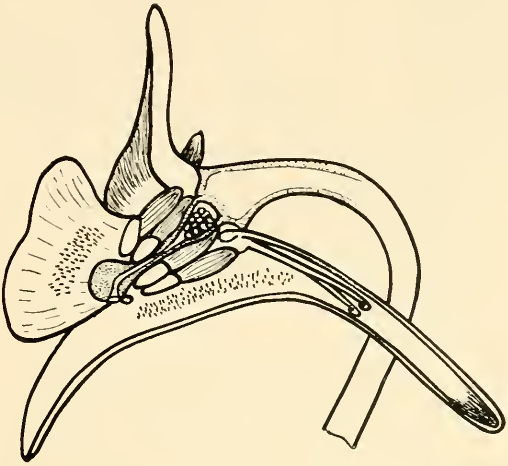


FIG. 1563.—*Viola calcarata*. Longitudinal section of flower illustrating the pollination mechanism.

Mention may be made here of the **Cucurbitales** which are mostly tropical herbaceous plants related to the last order through the Passifloraceae and Caricaceae. Many of them are climbers attaching themselves by tendrils.

The most important family is the **Cucurbitaceae** which includes about ninety genera and 750 species. They are mostly annual or occasionally perennial herbs bearing large unisexual flowers. Many are of economic importance, *e.g.*, *Cucurbita pepo*, the Pumpkin or Vegetable Marrow; *Cucumis melo*, the Melon; *C. sativus* (Fig. 1564), the Cucumber; *Citrullus vulgaris*, the Water Melon. Also included in this family is *Ecballium elaterium*, the Squirting Cucumber (see Fig. 1382). *Bryonia dioica* (White Bryony) is the only British example.

Fig. 1564.—*Cucumis sativus.* Flowering shoot with tendril.

A second family, the **Begoniaceae**, may be noted because of the important genus *Begonia*, many species of which are commonly cultivated. The flowers are unisexual (Fig. 1565). Many show remarkable powers of vegetative propagation by means of buds formed on detached leaves. They are mainly tropical in distribution.

Another order, the **Guttiferales**, was included by Engler in his Parietales, but is now generally separated on account of the axile placentation of the ovules. The order includes a number of not very large families mostly not represented in the British Flora. Certain species however are of economic importance.

The most important family is the **Theaceae**, which includes the genus *Camellia. C. sinensis* (Fig. 1566) is the tea plant, an erect, bushy shrub with smooth, leathery, oval leaves. The flowers are white and scented. It has been cultivated from very early times (probably before the sixth

FIG. 1565.—*Begonia semperflorens.* Left, female flower in side view showing the broadly winged, inferior ovary and cluster of stigmas. Right, male flower in face view.

FIG. 1566.—*Camellia (Thea) sinensis.* Tea plant. Shoot with flowers and fruit. Photograph supplied by courtesy of the Imperial Institute.

century A.D.) in India and China. The tea of commerce is obtained from the leaves and young shoots, the quality depending upon the age and preparation of the leaves. *C. japonica* (Fig. 1567), a native of China and Japan, is a common greenhouse shrub with handsome large red flowers.

FIG. 1567.—*Camellia japonica.* Flower.

In the family **Guttiferae** (Hypericaceae) is the genus *Hypericum* (Fig. 1568), with fourteen British species, which are mostly herbs of woods and damp places. *H. elodes* is an aquatic plant with hairy leaves and *H. androsaemum* is shrubby. The flowers are all yellow with three large fascicles of stamens and the fruit is a septicidal capsule except in the last-named species which has black berries. Most of the genera, however, are tropical trees and shrubs with resinous juice. A number are of economic importance. *Garcinia mangostana*, the Mangosteen, is a small tree up to 30 ft. high, with large oval leaves. The flowers may be either monoecious or dioecious. The fruit is about the size of an orange and somewhat flattened at the top and bottom. The skin is smooth and thick and purplish in colour.

FIG. 1568.—*Hypericum patulum.* Flower.

The flesh is white and the flavour is somewhat like that of a plum but more delicious. It only thrives in the region of the equator and is cultivated chiefly in the East Indies and Malaya. The fruit does not keep well and is seldom exported.

Garcinia hanburyi is the Gamboge Tree, a native of Siam, while *Pentadesma butyracea*, the Tallow Tree, yields a valuable fat. *Calophyllum inophyllum* yields Domba oil, and is known as the Alexandria Laurel. It is widespread in the eastern tropics. *Mammea americana*, the Mammee Apple, is a native of the West Indies. The fruits are eaten by the indigenous population but are of poor, subacid quality.

In the family **Dipterocarpaceae** we may mention two plants of economic importance: *Shorea robusta*, the Sal Tree of India, a magnificent timber tree which also yields Dammar resin; and *Dryobalanops aromatica* which is the source of Borneo Camphor. This substance forms yellow crystals between the wood elements. Several other genera also produce oils of local economic importance. They occur mostly in India and the East Indies.

Finally we may briefly mention the **Cactales** or as they are sometimes called the Opuntiales. The order includes the single family **Cactaceae**. The systematic relationship of the group is doubtful. Bentham and Hooker consider it related to the Passiflorales, while Engler places it near the Myrtiflorae. Rendle in his recent work follows Engler, while Hutchinson considers that the view of Bentham and Hooker is more correct and relates it to the Passifloraceae through the Cucurbitales.

As a whole the Cacti show very varied but remarkable adaptations to a xerophytic mode of life (Fig. 1569). They are uniformly succulent and range in size from small plants like rosettes (*Mammilaria*) to large columnar trees such as *Carnegiea gigantea* which may reach a height of 70 ft. by 2 ft. thick. A few live as epiphytes on forest trees, as for example *Rhipsalis*, while others again form an impenetrable scrub, *e.g.*, *Opuntia*, with flattened stem segments. Species of this genus became such a plague when introduced into Australia that considerable areas of Queensland became uninhabitable and the extermination of this Cactus, the Prickly Pear, provides one of the most remarkable stories of Biological Control (see Volume IV).

FIG. 1569.—*Melocactus communis*, with young fruits on top.

Though seldom seen because of their short duration, the flowers of many Cacti are surprisingly large and extremely beautiful (Fig. 1570). The great pink or red blossom of *Epiphyllum* (*Phyllocactus*) (Fig. 1571) which is so often cultivated in greenhouses is a case in point, while many of the tiny species produce flowers as large as the plant.

Fig. 1570.—*Echinopsis tubiflora.* Flower in face view. (See also Fig. 1111.)

Fig. 1571.—*Epiphyllum* (*Phyllocactus*) *ackermannii.*

The Cactaceae are an American family, the only exceptions being the African species of *Rhipsalis.* The Prickly Pears (*Opuntia*) are however extensively naturalized in many places, notably round the Mediterranean. Some of the Cacti are quite hardy and range as far as the north of British Columbia.

Nearly all Cacti are spiny, the spines possibly representing the leaves, which are not developed except in *Pereskia*, which has woody stems and succulent leaves.

ARISTOLOCHIALES

The Aristolochiales are Archichlamydeae in which the flowers are either monoecious or dioecious, cyclic, and either actinomorphic or zygomorphic. The perianth consists of a single whorl and may be either petaloid or fleshy, the parts being either separate or joined together. The stamens vary in number but are often a multiple of the number of perianth segments; they may be free or united with the style to form a central column or **gynostemium**. The ovary is inferior, four or six locular with axile placentation, or unilocular with parietal placentation. The ovules are numerous and possess two integuments. The fruit is a berry or capsule. The seed is provided with endosperm and sometimes with additional perisperm. The embryo is small.

The plants are either herbs or woody climbers with simple, alternate, exstipulate leaves. Some species are parasites, in which the vegetative structure is greatly reduced and may be even endophytic, while the flowers are often very large and conspicuous. The members of this order live chiefly in the tropics and are of particular interest on account of their parasitic representatives and their method of pollination.

According to Engler the order includes three families, Aristolochiaceae, Rafflesiaceae and Hydnoraceae. Hutchinson also includes the family Nepenthaceae, which Engler adds to the Sarraceniales. We shall follow Engler's system in this respect.

In the **Aristolochiaceae** the plants are mostly woody climbers, though some are herbs. There are five genera distributed through the tropics but extending into temperate regions (Fig. 1572). *Asarum europaeum* is a rare British perennial herb, while *Aristolochia clematitis* (Fig. 1573), a native of central and southern Europe, is established as a garden escape

FIG. 1572.—*Aristolochia elegans.* The perianth tube is greatly elongated into a coloured lip.

FIG. 1573.—*Aristolochia clematitis.* Flowering plant.

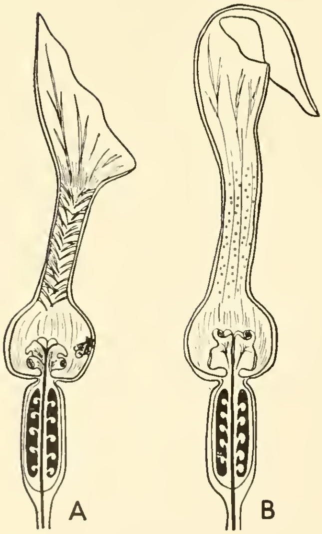


FIG. 1574.—*Aristolochia clematitis.* Pollination. A, Female stage with receptive stigmas. B, Later stage with stigmas rolled up and anthers dehisced. The perianth hairs have shrivelled up.

in parts of England. The pollination mechanism of this herbaceous type is of special interest (Fig. 1574). The flowers are long and tubular, several being produced together in the axil of a leaf. The flowers when young are vertical and bright yellow in colour. The perianth tube is produced above into a flat lip, while below it is swollen into a sort of bag. The slender middle tube is lined with downwardly projecting stiff hairs. Many flies and gnats find their way into the tube and cannot escape because of these hairs. They apparently fall in, for no nectar is secreted to attract them. The gynoecium ripens first and flies already covered with pollen are almost certain to blunder against the style in their attempt to escape. Later the anthers dehisce and the flies become liberally dusted with pollen. The hairs now shrivel and contract, leaving the way open for the flies to escape while at the same time the perianth droops so that the flowers hang downwards and the tip of the perianth closes over the mouth of the tube.

It is interesting to note the analogy between the condition in this family and in the entirely unrelated Araceae (see p. 2017). In the case of the Wild Arum, *Arum maculatum*, the hairs protect an inflorescence, while in this case they protect only a single flower.

Included in the **Rafflesiaceae** are some of the most remarkable of the parasitic flowering plants which, as a result of their mode of living, have lost all resemblance to a normal Angiosperm (Fig. 1575). The vegetative organs consist of a cellular tissue resembling a fungal mycelium which ramifies through the cambium region of the root, or occasionally the stem of the host plant. In the tissues of the host the flower buds develop by a local growth of the parasite tissue, until they ultimately burst out and appear at the surface. These flowers may be solitary, as in *Rafflesia*, or they may form an inflorescence as in *Cytinus*. The flowers are dioecious and vary enormously in size, the largest being *R. arnoldi* (Fig. 1576) in Sumatra, whose flowers measure a yard across. These flowers have a dull red perianth composed of five segments which are liberally spotted with yellow and surround a thick central ring (Figs. 1577 and 1578). In the centre of the male flower is an upright column which terminates just below the ring. This column is fringed by an indefinite number of anthers. The female flowers produce a large number of carpels, each containing a number of irregularly shaped cavities lined with small ovules (Fig. 1578). In *Cytinus* the ovules are borne on branched parietal placentae (Fig. 1579). The

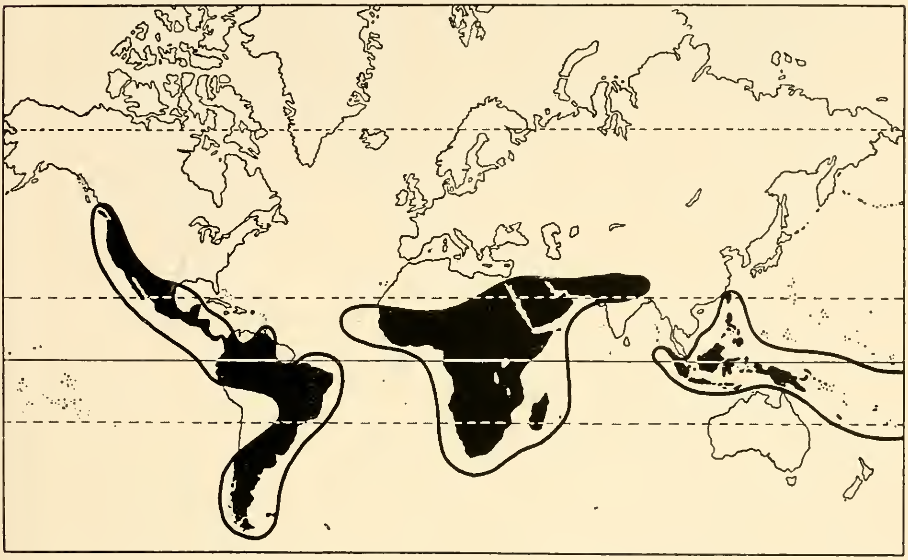


FIG. 1575.—Distribution of Rafflesiaceae. The area should now be extended to include North Island, New Zealand.

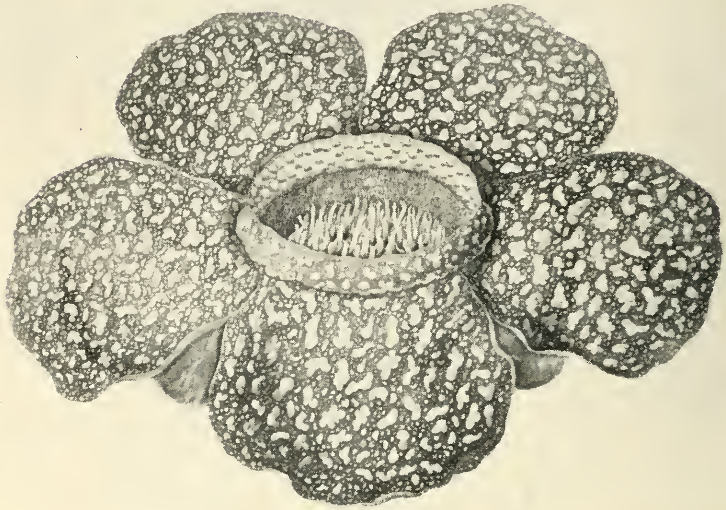


FIG. 1576.—*Rafflesia arnoldi.* Flower. (*From R. Brown, "Miscellaneous Botanical Works".*)

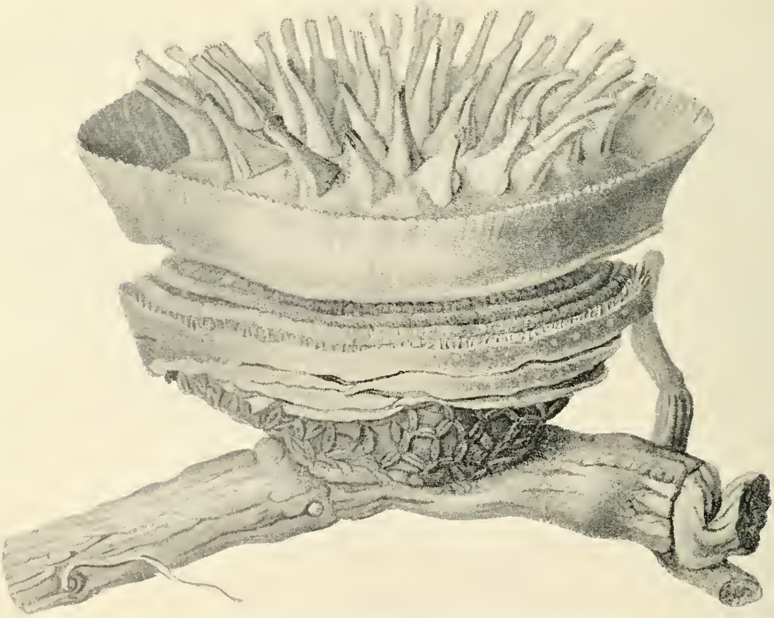


FIG. 1577.—*Rafflesia arnoldi.* Female flower with perianth removed, showing the ring, the outer surface of which is stigmatic. Inside the lower edge of the ring are numerous staminodes. The central processes may be vestigial styles but they are now without any function in pollination. (*From R. Brown, "Miscellaneous Botanical Works".*)

flowers emit the smell of decomposing flesh and are therefore visited by carrion-feeding flies who are said to effect pollination.

FIG. 1578.—*Rafflesia arnoldi*. Female flower in vertical section, showing the numerous ovuliferous cavities in the inferior ovary. These cavities are not normal carpellary loculi but are said to originate as intercellular spaces. (*From R. Brown*, "*Miscellaneous Botanical Works*".)

The third interesting family is the **Hydnoraceae** which are also parasitic in the roots of various trees and shrubs. There are only two genera, *Hydnora* which is found in Africa, and *Prosopanche* with one species found on the Pampas of the Argentine (Fig. 1580). The vegetative tissue consists of a branched, creeping, cylindrical or angular rhizome, which grows out from points of attachment on the roots of the host plant, which is often a species of *Acacia* or *Euphorbia*. The flowers (Fig. 1581) are elongated, solitary organs, which arise directly from the rhizome. They each consist of three or four thick, fleshy perianth leaves, which are united below and incurved above. The stamens are equal in number to the perianth segments, to which they are attached, and form a ring, on the upper side of which is a large number of pollen sacs. The ovary is inferior and unilocular containing numerous ovules. The small, undifferentiated embryo is surrounded both by endosperm and perisperm.

FIG. 1579.—*Cytinus hypocistus*. Longitudinal section of female flower with part of the perianth surrounding the style and stigmas. Below is the ovarial cavity showing branching placentae and numerous minute ovules.

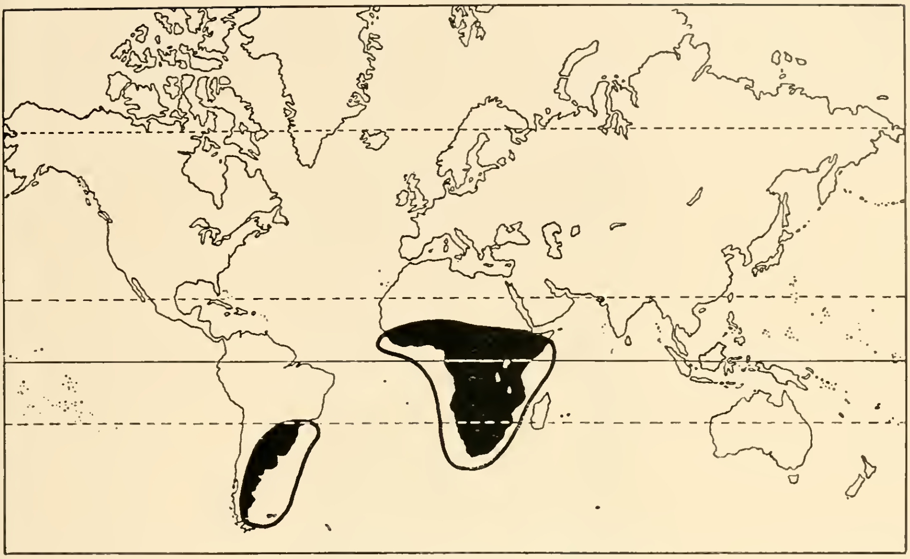


FIG. 1580.—Distribution of the Hydnoraceae.

FIG. 1581.—*Hydnora africana.* Flower in longitudinal section. (*After Hutchinson.*)

SARRACENIALES

The Sarraceniales are a small but interesting order of the Archichlamydeae in which the flowers are monoecious, except in *Nepenthes*, actinomorphic and hypogynous. There is usually a separate calyx and corolla. The gynoecium is tricarpellary, with parietal or axile placentation and indefinite ovules. The seeds are small and endospermic.

The plants are small and herbaceous or trailing; they inhabit moist situations and the leaves are modified in various ways for trapping and digesting insects and other small animals. We shall consider later the details of the various trap mechanisms employed (see Volume IV).

In the **Sarraceniaceae** there are three genera, *Sarracenia* (Fig. 1582) with seven species, restricted to the Atlantic coast of North America; *Darlingtonia*, a monotypic genus occurring in California; and *Heliamphora* with five species, found in British Guiana and Venezuela. Hence we see

Fig. 1582.—*Sarracenia* sp. Habit of flowering plant.

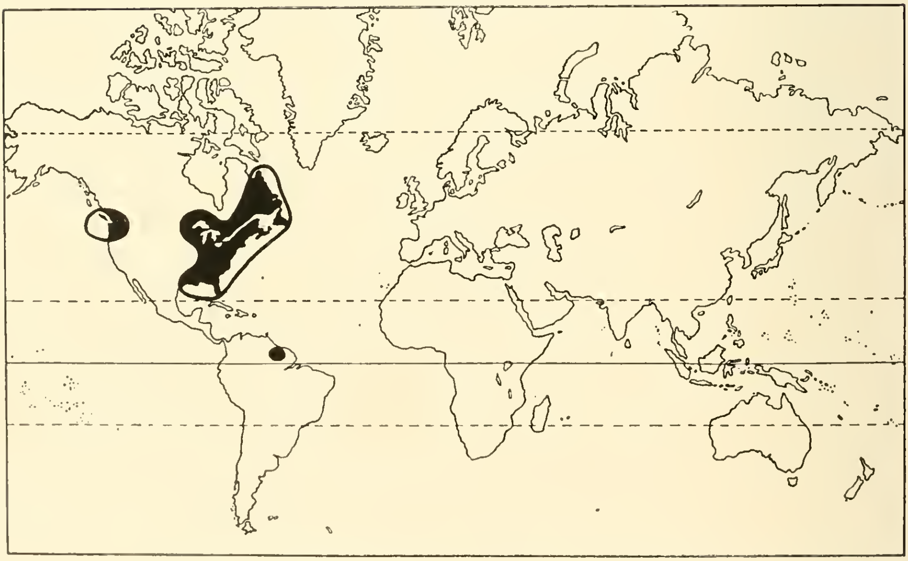


Fig. 1583.—Distribution of Sarraceniaceae.

that the Sarraceniaceae is essentially a New World family (Fig. 1583). The flowers (Fig. 1584) are remarkable chiefly because of the great development of the style, which in *Sarracenia* is expanded above the ovary into a large umbrella-like structure, which spreads over the stamens and has small stigmatic surfaces at the tips of its five lobes.

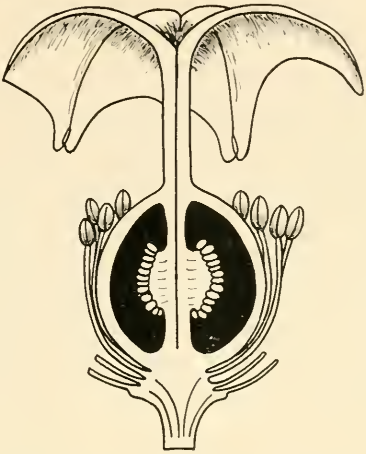


FIG. 1584.—*Sarracenia purpurea.* Longitudinal section of flower with perianth removed.

In the **Nepenthaceae** there is only one genus, *Nepenthes*, with about sixty species, which are distributed (Fig. 1585) in eastern tropical Asia, with the centre of distribution in Borneo, extending westwards to Mada-

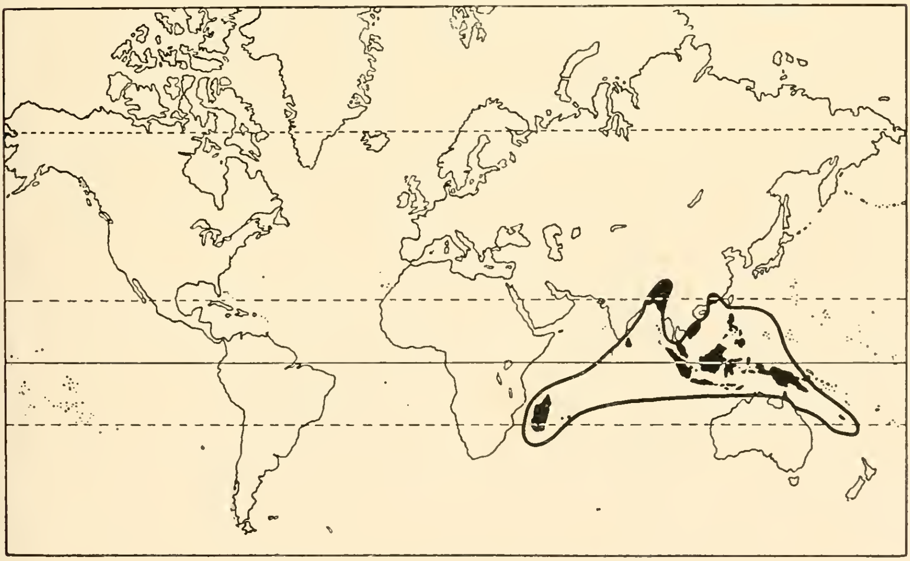


FIG. 1585.—Distribution of Nepenthaceae.

gascar, eastwards to the northern territory of Australia, and northwards into north-eastern Bengal and southern China. It would appear therefore that *Nepenthes* (Fig. 1586) must be regarded as the Old World representative corresponding to the Sarraceniaceae of the New World. They are slender plants which generally climb with the aid of their alternate leaves. The flowers (Fig. 1587) are small and dioecious, produced in racemes. The perianth consists of two dimerous whorls. In the male flowers there is a varying number of stamens; in the female there is a superior, four-chambered ovary with axile placentation. The family is placed in the Aristolochiales by some authors and separated thereby from the rest of the Sarraceniales. This is based chiefly upon the axile placenta-

FIG 1586.—*Nepenthes khasiana.* Plant with pitchers.

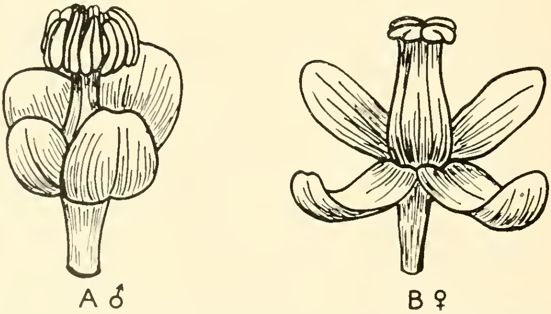


FIG. 1587.—*Nepenthes.* Male (A) and female (B) flowers.

tion, which distinguishes it from the Sarraceniaceae in which the placentation is parietal.

The third and last family is the **Droseraceae**. There are five genera with 100 species, all but three of which belong to the genus *Drosera*, the only genus of the order represented in the British Flora (Fig. 1588). This genus, which includes the Sundews, is widely distributed in temperate and tropical regions of the New and Old Worlds. Of the other three genera, all of which are monotypic, *Drosophyllum lusitanicum* grows wild in Morocco, Portugal and southern Spain; *Dionaea muscipula* (Venus' Fly-trap) (Fig. 1589) is confined to the south-eastern United States; while *Aldrovanda vesiculosa* occurs in central and southern Europe, north and east Asia, India (Bengal) and Australia (Queensland).

Fig. 1588.—*Drosera rotundifolia*. The commonest British species with basal rosettes of glandulose leaves.

The leaves in *Drosophyllum*, *Drosera* and *Dionaea* form a rosette on the ground and are modified to entrap flies (Fig. 1590) while in *Aldrovanda* the plant is a rootless aquatic in which the leaves are modified for the same purpose.

The flowers are hermaphrodite, actinomorphic and either pentamerous or rarely tetramerous, often with an increase in the number of the stamens and a reduction in the number of the carpels.

The ovules are numerous, anatropous with parietal or basal placentation.

This family, though obviously closely related to the others already

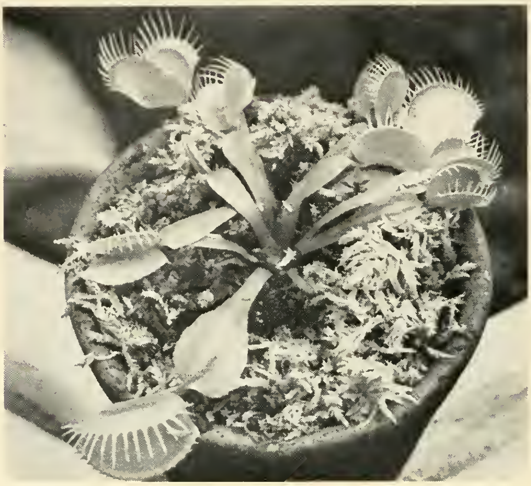


FIG. 1589.—*Dionaea muscipula.* Venus' Fly Trap. Cultivated plant with trap leaves open. Kew Gardens. Photograph supplied by *Picture Post* library.

mentioned, is considered also to be closely allied to the Parietales, in which it is sometimes placed. The family may therefore be regarded as a link between the Aristolochiales on the one hand and the Parietales and Rosales on the other, and hence quite apart from its importance from a bionomic standpoint it is also interesting phylogenetically.

FIG. 1590.—*Drosera binata* Cultivated plants with long forked leaves beset with large, adhesive, glandular hairs. Kew Gardens.

CENTROSPERMAE

The Centrospermae are Archichlamydeae with either hermaphrodite, monoecious or dioecious flowers, which are actinomorphic and usually pentamerous. The perianth is either single or double. The stamens are in one or two whorls and are generally either five or ten in number. In the former case they are generally opposite the petals. The ovary is usually superior, composed of from one to five carpels which are united to form a unilocular, rarely multilocular, ovary containing from one to many campylotropous ovules. The fruit is generally a capsule or nut, rarely a berry. The embryo is large and curved and the seed contains perisperm.

It is largely upon the campylotropous ovules, the curved embryo and the presence of perisperm that the apparently dissimilar genera are grouped together.

In the older classifications this order contained the following principal families: Chenopodiaceae, Amarantaceae, Phytolaccaceae, Portulacaceae, Aizoaceae, Nyctaginaceae and Caryophyllaceae. In more recent treatments, such as that of Hutchinson, the order is split up into a number of distinct orders. Thus the Chenopodiales are considered to include the Chenopodiaceae, Phytolaccaceae and Amarantaceae; the Caryophyllales include the Caryophyllaceae, Aizoaceae and Portulacaceae, while the Nyctaginaceae are excluded from the order. In Hutchinson's view the Caryophyllales are the more primitive group, arising from the Ranales through the Saxifragaceae; while the Chenopodiales as well as the Polygonales are considered to be derived from them.

We shall consider the Chenopodiaceae and Caryophyllaceae in detail, but first will briefly review the other families mentioned above.

The **Phytolaccaceae** include herbs, shrubs and trees with large, alternate leaves, occurring mostly in the tropics and subtropics. The carpels are free, which is exceptional in the order. *Phytolacca dioica* is used as a shade tree in Spanish countries and is known as Bella Sombra. Others, herbaceous species of the same genus, are sometimes cultivated in gardens (Fig. 1591). Secondary thickening is by successive bundle rings.

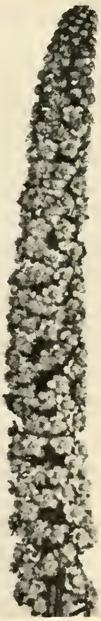


FIG. 1591.—*Phytolacca decandra.* Inflorescence.

The **Portulacaceae** are herbs and under shrubs which are often succulent. They are mainly American in origin. Among those cultivated for ornamental purposes may be mentioned *Portulaca grandiflora* (Sun Plant), an annual from Brazil; *Anacampseros arachnoides*, a succulent greenhouse plant from the Cape of Good Hope, and species of *Calandrinia* (Rock Purslane), which are pink or purple in colour and open only in the brightest sunshine. They are natives of Peru, California, Chile and Australia. *Claytonia perfoliata* (Fig. 1592) (Winter Purslane), a native of North America, is now naturalized in parts of Britain. It is botanically interesting because of its perfoliate leaves.

FIG. 1592.—*Claytonia perfoliata.* Flowers.

Finally the genus *Lewisia* contains a number of species which are cultivated as rock-garden plants. They are natives of North-eastern America and are calcifuge plants, needing a sandy soil and protection from excessive rain.

The **Aizoaceae**, or as they are sometimes called the Ficoidaceae, are mostly low-growing succulent herbs, found mainly in South Africa and the Mediterranean, while a few are native to South America, the West Indies and Australia. They are found chiefly on sandy seashores and in desert places. The best-known genus is *Mesembryanthemum* with about 350 species, of South African origin (Fig. 1593). They are mostly succulent

FIG. 1593.—*Mesembryanthemum spectabile.* Flower.

though *M. spinosum* develops thorns. Some like *M. crystallinum* are covered with glistening bladder-shaped hairs which earn that species the name of Ice Plant. It is widely distributed in South Africa, as well as in California, South and Western Australia and in the Mediterranean region. *M. edule* is interesting; it is a South African species which has become naturalized in Britain, occurring on the rocks by the seashore in the Isle of Wight, Cornwall and the Channel Islands. The fruits, which are capsules, contain a sweet pulp and are eaten in South Africa under the name of Hottentot Figs. The perianth in *Mesembryanthemum* consists of four sepaloid segments. The numerous apparent petals are really staminodes.

The **Nyctaginaceae** are placed by Hutchinson in his Thymelaeales. They are mostly shrubs or trees with flowers in cymose inflorescences surrounded by brightly coloured bracts: the calyx is tubular and often petaloid. They occur chiefly in tropical and temperate America. The best known is *Bougainvillea spectabilis* (Fig. 1594) which is a climbing, shrubby plant, native of Brazil. In this country it is often grown in greenhouses but in warmer countries it forms one of the most characteristic outdoor climbers, being cultivated wherever white settlements have been established. The brilliant purple or reddish bracts make the flower spikes extremely striking despite the fact that the flowers themselves are inconspicuous. The stem structure is anomalous, the cambium developing outside the original ring of vascular bundles. From it new closed bundles as well as intermediate xylem are formed; the phloem in these new bundles however is very poorly developed. Another important genus is *Mirabilis*. *M. jalapa* (the Marvel of Peru) is a well-known ornamental plant with tuberous roots and a fleshy stem 2 ft. to 3 ft. high. The flowers are tubular

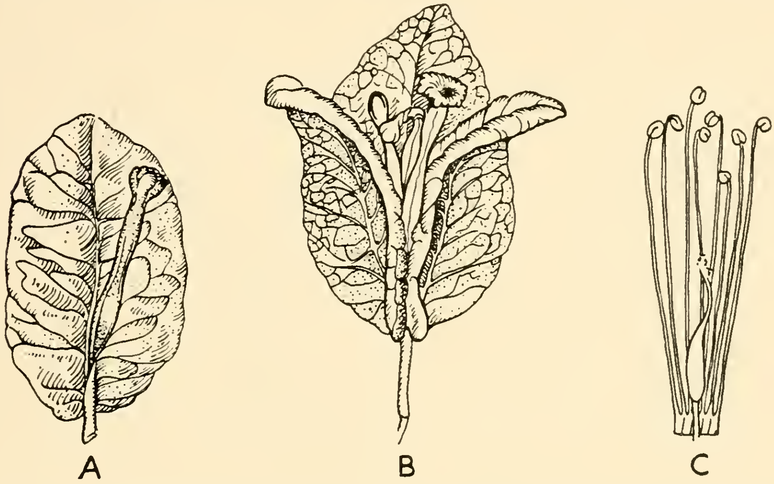


FIG. 1594.—*Bougainvillea spectabilis*. A, Single flower, adnate at the base to the large coloured bract, which serves as a wing for wind dispersal of the fruit. B, Three-flowered inflorescence with bracts. C, Sexual organs from a young flower. (*After Baillon.*)

and shaded red, yellow and white. Each flower is really the central flower of a three-flowered cyme of which the two lateral members are abortive. Around the base of the flower is a false calyx which is really the five partite involucre of the cyme.

Chenopodiaceae

The plants belonging to this family are widely distributed in maritime regions, occurring particularly on salt marshes, muddy foreshores and shingle beaches. Many of them are halophytes. Some of the species are the wild prototypes of commonly cultivated plants, some of which are used for food. Among the common British representatives we may mention *Beta maritima* (Sea Beet), *Salicornia stricta* (Glasswort or Marsh Samphire), *Salsola kali* (Prickly Glasswort), *Suaeda maritima* (Sea Blite), *Atriplex portulacoides* (Orache) and various species of *Chenopodium* (Goosefoot).

From the wild Beet have been cultivated the Garden Beet, the Sugar Beet and the Mangold Wurzel. *Chenopodium bonus-henricus* (All Good or

Fig. 1595.—*Atriplex hastata.* Flowering shoots.

Good King Henry) is cultivated for its leaves under the name of Mercury, while *Spinacia oleracea* is the Garden Spinach.

The plants are mostly annual or perennial herbs, occasionally shrubs or very rarely small trees. Many as we have seen above are halophytes, and as a result their anatomy has been considerably modified. Hairs are commonly developed and their shape and form is made use of in separating certain genera and species. In *Chenopodium*, *Salsola* and *Atriplex* these hairs are of peculiar structure, each consisting of a short stalk, bearing a large thin-walled end cell containing a clear watery sap. These terminal bladders easily collapse and form a peculiar mealy covering. They serve to store water at an early stage in the development of the plant but lose their contents when the structure on which they are borne reaches a certain age, afterwards acting as a protective covering.

In *Chenopodium* and *Atriplex* (Fig. 1595) the leaves are large and often hastate, but in many members of the family the leaves are greatly reduced and may be narrow and cylindrical in section. In *Salicornia* (Fig. 1596) the stems are apparently leafless, each internode ending in a narrow cuplike ring embracing the base of the one above. The internal anatomy shows clearly the outer cortex of these stem joints is foliar in origin and is derived from a decurrent development of the cuplike leaf-sheath of the pair of leaves at the node above.

A watery storage system of large cells containing sodium chloride and other mineral salts in solution is common in halophytic Chenopodiaceae. In dorsiventral leaves these cells occupy the upper and lower surfaces with the green palisade tissue lying in a layer between or even in some cases concentrated around the vascular bundles. In centric leaves, *e.g.*, *Salsola*, this water-storage tissue forms the bulk of the leaf while the assimilatory cells form a zone beneath the epidermis.

The **inflorescence** is frequently of a mixed type; racemes, panicles and spikes of small cymes are all common.

Fig. 1596.—*Salicornia stricta*. Entire plant.

The **flowers** are hermaphrodite, monoecious or actinomorphic and, except in *Beta*, hypogynous, with the parts arranged in fives. They are generally much reduced.

The **perianth** may consist of five sepals which are persistent after flowering. They may be united at their bases. Five sepals are present in the genera *Chenopodium*, *Beta* (Fig. 1597), *Salsola* and *Suaeda*: three or sometimes four in *Salicornia*, while in the female flowers of *Atriplex* there are only two.

FIG. 1597.—Floral diagram of *Beta*. Chenopodiaceae.

The **androecium** consists usually of the same number of stamens as there are calyx lobes, the stamens being inserted opposite the lobes. The filaments are free and the anthers two-celled. Staminodes are rare.

The **gynoecium** is syncarpous, composed of two or sometimes three carpels. The ovary is superior, unilocular, possessing a single basal, campylotropous ovule.

The **fruit** is a nut or akene enclosed in a persistent perianth. It is usually indehiscent or occasionally circumscissile.

The **seed** is usually endospermic, the embryo being curved or even spirally twisted in the endosperm.

The family is one of moderate size containing about seventy-five genera and 500 species showing an interesting geographical distribution. There are nine chief districts where the bulk of the genera occur, namely:

1. Australia. Low-lying salt plains.
2. The Pampas of South America.
3. The Prairies of North America.
4. The Mediterranean coast.
5. The Karroo in South Africa.
6. The Red Sea shore.
7. The south-west Caspian coast.
8. Central Asian deserts.
9. The salt steppes of eastern Asia.

The anatomical features of this family are important. Anomalous stem structure is general, and is due to the appearance of pericyclic rings or strips of cambium, which originate and lose their activity successively, forming secondary bundles and conjunctive tissue. Two extreme types are known: the one results in concentric zones of xylem and phloem, the other results in vascular bundles embedded in prosenchymatous conjunctive tissue and arranged in various ways either regularly or irregularly.

According to Volkens the family may be divided into two sub-families based on the way in which the embryo is arranged in the seed. These are the Cycloloboideae and the Spiroloboideae.

I. **Cycloloboideae**

The sub-family is characterized by the fact that the embryo is ring-shaped, horseshoe-like or semi-circular and wholly or partially immersed in endosperm. *Atriplex* (Fig. 1598), *Beta*, *Chenopodium*, *Salicornia*, *Spinacia*, *Kochia*, and *Corispermum*.

FIG. 1598.—*Atriplex* (*Obione*) *portulacoides*. Plants in flower on a shingle beach. Norfolk.

II. **Spiroloboideae**

This sub-family is separated from the former by the spirally twisted embryos which are either devoid of endosperm, or, where this is present, it is divided into two parts by the embryo. *Suaeda*, *Salsola* and *Haloxylon*.

The pollination mechanism has not been very fully investigated and there is considerable doubt as to whether wind or insects are the main agents of pollination. Since the flowers possess small, calyculate perianths, and are sometimes quite naked, they are comparatively insignificant and insects are not attracted to them. Volkens, who has made a special study of the family, considers that they are entomophilous and that wind pollination is of secondary importance. His reasons for this are, firstly, that the pollen is not easily dispersed; secondly, that the structure of the filaments of the anthers, the flower stalks, and the inflorescence are firm and rigid, not flexible and supple as in most anemophilous flowers; and thirdly, that the course of anthesis does not agree with that in anemophilous flowers, since the anthers do not dehisce all at once but open over an extended period.

The most obvious visitors to these flowers are not, however, the large flying insects normally associated with entomophily, but small bugs, aphids, flies and other creeping or crawling insects. It is possible that there is a slight nectar secretion from the glandular disc or from the papillae which cover this organ in certain genera. Alternatively they may merely enter the flowers to gain protection and to make use of the hiding-places which the flowers readily provide.

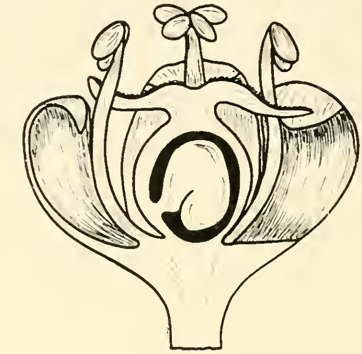


Fig. 1599.—*Beta maritima*. Longitudinal section of flower.

Salicornia is probably mainly self-pollinating. *Kochia* is thought to be pollinated by wind. In *Chenopodium* insects' visits only occur occasionally and self-pollination is usual. In *Beta* (Fig. 1599) the ovary is surrounded by a nectar-secreting disc and the flowers have been observed to be pollinated by hover flies. Finally in *Atriplex* it is uncertain whether wind or insects are the chief agents of pollination.

Automatic self-pollination is commonly found in the genera *Suaeda* and *Salsola*, though the latter is to some extent anemophilous. Included here is *Haloxylon ammodendron* which forms a striking feature on the central Asiatic steppes. It has a thick stunted trunk, sometimes reaching as much as 20 ft., which bears tufts of long, whiplike and apparently leafless branches. It is known as the Saxaul.

Caryophyllaceae (Silenaceae)

This family shows the highest floral expression of the Centrospermae and contrasts markedly with the Chenopodiaceae. It is well represented in the British Flora and many species are cultivated as ornamental garden flowers. The most widespread genus is *Stellaria*, which includes such common plants as the Stitchworts and the Chickweeds. Among others we may mention *Lychnis* (Fig. 1600) (Campion), *Spergularia* (Spurrey), *Arenaria* (Sandwort), *Sagina* (Pearlwort), *Cerastium* (Chickweed), *Silene* (Catchfly) and *Dianthus* (Pink).

Among cultivated plants we may mention particularly the genus *Dianthus*, from which the Pinks, Carnations, Picotees and Sweet William of our gardens have been derived. Various species of *Gypsophila* and *Lychnis* are also grown extensively for their flowers. The plants are mostly herbaceous with swollen stem nodes and opposite, simple, entire and usually exstipulate leaves. Many are annuals, but others form woody perennial growths near the ground or, in the warmer parts of the world, form small shrubs. The development of the leaves is unusual. At each node one leaf develops earlier than the other. This bears in its axil a more vigorous bud than on the other side and frequently it is only this bud which later develops.

FIG. 1600.—*Melandrium* (*Lychnis*) *dioicum*. Flower.

FIG. 1601.—Floral diagram of *Stellaria media*. Caryophyllaceae. All the antipetalous stamens are missing and two of the antisepalous stamens. There is great meristic variation in the family, the number of stamens varying from 1 to 10 and of carpels from 1 to 5.

The **inflorescence** is cymose and is usually a dichasium. Occasionally as in *Githago segetum* (Corn Cockle) the flowers are solitary.

The **flowers** (Fig. 1601) are actinomorphic, usually hermaphrodite and pentamerous, but occasionally unisexual or tetramerous.

The **calyx** is composed of five, rarely four, sepals which are either free or united together into a tube. They are imbricated, with membranous margins.

The **corolla** is made up of five, rarely four, petals or the petals may be absent. Unlike the sepals, the petals are never united together.

The **androecium** consists of ten, occasionally eight or fewer stamens which are arranged in two whorls. They are hypogynous or occasionally perigynous, and apparently obdiplostemonous, that is to say the stamens of the outer whorl appear opposite the petals rather than alternating with them. In some genera the stamens may be reduced to five, four or even one. The anthers are two-lobed and dehisce longitudinally.

The **gynoecium** consists of from two to five carpels, which are syncarpous, with free styles. The ovary is unilocular and superior; the ovules are usually numerous, campylotropous and arranged upon a central column, *i.e.*, the placentation is apparently free central (but see p. 1229). The carpels as judged by the positions of the styles are sometimes opposite the sepals as in *Viscaria* and *Spergula* and sometimes opposite the petals as in *Githago*. This has led to the suggestion that in the ancestral complete flower the gynoecium consisted of two whorls, of which one is now absent. In *Viscaria* it is the antipetalous, while in *Githago* it is the antisepalous whorl which is absent.

The **fruit** is generally a unilocular capsule which dehisces valvately at the apex, the seeds being scattered by the censer mechanism.

The **seeds** are endospermic and the embryo is curved or eccentric in the endosperm. The funicle is sometimes unusually conspicuous.

The family comprises some eighty genera and about 1,300 species which grow mostly in the temperate regions of the northern and southern hemispheres. A few are found in the tropics, mainly on mountain tops.

The chief distinguishing anatomical feature is that the stomata possess two subsidiary cells placed at right angles to the guard cells. So far as the stem is concerned, the cork is generally internal and there is often a ring of superficial sclerenchyma. Much of the xylem is frequently unlignified.

Biologically as well as morphologically the family falls into two distinct groups. The more advanced group is the Silenoideae and the less advanced the Alsinoideae.

I. Alsinoideae

In this sub-family the flowers are polysepalous and the stamens often perigynous; gynodioecism is common. The petals are small, white and simple. It is divided by Pax into a number of groups as follows:

(*a*) Fruit a capsule opening by teeth or valves.

1. *Alsineae.* The styles are free to the base and the leaves exstipulate. *Stellaria*, *Cerastium*, *Sagina* and *Arenaria*.
2. *Sperguleae.* The styles are free to the base but the leaves are stipulate. *Spergula* and *Spergularia*.
3. *Polycarpeae.* The styles are joined at the base. *Drymaria* and *Polycarpon*.

(*b*) Fruit an akene or nut.

1. *Paronychieae.* The flowers are all developed equally and the leaves are stipulate. *Corrigiola*, *Paronychia*, *Illecebrum* and *Herniaria*.
2. *Dysphanieae.* The flowers are all developed equally but the leaves are exstipulate and alternate. *Dysphania*.

3. *Sclerantheae.* The flowers are all developed equally but the leaves are exstipulate and opposite. *Scleranthus.*
4. *Pterantheae.* The flowers are in groups of three, the two lateral flowers being more or less abortive. *Pteranthus.*

Bentham and Hooker separate the last four of these groups as a distinct family, the Illecebraceae, but this now generally considered an unjustifiable separation of related groups.

II. Silenoideae

In this sub-family the flowers are gamosepalous and hypogynous. The petals are often red in colour and are differentiated into stalk and limb. There is often an out-growth or ligule forming a corona in the flower. The sub-family is divided into two groups.

1. *Lychnideae.* The calyx has commissural ribs. *Silene* and *Lychnis.*
2. *Diantheae.* There are no commissural ribs on the sepals. *Gypsophila, Dianthus, Saponaria* (Fig. 1602).

Fig. 1602.—*Saponaria officinalis.* Flowers.

A typical example of the Alsinoideae is the isomerous flower of *Spergularia arvensis*, in which the five simple white petals are succeeded by two whorls of five stamens, of which only one is sometimes developed, and five carpels. In certain other genera such as *Stellaria* (Fig. 1603) the flower is usually pentamerous but occasionally tetramerous and the carpels are reduced to three, but considerable variation may occur within a single species.

FIG. 1603.—*Stellaria holostea.* Stitchwort. Flower.

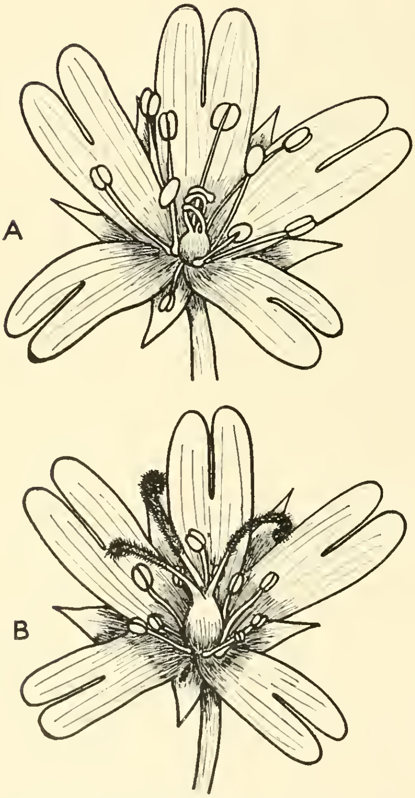


FIG. 1604.—*Stellaria graminea.* Pollination. A, Flower in male stage. B, Flower in female stage with expanded stigmas. (*After Knuth.*)

In many genera the petals are bifid and there is great variation in the number of the styles and the number of valves in the capsule.

The pollination mechanism is interesting. All the flowers secrete nectar and most are visited by flies and the less specialized bees, in contrast to the members of the Silenoideae in which long-tongued insects, such as butterflies and moths, are the chief visitors. This is because the long tubular calyx of the latter renders the nectar inaccessible to short-tongued insects.

Many of the flowers are dichogamous, in which case they are nearly always protandrous. Automatic self-pollination is probably possible in all species. Though the details differ appreciably in the different genera we may cite the condition in *Stellaria graminea* (Fig. 1604) as an example. In this flower five nectaries are arranged in the form of a green, fleshy ridge, at the base of each of the five outer stamens. The flowers are protandrous and when they open the five outer stamens bend inwards and dehisce while the five inner ones are still unripe and are curved outwards. The stigmas are also immature. Before the five outer stamens have withered the five inner dehisce but still remain directed outwards. As the stamens wither the styles elongate and the stigmas unfold above the stamens.

All but very small insects when trying to reach the nectar must become dusted with pollen in the younger flowers, whether they alight in the middle or at the edge. In older flowers they are bound to come into contact with the stigmas and thus effect pollination.

Failing cross-pollination the stigmatic surfaces bend back further until they come into contact with the anthers, to which some pollen remains adherent and thus self-pollination is ensured. This flower is normally pollinated by flies, small bees and beetles. In the Alps, where the Lepidoptera abound, it is sometimes visited by butterflies.

To the Diantheae belong all the more conspicuous members, many of which are cultivated in gardens. The flowers are pentamerous with two whorls of stamens. The styles are free and indicate the number of carpels involved in the gynoecium. These are five in *Lychnis*, three in *Silene* and two in *Dianthus* and *Saponaria*. The ovary is sometimes chambered at the base by septa which represent the lateral walls of the carpels.

Pollination (Fig. 1605) in this sub-family is effected by long-tongued insects, such as the larger bees, butterflies and moths. The nectar is concealed at the base of the deep tube formed by the sepals. We will take as

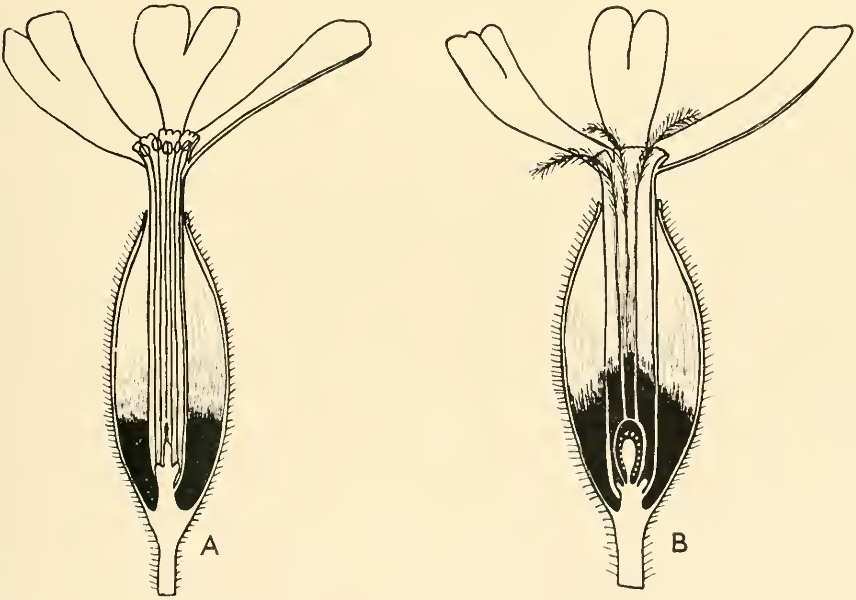


FIG. 1605.—*Melandrium album*. A, Male flower. B. Female flower. The deep calyx and the long claws of the petals form a floral tube which simulates the conditions in a sympetalous flower. (*After James and Clapham.*)

our example the common rock-garden Pink, *Dianthus deltoides*, the Maiden Pink.

The flowers (Fig. 1606) are protandrous and usually large and brightly coloured. The claws of the petals are long and winged and are held together so as to form a tube by the tubular calyx, which is itself generally surrounded by tough bracts which may prevent humble bees from attempting to reach the nectar by biting through the calyx. The nectar is concealed at the bottom of the corolla tube, which is so long and narrow that as a rule only the long tongues of butterflies can reach the bottom. The stamens and petals spring from a ridge of the receptacle which surrounds the base of the ovary. On the inner edge of this ridge is a yellow fleshy cushion which secretes the nectar. At the beginning of anthesis, the tubular passage formed by the corolla is made so narrow by the presence of the five inner stamens which it encloses, that only the fine proboscis of the insect can reach down it. The path to the nectar is indicated by nectar guides in the form of whitish spots on the rose-red petals. The five outer stamens elongate first, so that their anthers project out of the corolla tube when they dehisce, and after they have withered the inner five stamens elongate in a similar way. At all times the entrance to the tube is covered by the anthers so that the probing insect is sure to receive pollen on its head. When all the pollen has been shed the two styles, which up to now have remained twisted together in the corolla tube, elongate and their

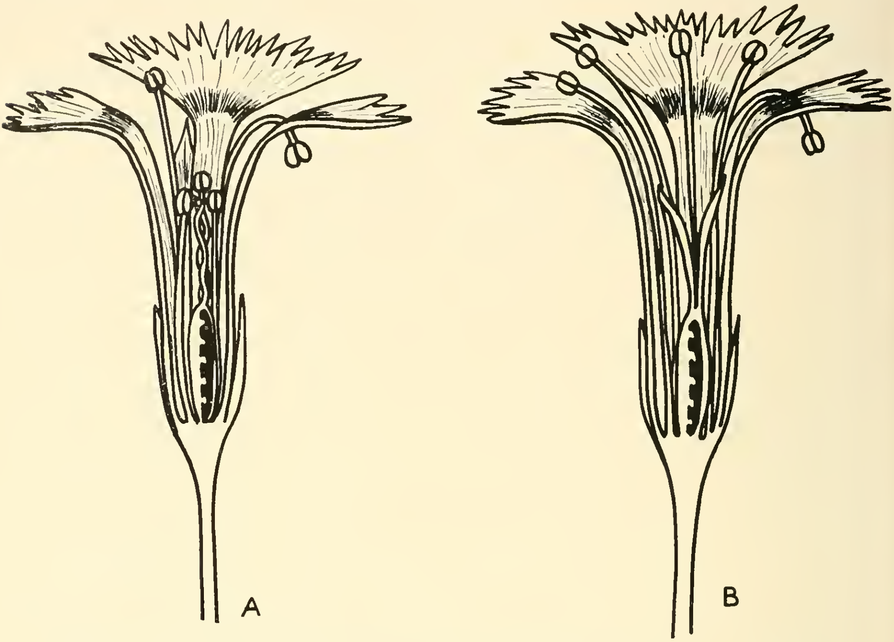


FIG. 1606.—*Dianthus deltoides.* A, Outer stamens elongating. B, Styles elongating.

stigmatic surfaces open out, occupying the same position as the anthers did previously. When the styles separate they remain spirally twisted so that the proboscis of an insect must touch a stigmatic surface from whatever side it may approach the flower. If the insect has previously visited a younger flower cross-pollination is thus ensured.

The genera *Silene* and *Dianthus* are widely distributed, the greatest number of species occurring in the Mediterranean region. The latter genus prefers dry exposed situations. Species of *Silene* occur on the mountains of Europe, tropical Africa and in Mexico, while those of *Dianthus* are absent from the New World. Certain species of *Silene* and *Lychnis* also occur in arctic regions.

The family is of little economic importance. Saponin is obtained from the roots and leaves of *Saponaria officinalis*, the Soap Wort, which is sometimes used for washing. Among the garden flowers already mentioned the genus *Dianthus* is the most important. Pinks are mostly derived from *D. plumarius*, Carnations from *D. caryophyllus* and Sweet William from *D. barbatus*.

The anthers of various genera are subject to attack by fungi: *Puccinia antherarum*, a Rust, and *Ustilago violacea*, a Smut. In both cases the anthers fail to produce pollen grains but liberate fungal spores instead. Reinfection is achieved by the insects normally concerned in cross-pollination.

PROTEALES

The Proteales are Archichlamydeae in which the flowers are either bisexual or unisexual as a result of abortion of part of the flower. The perianth is composed of one series of parts which is considered to be the calyx. It is often brightly coloured. There are four stamens opposite the calyx segments, the ovary is unilocular and the seed is devoid of endosperm.

The plants are usually woody and many are trees, though some would be better described as tall shrubs. The leaves are usually alternate, entire or pinnate. There is a single family, the **Proteaceae**, which is distributed in the drier parts of Australia and South Africa. It contains 960 species distributed among fifty genera.

We shall not consider the family in detail but will only refer to some of the more interesting members. One of the best-known members, already referred to in this book, is the genus *Hakea* which contains about 100 species, native to Australia. The seedlings show an interesting variation in their foliage. The cotyledons are round and somewhat fleshy, while the later leaves are either much divided or else form spiny needles. The anatomical structure of these needles is centric, with a peripheral palisade layer and large radial prop cells which span the assimilating tissues. Similar centric leaves are found in species of *Grevillea*, which is also a large Australian genus with about 170 species. Several species are cultivated in greenhouses in this country, the commonest being *G. robusta*, which grows into a fair-sized shrub with fern-like foliage. In Australia this species grows into a large tree, the Silky Oak, and it is extensively planted as a shade tree in Ceylon and elsewhere (Fig. 1607). The wood is of considerable economic importance. The flowers (Fig. 1608) of this genus are worthy of mention.

FIG. 1607.—*Grevillea robusta.* Silky Oak. Avenue in Australia.

FIG. 1608.—*Grevillea linearis* (left) and *G. bipinnatifida* (right). Flowering shoots.

The inflorescence is a raceme, two flowers being borne in each axil. The style projects from the bud as a long loop, while the immature stigma is retained within the perianth until pollen has been shed on to it (Fig. 1609). The style then straightens out bearing the pollen which it has collected from the anthers on its tip. Nectaries are developed at its base and pollination is effected either by insects or humming-birds. The stigmatic surface develops later, often as a disc formed laterally on the style.

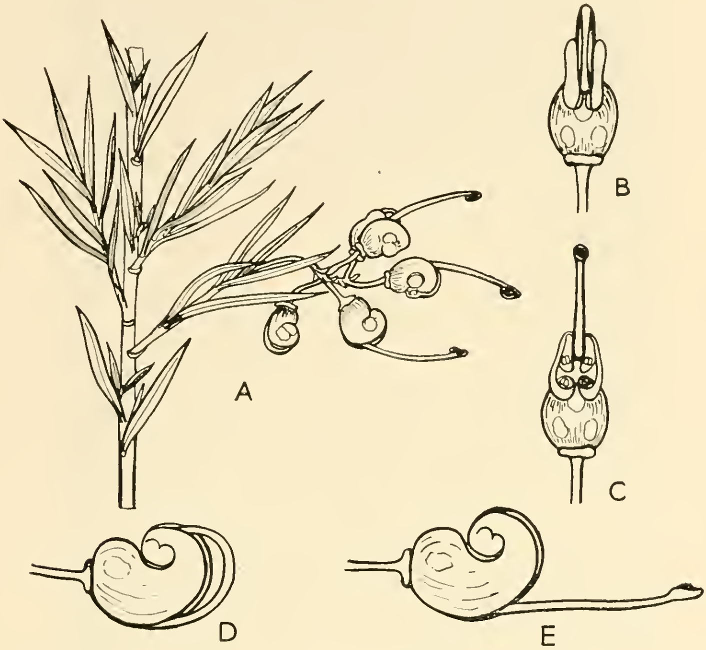


Fig. 1609.—*Grevillea linearis.* Pollination. A, Flowering shoot. B and D, Young unopened flowers with stigma still confined by the perianth. C and E, The style has forced open the perianth and straightened out, exposing the anthers which are held in pockets of the perianth segments.

In many genera such as *Protea* and *Banksia* the plants produce large heads of flowers (Fig. 1610) which are surrounded by large, often brightly coloured involucral bracts. A similar form of inflorescence is found in *Leucadendron*, a South African genus with seventy species. *L. argenteum* (Fig. 1611) is the Silver Tree, so called because of its silvery leaves which are covered with fine silky hairs. It is not uncommon around Cape Town.

The fruits produced in this family may be either follicles or nuts. The pericarp is usually thick and often woody. The fruits of the genus *Xylomelum* are known as woody pears and look edible at first sight. Examination shows however that they consist of a thick wall of woody tissue inside which are winged seeds. In the genus *Banksia* the fructification takes the form of a woody cone in which the dehiscent fruits are embedded.

The family as a whole is characteristic of dry situations and shows decided xerophytic tendencies. They form a very characteristic element in the flora of South Africa, especially the south-western portion of Cape Colony. A second centre of distribution is the dry south-western regions of Australia, whence they spread out to New Zealand, New Caledonia and eastern Asia. *Telopea speciosissima* is the national flower of Australia and is known as the Waratah. In contrast to the dense distribution in these areas only a few species occur in South America and none are found in north temperate regions; in fact the group is essentially a southern hemisphere one, as will be seen from the accompanying map (Fig. 1612).

Fig. 1610.—*Protea mellifera.* Inflorescence. Photograph supplied by Douglas Elliott, New Zealand.

FIG. 1611.—*Leucadendron argenteum.* The Cape Silver Tree. Branch with aggregate fruit.

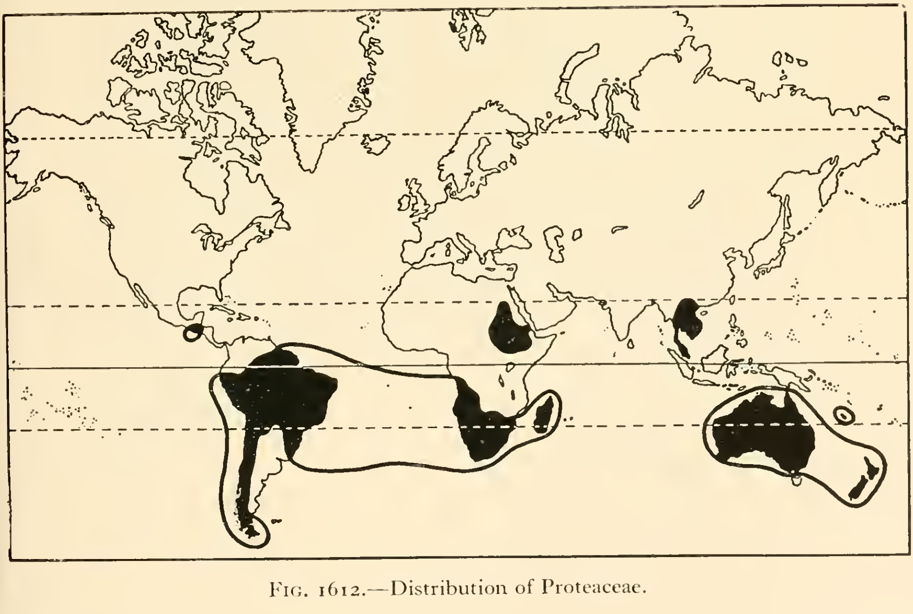


FIG. 1612.—Distribution of Proteaceae.

POLYGONALES

The Polygonales are Archichlamydeae which are essentially herbaceous plants, there being very few shrubby or arborescent types. The order is closely related to the Centrospermae on the one hand and the Piperales on the other. It contains the single family Polygonaceae and hence the characters of the family and of the order are the same.

The most characteristic feature is the peculiar sheathing membrane attached to the node, which is called an **ochrea** (see Chapter XXII). It clasps the stem above the leaf base and takes the place of stipules in protecting the bud during growth. The flowers are hermaphrodite, small and actinomorphic and are usually produced in large numbers on a compound inflorescence. The sepals vary from three to six and often enlarge and become membranous in the fruit; petals are absent.

The stamens vary from six to nine. The ovary is superior, composed of three or sometimes two united carpels, but it is unilocular and has a single

FIG. 1613.—*Rumex acetosella.* Sheeps' Sorrel. Flowering shoots.

FIG. 1614.—*Rheum.* Rhubarb. Part of an inflorescence with fruits.

orthotropous basal ovule. The fruit is a single, three- or two-winged nutlet. The seeds contain copious endosperm and often an eccentric embryo.

The **Polygonaceae** contain about forty genera and some 750 species, which live mostly in the north temperate zone. Among the more common genera which occur in Britain may be mentioned *Rumex* (Dock) (Fig. 1613) and *Polygonum* (Knotgrass). Several are of economic importance, *e.g.*, *Rheum rhaponticum* (Rhubarb) (Fig. 1614) and *Fagopyrum esculentum* (Buckwheat). *Muehlenbeckia platyclados*, a native of the Solomon Islands, has its stem and branches flattened in the form of cladodes.

Some of the genera rely upon wind for pollination, but *Rheum* and *Polygonum* are entomophilous, nectar being secreted at the base of the stamens. They are rendered conspicuous by the number of flowers in the inflorescence (Fig. 1615), and by the red and white colours of the sepals.

Fig. 1615.—*Polygonum sieboldii.* Inflorescence.

Anatomically the family is noteworthy on account of the occurrence of inversely orientated medullary bundles, especially in species of *Rumex* and *Rheum*.

The **Piperales**, as mentioned above, are closely related to the Polygonales. We shall not consider the order in detail but since they show several interesting features we may briefly describe them here. They are either herbs or shrubs with entire leaves containing oil glands. In the structure of the flowers they show certain resemblances to the Polygonales. The important families are the **Piperaceae** and the **Saururaceae**, which are however sometimes united together. The former is pan-tropical in distribution, but the latter family is restricted to three genera comprising four species distributed over eastern Asia.

Some authorities regard the Piperales as a very primitive order, deriving it from the Gnetales, and there are some anatomical features to support this view. In *Piper nigrum* (Fig. 899, Vol. I) the stem contains not only an external ring of bundles from which a zone of secondary wood may be formed but also a number of internal medullary bundles which may be either scattered or arranged in one or two rings. In the genus *Peperomia* the outer ring of bundles does not become united and the scattered arrangement of the medullary bundles recalls that of the Monocotyledons, except that the bundles are not closed. It also resembles closely the flowering stalk of *Anemone japonica* (see Chapter XXI). In *Peperomia*, too, resin and oil-secreting sacs are generally distributed both in the epidermis and in the ground tissue.

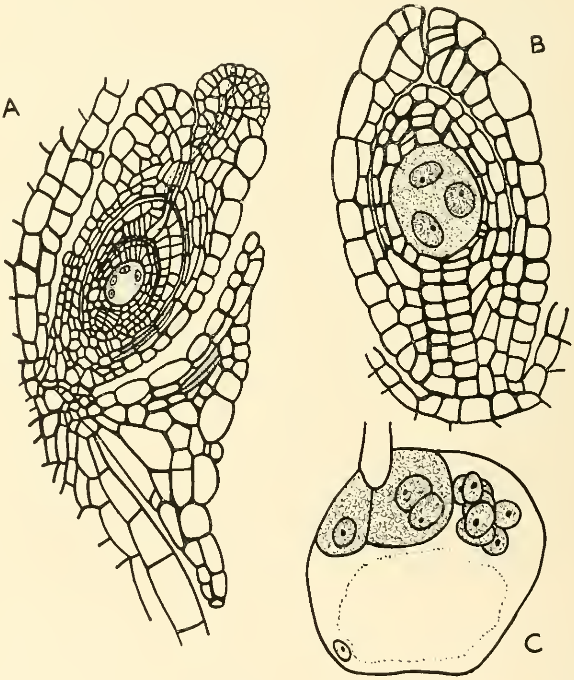


FIG. 1616.—*Peperomia pellucida.* A, Longitudinal section of ovule with four-nucleate embryo sac. B, Four-nucleate embryo sac, showing no polarity of nuclei. C, Embryo sac at fertilization stage. (*After Johnson.*)

In the structure of the ovules these genera are peculiar. In *Peperomia* (Fig. 1616) there is only a single integument and the female gametophyte is unusual. The first four nuclei formed are large and tetrahedrally grouped. From these sixteen nuclei are formed, one of which, at the micropylar end, forms the oosphere, while one adjacent nucleus functions as a synergid. Eight of the remaining nuclei unite after fertilization to form the primary endosperm nucleus. The remaining six preserve their parietal position and finally become enclosed in walls. There are no definite antipodal cells. It will be noted that there is a similarity between this and the behaviour in the embryo sac of *Gnetum*.

The plant of chief economic importance belonging to this family is *Piper nigrum*, a member of a large genus of some 700 species. It is a weakly growing climber, a native of Indo-Malaya where it is chiefly cultivated. It is propagated by cuttings, planted around live trees which serve as supports. These cuttings take about three years to reach a length of 15 ft. and are in full fruit for about six years thereafter. The berries are borne in clusters of about thirty. They are green at first, turning successively red and finally yellow when ripe. When they reach the red stage they are picked, spread out in the sun, and rapidly turn black. These berries when ground form the black pepper of commerce.

White pepper is made by soaking the black berries in water for several days till the outer coat can be rubbed off.

Several other species of *Piper* are in cultivation (Fig. 1617). *P. longum* is similar in appearance to *P. nigrum* and grows more quickly; the berries, however, are not so pungent. It is chiefly cultivated in India. *P. betle* is

FIG. 1617.—*Piper aduncum*. Brazil.

cultivated in the Middle and Far East and used in the preparation of Betel Pepper. *P. methysticum* is used in preparing the drink, Kava. Pepper Oil or Piperonal is the source of synthetic heliotrope essence.

URTICALES

The Urticales are Archichlamydeae in which the flowers are usually small and inconspicuous and are normally monoecious. The perianth is hypogynous and often greenish in colour, consisting of either four or five more or less united segments. The stamens are arranged opposite the perianth segments and are equal in number to them. The ovary is made up of either one or two carpels but is always unilocular and contains a single ovule. The fruit is either a drupe, a samara or a nut containing one seed. The embryo either occupies the whole of the seed or a fleshy or oily endosperm may be present.

Pollination is usually anemophilous or occasionally entomophilous.

The majority of the members of this order are trees, though shrubs and herbs also occur. They normally possess simple, alternate, leaves, while the inflorescences are generally cymose.

The limits of this order are clearly defined and most authorities agree which families should be included in it. Both Hutchinson and Rendle place the following families in the order: Ulmaceae, Urticaceae, Moraceae, Cannabinaceae and Eucommiaceae. Though the families are poorly represented in the British Flora we shall have to consider each in some detail on account of the economic importance of so many of their members.

The **Ulmaceae** are mostly trees, though in two genera some species are only bushes. Included in this family is *Ulmus*, the Elm, which grows into a large tree reaching a height of up to 150 ft. The leaves are simple, oval-shaped, asymmetrical and arranged alternately in two rows up the

FIG. 1618.—*Ulmus montana* (*U. glabra*). Inflorescences in early spring.

stem. The flowers are borne early in the spring in the axils of last year's leaves (Fig. 1618). They are monoecious, though frequently both kinds of flowers occur in the same inflorescence, the central ones being female and the lateral flowers, which develop later, being male, a point which distinguishes this genus from most of the others in the family. These flowers contain no nectar and are wind-pollinated. Each flower (Fig. 1619) consists of from five to seven polysepalous segments, inside which, and opposite to them, are a similar number of stamens. The ovary is made up of two carpels forming a single chamber, or occasionally two chambers. It contains a single anatropous ovule.

FIG. 1619.—*Ulmus montana.* Single flower.

The British species of *Ulmus* deserve a short note. In the first place there are a number of common but quite distinct species of which we may cite the following:

1. *U. procera* (*U. campestris*). English Elm. This is the largest and commonest species in southern England, which may be found either in rows, in hedges, or separately in parks. It is a hybrid and does not produce fertile seeds but propagates readily by suckers. In spite of its name it is not a native British species, but was traditionally introduced by the Romans. It does not occur spontaneously, but is widely planted for its timber and its stately form.
2. *U. sativa.* Small-leaved Elm. This species differs from *U. procera* only in the size of the leaves, which are smaller. It may in fact be only a variety. It occurs chiefly in the eastern counties.
3. *U. carpinifolia* (*U. nitens*). Smooth-leaved Elm. It is usually distinguished by the texture of the leaf which is smooth, and the veins not so clearly marked. It may be a variety of *U. glabra* and is restricted to the eastern counties.
4. *U. glabra* (including *U. montana*). The Wych Elm. It is a large tree with more or less arched branches. The leaves are sessile, acuminate, smooth and shiny on the upper surface, but with hairs in the vein-axils beneath. It frequently forms suckers and

a pendulous variety is known. Under very favourable conditions it may reach a height of 120 ft. It is a native of all parts of Great Britain.

5. *U. hollandica.* Dutch Elm. This is probably a hybrid between *U. glabra* and *U. nitens.* It has a short bole and widespreading branches, the lower limbs often being unusually long. It is a hedgerow plant readily propagating by suckers.

6 *U. stricta.* Cornish Elm. It is pyramidal in shape with narrow leaves. It is common in western Cornwall and occasionally found in southern England. According to some authorities this Elm is really a variety of *U. glabra* and is referred to as *U. glabra* var. *cornubiensis.* Another variety, *U. stricta* var. *sarniensis*, is the Jersey Elm, which is found in southern England and is frequently planted in the Channel Islands. It is probably not a native.

7. *U. americana.* American Elm. It is widely distributed in the United States and Canada and is sometimes planted in this country.

Many species of the genus *Ulmus* range widely in temperate regions and in Miocene times were common in Greenland. About 130 species are recognized.

In recent times the Elm has suffered exceptionally severely from a disease known as the Dutch Elm Disease, the cause of which is still open to question, though fungi certainly are associated with it. The result of an attack is the death of the tree and many fine trees both in this country and in Europe have succumbed to the disease. Elm wood is extensively used in carpentry, particularly for coffins, garden furniture and outdoor implements. It does not rot easily.

The **Urticaceae** are mostly herbs or small shrubs. They are a large family of some 480 species, generally tropical in distribution, occurring mainly in the New World and in Asia. In the East Indies species of this family form a notable proportion of the vegetation. In Great Britain there are only two genera, *Urtica*, with three species—*U. dioica* (Common Stinging Nettle), *U. urens* (Small Nettle), and *U. pilulifera* (Roman Nettle)—and *Parietaria* with the single species *P. diffusa* (Wall Pellitory). Both these genera are found chiefly in temperate regions.

In the Common Nettle (Fig. 1620) the sexes are separated in different plants, while in *U. urens* both sexes occur in the same inflorescence. The flowers are arranged in a panicle. Each male flower consists of a four-segmented perianth, with four opposite stamens. The latter are bent downwards and inwards in the bud, but when ripe spring violently upwards, the anthers turning outwards so that the loose pollen is liberated in a tiny cloud. Wind currents carry it to the female flowers. In the female flowers the lateral perianth segments are considerably larger than the antero-posterior ones, the ovary is unilocular and contains a single basal orthotropous ovule. The fruit is an akene, and the seed is rich in oily endosperm.

Not all the Urticaceae possess stinging hairs though they are present in the genera *Urtica*, *Urera* and *Laportea*. In the two latter genera the effect of the sting is serious and may cause severe injury to those who come into contact with the plants.

Fig. 1620.—*Urtica dioica*. Common Nettle. Male plant in flower.

Certain genera are used as a source of fibres, among the more important being *Boehmeria*. It is chiefly cultivated in China, where the fibres of *B. nivea* (China grass or Rhea) are obtained from the inner bark. They are possibly the toughest, longest and most silky of all vegetable fibres, reaching a length of up to 9 in. In the tropics a variety *tenacissima* is cultivated under the name of Ramie. Though these fibres are very valuable they are the most difficult to prepare. Smaller fibres up to 3 in. long can be obtained from the Stinging Nettles.

Anatomically the Urticaceae are of note because of the cystoliths which are found very commonly in the epidermal cells. They vary in shape in the different genera. A milky latex common in the Moraceae is absent from the Urticaceae.

The **Moraceae** are a family of some 900 species which are very widely distributed in the warmer parts of the world. There are some fifty-five genera, of which the genus *Ficus* is easily the largest. They are mostly trees or shrubs with stipulate leaves and many are of economic importance. The inflorescence (Fig. 1621) is cymose or racemose but is frequently modified. The flowers are unisexual. The perianth consists of four segments which are occasionally united. In the male flowers (Fig. 1622) there are

FIG. 1621.—*Broussonetia papyrifera.* Paper Mulberry. Young female inflorescences. The tree is the source of the Polynesian tapa cloth.

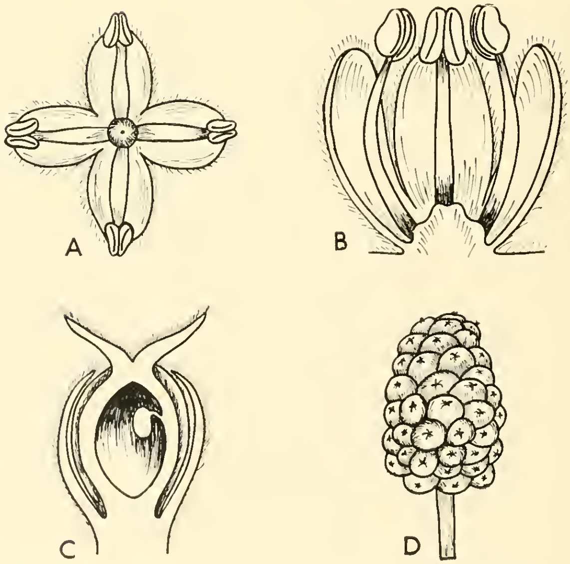


FIG. 1622.—*Morus nigra.* Mulberry. A and B, Male flowers. C, Female flower in section. D, Aggregate fruit. (*After Rendle.*)

four stamens arranged opposite the perianth segments. Though sometimes bent inwards in the bud they do not explode as in the Urticaceae. The gynoecium consists of two carpels, of which one aborts so that the ovary is unilocular and has a single pendulous ovule. The fruit is either an akene or a drupe but the single fruits are frequently aggregated together by the union of neighbouring flowers to form a pseudocarp, either as a result of modification of the receptacle or through the fusion of the swollen perianth segments. The seeds may be endospermic or non-endospermic and the embryo is usually bent.

There are no British examples, though several species are commonly grown in gardens. The best known of these is the Mulberry, *Morus*. The genus contains twelve species which are wild in north temperate regions and on the mountains of the tropics. The White Mulberry (*M. alba*) is a native of China. It has been cultivated in the Far East from the earliest times and was introduced into Europe in the twelfth century. The Black Mulberry (*M. nigra*) (Fig. 1623) has also been for long cultivated in Asia and parts of Europe. In 1548 it was introduced into England, the first tree being planted in the gardens of Syon House, near Richmond on the Thames. The cultivation of the Mulberry is closely bound up with the silk industry because its leaves provide the food of the silkworm caterpillar. Though *M. nigra* is chiefly used, it is said that better silk is obtained when the leaves of *M. alba* are used. The fruit is edible and ripens well in the south of England and Wales. The Mulberry forms a large spreading tree and is frequently used as a specimen tree on lawns; in later life the

FIG. 1623.—*Morus nigra*. Habit of tree.

trunk often becomes hollow and many fine trees have been lost by the collapse of the trunk during gales.

The genus *Ficus* (Fig. 1624) is a very large and important one with 800 species. The plants are mostly trees or shrubs with large, entire, alternate leaves, with stipules which envelop the buds and drop off soon after the latter have unfolded. The genus though widely distributed is most characteristic of the vegetation of the East Indies and Australasia. Many are epiphytes and produce adventitious aerial roots which eventually replace the primary root. These roots clasp the trunk of the supporting tree and by joining together they form a woody case in which the support soon perishes, leaving the epiphyte *Ficus* independent.

Fig. 1624.—*Ficus* sp. Giant tree at San Isidro, Chile.

The following are some of the principal species:

Ficus elastica is the India Rubber Tree. Though in cultivation it grows as a stout independent tree, it may be found in Nature as an epiphyte reaching a very large size. Buttress roots are often produced at the base which grows out in all directions and form woody walls only a few inches in thickness but about a foot in height. They may spread out 20 or more feet from the trunk. The leaves (Fig. 1625) are entire and of a leathery texture with a waxy surface which defies wetting. Caoutchouc is obtained from the latex, which is contained in latex canals distributed in the cortex and phloem. Adventitious roots descend from the branches and form great pillars which support the larger branches. It is cultivated particularly in India and Malaya.

Ficus benghalensis is the Banyan Tree (Fig. 826, Vol. I). It is a tree growing to an enormous size. From the larger branches adventitious roots grow down and if allowed will form pillars giving the appearance of additional trunks. As a result the trees may cover large areas. Tradition states that an army of 5,000 men have encamped under the cover of a single banyan tree, and one tree, consisting of 350 large and 3,000 small columns, has been recorded. The tree is sacred in India and the young prop roots are protected from injury by enclosing them in tubes of bamboo.

FIG. 1625.—*Ficus elastica.* The India Rubber Plant. Frequently grown for indoor decoration.

Ficus religiosa is the Peepul or Bo Tree. It is similar in appearance to the Banyan but the leaves have long, acuminate apices and no epidermal wax. It is also a sacred tree to the Buddhists for beneath its shade Buddha is said to have learned the vanity of existence and the mystery of the universe. At Dena Pitya in Ceylon is a Bo tree under whose shade lives a whole village of over a hundred huts.

Ficus sycomorus is the biblical Sycamore or Mulberry Fig. It is a relatively small, erect tree.

Ficus carica is the Mediterranean Fig. It is a small tree in which the fruits are pear-shaped (Fig. 1626). The species is commonly cultivated in this country and, though the best fruits are obtained in greenhouses, outdoor fruits can be obtained when the tree is planted against a warm wall. Commercial fig growing in this country is restricted mainly to the neighbourhood of Worthing.

FIG. 1626.—*Ficus carica*. The Fig. Branch with fruits.

Ficus repens is one of a number of climbing Figs, and supports itself by the aid of its adventitious roots in the same way as Ivy. These roots secrete a gummy substance containing caoutchouc and then absorb the fluid constituent, leaving the root firmly cemented to the support.

Ficus benjamina like certain other climbing Figs produces great clasping roots which are negatively phototropic and grow around the trunk of the support. These roots thicken and form a network which finally strangles the host. The roots may also form a trellis work over rocks and the same species may occur either as an epiphyte or as an independent tree.

In addition to providing raw material for the manufacture of rubber, certain species of *Ficus* produce Shellac by the punctures of a small hemipterous insect. The buttress roots are used by natives as planks for various purposes.

Numerous fossil leaves have been referred to the genus *Ficus*, and although some of these may really belong to other genera it seems certain that the genus extended to Greenland during Cretaceous times and was widely distributed in North America and Europe in the Tertiary period up to Miocene times.

Another important genus of this family is *Artocarpus*, with sixty species. Three species are cultivated mainly for their fruits. *A. incisa*, the Breadfruit (Fig. 1627), is a tree of particular importance in Polynesia where it grows to a height of about 50 ft. It has large, pinnatifid leaves, the male and female flowers being developed in separate inflorescences. The ripe fruit is yellow in colour, and 4 to 8 in. across, round or oval in shape. There are two forms of Breadfruit. In one the fruit is almost seedless, while the other contains many large seeds. The fruit is a pseudocarp, the flesh being formed from the axis of the inflorescence. The seedless variety is propagated from root cuttings. Analysis of the fruits shows a wide variation in carbohydrate content between 9 and 15 per cent. of the weight. The protein content is low, being about 1·5 per cent.

FIG. 1627.—*Artocarpus incisa.* Breadfruit Tree. Shoot with young fruits.

The Jack fruit (*A. integrifolia*) is similar to the Breadfruit, but differs in that the fruits in this species are borne on the trunk and not on the branches. The tree may reach 70 ft. in height and the aggregate fruits are very large, in fact they are probably the largest in the world, being oval in shape and 2 ft. in length, weighing up to 80 lb.

The third species is the Marang (*A. odoratissima*) which is a native of the Philippine Islands. The fruit is about 6 in. long and covered with short spines. The flesh is white, sweet, juicy and aromatic, with a pleasant flavour. It separates into segments each the size of a grape, which represent the individual fruits.

In addition to their important fruits the leaves of species of *Artocarpus* are used. The leaves are oval, about 2 ft. long, and dry very easily. When ground into a meal they form an excellent cattle food which has up to 24 per cent. of protein in it. The seeds are also ground and used for livestock, and though the protein yield is only 14 per cent., they contain some 64 per cent. of carbohydrates.

Several other genera are of economic importance and worthy of brief mention.

In the genus *Brosimum* the akenes are embedded in a fleshy receptacle which in *B. alicastrum* is used for food in the West Indies under the name of Bread-nut. *B. galactodendron* is the Cow-tree of Venezuela. The milky latex flows in considerable quantity and tastes very like ordinary milk and is used for that purpose by the natives. Several other species have useful wood, known as Snake Wood.

Broussonetia papyrifera, the Paper Mulberry of Japan, is used by the Polynesian natives to make Tapa or Kapa cloth. It is obtained from the inner bark. Sheets of this, prepared with the fibres crossed, are beaten together make a tough fabric.

Antiaris toxicaria is the famous Upas Tree of Java. The latex contains a very virulent poison and a century ago extraordinary stories of its effect were told. It was said that for a distance of several miles around the tree nothing could live. The noxious volcanic valleys with a high carbon dioxide content in the air were probably responsible for these stories.

Castilloa elastica, Ulé, is a native of Cuba. It yields caoutchouc and is the source of the Central American or Panama rubber.

Finally mention must be made of the genus *Cecropia* of which some forty-five species occur in tropical America. They are of particular interest because of the symbiotic association established between these trees and certain species of ants which inhabit the hollow stems. *C. peltata* (Fig. 1628) is the Trumpet Tree, so called because of the use made of its hollow stems by the Indians of Brazil.

The fourth family of the Urticales is the **Cannabinaceae**. It is a small family containing only two genera, *Humulus* and *Cannabis*, which are included by some writers in the Moraceae. They differ however from that family in having no latex. The plants are dioecious, and the flowers occur in cymose inflorescences, which contain many male or few female flowers. The male flower has a five-parted perianth and five opposite stamens, while the female flower has a small cuplike perianth and a unilocular ovary containing a single pendulous ovule. The embryo in *Humulus* is coiled while in *Cannabis* it is curved.

The genus *Humulus* contains two species, both of which are climbers. *H. lupulus* (Fig. 1629) is the Hop, which is widely cultivated. In this country Hop gardens are found particularly in Kent and Herefordshire. It is a perennial and in rich soil the shoots, generally called bines, grow to a height of 20 to 30 ft. in a year. Those used in commercial cultivation are varieties and are known by such names as Goldings, Grapes or White Blues. The bracts bear numerous yellow glandular hairs which secrete lupulin, an aromatic substance of a resinous nature to which they owe their value for flavouring beer. The Hop is wild in Europe and North America.

The second species, *H. japonicus*, is a native of China and Japan. It bears no lupulin glands and hence is of no economic value. It is cultivated as a decorative plant in gardens.

The genus *Cannabis* contains the single species *C. sativa*, Hemp (Fig. 1630). It is an annual plant, a native of central Asia. It is now widely

FIG. 1628.—*Cecropia peltata.* Trumpet Tree. Infrutescences. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

FIG. 1629.—*Humulus lupulus.* Hop. Shoot with fruiting catkins, with large papery bracts.

FIG. 1630.—*Cannabis sativa.* Hemp. Male plant on right and female plant on left, showing the sexual dimorphism.

cultivated in temperate regions on account of its use in textiles and for the long, strong bast fibres. In some countries it is grown for the narcotic resin obtained from the leaves, which acts like opium as a drug and a stimulant. From it is made an intoxicating drink, haschisch. It is also smoked, with or without tobacco, under the name of marihuana. In small quantities it produces excitement but increasing doses cause delirium and finally catalepsy. Stringent laws keep a check on its use and recently the sale of seed in Great Britain has been stopped.

The family **Eucommiaceae** is monotypic and contains the single genus *Eucommia* which is of some economic interest. *E. ulmoides* is a tree with alternate leaves and naked, unisexual flowers. It yields latex containing caoutchouc, while the bark produces a medicine valued by the Chinese. It has the distinction of being the only rubber-producing tree which is hardy, but its latex is, unfortunately, of no commercial value.

SALICALES

The Salicales are Archichlamydeae in which the flowers are unisexual and are produced in catkins. Each flower is subtended by a bract. The male flower is very reduced and consists of two or more stamens: the female flower of two carpels which are united to form a one-celled ovary with parietal placentation. The ovules are numerous and the seeds are covered with fine hairs. There is no endosperm and the embryo lies straight.

The order includes the single family Salicaceae, a point on which all authorities agree. They do not agree however on the systematic position of the order. The older view, which was supported both by Bentham and Hooker and also by Engler, was to relegate them to a separate group, the Apetalae, which were considered more primitive than the Archichlamydeae and closely related to the Gymnospermae. This view was based upon the very simple, incomplete flowers which they possessed, which were considered to be primitive. The more modern view as expressed by Hutchinson is to consider the flowers specialized but reduced and to relate them more closely with the Rosales, through the Hamamelidaceae. There is certainly much in favour of this view, which we shall follow.

Salicaceae

The family includes two types of shrubs or trees common in Britain which are collectively spoken of as the Willows and Poplars. Among the Willows we may mention *Salix caprea* (Common Sallow or Goat Willow) (Fig. 1631), *S. fragilis* (Crack Willow), *S. babylonica* (Weeping Willow), which is not a native, and *S. viminalis* (Osier). Several dwarf species such as *S. reticulata* and *S. herbacea* are common as alpine plants and are also found in the Arctic. Among the Poplars found in this country are *Populus nigra* (Black Poplar), *P. alba* (White Poplar), *P. tremula* (Aspen) and *P. nigra* var. *italica* (Lombardy Poplar) which is a fastigiate variety of the Black Poplar.

The **plants** are either large trees or shrubs, with alternate leaves which

Fig. 1631.—*Salix caprea*. Goat Willow. Left, male catkin. Right, female catkins.

are simple and deciduous. The stipules are small or foliaceous and often persistent.

The **flowers** (Fig. 1632) are either monoecious or dioecious and are densely arranged in erect or pendulous catkins which very frequently develop early in the year before the leaves appear. The flower (Fig. 1633) is

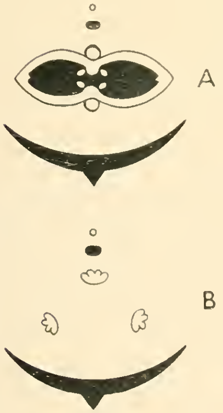


Fig. 1632.—Floral diagrams of *Salix*. A, Female flower. B, Male flower of *S. triandra*.

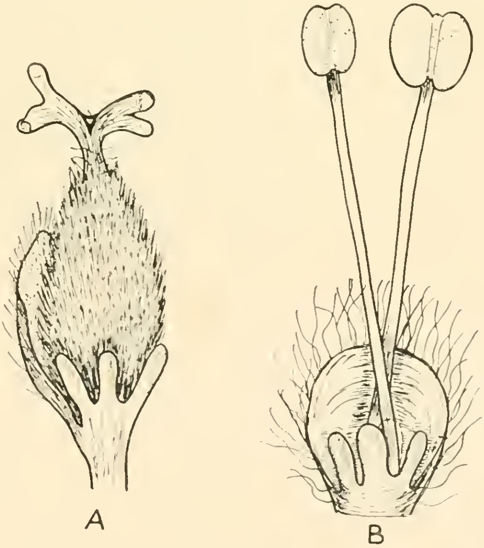


Fig. 1633.—*Salix reticulata*. A, Female flower with bract and basal nectaries. B, Male flower with bract and nectaries. (*After Goebel.*)

produced in the axil of a bract which is membranous and may be persistent.

The **calyx** is absent or may be represented by a small disc or by two glandular scales. There is no corolla present.

The **androecium** (Fig. 1633) in the male flower consists of two or more stamens each consisting of a slender filament and a bilocular anther which opens lengthwise.

The **gynoecium** in the female flower consists of a sessile ovary which is unilocular and composed of two carpels with two to four parietal placentas. The style is either bifid or tetrafid. The ovules are numerous and anatropous.

The **fruit** is a capsule which opens by two to four valves. The seeds are numerous and very small. Each is provided with a cluster of fine hairs, arising from the funicle, which envelop the seed and form a dispersal mechanism. There is no endosperm and the embryo is straight.

The family is a small one, containing two genera and about 180 species, which are widely distributed in the north temperate, subtropical and tropical regions. There are only two genera, *Salix* and *Populus*.

One of the constant features of the genus *Salix* is the origin of the cork cambium from the epidermis. This contrasts with the condition in *Populus*, where it arises from the hypodermis.

The pollination mechanism in the genus *Salix* is entomophilous, half-concealed nectar being present in the female flower, but this mechanism is the simplest found among insect-pollinated plants. The flowers are individually insignificant but by aggregation into catkins they become quite striking in appearance and are conspicuous objects on the bare trees in early spring. The male catkins with their bright yellow stamens are more noticeable than the female and will therefore be visited first by insects. On the other hand more nectar is secreted by the female flowers than by the male and hence these will be more carefully sought for. The combination of these two factors and the fact that few other flowers are open so early in the year, ensure a cross-pollination by numerous insects, including bees. Most of the species of *Salix* are interfertile and very many hybrids have been produced as a result of cross-pollination. Polyploidy is also a characteristic of the genus.

Members of this genus root remarkably readily from stem cuttings. Twigs put in a jug of water will soon form roots, while larger branches, cut and driven into the ground as posts, very soon root and become trees. Willows which line the banks of streams have often originated in this way from posts delimiting fields. Many species are cut down annually to provide young pliable shoots, called "withies", which are used in basket-making, others are allowed to grow and the wood employed in carpentry. Cricket bats are made from selected timbers of *Salix coerulea*. Along rivers the Willows are often pollarded, or cut off some 10 ft. above the ground. From the callus formed over the wound a crop of young shoots soon grows out, forming a bushy head. Dust and leaves accumulate among the branches, forming a nidus in which eventually a variety of plants grows: Hawthorns, Blackberries, Hedge Parsley, Nettles and many other plants may be discovered living epiphytically in this way in pollarded Willows.

The genus *Populus* is considerably smaller than *Salix*. It contains some twenty species, which are distributed in north temperate regions. Three species, *P. alba*, *P. canescens* and *P. tremula*, occur wild in Britain, but *P. nigra* and *P. serotina* are common as planted trees.

Unlike the genus *Salix*, the species of *Populus* are pollinated entirely by wind, though there is some evidence that the male flowers are often visited by pollen-collecting bees (Fig. 1634). The male and female catkins are long and pendulous and the bracts are toothed. There is a cup-shaped disc surrounding the essential organs, which secretes no nectar and is considered to represent the remains of a perianth.

FIG. 1634.—*Populus nigra*. Male catkins.

Closely allied to the Salicales are the **Garryales**, a small order containing a single family, the **Garryaceae**. They are trees or shrubs but differ from the Salicales in that the leaves are opposite, with the petioles connate at their bases. The flowers are less reduced and possess four sepals and four alternate stamens in the male flowers, which are arranged in long pendulous catkins. In the female flowers there are no sepals but only a unilocular ovary with two styles and containing two ovules which are pendulous from its apex. The fruit is a berry and the seed contains copious endosperm.

The family contains the single genus *Garrya* which has some eighteen species, distributed in North America and the West Indies. Several are cultivated, of which *G. elliptica* is the most common. It is an evergreen shrub (Fig. 1635) which grows to about 15 ft. and is the only species in which the flowers (Fig. 1636) are showy. It is often grown as a winter flowering shrub.

Fig. 1635.—*Garrya elliptica* with catkins growing on a wall.

Fig. 1636.—*Garrya elliptica*. Male catkins in flower.

A second order which may be conveniently referred to here is the **Myricales**. Like the last it is small and contains the single family **Myricaceae**, with the single genus *Myrica*. The genus contains some forty-five species which are widely distributed. One, *Myrica gale* (Fig. 1637) (Sweet Gale or Bog Myrtle), is a common low-growing shrub of bogs and moors in the British Isles. It is also found in Europe, Asia and America in the north temperate regions.

The flowers are either monoecious or dioecious and are protected by bracts, but in none of the flowers is a perianth found. The male inflorescence is an upright catkin and consists of up to twenty flowers, each being a group of four stamens between two bracteoles. The female flowers (Fig. 1638) are grouped in short catkins and comprise an ovary formed from two carpels bearing a pair of long stigmas. The two bracteoles are fused to the base of the ovary. The fruit is a drupe which secretes wax or resin from the

FIG. 1637.—*Myrica gale.* Bog Myrtle. Habit of male plant, with catkins, growing in a fen. Early spring.

FIG. 1638.—*Myrica gale.* Female plant. Leafy shoot with ovulate catkins.

epicarp. The embryo is surrounded by endosperm containing oil and protein.

The plants are all either trees or shrubs and are characterized by the alternate, simple leaves, which are often strongly aromatic. *M. gale* is used in medicine. *M. cerifera*, which grows in North America and is known there as Bay-berry or Wax-myrtle, is a source of wax which is obtained by boiling the fruits.

FAGALES

The Fagales are Archichlamydeae in which the flowers are dioecious and form catkins which may be either erect or pendulous. The calyx is much reduced or may be entirely absent. In the female flower there may be an involucre of bracts. The stamens vary from two to many and the ovary possesses from two to six loculi. There are one or two pendulous ovules in each loculus. The seed is non-endospermic.

This order includes several families among which we shall first refer briefly to the Fagaceae and then consider the Betulaceae in detail. Hutchinson splits up the Betulaceae into two families by separating out a number of genera into a new family, the Corylaceae.

The members of the **Fagaceae** are trees with alternate leaves. They may be either evergreen or deciduous. They are distinguished by the contracted dichasia of 3, 2 or 1 female flowers which are surrounded by a cupule with numerous imbricated scales or spines.

The family includes five genera, of which *Quercus* (Oak), *Castanea* (Sweet Chestnut), *Fagus* (Beech) and *Nothofagus* are the most important. The genus *Pasania* is widespread in Malaya and Polynesia.

In Britain two species of *Quercus* are considered indigenous, *Q. robur*, the Common Oak, and *Q. petraea*, the Sessile Oak (Fig. 1639), but several other species have been planted. Among commonly cultivated Oaks we may mention *Q. ilex*, the Holm or Holly Oak, which is evergreen. It is used as a timber tree and its bark is employed in tanning. *Q. cerris* (Turkey Oak) and *Q. alba* (Quebec Oak) are both valuable for their timber. The bark of *Q. suber* is used for making bottle cork. It occurs spontaneously in the Mediterranean regions and is cultivated in Portugal and Algeria. The bark of *Q. tinctoria* forms a yellow dye while *Q. aegilops* is important because the young acorns are employed in tanning. The genus includes some 300 species which are distributed through the north temperate regions, Indo-Malaya and around the Pacific.

The male catkins (Fig. 1640) are borne in the lower foliage or scale-leaf axils of the shoots of the current year, while the female flowers occur in the leaf axils of older shoots. The male flowers are single in the axils of the bracts and have no bracteoles. There are from four to seven perianth segments which are united at the base. The stamens are produced opposite them and are either equal to or more numerous than the perianth segments. The female flowers are solitary and each is surrounded by a cupule bearing numerous scales possibly formed by the union of bracteoles, but the

FIG. 1639.—*Quercus petraea.* Sessile or Durmast Oak. Habit of growth, showing short horizontal branches and the prolonged trunk which are characteristic of this species. Early spring.

Fig. 1640.—*Quercus robur* (*pedunculata*). Male catkins.

morphology of the cupule is open to various interpretations. The female flower itself has a tricarpellary gynoecium and generally six perianth segments. Pollination is anemophilous and eventually only one ovule matures so that the fruit is a one-seeded nut with a hard pericarp, the acorn, which is embedded in the cupule.

The genus *Castanea* contains about forty species which are distributed throughout the northern temperate regions. *C. sativa*, the Spanish chestnut, is extensively grown in Britain (Fig. 1641). The fruit consists of three nuts enclosed in a prickly cupule. These nuts are edible and have earned the tree the popular name of the Sweet Chestnut. The wood is valuable as timber and the bark in tanning.

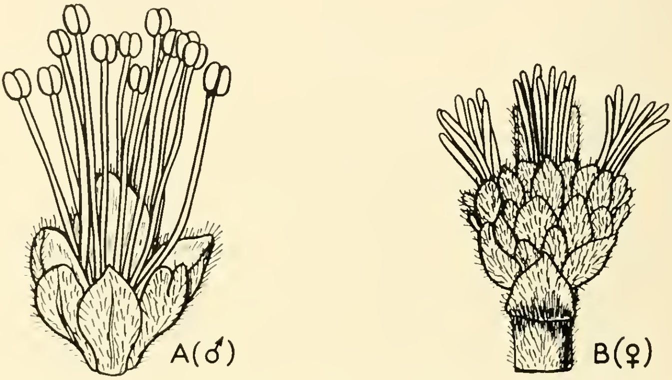


Fig. 1641.—*Castanea sativa.* Sweet Chestnut. A, Male flower. B, Cyme of three female flowers within the involucre which becomes spiny. (*After Wettstein.*)

The genus *Fagus* contains only four species, of which *F. sylvatica*, the common Beech, is the best known (Fig. 1642). It forms homogeneous woods, particularly on chalk, and is widely distributed throughout Europe. Though deciduous when grown as a tree it is noticeable that when kept cut as a shrub the Beech retains its withered brown leaves till the new ones open in the spring, a fact made use of by gardeners in planting Beech hedges for protecting young plants against wind.

Several varieties of the Beech are known. The Copper Beech differs in having a red pigment in the epidermal cells, the quantity of which varies considerably and hence the tint of the tree. Another variety is the Cut-leaved Beech in which the leaves are greatly dissected. Both varieties originated as mutations. Beech flowers (Fig. 1643) only produce fertile fruits once every few years.

The genus *Nothofagus* is restricted to twelve South American and Australasian species and is the southern counterpart of the genus *Fagus* in the north. *N. cunninghami*, the Myrtle Tree, produces valuable timber as does *N. fusca*, the Red Beech, in New Zealand.

Fagus and *Quercus* appear to be of ancient origin for fossil remains have

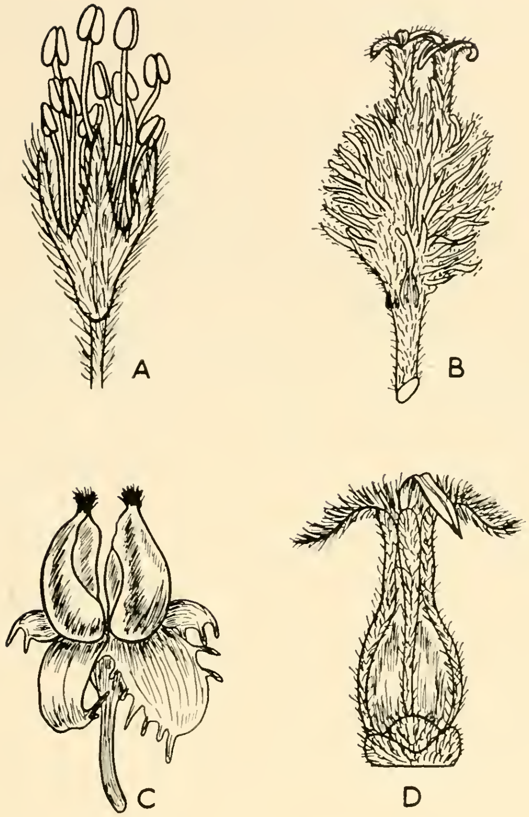


FIG. 1642.—*Fagus sylvatica.* Beech. A, Male flower. B, Cyme of two female flowers in spiny involucre. C, Fruits with open involucre. D, Female flower. (*After Wettstein.*)

FIG. 1643.—*Fagus sylvatica.* Shoot with female flowers.

been discovered in Cretaceous and Tertiary rocks showing that at that time the northern limit was extended to Greenland, Spitsbergen and Iceland.

Betulaceae

Several common British trees are included in this family. *Betula verrucosa* (Silver Birch), *Alnus glutinosa* (Alder), *Carpinus betulus* (Hornbeam), *Corylus avellana* (Hazel) are the best known.

The **plants** are either trees or shrubs, with alternate leaves bearing monoecious flowers in unisexual, catkin-like, compound inflorescences.

The **inflorescence** in the male is a catkin which terminates the growth of a branch in *Betula*, but in *Corylus* it is borne on a dwarf shoot. The bracts are arranged spirally and in the male the flowers are united to the bracts and bracteoles. In the female the catkins terminate leafy shoots and each consists of spirally arranged bracts in the axil of which is a dichasium of three flowers, the centre one of which is usually missing. Hence the inflorescence is really compound.

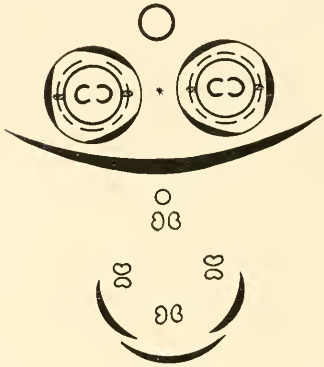


Fig. 1644.—Floral diagrams of *Corylus avellana*. Betulaceae. Female flower above; male flower below. (*After Eichler.*)

The **perianth** (Fig. 1644) when present consists of small scale leaves which vary in number and may be either free or united together. In the female flowers the ovary is inferior; the male flowers adhere to their bracts.

The **androecium** consists of from two to twelve stamens (Fig. 1645) each of which is divided nearly to the base.

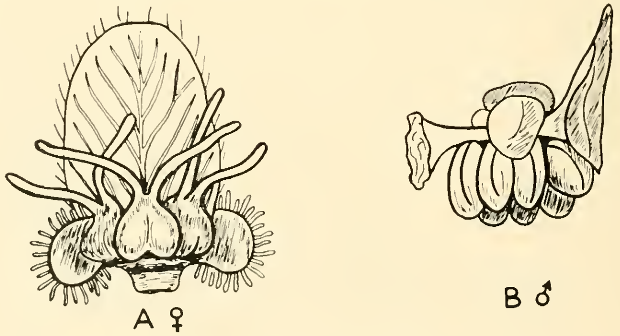


Fig. 1645.—*Betula*. Floral structure. A, Female flowers in cyme of three, each consisting of two joined carpels with two styles. B, Cyme of male flowers.

The **gynoecium** consists of a bilocular ovary with two styles. Each loculus contains one pendulous anatropous ovule with a single integument.

The **fruit** is a dry, indehiscent, one-seeded nut. The bracts during development undergo modification, forming a wing in *Carpinus* (Fig. 1646) or a cupule in *Corylus*.

FIG. 1646.—*Carpinus ovatus*. Shoot with female catkin furnished with large bracts which form the wings of the ripe fruits.

The **seed** is non-endospermic. The embryo possesses two large cotyledons which contain a reserve of oil.

The family is not a large one, but contains some six genera and about 105 species. At the present time the family is restricted chiefly to north temperate regions. A few American species extend southwards in the Andes as far as the Argentine.

The family is classified quite simply into two sub-families:

I. **Coryloideae**

The male flowers are in three-flowered cymes borne in the axil of a bract. A perianth is present. *Betula*, *Alnus*.

II. **Betuloideae**

The male flowers are in three-flowered cymes borne in the axil of a bract A perianth is present. *Betula*, *Alnus*.

The Coryloideae contain chiefly temperate genera. *Carpinus betulus* (Hornbeam) is common in Britain. The other twenty-one species of the genus occur chiefly in eastern Asia. The female catkins are terminal on long shoots while the males are themselves short shoots. In the axils of the latter are from four to twelve stamens but no bracteoles are present. In the female catkin there are two lateral flowers in each axil with six bracteoles and a minute epigynous perianth. The ovary is bilocular. The fruit is a one-seeded nut with a three-lobed leafy wing which is derived from the growth of the bract and two bracteoles, which form the side lobes.

Corylus avellana is the Hazel and is a shrubby plant often increased by suckers. It produces monoecious catkins, the male (Fig. 1647) ripening early, before the leaves. The females (Fig. 1648) are much smaller and are recognizable only by the bright red stigmas. Pollination is anemophilous but the chances of fertilization are probably enhanced by the fact that it occurs when the branches are bare of leaves. The nuts, which are sometimes referred to as Cob-nuts or Filberts, are edible and the plants have been cultivated from early times. The wood is elastic and is used for many agricultural purposes, for fixing down thatch, and for the construction of primitive implements. Hazel twigs are especially popular with water diviners in searching for water.

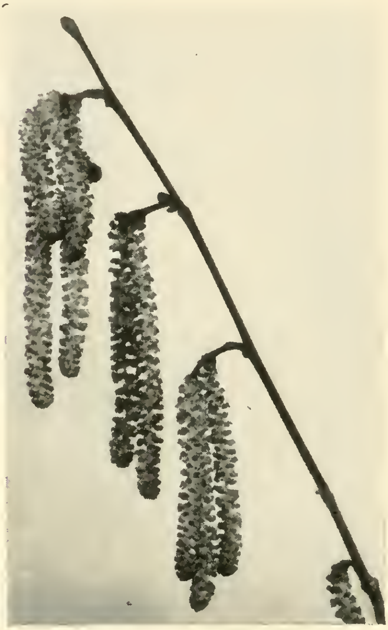


FIG. 1647.—*Corylus avellana.* Hazel. Male catkins open and shedding pollen.

FIG. 1648.—*Corylus avellana.* Female catkin with protruding stigmas.

In the Betuloideae the two common genera are both represented in the British Flora. *B. verrucosa* is the Common Birch while *B. nana*, the Mountain Birch, is a low shrub common in north temperate regions. Birch wood is tough and is much used in the making of wooden shoes. An oil prepared from the bark is used for tanning Russian leather to give it a peculiar fragrance. The bark of *B. papyracea* was used for making native Indian canoes in North America.

The genus *Alnus* contains twenty-five species which occur in the north temperate zone and in the Andes. *A. glutinosa* (Alder) (Fig. 1649) is common as a riverside British tree. Peculiar masses of coralloid rootlets are often found on the roots, which are stated to be caused by an organism *Schinzia alni* whose nature is uncertain, though it is probably related to the Actinomycetes. A symbiotic relationship has been postulated.

FIG. 1649.—*Alnus glutinosa.* Alder. Long male and short female catkins.

Another order which shows certain affinities with the Fagales is the **Casuarinales**. This is a small order containing the single family **Casuarinaceae** with the single genus *Casuarina*. The genus is widely distributed throughout the drier parts of Australia and Polynesia. Some thirty-five species are recognized. The plants are trees (Fig. 1650) composed of long slender branches which only produce whorls of scale leaves like those of *Equisetum*. The stems (Fig. 1651) are assimilatory and the cortex is deeply grooved, the chlorenchyma and stomata being distributed in the grooves in a way resembling that in *Cytisus*. The ridges are composed of thickened sclerotic cells giving the whole plant a markedly xeromorphic character.

The flowers are unisexual. The male flowers (Fig. 1652) are borne in terminal spikes on lateral branches. In these spikes the internodes are very short and the nodes are surrounded by cups formed from bracts, inside which are several stamens. Each is regarded as representing a male flower composed of one stamen with a two-leaved perianth and two

FIG. 1650.—*Casuarina equisetifolia.* Planted avenue in Chile.

FIG. 1651.—*Casuarina* sp. Part of transverse section of a stem, showing the sclerotic ridges with furrows between and with assimilatory palisade tissue on their flanks.

bracteoles. The female flowers (Fig. 1653) are produced in dense spherical heads and each flower is borne in the axil of a bract. It has no perianth but has two bracteoles and is made up of two carpels, only the anterior one of which is fertile and contains two or more ovules. The flowers are anemophilous and after fertilization the bracteoles become woody and enclose the winged akenes. The wood is remarkably hard and is known in Australia as She-oak or Beef wood. The young twigs are used to feed cattle.

FIG. 1652.—*Casuarina* sp. Spikes of male flowers.

FIG. 1653.—*Casuarina equisetifolia.* Short spikes of female flowers; bracteoles separating to release the winged akenes.

MYRTIFLORAE

The Myrtiflorae are Archichlamydeae with regular flowers, which are often monoecious. The corolla is polypetalous and pentamerous except in the Lythraceae where the flowers have six petals. The stamens may vary considerably in number, being very numerous in the Myrtaceae. The ovary may be unilocular or multilocular, with a single style, except in the Haloragidaceae. There are usually numerous anatropous ovules with axile placentation. The seed is usually non-endospermic. The plants may be trees, shrubs or herbs.

It will be seen from the above diagnosis that the limits of the order are very wide and it is not surprising therefore to find that some twenty-two families have been included in it. Several of these are of minor importance and we may leave them out of our consideration. According to Engler the following important families are included: Thymelaeaceae, Eleagnaceae, Lythraceae, Punicaceae, Lecythidaceae, Rhizophoraceae, Combretaceae, Myrtaceae, Onagraceae, Haloragidaceae, Hippuridaceae. To these Wettstein has added the Gunneraceae and the Callitrichaceae.

Hutchinson, in an attempt to get a more precise definition for the orders, has split up the Myrtiflorae into three orders, Thymelaeales, Lythrales and Myrtales. The latter name is used by Hutchinson in a different sense from that of Wettstein, who used it as equivalent to Myrtiflorae. There is much to be said for Hutchinson's views and we indicate below the arrangement of the families in the three orders recognized in his scheme.

Thymelaeales	Thymelaeaceae.
Lythrales	Lythraceae, Punicaceae, Onagraceae, Haloragidaceae, Callitrichaceae, Nyctaginaceae.
Myrtales	Lecythidaceae, Rhizophoraceae, Combretaceae, Myrtaceae.

It will be noted that Hutchinson excludes the Eleagnaceae, which he refers to the Rhamnales (p. 1813), while he includes in the Lythrales the family Nyctaginaceae which, following Engler, we have placed in the Centrospermae (p. 1717). The Gunneraceae he merges into the Haloragidaceae.

Were we considering all the families in detail it would be preferable to follow this classification but as we shall only fully describe the Onagraceae it seems desirable for convenience to make use of Engler's classification, whereby a brief mention may be made of a number of important families all embraced within the same order.

The **Thymelaeaceae** are a relatively small family with about thirty-eight genera and 550 species, which occur chiefly in temperate regions, particularly in Africa. Most of them are shrubs with entire, alternate leaves and racemose inflorescences. The flowers (Fig. 1654) are hermaphrodite

FIG. 1654.—*Daphne odora.* Flowers.

and may be either tetramerous or pentamerous. The perianth usually consists only of petaloid sepals, but a corolla is present in some genera. The flowers are strongly perigynous, the apparent perianth tube being due to the cup-shaped receptacle which often remains embedded in the fruit. The stamens may be equal in number to the sepals, or may be half or twice as many. The ovary is generally unilocular with one pendulous, anatropous ovule. The flowers are entomophilous, nectaries usually occurring at the base of the ovary.

Many of the species are found in dry situations, appearing frequently where the vegetation is periodically destroyed by fire. Such species often possess stout woody rhizomes which give off clumps of erect branches and terminate in brightly coloured inflorescences.

In Britain the family is represented by only two species, *Daphne mezereum* which, though very rare wild, is often planted in gardens, and *D. laureola*, the Spurge Laurel, which is a small, evergreen woodland shrub. The family is a natural one but shows no very close affinities with other groups.

The **Lythraceae** are a cosmopolitan family of some twenty-one genera and 500 species and are represented in Britain only by *Lythrum salicaria*, the Purple Loosestrife (Fig. 1655), *L. hyssopifolia* and *Peplis portula*, the Water Purslane.

FIG. 1655.—*Lythrum salicaria*. Purple Loosestrife. Flowering shoots.

Lythrum salicaria deserves some notice because of the complex pollination mechanism which it exhibits (Fig. 1656). Three forms of the flower appear, each on a separate plant. The flowers all possess six sepals and six petals, and are developed in verticillasters similar to those in the Labiatae. It is in the arrangement of the twelve stamens and in the length of the single style that the differences occur. (See also p. 1278.) The top figure represents a longitudinal section of the long-styled flower, the centre figure represents the mid-styled flower, while the lowest figure shows the short-styled flower. If S denotes the style and A the anthers we may represent the arrangement of these flowers in the following way. The numbers refer to the relative lengths of the organs.

Long-styled flower	*Mid-styled flower*	*Short-styled flower*
S.3	A.3	A.3
A.2	S.2	A.2
A.1	A.1	S.1

When the flowers are visited by insects there will be a tendency for pollen to be transferred from A.3 to S.3, from A.2 to S.2 and from A.1 to S.1 rather than a transference of pollen from anthers of one height to the style of another. It will be seen that this is assisted by the fact that the styles and anthers project sufficiently far out for the insect to alight directly on them.

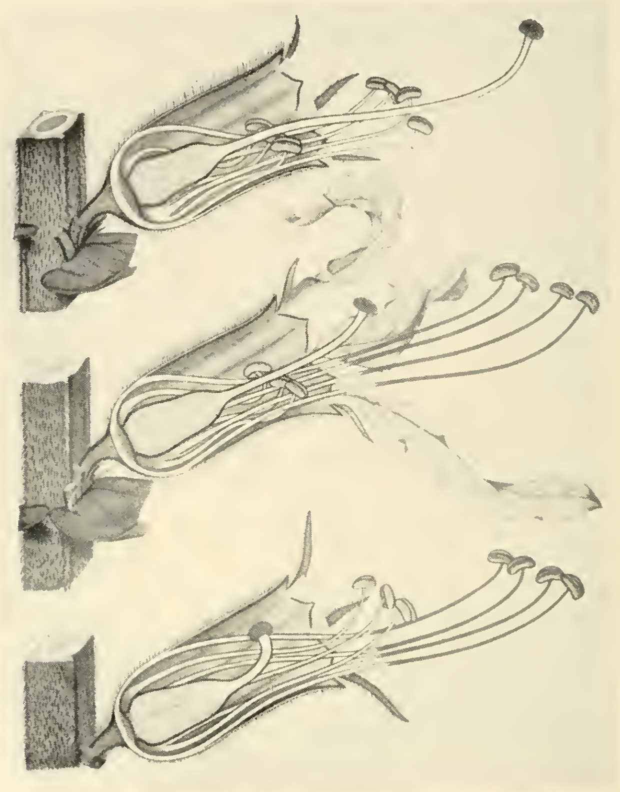


Fig. 1656.—*Lythrum salicaria.* Trimorphic flowers. For description see in text.

This complex system of cross-pollination is termed **trimorphism** and was originally investigated by Charles Darwin. As a result of a long series of experiments he was able to show that the number of seeds produced in the ovary was greatest when S.3 was pollinated by A.3, or alternatively S.1 by A.1. If S.2 or S.1 is pollinated by A.3 the fertility of the seeds is less and the same is true of any other similar cross. From this Darwin proposed the term **legitimate** for the crossing of a style by pollen derived from stamens of the same length, and **illegitimate** for crossings between organs of different length. The offspring of illegitimate fertilization behave as hybrids in so far as sterility is concerned. (See also p. 1279.)

The Lythraceae include a number of tropical trees whose timber is of economic value and we may mention *Physocalymma scaberrimum* from

Brazil which is the source of Tulip Wood, and *Lagerstroemia flos-reginae*, an important timber of eastern India. A constant feature of the stem anatomy is the presence of internal phloem and of bicollateral vascular bundles.

Lawsonia inermis occurs widely in the tropics. The leaves provide the cosmetic henna, which is used in the East to stain the fingernails red and as a hair wash. A similar red dye is obtained from the flowers of *Woodfordia floribunda*.

In the **Punicaceae** is the important genus *Punica* with two species, one of which, *P. granatum* (Fig. 1657), is the Pomegranate. It occurs wild from the Balkans to the Himalayas, and has been cultivated since earliest times on account of the fruit. This fruit (Fig. 1658) is a berry, with a thick leathery coat, which is divided into chambers by the thin walls of the carpels. The flesh of the fruit is derived from the pulpy outer coat of the seeds. It contains a refreshing, somewhat acid juice.

FIG. 1657.—*Punica granatum*. Pomegranate. Flowers on bush.

FIG. 1658.—*Punica granatum*. Shoot with ripening fruit. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

The **Haloragidaceae** (Myriophyllaceae) are a small family containing seven genera and about 170 species. In Britain the family is represented by the genus *Myriophyllum*. It contains submerged water plants with whorls of much divided leaves, which are developed on shoots arising from creeping rhizomes. These leafy stems contain large air cavities. The inflorescences project above the water and the flowers are anemophilous. Hibernating winter buds are often produced.

Another interesting genus is *Gunnera*, which is restricted to the southern hemisphere (Fig. 1659). Several of the species produce enormous leaves several feet across (Fig. 1660), and are the largest herbaceous plants known.

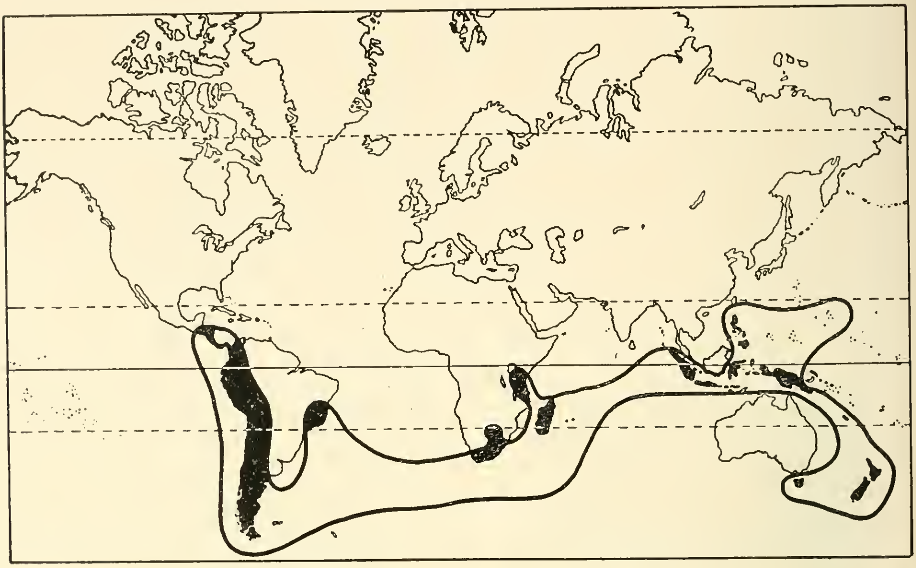


FIG. 1659.—Distribution of *Gunnera*. (*After Hutchinson.*)

FIG. 1660.—*Gunnera manicata* in cultivation in Britain. The leaves are probably the largest borne by any herbaceous plant.

The stems are short and subterranean and are truly polystelic, each vascular strand being surrounded by its own endodermis. In *G. manicata* pockets in the stem cortex contain the Blue-green Alga, *Nostoc gunnerae.* It is frequently cultivated in large gardens as a lakeside plant. The flowers are produced on large fleshy axes and are individually inconspicuous (Fig. 1661). The two petals are but slightly larger than the two minute sepals. The two stamens are free, with short filaments, while the ovary is composed of two carpels but is unilocular and contains one ovule. The embryo is tiny and is buried in the endosperm at the upper end of the seed. This general reduction of parts as compared with the other members of the family is further seen in the embryo sac, which only contains four nuclei. The genus *Hippuris*, though separated into a monotypic family by Engler, is now usually included here. *H. vulgaris*, the Mare's-tail, is widely distributed through Arctic and temperate regions and is also found in Antarctic America.

FIG. 1661.—*Gunnera manicata.* Inflorescence, which comes up directly from the underground stem.

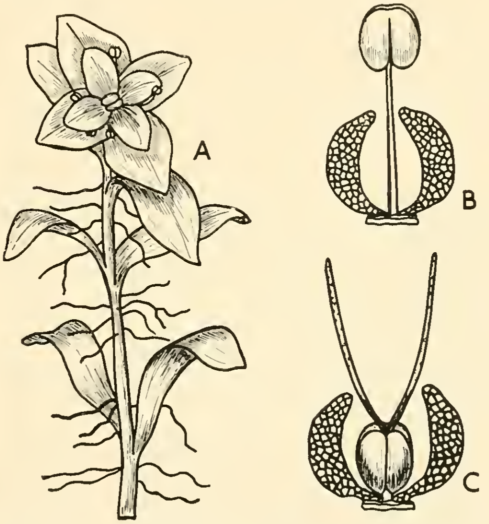


FIG. 1662.—*Callitriche obtusangula.* A, Flowering shoot with terminal rosette of leaves. B, Male flower with two bracteoles and one stamen. C, Female flower with two bracteoles and two united carpels.

The **Callitrichaceae**, sometimes included in the Haloragidaceae, comprises the single genus *Callitriche* (Fig. 1662) which contains small herbaceous plants mostly found submerged in fresh water all over the world. Some consider that only one or two species exist which are divisible into nearly 100 varieties. Others elevate these varieties to species rank. We have already referred to the group in connection with the Centrospermae to which they may be related. Others such as Engler and Warming would relate them to the Euphorbiaceae. They have also been included in the Labiatae on account of their fruit of four nutlets.

The **Lecythidaceae** contain a number of genera of more than passing interest. The family is represented mainly by trees and shrubs. It contains about eighteen genera and some 150 species. The leaves are large and are often produced in bunches at the ends of the branches. Among the more important genera is *Bertholletia* which contains two species found in South America and the West Indies. The fruit (Fig. 1663) is a large woody capsule containing seeds each having a hard woody testa and an oily endosperm. This seed is the Brazil Nut of commerce, for the complete fruit is seldom seen in this country. The fruit is indehiscent and is closed by a plug formed from the hardened calyx and it is through this opening that the seedlings grow out during germination, as the seeds germinate inside the capsule after it has fallen to the ground. In the genus *Lecythis* itself, the fruit is a large woody capsule which opens by a lid. The fruit is the famous Monkey Pot, used to catch monkeys who insert their hands to get the seeds and cannot withdraw them without letting go of the seed, which they will not do. The oily seeds it contains are eaten in the tropics as Sapucaia Nuts. Other species of this genus are used for timber. The Anchovy Pear (*Grias cauliflora*) is cultivated in the West Indies.

FIG. 1663.—*Bertholletia excelsa.* Brazil Nut. Woody capsule cut in half showing the contained seeds.

FIG. 1664.—*Couroupita guianensis.* Cannon Ball Tree. Large woody capsules. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

The genus *Couroupita* contains nine American species. *C. guianensis* possesses flowers which are borne on the older wood and are followed by large spherical woody spheres to which the name "Cannon Balls" has been given (Fig. 1664).

The family is characterized by the presence of a series of cortical bundles which run up as separate traces into the leaf and remain distinct not only in the midrib but in the larger veins as well.

The **Rhizophoraceae** include a number of interesting plants collectively referred to as the Mangroves. They form a very characteristic vegetation on muddy coasts and estuaries in the tropics. The family is a small one containing about twelve genera, with some sixty species. They are all woody plants with simple, often leathery, leaves. It is however their tendency to produce large aerial prop-roots, after which the main roots and the base of the stem disappear, which has gained them such a reputation, for these prop-roots (see Fig. 825, Vol. I) form an almost impenetrable jungle, while at the same time lifting the functional stems above the sea at high tide. At low tide they bridge over the evil-smelling estuarine mud.

The best-known genus is *Rhizophora* (Fig. 1665) and it is interesting particularly on account of the germination of the seeds while still attached to the parent tree (Fig. 1666). In section at a young stage the embryo consists of a very large hypocotyl whose free end is directed downwards

FIG. 1665.—*Rhizophora conjugata.* Leafy shoot with flowers and fruits, the latter showing outgrowing seedlings. Below, similar fruits and seedlings of *Bruguiera caryophylloides.* (*After Karsten.*)

FIG. 1666.—*Rhizophora mucronata.* Fruits with fully developed seedlings attached. The middle one has been dropped from the fruit and shows the terminal plumule.

and passes out through the micropyle, and the united cotyledonary tube which surrounds the plumule. The cotyledon is provided with a ring of vascular bundles which are continuous with those of the hypocotyl and the whole of its external surface is covered by absorbent cells which take up food material from the endosperm. This food is entirely used in the development of the hypocotyl which grows fatter and longer until it may be 1 or 2 ft. long. Finally the vascular bundles between the cotyledon and the hypocotyl are ruptured, the embryo falls away and its lower end plunges into the mud and forms roots. Meanwhile the now liberated plumule grows out and forms a stem with leaves. Later the prop-roots arise both from the epicotyledonary stem and also from the hypocotyl. Later still the primary root dies and its function is assumed by the prop-roots. It is interesting to note that these are liberally supplied with lenticels which probably function as pneumatothodes.

The family is essentially a tropical one, occurring chiefly in Asia, Australia and the East Indies. *Rhizophora mangle* occurs in America and West Africa.

Poga oleosa which occurs in French Equatorial Africa is the source of the Poga Nuts which occasionally find their way into Britain.

Hutchinson considers that the family shows affinities to the Malvales and may provide a connecting link between the two orders.

The **Combretaceae** are another family of tropical and subtropical trees and shrubs which are of some economic importance on account of their fruits. *Terminalia chebula* and certain closely allied species provide the Myrobalan Nuts which are an important article of commerce in India. They are used for dyeing, tanning and also in medicine. *T. glabra* provides good timber. Other genera form beautiful climbers some of which are in cultivation. *Combretum butyrosum* yields a butter-like substance known in Central Africa as Chiquito which is used as butter by the natives.

We now come to the **Myrtaceae** which are a large and very important family. It is not represented in the British Flora although many species are commonly cultivated in gardens and greenhouses. It is essentially a tropical and subtropical family, containing about ninety genera and over 2,800 species. They are all woody plants, many forming large shrubs or trees, with entire, leathery leaves. The presence of bicollateral vascular bundles is a constant feature in the group, and many species possess spherical glands containing essential oils. These glands, which are formed lysigenously, are developed not only in the leaves but also in the young stems and in the floral organs and fruits.

The flowers (Fig. 1667) are sometimes solitary in the leaf axils but more generally they are produced in cymose inflorescences. They are hermaphrodite, regular, actinomorphic and usually epigynous. The calyx normally consists of either four or five sepals, alternating with four or five free petals. There are a large number of stamens which are inserted in whorls on the raised edge of the receptacle. The ovary may have one to many loculi containing two or many pendulous, anatropous or campylotropous ovules. The form of the fruit varies very greatly and serves as the basis of classification within the family.

FIG. 1667.—*Myrtus communis.* Flowering shoot.

The Myrtaceae are divided into two main groups according to the nature of the fruit.

I. Myrtoideae

In which the fruit is a berry or more rarely a drupe. Many are of economic importance as cultivated fruits. *Myrtus*, *Psidium*, *Pimenta*, *Eugenia*.

II. Leptospermoideae

In which the fruit is dry and few are of economic importance on that account. *Eucalyptus*, *Metrosideros*, *Callistemon*, *Melaleuca*, *Darwinia*, *Leptospermum*.

The genus *Myrtus* is represented by some seventy species, of which *M. communis* is the best known, being extensively cultivated and long naturalized in Europe. Most of the species are shrubs of tropical or subtropical origin.

The genus *Psidium*, with over 110 species, is found in America and the West Indies. Many are cultivated in the tropics on account of their fruits. *P. guajava* (Fig. 1668) is the Guava which forms a tree up to 30 ft. high. The fruit is eaten and is largely used for the confection Guava jelly and in cookery. *P. cattleianum* is the Strawberry Guava and grows in cooler climates than the former species. The sugar content of these fruits is relatively low, being less than 6 per cent. Several other species are cultivated in the countries in which they are native.

FIG. 1668.—*Psidium guajava.* Guava. Shoot with fruits. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

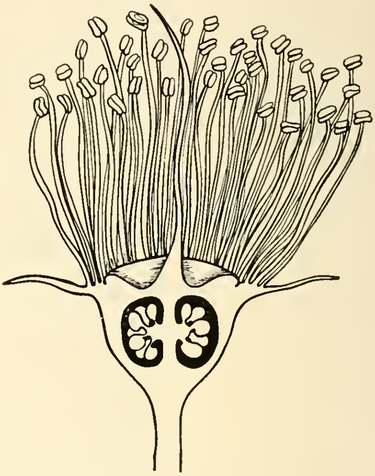


FIG. 1669.—*Eugenia jambos.* Flower in longitudinal section. (*After Baillon.*)

In the genus *Pimenta* the most important species is *P. officinalis.* The unripe fruits of the plant if dried rapidly yield Allspice, which consists of small, dark brown berries used in flavouring.

There are a number of important species included in the genus *Eugenia*, probably the best known being *E. caryophyllata*, the young flower buds of which are collected and dried to produce the Cloves of commerce. *E. uniflora* is the Pitanga, which is a native of Brazil and forms in that country the equivalent of the European Cherry. *E. jambolana*, the Jambolan, is cultivated in the East Indies and is often referred to as the Java Plum. *E. jambos* (Fig. 1669) is the Rose Apple which forms an ornamental tree in the tropics. The flowers are white and are produced in racemes. The fruits are about an inch and a half in diameter and apricot yellow in colour. They contain nearly 12 per cent. of the dry weight as sugars. The plant is indigenous in the East Indies but has been extensively planted. *E. malaccensis*, the Otaheite Apple, is a native of Malaya, but has been introduced into Hawaii and now constitutes one of the most important species. The fruits are oval and 2 to 3 in. long. The flesh is crisp and apple-like with a refreshing sub-acid flavour. About 7 per cent. of the dry weight is sugar. *E. uniflora* is the Surinam Cherry (Fig. 1670).

The genus *Eucalyptus*, with 230 species, is almost entirely restricted to

FIG. 1670.—*Eugenia uniflora.* Surinam Cherry. Shoot with fruits. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

Australia, where it forms one of the most characteristic features of the vegetation. The largest is *E. regnans* which may reach a height of over 300 ft. and a girth of 30 ft. at 6 ft. from the base. Several species have been introduced into this country but they are not completely hardy. *E. globulus*, the Blue Gum, survives in the warmer parts forming a tree up to some 50 ft. For the first few years it produces only juvenile leaves which are connate and oval; later this foliage is replaced above by sickle-shaped leaves of the permanent foliage. The tree has been known to flower in this country.

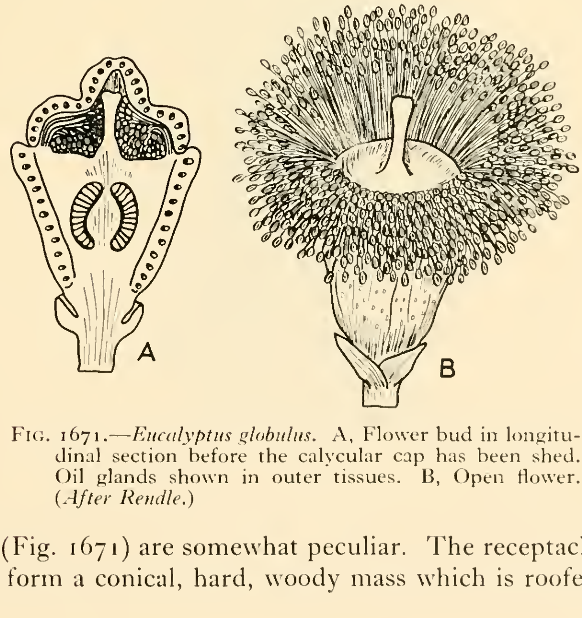


FIG. 1671.—*Eucalyptus globulus.* A, Flower bud in longitudinal section before the calycular cap has been shed. Oil glands shown in outer tissues. B, Open flower. (*After Rendle.*)

The flowers (Fig. 1671) are somewhat peculiar. The receptacle unites with the ovary to form a conical, hard, woody mass which is roofed over at the top by the sepals which form a cap. The stamens are borne on the margin of the receptacle and at an early stage are folded in around the style. The sepal cap drops off as a whole and after it is shed the stamens open up, forming a fringe around the single style. After fertilization the receptacle contributes to the formation of a loculicidal capsule which liberates, in some species, winged seeds.

E. globulus yields the Oil of Eucalyptus, as do certain other related species. For this reason they are of economic importance and are extensively planted, particularly in California and Italy. They are supposed to keep away malaria mosquitoes. As might be expected many species provide valuable timber.

Several species of *Metrosideros* and *Melaleuca* yield valuable timbers, while *Melaleuca leucadendron* yields Cajeput oil. Finally species of *Callistemon* are often cultivated on account of their peculiar inflorescences which has earned them the name of Bottle-brushes (Fig. 1672).

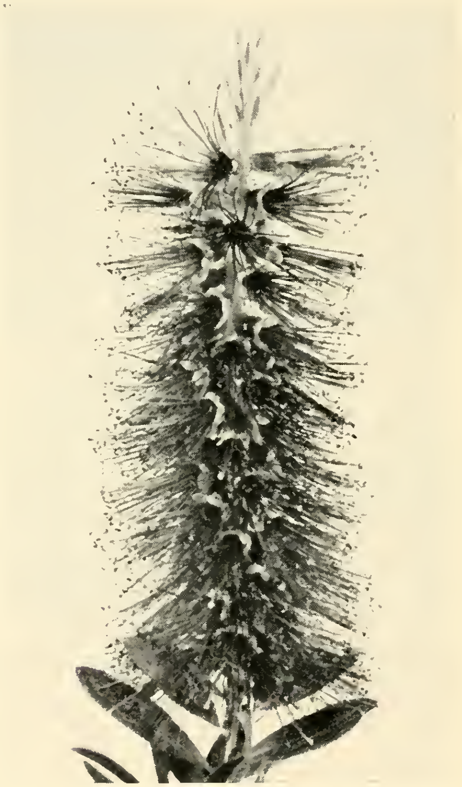


Fig. 1672.—*Callistemon lanceolatus*. Flower spike with long scarlet stamens.

Turning from the Myrtaceae to the last family of this order, the **Melastomaceae**, we have a large group of plants arranged in 200 genera and about 2,500 species, which live in the tropics and subtropics, particularly in South

America. They are distinguished from the Myrtaceae by the absence of oil glands and by the fact that the anthers dehisce by apical pores. There are three prominent longitudinal veins on the leaves connected by pinnate side branches, a vegetative feature which is strikingly characteristic of the family. Bicollateral and concentric, cortical, and medullary vascular bundles occur. Many species are cultivated on account of their flowers, particularly the genera *Medinilla* and *Centradenia* which are common greenhouse plants. None has any great economic importance.

Onagraceae (Oenotheraceae)

This family, which is sometimes called the Oenotheraceae, is represented in the British Flora mainly by the Willow-herbs but several well-known cultivated plants also belong to the family, among which we may mention *Fuchsia*, *Clarkia* and *Godetia*. Among the common British species are *Epilobium angustifolium* (Rose-bay Willow-herb), *E. hirsutum* (Hairy Willow-herb), and *E. parviflorum* (Hoary Willow-herb), *Oenothera biennis* (Evening Primrose) and *Circaea lutetiana* (Enchanter's Nightshade).

The **plants** are mostly herbaceous with alternate or opposite leaves and axillary or terminal racemose inflorescences. Many are annuals, others biennials, while the family also includes certain shrubby genera such as *Fuchsia*.

The **flowers** (Fig. 1673) are hermaphrodite, actinomorphic or occasionally zygomorphic, tetramerous or occasionally dimerous and epigynous.

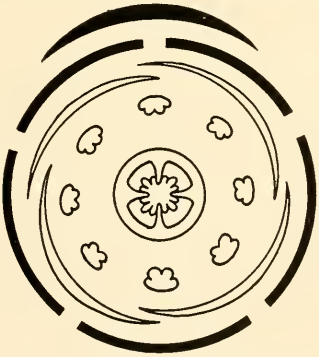


FIG. 1673.—Floral diagram of *Epilobium hirsutum*. Onagraceae.

The **calyx** is composed of two or four sepals, superior and sometimes petaloid as in *Fuchsia*.

The **corolla** is composed of two or four petals or is occasionally absent. The petals may be contort or imbricate.

The **androecium** consists of as many or twice as many stamens as there are sepals, the anthers are two-chambered and open lengthwise. The pollen grains are triangular or rectangular in outline, with three or four germ pores.

The **gynoecium** is polycarpellary, syncarpous and composed of two or generally four carpels. The ovary is inferior, with two or four loculi. There may be one ovule in each loculus (*Circaea*) or there may be numerous anatropous ovules with axile placentation.

The **fruit** is a capsule, a berry or a nut. Most frequently it is a capsule which splits loculicidally, leaving a central column which bears the seeds.

The **seeds** are non-endospermic and there is often a hairy aril. The embryo is nearly straight.

The family comprises forty genera and contains some 500 species which are distributed mainly in temperate and subtropical regions though a few are found right into the tropics.

The chief anatomical feature is the presence of internal phloem which may either closely adjoin the system of vascular bundles or may form small medullary groups.

The classification within the family is simple, two sub-families only being recognized. The genera are distributed as follows:

I. Trapeoideae

The ovary is only partly inferior and possesses two loculi. The fruit is thorny. *Trapa*.

II. Oenotheroideae

The ovary is truly inferior and there are from one to four loculi. *Epilobium*, *Jussiena*, *Ludwigia*, *Oenothera*, *Clarkia*, *Godetia*, *Fuchsia*, *Lopezia*.

Trapa natans, the Water Chestnut, is an annual water plant with rhomboid floating leaves and submerged adventitious roots which are peculiar in that they possess chlorophyll and assimilate. The genus is anomalous in many respects and may represent an ancient type which was more widely distributed in the Tertiary period. Later, to judge by fossil fruits, it extended over a wide range of northern and central Europe. The fruits are large, prickly nuts which are used as food in China.

The genus *Epilobium* is the largest in the family and contains about 160 species, of which some nine are found in Britain. The pollination mechanism is interesting. Bees and species of the Lepidoptera are chiefly concerned, and, in British Epilobia, it is possible to trace a transition from large-flowered species which are normally cross-pollinated by insects, to small-flowered types which are usually self-pollinated. We shall refer to a similar series in the genus *Geranium*, but it will be necessary to consider this example also in some detail.

In *Epilobium angustifolium* the purple-red flowers open between 6 and 7 a.m. and are completely protandrous. Nectar is secreted by the fleshy green top of the ovary and is protected from rain by the bases of the filaments which converge to form a hollow cone, which encircles the base of the style. Where the style leaves this cone it is covered with hairs which prevent the entry of rain, though the proboscis of an insect can push between them. In the young flowers the stamens are covered with pollen grains which are bound together by viscid threads. These stamens bend outwards and permit insects to alight on them (Fig. 1674). Later the dehisced stamens curve downwards, while the style, which at first is quite short, now elongates and four divergent stigmas are produced which form the only alighting place for visiting insects. Hence insects coming from younger flowers will pollinate the stigmas with pollen borne mainly on their feet.

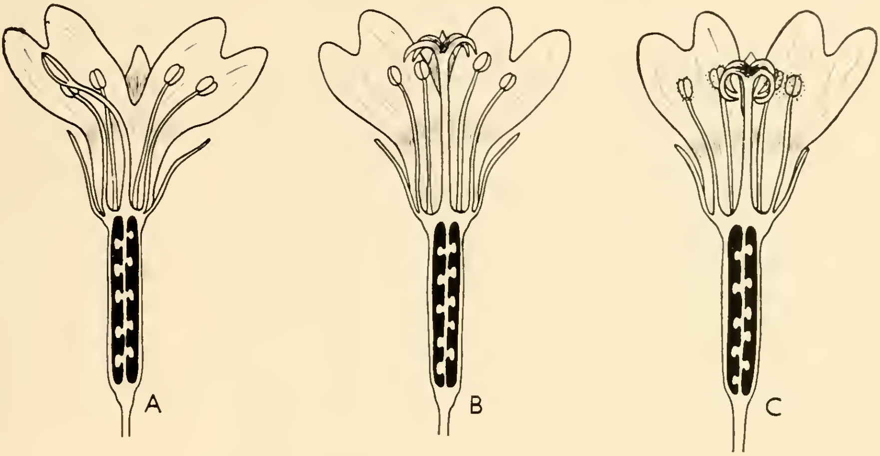


Fig. 1674.—*Epilobium hirsutum.* Three successive stages in anthesis. A, Stamens spreading, stigmas still immature. B, Stigmas expanded, above the level of the stamens. C, Stigmas recurved. Self-pollination is now possible.

In *Epilobium hirsutum* the flowers vary somewhat in size; in the large-flowered forms the stamens ripen first and the style is long and curved in such a way that self-pollination is impossible. In medium-sized flowers, both the style and stigmas ripen at the same time, the style is straight and should insect visits fail, the stigmas bend back so that they touch the anthers of the longest stamens, making self-pollination possible. In the small flowers the stigmas are produced at the same level as the longest stamens and automatic self-pollination is almost inevitable.

Finally in *Epilobium parviflorum* the flowers are quite small and are rarely visited by insects. Four of the stamens are longer and four shorter than the style. An insect visiting the flower may effect cross-pollination, but if that fails the style is almost certain to receive pollen from the shorter stamens. This condition is similar to that in *E. collinum* in which automatic self-pollination inevitably occurs on the first day of anthesis, the stamens being of a length suitable for the anthers to touch the stigmas.

The seeds of the Willow-herbs are characterized by a group of long hairs which develop from the chalazal end of the seed. These plumed seeds are liberated successively from the capsule and ensure a very wide

FIG. 1675.—*Epilobium angustifolium.* Flowering shoot.

distribution of the offspring. *E. angustifolium* (Fig. 1675) is a characteristic plant of burnt heaths, being one of the first plants to reappear after a fire, as likewise in coniferous forests. In North America it is known as Fire Weed. Similarly it was found to be one of the earliest arrivals on those parts of large cities which were wrecked as a result of bombing.

The genus *Jussieua* contains some fifty species of marsh and aquatic plants in which special aerating tissue is well developed. Both in the stem and in the water roots the stele is very small but a large lacunar cortex or aerenchyma is developed. In *J. repens* two kinds of roots may develop in plants growing in water. The one type are ordinary roots, the other type (Fig. 1676) grow upwards until they reach the surface and the bulk of the tissue consists of

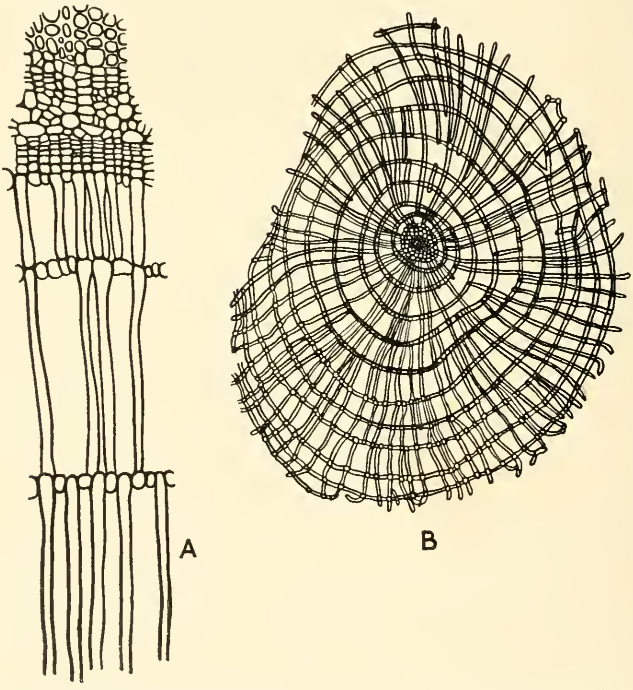


FIG. 1676.—*Jussieua peruviana.* A, Transverse section of aerial root showing part of the stele and the aerenchymatous cortex. B, *J. repens.* Transverse section of aerial root. (A, *after Schenck.* B, *after Goebel.*)

aerenchyma. If the plants are grown on land this aerenchyma is not produced.

Another marsh genus is *Ludwigia*, which is represented in Britain by a single very rare species.

The genus *Oenothera* (Fig. 1677), the Evening Primrose, has gained a reputation in genetical studies on account of the work done on the theory of mutations. De Vries was the first to demonstrate the existence of mutation from his study of Evening Primrose in Amsterdam. Later Gates and others investigated very elaborately the cytology of the group and attempted to relate this cytology with the genetics. The subsequent discovery that many of the species studied so carefully were natural hybrids tended to discountenance some of the work though it is still looked upon as of considerable importance. *O. biennis* and several other species open their large bright yellow flowers at dusk. They emit scent in the evenings and are visited by night-flying long-tongued moths.


FIG. 1677.—*Oenothera biennis*. Inflorescence.

Both the genera *Clarkia*, with eight North American species, and *Godetia* with twenty-five Western American species, are extensively used in this country as annual bedding plants.

The genus *Fuchsia* is essentially composed of shrubs. There are some sixty-five species distributed in South and Central America and in New Zealand. Many have long racemes of flowers in which the calyx is petaloid and bends backwards to expose the corolla. Frequently the two whorls are of different colours. Many have been cultivated and hybrids have been produced in which the calyx and corolla possess contrasting colours, white and red, or red and blue. The flowers are pollinated in this country by bees but in their native countries humming-birds play an important part. A few are wind-pollinated. None is completely hardy in this country though *F. riccartoni* (Fig. 1678) is hardy in southern districts, and in sheltered parts of Cornwall and western Scotland forms large, thick hedges. Elsewhere it does best as a wall shrub.

FIG. 1678.—*Fuchsia riccartoni.* Flowering shoot.

The genus *Lopezia* contains fifteen Central American species. Their chief interest lies in their mechanism for pollination. The flowers are truly zygomorphic, the two upper petals being bent upwards a little way from the base and in the bend is an apparent drop of nectar, which in reality is a glossy piece of hard tissue. Nectar is actually secreted at the base of the flower. There are two stamens of which only the posterior one is fertile, and opposite it is a petaloid staminode. In the early stage the style is undeveloped and insects alight on the stamens. Later the style grows up in place of the stamen, which now bends upwards out of the way. In *L. coronata* there is an upward tension in the posterior stamen and a downward one in the anterior one. When an insect alights on a flower an explosion occurs.

Finally in the genus *Circaea* we have small herbaceous plants in which the flowers are typically dimerous and represent the extreme case of reduction in the family. In this genus the ovary is either one- or two-locular with only one ovule in each loculus. The fruit is indehiscent and nutlike and bears numerous bristles. Both *Circaea lutetiana* and *C. alpina* are widely distributed in Europe and western Asia. In *C. lutetiana* (Fig. 1679) the flowers are pollinated by hover flies. Two stamens project one on each side of the pendulous flower and between them is the style which projects rather further and bears a terminal knobbed stigma. These three structures serve as an alighting platform on which the insect must support itself while reaching for the nectar, secreted from a ring at the base of the style. Since the style is somewhat longer, most insects alight on it first, and it therefore receives the pollen from another flower, after which the insect's body becomes dusted with pollen from the anthers as it forces its way towards the nectar. Self-pollination is exceptional for it rarely happens that the stigma comes into contact with a dehisced anther.

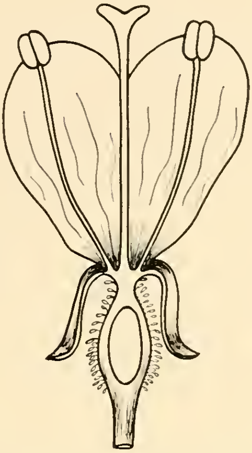


Fig. 1679.—*Circaea lutetiana.* Flower in longitudinal section.

MALVALES

The Malvales are Archichlamydeae in which the flowers are bisexual, regular, hypogynous, actinomorphic and pentamerous. Both the androecium and gynoecium may show a great increase in the number of parts. There are five sepals which are valvate in the bud and either free or united in the mature flower. The petals are free and often imbricately twisted. The stamens are arranged in two whorls, though those of the outer whorl may be absent or replaced by staminodes. The inner whorl may be composed of numerous stamens often with their filaments united to form a column around the style. The number of carpels is variable but they are united to form a multilocular ovary, each loculus having one to many anatropous ovules.

The order includes many trees and shrubs as well as herbaceous plants, with alternate, stipulate leaves. Stellate hairs are very common in the younger parts and mucilage-containing cavities are often formed in the cortex.

The arrangement of the families within the order varies somewhat among different authors. Engler, Rendle and Wettstein include the following common families: Tiliaceae, Bombacaceae, Sterculiaceae and Malvaceae. Hutchinson separated the first three into an independent order which he calls the Tiliales, and retains Malvaceae with certain small families in the Malvales. We shall consider the Malvaceae in detail but may first mention certain important points about the other three families.

Rendle considers that the Malvales show a relationship with the Guttiferae in their regular, hypogynous, pentamerous flowers and also in the structure of the androecium. On the other hand he thinks they may be related to the Euphorbiales in the structure of the ovary and in the endotrophic course of the pollen tubes.

The **Tiliaceae** are an important family with thirty-five genera and about 380 species, occurring mainly in tropical and temperate regions of south-eastern Asia and Brazil. They are mostly trees or shrubs with alternate, stipulate leaves. The inflorescence (Fig. 1680) is cymose though in such genera as *Tilia* it may be complexly modified. The family is distinguished from the Malvaceae, first because the stamens are either free or only united at the base and secondly because the anthers have only two pollen sacs instead of four as in the Malvaceae.

FIG. 1680.—*Tilia cordata*. Flowering shoot.

Tilia vulgaris is the Common Lime (Fig. 1681) which is frequently planted in this country, while *T. americana* is the Basswood, a native of North America, but often cultivated in Britain. *Corchorus capsularis*, an annual which grows about 10 ft. high, is a native of India. The stems are cut and retted in water and the fibres beaten out. They provide the Jute or Gunny of commerce. Commercial fibres are also obtained from species of *Grewia* and *Triumfetta.* The hard phloem fibres of the Common Lime supply the Bast used by gardeners in tying plants.

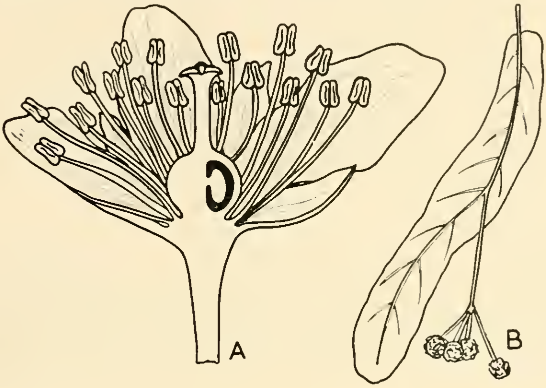


FIG. 1681.—*Tilia vulgaris.* Lime. A, Vertical section of flower. B, Inflorescence with adnate wing-bract.

The **Bombacaceae**, which are a small family of some twenty genera and 140 species, include several interesting plants. They are mostly very tall trees with thick trunks. One of the best-known supplies the Kapok of commerce. This is *Eriodendron anfractuosum* which is widely distributed in the tropics. The Kapok is obtained from the silky hairs which envelop the seeds. In contrast to this is *Durio zibethinus*, the Durian, which has been cultivated in Malaya for the edible fruits, possibly since the fifteenth century. The flowers are produced in cymes and the fruits are oval in shape and about 6 in. long. They are covered externally by woody protuberances. There are four loculi and each has several seeds surrounded by a clear, pale brown, custard-like pulp with a strong odour and a rich taste which is not usually attractive to Europeans. The ash contains up to nearly 25 per cent. of sugar. Despite its unpleasant smell the Durian is very greatly esteemed among the natives.

Another member of the Bombacaceae is *Ochroma lagopus* which is a native of South America and the West Indies. The seeds are embedded in hairs which are employed in the preparation of floss. The wood is composed of large elements with unusually thin walls, and as a consequence it is extremely light. It is sold under the name of Balsa or Cork wood and is used extensively in model-building, particularly in the wooden parts of model aeroplanes.

Also included in this family is the Silk Cotton Tree or Semul, *Bombax*

FIG. 1682.—*Adansonia digitata.* Above, winter aspect. Below, summer aspect. Limpopo Valley. Photographs supplied by Dr. Pole Evans.

malabaricum, a native of Ceylon and India. In addition to the hairs, which are employed in the preparation of a crude cotton, the trunk, owing to the softness of the wood, is hollowed out, and is used for making canoes. *Adansonia digitata* (Fig. 1682) also belongs to this family. It is widely distributed in tropical Africa (Fig. 1683) and is known as the Baobab, or

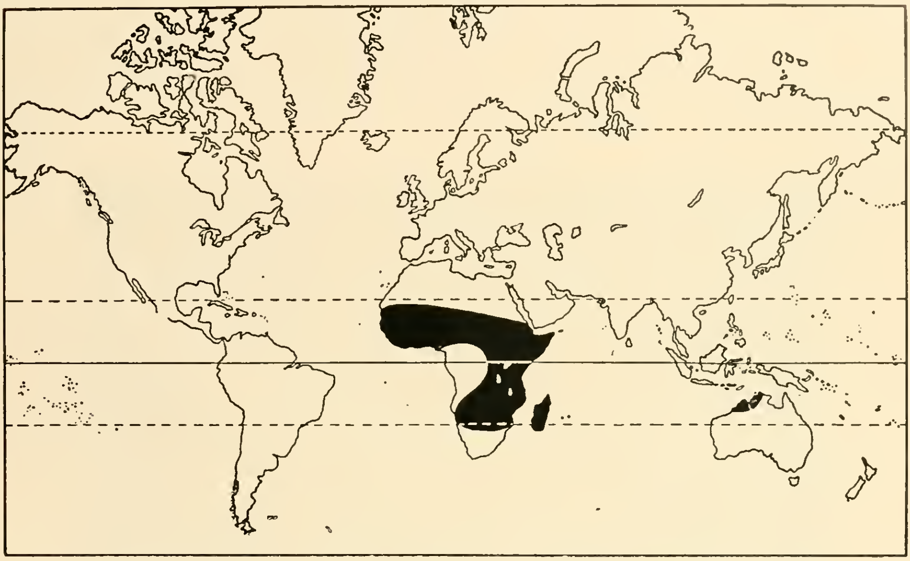


FIG. 1683.—*Adansonia* distribution. (*After Hutchinson.*)

FIG. 1684. — *Adansonia digitata*. Branch with flowers and fruit. (*After Pechuel-Lösche, from Engler-Prantl.*)

Monkey Bread. The trunk is quite short but of enormous thickness. The fruits are large, woody, indehiscent capsules with interior pulp which is edible (Fig. 1684).

A third family included here is the **Sterculiaceae**. It is a fairly large family with about forty-eight genera and 660 species. Most of them are trees or shrubs or occasionally climbers. The most important is *Theobroma cacao*, a native of tropical America which is now mainly cultivated in the Gold Coast. It bears large reddish-yellow fruits directly on the older branches (Fig. 1685). It is from these fruits that the Cocoa of commerce is prepared by grinding the seeds after they have been fermented and roasted. The pressed seeds are also used in the preparation of Cocoa-butter, for in this case the fats are solid at ordinary temperatures.

FIG. 1685.—*Theobroma cacao.* Old branches bearing flowers and fruit simultaneously. Photograph supplied by courtesy of Messrs. Cadbury Ltd.

Cola acuminata provides the Kola nuts which form one of the principal trades in West Africa. It is very common in forests but is rarely cultivated. The nuts contain caffein and when chewed help to overcome fatigue. They are used in some refreshing drinks.

Malvaceae

This family includes a number of British species though it is more widely distributed in the warmer parts of the world. Among the British species we may mention *Malva moschata* (Musk Mallow), *M. rotundifolia* (Dwarf Mallow) and *M. sylvestris* (Common Mallow), *Lavatera arborea* (Tree Mallow) and *Althaea officinalis* (Marsh Mallow).

Several are commonly cultivated in gardens, for example, the Hollyhock, *Althaea rosea*, while species of *Abutilon* and *Hibiscus* are grown in all gardens in warm climates. However by far the most important member of the family is the genus *Gossypium*, from which the various sorts of Cotton are prepared.

The **plants** are herbs or shrubs with alternate, round or palmate, stipulate, multicostate leaves which often bear stellate hairs. Mucilage sacs occur abundantly in the tissues.

The **flowers** (Fig. 1686) may be solitary or produced in cymose inflorescences. They are regular, hermaphrodite and hypogynous.

The **calyx** is usually gamosepalous and pentamerous. An epicalyx is often present and consists of five segments which are either bracteoles or may be formed from the fused stipules of the sepals.

The **corolla** is usually regular, polypetalous and pentamerous. The petals are usually adherent to the base of the stamen tube and are twisted in aestivation.

Fig. 1686.—Floral diagram of *Malva*. Malvaceae.

The **androecium** is made up of an indefinite number of monadelphous stamens each bearing half an anther (Fig. 1687). These are derived by the copious branching of five antipetalous stamens. The outer whorl has

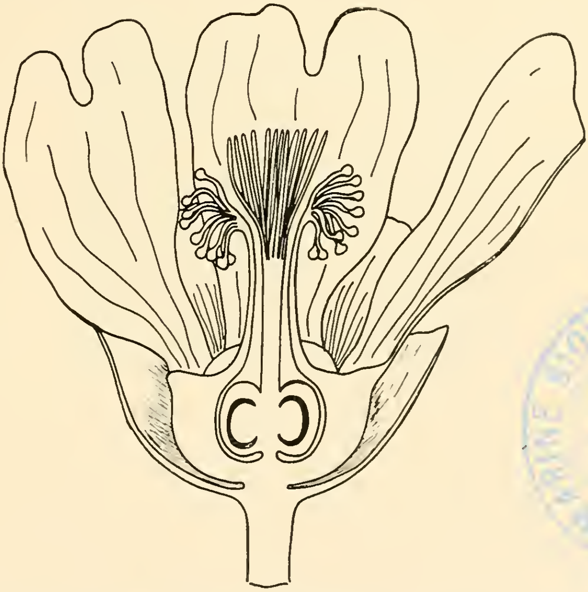


Fig. 1687.—*Malva*. Longitudinal section of flower. (*After Rendle.*)

been lost, though in *Hibiscus* it is represented by five staminodes. The anthers dehisce transversely. The pollen grains are large and echinulate.

The **gynoecium** is polycarpellary and usually syncarpous, being made up of five or more carpels. The styles are united but the stigmas are free. The ovary is superior and multilocular. The ovules vary from one to many in each loculus. Placentation is axile.

The **fruit** is usually a schizocarp which splits into a large number of mericarps, the number being equal to the number of carpels. In *Hibiscus* and *Gossypium*, the fruit is a capsule which dehisces loculicidally.

The **seed** is buried in a hairy covering formed from the testa. Endosperm is scanty and the embryo possesses large, much-folded cotyledons.

The family contains some thirty-five genera with about 700 species. Though some genera occur as far north as Russia and Sweden, the number of species increases towards the tropics. In the south, species of *Plagianthus* are found as far as New Zealand. In the Andes certain species reach a considerable altitude, assuming a dwarf alpine habit.

The chief anatomical characteristics of the family are the wedge-shaped masses of phloem which are divisible into hard and soft bast resembling the condition in *Tilia*. Secondly the presence of stellate epidermal hairs and finally the mucilage-containing organs which may be either epidermal cells or lysigenously formed cavities. In many genera the leaves are bifacial.

The classification within the family is simple:

I. **Malopeoideae**

The carpels are arranged in vertical rows, as a result of division by horizontal transverse walls.

1. *Malopeae*. The only tribe. Included here are the genera: *Malope*, *Kitaibelia*.

II. **Malvoideae**

The carpels are arranged in a single plane.

1. *Malveae*. There are as many styles as carpels, and the fruit is a schizocarp. *Abutilon*, *Lavatera*, *Althaea*, *Malva*, *Anoda*, *Sidalcea*, *Malvastrum*, *Plagianthus*.
2. *Ureneae*. There are twice as many styles as carpels and the fruit is a schizocarp. *Urena*, *Goethea*, *Pavonia*.
3. *Hibisceae*. The fruit is a capsule. *Hibiscus*, *Gossypium*.

The Malopeae are the less important group. *Malope* is a Mediterranean genus, with three species, which is characterized by the three large leaves of the epicalyx. *Kitaibelia* is monotypic and is found in the Lower Danube area. Both genera are cultivated as ornamental flowers. In the Malveae are most of the common herbaceous genera, of which *Malva* (Fig. 1688), *Althaea* and *Lavatera* occur wild in Britain. *Abutilon* is shrubby and rather tender but several species are cultivated in the milder parts of the country. There are about 100 species, found chiefly in the tropics and subtropics.

Fig. 1688.—*Malva sylvestris.* Flower in early stage of anthesis.

There is no epicalyx and the flowers (Fig. 1689) are characterized by the fact that the stamens do not bend down and the styles emerge through the anther group. Many of the species are naturally pollinated by humming-birds. *A. avicennae* is cultivated in China on account of the "China Jute" which is obtained from it at the rate of a ton per acre. *A. indicum* and *A. asiaticum* are cultivated in India for the same purpose.

Fig. 1689.—*Abutilon megapotamicum.* Flower.

The genus *Malva* is interesting on account of the various types of pollination mechanism which it exhibits (Fig. 1690), which may be considered as representative of the family as a whole. The corolla is large and brightly coloured and the flowers are rendered conspicuous by the pyramid of stamens in the centre. Nectar is secreted either at the base of the petals or at the bottom of the calyx.

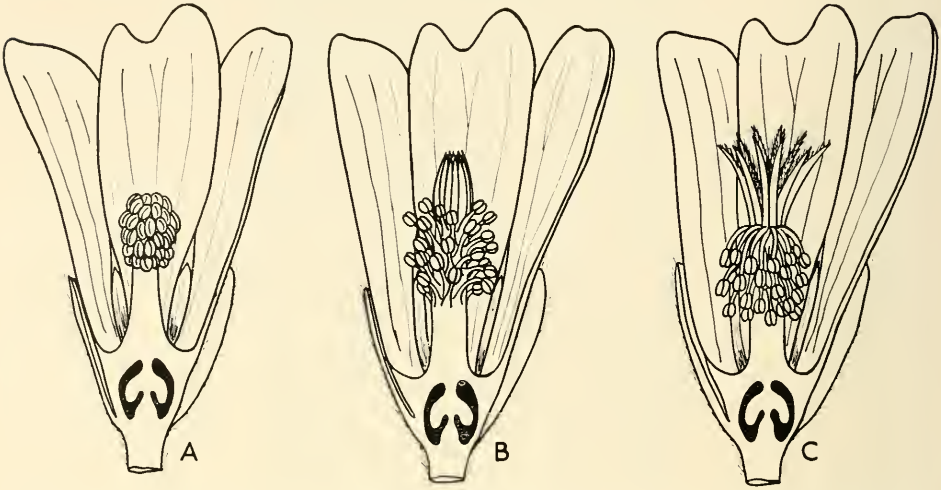


Fig. 1690.—*Malva sylvestris*. Longitudinal sections of flower in three successive stages of anthesis. See in text for pollination mechanism. (*After Knuth.*)

In *M. sylvestris* the red petals are marked with dark stripes which act as nectar guides and above the nectaries are hairs which serve for protection against flies. In the early stage the anthers form a pyramid in the centre of the flower, the filaments being united into a tube below. The immature styles are completely enclosed in this tube so that at an early stage the centre of the flower is entirely filled with ripe anthers. As the latter dehisce they bend outwards and downwards while the stigmas grow up until they occupy the position previously held by the anthers. Insects therefore on visiting a young flower will be liberally dusted with the large, spiny pollen grains, while on visiting an older flower this pollen will be shed on to the stigmatic surfaces. Self-pollination is excluded, for the anthers have bent well out of the way before the stigmas open. The flowers are largely visited by humble bees.

In *M. rotundifolia* the flowers are considerably smaller and are often covered by the large round leaves. In structure they are similar to *M. sylvestris* but owing to their position they are rarely visited by insects. In this species, therefore, after the anthers have opened, the stigmas grow up but instead of the stamens all bending downwards, they remain more or less erect and the stigmas curl back and ultimately come into contact with the anthers. Müller suggests that "in the struggle for existence *M. rotundifolia* has the advantage in being content with poorer soil, in the appearance of its flowers from one to several weeks earlier, and in the possibility of regular self-pollination; *M. sylvestris* on the other hand, in its more vigorous growth, and much greater attraction for insects".

Plagianthus betulinus, a native of New Zealand, is used for timber under the name of Ribbonwood; other species, and especially *Plagianthus* (*Hoheria*) *lyalli* (Fig. 1691), the Lacebark, are common cultivated shrubs or small trees in this country.

FIG. 1691.—*Hoheria lyalli*. Flowering shoot.

In the Ureneae, the three genera mentioned all exhibit interesting features. *Urena* itself contains three tropical species. The fruit is a schizocarp in which the individual segments are provided with hooks. *U. lobata* is of commercial importance on account of its fibres. In Brazil it is used in the preparation of the bags required to hold the locally produced coffee. It is also cultivated for its fibres in Africa and India. *U. simulata* is cultivated in northern Nigeria for making rope.

The genus *Goethea* is represented by two Brazilian species. The flowers are brightly coloured, as is also the epicalyx, and the flower buds may remain for years in a dormant state so that flowers may appear to be produced on the old wood of stem and branches. The genus *Hibiscus* is a large one with about 160 tropical and subtropical species. *H. sinensis* is cultivated in gardens all over the world. The flowers vary in colour from yellow to white and red, and a number of varieties have been recognized as garden forms. Structurally the flowers are interesting because the five antisepalous stamens are represented by teeth at the top of the stamen tube. The fruit is a loculicidal capsule. A number of species are of economic importance; *H. esculentus*, which is known locally as Okra, produces fruits which, when young, are mucilaginous and used as a vegetable in soup. This and a number of other species yield jute-like fibres several of which have been grown on a commercial scale in different parts of Africa.

Finally we come to the genus *Gossypium*, which is by far the most important economically. Species of *Gossypium* provide the Cotton of commerce, which is obtained from the hairs covering the seeds. The cotton plant is naturally a perennial shrub or a small tree but is generally grown as an annual. The flowers vary in colour but are generally white or yellow in the American, yellow with crimson spots in the Egyptian, and purplish red in the Indian varieties. A number of different species are involved therefore in the production of cotton and we shall consider the matter more closely in Volume IV. In the meantime, we may note that *G. barbadense* is the Sea-Island Cotton, *G. peruvianum* is the South American Cotton, *G. hirsutum* the Short Staple Cotton, *G. herbaceum* is the East Indian Cotton and *G. arboreum* is the Tree Cotton of tropical Africa. It must be pointed out however that some confusion has existed regarding the identity and limits of these species and most of the forms now in cultivation are hybrids.

SAPINDALES

The Sapindales are Archichlamydeae with the following characters. The flowers are usually actinomorphic. The sepals are imbricated or occasionally valvate, petals are usually present and imbricated in the bud. The ovary is superior, with one or two ovules in each loculus, and the seeds may or may not have endosperm. The plants are mostly trees or shrubs, with non-glandular leaves which may be either simple or compound.

This order, as originally defined by Engler, is obviously not a very united one and most modern authors subdivide it into two distinct orders by relegating a number of the families into a separate order, the Celastrales. This method is followed by both Rendle and Hutchinson. According to this later and better system the arrangement of the principal families is as follows:

Sapindales: Anacardiaceae, Sapindaceae, Aceraceae, Hippocastanaceae.
Celastrales: Celastraceae, Aquifoliaceae, Staphyleaceae, Empetraceae.

The Sapindales in this more restricted conception are trees or shrubs with compound leaves and numerous flowers. These flowers are either unisexual or bisexual, actinomorphic or less often zygomorphic, hypogynous and generally pentamerous. The ovary is composed of two or three carpels with one or two ovules in each loculus. The embryo is large and endosperm is absent. The Celastrales on the other hand are trees or shrubs with simple leaves and whitish flowers. The flowers are usually bisexual, either tetramerous or pentamerous and actinomorphic. The ovary is plurilocular, containing one or two ovules in each loculus. The embryo is small within a fleshy endosperm.

We shall not consider any one of the families in detail but shall refer briefly to certain of the more important ones.

The **Anacardiaceae** are a family of about sixty genera and 500 species whose distribution is mainly tropical, although a few are found in southern Europe. They are mainly trees or shrubs and are characterized by the resin canals which are present in the wood. The flowers are hermaphrodite though they may become unisexual by reduction of the parts. There may be from three to seven petals, though the corolla may be absent, and the stamens are often double the number of the petals. The ovary is superior and contains a single, solitary, pendulous ovule. The flowers are sometimes epigynous. The fruit is usually a drupe and the seed has little or no endosperm, while the embryo has fleshy cotyledons.

Among the numerous plants of interest which belong to this family we may mention first the genus *Rhus*, of which there are about 130 species widely distributed in warm temperate and subtropical regions. In this country the best known is *R. cotinus* (Fig. 1692), the so-called Burning Bush or Wig Tree, which forms a large shrub often grown in gardens. The name Wig Tree has been given to the plant because of the way the fruits ripen. The stalk of each drupe remains smooth, but the sterile part of the panicle lengthens and becomes hairy. When ripe the stalks become detached at the joints and the whole inflorescence with the fruits attached falls to the ground and may be blown about. These structures have the semblance of grey wigs. The wood yields the yellow dye known as "Young Fustic". *R.*

FIG. 1692.—*Rhus cotinus.* Inflorescence.

toxicodendron is a climbing plant which clings in a way similar to Ivy and is spoken of as Poison-ivy. It is common in North America and is notorious for producing an acute dermatitis if touched. *R. vernicifera* is a native of Japan. It is a small tree which yields lacquer which is obtained by notching the trunk. *R. succedanea*, also native of Japan, is spoken of as the Wax Tree, because the crushed berries yield a yellow wax. *R. typhina* is the Sumach, a magnificent tree which is common in North America and is now widely cultivated.

The genus *Anacardium* contains eight species, of which *A. occidentale* is the most important. It is largely cultivated as the Cashew Nut. The flowers are polygamous and the ovary consists of a single carpel which produces a kidney-shaped nut (Fig. 1693), with a hard acrid coat. The receptacle below the gynoecium swells up into a pear-shaped structure which is fleshy and edible. The stem yields a gum. The plant is a native of tropical America.

FIG. 1693.—*Anacardium occidentale.* Cashew Nut. Fruit borne upon the large, fleshy receptacle.

Even more important and better known is *Mangifera indica* (Fig. 1694), the Mango, which is cultivated in most parts of the tropics. In fact records indicate that it has been known for its fruits for as far back as 5,000 or 6,000 years. The tree is a large one, up to 70 ft. in height, and as much as 5 ft. thick. It grows very rapidly and endures any amount of pruning. These prunings are often used not only for firewood but also for charcoal. The solitary carpel develops into a drupe with a fibreless mesocarp which contains up to 20 per cent. of sugar. The unripe fruit is rich in pectin and is valuable in jam making. Both the leaves and also the unripe fruits are used for cattle feed, the fruits being dried and ground. There are a number of recognized cultivated varieties. The genus contains some thirty species with their centre of distribution in Indo-Malaya.

FIG. 1694.—*Mangifera indica.* Mango. Trees in the Jardim Botanico, Rio de Janeiro.

Another genus of economic importance is *Pistachia.* There are only five species, which are very widely distributed. The flowers are apetalous and dioecious. *P. vera*, which is of Mediterranean origin, yields fruits which are sold as Pistachio nuts. *P. terebinthus* yields China Turpentine, while *P. lentiscus* produces a mastic resin. A somewhat similar resin is produced by *Schinus molle*, the "Pepper" Tree, which is a native of Central and South America and is planted everywhere in dry countries.

From this brief survey it will be realized that this family includes a remarkable number of important economic plants.

The **Sapindaceae** are a large family, with about 1,000 species grouped into some 120 genera. They are mostly trees or shrubs, though a number have adopted climbing methods of growth, usually forming lianas with anomalous secondary growth. In *Serjania*, for example, there is a ring of vascular bundles surrounded by a varying number of rings of outer bundles each with its own pith. Both central and peripheral bundle rings develop their own cambia and form secondary wood independently of one another (Fig. 1695). Tendrils are axillary and represent modified axes of inflorescences which fork at their apices, the branches being flattened and much inrolled. The internal tissues generally contain special cells which secrete resinous or latex-like material. The flowers are unisexual though bisexual flowers may occur in which the stamens are functionless. These flowers show a tendency towards zygomorphy, are tetramerous or pentamerous and are polygamous. The stamens are usually arranged in two whorls and are often reduced to eight and inserted in a disc around the ovary. The latter is trimerous and contains one ascending ovule in each loculus. The fruit may be either a dry capsule or nut or a fleshy berry or drupe. The seed may develop an aril and is non-endospermic.

Fig. 1695.—*Serjania* sp. Transverse section of an old stem with four distinct masses of secondary wood, each developing from a separate cambial ring.

Serjania and *Paullinia*, with 175 and 121 species respectively, are two important American genera both of which form lianas with watch-spring-like tendrils. They both produce winged, dry fruits.

Among species which are of some economic importance first place must be given to *Litchi chinensis* (Fig. 1696). It has been cultivated in China for at least 2,000 years. It is an ornamental tree growing to 40 ft. in height with a broad round crown and light, glossy, green foliage. The flowers are small and unattractive and the fruits are produced in loose clusters of from two to twenty. Each is oval in shape, about $1\frac{1}{2}$ in. in diameter. When ripe it is rose-red in colour. The seed is large but is surrounded with a translucent fleshy mass which is really an aril. It has a white, juicy consistency and a flavour resembling a grape. The total sugar content is about 15 per cent.

Very similar in structure is the genus *Nephelium* which contains about

FIG. 1696.—*Litchi chinensis*. Fruiting shoots. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

twenty-five Indo-Malayan species, which are cultivated for their fruits. *N. longana* is the Longan, and *N. lappaceum* the Rambutan.

Many of the species of the family form large forest trees whose timber is becoming increasingly used and exported. *Schleichera trijuga*, the Ceylon Oak, not only produces good timber but its seeds are edible, and oil may be pressed from them. It furnishes Mirzapore Lac, a varnish which is esteemed for its high quality. Species of *Sapindus* (Fig. 1697), which occur both in tropical Asia and America, yield saponin which produces a lather in water. *S. saponaria* is the American Soap Tree, in which only two segments of the fruit develop.

Compared with the last two families the **Aceraceae** are quite a small one, with only two genera containing somewhat more than 150 species. These genera are *Dipteronia* with one species in central China, and *Acer* which includes all the rest.

The genus *Acer* is not only well known on account of the

FIG. 1697.—*Sapindus marginalis*. Compound leaf and infrutescence. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

species which are commonly cultivated, it is also of considerable economic importance not only for its timber but also because of the Maple Sugar which it yields.

Acer campestris is the Field Maple, a common British plant which forms a large shrub or small tree. The flowers (Fig. 1698) are produced in racemes; they are pentamerous with eight stamens developed in two whorls, while the ovary is composed of two carpels with two collateral or superimposed ovules in each loculus. The fruit is a schizocarp composed of two one-seeded samaras.

FIG. 1698.—*Acer pseudoplatanus*. Inflorescence.

Acer pseudo-platanus, the Sycamore, is a large forest tree common in Britain though not a native. The inflorescence is a raceme. The leaves are palmate and are frequently attacked by the fungus *Rhytisma acerinum* which causes large black spots resembling tar.

Acer saccharinum, the Sugar Maple, grows in the eastern United States and Canada. It yields from 2 to 4 lb. of maple sugar a year. This sugar is obtained mainly in the early spring by boring holes in the trunk, and collecting and evaporating the liquid exuded from the xylem.

Acer negundo, another species closely resembling the Sycamore, is commonly cultivated in this country. It is dioecious, the male inflorescence being an umbel while the female inflorescence is raceme. Pollination is by long- or short-tongued insects which collect the nectar which is exuded copiously. The lateral buds, as in the Plane, are protected by the base of the petiole. Many small and beautiful species of *Acer* are cultivated in Japan. Some of these are quite small bushes, with finely dissected leaves which may be red or variegated in colour. The species of *Acer* generally produce good timber and in this country Maple wood is used in the manufacture of furniture and also in turnery. Good charcoal can also be manufactured from the waste timber.

The Aceraceae are well represented in the Tertiary strata and fossil species appear to have been widely distributed in circumpolar regions during the Oligocene. From this it has been deduced that the family is of Arctic origin and travelled south during Tertiary times till it was more widely distributed than it is today.

The **Hippocastanaceae** are a small family closely allied to the Aceraceae, and are important chiefly because they include the genus *Aesculus* which is distributed in north temperate regions and in South America. The most important is *A. hippocastanum*, the Horse Chestnut (Fig. 1699), which is the only present-day European species, growing wild in Greece and Anatolia. In Pliocene times it was widely distributed in central Europe. The tree was introduced into cultivation in 1576 and was first planted in England a century later. At the present time a number of hybrids are in cultivation produced by crossing this species with *A. carnea*, a North American species. Other American species, *A. pavia* with red flowers and *A. glabra* with yellow flowers, are also extensively grown. The seeds are large and are enclosed in a leathery capsule which may be spiny or smooth according to the species. Oil can be expressed from the seeds which was formerly used as a cure for

FIG. 1699.—*Aesculus hippocastanum.*
Horse Chestnut. Inflorescence.

rheumatism. The roots contain saponin and those of certain species are crushed and used in washing woollen goods. The family includes two genera, *Aesculus* with twenty-five species and *Billia* with two. The family is essentially American in distribution. Floristically it may be separated from the Aceraceae by the irregular, obliquely zygomorphic flowers and the tricarpellary gynoecium. For the pollination, see Fig. 1700.

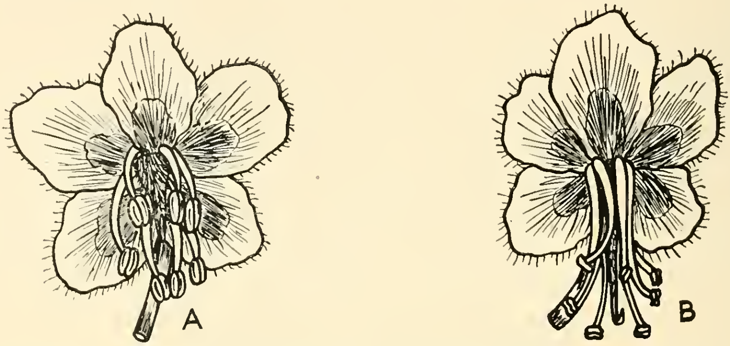


FIG. 1700.—*Aesculus hippocastanum*. Pollination. A, Flower in early stage with stamens elongating. B, Later stage with anthers withered and style elongating from among them.

Turning to those families which comprise the **Celastrales** we may consider first the **Celastraceae**. Although this family contains thirty-eight genera and 480 species, few are well known or of economic importance, and we shall confine our remarks to the genus *Euonymus* of which there are 100 species distributed in the north temperate region and south-eastern Asia.

One species, *E. europaeus* (Fig. 1701), occurs in Britain where it is known as Spindle Tree. Several species produce curious corky outgrowths on the stem. The flowers are bisexual or may become unisexual by abortion of the parts. The perianth is often small and inconspicuous, consisting of four sepals and petals enclosing four stamens. The fruit is a five-parted loculicidal capsule which splits to expose red seeds with orange-coloured arils, which ensure dispersal by birds. The wood is used in the manufacture

FIG. 1701.—*Euonymus europaeus*. Spindle Tree. Flowering shoot.

of pegs and spindles and produces good charcoal. *E. japonicus*, commonly grown in gardens, is an evergreen hardy shrub with oval, glossy leaves. A few other species of the genus are lianas. *Euonymus europaeus* is the winter home of certain species of black aphids which in summer attack sugar beet, and energetic attempts are being made to eradicate spindle trees from Britain on this account.

The **Aquifoliaceae** are another small family with five genera and 300 species, which are widely distributed in temperate and tropical regions (Fig. 1702). They are mostly shrubs and trees with leathery, alternate leaves and unisexual flowers which are generally tetramerous. The chief genus is *Ilex*. *I. aquifolium* (Fig. 1703) is the Holly, and occurs wild in Britain. The plants are monoecious, but in the female flowers the sterile stamens are often so large that the flowers appear to be hermaphrodite. *I. paraguensis* is a South American species whose leaves and twigs are used in the preparation of Maté, which is used in South America as a beverage in the same way as tea. It is imported on a small scale into this country.

FIG. 1702.—Distribution of *Ilex aquifolium*.

The two other genera of the family are *Nemopanthus* with one species in the eastern mountains of North America and *Phelline* with twelve species in New Caledonia.

The **Staphyleaceae** are a small family, containing six genera and only twenty species, which may be mentioned on account of *Staphylea pinnata* (Fig. 1704), a small tree or large shrub commonly cultivated in gardens because of its panicles of fragrant white flowers, which are produced early in the spring. These flowers are pentamerous with a trilocular ovary. The fruit is a soft, inflated capsule.

FIG. 1703.—*Ilex aquifolium.* Flowering shoot.

FIG. 1704.—*Staphylea pinnata.* Inflorescence.

The **Empetraceae** are an even smaller family with three genera, *Corema*, *Empetrum* and *Ceratiola*. *Ceratiola* is monotypic, while *Empetrum* and *Corema* have two species each. *Empetrum nigrum* occurs in Britain and is called the Crow-berry. It is a typical component of peaty moorland vegetation. The flowers are produced on spur shoots and are trimerous. The leaves show xerophytic modifications, with a well-developed cuticle and stomata sunk in deep grooves, lined with hairs, formed by the downwardly rolled leaf margins.

We may also refer here to the **Buxaceae**, a small family whose systematic position is very doubtful. Placed in the Sapindales by Engler, it was included in the Euphorbiales by Rendle and in the Hamamelidales by Hutchinson. It is a family of evergreen shrubs with leathery leaves and no latex. There are six genera and about thirty species widely distributed in the temperate and tropical parts of the world.

The genus *Buxus* includes *B. sempervirens* (Fig. 1705), Box, which occurs wild in certain southern countries and is often cultivated. It grows very slowly and the box hedges which are found in the gardens of old mansions may have been planted for several hundred years. The wood is very firm and close grained and is largely used in turning and for wood-block engraving. The common name is a corruption of the German " Buchs " (Books), from the last-named use.

Fig. 1705.—*Buxus sempervirens.* Box. Left, a flowering shoot. Right, a shoot with ripe capsules.

Somewhat closely allied to the Sapindales, though occupying a doubtful position, are the **Santalales.** The members of this order may be trees, shrubs or herbs and many of them are parasitic. Leaves when present are opposite but they may be reduced to scales. The floral parts are often reduced, the ovary is inferior, the placentation axile and the ovules few in number. The seeds have abundant endosperm and the embryo is straight. As originally constituted the order contained some eight families, to three of which we shall refer briefly, the Loranthaceae, Balanophoraceae and Santalaceae.

The **Loranthaceae** are a family of parasitic shrubs with green leaves, but deriving the greater part of their food as parasites. There are thirty genera and about 520 species, occurring in temperate and tropical regions.

FIG. 1706.—*Viscum album*. Mistletoe. Habit of plant growing on the branch of an apple tree.

The only British genus is *Viscum*; *V. album* (Fig. 1706) is the Mistletoe. The plants are attached to their hosts by suckers which have been variously interpreted, but are generally thought to be adventitious roots greatly modified as organs of absorption. A few species root in the ground but most live on trees. Some species are unselective, others can only live on the wood of one or two species. The vegetative parts of *Arceuthobium* are endophytic in the host plant, as in the Rafflesiaceae.

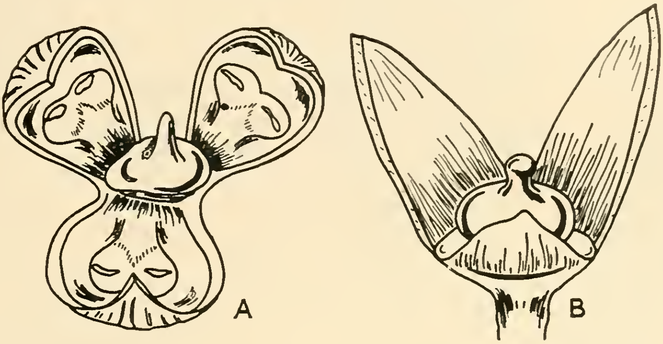


Fig. 1707.—*Viscum album.* Flowers. A, Male flower. B, Female flower. (*After Hutchinson.*)

The flowers (Fig. 1707) are dimerous, or trimerous, the parts being either free or united. In some genera, included in the sub-family Viscoideae, the flowers are small and inconspicuous, while in the Loranthoideae they may be large and brilliantly coloured. The stamens are equal in number to the segments of the corolla and the anthers consist of a large number of separate pollen sacs. The ovary is unilocular with a large central placenta bearing numerous ovules.

The **Balanophoraceae** are a small family of root parasites which are leafless and devoid of chlorophyll. There are fifteen genera and forty species which are typically tropical in distribution. The plant (Fig. 1708) is attached to the roots of its host by suckers developed from an underground tuberous stem. From it springs the inflorescence, though in some species the flowers may develop within this tuber and break out through it. The inflorescence grows up above the soil in the form of a spike or head, beset with scale leaves, and bears unisexual flowers. The male flowers have a perianth of three or four parts which are united into a tube, with an equal number of stamens. The female flowers are generally devoid of any perianth segments and consist of a gynoecium composed (Fig. 1709) of one to three carpels which unite to form a unilocular ovary. The ovules are naked and may be reduced to embryo sacs embedded in a common mass of tissue called the **mamelon.** Little is known about the pollination mechanism, but one, *Sarcophyte sanguinea*, emits the smell of decaying fish and may be visited by insects. Others are thought to be also entomophilous.

The largest genus is *Balanophora*, which contains eleven species scattered through Indo-Malaya, Polynesia and Australia.

The **Santalaceae** are semi-parasitic herbs, shrubs or trees with green leaves, some of which live as epiphytes, others as root parasites. The only

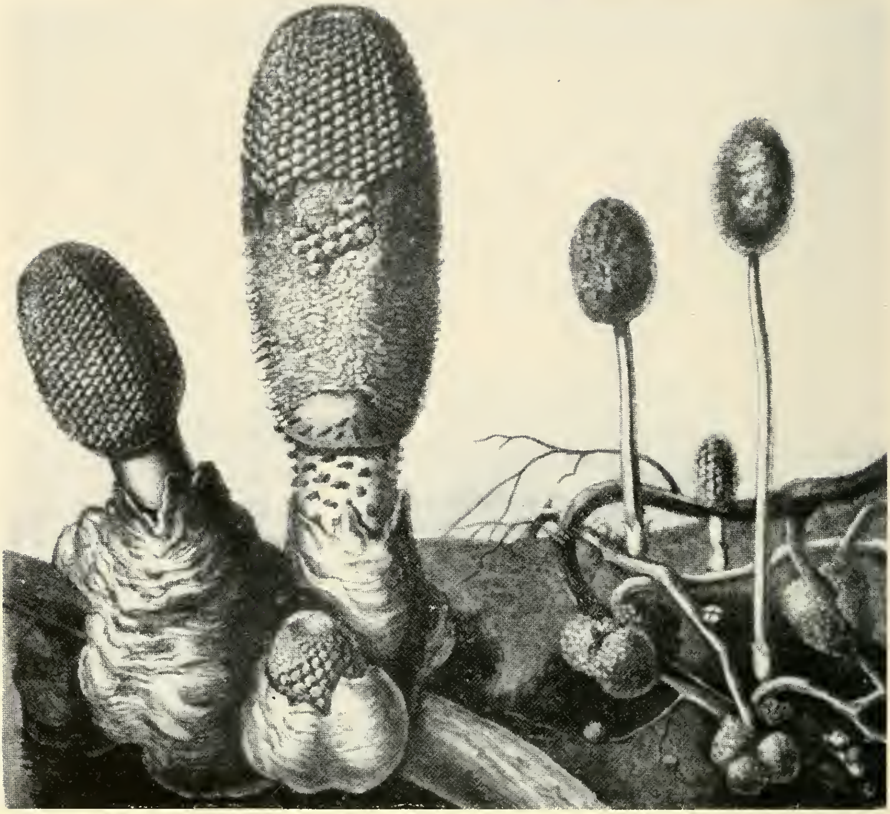


Fig. 1708.—Habit of two members of the Balanophoraceae. Left, *Rhopalocnemis phalloides*. Java. Right, *Helosis guj mensis*. Mexico. (*After Kerner and Oliver.*)

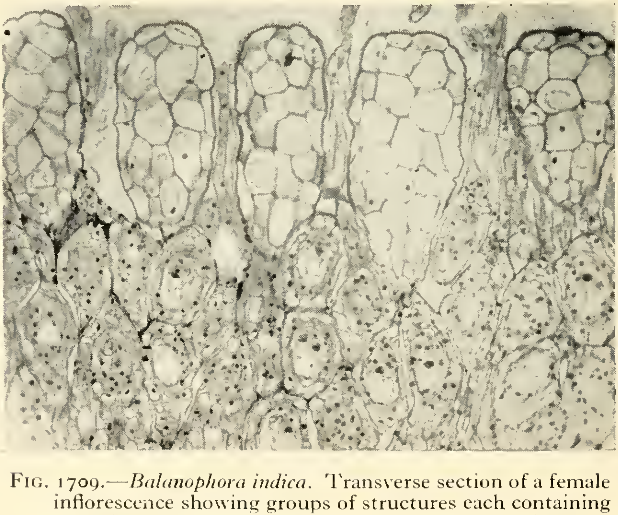


Fig. 1709.—*Balanophora indica*. Transverse section of a female inflorescence showing groups of structures each containing an embryo sac and having long, stylar projections between the lobes of large celled vegetative tissue. These structures are either naked nucelli or uniovulate carpels in which nucellus and carpel wall are completely united, forming a mamelon.

British example is *Thesium humifusum* (Fig. 1710) (Bastard Toadflax) which is a root parasite on grasses. This genus which contains about 235 species has its centre of distribution in South Africa. The genus *Santalum*, with ten Indo-Malayan and Polynesian species, consists of large, parasitic trees.

Fig. 1710.—*Thesium humifusum.* Habit of plant.

S. album is the source of the fragrant Sandalwood, which is used in cabinet-making. A perfumed oil may be distilled from it. The fruits of several species possess edible, sweet pericarps. Species of *Exocarpus* are valuable for their timber, while the hard nuts are borne on fleshy, edible stalks and are called Australian Cherries.

It is convenient here to refer to another small order, the **Rhamnales**. They show a marked similarity to the Celastrales but the tendency to form unisexual flowers is more pronounced and they are sometimes apetalous. The gynoecium usually consists of five carpels, more rarely two, which are united to form a chambered ovary, each loculus of which contains two anatropous, ascending ovules. The plants are either shrubs or trees with a tendency to become lianas. Two families are included, the Rhamnaceae and the Vitaceae.

The **Rhamnaceae** contain about forty genera and 500 species which are very widely distributed. *Rhamnus* contains 100 species of which two are wild in Britain. *R. catharticus* (Buckthorn) which grows chiefly on the chalk in southern England and *R. frangula* which is widely distributed in England although rare in Scotland. Its centre of distribution is central Europe. Another genus, *Zizyphus*, with forty species, occurs in Indo-Malaya. The plants are stipulate, the stipules being developed as thorns, one of which turns upwards and the other downwards. Sometimes only one develops. *Z. vulgaris* and *Z. lotus* have edible fruits, the former being known as the French Jujube (Fig. 1711). The latter was the food of the legendary Lotus eaters. *Z. chloroxylon* of Jamaica provides a hard, tough timber known as Cogwood.

FIG. 1711.—*Zizyphus jujuba.* Fruiting shoot. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

Species of the genus *Colletia* occur in South America and are peculiar in having two buds developed in each axil. The upper forms a thorny cladode while the lower may produce a flower or a branch of unlimited growth. In some species the flattened spiny cladodes bear small deciduous leaves. In such forms the flowers (Fig. 1712) develop on the cladodes, which are produced in opposite pairs. *C. cruciata*, the Anchor Plant, is a garden shrub.

FIG. 1712.—*Colletia cruciata.* Shoots with spiny cladodes bearing flowers.

The North American genus *Ceanothus* (Fig. 1713), the Californian Lilac, contains forty species. Many are deciduous but a few are evergreen with small ovate leaves and bright blue or pink flowers crowded into dense inflorescences. The flowers are epigynous. Several species are commonly cultivated in gardens.

FIG. 1713.—*Ceanothus dentatus.* Shoot with inflorescence.

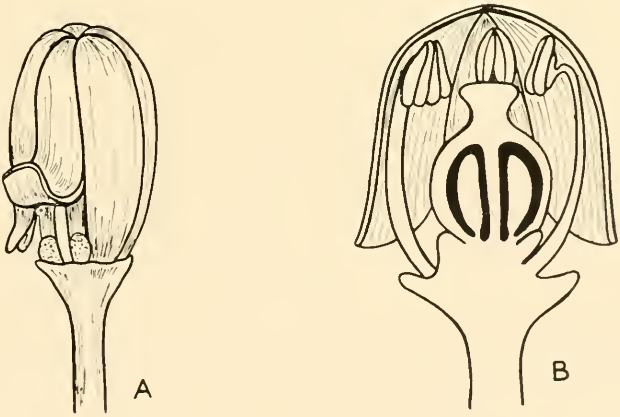


FIG. 1714.—*Vitis vinifera.* Flowers. A, Abscission of the perianth. B, Longitudinal section of flower, showing coherent perianth being shed in one piece. (*After Le Maout and Decaisne.*)

The second family is the **Vitaceae**, which are a family composed of 450 species arranged in eleven genera. The largest genus is *Cissus*, with 325 species widely distributed in the tropics and subtropics. The best known however is *Vitis*, the vine (Fig. 1714), a genus once considered to contain abouty forty species, but now split into several distinct genera. The plants are tendril-climbing shrubs, which is the chief feature which separates them from the Rhamnaceae. These tendrils (Fig. 1715) terminate the main axis, which is continued by the growth of the uppermost lateral bud, so that the tendril and leaf appear to be borne on opposite sides of the shoot, forming a sympodium. The inflorescence occupies the same position as a tendril. These tendrils may either terminate in a coiled, tactile tip or a cushion-like adhesive disc. The fruit is a berry containing from one to four seeds and is adapted for bird distribution. The plants occur all over the northern hemisphere, though they may also be found at considerable altitudes on tropical mountains. Species of *Cissus* however are sometimes desert and steppe plants, in which the vegetative tissues become adapted for water storage.

Fig. 1715.—*Vitis vinifera.* Axial tendrils.

Several are of economic importance, the chief of which is *Vitis vinifera*, the Grape-vine (Fig. 1716), which is wild in Asia Minor. Currants and raisins are the dried fruits of varieties cultivated along the warm Mediterranean coast. They have an abnormally high sugar content. The name currant is a corruption of Corinth where the variety was first grown. In the United States *V. labrusca* (Fox-grape) is cultivated and several varieties

FIG. 1716.—*Vitis vinifera.* Longfield Vinery, Guernsey, containing 25,000 bunches of grapes. Photograph supplied by courtesy of Mr. de Garis.

have been sent to Europe to serve as stocks for grafting the European varieties, because they withstand the attacks of *Phylloxera* better than the European ones. It was in a vineyard of Bordeaux that the mixture of copper sulphate and lime was first used as a deterrent to prevent the populace from picking the grapes and was afterwards discovered to ward off mildew attack. This fungicide later became known as the famous Bordeaux Mixture. *Parthenocissus quinquefolia* is the Virginia Creeper, well known because of its brilliant red autumn foliage, while

FIG. 1717.—*Ampelopsis veitchii* (*Parthenocissus* or *Vitis inconstans*). Young shoots with branched, axial tendrils which end in adhesive discs.

P. veitchii or *Ampelopsis veitchii* is the Ampelopsis Creeper which climbs by suctorial discs (Fig. 1717). It also has red autumn foliage.

GERANIALES

The Geraniales are Archichlamydeae in which the flowers are bisexual, actinomorphic or rarely zygomorphic. The floral parts are pentamerous and cyclic. The sepals are imbricated in the bud, free or sometimes united at the base, and may be persistent. The petals are imbricated in the bud, but are always free. The stamens are arranged in two whorls, generally consisting of five stamens, becoming obdiplostemonous by abortion of the outer whorl; or they may be numerous, when the filaments are either free or united into a tube or ring at their base. The gynoecium consists of three to five carpels, which form a plurilocular ovary. The ovules are axile in attachment, pendulous and anatropous in form, with the micropyle directed outwards. The ovules are provided with two integuments.

The limits of this Order are very wide. According to Engler it includes some twenty families, while both Wettstein and Rendle exclude the whole of Engler's sub-order, Tricoccae, and regard the families included in it as a separate order. Hutchinson on the other hand further splits up the order as Engler conceived it. It is obvious that there is a considerable diversity of form within the order, the more so when it is allowed to embrace the large number of families included by Engler. On the other hand distributing the families between three orders, Geraniales, Malpighiales and Euphorbiales, as is done by Hutchinson, would be too elaborate a system for us to adopt here. It seems therefore most convenient to follow Wettstein in this matter. Under his system the Geraniales, or Gruinales, as he terms them, include the following important families: Linaceae, Oxalidaceae, Geraniaceae, Tropaeolaceae, Balsaminaceae, Erythroxylaceae, Malpighiaceae and Zygophyllaceae.

Most of the plants are herbaceous, occasionally woody or climbers, usually with simple, alternate leaves with or without stipules. The order shows a gradual transition from actinomorphy to zygomorphy.

We shall consider the family Geraniaceae in detail but before doing so we may refer briefly to some of the more important features exhibited by the other families.

The **Linaceae** are a small family of some 150 species, the majority of which belong to the genus *Linum*. Most of the species are herbs or small shrubs with small entire, alternate leaves often provided with stipules. In the genus *Linum* (Fig. 1718) are some ninety-five species, four of which occur in Britain. *L. catharticum*, the Purging Flax, is an annual which extends to Arctic Europe; *L. usitatissimum*, the Common Flax, which is native of the country between the Persian Gulf, the Caspian Sea and the Black Sea; *L. perenne* (Fig. 1719), the Blue Flax; *L. angustifolium* and *L. grandiflorum* which is cultivated in gardens. The seeds have a mucilaginous testa, which swells on wetting and yields an oil on pressure which is sold commercially as Linseed Oil. The residue is made into a hard cake which is broken up and used as a source of protein for feeding cattle. The chief importance of the species *L. usitatissimum* lies in the fibres, which are used in the production of linen, the short fibres being made into tow. The genus is widely distributed in temperate and subtropical regions.

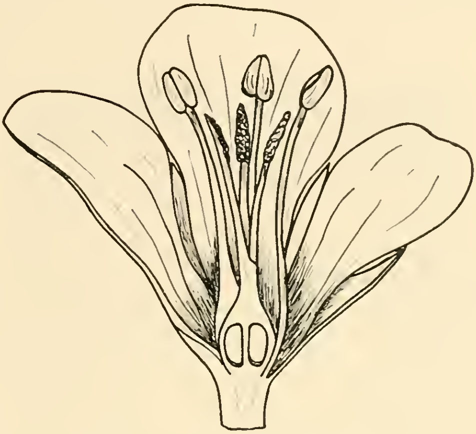


FIG. 1718.—*Linum.* Vertical section of the flower.

FIG. 1719.—*Linum perenne.* Flower.

Radiola linoides (All-seed) belongs to a monotypic genus. It is common in Europe and occurs rarely in Britain. In the genus *Hugonia* the lower twigs of the inflorescence are modified into hooks for climbing. There are eleven tropical species.

The **Oxalidaceae** are closely allied to the Geraniaceae, from which they differ in having ten stamens united at their base, in having five styles and in the mode of dehiscence of the fruit. The family is essentially a tropical one with seven genera and some 850 species. There is only one British representative, *Oxalis acetosella*, the Wood Sorrel (Fig. 1720). In many species the flowers are trimorphic (Fig. 1721), there being three kinds of plants, those with long style and medium- or short-length stamens; secondly those with medium or short styles and with long and medium stamens; and thirdly those with long or medium styles and short or medium stamens. In *O. bupleurifolia* and some other species, the ordinary leaves are replaced by phyllodes. The tubers of *O. deppi* and others are used for food. Many species develop subterranean, cleistogamic flowers if the normal flowers fail to set seeds. Oxalic acid may be prepared from *Oxalis acetosella*, where it occurs in the leaves in the form of the Potassium salt.

FIG. 1720.—*Oxalis acetosella.* Wood Sorrel. Flower.

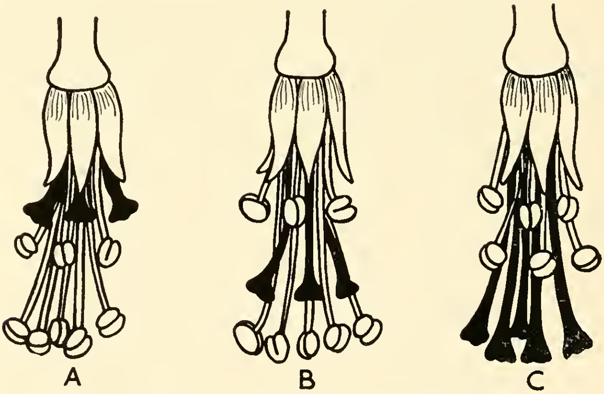


FIG. 1721.—*Oxalis speciosa.* Trimorphic flowers. A, Short styles, long stamens. B, Medium styles, long stamens. C, Long styles, short stamens. (*After Darwin.*)

The genus *Biophytum*, containing some sixty tropical species, is interesting because of the sensitive, pinnate leaves possessed by many of them. These leaflets bend down when touched, in a way similar to that in *Mimosa pudica*. Many species of *Oxalis* exhibit nyctinastic movement. Another genus worthy of mention is *Averrhoa*, whose two species are trees which are cultivated in the tropics for their berries, which taste much like Gooseberries. They are known as Carambola (*A. carambola*) and Bilimbi (*A. bilimbi*) respectively.

The **Tropaeolaceae** are a small family with the single genus *Tropaeolum* (Fig. 1722). There are about fifty species occurring chiefly in South and Central America (Fig. 1723). Most of them are herbs climbing by sensitive petioles, with compound or peltate laminae. The flowers (Fig. 1724) show an advanced character in that they are zygomorphic, with a posterior spur formed by the axis under the posterior sepal, to which two lateral sepals unite to contribute to form the large spur. The embryogeny is abnormal in that the suspensor becomes much elongated and grows out of the micropyle, where it bears two long appendages or haustoria, one of which grows into the tissue of the placenta and absorbs nourishment for the developing embryo, while the other grows into the ovary cavity and may serve as an organ of respiration. The embryo and its cotyledons finally fill the seed coat, there being no endosperm. Several species of *Tropaeolum* are commonly cultivated in gardens. The common garden Nasturtium or Indian Cress is *T. majus*; the Canary Creeper is *T. peregrinum*; while the red *T. speciosum* also thrives in sheltered positions. It is a tuberous-rooted perennial, as is also *T. polyphyllum*.

FIG. 1722.—*Tropaeolum majus*. Garden " Nasturtium ". Left, flower in face view. Right, flower in profile showing the spur.

In the **Balsaminaceae** there are two genera, *Impatiens* with about

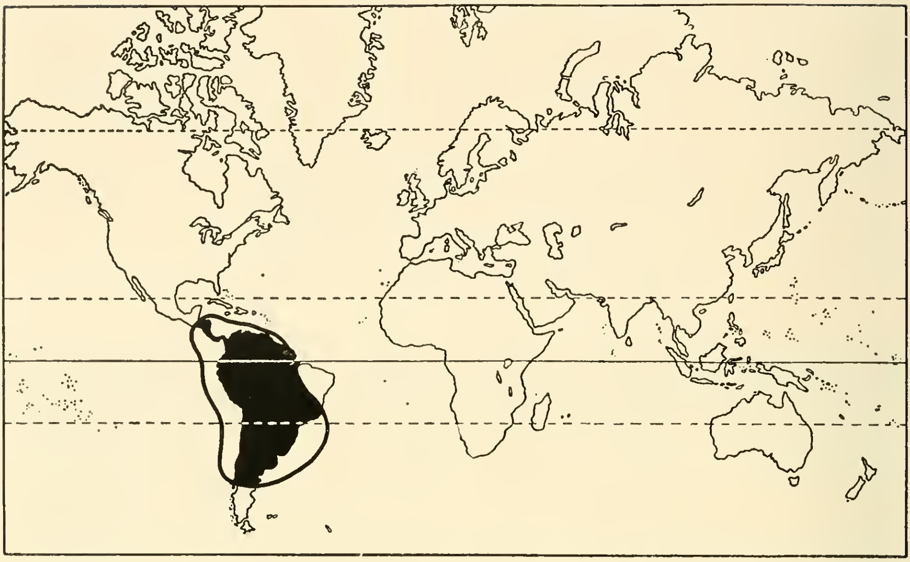


FIG. 1723.—Distribution of *Tropaeolum*.

FIG. 1724.—*Tropaeolum majus*. A, Younger flower, stamens extruded. B, Older flower with stigma extruded. The stamens enlarge in succession, to occupy the centre of the flower. When all are exhausted they bend aside and the stigma comes forward into the centre.

430 species and *Hydrocera*. They are all herbs, with watery translucent stems and alternate leaves. The flowers are hermaphrodite and zygomorphic, a spur being formed by the greatly enlarged posterior sepal. The slender pedicel is often twisted so that the spur becomes anterior, that is to say, the flower is **resupinate.** Cleistogamic flowers are often produced.

The chief interest in the family is the explosive nature of the capsule at the time of maturity. In *Impatiens noli-tangere* (Fig. 1725) the capsule has a fleshy pericarp, the cells of the outer layer of which are highly turgid.

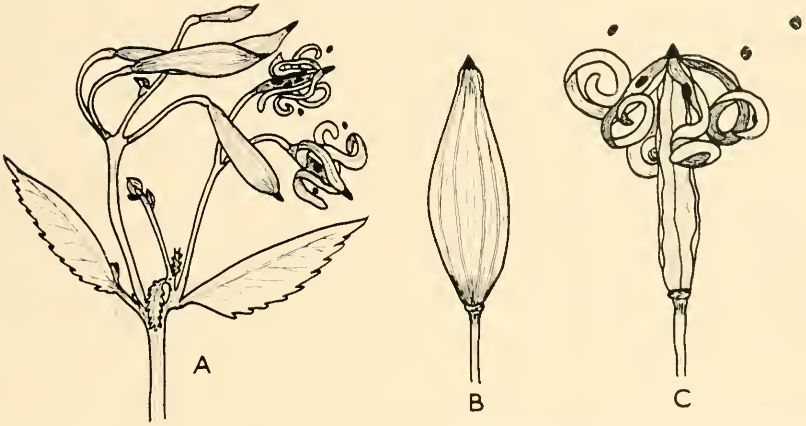


Fig. 1725.—*Impatiens noli-tangere.* A, Shoot with capsules, two of which have dehisced. B, Ripe capsule. C, Capsule dehiscing. The carpel valves roll up elastically and throw off the seeds with considerable force.

This puts a great strain on the whole structure. Dehiscence is septifragal and is started by the least touch on the ripe fruit. The valves roll up inwards with great violence, starting at the base, with the result that the seeds are shot out in all directions.

I. noli-tangere is the only British species, though *I. fulva*, a North American species with orange flowers, and *I. roylei*, a Himalayan species with pink flowers, have become naturalized. *I. balsamina* (Balsam), an East Indian species, is often grown in gardens. *Hydrocera* is represented by a single species, a marsh plant found in India and Java.

The **Erythroxylaceae** are a small family with two genera and 200 species. They are shrubs or trees with alternate, entire leaves. The only important member which we must mention is *Erythroxylum coca*. The leaves of this plant are of extreme economic importance as the chief source of cocaine.

The **Malpighiaceae** are a family of woody plants found mainly in South America. There are some fifty-five genera containing about 650 species (Fig. 1726). Many of them are climbers and form lianas with very complex and abnormal anatomy. The simplest of these abnormalities is the development of phloem islands in the xylem, which occurs in all the species

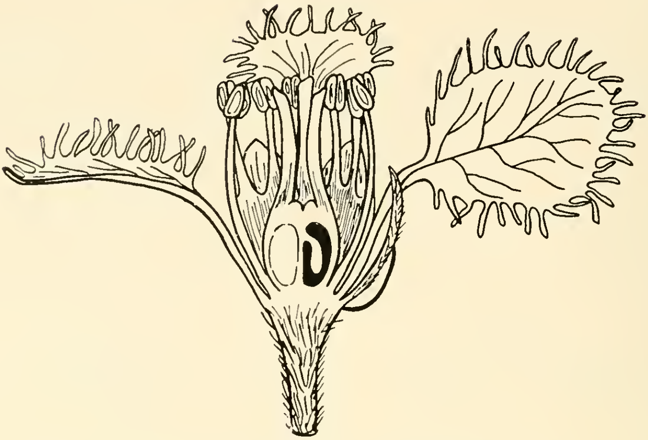


FIG. 1726.—*Camarea ericoides.* Malpighiaceae. Flower in longitudinal section. (*After Baillon.*)

of the genus *Dicella.* This phloem appears to arise from the cambium which for a time may cut off phloem elements internally, thereafter reverting to xylem formation. In many of the lianas grooves appear in the xylem which are themselves lined with cambium and in some genera there are furrows in the stem corresponding to these xylem grooves (Fig. 1727). The most elaborate condition is seen in the stems of *Stigmatophyllon* in which the xylem at first grows in thickness by the activity of a normal cambium and is surrounded by a rather wide circular phloem. The xylem contains abundant xylem parenchyma and broad medullary rays with the result that the xylem appears to be broken up

FIG. 1727.—*Tetrapteris.* Malpighiaceae. Transverse section of an old stem showing the dissected xylem masses. (*After Schenck.*)

into strands. Later, as a result of cell division of the parenchyma cells, new cambial layers are produced in association with these strands and form additional bundles of xylem and phloem.

Apart from these anomalous stem structures, the morphology of the leaf calls for special mention, though abnormalities do not occur in all members of the family. The leaf may be either centric or bifacial and the assimilatory tissue consists of one layer of palisade cells. In some forms however the upper epidermis may be two or even three cells thick and from the outer layer there may arise stellate hairs. The lower epidermis is often papillose. The stomata often have a pair of subsidiary cells parallel to the pore.

The genus *Byrsonima* is widely distributed in Central and South America. It contains about 120 species, several of which are of economic importance. *B. spicata* which occurs in the West Indies is known as the Shoemaker's Bark; the bark of the tree being tanned and used in place of leather.

The **Zygophyllaceae** are a small family of woody perennials containing about twenty-two genera and 160 species. They are mostly tropical and subtropical in distribution and live either under xerophytic or halophytic conditions. The leaves are opposite, stipulate and usually hairy, fleshy or leathery in structure. They form one of the chief components of the vegetation of the salt deserts.

The anatomical features reflect the ecological habitat of the plants. The leaves are often centric, with a central thin-walled water-storage

FIG. 1728.—*Guaiacum officinale*. Shoot with flowers and a fruit. (*After Berg and Schmidt, from Rendle.*)

tissue surrounding the vascular bundles. In other types mucilage cells are scattered through the mesophyll. Other features of anatomical interest are the production of cork from the epidermis and the presence of resinous material stored up in the heart wood.

One species of economic importance is *Guaiacum officinale* (Fig. 1728) (Lignum Vitae), a small tree which is found growing in the dry coast areas of the West Indies and Central America. The greenish-brown heart wood yields a bitter resin which is used medicinally and also as a test reagent. *Tribulus terrestris* develops spiny, schizocarpic fruits which are readily carried about by animals. It is found in dry sandy districts of southern Europe, central Asia and tropical Africa. *Porliera hygrometrica* shows an interesting physiological behaviour. The leaflets spread out horizontally by night, but by day they fold up in pairs and thus avoid excessive transpiration. It is a native of Mexico and the Andean region of South America. *Larrea mexicana* is the so-called Tar Bush or Creosote Plant, which forms a dense scrub vegetation and serves to bind loose sand together. It has an offensive smell which prevents animals from eating it. The seeds of *Peganum harmala* yield a dye known as Turkey Red.

Geraniaceae

The family is a small one but is fairly well represented in the British Flora. The best-known genera are *Geranium* (Crane's-bill) and *Erodium* (Stork's-bill); both are represented in Britain by a number of species, of which we may mention Herb Robert (*G. robertianum*), Meadow Crane's-bill (*G. pratense*) and Mountain Crane's-bill (*G. sylvaticum*).

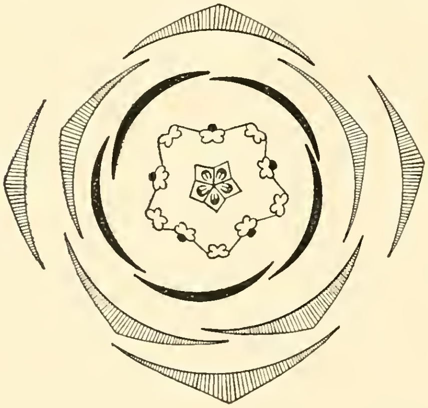


FIG. 1729.—Floral diagram of *Geranium pratense*. Geraniaceae. (*After Eichler.*)

It should be noted that the so-called Geraniums so extensively grown in gardens and greenhouses belong to the genus *Pelargonium*, which is South African.

The **plants** are mostly annual or perennial herbs with swollen, jointed nodes often covered with glandular hairs. The leaves may be either alternate or opposite. They may be palmate but many are palmatisect and most are stipulate.

The **flowers** (Fig. 1729) may be solitary or may be borne in cymose inflorescences, generally composed of a small number of flowers. They are usually actinomorphic, pentamerous and hypogynous.

The **calyx** is polysepalous and consists of five persistent sepals which are well developed and green in colour. They are imbricated in the bud.

The **corolla** is polypetalous (Fig. 1730), consisting of five petals often of large size and brightly coloured; they are also imbricated in the bud.

FIG. 1730.—*Geranium pratense.* Flower.

The **androecium** consists usually of ten stamens, obdiplostemonous in *Geranium*, consisting of five short outer and five long inner ones. In *Erodium* there are only five, those opposite the petals being represented by scaly staminodes. In *Pelargonium* only two to four of the stamens are fertile and in certain species of *Geranium*, *e.g.*, *G. pusillum*, some of the stamens have no anthers. A nectary is present at the base of some of the stamens.

The **gynoecium** is syncarpous, composed usually of five carpels which unite to form a chambered ovary and pass upwards to form a well-developed compound style or " beak ", which divides at the top into an equal number of slender stigmas. One or two ovules are present in each loculus; each is pendulous and anatropous with the micropyle directed outwards.

The **fruit** is a schizocarp. The five carpels with their long persistent styles, here referred to as **awns**, separate from the central column. In *Geranium* the one-seeded parts or **cocci** are dehiscent and the styles roll up with considerable force so that the seeds are shot out. In *Erodium* and *Pelargonium* the parts are indehiscent but the sharp-pointed awns are hygroscopic and twist up like corkscrews in dry weather. This not only assists in distribution but also forces the seed into the ground.

The seed contains but little endosperm and the embryo is more or less bent with the cotyledons rolled or folded on each other. These cotyledons may become green while still enclosed in the seed coat.

The family comprises some eleven genera containing about 750 species. They are widely distributed in north temperate regions. The genus

Geranium (Fig. 1731), of which there are about 300 species, covers the widest range. *G. pratense*, *G. sylvaticum*, and *G. robertianum* extend into the Arctic, while *G. patagonicum* and *G. magellanicum* are found within the Antarctic. Eleven species of this genus occur wild in Britain.

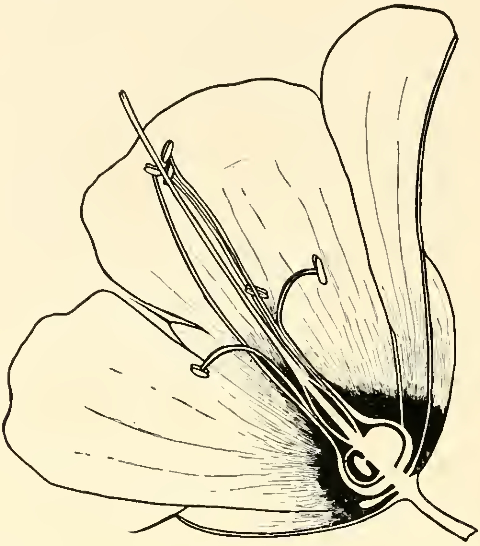


FIG. 1731.—*Geranium pratense.* Longitudinal section of flower. (*After James and Clapham.*)

The genus *Erodium* is also a large one, with about sixty-five species, of which three are found in Britain. The genus *Pelargonium* with about 250 species is found mainly in South Africa.

The genera of the Geraniaceae fall naturally into five sub-families.

I. Geranioideae

Ovary beaked, sepals free, imbricated. Ovary containing one or rarely two ovules in the loculus. *Geranium*, *Erodium*, *Pelargonium*, *Monsonia*, *Sarcocaulon.*

II. Biebersteinioideae

Ovary not beaked, sepals free, imbricated, ovary containing a single eed. *Biebersteinia*, native of central and western Asia.

III. Wendtioideae

Ovary not beaked, sepals free, imbricated, ovary containing two to many seeds. *Rhynchotheca*, *Wendtia*, *Balbasia*, occurring mainly in South America.

IV. Vivianoideae

Ovary not beaked, calyx tubular, fruit a capsule. *Viviania*, found in the Andes.

V. Dirachmoideae

Ovary not beaked, carpels eight, calyx tubular. *Dirachma*, which contains a single species, found on the island of Socotra, off East Africa.

The flowers of the genus *Geranium* show interesting pollination mechanisms (Fig. 1732). In general the larger the flowers the more insect visitors are relied upon and the more probable is cross-pollination. In the

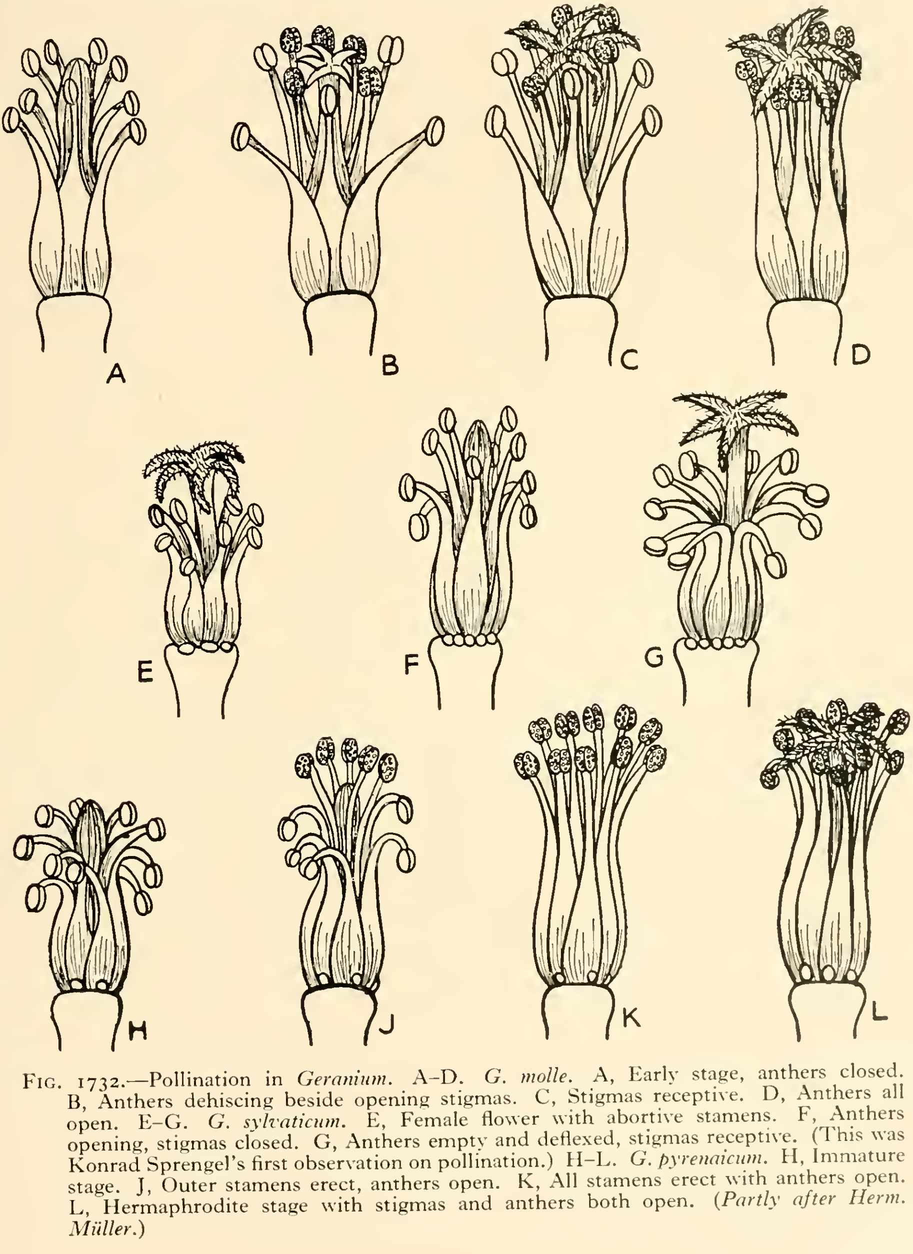


FIG. 1732.—Pollination in *Geranium*. A–D. *G. molle*. A, Early stage, anthers closed. B, Anthers dehiscing beside opening stigmas. C, Stigmas receptive. D, Anthers all open. E–G. *G. sylvaticum*. E, Female flower with abortive stamens. F, Anthers opening, stigmas closed. G, Anthers empty and deflexed, stigmas receptive. (This was Konrad Sprengel's first observation on pollination.) H–L. *G. pyrenaicum*. H, Immature stage. J, Outer stamens erect, anthers open. K, All stamens erect with anthers open. L, Hermaphrodite stage with stigmas and anthers both open. (*Partly after Herm. Müller.*)

small-flowered species self-pollination may become the rule. They all contain nectar, which is secreted from nectaries developed at the base of the stamens. The flowers are mostly protandrous and the greater the prospect of insect visits the more marked is the dichogamy. In addition to the large hermaphrodite flowers there are small female ones developed in some species.

In *Geranium palustre* the flowers are markedly protandrous and the nectar is secreted by glands at the bases of the five inner stamens. Nectar guides are present on the petals, while hairs at their bases prevent raindrops from reaching the nectar. The five inner stamens ripen first and then the five outer ones. Only when all ten have shed their pollen do the stigmas mature for previously they have been tightly closed together, but now they open out and project from the centre of the flower. After dehiscing, the stamens all bend outwards so far that self-pollination is impossible. The condition in *G. pratense* is the same.

In *Geranium pyrenaicum* the nectar is enclosed in glands at the bases of the five outer stamens. These stamens grow up first, overtopping the immature stigmas, and the anthers turn outwards and dehisce. At this stage the five inner stamens curve downwards so that their anthers are well out of the way of visiting insects. A day later the inner stamens grow up and dehisce so that the closed styles are now surrounded by all ten stamens which are liberating ripe pollen. A day or two later the stigmas begin to separate and they open out to lie level with the anthers. Hence if all the pollen has not been removed by insects, self-pollination is now possible, and is as likely as cross-pollination. If on the other hand insect visits have been numerous all the pollen will have already been removed and cross-pollination rendered certain.

In *Geranium molle* the stigmas are, as usual, closely pressed together in the centre of the flower and the anthers closed and arranged outside the stigmas. This condition is followed by the incurving of the outer whorls of stamens, which bend in towards the centre of the flower and lie over the immature stigmas. Even before these anthers have dehisced, however, the stigmas begin to grow up and expand between the stamens so that self-pollination becomes possible. At this stage the inner stamens begin to curve inwards and the anthers dehisce. Hence at this stage an insect visiting the flower touches the anthers and stigmas at the same time and can achieve cross-pollination or self-pollination equally easily.

Finally in *Geranium pusillum* only the five stamens which alternate with the petals bear anthers and are provided with basal nectaries. When the flower opens the stamens are all erect and before the anthers split, the five styles have opened out between them. Hence, at this stage the flower is essentially female, but soon after the anthers split and the stigmas spread out further, so that they are almost inevitably dusted with pollen as it is shed. Finally the anthers bend over till they touch the stigmas. At this stage pollen may be received by a visiting insect, but if the flower was not cross-pollinated before its anthers matured, self-pollination is certain.

This series is interesting because, as the size of the flowers diminishes and they become less likely to receive insect visits, provision is made that, in the event of cross-pollination failing, self-pollination becomes inevitable.

Before leaving the pollination mechanisms in this family we must refer to the peculiar condition found in *Erodium cicutarium*. It has been clearly shown in this species that two distinct kinds of flowers occur, which are associated with two methods of pollination. The first is termed var. *genuinum* and in this the petals are uniformly red and of equal size, though the upper ones are sometimes rather shorter and darker in tint than the lower. The nectaries are developed as in *Geranium*. Although ten stamens are formed, only the five opposite the petals develop anthers. Of these, three are longer and while the anthers dehisce they lie close to the stigmatic branches. Later the two others dehisce similarly so that automatic self-pollination is inevitable. Moreover this process takes place early in the morning, within an hour of the opening of the flowers, and by midday the petals have been shed. Since the variety is self-fertile good viable seeds are formed.

The second variety, which is termed *pimpinellifolium*, is entomophilous. The flowers are larger and the two upper petals are small and broad as compared with the three lower ones, which are elongated to provide a platform for alighting insects. At first the centre of the flower is closed by the stamens, but the nectar is obtainable between the stamens and the two upper petals. Then the three upper and, later, the two lower anthers dehisce, while the stamens curve further and further outwards. At this stage the style is quite short and undeveloped. The day after the anthers have dehisced the styles grow up and expand. Thus, normally, self-pollination is prevented, though occasionally, if cross-pollination is not successful, the stamens may bend inwards making self-pollination possible.

The Geraniums of our gardens have been artificially produced as hybrids of the genus *Pelargonium*. The so-called zonal pelargoniums have been produced by crossing *P. zonale* with *P. inquinans*, while many of the larger-flowered varieties have originated from crosses with *P. grandiflorum*. Some possess specially scented leaves, as for example *P. crispum* which is lemon-scented, *P. tomentosum* which is peppermint-scented and *P. fragans* which has the scent of nutmeg. *P. endlicherianum* is the only species which is hardy in Britain. It is a bushy perennial, growing about 2 ft. high with rose-red flowers.

We may refer briefly here to the small but important order the **Rutales**, which contains the families Rutaceae and Meliaceae. The members of this order are trees, shrubs or climbers, but rarely herbs. The leaves are dotted with glands and may be either simple or compound.

The **Rutaceae** are a small family with about 100 genera and 800 species, which are widely distributed in warm temperate regions. The flowers are regular or occasionally slightly zygomorphic and there are usually either four or five sepals and the same number of petals. The stamens are often double the number of petals and the ovary is composed of four or five carpels with one or two ovules in each loculus.

The most important genus is *Citrus*, which contains ten species distributed throughout the Old World. They are trees or shrubs with simple leaves. Axillary spines derived from a leaf of a branch shoot occur in most species. The calyx and corolla are composed of from four to eight segments (Fig. 1733). The stamens are joined in irregular bundles corresponding in position to the sepals and the gynoecium consists of six or more carpels. The fruit is a large berry, or hesperidium, with a leathery pericarp and the flesh is formed of succulent hairs which grow out from the inner layers of the pericarp.

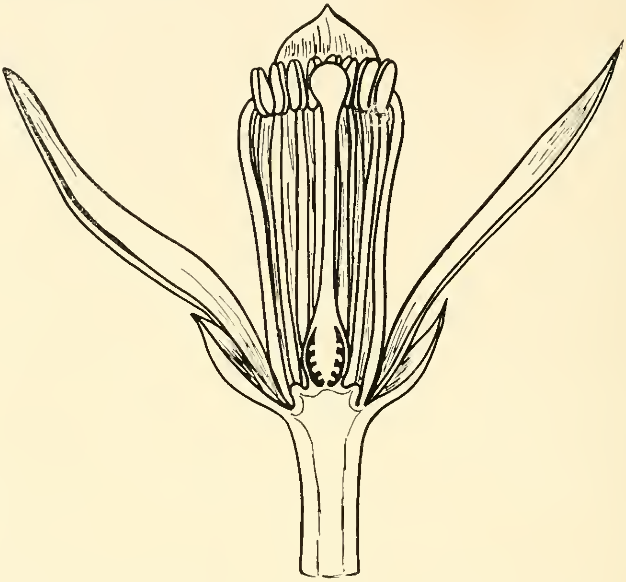


FIG. 1733.—*Citrus medica* var. *limonum*. Lemon. Flower in longitudinal section.

The Citrus fruits form a very important article of commerce. *C. aurantium* is the Orange, which probably originated in northern India and Assam. It has been in cultivation possibly since 1500 B.C. *C. limonum* is the Lemon. That at present in cultivation was derived from a variety collected in Peking in 1908 and is considered far superior to the older forms. *C. medica* is the Citron, and, according to some, the Lemon, the Lime and the Sweet Lime are varieties of it, the last two being botanically var. *acida* and var. *limetta* respectively. *C. decumana* is the Shaddock or Pomelo, while a variety, or possibly a separate species, *C. paradisi*, is the Grapefruit. This important fruit is thought to have originated from a West Indian sport from the Shaddock. The Mandarin Orange is *C. nobilis*, while a number of hybrids are also cultivated. The whole question of the Citrus fruits will be more fully considered in Volume IV.

Fig. 1734.—*Ruta graveolens.* Garden Rue. Flowering shoot.

Among the members of the Rutaceae we may mention *Ruta graveolens* (Rue) (Fig. 1734), a strong-smelling herb with yellow flowers often cultivated in Britain, and *Choisya ternata* (Fig. 1735) which is a common garden shrub.

Fig. 1735.—*Choisya ternata.* Mexican Orange Blossom. Flowering shoot.

The **Meliaceae** are an exclusively tropical family, notable mainly for their timber. The family includes forty genera and 600 species. *Swietenia mahogani*, a native of the West Indies and Central America, is the original source of Mahogany. African Mahogany is obtained from *Khaya senegalensis*. *Cedrela odorata*, also a West Indian tree, provides the Cedar wood of commerce, while *Melia azedarach* is also an important timber tree.

EUPHORBIALES

The Euphorbiales are Archichlamydeae in which the flowers are usually dioecious and hypogynous. They are generally actinomorphic, consisting of a single whorl of free perianth leaves or occasionally the flowers may be naked. The stamens are inserted opposite the perianth segments when present, and are generally equal in number to them. Pollination is anemophilous. The ovary consists of three carpels, which unite to form three loculi, the placentation is axile, each loculus containing one or two pendulous, anatropous ovules, each possessing a ventral raphe. The growth of the pollen tube is endotrophic.

The classification varies considerably according to the views of various authorities. According to Hutchinson, who is responsible for the name Euphorbiales, it embraces the single family Euphorbiaceae. According to Wettstein and Rendle the Euphorbiaceae are included in the Tricocceae which also include, according to Wettstein, the Buxaceae, and according to Rendle the Buxaceae and the Callitrichaceae. Engler on the other hand includes the Euphorbiaceae in his Geraniales, in the sub-order Tricocceae, and the Callitrichaceae in the sub-order Callitrichineae. He places the Buxaceae in the Sapindales. Hutchinson separated the Euphorbiaceae sharply from the other two families, referring the Buxaceae to the Hamamelidales, a separate order made by him for certain of the Rosales (see p. 1646), and puts the Callitrichaceae in the Lythrales, an order separated from the older Myrtiflorae.

Since we are only concerned here with the Euphorbiaceae, and since that family is so distinct from the Geraniales, it seems best to follow Hutchinson and use the order Euphorbiales as a monotypic one. The Buxaceae and the Callitrichaceae have already been referred to. (See p. 1809 and p. 1773.)

Euphorbiaceae

The family is essentially a cosmopolitan one though a number of small herbaceous types occur in Britain. There are two British genera: *Euphorbia* with some sixteen species, and *Mercurialis*, which is only represented by two species. Among the more common members we may mention *Euphorbia helioscopia* (Fig. 1736), the Sun Spurge; *E. paralias*, the Sea Spurge; *E. peplus*, the Petty Spurge; *E. peplis*, the Purple Spurge; and *E. amygdaloides*, the Wood Spurge. *Mercurialis perennis* is the Dog's or Herb Mercury.

The **plants** vary very greatly in form and size and we should gain a very wrong impression of the family merely from a study of the British representatives. The latter are mostly small herbs, rarely growing above a

FIG. 1736.—*Euphorbia helioscopia.* Sun Spurge. Group of cyathia seen from above.

couple of feet. In other parts of the world, however, Euphorbias may grow into small trees or bushes, while in desert regions in Africa and elsewhere they form large cactus-like plants, many feet in height, with thick fleshy stems and leaves reduced to spines. In Australia many heath-like Euphorbias are quite common. Species of the genus *Tragia* are tropical climbers while the genus *Phyllanthus* contains plants ranging from large trees to annual herbs.

The form and position of the leaves are very variable. In many they are reduced to spines, in some they are replaced by cladodes. Where the leaves are normal they may be arranged either oppositely or alternately and vary very greatly in shape.

Nearly all the members of the family possess large laticiferous vessels.

The **inflorescence** may be racemose or cymose and is often complex in form. The peculiar but very characteristic inflorescence of *Euphorbia* is termed a **cyathium** (Fig. 1737) which is modified from a cyme and simulates a simple flower, the bracts being arranged like a perianth.

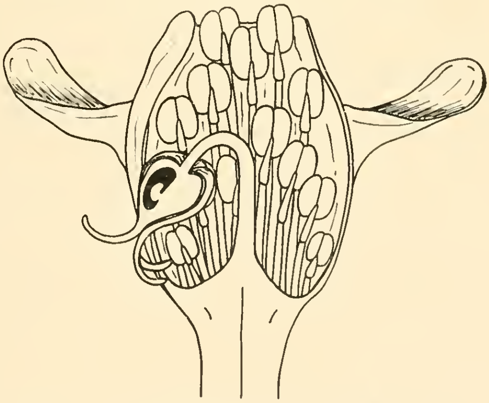


FIG. 1737.—Cyathium of *Euphorbia* in longitudinal section.

The **flowers** (Fig. 1738) are dioecious or monoecious and generally much reduced. For example in *Euphorbia* the male flowers consist of a single stamen. Occasionally, as in the genus *Croton*, both calyx and corolla are present but more often one or both are wanting.

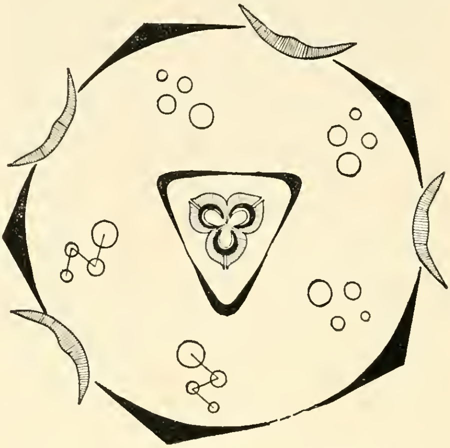


Fig. 1738.—Floral diagram of *Euphorbia peplus* (cyathium). (*After Eichler.*)

The **androecium** varies in number of parts from one to many. Frequently they may be equal in number to the perianth segments.

The **gynoecium** is usually tricarpellary and syncarpous. The ovary is trilocular and superior. There are one or two pendulous, anatropous ovules in each loculus.

The **fruit** is a schizocarp, often breaking violently and dehiscing into one-seeded cocci.

The **seed** is endospermic and frequently has a caruncle developed from the micropyle. The cotyledons either lie flat in the endosperm or are bent or folded. The relative breadth of the cotyledons is used as a character in classification within the family.

The family is a large one with about 220 genera and some 4,000 species. It is world-wide in distribution. The chief centre is in Indo-Malaya but, with the exception of the Arctic, members of the family occur almost everywhere. Their ubiquity, coupled with their very great variety of form, makes them a very interesting family systematically, moreover many are of great economic importance. There are no anatomical features which are characteristic of the whole order but a laticiferous system is found in the majority and is of great economic importance. The following is an outline of the classification of the family according to Pax.

A. PLATYLOBEAE

Cotyledons much broader than the radicle.

I. Phyllanthoideae

There are two ovules in each loculus. Laticiferous tissue and internal phloem are absent.

1. *Phyllantheae.* The embryo is large, little shorter than the endosperm. In the male flower the calyx is imbricated. *Phyllanthus, Wielandia, Petalodiscus, Hymenocardia, Bischofia, Toxicodendrum, Aporosa, Baccaurea.*
2. *Bridelieae.* The embryo is large, little shorter than the endosperm. In the male flower the calyx is valvate. *Bridelia.*
3. *Daphniphylleae.* The embryo is short, about one-quarter as long as the endosperm. *Daphniphyllum.*

II. Crotonoideae

There is one ovule in each loculus. Laticiferous tissue and internal phloem are usually present.

1. *Crotoneae.* The stamens are bent sharply inwards in the bud. The calyx of the male flower imbricate or valvate, corolla generally present. *Croton.*
2. *Acalypheae.* The stamens are erect in the bud, the calyx of the male flowers valvate, and the inflorescence racemose, axillary or terminal. *Mercurialis, Argithamnia, Acalypha, Mallotus, Ricinus, Alchornea, Macaranga, Pera, Dalechampia, Caperonia* and *Tragia.*
3. *Jatropheae.* The stamens are erect in the bud, the calyx of the male flower valvate or almost imbricated. These flowers may or may not have a corolla. The inflorescence is a dichasium. *Hevea, Jatropha, Aleurites.*
4. *Manihoteae.* The stamens are erect in the bud, the calyx of the male flowers is usually valvate and the inflorescence is racemose, being either a terminal spike or a raceme. *Manihot.*
5. *Cluytieae.* The stamens are erect in the bud, the calyx of the male flowers is imbricated and they possess a corolla. The inflorescence is cymose. *Codiaeum, Cluytia.*
6. *Gelonieae.* The stamens are erect in the bud, the calyx of the male flowers is imbricated, the flowers are apetalous and the laticiferous tissue is segmented. *Gelonium.*
7. *Hippomaneae.* The stamens are erect in the bud, the calyx of the male flowers is imbricated, the flowers are apetalous, but the laticiferous tissue is not segmented. *Stillingia, Hura, Hippomane, Sapium, Mabea.*
8. *Euphorbieae.* The inflorescence is a cyathium. *Euphorbia, Anthostema, Synadenium.*

B. STENOLOBEAE

Cotyledons as broad as the radicle.

I. Porantheroideae

There are always two ovules in the loculus. *Poranthera.*

II. Ricinocarpoideae

There is only one ovule in each loculus. *Ricinocarpus, Dysopsis.*

It is impossible in so large a family to consider in any degree of detail all the various types of information available. Many of the genera are of interest on account of their floral structure, others show abnormal anatomical peculiarities, while many are of economic importance. From this plethora of material we can only pick out some of the more striking features.

In the Phyllanthoideae are included the greater proportion of the species, and it is them which we must chiefly consider. The tribe Phyllantheae includes a considerable number of genera, which possess cladodes, a feature which makes them popular greenhouse plants in this country. Some are quite small annuals, while others grow into trees.

FIG. 1739.—*Phyllanthus pulcher*. Habit showing branches of limited growth which have the aspect of compound leaves but bear flowers.

FIG. 1740.—*Phyllanthus montanus* (*xylophylla*). Cladodes with marginal nodes, some bearing fruits.

The genus *Phyllanthus* (Figs. 1739 and 1740) is a large one containing some 500 species which are found both in temperate and tropical regions. *P. cyclanthera* is interesting because the filaments and also the anthers are united into a ring, as in the genus *Cyclanthera* which belongs to the Cucurbitaceae. *P. pulchra* and *P. glaucescens* are frequently found cultivated in collectors' greenhouses.

In *Wielandia*, which is a monotypic genus found in the Seychelle Islands, the flowers are pentamerous, the two outer whorls forming a calyx and corolla. These are followed in the male flowers by a whorl of five stamens, while in the female flowers there are five carpels. The genus *Petalodiscus* is represented by five species, all occurring in Madagascar. *Bischofia* is a monotypic genus found in Polynesia. The bark is used medicinally. Other large genera included are *Antidesma*, with 150 palaeotropical species, and *Baccaurea* with sixty species occurring in Africa, Asia and Polynesia.

In the Crotonoideae, the single genus *Croton* is important. It is a large tropical genus containing about 600 species. A pentamerous calyx and corolla are present though the latter may be absent from the female flowers. The stamens are very numerous, some species having as many as a hundred. The females normally have three carpels.

C. tiglium, found in Asia, is the source of Croton Oil which is expressed from the seeds. It is used as a powerful purgative drug. *C. cascarilla* and *C. eleuthera* are the source of Cascarilla Bark which is used as a tonic. They are cultivated in the West Indies. *C. lacciferus*, which grows in India and Ceylon, yields a lac which is used in high-class varnishes. Several of the Brazilian species provide Dragon's Blood resin. In the large tribe Acalypheae are a number of important genera. It includes the two British genera *Euphorbia* and *Mercurialis* (Fig. 1741) and also many tropical genera. *Euphorbia* itself is a genus of some 750 species. Though the British species show a considerable family resemblance to one another, the same can scarcely be said of those from warmer climates. Many of them live under dry conditions and are succulent in character and devoid of leaves. Under such conditions therefore they resemble very closely some of the Cacti. Many are armed with thorns, and in general it is the stem which becomes fleshy. Laticiferous tissue is present and the succulent *Euphorbia splendens* (Fig. 1742) is often used botanically to illustrate this structure on account of the thick-walled tubes with dumb-bell shaped starch grains which it

FIG. 1741.—*Mercurialis perennis.* Left, flowers on female plant. Right, male plant.

contains. *Euphorbia pulcherrima* is the Poinsettia so frequently grown in greenhouses for the sake of its large scarlet bracts.

FIG. 1742.—*Euphorbia splendens.* Apex of one of the succulent stems with an inflorescence.

The pollination mechanism employed in the genus is worthy of note. The inflorescence, which behaves in pollination like a single flower, is strongly protogynous. The three bilobed stigmas emerge first from the involucre and may be dusted with pollen if the flower is visited by an insect. Later, when the ovary on its long, curved pedicel has grown out and hangs down below the involucre, the stamens gradually elongate one after another, and come to occupy the place where the ovary formerly was situated. Pollination is generally effected by flies, though wasps and beetles visit the flowers occasionally. They are attracted by glands situated on the involucre which secrete nectar in a completely exposed layer. Apparently the inconspicuous nature of the flowers keeps away bees, but where large masses of flowers are found together, bee visits do sometimes occur.

Among the genera not found wild in Britain the most familiar is *Ricinus.* The genus is monotypic. *R. communis* is a shrub in the tropics but when found in Europe it is herbaceous. The plants (Fig. 1743) are monoecious and the androecium is peculiar, for the stamens are branched, treelike structures, with the anthers borne on short terminal branchlets. The fruit explodes, when ripe, into the separate carpels, which at the same time open and drop the seeds. These seeds possess a caruncle and contain a large quantity of oily endosperm which is used medicinally as the source of Castor Oil. It is also employed as a lubricant. The plant is a native of Africa but on account of its economic use it is widely cultivated. It is grown under glass in this country on account of its highly decorative foliage. The genus *Acalypha* is notable for having stamens with long appendages. It is a large tropical and subtropical genus with some 400 species.

FIG. 1743.—*Ricinus communis.* Castor Oil Plant. Left, male flower with branched stamens. Right, female flower. (*After Baillon.*)

Mallotus phillipinensis, which is found from Ceylon to Australia, is of economic importance because Kamala dye is obtained from the capsules. The genus is a large one containing some 120 species and is widely distributed in the tropics. Another interesting member of this group is *Alchornea ilicifolia* of which only female plants are in cultivation. These however produce viable seeds due to the formation of embryos from buds produced from the nucellus around the embryo sac. *Macaranga caladifolia* is peculiar in that the hollow peduncles are inhabited by ants.

Mention must also be made of *Dalechampia roezliana* which is extensively cultivated. It has a very complex inflorescence, the whole of which is enclosed in two large outer bracts which are coloured white or pink. On the axis above them is a smaller bract in the axil of which is a three-flowered cyme of female flowers. Above this is the male inflorescence which starts with four bracts, above which are about a dozen male flowers and posterior to them a yellow cushion of rudimentary flowers which may secrete a resin. In Brazil this resin is used by bees to make their nests for which reason bees regularly visit the flowers.

In the tribe Jatropheae is included the very important genus *Hevea*, which contains some twenty American species. The most important of these is *H. brasiliensis* (Fig. 1744), the source of the best Para rubber, which is largely exported from the Amazon valley. Towards the end of the last century seedlings were introduced into Ceylon and from there to Malaya, thus gradually diverting the rubber industry to that part of the world. The tree is a large one, usually with a long straight trunk from which the latex is obtained by tapping. We shall refer in detail to the process of extracting this latex in Volume IV. Several other genera of the Euphorbiaceae yield caoutchouc from which rubber can be prepared and we may mention *Mabea*, *Manihot* and *Sapium*, but in none is the yield so large or the rubber as good as that obtained from *Hevea brasiliensis*.

FIG. 1744.—*Hevea brasiliensis*. Rubber plantation in Ceylon. Photograph supplied by courtesy of the Imperial Institute.

The genus *Jatropha* deserves mention. There are about 200 tropical and subtropical species. *J. podagrica* is a xerophyte with a swollen stem which consists mainly of water-storage tissue. Other species are widely cultivated as ornamental plants while *J. curas* is the Physic nut. *Aleurites moluccana* and *Sapium sebiferum* yield oils and fats.

Another genus of great importance is *Manihot* (Fig. 1745). There are about 150 species, occurring from Mexico to South America. They are either shrubs or herbs. *M. palmata* is the Sweet Cassava or Mandioc and *M. utilissima* (Fig. 1746) is the Bitter Cassava. Both are extensively cultivated in the tropics on account of the valuable starchy food (arrowroot and tapioca) obtained from the large tuberous roots. We shall refer to their preparation in Volume IV.

M. glaziovii provides the Ceara rubber of commerce which is obtained by tapping in a manner similar to that employed for Para rubber.

Codiaeum variegatum is the source of the " Crotons " so often cultivated in greenhouses on account of their magnificent foliage. Other species are employed for making hedges in the tropics.

From the above rather long account of the family it will be seen that not only is it represented by many large genera, but that many and varied are the uses made of them by man. The chief centre of geographical distribu-

FIG. 1745.—*Manihot utilissima.* Habit of the plant. (*After Engler-Prantl.*)

tion of the family is clearly the Indo-Malayan region, but, in addition, a number of New World genera occur, particularly in Brazil. Members of the Stenolobeae are found in Australia, with the exception of the monotypic genus *Dysopsis*, which occurs in the Andes and on the island of Juan Fernandez.

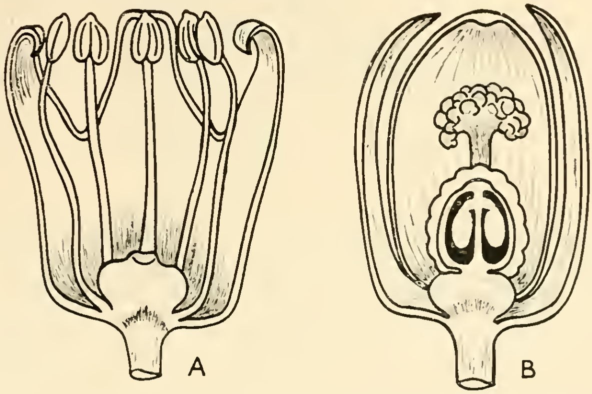


FIG. 1746.—*Manihot.* Flowers in longitudinal section. Left, male. Right, female. (*After Tussac.*)

It is perhaps not inappropriate to refer briefly here to another order, the **Juglandales**. Its systematic position is far from clear. According to Hutchinson it may have had its ancestry in the Sapindales. On the other hand Engler and Rendle include it among the apetalous families, placing it near the Garryales. According to Rendle the order includes two families, the Myricaceae and the Juglandaceae. Engler on the other hand separates the Myricaceae in a distinct order, the Myricales. It is certainly true that the Myricaceae show considerable affinities with the Salicales and Garryales on the one hand and with the Fagales on the other. Hutchinson considers that these families may represent reduced forms which originated from the Rosales through the Hamamelidaceae. While the question is a very obscure one and outside the scope of this book we have referred briefly to the Myricales under the Salicales (see p. 1756). Hence in this treatment the Juglandales will be regarded as possessing only a single family Juglandaceae.

In the **Juglandaceae** the flowers are monoecious. The male inflorescence consists of a many-flowered catkin, each flower being borne in the axil of a bract and composed of a perianth of scale leaves and from three to forty stamens. In the female flower (Fig. 1747) the bract and bracteoles are fused to the inferior ovary, as are also some four rudimentary perianth leaves. The ovary consists of two carpels with a pair of large stigmas. The fruit is a nut or drupe with a thin epicarp and fleshy mesocarp; the endocarp is hard and may give rise to either two or four incomplete septa.

Fig. 1747.—*Juglans regia.* Female flowers.

There are six genera and about forty species in the family. They are trees usually with large compound leaves and are found in the warmer parts of the north temperate regions. There is evidence that in Cretaceous times the family extended as far north as Greenland.

The most important members are the Walnuts; *Juglans regia* is the Common Walnut while *J. nigra* is the Black Walnut. Species of the genus *Carya* provide the Hickory or Pecan nuts of commerce.

UMBELLIFLORAE

The Umbelliflorae are Archichlamydeae in which the flowers are hermaphrodite, polypetalous and epigynous. They are tetramerous or pentamerous, with one series of stamens, and the gynoecium is inferior, composed of two carpels. There is a single ovule in each loculus which is anatropous and pendulous, possessing a single integument and an outwardly directed micropyle. The seed is endospermic and the embryo small.

The plants are mostly herbaceous, though a few are woody and the leaves are often compound and much divided. The flowers are usually small and are arranged in umbels. Oil or resin canals are often present.

This order is characterized by a simplification of the structure of the flower and is sharply defined. It contains only three families, Araliaceae, Umbelliferae and Cornaceae. We shall consider the Umbelliferae in detail but will first indicate certain points of interest in the other two families.

The **Araliaceae** are a small family, containing about fifty-five genera and some 700 species, which are chiefly tropical, with their centres of distribution in Indo-Malaya and tropical America. The plants are usually trees or shrubs; many are climbers. The leaves are usually alternate, often large and compound, with small stipules. The flowers are small but are developed in large compound umbels. Each flower has four very small sepals, five petals and stamens and the gynoecium consists of five carpels forming a quinquelocular ovary, each loculus having a single, pendulous ovule. The fruit is a drupe.

The most important genus is *Hedera*, with six temperate species; *H. helix* (Ivy) is a root climber with dimorphic leaves, those on the vegetative shoots being palmate and those on the flowering shoots being simple. The flowers (Fig. 1748) are not conspicuous but develop late in the year and are pollinated by flies and hive bees. It is a native of Europe

FIG. 1748.—*Hedera helix*. Ivy. Flowering shoot with unlobed leaves.

and Asia Minor. Many cultivated varieties are commonly grown in Britain. *Fatsia japonica* (Fig. 1749) is a favourite room-plant with large palmate leaves.

FIG. 1749.—*Fatsia japonica.* (Commonly called *Aralia sieboldii.*) Flowering shoot.

Tetrapanax papyrifera, a native of Formosa, is of economic importance for the Chinese prepare thin " rice paper " from the pith. *Aralia quinquefolia* is also important, for the Chinese obtain their famous aphrodisiac, ginseng, from its roots. *A. nudicaulis* is the Virginian Sarsaparilla.

The **Cornaceae** are a little family with only 100 species separated into fifteen genera. They are mostly shrubs, growing in temperate regions or on tropical mountains. The flowers are either tetramerous or pentamerous and closely similar to those of the Araliaceae. The fruit is a drupe or occasionally a berry, as in *Aucuba*.

The most important genus is *Cornus*, which contains about sixty species. Two occur wild in Britain, they are *C. sanguinea* (Dogwood) and *C. suecica*, a small perennial herb of the Scottish Highlands. Several other species are of economic importance; *C. mas* (Cornelian Cherry) (Fig. 1750), which is wild in Europe and Asia Minor, produces fruits which make a good jam, while *C. florida*, a North American tree, is valuable for its timber.

Species of the genus *Aucuba* are well-known garden shrubs. *A. japonica*, sometimes called the Japanese Laurel, is a dioecious evergreen shrub with large, often spotted leaves and was a characteristic plant of Victorian shrubberies. The genus *Griselinia* contains eight species in New Zealand and South America. Several are cultivated in gardens.

FIG. 1750.—*Cornus mas.* Cornelian Cherry. Inflorescences in early spring.

Davidia involucrata (Fig. 1751) is a small tree up to 30 ft. in height which was introduced towards the end of the last century into this country from China. The leaves are cordate and the small flowers are produced in tightly packed, globular heads, which are surrounded by two large, leafy, white bracts, sometimes 6 in. in length. Because of these bracts the tree in full flower appears as if covered with giant butterflies.

FIG. 1751.—*Davidia involucrata.* Handkerchief Tree. Inflorescence with large white bracts.

Umbelliferae (Daucaceae)

This is a very large and important family which is easily recognized by the form of the inflorescence and the shape of the fruit. Many are of economic importance and others are cultivated on account of their floral beauty. Many are common British weeds.

Among the well-known species we may mention *Daucus carota* (Wild Carrot), from which the various forms of cultivated carrots have been produced; *Carum petroselinum* (Parsley), *Carum carvi* (Caraway), and *Conium maculatum* (Hemlock). Other common types are *Apium graveolens* (Wild Celery), *Oenanthe fistulosa* (Water Dropwort), *Crithmum maritimum* (Samphire), *Aethusa cynapium* (Fool's Parsley), *Heracleum sphondylium* (Cow Parsley), *Myrrhis odorata* (Sweet Cicely), *Conopodium denudatum* (Earthnut), *Anthriscus sylvestris* (Hedge Parsley) and *Caucalis anthriscus* (Chervil). Other less common members of the family are *Hydrocotyle vulgaris* (Marsh Pennywort), which occurs in wet places; *Eryngium maritimum* (Sea Holly), which is found on sand and shingle, and *Sanicula europaea* (Wood Sanicle), which lives in calcareous woods.

The **plants** are mostly herbs or occasionally shrubs, with green fistular stems which are often ribbed and angled. The leaves are alternate, amplexicaul and often much divided.

The **inflorescence** (Fig. 1752) is either an umbel or a compound umbel. These compound umbels are sometimes cymose in character and a terminal flower may occur, as in *Daucus carota*. Occasionally, as in *Eryngium*, the inflorescence may be a cymose head.

Fig. 1752.—*Heracleum sphondylium*. Hogweed. Compound umbel seen from above.

The **flowers** (Fig. 1753) are usually hermaphrodite and regular, but unisexual flowers may be found in some inflorescences and the outer flowers of the umbel are often irregular and zygomorphic.

The **calyx** is small and consists of five minute sepals, the odd sepal being posterior. In many the calyx is absent.

The **corolla** (Fig. 1754) is polypetalous, with five petals which are usually white or yellow in colour. They may vary in size, two being longer than the other three. The tips are often reflexed.

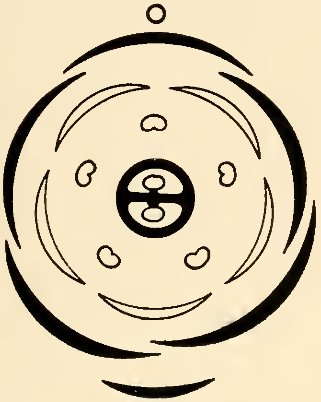


FIG. 1753.—Floral diagram of *Eryngium*. Umbelliferae. (*After Eichler.*)

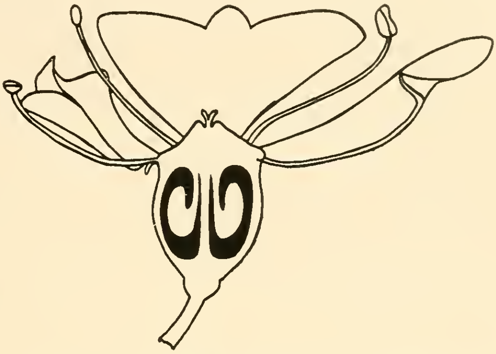


FIG. 1754.—*Heracleum*. Flower in longitudinal section.

The **androecium** is composed of five stamens and the anthers are introrse. The pollen grains are ellipsoidal with three equatorial stoppers over pores through which pollen tubes may emerge.

The **gynoecium** is bicarpellary and syncarpous. The ovary is bilocular

FIG. 1755.—*Foeniculum vulgare*. Fennel. Transverse section of the cremocarp fruit.

with one pendulous, anatropous ovule in each loculus. On top of the ovary is a nectar disc surrounding the two stigmas.

The **fruit** (Fig. 1755) is a cremocarp. The ovary splits into two mericarps which remain temporarily attached to the top of the axial prolongation, or carpophore, between them. Each mericarp is usually marked by five longitudinal ridges or **costae**, which contain the vascular bundles, and between the costae are furrows or **valleculae** under which lie special oil ducts or **vittae**. Secondary costae and vittae may occur between the primary ones.

The **seed** is endospermic, the reserve consisting mainly of oil and protein. The embryo is minute.

The family contains about 200 genera with about 2,700 species which are distributed throughout the north temperate regions. Many are found in Britain. The family exhibits certain anatomical features which are worthy of mention. The most important is the occurrence of schizogenous resin canals similar to those in the Araliaceae. Collenchymatous strands are found in the primary cortex corresponding to the ribs of the stem. The pith is absent except at the nodes. Cork formation, where it occurs, is usually superficial. Branched hairs of various forms occur in many genera.

The classification of the family is fairly complex, due to the number of genera, while the generic distinguishing characters are small owing to the uniformity of the family.

I. **Hydrocotyloideae**

Fruits with woody endocarp and no free carpophore. Vittae absent or in the main ribs only.

1. *Hydrocotyleae.* Fruits laterally flattened, with narrow surface of union. *Hydrocotyle*, *Azorella.*
2. *Mulineae.* Fruit with flattened or rounded beak. Found in the southern hemisphere only. *Bowlesia*, *Mulinum.*

II. **Saniculoideae**

Endocarp soft, epicarp rarely smooth. Style long, with capitulate stigma, surrounded by a ring-like disc.

1. *Saniculeae.* Ovary bilocular, fruit two-seeded with a broad surface of union. Vittae well marked. *Eryngium*, *Astrantia*, *Sanicula.*
2. *Lagoecieae.* Ovary unilocular and fruit one-seeded. Vittae indistinct. *Lagoecia*, *Arctopus.*

III. **Apioideae**

Endocarp either soft or hardened by a subepidermal fibrous layer. Style situated on the apex of a disc.

A. Primary ridges of the fruit projecting, the lateral ones sometimes wing-like. Secondary costae absent.

1. *Echinophoreae.* Secondary umbels with several female flowers surrounded by male ones. Fruit enclosed by the hardened stalks of the male flowers. *Echinophora.*

2. *Scandicineae.* Flowers all generally hermaphrodite, seeds at the surface of union deeply forked or hollow. Crystal layer present in the parenchyma around the carpophore. *Chaerophyllum, Anthriscus, Scandix, Torilis, Myrrhis.*
3. *Coriandreae.* Flowers generally all hermaphrodite, seeds at the surface of union deeply forked or hollow. Crystal layer absent. Fruit nutlike with woody epidermal layer. *Coriandrum.*
4. *Smyrnieae.* Flowers generally all hermaphrodite, seeds with a narrow surface of union and mericarp rounded outwards. *Smyrnium, Conium.*
5. *Ammineae.* Flowers generally all hermaphrodite, seeds flattened at surface of union, primary costae all alike, seeds semi-circular in section. *Bupleurum, Apium, Petroselinum, Aciphylla, Carum, Cicuta, Pimpinella, Seseli, Foeniculum, Oenanthe, Ligusticum, Aethusa.*
6. *Peucedaneae.* Flowers usually hermaphrodite. Seeds narrow in section flattened at surface of union, lateral costae much broader and often forming wings. *Angelica, Ferula, Heracleum, Peucedanum, Dorema, Pastinaca.*

B. Lateral costae equal to or larger than the primary ones. Vittae in furrows or on secondary well-marked costae.

7. *Laserpitieae.* Secondary costae often expanded into broad, undivided or wavy wings. *Laserpitium, Thapsia.*
8. *Dauceae.* All costae provided with spines. *Daucus.*

The Hydrocotyloideae are a relatively small sub-family of which the genus *Hydrocotyle* is the most important. There are seventy-five species, cosmopolitan but mainly restricted to the southern hemisphere. *H. vulgaris* occurs in Britain and is widely distributed in Europe, western

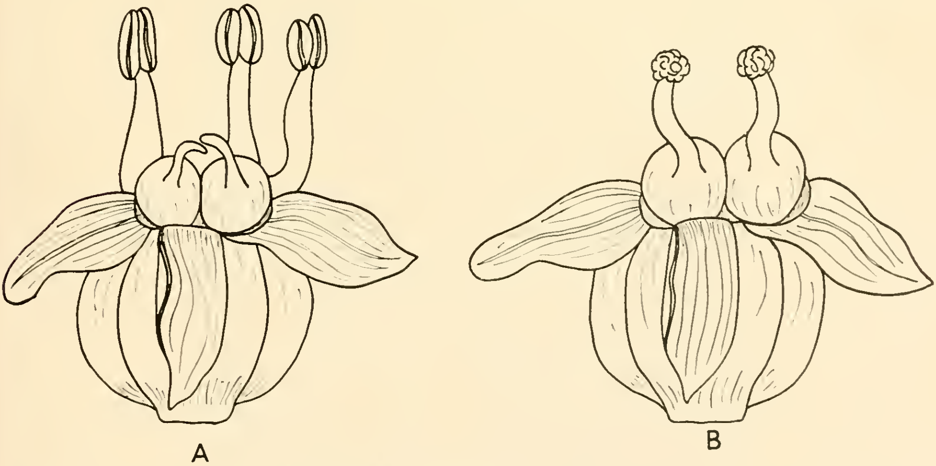


FIG. 1756.—*Hydrocotyle vulgaris.* Marsh Pennywort. Pollination. Left, early, staminal stage. Right, later female stage. (*After Knuth.*)

Asia and North Africa. The inflorescence is much reduced and may consist of only a single flower. The leaves are simple and peltate. *Azorella* contains about seventy species of cushion-like plants, found only in the southern hemisphere.

The pollination of *Hydrocotyle vulgaris* (Fig. 1756) is apparently by minute flies. The flowers are extremely inconspicuous and self-pollination often takes place. The anthers dehisce first in slow succession and the stigma matures before the last anther has discharged its pollen. In fact, it automatically comes into contact with the last stamen, so that, unless cross-pollination has occurred before, self-pollination is automatic. The nectar is completely exposed.

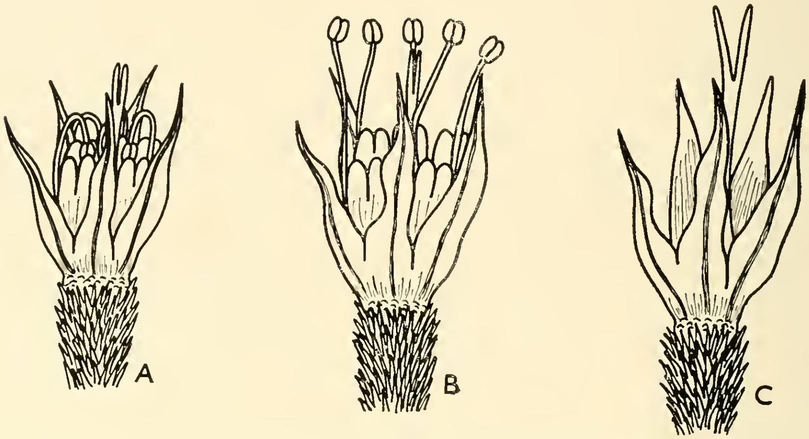


FIG. 1757.—*Eryngium.* Pollination. Stamens developed first, then dropped. In C the stigmas expanding. (*After Knuth.*)

In the Saniculoideae the best-known genus is *Eryngium*, (Fig. 1757), with 220 species in temperate and subtropical regions. The flowers are blue and are visited by bees. The inflorescence is surrounded by a spiny involucre which prevents soft-bodied animals reaching the nectar by climbing up the flowers (Fig. 1758). The stamen filaments are incurved in the bud so that the anthers are enclosed in the corolla which is itself long and stiff. Meanwhile the ten-rayed disc begins to secrete nectar. First the anthers uncurl and project beyond the corolla and then the tips of the petals also uncurl so that only long-tongued insects can force their way to the nectar and in the process they become dusted with pollen.

After the anthers have shed their pollen and dropped off, the style elongates and the stigmatic branches diverge beyond the petals so that they are in a suitable position to be pollinated by a visiting insect.

Eryngium pandanifolium is of economic importance, for the leaves yield Caraguata fibre. It belongs to a group of species in which the foliage is reduced to a radical cluster of long phyllodes with toothed margins. Their linear form and parallel venation give to the plants the aspect of Monocotyledons.

Fig. 1758.—*Eryngium oliverianum.* Inflorescence with large spiny bracts.

Fig. 1759.—*Astrantia major.* Umbels of flowers with pink bracts.

The genus *Sanicula* contains some forty cosmopolitan species though none is found in Australia. The flowers are formed in cymose umbels and the fruits are hooked, being adapted for animal distribution. The sepals are better developed in this genus than in most and are slightly imbricated.

In the genus *Astrantia* (Fig. 1759) the simple umbel is enveloped in large, coloured involucral bracts, which increases greatly the attractive appearance of the inflorescence.

The third sub-family, the Apioideae, is by far the largest, containing many common herbs, some of which have already been mentioned. It is impossible to consider even all the common genera here. We may note a few which are of economic importance. *Apium graveolens* has been cultivated and improved to provide the common vegetable Celery. *Daucus carota* is the wild plant from which all the long- and stump-rooted carrots have been derived. Both the above occur wild in Europe and western Asia. *Pastinaca sativa*, also native of Europe and Asia, has given us the Parsnip. All these are naturally biennials, producing their storage roots and radical leaves in the first year and developing their flowering spikes at the expense of reserve food stores in the second year. The seeds of various species are also used, chiefly in cooking. Caraway seeds come from *Carum carvi*; Dill seeds from *Peucedanum graveolens*; Coriander seeds from *Coriandrum sativum*; and Anise from *Pimpinella anisum*. Fennel, which is used in flavouring soups, is obtained from the leaves of *Foeniculum capillaceum*; while Gum Ammoniacum is a resin obtained by puncturing the stem of *Dorema ammoniacum*. *Conium maculatum*, which is found wild in Britain, is the source of the alkaloid drug coniine, which is derived from the seeds. It has been known from early times as Hemlock.

The pollination mechanisms exhibited by members of the family as a whole fall into a number of distinct types, most of which are found in the sub-family Apioideae.

1. Flowers almost homogamous

This type we have already referred to, since it is best illustrated by *Hydrocotyle vulgaris*.

2. Strongly marked protandrous dichogamy

This is probably by far the most common in the family. The inflorescences rather than the individual flowers attract insects, which attraction is enhanced by an ethereal secretion which is noticeable to the insect. The nectar is completely exposed, and is secreted on a disc in the centre of the wide-open flower and is therefore accessible to quite small flies. The stamens develop first and the anthers have discharged all their pollen well before the flowers of the same umbel have spread their styles and developed their stigmas. Thus self-pollination is entirely excluded.

3. Andromonoecism

In this type both male and hermaphrodite flowers are present, and the male flowers often have longer stalks than the hermaphrodite ones. This type is well illustrated by *Torilis*, *Astrantia*, *Anthriscus* and *Scandix*.

A somewhat special arrangement is seen in *Chaerophyllum aromaticum* and was described by Kerner as **geitonogamy** (Fig. 1760). In this species each umbel contains one central and three to five marginal, hermaphrodite flowers, while the intervening space is occupied by about twenty pseudo-hermaphrodite ones. The hermaphrodite flowers develop first and their anthers have fallen and their stigmas matured before dehiscence in the pseudo-hermaphrodite flowers occurs. As the pollen is shed from these latter flowers it may fall on the stigmas of the now female flowers and ensure cross-pollination.

Fig. 1760.—*Chaerophyllum aromaticum.* A, Hermaphrodite flowers open, male flowers still closed. B, Male flowers open and dropping pollen on the stigmas of the hermaphrodite flowers, which have lost their stamens. (*After Kerner and Oliver.*)

4. Monoecism

In this type, which is illustrated by the southern European genus *Echinophora*, a single female flower is surrounded by a number of male ones. As already mentioned the spiny stalks of these male flowers later enclose the fruit.

5. Dioecism

This simple condition is exhibited only by two genera, *Aciphylla* with twenty-five species in Australia and New Zealand and *Arctopus* with three species in South Africa.

6. Trimonoecism

This is illustrated by *Ferula*, where the main umbel and its primary branches all bear flowers with rudimentary stamens, but the anthers produce a few viable pollen grains. The styles are fertile. Later, male flowers with functional anthers and normal stamens develop in lateral umbels.

In general, therefore, it may be said that, while cross-pollination is the rule in the family, it is achieved more by the way in which the flowers develop than in any specialization to particular visitors. Thanks to the production of large numbers of flowers and plenty of nectar all kinds of insects visit the flowers, and such flowers as the Carrot are probably visited by a larger range of insect life than almost any other species. Apart from its unique pollination mechanism, the genus *Ferula* is worthy of special mention. There are some sixty species occurring in southern Europe and central Asia. *F. communis* (Grain Fennel) only flowers after storing up material for a number of years. *F. narthex* and *F. asafoetida* are the source of the drug asafoetida, which is obtained by notching the roots. In Persia it is used under the name of " food of the gods" as a condiment and also as a stimulant. *F. rubricaulis* is the source of Gum Galbanum which has medicinal properties.

CHAPTER XXIX

THE DICOTYLEDONES: METACHLAMYDEAE

The Metachlamydeae or Sympetalae are distinguished from the Archichlamydeae by the more or less complete fusion of the petals to form a tubular corolla. This is achieved either by the lateral union of the petals or by the development of their common base, by which the stamens are usually also elevated on the side of the corolla tube. There seems little doubt that the development of this tubular corolla results in a very close interplay between insect pollinators and the plant. A tubular corolla with nectar secreted only at its base prevents access to the nectar to all but long-tongued insects, while at the same time it serves to protect the pollen from rain, and confines the anthers to a position suitable for pollination when occasion occurs. Though fundamentally the tubular corolla has apparently originated similarly in all the families, in the more advanced members it has become secondarily modified in a number of sharply contrasting ways.

Associated with this sympetalous condition there has been a reduction in the number of floral whorls as well as in the number of parts in each whorl. The flowers are normally pentamerous, so far as the sepals and petals are concerned, but there is frequently only a single whorl of stamens and of the five stamens typically present one or more may be reduced to staminodes or may be absent altogether. In the majority of the families the ovary is composed of two carpels and the number of ovules in each loculus is frequently small. The ovules themselves frequently possess only a single integument.

The flowers are arranged in various inflorescences, are seldom solitary and show a marked tendency to zygomorphy. In the highest families capitula are produced with a corresponding reduction in the size of the individual florets.

It is now generally agreed that the Metachlamydeae represent an advance on the Archichlamydeae. They are a natural culmination of the evolutionary trends exhibited within the latter families. It is however extremely improbable that they are a monophyletic group. They represent rather the ends of a number of separate evolutionary lines which arose in the Archichlamydeae, all tending in the same direction. Whether each of the families represents a single evolutionary series or whether each family is itself polyphyletic is a matter of dispute. The true interrelationships of the various families which comprise the Metachlamydeae have not yet been settled, and their classification is still subject to considerable diversity of opinion.

ERICALES

The Ericales are Metachlamydeae in which the flowers are either pentamerous or tetramerous, regular in form and hermaphrodite. The stamens are generally free from the petals and both they and the petals are inserted around the margin of a nectar-secreting disc. The petals are usually united into a bell-shaped tube, but sometimes they are free. The ovary is multilocular and either superior or slightly inferior. The placentation is axile and the ovules have a single integument. The seeds are small but endospermic: the embryo is straight. The plants are usually shrubs or small trees with leaves which are either thick and leathery or minute and folded and decidedly xeromorphic in character. They occur mainly in cool and temperate climates and are characteristically intolerant of lime in the soil.

There is a considerable degree of uniformity of opinion regarding the families which should be included in this order. The chief difference of opinion lies in the limits to be assigned to the Ericaceae. Wettstein and Engler both recognize the family Pyrolaceae, which Hutchinson includes in the Ericaceae, while the latter splits off the Vacciniaceae, which the former writers regard as a sub-family of the Ericaceae. Hutchinson on the other hand has followed Bentham and Hooker in recognizing the family Monotropaceae, which includes those genera which are saprophytic in habit.

Fig. 1761.—*Pyrola rotundifolia.* Habit of flowering plant.

Fig. 1762.—*Monotropa hypopithys.* Colourless inflorescence emerging from ground under Birch.

In this connection we shall follow Engler as regards both the families included in the order and also in the limits which he sets for the Ericaceae. Of the families which he includes we shall mention only three, Pyrolaceae, Epacridaceae and Ericaceae. Before considering the Ericaceae in detail we may briefly refer to the other two families.

The **Pyrolaceae** include some thirty species grouped in ten genera. They are confined to the Arctic and cold north temperate regions. Two genera occur in Britain, *Pyrola* (Fig. 1761) and *Monotropa* (Fig. 1762). The former is an evergreen plant with a creeping rootstock. The latter is a colourless saprophyte occurring rarely in Birch and Beech woods. Below ground it has a much-branched root system, covered by an ectotrophic mycorrhiza, while the flowering shoots originate from adventitious buds. Similar modifications occur in *Moneses uniflora* in which there is no stem, the solitary flower arising from a bud on the roots. These and other examples of the family show remarkable specialization and reduction in floral structure, and it is interesting to note that among other features of reduction no cotyledons are produced by the embryo.

The **Epacridaceae** are a larger family containing about 350 species, distributed chiefly in Australia and Tasmania, but extending eastwards to South America and westwards to India. They strongly resemble the Ericaceae in habit. It is interesting to find that while their centre of distribution is clearly Australia, that of the Ericaceae is mainly in Africa (*Erica*) and western China (*Rhododendron*). They may thus be said to be the Australian counterpart of the Ericaceae. Several are cultivated in this country as greenhouse shrubs.

Ericaceae

The Ericaceae are a widely distributed family of woody shrubs with alternate, opposite or verticillate leaves, which form an important facet of the flora of moorlands. Many are alpine plants and most of them are evergreens. The family is represented in Britain, firstly by the Heather and Ling which abound on almost every common or moorland. To a somewhat less extent it is also represented by the Cranberry and the Whortleberry or Bilberry which, though not as widespread as the former plants, cover wide stretches of country, particularly in western and northern districts. In the second place the family is represented by introduced plants, particularly the Rhododendrons and Azaleas, one of which, *R. ponticum*, has multiplied naturally in many parts of the western counties and in the Scottish highlands to such an extent that it forms the dominant shrub of the pine woods.

A number of species of Heather occur in this country, *Erica cinerea* (Bell Heather), *E. tetralix* (Cross-leaved Heath), and *Calluna vulgaris* (Ling) being the most important. *Vaccinium myrtillus* (Fig. 1763) is the Whortleberry or Bilberry, while other related species are *V. vitis-idaea* (Cowberry), *V. oxycoccus* (Cranberry) and *V. uliginosum* (Bog Whortleberry). In the highlands of Scotland two species of *Arctostaphylos* occur: *A. uva-*

ursi (Red Bearberry) and *A. alpina* (Black Bearberry); *Andromeda polifolia* (Wild Rosemary) and *Arbutus unedo* (Strawberry Tree), though rare as wild plants, are often cultivated. The latter grows in natural woods in western Ireland.

FIG. 1763.—*Vaccinium myrtillus.* Bilberry. Shoot with young fruits.

The **plants** are usually woody shrubs with leathery, evergreen, simple leaves usually showing marked xerophytic characters. Many of the leaves are characteristically rolled towards the abaxial surface, and the stomata are restricted to the groove so formed and are further protected by branched

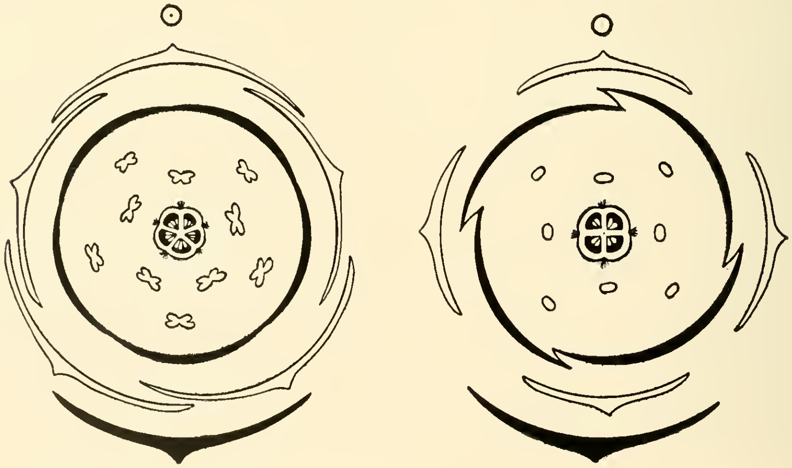


FIG. 1764.—Floral diagrams of Ericaceae. A, *Vaccinium vitis-idaea*. B, *Erica carnea*. (*After Eichler.*)

hairs. The roots of many species have been shown to be inhabited by endotrophic mycorrhizal fungi.

The **inflorescence** is usually racemose, though the number of flowers in the inflorescence is often small.

The **flower** (Fig. 1764) is hermaphrodite, regular and actinomorphic, occasionally slightly zygomorphic, usually hypogynous, except in *Vaccinium* where it is epigynous.

The **calyx** is pentamerous or tetramerous, gamosepalous and persistent, and except in *Vaccinium* hypogynous.

The **corolla** is regular or slightly zygomorphic in *Rhododendron*. It is tetramerous or pentamerous and gamopetalous, usually globose or broadly campanulate; imbricated in aestivation and often persistent as in *Calluna* and *Erica* (Fig. 1765).

The **androecium** is composed of either eight or ten stamens, rarely five, as in *Azalea*. They are obdiplostemonous and hypogynous except in *Vaccinium*. The anthers possess hornlike appendages and open by apical pores or slits. The pollen grains remain together in their tetrads and form a powdery or sticky mass, which often comes out of the apical pore in long strings.

The **gynoecium** is composed of four or five syncarpous carpels, forming an ovary with four or five loculi, which is superior except in *Vaccinium*. Each loculus contains from one to many anatropous ovules with axile placentation. The style is simple but the stigma is either capitate or four- or five-lobed.

The **fruit** may be a berry or a capsule, the latter splitting either septicidally or loculicidally.

The **seed** is small and contains endosperm. The embryo is also small and straight.

Fig. 1765.—*Erica carnea*. Longitudinal section of flower. The anthers are exserted and surround the immature stigma.

The family is cosmopolitan in distribution occurring all over the world except in deserts or hot, damp tropical regions. There are about fifty genera containing some 1,350 species. Owing to their number and their social habit, they form a quite characteristic part of the vegetation of certain regions of the world. The sub-family Ericoideae (Fig. 1766) is restricted to Europe and Africa, but these two areas are now separated from one another by the Sahara Desert which contains no species. The Rhododendroideae have their centre of distribution in the Himalayas and south-west China. The Arbutoideae and the Vaccinioideae are found chiefly in north temperate regions, having several species with circumpolar distribution. According to Drude the Ericaceae are divided into the following sub-families:

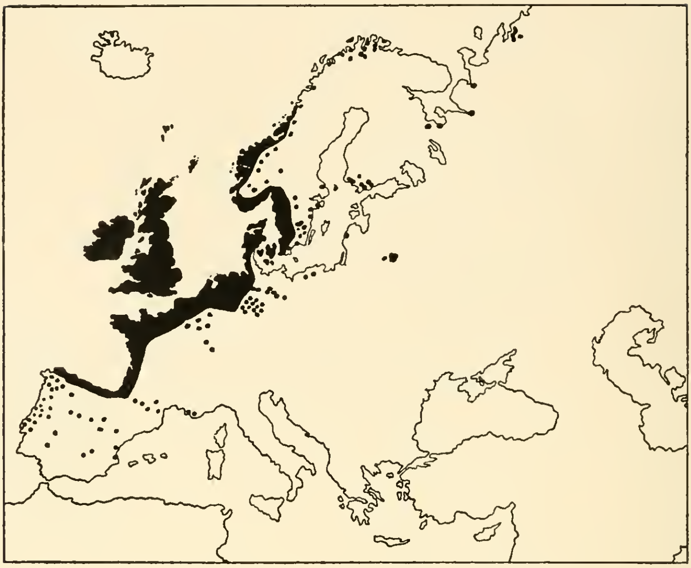


FIG. 1766.—Distribution of *Erica* in Europe.

I. Rhododendroideae

Capsules splitting septicidally, seeds often winged, with a loose, ribbed coat. Stamens with upright, long, adnate anthers without appendages. Corolla falling after flowering and slipping forward over the other floral parts, ensuring self-pollination if necessary. *Ledum*, *Rhododendron* (Fig. 1767), *Loiseleuria*, *Kalmia* (Fig. 1768), *Phyllodoce* and *Daboecia*.

FIG. 1767.—*Rhododendron ponticum.* Umbellate inflorescence.

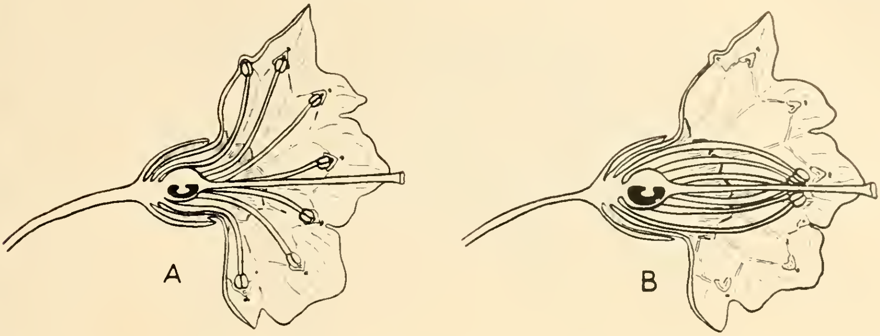


FIG. 1768.—*Kalmia latifolia.* Flowers in longitudinal section. A, Young stage with open anthers displayed. B, Older stage with stamens connivent and stigma receptive.

II. **Arbutoideae**

Berry, or capsule splitting loculicidally, seeds triangular or ovate. Anthers much folded or with appendages. Pollen shed from the tops of the anthers. Ovary superior. *Cassiope*, *Andromeda*, *Epigaea*, *Pernettya* (Fig. 1769), *Gaultheria*, *Arbutus* and *Arctostaphylos.*

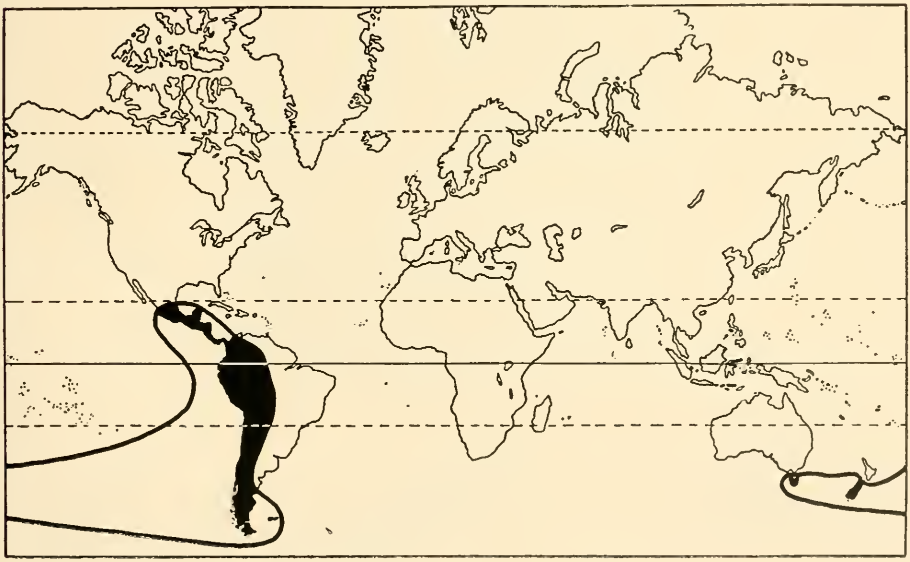


FIG. 1769.—Distribution of *Pernettya.*

III. **Vaccinioideae**

Berry, or capsule splitting loculicidally. Seeds triangular or oval. Anthers folded, with peglike appendages, or prolonged into tubes. Ovary inferior. *Vaccinium*, *Pentapterygium*, *Agapetes*, *Macleania* (Fig. 1770).

FIG. 1770.—*Macleania insignis.* Flowering shoot.

IV. **Ericoideae**

Nut, or capsule splitting loculicidally, seeds round, anthers with short connectives and with appendages. Corolla persistent. *Erica*, *Calluna*, *Eremia* and *Salaxis*.

The Rhododendroideae include about seventeen genera and 850 species, of which the genus *Rhododendron* is by far the largest, with about 800 species. It is characteristically an eastern Asiatic genus occurring particularly in the Himalayas and south-western China. Many of the species, introduced by collectors, are cultivated in this country, and contribute a most remarkable variety of evergreen shrubs. Some species become almost wild in parts of England. Many hybrids have been produced in cultivation and the identification and naming of these varieties has become an extremely complex matter.

The flowers (Fig. 1771) are protandrous and usually brightly coloured.

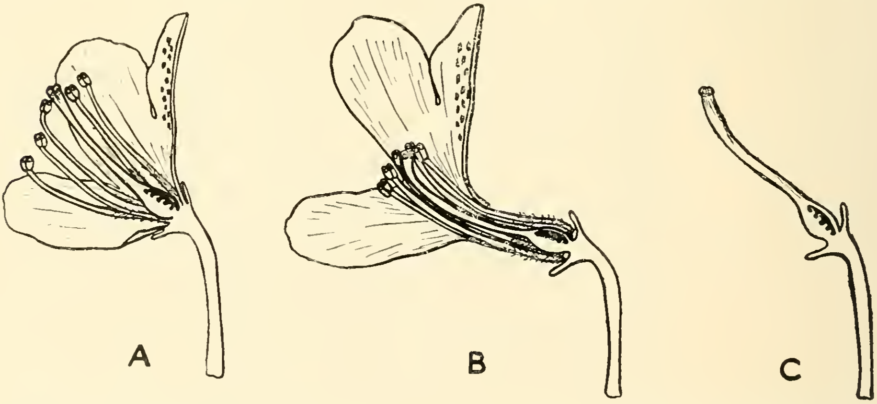


FIG. 1771.—*Rhododendron.* Pollination. A, Young, staminal stage. B, Corolla detached at the base and falling off, thus drawing the anthers on to the stigma and causing self-pollination. C, Ovary with persistent style, after anthesis.

Nectar is secreted by a swelling at the base of the ovary, and is often protected by erect hairs on the filaments of the stamens. Pollination is effected by humble bees who are forced to crawl over the stamens and stigma to reach the nectar. As the longest stamens project beyond the stigma, automatic self-pollination is possible if insect pollination fails. In many species the pollen grains remain cemented together in tetrads. The tetrads are also loosely held together by threads of viscin.

The second sub-family, the Arbutoideae, is smaller, containing some 250 species distributed among twenty genera. They are chiefly north temperate and Arctic species. The largest genus, *Gaultheria,* with 100 species, occurs in America, from the Andes, through central South America to Chile. A few species, *e.g.,* *Arctostaphylos alpina* and *A. uva-ursi* and *Andromeda polifolia,* are Arctic or alpine species found in Britain. The Strawberry Tree, *Arbutus unedo* (Fig. 1772), inhabits natural woodlands near Killarney. It is one of the group of so-called Lusitanian species found in the extreme west of the British Isles.

FIG. 1772.—*Arbutus unedo.* Shoot with flowers and fruits.

In these genera the flowers are usually homogamous or slightly protogynous and nectar is secreted at the base of the corolla. In *Arctostaphylos uva-ursi* (Fig. 1773) the nectar does not remain in the nectary but collects in ten pits which surround it, in the base of the corolla. It is prevented from running down the petals by the dense covering of hairs which are developed on the filaments of the stamens. The stamens are highly modified. At the base the filament is narrow and tubular, but immediately above it swells out and is covered by hairs. It narrows again and at its apex bears an anther with two inwardly directed anther lobes with long tail-like appendages, which extend outwards to the corolla. Only the most skilful Humble Bee and Hive Bee are able to get at the nectar by probing with their probosces through the tubular opening in the pendulous flowers. If the insect's head is covered with pollen it is almost certain to touch the stigma, which lies centrally just below the opening of the corolla. As the proboscis is thrust further down it meets the appendages of the anthers causing pollen to be shaken on to the insect's head. Thus cross-pollination is almost certainly ensured. Since the flowers are pendulous, pollen at the end of anthesis may become loose and fall on the stigma, so that as a last resort self-pollination may occur.

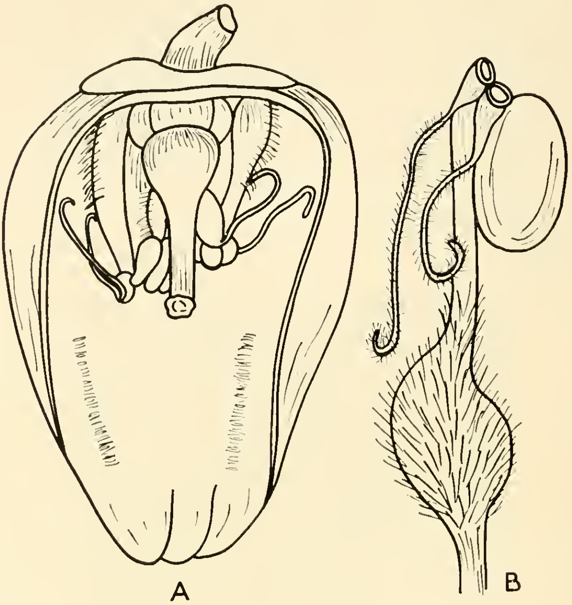


FIG. 1773.—*Arctostaphylos uva-ursi*. A, Longitudinal section of flower in bud stage. B, Stamen with apical dehiscence pores and filamentous appendages. (*After Knuth.*)

As already mentioned, the members of the Vaccinioideae are sometimes separated as a distinct family. The genera are mostly temperate in distribution or occur on the tops of tropical mountains, and are usually modified as xerophytes or epiphytes. The 350 species are distributed among about twenty-five genera, of which *Vaccinium*, with 100 species, is the best known.

The flowers are feebly protandrous, with concealed nectar, and are pollinated by bees. In *V. myrtillus* (Fig. 1774) the flowers are bright green in colour with a reddish tint, and are quite devoid of scent, but despite this they are very rich in nectar. The pendulous corolla is contracted at its tip so that only the proboscis of a bee can enter and reach the base of the flower. The capitate stigma projects a little from the mouth of the flower in a position suitable for receiving pollen before the insect reaches the anthers, which cluster around the style inside the bell-shaped flower. Each anther has two long basal appendages, which diverge outwards and touch the inner wall of the corolla. When the bee's proboscis touches them it causes the dry pollen in the anthers to fall out on to the insect's head. Nectar is secreted by a white annular swelling at the base of the style. As in previous examples, should cross-pollination fail, self-pollination is possible by the pollen falling on the stigma, since the flowers are pendulous.

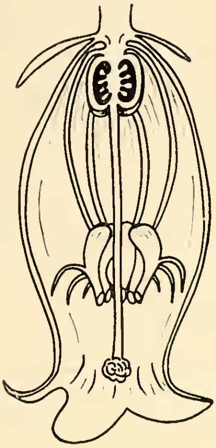


FIG. 1774. — *Vaccinium myrtillus.* Flower in longitudinal section. For pollination see in text.

FIG. 1775.—*Erica carnea.* Flowering shoot in early spring.

The fourth sub-family, Ericoideae, contains sixteen genera and 600 species, of which about 500 belong to the genus *Erica.* The majority are confined to the Cape but several are found in this country, *e.g.*, *Erica cinerea*, Heather, and *E. tetralix*, Cross-leaved Heath. *Calluna vulgaris*, Ling, is widespread in Europe and is interesting because of the endotrophic mycorrhiza which it possesses. Many species of *Erica* (Fig. 1775) are cultivated in gardens, and special Heather gardens are sometimes planted in which, by a careful selection of species, flowers may be obtained all the year round.

In *Erica tetralix* the flowers are pendulous and pink in colour and are pollinated by bees. The nectar is secreted at the base of the flower and a proboscis 7 mm. long is necessary to reach it. The pollination mechanism is essentially similar to that of the previous examples. Heather honey is very important commercially, for the plants are in flower later than most other nectar-producing species and the removal of hives to moorlands early in August is a feature of commercial honey production. It may be noted that in addition to collecting nectar, the bees gather the slate-grey pollen as food for their larvae. Heather honey contains a higher proportion of protein than ordinary mixed honeys.

EBENALES

The Ebenales are Metachlamydeae in which the flowers are bisexual or dioecious, regular, usually tetramerous and gamopetalous. The stamens are inserted in the corolla tube, the ovary is usually superior and multilocular and placentation is axile with one or two ovules in each loculus. The embryo is usually straight and is surrounded by endosperm.

The plants are mainly tropical in distribution. They are mostly woody with leathery leaves. Some four families are included in the order. The Sapotaceae are separated from the remaining three by the presence in the stems and leaves of a laticiferous system. The other three families are the Ebenaceae, Styracaceae and Symplocaceae.

We shall not consider any family in detail but will refer briefly to certain features of interest in the families which are of economic importance.

The **Sapotaceae** contain about thirty-five genera and 600 species and are mostly trees. The flowers are solitary or in cymose inflorescences. Calyx and corolla vary in the number of their parts, being either 2+2, 3+3, 4+4 or 5. The stamens are in two or three whorls, the outer whorl often

FIG. 1776.—*Achras sapota*. Sapodilla. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

being reduced to staminodes or entirely absent. The gynoecium is syncarpous and multilocular. The fruit is a berry, often with a sclerenchymatous outer layer. These sapotaceous, tropical fruits often reach a considerable size and are locally of economic importance. Among the more common we may mention *Achras sapota* (Fig. 1776), the Sapodilla, which is one of the best tropical American fruits. The tree is evergreen, reaching 75 ft. in height. The bark contains a latex known as chicle which is obtained by tapping and is used as a base for chewing-gum. The fruit is oval or conical, 2 to 3½ in. in diameter, the skin is thin and rusty brown in colour, the flesh is translucent and contains about 14 per cent. of sugar, mostly sucrose. *Chrysophyllum mammosum*, the Sapote, is also of importance in Central America. The fruit is elliptical or oval in shape, 3 to 6 in. long and russet brown in colour. The taste is very sweet, without any acid flavour. *C. viride*, the Green Sapote, is considered by experts to be superior to the last in flavour but is much more limited in distribution, being found only in the highlands of Guatemala, Honduras and Costa Rica. The Star Apple (*C. cainito*) is common in Cuba, Jamaica and other parts of Central America and is regarded as a valuable fruit which may either be eaten fresh or made into jam. Other sapotaceous fruits include *Lucuma nervosa* (Canistel), *L. salicifolia* (Yellow Sapote), *L. obovata* (Lucmo) and *L. carinito* (Abiu).

Species of the genus *Sideroxylon* produce a useful timber known as Ironwood. This genus which contains about 100 species is found in tropical and subtropical parts of the Old World. The latex of such genera as *Payena*, found in Malaya, and *Mimusops*, which is widely cultivated in the tropics, is a source of Gutta Percha.

The **Ebenaceae** are a small family with five genera and about 350 species. The species are important chiefly because of the very hard wood, which is usually black or more rarely green in colour. Ebony is the heartwood of various species of *Diospyros*. This genus, which contains 200 species, is widely distributed in the tropics, especially in the Old World. *D. reticulata*, occurring in Mauritius, and *D. ebenum* in Ceylon, yield the finest ebony. *D. quaesita*, also in Ceylon, yields Calamander wood, while *D. embryopteris* of India provides a sticky pulp used for caulking. This genus also yields several valuable fruits. *D. kaki*, the Japanese Persimmon, is a tree up to 40 ft. in height which, though native of eastern Asia, is now cultivated in America. The fruit is oval or conical, about 3 in. in diameter, with an orange-coloured pulp, and contains about 15 per cent. of sugar. A number of cultivated varieties are recognized. *D. ebenastri* is the Black Sapote, which is restricted to Mexico where the fruit is regarded as of equal merit to that of *D. kaki*. *D. discolor*, the Mabolo, is valued in Malaya for its fruits. *D. lotus* is the Date Plum of the eastern Mediterranean region. These trees are distinguished from those of the Sapotaceae by the absence of any laticiferous system.

The **Styracaceae** are a small family of eight genera and 120 species which are widely distributed in the warm climates. *Styrax* (Fig. 1777) with 100 species yields resins. *S. officinalis* of the Mediterranean region is the source of Storax, a resin much used in ancient times, while *S. benzoin* which occurs in Sumatra yields the fragrant Gum-benzoin which is used medicinally and in the manufacture of incense. It is obtained from cuts in the bark.

FIG. 1777.—*Styrax japonica.* Flowering shoot.

The family **Symplocaceae** includes only one genus, *Symplocos*, which is separated on account of the inferior ovary. There are some 300 species with their centre of distribution in India; thirteen species are found in New Caledonia.

PRIMULALES

The Primulales are Metachlamydeae in which the flowers may be either unisexual or bisexual. Both calyx and corolla are pentamerous. There are usually five epipetalous stamens. The ovary is superior, or rarely inferior, and unilocular. The ovules are indefinite in number and are either attached basally or exhibit free-central placentation. The seeds are small with a straight embryo surrounded by endosperm.

The plants are herbs, shrubs or trees with simple entire leaves.

The limits of the order are uniformly interpreted. According to Engler there are three families, of which one, the **Theophrastaceae**, contains about seventy species confined to the tropical regions of America. The second family, the **Myrsinaceae**, is also tropical and subtropical in distribution. It contains about 1,000 species, but few of them can lay claim to any special importance, except *Aegiceras majus*, a common mangrove tree, and *Ardisia crenata*, which harbours colonies of nitrogen-fixing bacteria in its leaves. The third family is the Primulaceae which we shall consider in detail.

Primulaceae

The plants which compose this family are herbs, with simple leaves and often with solitary flowers. They frequently perennate by means of rhizomes or tubers. The leaves are opposite or alternate, frequently radical and usually entire.

The family includes a number of common wild flowers, of which we may mention the following: nine genera are represented in the British Flora: *Primula*, which includes *P. vulgaris* (the Primrose), *P. elatior* (the Oxslip) and *P. veris* (the Cowslip); *Lysimachia*, which includes *L. vulgaris* (Yellow Loosestrife), *L. nemorum* (Yellow Pimpernel) and *L. nummularia* (Moonwort or Creeping Jenny); *Glaux*, with the single species *G. maritima* (Sea Milkwort); *Hottonia palustris* (Water Violet); *Anagallis*, with two species, *A. arvensis* (Scarlet Pimpernel) and *A. tenella* (Bog Pimpernel); *Centunculus minimus* (Chaff-weed); *Trientalis europaea* (Chickweed Wintergreen); *Samolus valerandi* (Brookweed); and finally *Cyclamen hederifolium* (Cyclamen) which is not really native in this country.

Many other species are cultivated in gardens, in particular those of the genus *Primula* (Fig. 1778). The centre of distribution of this genus appears to be Assam and south-eastern Asia, where on the mountain-sides meadows largely populated with species of *Primula* form a conspicuous feature. In recent years the introduction of many of these plants as garden flowers has been made possible by the activities of such well-known plant collectors as Farrar, Kingdon Ward, Ludlow, Sherriff and others.

Fig. 1778.—*Primula vulgaris.* Primrose. In a Cambridgeshire woodland.

The **plants** are herbaceous, sometimes annual, but more usually perennial, perennating by sympodial rhizomes as in *Primula*, or tubers formed from the swollen hypocotyl as in *Cyclamen*. The plants often have a rosette of radical leaves, though there may be an erect or creeping stem as in *Lysimachia*. The leaves are generally simple, often toothed, but in *Hottonia* the submerged leaves are finely divided. In other genera the leaves may be opposite, alternate or whorled.

The **inflorescence** may consist of an umbel, a raceme, or a panicle, though in many the flowers are solitary.

The **flowers** (Fig. 1779) are usually regular, actinomorphic, hermaphrodite or occasionally unisexual by reduction. Many are heterostyled.

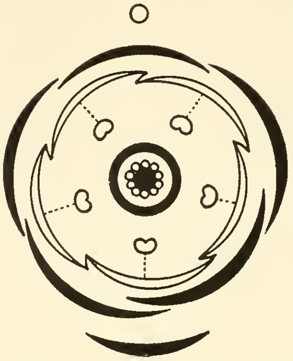


Fig. 1779.—Floral diagram of *Primula*. Primulaceae.

The **calyx** is gamosepalous and persistent, composed of five or sometimes four segments, which are represented by points on the calyx tube.

The **corolla** is gamopetalous, regular, composed of five or occasionally four petals, which may be united basally into a tube but spread out and separate above. In *Glaux* the corolla is absent, the sepals being coloured. The **androecium** consists of five or more rarely four stamens, which are arranged opposite the petals, and are attached to them or to the base of the corolla tube. The anthers are introrse and dehisce longitudinally.

The **gynoecium** is polycarpellary being made up of five fused carpels, syncarpous, with a single simple style and capitate stigma. The ovary is unilocular and superior. The ovules are anatropous and numerous and the placentation is free-central.

The **fruit** is a capsule, which may dehisce by five valves as in *Primula*, or with circumscissile dehiscence, forming a pyxidium as in *Anagallis*.

The **seed** is endospermic but small in size and the embryo is straight.

Exceptions to the above description are found in certain species. Thus, for example, the calyx may be composed of from five to nine sepals in *Trientalis*, five or six in *Lysimachia* and four to five in *Centunculus*. The flowers of the genus *Coris* are zygomorphic.

The single whorl of stamens opposite the petals is interpreted as the remnants of an earlier two-whorled condition, in which the outer whorl has disappeared. This idea receives support from the fact that in *Samolus* and in *Soldanella*, a whorl of scales is present opposite the sepals, which may be the remnants of an outer stamen whorl. Anatomically the family exhibits certain important features. Firstly there is the frequent development of either simple or compound glandular hairs; secondly the common occurrence of Casparian Bands on the radial walls of the endodermal cells in the stem, and thirdly the absence of specialized cells around the stomata.

The family contains some twenty-five genera and about 550 species which are very widely distributed though they are most common in north temperate regions.

The family is subdivided into the following tribes on the position of the ovary, the aestivation of the corolla and the floral symmetry.

1. Primuleae

Ovary superior, capsule with valvate dehiscence, corolla lobes imbricated in the bud. *Primula*, *Androsace*, *Soldanella*, *Dodecatheon* and *Hottonia.*

2. Cyclamineae

Ovary superior, capsule with valvate dehiscence, flowers with reflexed petals. The plants arise from tubers derived from the hypocotyl. Only genus *Cyclamen*.

3. Lysimachieae

Ovary superior, capsule with valvate dehiscence or a pyxidium. Corolla lobes contorted in the bud. *Lysimachia*, *Trientalis*, *Centunculus*, *Anagallis* and *Glaux*.

4. Samoleae

Ovary partly inferior. Only genus *Samolus*.

5. Corideae

Flowers zygomorphic, calyx spiny. Only genus *Coris*.

Among the Primuleae the largest genus is *Primula*, with about 300 species. This genus is widely distributed in the north temperate regions, occurring particularly in the mountainous districts of northern India and China. Besides the five species which occur wild in Britain many are cultivated either in gardens or in greenhouses. *P. sinensis* and *P. japonica* are among the more important of the greenhouse forms. The genetical nature of these species, and their mutant forms, has formed the subject of very extensive studies carried out in recent years at the John Innes Horticultural Institute. As a result of this work, not only has the cytological complement of the species been minutely investigated, but a number of new races of considerable horticultural value have been produced.

The flowers of *Primula* (Fig. 1780) are dimorphic and heterostylous. Darwin showed that legitimate pollination, in which the stigma of the long-

FIG. 1780.—*Primula sinensis*. Left, thrum-eyed flower. Right, pin-eyed flower.

or short-styled flower receives pollen produced at the same level in the flower, by the anthers of the long or short stamens respectively, produced a higher degree of fertility than illegitimate pollination. Such species as *P. officinalis*, *P. japonica* and *P. auricula* (Garden Auricula) are very infertile when insect visits are prevented, but completely fertile when such insects are allowed, or artificial pollination permitted. He found that the legitimate pollination was about one and a half times as fertile as the illegitimate type. Later it was found by Hildebrand that when the flowers are artificially self-pollinated, fertility is at a minimum. When the parents are both long-styled, the offspring are also predominantly long-styled, and similarly in the case of short-styled flowers. Crosses between long- and short-styled forms gave a progeny with long- and short-styled flowers in approximately equal numbers.

Most of the species of *Primula* (Fig. 1781) are pollinated by Humble Bees and similar long-tongued insects, though Humble Bees have been observed to perforate the corolla tube in their search for nectar. In *P. vulgaris*, the typical heterostylous condition is well seen, and it is interesting to note that there are microscopic differences between the size and shape of the stigma in the two forms, and also in the diameter of the pollen grains; those of the short-styled flowers being larger than those of the long-styled ones.

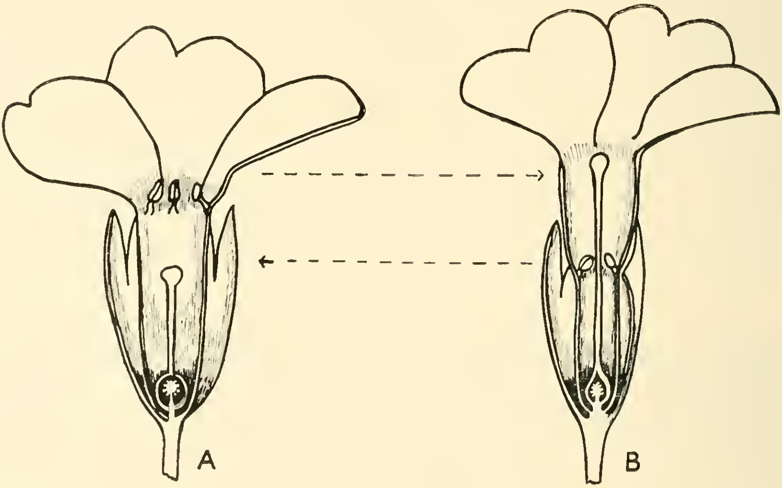


Fig. 1781.—Heterostylous *Primula* flowers, in longitudinal section. Left, short-styled, thrum-eyed. Right, long-styled, pin-eyed. Legitimate pollination follows the directions shown by the arrows.

Hybrids between closely allied species of *Primula* are not equally fertile, for the sterility of the pollen increases as the affinity of the stocks becomes more remote.

The following table illustrates this point clearly:

Hybrid	*Normal pollen in per cent.*	*Shrivelled pollen in per cent.*
P. vulgaris x *P. officinalis*	26·5–33	73·5–67
P. elatior x *P. officinalis*	31–36	69–64
P. elatior	33	67
P. vulgaris x *P. elatior*	66–69	34–31
P. acaulis x *P. elatior*	78	22

These results are confirmed by the number of seeds developed in the various examples.

The genus *Hottonia* contains two species, both of which are water plants with finely divided submerged leaves. *H. palustris* (Fig. 1782) (Water Violet) is widely distributed from Siberia through Europe including Britain, while *H. inflata* is found in North America along the Atlantic coast. The flowers (Fig. 1783) are heteromorphic, with concealed nectar secreted at the base of the ovary and stored in the corolla tube. Pollination is effected mainly by two-winged flies.

Among the other genera included in this tribe we may mention *Soldanella*, with six species found in the European Alps, *Dodecatheon*, with thirty species found in Pacific North America, and *Androsace*, with ninety species in the mountains of north temperate regions.

The Soldanellas are famous for their habit of thrusting their flowers up through the fringes of the melting snow in the high Alps. The flowers are pendent and are of two kinds. In some species the corolla is wide and bell-like and in these the nectar is protected by an interior ring of corolla scales. In others the corolla is tubular and narrow and the protective scales are absent.

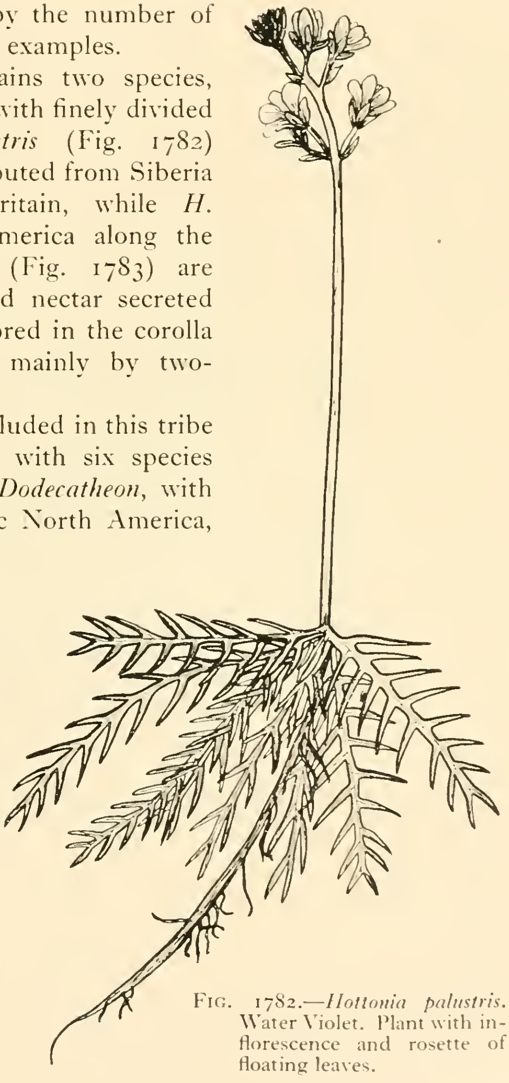


FIG. 1782.—*Hottonia palustris.* Water Violet. Plant with inflorescence and rosette of floating leaves.

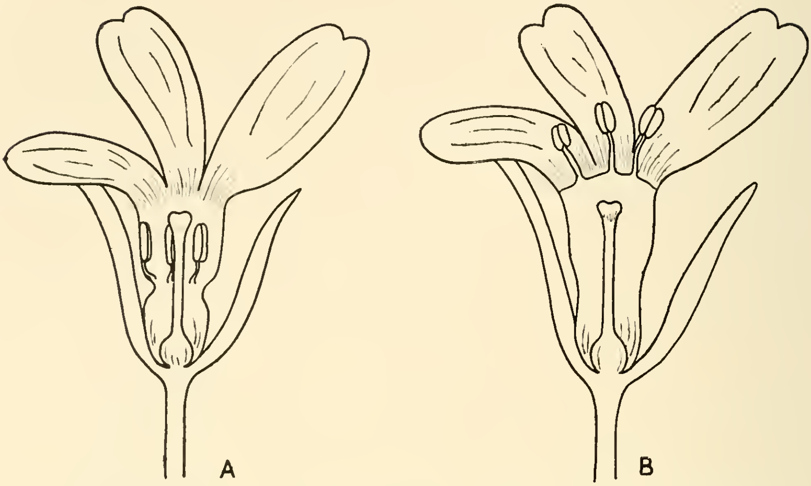


Fig. 1783.—*Hottonia.* Flowers in longitudinal section to illustrate pollination. The flowers are heteromorphic with regard to stamen length. A, Short stamens. B, Long stamens. (*After Knuth.*)

The tribe Cyclamineae contains the single genus *Cyclamen* (Fig. 1784) with sixteen species, which occur chiefly in the Mediterranean region. There is a stout corm or tuber originating from the hypocotyl, from which the leaves and flower stalks arise annually. The flowers are pendulous and the petals reflexed. The pollination mechanism (Fig. 1785) is interesting, and recalls that in *Erica.* At first the flowers are entomophilous, the anthers clasping the style, and the pollen is covered with a sticky oil. Later this pollen becomes powdery and the angle at which the flower hangs becomes more acute, so that the pollen grains fall on the style when the flower is shaken by the wind. After pollination the stalk usually coils up spirally, drawing the ripening fruit into the soil. (See Fig. 1431.) In *C. persicum* the stalk bends over and actually forces the fruit into the ground. Cleistogamic flowers are sometimes produced in this genus.

Fig. 1784.—*Cyclamen neapolitanum.* Flowers.

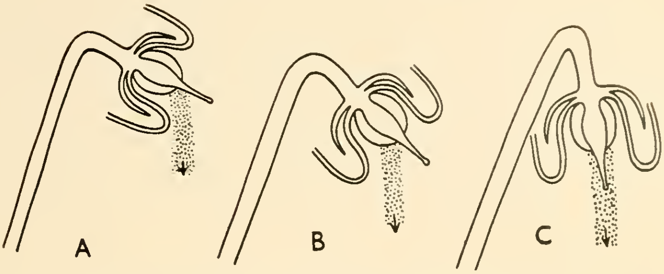


FIG. 1785.—*Cyclamen* pollination, showing the change of position of the stigma in relation to the direction of pollen drop. (*After Knuth.*)

The Lysimachieae contain a number of genera, several of which are represented in the British Flora. *Lysimachia* with over 100 species is widely distributed in temperate regions and in the mountains of the tropics. The flowers (Fig. 1786) are mostly yellow in colour and are visited by insects for their pollen, which is either collected or eaten by bees. *Anagallis* with twenty-four species is almost cosmopolitan. In *A. arvensis* the flowers open early in the morning in sunny weather; the five divergent anthers become covered with discharged pollen and the style is bent in such a way that the stigma must come into contact with any insect visiting the flower. Later in the day the flower closes, bringing the anthers into

FIG. 1786.—*Lysimachia punctata.* Flowering shoot.

contact with the stigma, so that automatic self-pollination regularly takes place, and, since few insects visit the plant, this is probably the normal method of pollination. In dull weather the flowers never open and self-pollination takes place pseudo-cleistogamously.

In the tribe Samoleae is the single genus *Samolus* with nine species, of which *S. valerandi* (Fig. 1787) is cosmopolitan in damp ground, often by the seashore. The flowers are small and the ovary semi-inferior. Self-pollination is almost inevitable, for the stigma and anthers develop at the same level and at the same time.

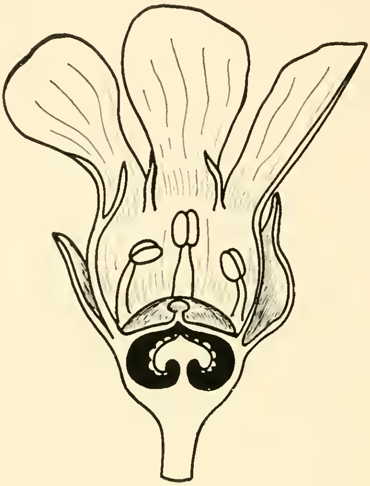


Fig. 1787.—*Samolus valerandi.* Longitudinal section of flower.

OLEALES

The Oleales are Metachlamydeae in which the flowers are hermaphrodite or unisexual by reduction, regular and generally tetramerous, the petals being either free or united into a tube. The stamens are often reduced to two. The ovary is superior, composed of two united carpels, and forming a bilocular structure, each loculus having one or two pendulous, or basally attached, anatropous ovules. The ovules usually have only a single integument. The plants are mostly woody shrubs, with opposite, simple or pinnate leaves, and have flowers in small racemes.

The various systems of classification differ in their interpretation of the limits of the order. Bentham and Hooker called the Oleales the Gentianales and included in it the families Oleaceae, Loganiaceae, Gentianaceae, Apocynaceae and Asclepiadaceae. Engler combined the same families under a different order which he called the Contortae. Wettstein pointed out that there are essential differences between the Oleaceae and the remaining families; such as the placentation of the ovules, and the absence of internal phloem, and the dimerous androecium, which he considered to be an advanced character. Hence he separated the Oleaceae, with the additional family Salvadoraceae, as the Oleales, while retaining Engler's Contortae for the other four families. This view was followed by Rendle. Hutchinson placed the Oleaceae and Loganiaceae in the Loganiales and the Apocynaceae and Asclepiadaceae in the Apocynales, while the Gentianaceae he placed in the Gentianales between the Compositae and the Primulaceae.

In this book we shall consider in detail only the Oleaceae and shall refer briefly to certain features of interest in other families; hence for convenience, though not necessarily on systematic grounds, we shall treat them under the heading of the Oleales.

The **Loganiaceae** are a small tropical family with thirty-five genera and about 600 species, which are characterized by having flowers with four or five petals and stamens, a bilocular ovary and ovules indefinite in number. The fruit is a capsule, berry or drupe and the seeds are endospermic. The plants are mostly trees or shrubs, which bear cymose inflorescences. The best-known genus is *Buddleia* with about 100 species which are generally distributed in the subtropics (Fig. 1788). Several species are commonly cultivated in gardens, the most common being *B. variabilis* (Fig. 1789), a native of China, which bears long inflorescences of mauve flowers, and *B. globosa* (Fig. 1790) which comes from Chile and Peru and produces balls of orange-yellow flowers. Several other Chinese Buddleias are in cultivation, but they are delicate and require protection in winter. The flowers are pollinated by butterflies, and in the late summer attract large numbers of

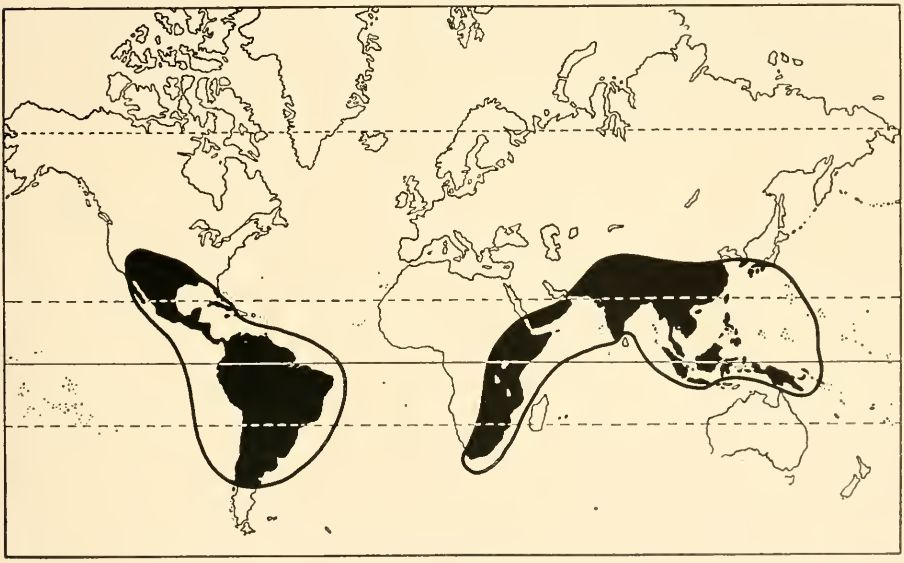


FIG. 1788.—Distribution of *Buddleia*.

Red Admiral, Peacock, Painted Lady and Tortoiseshell butterflies to the bushes.

Fig. 1789.—*Buddleia davidi* (*B. variabilis*). Long inflorescence of mauve flowers.

Fig. 1790.—*Buddleia globosa*. Globular inflorescence of orange flowers.

The second important genus is *Strychnos*, which contains about 200 species, widespread in the tropics. *S. nux-vomica* is an erect tree, occurring in India and Ceylon. The fruits yield the alkaloids strychnine and brucine. *S. ignatia* produces seeds known as Ignatius Beans, which are used in India as a remedy for cholera. *S. toxifera* is the source of Curare poison, which is used by the South American Indians to poison their arrows. It is obtained from the bark by scraping and maceration in water. The seeds of *S. potatorum* are used to purify dirty water for drinking. They are rubbed on the inside of the vessel and cause precipitation of colloidal matter in suspension.

While some of the species are trees, others are climbing shrubs with hooked tendrils which are modified axillary shoots. If the hook becomes attached to a support it thickens after closing around it and then becomes lignified. Other species have axillary thorns. *Gelsemium sempervirens*, which is found in south-eastern United States, contains the alkaloid gelsemin in its rootstock.

The **Gentianaceae** are another rather small family with seventy genera containing about 800 species. They are mostly annual or perennial herbs (Fig. 1791), with opposite leaves and cymose inflorescences. Many perennate by underground rhizomes. Many of the species are found in

FIG. 1791.—*Gentiana campestris.* Field Gentian. Iona.

alpine situations, while a few occur as halophytes. The Asiatic genus *Crawfurdia* is a climber. Certain genera live as saprophytes. They are found chiefly among the American species, though the condition is also known among certain Asiatic and African forms. In these cases the plants are small herbs in which the leaves are reduced to scales. *Menyanthes trifoliata* (Fig. 1792), the Bog Bean, has alternate leaves and this genus together with *Limnanthemum* (Fig. 1793) is sometimes separated into a distinct family. They are aquatic or marsh plants, and large idioblasts are developed in the floating leaves. Anatomically they are also separated by the vascular bundles, which in *Gentiana* are bicollateral, while in *Menyanthes* they are simply collateral. The flowers are adapted to insect pollination, and are usually brightly coloured. The fruit is a capsule, containing many minute seeds. A mycorrhizal fungus appears to be present, at least in many species, and is suspected of assisting germination. Recent experiments on vernalization of the seeds have proved particularly successful, for the germination of *Gentiana* seed is notoriously difficult.

The **Apocynaceae** are a rather larger family with about 1,000 species distributed among 130 genera. They are mostly found in the tropics but a

FIG. 1792.—*Menyanthes trifoliata.* Bog Bean.

FIG. 1793.—*Limnanthemum peltatum* (*Nymphoides peltatum*). A single plant with floating leaves.

few, as for example *Vinca* (Periwinkle) (Fig. 1794), are commonly naturalized in this country. Most of the genera are shrubs or twiners, and in the tropics they form large lianas. The vascular bundles are bicollateral and latex is always present. The flowers are usually produced in panicles, but are rarely solitary.

FIG. 1794.—*Vinca minor*. Lesser Periwinkle. Flower.

The **Asclepiadaceae** are also a fairly large family containing nearly 2,000 species arranged in 280 genera. They are mostly erect herbs or woody climbers but some are succulent. They are mainly tropical in distribution occurring especially in the drier parts of Central and South America. Anatomically they resemble the Apocynaceae in having bicollateral bundles and latex. They also frequently possess a mycorrhizal fungus in their roots. The flowers are remarkably uniform, with three whorls of five alternating sepals, petals and stamens. The ovary is bicarpellary and the ovaries remain free, though the two styles are united into a common stigma. The fruit consists of a pair of follicles. Few of the genera are commonly grown in this country, but we may mention *Stapelia*, which is sometimes grown as a succulent, and *Ceropegia*, which has already been referred to on account of the swollen, aerial tubers which it produces at intervals along its stem. These serve as a means of vegetative propagation. Species of *Asclepias* (Fig. 1795) are woody plants sometimes cultivated in greenhouses on account of their bright red flowers which last for several weeks.

The pollination mechanism of Asclepiadaceae calls for special comment, for it is unique and is one of the most remarkable among flowering plants. In *Vincetoxicum officinale* the ovary is surrounded by a fleshy column, formed by the fusion of the stamens, and is covered by a fleshy disc, under which are the entrances to the five stigmas. On the staminal column are

FIG. 1795.—*Asclepias curassavica.* Inflorescence.

borne five anthers, and below these externally are five appendages which are fused together to form a cuplike corona. The anthers are closely associated with the top of the style and each of them contains a pair of platelike pollinia which lie in the upturned side. The connective is produced upwards into a triangular membranous appendage, which is closely applied to the top of the stylar knob. Each side of the anther is continued into a leaflike wing, narrowing gradually above and vertical to the column of filaments. The adjoining wings of every two anthers enclose between them a narrow slit which widens below. These slits open internally into the stigmatic cavity which is partly bounded by the stigmatic surface on the underside of the terminal expansion of the style. Lying in the upper part of each slit, and visible externally, is a dark, bilaterally symmetrical, shiny body which consists of a thin, hard, horny plate (Fig. 1796). Its sides are

FIG. 1796.—*Asclepias.* Transverse section of one of the horny clips in which the legs of insect visitors are trapped.

bent so that the edges lie close together and in the middle of its lower border is a wedge-shaped slit. Two pollinia, lying in the adjacent loculi of two different anthers, are attached by bands to this clip.

Nectar is secreted abundantly and when a fly tries to suck the nectar secreted in one of the coronal pits situated immediately below one of the clips, its extended proboscis, beset with erect bristles, will be guided upwards into the slit between adjacent anther wings until it is held fast in the clip. When the insect withdraws its proboscis with a jerk, it pulls away the clip and the two pollinia attached to it. At first the pollinia are sharply divergent, but as the bands dry, they become closely appressed. Should such an insect visit another flower, the pollinia are readily thrust into one of the slits and guided by them will slip into the stigmatic chamber, thus effecting cross-pollination, for, on this occasion, when the insect withdraws its proboscis the pollinia are torn away from the band connecting them to the clip, while at the same time a new clip with fresh pollinia becomes fastened on to the proboscis. Two-winged flies allied to the house fly are the most efficient and are the chief agents of pollination.

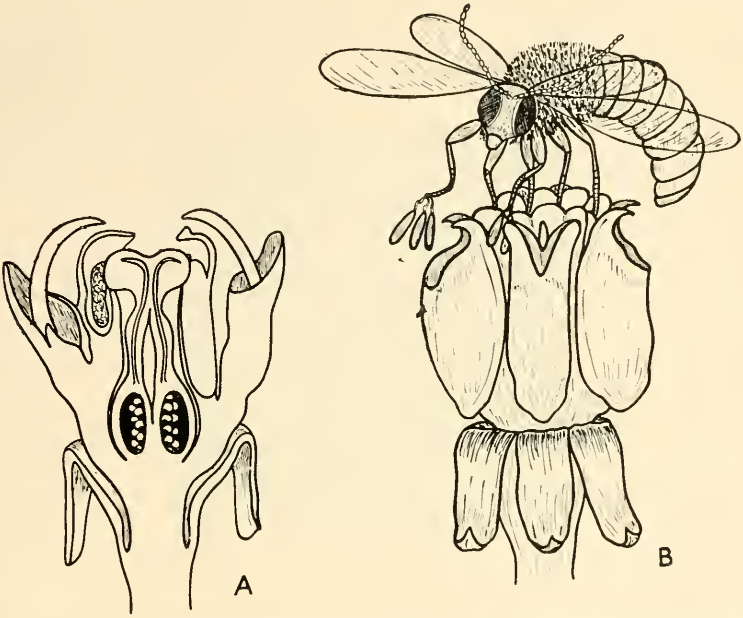


Fig. 1797.—*Asclepias curassavica.* Pollination. A, Longitudinal section of flower. B, Insect with pollinia attached to its legs.

Species of *Asclepias* (Fig. 1797), *e.g.*, *A. syriaca*, are adapted to bee pollination. Here it is the legs rather than the proboscis which become caught by the clips. A bee probing for nectar tends to slip on the smooth flower till its legs get a firm grip on a slit. When it lets go and draws up its legs, the claw is guided upwards in the slit, and it carries away the clip with the attached pollinia. In visiting another flower the pollinia become introduced into the slits which lead to the stigmas, cross-pollination is effected and another clip becomes attached as the bee leaves. It has been proved that self-pollination is impossible, for pollen is completely infertile on the stigmas of the same flower or even on plants raised vegetatively from the same stock.

A. curassavica is pollinated by butterflies, the clips becoming attached to the feet. Müller depicts an insect with as many as eleven clips and eight pollinia attached to a single limb.

The genus *Stapelia* has also a similar pinch-trap mechanism, and emits a carrion odour attactive to flies, which effect cross-pollination by means of their probosces. Cleistogamy is said to occur in this genus.

Other well-known genera of this family with clip pollination mechanisms are *Ceropegia* (small flies), *Hoya* (Fig. 1798) (bees), *Araujia* (humble bees) and *Gomphocarpus* (hive bees).

FIG. 1798.—*Hoya carnosa.* Flower in face view.

Oleaceae

The members of the Oleaceae are mostly trees or shrubs which are widely distributed both in temperate and tropical regions. Many are cultivated in Britain, and some, though not native, have become so familiar that they form an accepted part of our flora.

Among the truly British members we may mention first the Ash (*Fraxinus excelsior*). *Ligustrum vulgare* (Privet) also occurs wild, though it is best known as an evergreen garden shrub which is extremely accommodating, in that it will grow almost anywhere, and will withstand cutting almost indefinitely. The golden privet, a form in which the leaves are yellow-orange, is frequently planted as an ornamental shrub. Among other commonly planted genera are *Syringa* (Lilac), *Forsythia*, *Jasminum* (Jasmine) and *Olea* (Olive).

The **plants** are woody with opposite, decussate, simple or compound leaves and are sometimes evergreen. Several buds are often developed serially in the leaf axils. These may produce either branches or flowers. Extra-floral nectaries have been described in some species.

The **inflorescence** is racemose or cymose containing a large number of small flowers. Each flower stands in the axil of a bract and is subtended by a pair of lateral bracteoles.

The **flowers** (Fig. 1799) are regular, tetramerous and usually hermaphrodite, but they may be polygamous in *Fraxinus* or dioecious as in some species of *Olea*.

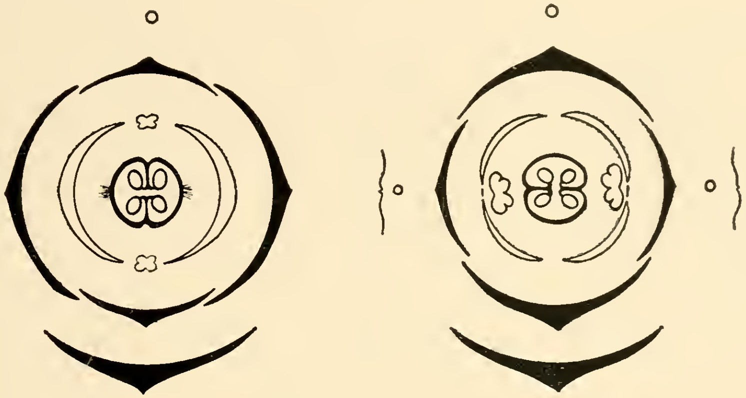


FIG. 1799.—Floral diagrams of Oleaceae. Left, *Fraxinus dipetala.* Right, *Olea europaea.* (*After Eichler.*)

The **calyx** is gamosepalous, valvate in aestivation and composed of four sepals, or five to ten in *Jasminum*, or absent in *Fraxinus*.

The **corolla** is regular and gamopetalous (Fig. 1800), usually tubular and composed of four petals or five to six in *Jasminum*. Aestivation is valvate except in *Jasminum* where it is imbricate.

The **androecium** is composed of two free stamens usually placed transversely but sometimes median. In a few genera four stamens occur. They are epipetalous and inserted on the base of the corolla. The anthers dehisce laterally by a longitudinal slit.

The **gynoecium** is bicarpellary and syncarpous, the carpels alternating with the stamens and therefore usually median. The ovary is bilocular and superior, each loculus containing two ovules which may be pendulous or ascending (*Jasminum*). *Fraxinus* has three ovules in each loculus, the two laterals being abortive. In *Forsythia* four to ten ovules may be present.

The **fruit** varies greatly; in *Forsythia* and *Syringa* it is a loculicidal capsule; in *Ligustrum*

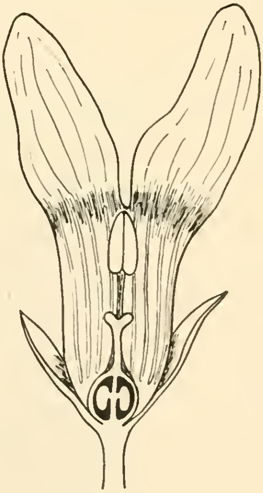


FIG. 1800.—*Forsythia suspensa.* Longitudinal section of flower.

and *Jasminum* a berry; in *Olea* a drupe; in *Fraxinus* a samara. The berry in *Jasminum* is vertically constricted giving the appearance of a double structure.

The **seeds** are endospermic, the reserve material being oil, except in *Jasminum*, and the embryo is small and straight.

The family contains about 400 species distributed among twenty-one genera. They are found in temperate and tropical regions but the main centres of distribution are Indo-Malaya and the Sino-Japanese region. Economically the most important genus is *Olea*, for *O. europaea* is the Olive of commerce. It is a tree which may reach a very great age. It is probably a native of Abyssinia whence it was introduced into the Mediterranean regions of Europe during the first century before Christ. The olive oil is obtained by pressing the fleshy fruits. There are actually two forms which may be distinct species. The wild form has thorny twigs and small fruits, while the cultivated form is smooth and has large fruits. *O. laurifolia* yields good timber known as Black Ironwood. The presence of peltate hairs is an anatomical feature common to all members of the family, while the absence of bicollateral bundles distinguishes this family from the Gentianaceae, Loganiaceae, Apocynaceae and Asclepiadaceae, and the absence of laticiferous tissue separates it from the Styracaceae and Ebenaceae. Sclerenchymatous fibres often occur in the leaf mesophyll.

The family is classified as follows, mainly on the nature of the fruit and on the position of the seed.

I. Oleoideae

Seeds pendulous. Fruits not vertically constricted.

1. *Fraxineae.* Fruit a samara. Only genus *Fraxinus.*
2. *Syringeae.* The fruit is a loculicidal capsule. *Syringa* and *Forsythia.*
3. *Oleeae.* The fruit is succulent, either a berry or a drupe. *Olea* and *Ligustrum.*

Fig. 1801.—*Jasminum officinale.* Flowering shoot.

II. Jasminoideae

The seeds are erect, and the fruit divided into two parts by a vertical constriction, except when one carpel fails to develop. *Jasminum* (Fig. 1801).

The Oleoideae include about half the known species of the family. Economically, in addition to the Olive the only important genus is *Fraxinus* (Fig. 1802). The Common Ash is valuable for its wood, which is close-grained and non-splitting and is employed in the manufacture of handles for implements. There are some sixty species of *Fraxinus* which are distributed in North America, eastern Asia and southern Europe. The genus *Syringa* (Fig. 1803) includes the Lilacs of horticulture which are mostly derived from *S. vulgaris*. There are about thirty species distributed through Europe and Asia. *Forsythia* (Fig. 1804), which is widely grown in gardens because of its bright spring flowers, is a native of China. *Ligustrum*, with fifty species, is found in Europe, Asia and Australia. *L. vulgare*, Privet, is much used in hedges.

FIG. 1802.—*Fraxinus excelsior*. Ash. Left, female inflorescence. Right, male inflorescence.

The pollination mechanism in the sub-family varies. *Fraxinus* is wind-pollinated, *Syringa* and *Ligustrum* are hermaphrodite and in the absence of insect-pollination many become self-pollinated. *Jasminum* and *Forsythia* are pollinated by insects. We may consider two examples.

In *Syringa* (Fig. 1805) the flowers are homogamous and the individual flowers are aggregated into large conspicuous inflorescences. The corolla tube is about a centimetre long and about 2 mm. in diameter. The lower 2 to 4 mm. of the tube is filled with nectar which is liberally secreted by the

FIG. 1803.—*Syringa vulgaris*. Lilac. Inflorescence.

FIG. 1804.—*Forsythia viridissima*. Flowers.

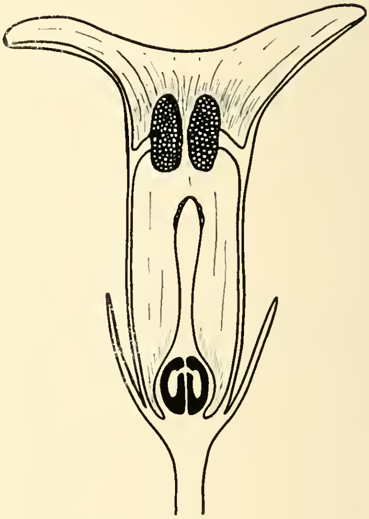


FIG. 1805.—*Syringa*. Flower in longitudinal section. For pollination see in text

ovary. The anthers are attached to the petals near the top of the tube and well above the top of the style. It would appear therefore that when the insect thrusts its proboscis into the flower to suck the nectar, the pollen would be transferred from the anthers to the stigma. In practice however this does not occur, because the pollen grains do not adhere to the dry proboscis, but only to one wetted with nectar and hence the pollen is picked up only during the withdrawal of the proboscis, and therefore after it has passed the level of the stigma. Hence cross-pollination is usually effected, but, should it fail, pollen will eventually fall on the stigma from the anthers above and self-pollination is thereby ensured.

In *Forsythia* the yellow flowers are homogamous, appearing early in the year before the leaves. Nectar is concealed. Darwin thought that a heterostylous condition occurred in *Forsythia*, but in gardens it is found that *F. suspensa* is only short-styled whereas *F. viridissima* is long-styled. The seeds from *F. suspensa* often produce *F. intermedia* which is apparently a hybrid. In *F. viridissima* the style usually projects beyond the stamens so that insects must first touch the style before meeting the mature anthers, thereby effecting cross-pollination. In some flowers however the style is so short that the stigma touches the anthers and self-pollination is inevitable. The visitors are mainly bees.

Another order, the **Plantaginales**, is somewhat nearly related to the Oleales. It contains the single family **Plantaginaceae**. The members of this family are annual or perennial herbs. The flowers are developed in close heads or spikes and are usually hermaphrodite. There are four sepals, four petals and four stamens, the latter having very long filaments with versatile anthers containing much powdery pollen. The gynoecium has two loculi containing many anatropous ovules. The fruit is a capsule with circumscissile dehiscence; occasionally it is a nutlet. Pollination is usually by wind. The chief genera are *Plantago* (Plantain) and *Littorella* (Fig. 1806) in which the flowers are monoecious. Many consider that the family represents a degraded type, originating from the Scrophulariaceae. *Plantago* is notable for its strongly marked protogyny.

A further small order, the **Campanulales**, may also be mentioned here. Their systematic position is uncertain, but they may be considered as somewhat distantly related to the Compositae. The order includes several small families of which the only important one is the **Campanulaceae**. This family contains about sixty genera and 1,000 species. They are temperate and subtropical herbs with alternate leaves, containing latex. The inflorescence is generally racemose, though occasionally the flowers may be solitary or cymosely arranged. The flowers (Fig. 1807) are hermaphrodite, regular and pentamerous. In some, the odd sepal is anterior due to the twisting of the bud through 180°. There are five stamens whose anthers may be united. The gynoecium is multilocular and bears many

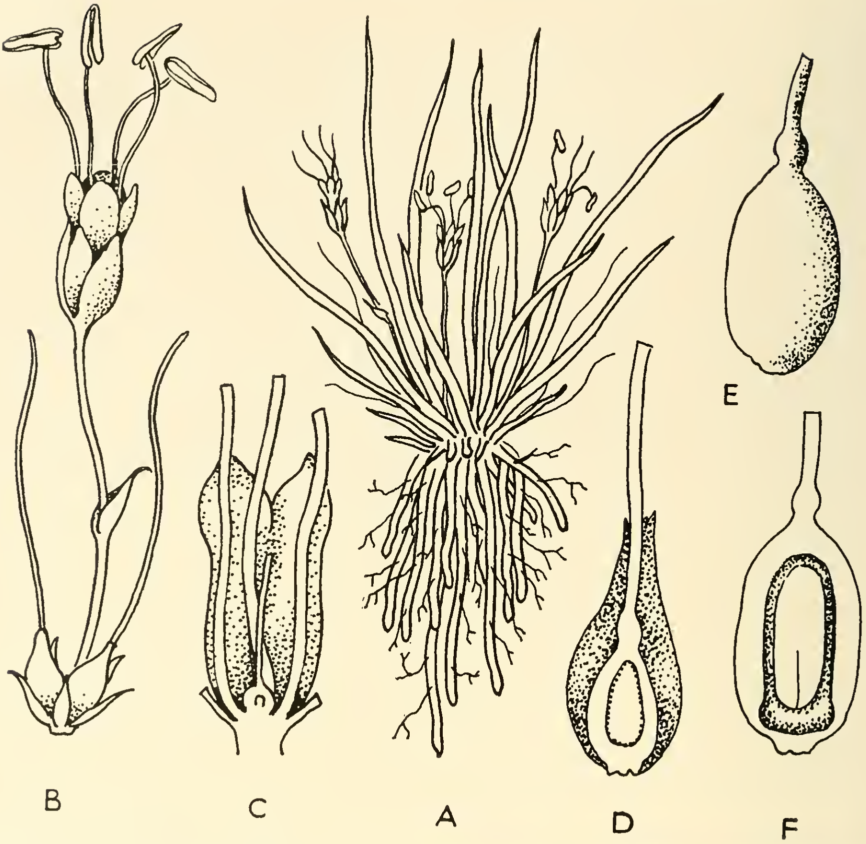


FIG. 1806.—*Littorella uniflora.* A, Flowering plant. B, Male flower with two female flowers at base. C, Male flower in section showing abortive carpel. D, Female flower in section. E, Fruit. F, Fruit in section. (*After Engler-Prantl.*)

FIG. 1807.—*Campanula persicifolia.* Flowers.

anatropous ovules with axile placentation. The fruit is usually a capsule or rarely a berry. The seed is endospermic.

A number of genera are grown in gardens. *Phyteuma*, *Jasione*, *Platycodon* and *Lobelia* may be mentioned, but by far the commonest is *Campanula* with 300 species, eight of which, including *C. rotundifolia* (Harebell), occur in Britain.

Fig. 1808.—*Statice limonium* (*Limonium vulgare*). Inflorescence.

Another small order, the **Plumbaginales**, contains the single family **Plumbaginaceae** with some ten genera and about 260 species. The plants are perennial shrubs or herbs, with narrow leaves often possessing water glands. The flowers are regular and pentamerous. The calyx is persistent and the stamens are opposite the petals. The ovary is superior, unilocular and contains a single ovule.

Among the common genera is *Statice* with about 130 species which are cosmopolitan in distribution but are found chiefly in salt marshes and on steppes. *S. limonium* is the Sea Lavender (Fig. 1808) which is common in Britain. The flowers are often heterostylous. The closely related *Armeria* (Sea Pink or Thrift) is found in similar situations. *Plumbago*, with ten

Fig. 1809.—*Ceratostigma willmottianum*. Inflorescence.

cosmopolitan species, possesses racemose inflorescences. It is sometimes cultivated in gardens. Species of *Ceratostigma* (Fig. 1809) are also cultivated for their fine blue flowers. There are ten species, found in China and Japan, which possess compound racemose inflorescences.

BORAGINALES

In an attempt to split the order Tubiflorae into a number of smaller groups Hutchinson has suggested the introduction of a number of separate orders of which the Boraginales is one. In this work we have not thought it advisable to go as far as Hutchinson, more especially because it would be necessary to consider a number of relatively unimportant families if a clear idea of Hutchinson's method was to be given. We have, however, retained Hutchinson's order names as far as possible and will discuss the following four orders, Boraginales, Solanales, Personales and Lamiales, all of which were included by Engler in the Tubiflorae. While it is desirable to divide the Tubiflorae into smaller groups it is important to appreciate that the four orders are closely related and are thought to have a common origin from regular, isostemonous flowers in which there has been an increasing tendency towards the development of zygomorphy.

In the Boraginales the corolla is actinomorphic, but a more interesting feature is the reduction and specialization of the gynoecium, in which the ovary, which was originally bilocular, becomes divided by a false septum into four uniovular segments. In the Solanales, the flowers are regularly isostemonous, with a bilocular multi-ovulate ovary; while in Personales and Lamiales the corolla shows marked zygomorphy, with a reduction in the number of ovules in the Lamiales but a multi-ovulate ovary in the Personales.

We may define the **Boraginales** as Metachlamydeae in which the plants are mostly herbaceous, or rarely woody, with an actinomorphic corolla and epipetalous stamens which alternate with the corolla lobes. The ovary is bicarpellary, often deeply lobed, with a gynobasic style and paired ascending ovules.

As recognized by Hutchinson this order does not include the families Polemoniaceae or Hydrophyllaceae which he separates into a distinct order, the Polemoniales. This differs mainly in the numerous sessile ovules and in the axile placentation. The **Polemoniaceae** are a small family occurring mainly in the New World and consists of about 300 species. They are mostly annual or perennial herbs or occasionally climbers. Among common garden plants belonging to the family we may mention *Phlox* (Fig. 1810), various species of which are common in gardens, *Polemonium* which is also grown as a herbaceous garden plant and *Cobaea scandens* (Fig. 1811) which is a greenhouse tendril-climber, often planted out during the summer. The flowers are protandrous, greenish at first with an unpleasant smell and adapted to fly-pollination. Later they become purple with a sweet, honey scent and are pollinated by bees.

FIG. 1810.—*Phlox*. Herbaceous garden form. These favourite garden plants are mostly hybrids of *P. paniculata* and *P. maculata*.

FIG. 1811.—*Cobaea scandens*. Flower.

The **Hydrophyllaceae** are also mainly North American in distribution. The family contains about 200 species most of which are annual or perennial herbs, with parietal placentation. Species of *Nemophila* are grown in gardens. *Hydrophyllum canadense* is used as an antidote for Poison Ivy and for various skin diseases.

The **Boraginaceae** are a large family with about 1,600 species, included in some ninety genera. The plants are mostly annual or perennial herbs, more rarely trees or shrubs, usually with simple, alternate leaves and flowers which are arranged in scorpioid cymes. Rough bristles are a notable feature of the vegetative parts. The flowers are hermaphrodite, only rarely zygomorphic, and hypogynous. The sepals are five in number, usually free or united into a bell-shaped tube. The corolla is tubular and composed of five petals, and in *Symphytum* there is an inner corona formed of petal lobes. The stamens are equal in number to the petals and alternate with them. The gynoecium is composed of two carpels which are initially unilocular, but, by the growth of false septa, the ovary becomes divided into four uniovulate segments with a single gynobasic style. The ovules are more or less erect with orthotropous micropyles. The fruit consists of four nutlets, or more rarely drupes. The seeds may or may not be endospermic and the shape of the embryo is variable.

The family is represented in Britain by a number of genera. Among the more important and best known are *Borago* (Borage), *Myosotis* (Forget-me-not), *Symphytum* (Fig. 1812) (Comfrey), *Anchusa* (Fig. 1813) (Alkanet), *Cynoglossum* (Hound's Tongue), *Echium* (Viper's Bugloss), *Heliotropium* (Heliotrope) (Fig. 1814).

Fig. 1812.—*Symphytum officinale.* Comfrey. Flowering shoot.

Fig. 1813.—*Anchusa italica.* The blue garden *Anchusa.*

Fig. 1814.—*Heliotropium peruvianum.* Garden Heliotrope. Inflorescence.

Many are cultivated in gardens, particularly those from the Mediterranean region. *Alkanna tinctoria* yields Alkanet Root, while species of the genus *Cordia*, many of which are trees, yield the valuable tropical American timber known as Aloewood and Princewood.

SOLANALES

The Solanales are Metachlamydeae in which the plants are mainly herbs or twiners, with alternate leaves. The flowers are usually actinomorphic and pentamerous, and the ovary is superior, containing numerous or solitary ovules grouped in one to five loculi. The seed is endospermic and the embryo is generally curved.

The order contains two important families: the Solanaceae, which we shall consider in detail, and the Convolvulaceae.

The **Convolvulaceae** were separated by Rendle into a distinct order, the Convolvulales, which he also separated from the Tubiflorae. Engler on the other hand included the family in the Tubiflorae. It is a family of about 1,100 species divided among fifty genera. They are annual or perennial herbs often growing by twining up other vegetation. The flowers are often showy and are either borne singly in the axils of the leaves or in axillary dichasia. The family is notable for having both latex and bicollateral bundles. The flowers are hermaphrodite and actinomorphic; and bracts often form an involucre. The sepals are often free but the petals are joined to form a funnel-shaped, pentamerous corolla. There are five stamens inserted towards the base of the corolla tube. The anthers have two loculi. The ovary contains one to four loculi with either solitary or paired ovules. The fruit is either a berry, a nut or a capsule. The cotyledons are large and folded or crumpled in the seed, which is endospermic.

Wettstein suggests that the Convolvulaceae may have had a distinct origin from the other groups of the Tubiflorae and considers them as allied phylogenetically to the Malvales or Geraniales. Hutchinson appears to favour a close relationship of the Geraniales with the Convolvulaceae and places the latter family among the Tubiflorae.

A number of interesting plants belong to this family. *Convolvulus* (Fig. 1815) itself shows great variety of habit. Usually it is a twiner, but in dry parts of Palestine and Arabia it becomes a spiny shrub. There are three British species, two of which are usually placed in the related genus *Calystegia*, *i.e.*, *C. sepium*, the Common Bindweed, and *C. soldanella*, the Sea Bindweed. The genus *Ipomoea* is very similar to *Convolvulus*, but often develops a perennial tuberous rhizome. In some, *e.g.*, *I. batatas*, the lateral roots become fleshy and this plant is grown in the tropics as a vegetable under the name of the Sweet Potato. The tubers are rich in both starch and sugar.

The genus *Cuscuta* (Fig. 1816) includes a number of parasitic climbing plants collectively termed Dodder. Many cause considerable damage to the plants on which they live. *C. trifolii* on Clover and *C. epithymum* on

Fig. 1815.—*Convolvulus* (*Calystegia*) *sepium*. Bindweed.

Fig. 1816.—*Cuscuta europaea*. Dodder. Twining stems and inflorescences.

Gorse and other plants are among the more common. The plants are climbers with pink, yellow or white filamentous stems. The seed on germination produces a thin leafless stem which grows upright and then curves and rotates to encounter a host (Fig. 1817). If it fails to make contact it collapses to the ground and remains quiescent for several weeks only to renew its activity again later. If it again fails to find a host, the seedling dies. After attachment to a suitable host by haustoria has been established the parasite loses its connection with the soil. We shall consider the structure in greater detail in Volume IV.

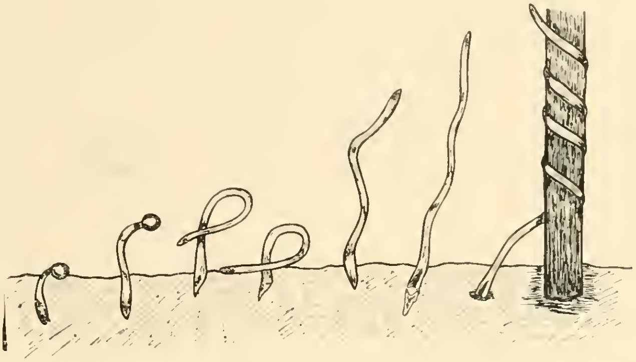


FIG. 1817.—*Cuscuta*. Stages in the germination and development of the seedling. (*After Kerner and Oliver.*)

Solanaceae

The members of this family are mostly herbaceous plants, many of which are annual, some are climbers and a few are woody. The leaves are alternate, simple or compound. Stipules are absent. Adnation of leaves or of bracts to their axillary shoots is common in the family and results in complex changes in the plant form.

The family includes a number of common or well-known plants, many of which are found wild in Britain. Among the common British species we may mention *Solanum dulcamara* (Bitter Sweet), *S. nigrum* (Woody Nightshade), *Atropa belladonna* (Deadly Nightshade) and *Hyoscyamus niger* (Henbane). Other species commonly grown in Britain are: *Datura stramonium* (Thorn Apple), *Solanum tuberosum* (Potato), *Nicotiana tabacum* (Tobacco), *Lycium halamifolium* (Tea plant) (not to be confused with *Camellia sinensis*, the Tea Bush from which the beverage is obtained), *Mandragora officinalis* (Mandrake) and *Physalis alkekengi* (Winter Cherry). In addition there are a number of other economic species which in this country must usually be grown under glass. Of these we may mention *Solanum lycopersicum* (Tomato), *S. melongena* (Aubergine or Egg Plant), *Capsicum* spp. (Chillies) and *Physalis peruviana* (Cape Gooseberry).

The **inflorescence** is usually cymose, with the bracts sometimes adnate to the axillary flowers.

The **flowers** (Fig. 1818) are usually actinomorphic, pentamerous and hermaphrodite.

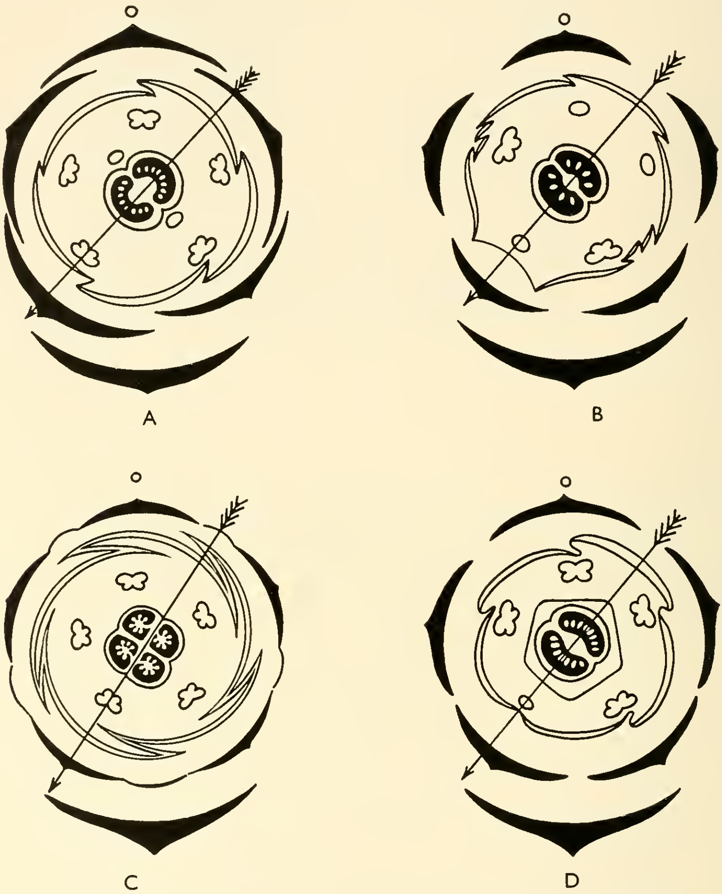


Fig. 1818.—Floral diagrams of Solanaceae. A, *Petunia nyctaginiflora*. B, *Schizanthus retusus*. C, *Datura stramonium*. D, *Salpiglossis sinuata*. (*After Eichler*.)

The **calyx** is gamosepalous, and five-cleft, persistent.

The **corolla** is gamopetalous (Fig. 1819), usually five-lobed and the lobes either folded, contort or valvate.

The **androecium** consists of five stamens which are epipetalous and alternate with the lobes of the corolla. The anthers are sometimes connate, two-chambered and opening either by a longitudinal split or by an apical pore.

The **gynoecium** is bicarpellary and syncarpous and the ovary is usually bilocular but occasionally becomes multilocular by the development

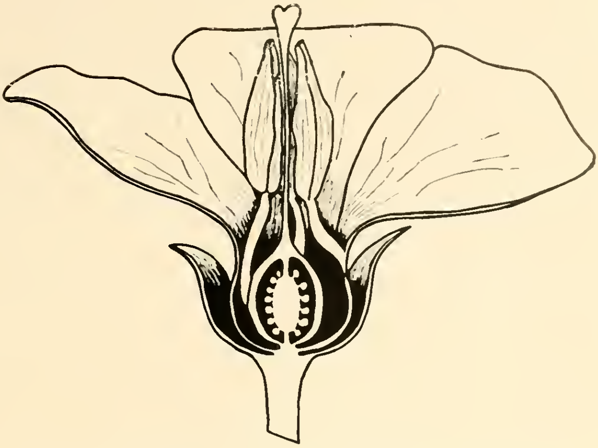


FIG. 1819.—*Solanum tuberosum.* Flower in longitudinal section.

of false septa. The two carpels are placed obliquely in the flower and not in the median plane. The placentation is axile. The ovules are numerous.

The **fruit** is either a capsule or a berry.

The **seeds** are endospermic and the embryo is generally curved.

The family contains about eighty-five genera with about 2,000 species which are distributed mainly in the tropics, although there are a number in temperate climates. They are mostly herbaceous although in the genus *Solanum* (Fig. 1820) a few species form shrubs, trees or climbers.

FIG. 1820.—*Solanum crispum.* Flower in face view.

Certain anatomical characteristics of the family are important. Intraxylary phloem is normal in the stems, and is frequently accompanied by sclerenchymatous fibres, while the secondary xylem contains no fibres.

In certain genera, *e.g.*, *Datura*, *Scopolia* and *Atropa*, there is no intraxylary phloem in the roots.

The leaves of the Solanaceae are usually alternate on the vegetative branches but become opposite in the flowering shoots. Both the branching and the leaf arrangement are, however, subject to many irregularities produced by adhesion, that is the adnation of leaves and shoots to the main axis, in varying degrees. Thus, leaves are frequently adnate to the whole of the internode above, so that they appear at the node above their point of origin, while in *Solanum nigrum*, and other species, the inflorescence peduncle is partly adnate to the axis and appears to be attached to the middle of an internode.

The family is of considerable economic importance. We have already referred to a number which are used as vegetables. Others yield drugs, as for example *Atropa* (Fig. 1821), *Hyoscyamus*, *Solanum* and *Datura*. Many are cultivated in gardens as semi-hardy perennials or as annuals. Among the best known are *Petunia*, *Nicotiana*, *Salpiglossis*, *Schizanthus* and *Datura*.

FIG. 1821.—*Atropa belladonna*. Deadly Nightshade.

According to Wettstein the family is classified as follows, the chief characters being the shape of the embryo and the nature of the gynoecium.

I. Solanoideae

Embryo curved through more than a semi-circle. All five stamens fertile and equal or only slightly unequal.

1. *Nicandreae*. Ovary three- or four-chambered, the walls of the loculi dividing the placentae unequally. *Nicandra*, a native of Peru, but cultivated widely as a garden plant.
2. *Solaneae*. Ovary two-chambered. This tribe contains the largest number of the genera and is sometimes further subdivided.

Lycium, *Atropa*, *Hyoscyamus*, *Physalis*, *Capsicum*, *Solanum*, *Mandragora*.

3. *Datureae*. Ovary four-chambered, the walls of the loculi dividing the placentae equally. *Datura*, *Solandra*.

II. **Cestroideae**

The embryo is either straight or if curved the curvature is less than a semi-circle.

1. *Cestreae*. Androecium of five stamens, all of which are functional. *Cestrum*, *Nicotiana*, *Petunia* (Fig. 1822).

FIG. 1822.—*Petunia* "*hybrida*" of gardens. The garden forms are mostly hybrids of *P. nyctaginiflora* and *P. violacea*.

2. *Salpiglossideae*. Androecium of five stamens, only two or four of which are fertile and these are always of unequal length. *Salpiglossis*, *Schizanthus*, *Brunfelsia*.

The Solanoideae are by far the larger of the two sub-orders and include most of the genera of economic importance. *Solanum* is the largest genus with about 1,200 species, most of which are herbs. The corolla is rotate and the fruit a many-seeded berry. The anthers form a cone in the centre of the flower and dehisce by apical pores. The pollination is sometimes effected by bees. In *S. tuberosum* (Fig. 1823) the flowers are white or pale violet and are erect by day but droop by night. When the flower is visited the stigma is touched first, hence favouring cross-pollination. There is however no nectar and the quantity of pollen is small. Self-pollination therefore is customary and it appears to be effected either by the folding of the corolla or by curvature of the style which brings it into the line of falling pollen. In *S. dulcamara* there are capitate projections on the receptacle which occur in pairs at the base of the corolla lobes. Like the recep-

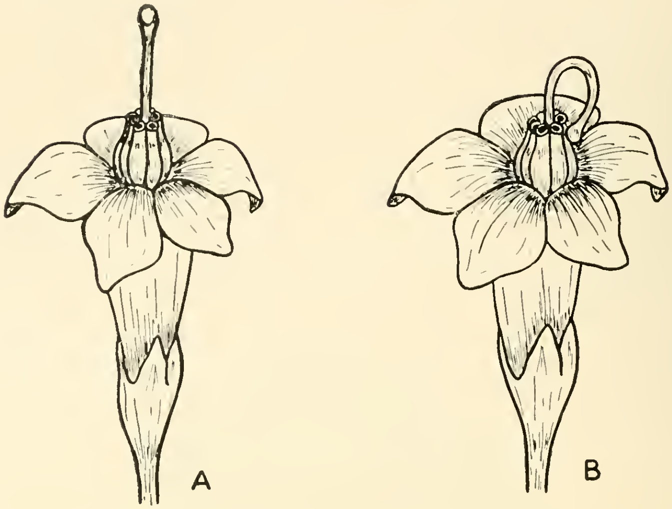


FIG. 1823.—*Solanum tuberosum.* Flowers illustrating pollination. See in text.

tacle itself they are shining and look damp, giving the suggestion of nectaries, though they are not secretory, and insects visit the flowers in their search for nectar. The insect trying to find the nectar shakes pollen out of the sacs on itself and cross-pollination may thereby be effected.

In the genus *Datura* nectar is secreted at the base of the ovary and is concealed in the lowest, contracted part of the bell-shaped corolla. The flowers (Fig. 1824) are protogynous and are visited by humble bees. The genus contains fifteen species most of which are shrubs, herbs or occasionally trees in subtropical countries. Stramonum is obtained from *D. stramonium*, but the species is also interesting because of the mutant races which have been discovered. *Datura* is one of the few genera in which a mutant with less than the basic number of chromosomes has been discovered. *D. stramonium* has fourteen chromosomes but a number of mutants have been found by Blakeslee each corresponding to the loss of a different single chromosome.

FIG. 1824.—*Datura stramonium.* Flowering shoot.

The genus *Physalis*, with forty-five species, is found in the warmer parts of North and South America. It is peculiar because of the large, coloured, bladder-like structure which is formed from the calyx and encloses the ripe (see Fig. 1132), edible berry. The structure is often bright red and the plant is often grown in gardens under the name of Chinese Lanterns.

The genus *Capsicum* has a peculiar distribution. Thirty species are recorded from South and Central America, while one species, sometimes separated as a genus *Tubocapsicum*, is found in Japan. *C. annuum* is the commonly cultivated species, its fruits yielding Chillies or Red Pepper. When these are dried and powdered they are sold as Cayenne Pepper.

There are about 100 species of the genus *Lycium*, most of which are shrubs or trees. The plants are widely distributed in temperate regions of both hemispheres. They are often thorny, with a narrow, bell-shaped corolla, and the fruit is a berry. *L. halamifolium* is a straggling climber often occurring as a semi-naturalized plant in this country. We have already referred to its popular name of Tea plant. It is reported to have been introduced in error for the true Tea bush.

FIG. 1825.—*Nicotiana tabacum.* Inflorescence.

In the Cestreae by far the most important genus is *Nicotiana*. There are some fifty species, occurring in America and Polynesia with one species in Australia. *N. tabacum* (Fig. 1825) is cultivated in many tropical countries and more particularly in the United States, Cuba, Sumatra, Egypt and Brazil. Other species, including *N. rustica*, are also grown. Different varieties of *N. tabacum* are used in the preparation of cigar, pipe and cigarette tobacco, *N. rustica* being now chiefly employed as a source of

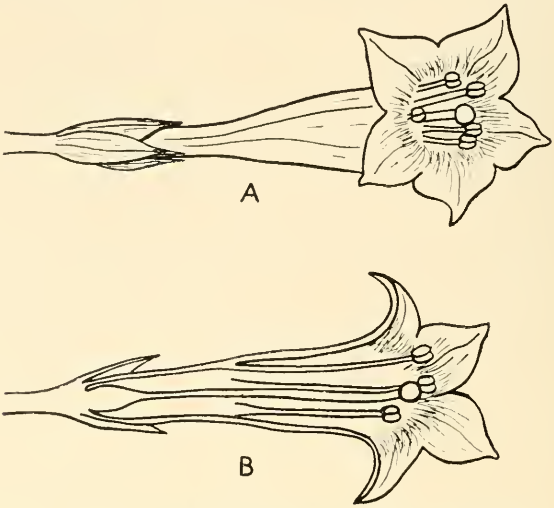


FIG. 1826.—*Nicotiana tabacum.* Flowers illustrating pollination. See in text.

FIG. 1827.—*Schizanthus wisetonensis.* Garden forms which are hybrids of *S. pinnatus* and *S. grahami.*

commercial nicotine. *N. affinis* and others are used as half-hardy annuals in garden bedding. The common flower colours are red and white. The flowers are night-scented and secrete nectar. When they open (Fig. 1826) the stigma is mature and the anthers dehisce at the same time or later. The stamens differ in length in the various species, but there are usually four stamens of the same length and one, the posterior, which is shorter. Occasionally two are higher than and two at the same level as the style. Cross-pollination is sometimes effected by night-flying moths, particularly in the white form of *N. affinis*. In *N. tabacum* self-pollination generally occurs though bees have been observed to visit the flowers occasionally.

Species of the genus *Salpiglossis* are cultivated as half-hardy annuals in gardens for the sake of the large flowers bright with coloured markings. There are eight South American species. The genus *Schizanthus* (Fig. 1827) also provides cultivated species often grown for decoration in greenhouses or as a summer annual. There are eleven species all found in Chile.

The genus *Cestrum* with about 150 species occurs in America; some are grown as wall-shrubs in gardens, but they are usually treated as greenhouse subjects.

Personales

As already explained, this order is used by Bentham and Hooker and by Hutchinson to include the following families: Scrophulariaceae, Orobanchaceae, Lentibulariaceae, Gesneriaceae, Bignoniaceae, Acanthaceae and the less important order Pedaliaceae in which are included several species whose fruits we have already mentioned. (See p. 1565.)

The order may be characterized by the alternate or opposite leaves, the invariably zygomorphic corolla, the reduction in the number of stamens to four or two. The ovary contains numerous ovules, which generally have axile placentation.

The order includes a number of important families, as will be seen from the above list, and though we shall consider only the Scrophulariaceae in detail we shall first consider more briefly the important features of the other families.

The **Orobanchaceae** are all parasites living usually on the roots or stems of Angiosperms (Fig. 1828). The leaves are alternate and are never green. They are reduced to fleshy scales at the base of the stem and may be greatly reduced in the flower spike. The flowers are solitary in the axils of bracts and form large racemose inflorescences. The flowers are strongly zygomorphic, hermaphrodite and dusky yellow or violet in colour. The androecium consists of four stamens, in two pairs, of which the anterior is longer. The ovary is superior and unilocular, with four parietal placentae which bear numerous ovules. The seeds are very small, but are endospermic and contain minute embryos. Pollination is by insects which are attracted by nectar secreted at the base of the flower.

The species are almost confined to the northern hemisphere and are most plentiful in the warmer parts of Europe and Africa. About a dozen

FIG. 1828.—*Orobanche elatior.* Emergent inflorescence.

species occur in Britain, among which *Lathraea* and *Orobanche* are the best known. *Lathraea squamaria* (Toothwort) (Fig. 1829) occurs as an obligate parasite on the roots of Hazel, Elm, Beech and other trees. It has a thick stem which is covered below by fleshy scale-leaves. These scales are hollow and contain a labyrinthine cavity opening to the exterior by a small pore on the lower surface near the point of attachment. Secretory glands line this cavity and it has been suggested that it may function to catch insects and that previous to its parasitic life the Toothwort was an insectivorous plant. There is no positive evidence for this, however. The flowers are borne on the end of racemose inflorescences and are brownish white in colour with purple bands. These flowers are all twisted round to one side of the inflorescence, in the direction of the strongest light. The flowers are protogynous and, in the first stage, the four stamens are curled up with their anthers lying inside the lower lip of the corolla (Fig. 1830), while the yellow stigma occupies the centre of the flower. In this stage the flowers are pollinated by humble bees. Later the stigmas shrink and the centre of the flower is occupied by the stamens, while the corolla tube elongates to double its length. Cross-pollination is therefore effected, as the bees search the

FIG. 1829.—*Lathraea squamaria.* Inflorescences.

flowers for nectar secreted near the base of the ovary. If cross-pollination fails, the anthers may be carried outside the flowers by the elongation of their filaments, when wind-pollination of the upper flowers of the inflorescence is made possible.

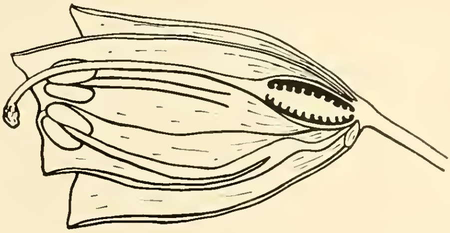


FIG. 1830.—*Lathraea squamaria.* Longitudinal section of flower to illustrate pollination. See in text.

Lathraea clandestina (Fig. 1831), with large purple flowers, is parasitic on Willow and allied shrubs. It is occasionally cultivated in shrubberies. The fruit is a capsule which opens explosively.

The genus *Orobanche* (Broomrape) contains about 100 species which are parasites found in temperate and subtropical regions. Several occur in Britain. Some parasitize only a single host plant, for example *O. elatior* occurs on *Centaurea* and *O. hederae* on Ivy. Others, like *O. apiculata*, are less restricted in the plants they parasitize.

FIG. 1831.—*Lathraea clandestina.* Emergent inflorescences.

The family contains a number of other genera most of which are tropical and among these may be mentioned *Christisonia* in Asia on Bamboos and *Aeginetia*, which occurs on Sugar Cane, in south-eastern Asia.

The **Lentibulariaceae** are a small family containing five genera with about 250 species, of which one genus, *Utricularia*, contains over 200. One other important genus, *Pinguicula*, contains about thirty species. Both these genera are represented in the British Flora. *Utricularia* (Fig. 1832), the Bladderwort, is represented in Britain by four species while there are also four British species of *Pinguicula* (Fig. 1833), the Butterwort. Both genera possess the carnivorous habit, though the mechanism of capture in each genus is completely different. *Utricularia* is a submerged, rootless water plant in which bladders are developed on the finely divided leaves. The flowers rise above the water and are hermaphrodite and zygomorphic. Calyx and corolla consist of five united parts. There are only two stamens and the ovary consists of two carpels forming a single loculus in which numerous ovules are borne on a free-central placenta. The fruit is a capsule opening by valves. In the germination of the embryo it is impossible to differentiate between stem and leaf, for it produces an irregular cell-mass on which arises the leaf rudiments, and no primary root is formed.

Pinguicula is a genus of perennial herbs characteristic of marshy ground and bearing sparse roots. The leaves are large and form a rosette, from which a one-flowered, axillary flower spike arises. The embryo generally produces only one cotyledon.

Utricularia is widely distributed in tropical and temperate regions, but

Fig. 1832.—*Utricularia minor.* Vegetative branch bearing traps.

Fig. 1833.—*Pinguicula vulgaris.* Habit of plant in flower. Photograph by Mr. Harold Bastin.

Pinguicula is restricted to northern temperate parts of the world. Their carnivorous habits will be described in detail in Volume IV.

The other three genera are *Genlisea*, a tropical American and African genus, *Polypompholyx* in tropical Australia, and *Biovularia* which occurs in the West Indies. All are insectivorous.

The **Gesneriaceae** are a much larger family, with over 1,100 species and 100 genera. They are mainly tropical and subtropical herbs and shrubs. Several are cultivated in gardens, *e.g.*, *Streptocarpus* (Fig. 1834), *Ramondia* and *Sinningia speciosa* which, under the name of Gloxinia, is often grown as a stove plant on account of its large trumpet-shaped flowers of red or purple. Many forms with bicoloured flowers have been produced in cultivation. (Germination of *Streptocarpus*, see p. 1596.)

FIG. 1834.—*Streptocarpus* sp. Flowers.

FIG. 1835.—*Columnea schiedeana.* Flower, scarlet and yellow.

Species of the genus *Columnea* (Fig. 1835) are occasionally seen in this country as greenhouse climbers with succulent leaves. There are about seventy-five species in tropical America, several of which live as epiphytes. Anisophylly frequently occurs, large and small leaves forming opposite pairs.

The Orobanchaceae are by some considered to be parasitic degenerate forms of the Gesneriaceae. The latter family is also closely allied to the Bignoniaceae and the Scrophulariaceae.

The **Bignoniaceae** are a somewhat smaller family than the last with some 600 species arranged in over 100 genera. The plants are mostly trees or shrubs or woody climbers forming large lianas. These latter comprise a large proportion of the climbers of the tropical American forest. Many, especially those in Brazil, are pollinated by humming-birds. The anatomy of these stems is anomalous, the xylem being more or less divided into wedge-shaped masses separated by parenchyma. The fruits are capsules and the seeds are winged. Endosperm is absent. There are no British representatives, but several are cultivated. *Catalpa bignonioides* (Fig. 1836) forms a fine tree and good specimens can be seen in this country, for example in Parliament Square, London. *Eccremocarpus scaber* (Fig. 1837) is a

FIG. 1836.—*Catalpa bignonioides.* The long capsule fruits.

FIG. 1837.—*Eccremocarpus scaber.* Inflorescence.

Fig. 1838.—*Acanthus mollis.* A young, developing inflorescence.

Fig. 1839.—*Beloperone* sp. Probably *B. angustiflora.* Inflorescence with large bronze-coloured bracts.

Fig. 1840.—*Martynia fragrans.* Inflorescence.

perennial climber with orange flowers, which is frequently grown in gardens. *Tecoma radicans*, the Trumpet Flower, is a favourite self-clinging climber on house walls in warm climates.

The **Acanthaceae** are a family of herbs or shrubs with about 2,000 species and 250 genera found in the warmer parts of the world. Some are seen in this country as hothouse plants, which are grown on account of their large spikes of bright-coloured flowers often with large coloured bracts. Others, as for example, *Acanthus mollis* (Fig. 1838), can be cultivated in the open in the warmer parts of Great Britain. In some the attractive appearance of the plant is enhanced by the coloured bracts (Fig. 1839).

The **Pedaliaceae** are a small family of annual or perennial herbs which includes only about sixty species divided among twenty genera. They occur mainly in South Africa, Madagascar, Indo-Malaya and Australia. *Sesamum indicum* (Sesame) is widely cultivated for its oily seeds. Two genera, *Harpagophytum* and *Martynia* (Figs. 1840 and 1841), have already been referred to (p. 1565) because of their elaborate barbed fruits.

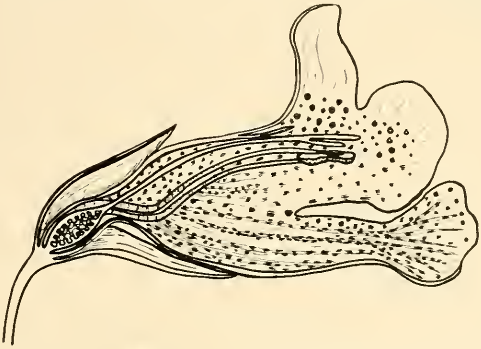


Fig. 1841.—*Martynia*. Longitudinal section of flower. The two stigmatic lobes are normally spreading but close up on being touched, thus trapping pollen from visiting insects.

Scrophulariaceae

The members of the Scrophulariaceae are predominantly herbs, mostly perennial, while trees and shrubs are rare. The flowers show a wide range of structure which is reflected in the method of classification within the family. The family is found in all climates but most abundantly in temperate regions and very rarely either near the equator or towards the poles (Fig. 1842). Some members of the family are parasitic and others semi-parasitic.

There are many common genera in the British Flora, while many more are commonly cultivated in gardens. Familiar British examples are *Digitalis* (Foxglove), *Veronica* (Speedwell), *Scrophularia* (Fig Wort), *Linaria* (Toadflax), *Verbascum* (Mullein). Among the semi-parasitic genera found in Britain are *Euphrasia* (Eyebright), *Pedicularis* (Lousewort), *Melampyrum* (Cow-wheat), *Rhinanthus* (Yellow Rattle) and *Bartsia*.

Among the commonly cultivated genera are *Antirrhinum*, *Mimulus*, *Calceolaria*, *Nemesia*, *Collinsia* and *Pentstemon*.

FIG. 1842.—Distribution of *Digitalis purpurea* in Europe.

The **plants** are herbaceous or rarely shrubby, with leaves arranged opposite, alternate or verticillate. Stipules are absent. The stems may be prostrate but are more usually erect. Some are climbers.

The **inflorescence** varies considerably, it may be racemose or a spike, but often the lateral branches of inflorescences have the flowers arranged in cymes. Occasionally the flowers are solitary and axillary. Bracts and bracteoles are usually present.

The **flowers** (Fig. 1843) are hermaphrodite and zygomorphic. They are fundamentally pentamerous, but the typical condition is often obscured by the suppression and fusion of the parts.

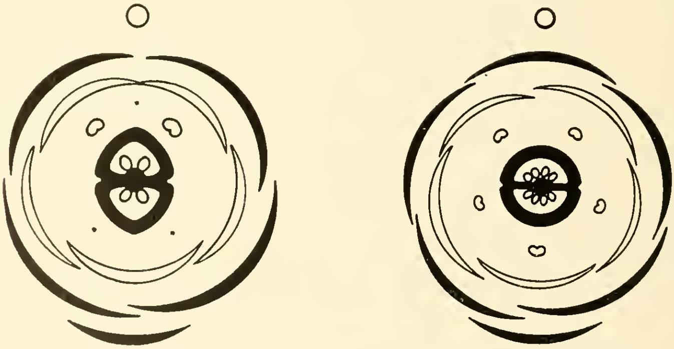


FIG. 1843.—Scrophulariaceae, floral diagrams. A, *Veronica chamaedrys*. B, *Verbascum nigrum*. (*After Eichler.*)

The **calyx** is gamosepalous, usually consisting of five lobes. In *Veronica* and *Calceolaria* the posterior sepal is suppressed. The calyx is usually persistent.

The **corolla** is gamopetalous, hypogynous and usually two-lipped. In *Verbascum* it is nearly regular, while in *Antirrhinum* and *Linaria* it is bilabiate and personate. In *Veronica* it is rotate and four-lobed, owing to the fusion of the posterior pair of petals.

The **androecium** is usually composed of four stamens which are didynamous and epipetalous. In *Verbascum* the posterior stamen is present and functional; in *Scrophularia* and *Pentstemon* it is represented by a staminode while in *Veronica* and *Calceolaria* there are only two stamens, for the anterior pair are also suppressed.

The **gynoecium** is bicarpellary and syncarpous. The style is single and the stigma two-lobed or entire. The ovary is superior and bilocular, the partition lying in the transverse plane. The placentae are axile and bear numerous anatropous ovules.

The **fruit** is a capsule which either dehisces loculicidally or else the walls may split only at the base or at the apex of the capsule, forming pores through which the seeds are distributed.

The **seeds** are endospermic and numerous, and the embryo is either straight or slightly curved.

Anatomically the family is characterized by the rich development of epidermal hairs, often borne both on the stems and leaves. The stem is round except in some species of *Scrophularia* and in *Collinsia* in which it is four-angled. This, together with the form of the leaves and the fact that the flowers are borne in verticillasters, gives this latter genus a superficial resemblance to the Labiatae, though the flowers resemble the Papilionaceae.

The family is an important one, although it is by no means one of the largest families. There are about 3,000 species which are arranged in about 220 genera.

According to Wettstein the family is classified as follows:

I. **Pseudosolanoideae**

The two posterior corolla lobes cover the lateral lobes in the bud. Leaves alternate. Five stamens often present.

1. *Verbasceae.* Corolla with very short tube or none, rotate or shortly campanulate. *Verbascum* and *Celsia.*
2. *Aptosimeae.* Corolla with long tube. *Aptosimum.*

II. **Antirrhinoideae**

The lower leaves, at least, opposite; the posterior stamen either absent or represented by a staminode.

1. *Calceolarieae.* Corolla-two lipped, the lower lip being large and concave. *Calceolaria.*
2. *Hemimerideae.* Corolla with no tube, spurred or saccate at the base. *Alonsoa, Hemimeris.*
3. *Antirrhineae.* Corolla two-lipped, tubular or sometimes spurred or

saccate at the base. *Linaria*, *Antirrhinum*, *Nemesia* and *Rhodochiton*.

4. *Cheloneae*. Corolla two-lipped but not spurred or tubular. Fruit a capsule or a many-seeded berry. Inflorescence cymose. *Collinsia*, *Pentstemon*, *Scrophularia*, *Paulownia* and *Chelone*.
5. *Manuleae*. Corolla two-lipped but not spurred or saccate. Fruit a capsule. Inflorescence not cymose, usually simple. *Manulea Zaluzianskia* and *Lyperia*.
6. *Gratioleae*. Corolla two-lipped, flowers solitary or in racemose inflorescences. *Mimulus*, *Gratiola* and *Torenia*.
7. *Selagineae*. Corolla two-lipped. Fruit a drupe or indehiscent. *Selago*, *Hebenstretia*.

III. **Rhinanthoideae**

Corolla teeth all flat and divergent or the two upper ones erect.

1. *Digitaleae*. Two upper corolla lobes often erect. Not parasitic. *Veronica*, *Digitalis*, *Sibthorpia*.
2. *Gerardieae*. Corolla lobes flat and divergent or two upper ones erect. One anther lobe often reduced. Often parasites or semi-parasites. *Gerardia*, *Harveya*, *Hyobanche*.
3. *Rhinantheae*. (Sometimes considered as a separate family.) Upper corolla lobes forming a helmet-like lip. Parasites or semi-parasites. *Melampyrum*, *Bartsia*, *Rhinanthus*, *Euphrasia*, *Pedicularis*, *Odontites*, *Tozzia*, *Castilleja*.

The members of the sub-family Pseudosolanoideae may be typified by the genus *Verbascum*. The plants are large perennial or biennial herbs with stout tap roots. The inflorescence is racemose but the lateral flowers are often replaced by condensed dichasia. The corolla is nearly regular and the flowers are open, with a very short tube. The plants are essentially north temperate in distribution. Six species occur in Britain where they are known as Mulleins.

The flowers are pollinated by bees and flies. Nectar is secreted sparingly on the inside of the petals. The bright yellow colour of the flowers is further enhanced by the densely hairy stamens, which may be of a different colour from the petals. The stamens and style project freely and pollination by insects is a rather haphazard business, though usually the stigma ripens first. Self-pollination however is quite efficient, in fact it is sometimes produced automatically by the movement of the stamens towards the style as the flowers fade. (See also p. 1311.)

The Verbasceae are usually considered to be closely related to the Salpiglossideae and hence serve as a link connecting the Scrophulariaceae with the Solanaceae. They differ markedly however in the transverse position of the septum in the Scrophulariaceae and its oblique position in the Solanaceae.

In the Antirrhinoideae we find a number of genera of more or less common plants, some of which are found wild in Britain and others are often cultivated in gardens. The genus *Calceolaria* contains about 200 species mainly in South America. Many are cultivated and a large number of ornamental hybrids have been produced. The genus *Antirrhinum* which contains thirty-three species is widely distributed in the northern hemisphere. One species, *A. majus* (Fig. 1844), the Snapdragon, is found in Britain but is probably an escape. Many hybrid forms have been produced which are generally used in summer bedding. The recent spread of a Rust (*Puccinia antirrhini*) has caused great losses among these bedding plants and somewhat reduced their popularity. Rust-resistant varieties have recently been produced.

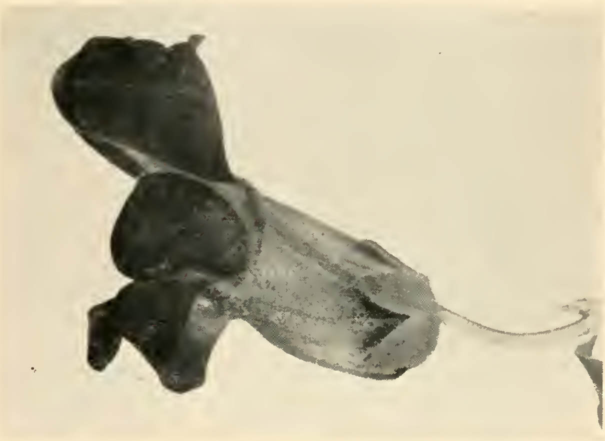


FIG. 1844.—*Antirrhinum majua.* Snapdragon. Flower in profile, showing " personate " form.

The pollination mechanism in the Snapdragon (Fig. 1845) is worthy of special mention. These flowers can only be pollinated by humble bees, for the entrance is completely closed by the upper and lower lips of the corolla. The lower lip possesses two swellings which serve as an alighting platform and fit into two depressions in the upper lip. The anthers are enclosed within the corolla and lie closely against the upper lip. When ripe, the pollen is liberated in two rounded balls which adhere to the back of a bee which visits the flower to reach the nectar secreted at the base of the ovary. Visits by small insects, including small bees which would not effect pollination, is prevented by the closed flower, for only a humble bee is heavy enough to depress the lower lip and thus gain access to the nectar. Small bees may sometimes visit the older flowers, which are not entirely closed, in the hope of finding a little residual nectar. Humble bees sometimes rob the flowers by biting through the corolla tube and sipping the nectar from the outside. Should cross-pollination fail self-pollination is possible in some species by pollen adhering to the hairy lining of the lower lip, which is brought into contact with the style.

Both in species of *Antirrhinum* and also in *Linaria*, nectar guides are

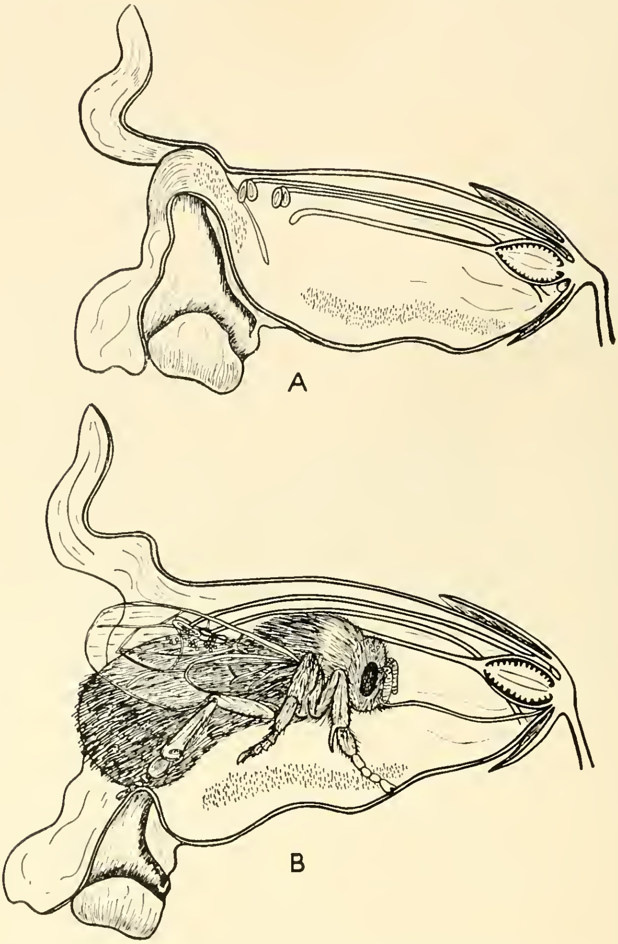


FIG. 1845.—*Antirrhinum majus.* Flowers in longitudinal section showing how the entrance is forced open by humble bees.

present on the lower lips of the flowers. In *Linaria* (Fig. 1846) (Toadflax) nectar is secreted at the base of the ovary and stored in the spur. In this genus should pollination fail, cleistogamic flowers are occasionally produced.

The zygomorphic character of the flowers of this sub-family shows considerable variation. In *Linaria* the single anterior petal is spurred. In *Diascia* there is a spur on each of the anterior lateral petals. In *Calceolaria* the spur is short but is formed as in *Linaria*, from the anterior petals. In *Antirrhinum* the two carpels are unequal in size, the anterior being considerably the larger. Peloric anomalies occur in *Linaria*, the flowers becoming actinomorphic by the formation of spurs on all the petals.

The genus *Scrophularia* is common in north temperate regions. There

FIG. 1846.—*Linaria vulgaris.* Yellow Toadflax. Flowers, with long spurs.

are about 130 species, three of which occur in Britain, under the name Figwort. The flowers are reddish-brown in colour and are borne on compound inflorescences, the main branching being racemose and the secondary shoots dichasial. In *S. nodosa* the flowers are protogynous and nectar is secreted by glands situated in the base of the widely open corolla. These flowers are almost exclusively visited by wasps, both in Europe and in North America (Fig. 1847). Should pollination by their agency fail the stigma remains receptive and self-pollination may be effected by pollen from the ripe anthers falling upon the stigmatic surface from above. Cleistogamic flowers are said to be produced occasionally by this species.

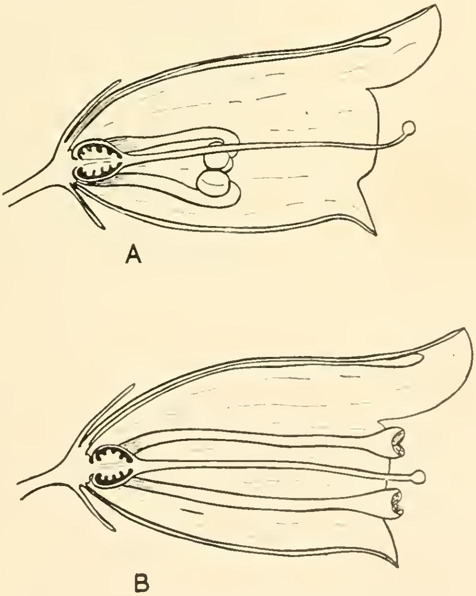


FIG. 1847.—*Scrophularia nodosa.* A, Early stage with stigma extruded and receptive. B, Stamens elongated, when self-pollination becomes possible.

The third sub-family, the Rhinanthoideae, includes all the semi-parasitic genera such as

Euphrasia, *Rhinanthus*, *Melampyrum*, *Odontites*, *Pedicularis* and *Bartsia*. According to Heinricher these constitute a series of parasitic forms which he considers culminates in *Lathraea*, now generally included in the Orobanchaceae. We shall discuss the parasitic habit of these genera in Volume IV.

In addition this sub-family also includes two important non-parasitic genera, *Digitalis* and *Veronica*. The genus *Digitalis* contains some 250 species, common in Europe and western Asia, while *Veronica* is represented by over 200 species which occur chiefly in north temperate regions and also in New Zealand and Australia. The southern species are nearly all shrubby and are separated by many authorities under the generic name of *Hebe*.

In *Digitalis purpurea* (Fig. 1848), the Common Foxglove, the large, purplish flowers are very conspicuous, more especially because they develop in long unilateral racemes. Their shape and the way in which the flowers hang prevent rain from accumulating in the corolla tube. There are nectar guides in the throat of the corolla which take the form of dark purple spots surrounded by white margins. The lower lip is also provided with numerous fine bristle-like hairs. Whether these serve to prevent the entrance of small insects who might steal the nectar, or whether they serve as a grip for large visiting insects is not known, maybe they have both functions.

FIG. 1848.—*Digitalis purpurea*. Foxglove. Inflorescence.

Nectar is secreted at the base of the ovary and stored in the base of the corolla tube, which is itself proportioned to the body of a humble bee, the only insect which normally visits the flower (Fig. 1849). The style and stamens lie against the upper side of the corolla tube. The two long stamens dehisce first, followed by the shorter ones, and it is only after the latter have completely liberated their pollen that the stigma becomes receptive. Should the flower not be visited by an insect, self-pollination is possible, for as the stigmatic lobes diverge they come into contact with the stamens.

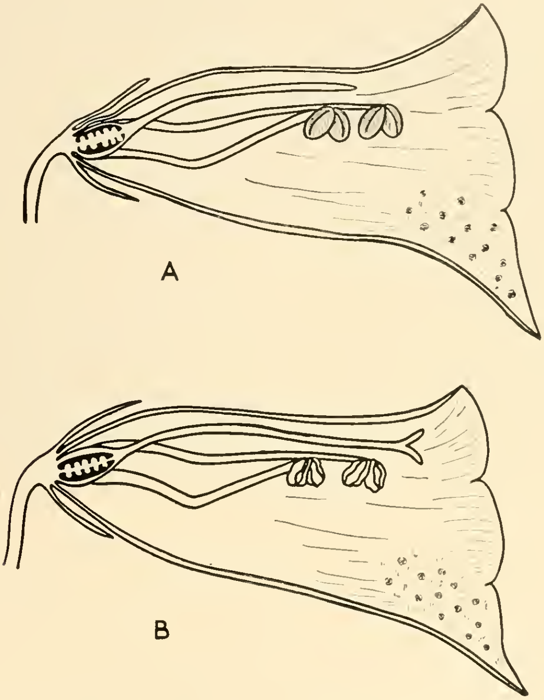


Fig. 1849.—*Digitalis purpurea.* Flowers in section, to illustrate pollination. See in text.

Most of the other genera in this sub-family are visited by humble bees and their flowers are adapted to receive them. There are however exceptions. The alpine *Rhinanthus angustifolius* is specially modified for butterfly-pollination. The nectar is secreted at the base of the ovary and stored in the corolla tube. To reach this nectar the insect must thrust its proboscis into the flower and in so doing the head is dusted from above by the anthers which lie protected from rain beneath the upper lip of the corolla. As compared with other species of *Rhinanthus*, the entrance is too narrow for the proboscis of any but butterflies to penetrate. In other species a wider opening is formed by the upper lip which thereby admits both humble bees and butterflies. The genus *Euphrasia* (Fig. 1850) is mostly visited by hive bees, the flower tube being considerably shorter than in most other genera.

Fig. 1850.—*Euphrasia officinalis* agg. Eyebright. Colony of plants in turf. Iona.

The genus *Veronica* (Fig. 1851) possesses flowers very different from those we have been considering. The corollas are mostly blue in colour, occasionally red or white, and consist of four lobes which are only united

Fig. 1851.—*Veronica pectinata*. Inflorescences.

at the base into a very short tube. The posterior sepal is missing and the two posterior petals are fused into one large member. There are only two stamens which, with the style, project considerably beyond the flower. The flowers (Fig. 1852) are mostly pollinated by hover flies which alight on the stamens. A fly visiting a flower finds the lowermost corolla lobe the most convenient place to settle and in doing so comes into contact with the stigma, which is projecting slightly downwards. At the same time the visitor seizes the filaments of the stamens, drawing them together and thereby dusting the lower surface of its body with pollen. In this way it follows that, although style and stamens mature at the same time, the style is pollinated by pollen from the body of the fly before it becomes dusted with the pollen of that flower. According to Kerner in those species in which the flowers develop in spikes geitonogamy may also take place.

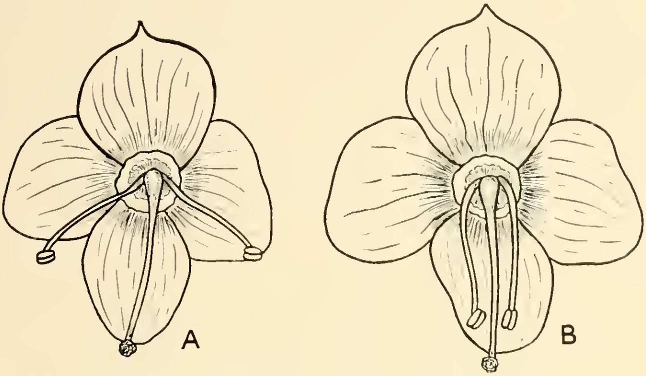


FIG. 1852.—*Veronica.* Flowers to illustrate pollination. See in in text.

LAMIALES

The Lamiales may be defined as Metachlamydeae in which the leaves are mostly opposite or in whorls, the corolla is zygomorphic and fundamentally pentamerous, the stamens fewer than the corolla lobes, the ovary deeply lobed with a gynobasic style, and ovules are mostly paired.

This order as treated by Hutchinson includes five families, one of which, the Selaginaceae, we have already dealt with as a tribe of the Scrophulariaceae. Two only need be considered here, the Verbenaceae and the Labiatae.

The **Verbenaceae** are a small family of eighty genera and about 800 species, which are almost entirely tropical or subtropical in distribution. Only *Verbena officinalis* occurs in Britain. It is a small herbaceous plant with long flower spikes bearing rather inconspicuous violet flowers and is interesting for having been the object of superstitious veneration from the earliest times. It was long held to be highly sacred and to possess magical powers.

Several species are of economic importance, particularly *Tectona grandis* which is a large forest-tree occurring especially in Java and Burma. It is the source of Teak, a hard and very durable wood used especially in shipbuilding. The wood sinks in water unless thoroughly dried, which in India is effected by removing a ring of bark and sapwood from the base of the tree. The tree soon dies and thereafter is left standing for two years before being cut, by which time it is completely dry. Another interesting genus is *Avicennia*, with three species which are normal inhabitants of mangrove swamps and extend into the subtropics. The stems of this shrub increase in thickness by the repeated production of new cambia outside the original one. *Caryopteris mastacanthus* (Fig. 1853) is grown in gardens. It is a low-growing shrub with heads of violet flowers, blooming in the autumn.

Fig. 1853.—*Caryopteris mastacanthus*. Flowering shoot with axillary inflorescences.

The flowers of the Verbenaceae are generally pentamerous, though reduction in the number of stamens is very common. *Tectona* is exceptional in having five. The gynoecium usually comprises two carpels, but there are four in *Duranta*, and five in *Geunsia*. The loculi are frequently divided into one-seeded portions by false septa which have been developed secondarily. The fruit is generally a drupe, sometimes a capsule. The family is distinguished from the Labiatae by the terminal and not gynobasic style and the undivided ovary.

Labiatae (Lamiaceae)

This family consists almost entirely of herbs inhabiting the temperate regions. In warmer lands there are a few shrubs but trees are extremely rare. In America a few species of the genus *Scutellaria* climb, but these are exceptions. The characteristics of the family are very clearly defined making most of the members easily recognizable.

In Britain the family is represented by a number of common genera of which the Deadnettle (*Lamium*), Wild Sage (*Salvia*), the Mints (*Mentha*) and Thyme (*Thymus*) are the best known. Among other common genera we may mention *Ajuga* (Bugle), *Stachys* (Betony), *Galeopsis* (Hemp Nettle), *Scutellaria* (Skullcap), *Origanum* (Marjoram) and *Lycopus* (Gipsywort). Mint, Thyme and Sage are among the commonest plants used as flavourings, but most Labiatae are more or less aromatic.

The **plants** characteristically possess square stems and bear opposite, decussate, simple leaves. Most possess epidermal glandular hairs or internal glands from which are derived the volatile oils which give them their value in cookery.

The **inflorescence** (Fig. 1854) is a specialized type of cyme, referred to as **verticillaster**, which is really a condensed dichasium of scorpioid cymes in which the axis has become telescoped. (See p. 1078.)

Fig. 1854.—*Lamium galeobdolon*. Archangels. Flowers in verticillasters.

The **flowers** (Fig. 1855) are hermaphrodite, zygomorphic and pentamerous though certain parts are often suppressed in individual genera.

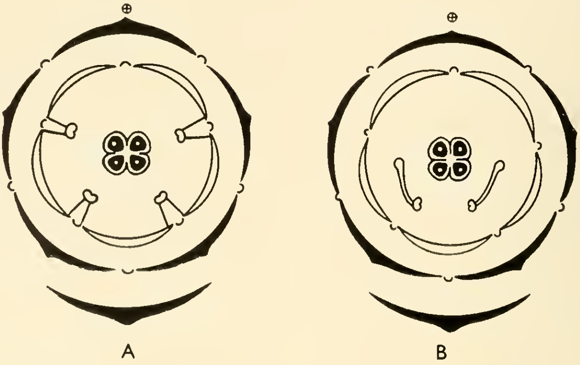


Fig. 1855.—Floral diagrams of Labiatae. A, *Lamium album*. B, *Salvia officinalis*. (*After Eichler.*)

They may be either axillary or whorled. In some genera, *e.g.*, *Thymus*, *Nepeta* (Fig. 1856) and *Prunella*, separate female flowers occur in addition to hermaphrodite ones, a condition known as gynodioecism which probably promotes cross-pollination.

Fig. 1856.—*Nepeta musseni*. Inflorescence.

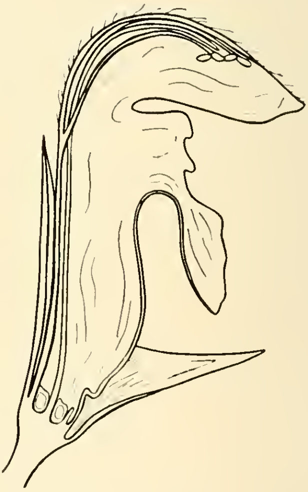


Fig. 1857.—*Lamium album*. Flower in longitudinal section. Young stage before the extrusion of the stigmas, which are still covered by the hood of the corolla.

The **calyx** is persistent, gamosepalous, tubular or funnel-shaped, composed generally of five sepals. In certain genera it may be two-cleft.

The **corolla** is usually zygomorphic and two-lipped (Fig. 1857), though in *Mentha* it is nearly regular. It is gamopetalous, hypogynous, tubular and four-lobed, the two posterior petals being united to form the upper lip.

The **androecium** consists of four epipetalous and didynamous stamens, the fifth being suppressed. The fifth posterior stamen is sometimes (*Salvia*) represented by a staminode, while in *Lycopus* and *Salvia* the two upper stamens are also suppressed. In *Coleus* the stamens are monadelphous.

The **gynoecium** is bicarpellary and syncarpous, but at a very early stage in the development of the ovary a constriction is produced which divides the ovary into four segments each containing a single ovule. The style is bifid and gynobasic except in the Ajugoideae and *Prostanthera*. The placentation is axile or basal.

The **fruit** is a carcerulus consisting of four nutlets which are either free or united in pairs.

The **seed** is usually non-endospermic and the embryo is usually straight.

The family is a large one represented by nearly 200 genera containing over 3,000 species generally distributed in warm and temperate regions, and is particularly well represented in the Mediterranean region. Some small groups are restricted to Australia and Tasmania, India, China, Malaya and Central America. Many occur under semi-desert conditions and are sometimes characterized by small needle-shaped leaves in which the stomata are restricted to hair-covered grooves on the lower surface.

The family is of considerable economic importance on account of the volatile oils, obtained from the leaves, many of which are used in perfumery. Among the more important of these are Lavender, Rosemary, Peppermint and Patchouli. Several genera, as already mentioned, are used as culinary herbs, while *Stachys sieboldii* produces edible tubers known as Chinese Artichokes.

The family is subdivided by Briquet in the following somewhat elaborate way.

I. Ajugoideae

Style not gynobasic; fruit consisting of nutlets with lateral placentation. Seed non-endospermic.

1. *Ajugeae.* Corolla various, upper lobe if present rarely concave. Stamens four to two, anthers bilocular. Nutlets more or less wrinkled. *Teucrium*, *Ajuga*.
2. *Rosmarineae.* Corolla strongly two-lobed with upper lobe concave and arched. Stamens two, anthers unilocular. Nutlets smooth. *Rosmarinus*.

II. Prostantheroideae

Style not gynobasic; fruit consisting of nutlets with lateral placentation, seed endospermic. Only genus *Prostanthera*.

III. Prasioideae

Style gynobasic; fruit consisting of nutlets with basal placentation, drupaceous, with fleshy or thick epicarp and hard endocarp. *Stenogyne*, *Gomphostemma* and *Prasium*.

IV. **Scutellarioideae**

Style gynobasic; fruit consisting of nutlets with basic placentation, dry, with seeds lying more or less transversely. *Scutellaria*, *Salazaria*.

V. **Lavanduloideae**

Style gynobasic; stamens four, unilocular at the tips, fruit consisting of dry nutlets with erect seeds and embryos with short, straight, superior radicles. Only genus *Lavandula*.

VI. **Stachydoideae**

Style gynobasic; stamens ascending or spreading and projecting straight forward; fruit consisting of nutlets with small basal attachments.

This sub-family is divided into twelve tribes of which we may mention the following which are represented in the British Flora.

1. *Marrubieae*. Sepals united; calyx bilabiate with entire lip. Corolla bilabiate or almost actinomorphic. Stamens four or two. *Marrubium*.
2. *Nepeteae*. Sepals united, tube fifteen-ribbed. Corolla bilabiate. Stamens four, the posterior pair larger or sometimes the only ones developed. *Nepeta*.
3. *Stachyeae*. Sepals united, calyx tube five- to ten-ribbed. Upper lip of corolla concave or helmet-shaped. Stamens four, lying parallel to one another under the upper lip. *Prunella*, *Galeopsis*, *Melittis*, *Lamium*, *Ballota*, *Stachys*.
4. *Salvieae*. Sepals united, calyx campanulate or tubular. Corolla bilabiate with sickle-shaped or helmet-shaped upper lip. Only the two anterior stamens fertile. *Salvia*.
5. *Saturejeae*. Calyx generally five-toothed, sometimes bilabiate. Corolla with flat lobes, either actinomorphic or bilabiate. Stamens four to two, equal in length, or the anterior ones longer. *Calamintha*, *Origanum*, *Thymus*, *Mentha*, *Lycopus*.

VII. **Ocimoideae**

Style gynobasic. Stamens descending and lying upon the lower lobe of the corolla or enclosed by it. Fruit consisting of nutlets with short basal attachment. *Hyptis*, *Ocimum*.

VIII. **Catopherioideae**

Style gynobasic; fruit consisting of dry nutlets; seeds erect. *Catopheria*.

The Ajugoideae include several common British genera. *Ajuga* contains some thirty species distributed through temperate regions, three of which are found in Britain, *A. reptans* (Bugle) and *A. chamaepitys* (Ground Pine) being the more common. Cleistogamic flowers have been described in *Ajuga* but are not common. In the genus *Teucrium* there are about 100 cosmopolitan species, four of which are found in the British Isles. *T.*

scorodonia (Wood Sage) is the most common. *Rosmarinus officinalis* (Rosemary) is the only species of the genus and is a xerophytic shrub inhabiting the Mediterranean region.

The pollination mechanism in this group differs from that most typical of the family as a whole. We may consider *Teucrium scorodonia* (Fig. 1858) as an example. The greenish-yellow flowers are arranged in terminal and axillary racemes. The corolla tube (Fig. 1859) is about 10 mm. long, almost half of which may be filled with nectar. In the early stage the stamens, which lie against the back of the corolla tube, project straight out of the flower, in company with the bifid style. The anthers however lie slightly in front of the style. In this stage pollen will be shed on to the head of a bee entering the flower in search of nectar. Later the anthers wither and bend backwards, while the lip of the style bends forwards so that the positions are reversed and the style will come into contact with the insect visitor. When the lower flowers of the inflorescence are in the later or female stage, the upper flowers still have functional anthers. Hence an

FIG. 1858.—*Teucrium scorodonia.* Woodsage. Inflorescence.

insect working regularly up the spikes from below brings pollen from other plants to the stigmas. Humble bees usually behave in this way, working up from below rather than downwards from the top of an inflorescence.

Fig. 1859.—*Teucrium*. Flowers to illustrate pollination. See in text.

Automatic self-pollination can only occur if the change in position of stamens and style takes place before all the pollen has been liberated.

The Scutellarioideae are a small sub-family in which the most common genus is *Scutellaria* with 200 cosmopolitan species. *S. galericulata* and *S. minor*, the Skull Caps, are found in Britain. The flowers are paired in the axils of the leaves, a feature which distinguishes this genus from the rest of the family.

The Lavanduloideae contain the single genus *Lavandula* with twenty species distributed between the Mediterranean and India. From the common species *L. vera* is obtained the Oil of Lavender, which is prepared by the distillation of the flowers. The flowers are protandrous, nectar being secreted in considerable quantities. Pollination is effected chiefly by bees, but the flowers are also visited by long-tongued insects, particularly by humming-bird hawkmoths.

The Stachydoideae, as already pointed out, are a large sub-family embracing a number of tribes. The inflorescence is made up of paired cymose inflorescences each consisting in *Salvia* of a three-flowered dichasium, or more generally branching and becoming modified into a pair of monochasia. In either case the axes are contracted so that the flowers appear to be produced in whorled clusters. The bracts may be simple or highly differentiated, as in *Monarda* (Fig. 1860). The flowers show considerable variation, with corresponding differences in the pollination mechanisms.

In general the three anterior petals form a lip while the two posterior petals form an arched hood, protecting and enclosing the stamens and stigma. The number of stamens is either four, or reduced to two.

FIG. 1860.—*Monarda didyma.* Bergamot. Inflorescence, with coloured bracts.

The flowers are often brightly coloured, generally blue or red, and are adapted to butterfly- and moth-pollination, though most of the British species have shorter tubes and are adapted to pollination by bees. Cleistogamic flowers are found in *Salvia* and *Lamium*, while in *Lycopus virginicus* autumn flowers occur which are buried below the soil, where fruits are produced as a result of self-pollination.

The genus *Salvia* (Fig. 1861) shows an elaborate pollination mechanism which varies somewhat in different species. The flowers are generally protandrous and are adapted to pollination by humble bees or hive bees. In *S. pratensis* (Fig. 1862) the corolla is bright blue in colour and is directed horizontally. The nectar is secreted by the fleshy base of the ovary. The lower lip of the corolla forms a platform while the upper lip serves to protect the fertile anther lobes.

The flowers are protandrous and have two fertile stamens only, with short filaments which are inserted on the corolla tube. Each filament bears a versatile anther with a transversely elongated connective. One limb of the connective is very long and turned upwards, bearing a fertile half-anther which is hidden below the upper corolla lip. The other limb of the connective is much shorter, points downwards and ends in a sterile plate of tissue, lying across the entrance to the basal, tubular part of the corolla. The sterile plates of the two stamens are joined and in the normal position they block access to the nectar. The whole arrangement forms a bent or bell-crank lever, pivoting on the tips of the stamen filaments.

FIG. 1861.—*Salvia sclarea.* Clary. Inflorescence with old flowers showing the long exserted styles and bifid stigmas.

When an insect thrusts its head into the flower the sterile anther plates are pushed upwards and backwards so that the fertile anther lobes covered with pollen are brought forwards and downwards. By the same action entrance is gained to the nectar and pollen is liberally dusted on to the back

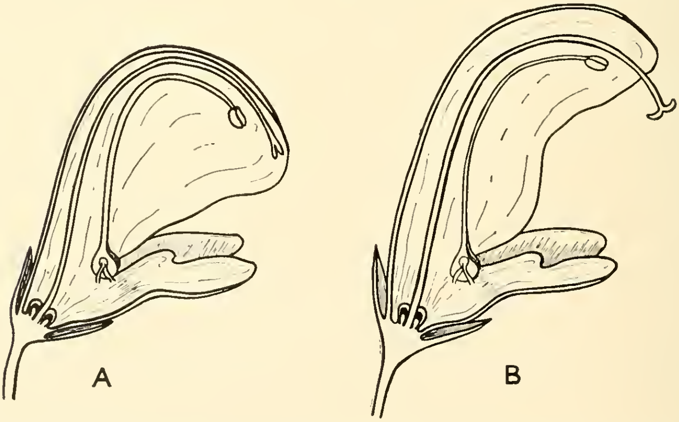


FIG. 1862.—*Salvia pratensis.* Flowers in longitudinal section, to illustrate pollination. A, Younger, and B, older stages, showing the hinged stamens and the later extrusion of the stigmas. See in text.

of the visitor. When the insect withdraws its head the pressure on the lever is released and the anthers return to their former position.

In an older flower in which the bifid stigma is mature we find that the style has elongated and now occupies a position in the front of the flowers where it must inevitably be brushed by an insect visiting the flower. Variations in the form of the flowers are known, large-flowered and small-flowered hermaphrodite types occurring as well as large and small female forms in which the lever mechanism is greatly reduced.

In the genus *Lamium* the mechanism is simple. Here the flowers are only visited by bees and the shape of the corolla exactly fits the body of the insect. Nectar is secreted at the bottom of the corolla tube and is usually protected by a circle of hairs above the secretion. The upper lip shelters the anthers while the lower lip serves as a platform for visitors. The stigma is bifid, one lobe lying directed horizontally outwards and the other turned vertically downwards. When a bee enters the flower it first touches the lower lobe of the bifid stigma and afterwards the anthers, which mature simultaneously. The second lobe of the stigma is directed out of the flower and therefore lies between the anthers. Should cross-pollination fail, the flower is almost certain to be self-pollinated owing to the simultaneous maturation and close proximity of the stigma and anthers. Insect visits are however frequent and few flowers are ever missed. Short-tongued bees unable to reach the nectar by the orthodox method sometimes perforate the corolla tube.

RUBIALES

The Rubiales are Metachlamydeae in which the flowers are hermaphrodite and either actinomorphic or zygomorphic, and the parts arranged either in fours or fives. The stamens are usually equal in number to the corolla lobes, occasionally fewer. There may be five carpels but that number is usually reduced, often to one. The ovary is inferior, with one or more chambers containing from one to many anatropous ovules with axile placentation. The seeds mostly contain endosperm.

The plants are trees, shrubs or rarely herbs with opposite entire leaves and occur mainly in the tropics.

The group is a natural one and the families included in it show a gradual reduction in the number of floral parts and an increasing tendency to zygomorphy as a result. There is some difference in opinion as to the precise line to be drawn between the Rubiales and the following order, the Asterales. Rendle, following the older treatment of Engler, recognizes five families in the order, while Hutchinson includes only the first two, the three others being transferred to the Asterales. Here we shall follow Hutchinson and retain only the families Rubiaceae and Caprifoliaceae in the Rubiales.

The **Rubiaceae** are a large and cosmopolitan family containing nearly 400 genera and 4,500 species. Many are found in the tropics but some extend their range to temperate regions while a few are found under sub-Arctic conditions. The flowers of the Rubiaceae are hermaphrodite, usually actinomorphic and either tetramerous or pentamerous, with five or four stamens and two carpels. The corolla is tubular and the stamens are inserted on the corolla tube, the anthers being introrse and bilocular. The ovary is covered by a fleshy disc, is usually inferior and contains usually two loculi with one to many anatropous ovules. The fruit is a capsule, drupe or berry; the seeds have a straight embryo lying in cartilaginous or horny endosperm. They are mostly shrubs or trees but those occurring in Britain are herbs. These herbaceous types all belong to a single tribe, the Galieae, which occupy a somewhat anomalous position within the family. In this tribe the stipules are leaflike and are grouped with the true leaves into whorls on the stem, distinguishable from the leaves by having no buds in their axils. Species of *Galium* (Fig. 1863) (Bedstraw) are common in Britain, *G. aparine* (Cleavers) being well known as a scrambler, climbing by stiff recurved hairs. Among the other genera included in this tribe are *Asperula* (Woodruff), *Sherardia*, *Crucianella* (see Fig. 1254) and *Rubia*. *Rubia tinctoria* (Madder) contains the dyes alizarin and purpurin in the roots, for which it was formerly cultivated in India.

FIG. 1863.—*Galium erectum*. Paniculate inflorescence of small, white flowers.

One of the most important genera belonging to the family is *Coffea* (Fig. 1864) which contains forty-five species especially common in Africa. *C. arabica*, Arabian coffee, is now largely cultivated in Brazil, Java and the

West Indies, while *C. liberica*, Liberian coffee, is also cultivated though on a less extensive scale. From 1850 to 1880 coffee formed the main agricultural crop in Ceylon but was largely destroyed as a result of attack by the rust-fungus *Hemileia vastatrix*.

FIG. 1864.—*Coffea arabica*. Flowers and fruits. Ceylon. From a commercial photograph.

Closely allied to *Coffea* are a group of genera grouped together in the tribe Psychotrieae which are biologically interesting. The genus *Psychotria* itself contains about 600 species widely distributed in the tropics. Many possess small nodules on the leaves (Fig. 1865) containing bacteria which are thought to fix atmospheric nitrogen. The genera *Hydnophytum*, which comprises thirty species in eastern Asia, New Guinea and Fiji, and *Myrmecodia* (Fig. 1866) with twenty species in Indo-Malaya, are epiphytes. In both of these genera the base forms a large tuber which is anchored to the support by adventitious roots. This tuber is mainly composed of cork and is penetrated by numerous passages inhabited by ants. These passages are formed at an early stage in the hypocotyl which swells into a small tuber, in which a hollow axial cylinder of phellogen is formed which cuts off cork on its *inner* side and parenchyma on its outer side, thus increasing the size of the tuber while at the same time forming a hollow space lined by cork. On the outside of the tuber there is a second phellogen which cuts off cork outwards in the usual way. As the tuber grows more phellogens appear, cutting off more internal cork and thus producing more chambers in communication with the older ones. Though these cavities are inhabited by ants it is not known whether they serve any useful purpose to the plant. The tuber itself may be merely a water-storage organ.

FIG. 1865.—*Psychotria bacteriophila.* Above, foliage showing the bacterial colonies as dark spots on the leaves. Below, a section through one of the colonies. The bacteria enter what was originally a schizogenous secretory cavity, in which they multiply and the cavity enlarges.

FIG. 1866.—*Myrmecodia echinata.* A young plant showing the early formation of the stem tuber containing the hollow passages in which the ants live. (*After Treub.*)

Hollow swollen internodes occur in the genera *Nauclea* and *Duroia.* In the latter genus, which contains ten South American species, the stems are swollen just below the inflorescence. This swollen region is hollow and entrance is gained by two longitudinal slits. It becomes inhabited by ants which bite through the thin base of the slits to gain admission. In one species, *D. saccifera*, the ant houses occur in the leaves, where two pear-shaped outgrowths are formed on the under surface. The entrance is on the upper side of the leaf and is protected by a little flap of tissue.

The origin of the Rubiaceae may probably be found in the Umbelliflorae, which also show tetramerous to pentamerous flowers which are tetracyclic and epigynous, a more or less suppressed calyx, a fleshy disc covering the ovary, anatropous ovules with a single integument and an embryo containing endosperm.

The **Caprifoliaceae** (Loniceraceae) are a much smaller family with only twelve genera and about 400 species, most of which inhabit north temperate regions. They are mostly woody plants with decussate leaves and cymose inflorescences of showy flowers (Fig. 1867).

The flowers are hermaphrodite, actinomorphic or zygomorphic and usually pentamerous but with a reduced number of carpels. The calyx is usually small, consisting of five lobes or teeth. The stamens are inserted on the corolla tube and the anthers are usually introrse. The ovary is inferior, one to five locular, with one to many pendulous ovules. The fruit is a berry or drupe, except in *Diervilla* where it is a capsule. The seed contains a straight embryo embedded in fleshy endosperm.

There are a number of well-known genera in this family, among the commonest being *Sambucus*, with *S. nigra* (Elder); *Viburnum*, including *V. lantana* (Wayfaring Tree), *V. opulus* (Guelder Rose), and many cultivated species (Fig. 1868); *Symphoricarpus*, with *S. racemosus* (Snowberry);

Fig. 1867.—*Lonicera periclymenum.* Honeysuckle. Inflorescence.

Diervilla, species of which are cultivated in gardens under the name of *Weigelia*; *Lonicera*, which includes *L. periclymenum* (Honeysuckle); and *Leycesteria*.

Fig. 1868.—*Viburnum tomentosum.* Umbellate inflorescence with enlarged, sterile, irregular flowers. See also Fig. 1089 and reference there in text.

In addition we may mention *Linnaea borealis*, a creeping plant of the north temperate regions, named after Linnaeus.

The inflorescence varies; in *Leycesteria formosa* (Fig. 1869) it is cymose; in *Lonicera* the central flower is often suppressed, while in *Symphoricarpus* and *Diervilla* the inflorescence appears to be a spike or raceme. The flowers are insect-pollinated and many possess conspicuous white corollas which are often strongly scented at night and are attractive to night-flying moths. The stigma is usually longer than the stamens, thereby preventing self-pollination.

FIG. 1869.—*Leycesteria formosa.* Raceme of two-flowered cymes, with coloured bracts.

The family is mainly found in northern latitudes, only a few species being found in the southern hemisphere. Numerous leaf impressions of *Viburnum* have been described from the Tertiary rocks of North America.

ASTERALES

The Asterales are the highest group of the Metachlamydeae, at least from some evolutionary standpoints. The plants are almost all herbaceous or slightly shrubby, very few are trees and many are annuals. The leaves are very diverse in shape and are never associated with stipules. The flowers are generally closely crowded together in heads or capitula surrounded by involucral bracts. They are individually small and the anthers are united to form a ring around the style. The ovary is inferior, bicarpellary but unilocular and with a single ovule, except in Valerianaceae where there are three carpels, only one of which remains functional, and in Adoxaceae, where there may be five. The embryo completely fills the seed except in *Adoxa*, where there is endosperm present.

As here treated the order contains four families, Adoxaceae, Valerianaceae, Dipsacaceae and Compositae, but this treatment, while following Hutchinson, differs from that of other authorities. Both Engler and Rendle place the Compositae in the Campanulales while the Dipsacaceae, Valerianaceae and Adoxaceae are included in the Rubiales. Eichler places *Adoxa* in the Caprifoliaceae while other workers have suggested that it has a relationship with the Saxifragaceae or the Araliaceae.

We shall first refer briefly to the families Adoxaceae, Valerianaceae and Dipsacaceae and then consider the great family of the Compositae in some detail.

The **Adoxaceae** contain the single species *Adoxa moschatellina* which is a small herb arising from a perennial rhizome. The radical leaves are ternately divided and the flowering stalk bears one pair of similar leaves. At the apex of the stalk is a head of five small, greenish-white, hermaphrodite flowers. The terminal flower is usually tetramerous while the other four are pentamerous. The calyx is formed of three sepals, while the corolla comprises usually five small petals. The stamens, which may number four, five or six, appear to be double owing to a split which begins near the base, so that each bears half an anther. The ovary is more or less inferior and contains four or five loculi with a single pendulous ovule in each loculus. The short styles are equal in number to the loculi. The fruit is a drupe and the seeds contain minute embryos embedded in endosperm.

The flowers are pollinated by small insects which are attracted by the muskysmell and by nectar which is secreted around the base of the stamens.

As has already been pointed out the position of *Adoxa* is somewhat dubious and it is placed here mainly on account of the single pendulous ovule in each loculus. The plant is widely distributed over north temperate regions and is not uncommon in Britain.

The **Valerianaceae** comprise some ten genera and nearly 400 species which occur mostly in north temperate regions. The plants are very rare in Africa and absent from Australia. Most of the species are herbs though a few are shrubby, with opposite leaves and small flowers in cymose inflorescences. *Valeriana* (Fig. 1870), *Valerianella* and *Centranthus* are found in Britain. *Centranthus ruber* (Fig. 1871) is really an escape from cultivation for its home appears to be the Mediterranean region. It has however for long become naturalized on old walls. It may be found in three forms, one deep red, one white and, by far the most common, one pink. *Valerianella olitoria* (Lamb's Lettuce) is used in salads, while Spikenard, one of the most prized perfumes of antiquity, was prepared from the young shoots of *Nardostachys jatamansi*, a native of the Himalayas.

The flowers may be hermaphrodite or unisexual and somewhat zygomorphic. The calyx is represented by an epigynous ring. The corolla is tubular, often saccate at the base; the stamens in the corolla tube alternate with the lobes and vary between one and four. The ovary is inferior and made up of three united carpels though only one loculus is fertile and contains a single pendulous ovule. The fruit is dry, indehiscent and one-seeded. The embryo is straight and possesses no endosperm.

The pollination mechanism is elaborate and may even extend to a condition of dimorphism. The small flowers, rather inconspicuous separately, are aggregated into large heads. Each flower possesses nectar

Fig. 1870.—*Valeriana pyrenaica.* Inflorescence.

Fig. 1871.—*Centranthus ruber.* Inflorescence.

which is contained in the corolla sac. It is therefore accessible only to insects with fairly long tongues. In *Valeriana dioica* (Fig. 1872) cross-

Fig. 1872.—*Valeriana dioica.* A, Inflorescence. B, Male flower with rudimentary stigma. C, Female flower with rudimentary stamens.

pollination is ensured by dioecism, there being four different kinds of flowers: firstly, male flowers with no stigma and with a large corolla; secondly, male flowers with a rudimentary stigma and a small corolla; thirdly, female flowers with vestiges of stamens and small corollas; and finally female flowers with no stamens and even smaller corollas. In *V. officinalis* the anthers develop first and the trifid style later, thus ensuring cross-pollination.

In *Centranthus ruber* (Fig. 1873) the corolla tube is divided longitudinally by a septum into two parts, in one of which is the style. Only one stamen develops. In the first stage this stamen lies in the mouth of the flower covering over the immature style. Later after the pollen has shed, it bends backwards over the corolla and the bifid stigma now occupies the centre of the flower. Thus an insect visiting a young flower in search of the enclosed nectar will touch the anther with its head but when visiting an older flower will encounter the stigma and deposit pollen on it.

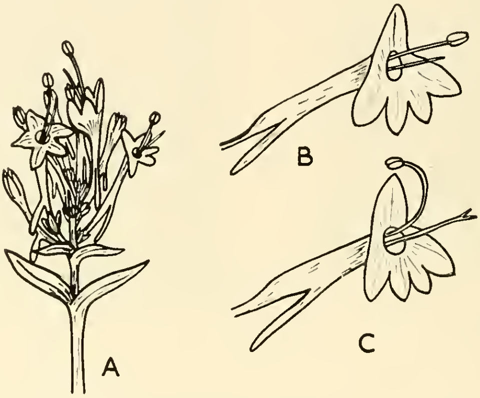


Fig. 1873.—*Centranthus ruber.* A, Group of flowers showing spurs and exserted stamens. B, Flower in first, male stage. C, Flower in later, female stage with stamen recurved and stigmas expanded.

The **Dipsacaceae** are mainly centred in the Mediterranean region, but spread thence over a wide area and even reach South Africa. Several species are found in Britain. The family contains ten genera and about 150 species. They are mostly herbs, with opposite leaves, but a few are shrubs. The flowers are hermaphrodite and zygomorphic. The calyx is epigynous or divided into pappus-like segments, and each flower has a cup-shaped involucre made up of a pair of bracteoles. The corolla is divided into four or five lobes of varying sizes. The stamens are basically four but the number may be reduced by abortion. These alternate with the corolla lobes, and are inserted at the bottom of the tube. The filaments may be free or may be united in pairs. The ovary is inferior and unilocular but derived from two carpels. There is a single pendulous ovule. The fruit is dry and one-seeded, enclosed in the involucre and often crowned by the persistent calyx. The embryo is straight and lies in a scanty endosperm.

The commonest genus is *Scabiosa* (Fig. 1874), several species of which are cultivated in gardens. Three British species were originally included in this genus but one is now placed in *Knautia*. *Cephalaria tatarica* (Fig. 1875) is yellow in colour and is often cultivated, but most of the flowers in the family are blue or red in colour. The genus *Dipsacus* includes *D.*

FIG. 1874.—*Scabiosa caucasica*. Capitulate inflorescence with greatly enlarged marginal flowers.

FIG. 1875.—*Cephalaria tatarica*. Two capitula showing enlarged exterior flowers. Right, flowers in male stage with stamens exserted. Left, flowers with exserted styles.

fullonum, the Fuller's Teasel, the hooked bracteoles (Fig. 1876) of which are used to raise the nap on woollen cloth after weaving.

The family is entirely absent from America, Australia and Polynesia.

FIG. 1876.—*Dipsacus fullonum*. Teazle. Inflorescence with long involucral bracts and numerous hooked bracteoles which subtend the individual flowers.

Compositae (Asteraceae)

This is the largest and most widely distributed of all families of the Angiosperms and probably represents the highest stage in the evolution of the Dicotyledons. It has been estimated that there are some 13,000 species, which is approximately 10 per cent. of the Flowering Plants. Although the family is so large its members show a marked similarity in floral structure, so marked in fact that they cannot be confused with those of any other family, although they have a superficial resemblance to members of the Dipsacaceae.

The variety of habitats which the species occupy is extremely diverse, while even within the confines of a single genus they display a corresponding variety of forms. It is interesting to note that the shrubby species often form an important feature of the Composite flora of oceanic islands.

Of this vast assemblage of species only comparatively few are represented in the British Flora, but, even so, the number of common species is considerable and it is impossible here to do more than mention a few of the most obvious. Among the commonest weeds are the Dandelion (*Taraxacum officinale*) (Fig. 1877), Daisy (*Bellis perennis*), Hawkweeds (*Hieracium*), Sow Thistle (*Sonchus*), Thistle (*Carduus*), Yarrow (*Achillea*), Scentless Mayweed (*Matricaria inodora*), Groundsel (*Senecio vulgaris*), Ragwort (*Senecio* *jacobaea*), Oxeye Daisy (*Chrysanthemum leucanthemum*) and Mugwort (*Artemisia vulgaris*). Several are commonly grown as vegetables, such as Chicory (*Cichorium intybus*), Lettuce (*Lactuca*), Salsify (*Tragopogon porrifolium*), or as herbs, such as Tansy (*Tanacetum vulgare*) and Wormwood (*Artemisia absinthium*). Many common garden flowers are represented by species of the family and we can do no more than cite a few common examples: Michaelmas Daisies (*Aster*), Chrysanthemums (*Chrysanthemum*), Sunflowers (*Helianthus*), Cornflowers (*Centaurea*), Golden Rod (*Solidago*) and Everlastings (*Helichrysum*).

FIG. 1877.—*Taraxacum officinale.* Dandelion. Capitulum in which all the flowers except a few in the centre have liguliform, *i.e.*, strap-shaped, extensions of the corolla.

The **plants** are herbaceous or shrubby, rarely trees, usually with alternate leaves. Stipules are absent. There is great diversity of form. *Senecio*, which is the largest genus, having over 2,500 species, besides including annual and perennial herbs, may be a climber, as *S. macroglossus* in South Africa; a shrub, as *S. hastata*, found in the Mediterranean region; a tree, as *S. johnstonii* in Central Africa; a succulent, as *S. articulata* found in South Africa, and a marsh plant, as *S. aquatica* in this country. True water plants are rare in the family, though Hutchinson mentions four species, widely separated both in systematic position and also in geographical distribution, which suggests that an aquatic habit has recently developed independently several times in the family. These four species are all small herbs with slender stems and much dissected submerged leaves.

There is frequently a tap-root, which may bear adventitious buds, as in the Dandelion, where they serve as a means of rapid propagation. Alternatively the roots may be tuberous, as in *Dahlia*, or stem tubers may develop on a rhizome as in *Crepis bulbosa* and *Helianthus*, those of *H. tuberosus*, the Jerusalem Artichoke, being edible. Runners or stolons are often produced, as in *Achillea*.

The leaves may form a rosette at the base of the plant as in the Daisy and Dandelion, or they may be produced alternately up the stem. They are often large in relation to the plant. In some species the leaves may become spiny or in extremely xerophytic types, needle-shaped. Narrow, parallel veined leaves occur in a few genera. Though stipules are absent, auricles occur at the leaf bases in some genera and decurrent leaves are widely distributed.

FIG. 1878.—*Doronicum pardalianches.* Leopards' Bane. Capitulum with well-marked differentiation of small disc florets and marginal ray florets with liguliform corollas.

The **inflorescence** (Fig. 1878) is with few exceptions a capitulum containing numerous small flowers called **florets**, surrounded and protected by an involucre (Fig. 1879). The disc may be either flattened or convex.

The florets (Fig. 1880) may be all alike, or there may be a central group of disc florets surrounded by marginal ray florets, but in all instances the youngest flowers lie towards the centre of the capitulum. Small scaly bracts or **paleae** often occur between the florets, usually subtending them.

The capitula themselves may be arranged in racemes, panicles or spikes, forming thereby compound inflorescences which may themselves simulate capitula. In most of these cases the individual capitula have only a few florets or may be reduced to one only, as in *Echinops*.

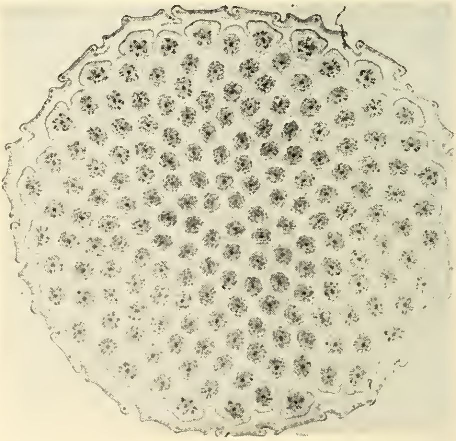


FIG. 1879.—*Taraxacum.* Transverse section of a capitulum with florets all sub-similar, surrounded by a ring of involucral bracts.

The **flowers** (Fig. 1881) are epigynous and usually pentamerous; they may be actinomorphic or zygomorphic, and may be either hermaphrodite, monoecious or even sterile.

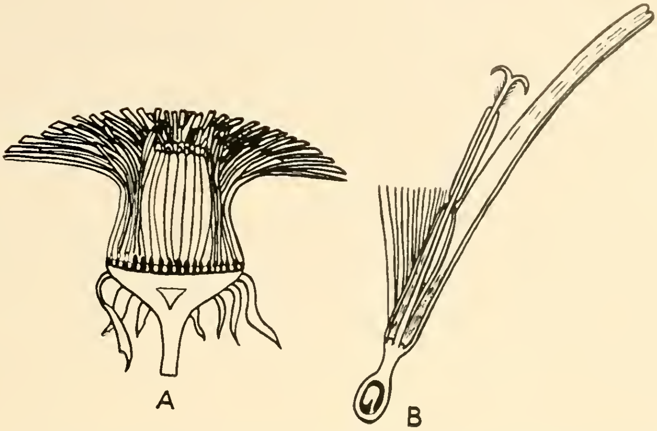


FIG. 1880.—*Taraxacum*. A, Vertical section of a capitulum showing the flattened receptacle and the bracts of the surrounding involucre. B, Single floret showing the inferior ovary, pappus hairs, strap-shaped corolla and stamens with anthers closely surrounding the style, which terminates in two stigmatic lobes.

The **calyx** is either absent or is represented merely by a ring of minute teeth or by a pappus borne on top of the ovary.

The **corolla** is gamopetalous and may be either tubular, ligular or labiate and is valvate in aestivation.

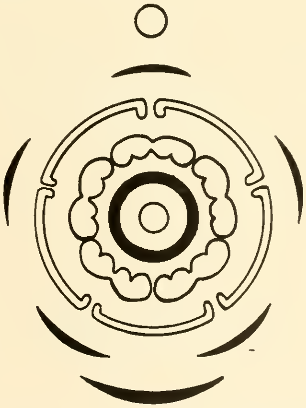


FIG. 1881.—Floral diagram of *Carduus crispus*. Compositae. (*After Eichler.*)

The **androecium** consists of five stamens which are epipetalous and syngenesious, *i.e.*, the anthers are fused together laterally to form a tube. The anthers are bilocular and dehisce introrsely by longitudinal slits.

The **gynoecium** is bicarpellary and syncarpous, the style is filiform or slender and the stigma is bifid. The ovary is inferior and unilocular, containing a single anatropous ovule with basal placentation.

The **fruit** is a cypsela. The pappus when present may be sessile or may after fertilization be carried up on a tubular stalk. It is frequently hygroscopic.

The **seed** is non-endospermic and completely fills the fruit, its coat being fused with that of the pericarp. The embryo is straight with a short radicle and flat or semi-circular cotyledons.

According to Willis the family contains 900 genera and over 13,000 species, with a world-wide distribution.

The anatomical features of the family are worthy of note, particularly the frequent occurrence of schizogenous canals in stem, root and leaf, which are widely distributed in the different tribes of the Tubulifloreae, while laticiferous vessels occur in the Cichorieae.

The family has been variously divided up by different authors and here we shall adopt the system proposed by Hoffmann.

I. Tubulifloreae

Corolla of disc florets never ligulate. Laticiferous vessels absent but schizogenously produced oil canals often present.

1. *Vernonieae.* Capitulum homogamous, florets tubular, regular, with five narrow lobes, never yellow in colour. Anthers arrow-shaped at the base, pointed or rarely tailed, with filaments inserted high above the base. Style generally divided into two long, pointed stigmas, hairy on the outside. Pappus usually copious and setose. *Vernonia* and *Elaphantopus.*

   The members may be herbs, trees or shrubs usually with alternate leaves. They occur mostly in tropical America though some are found in Africa and Asia. The tribe is not represented in Europe.

2. *Eupatorieae.* Capitulum homogamous, corolla tubular and regular, with five short teeth, never pure yellow in colour. Anthers blunt at the base and basifixed. Stigmas long but blunt or flattened at the tip, covered with very short hairs. Pappus of five or more bristles or scales, but sometimes absent. *Eupatorium*, *Mikania* and *Adenostemma.*

   The members of the tribe are herbs or shrubs which occur chiefly in the New World, though *Eupatorium cannabinum* (Hemp Agrimony) is British. Species of *Mikania* occur mostly in Brazil where some are climbers.

3. *Astereae.* Capitulum heterogamous or homogamous, with female or sterile ray florets and bisexual or male disc florets. All or nearly all central flowers tubular. Anthers blunt at the base and basifixed. Stigmas flattened, with marginal rows of papillae and terminal hairy sterile portions. *Bellis*, *Aster*, *Olearia*, *Solidago*, *Erigeron*, *Baccharis*, *Callistephus* and *Conyza.*

   The plants are mostly herbaceous, world-wide in distribution, though more common in the New World than the Old World, and more typical of temperate than tropical regions. We shall discuss certain points about this tribe later.

4. *Inuleae.* Capitula heterogamous or homogamous, corolla in tubular florets has a limb with four or five teeth. Usually yellow in colour. Anthers tailed at the base. Pappus usually setose with simple or plumose bristles. *Blumea*, *Filago*, *Antennaria*, *Gnaphalium*, *Helichrysum*, *Leontopodium*, *Tarchonanthus*, *Raoulia*, *Odontospermum* and *Pulicaria*.

The plants are very varied in form. They generally have alternate leaves, often with woolly hairs; others are heath-like. The species are very widely distributed. Several of these genera include well-known plants. *Leontopodium alpinum* is the Edelweiss, *Odontospermum pygmaeum* is a " Rose of Jericho ", a small shrubby plant in which the involucral bracts close up over the flowers in dry weather and open out again when damp thus allowing the ripe fruits to escape at a time most suitable for germination. *Helichrysum* (Fig. 1882) is a large genus of some 400 species, found chiefly in South Africa and commonly grown in gardens under the name of Everlastings, on account of the stiff, papery nature of the florets. Some are brightly coloured. The genus *Raoulia* contains some twenty New Zealand species which are woolly herbs growing in dense mats or white cushion-like masses, sometimes referred to as Vegetable Sheep.

FIG. 1882.—*Helichrysum bracteatum.* Everlasting. Capitulum after anthesis with the dry, coloured bracts and ray florets incurved over the disc.

5. *Heliantheae.* Capitula heterogamous or rarely homogamous, with female or sterile ray florets and hermaphrodite or sterile disc florets. Corolla of disc flowers actinomorphic, generally yellow. Involucral bracts often imbricated, and not membranous at the margins. Anthers usually rounded at the base, with basally inserted filaments. Style possessing a crown of hairs above the division. Pappus not hairy. Receptacle covered with scaly bracts. *Helianthus*, *Dahlia*, *Silphium*, *Zinnia*, *Xanthium* (Fig. 1883), *Espeletia*, *Coreopsis*, *Rudbeckia*, *Siegesbeckia*, *Bidens*, *Cosmos*, *Ambrosia* (Fig. 1884) and *Galinsoga*.

FIG. 1883.—*Xanthium spinosum.* Cocklebur. The female capitula contain only two flowers and are surrounded by a spiny involucre.

The plants are usually herbaceous and are mainly American, though some of the genera are represented in the Old World, occurring both in temperate and tropical climates. Only three are found in Britain. We shall refer again later to certain features of this tribe.

6. *Helenieae.* Capitulum heterogamous or rarely homogamous, with female or sterile ray flowers and hermaphrodite or sterile disc florets. Involucral bracts imbricated and not membranous at the margins. Anthers usually rounded at the base, filaments basifixed. Style with long hairs above the fork. Pappus not hairy. Receptacle *without* scaly bracts. *Helenium*, *Gaillardia* and *Tagetes*.

FIG. 1884.—*Ambrosia artemisiaefolia.* Ragweed. Flowering shoot.

The plants are herbaceous, occurring mainly in Mexico and the Pacific coast of North America. Several species are cultivated in gardens. *Tagetes erecta* is the African Marigold.

7. *Anthemideae.* Capitulum heterogamous or rarely homogamous, with female or sterile ray florets and fertile or sterile disc florets. Corolla of disc flowers regular, with five or rarely four short lobes. Involucral bracts *with* membranous tip and edges. Anthers usually rounded at the base, with basifixed filaments. Style with long hairs above the fork. Pappus absent or reduced to a ring or cup. *Achillea*, *Anthemis*, *Chrysanthemum*, *Matricaria*, *Artemisia*, *Tanacetum.*

The plants are generally herbaceous but occasionally shrubby, with alternate, pinnate leaves. Many are found in Britain and on the whole the tribe is more widely distributed in the Old World than in the New.

The tribe is divided into two sections, the Anthemidineae in which there are floral bracts on the receptacle and the Chrysanthemidineae in which they are absent. Many species are cultivated and some are of economic importance. *Anthemis nobilis* is the source of Chamomile, *Artemisia* and *Tanacetum* are used as herbs. Species of *Chrysanthemum* occur wild in Britain; *C. leucanthemum* is the Oxeye Daisy, *C. segetum* is the Corn Marigold while *C. parthenium* is Feverfew. *C. indicum* and *C. sinense* which are native of China and Japan are the parents of the cultivated Chrysanthemums.

8. *Senecioneae.* Capitula homogamous or heterogamous. Involucral bracts united into a cup with additional outer scales. Anthers usually rounded at the base, filaments basifixed. Style with long hairs below the fork. Pappus hairy. Receptacle generally without floral bracts. *Tussilago*, *Senecio*, *Petasites*, *Arnica*, *Doronicum* and *Cineraria*.

Fig. 1885.—*Senecio jacobaea.* Ragwort.

The plants may be herbs, shrubs or trees with alternate leaves, occurring mostly in the Old World. The genus *Senecio* (Fig. 1885) is by far the largest, with over 2,500 species, exhibiting almost every type of habit. Several species, as already mentioned, occur in Britain. *Tussilago farfara* is the Coltsfoot while *Petasites fragrans* (Winter Heliotrope) and *P. officinalis* (Butterburr) also occur in Britain. All three spread rapidly by rhizomes. Coltsfoot leaves are used as a substitute for tobacco. *S. cruenta* is the source of the greenhouse "Cinerarias" and not the genus *Cineraria* as might be expected. The former is a native of the Canary Islands.

9. *Calenduleae.* Capitula heterogamous. Ray florets usually ligulate and female, disc flowers male or sterile. Anthers pointed at the base. Style undivided. Pappus absent. Receptacle without scales.

The only genus included in this tribe is *Calendula*, the species of which are annuals or perennials, occurring mainly round the Mediterranean. *C. officinalis* is the Marigold, frequently cultivated in gardens and formerly used as a culinary herb. A variety is known in which each principal capitulum is surrounded by others which spring from the axils of the involucral bracts.

10. *Arctotideae.* Capitula heterogamous with ray florets ligulate, female or sterile and disc florets male or sterile. Anthers blunt at the base, filaments inserted above the base. Style thickened at or above the point of division or having a circle of hairs. Pappus absent or if present not hairy.

Included in this tribe are the genera *Arctotis* and *Gazania*, which are found chiefly in the tropics and in South Africa and Australia.

11. *Cynareae.* Capitula homogamous or with sterile, rarely female, non-ligulate ray florets. Anthers usually tailed. Style thickened or possessing either below or at the point of division a circle of hairs. Involucre composed of many series of bracts increasing in length inwards and often spiny. Receptacle usually bearing bristles. *Echinops*, *Arctium*, *Carlina*, *Carduus*, *Cirsium*, *Cynara*, *Centaurea*, *Carthamus*, *Saussurea*, *Serratula* and *Silybum*.

The plants are mainly herbaceous with their chief centre of distribution in the Mediterranean region. The tribe includes a number of British species many of which are known under the general name of the Thistles.

The inflorescence is often compound and the leaves prickly or spiny. We shall refer to this tribe later.

12. *Mutisieae.* Capitula homogamous or heterogamous. Ray florets either absent or two-lipped, disc florets actinomorphic with deeply divided limb or two-lipped. *Barnadesia*, *Mutisia*, *Gerbera* and *Stifftia*.

The tribe is mainly developed in the Andean region of South America, though species of *Gerbera* are found in Africa, Asia and Tasmania. The genus *Mutisia* includes a number of shrubby climbers some of which are cultivated in gardens in this country.

I. Liguliflorae

Corolla of all flowers ligulate. Oil-containing passages rare, but anastomosing laticiferous vessels present.

1. *Cichorieae.* Capitula homogamous. Corolla ligulate and five-toothed.

Anthers sagittate at the base. Style slender and papillose. Fruit an akene, usually narrow or flat, sometimes with a slender beak bearing a pappus which may have one or more rows of simple or plumose bristles. *Cichorium*, *Picris*, *Hieracium*, *Leontodon*, *Taraxacum*, *Lactuca*, *Tragopogon*, *Scorzonera*, *Sonchus*, *Dendroseris*, *Fitchia*, *Lapsana*, *Hypochaeris* and *Rhagadiolus*.

The plants are mostly herbaceous or occasionally shrubby. Trees occur only in the isolated allied genera *Fitchia* (Polynesia) and *Dendroseris* (Juan Fernandez). The species are widely distributed, though mainly in the Old World with the chief regions of concentration in the Mediterranean. Others are centred in Western America and Mexico. There are a large number of British species and many are cultivated either for their floral effect or as vegetables. We shall refer again to this tribe below.

The presence or absence of laticiferous tissue is a valuable distinguishing feature between the two main subdivisions of the Compositae and where it is absent oil-glands are usually found. Inulin is present as a storage carbohydrate in many genera, occurring either in root tubers, *e.g.*, *Dahlia*, or in the rhizome, *e.g.*, *Helianthus tuberosus*. The anatomy is normal and anomalous structures are rare. The plants are efficient colonizers of new ground and are often pioneers in vegetation, mainly because of the air-borne fruits, the rapid germination and the very short life-cycle possessed by many species. Groundsel is an excellent example of this. Moreover the fruit will develop and ripen even after the plants are dead, a feature which can be well observed among dried herbarium specimens, which though picked in flower often bear mature seeds by the time they are dry enough to be mounted.

The condensation of the inflorescence to a capitulum represents a high, if not the highest, expression of dicotyledonous development and it is customary to consider the Compositae as the most advanced family of the Dicotyledons. Despite this, geological evidence indicates that species resembling those of the present day occurred in Tertiary rocks as far back as the Oligocene, an early period for so advanced a family.

The success of the Compositae in the vegetation of the world may be in part, at least, attributed to the admirable adaptation of the flowers to cross-pollination by a great variety of insects. Müller points out that only the Umbelliferae can compare with the Compositae in this respect, but that whereas in the former family the nectar is exposed to rain on the epigynous disc, the nectar in the Compositae is secreted at the base of a narrow tubular corolla. Here it accumulates, rising up the tube as more is secreted. In this way the type of insect which can obtain it will depend on the amount of nectar secreted by each individual flower and the nature of the preceding visitors. Hence it is a matter of chance whether the flowers will supply a particular visitor and many insects visit and pollinate the flowers without receiving any reward for their services. Observations show however that the flowers are mainly visited by insects belonging to what are generally regarded as the more advanced orders of insects. If it is correct to suppose that insects and flowers were evolved simultaneously side by side, that state of affairs is what we might expect.

Apart from particular pollination mechanisms to which we shall refer later, the success of the Compositae lies generally in the aggregation of the flowers into compact heads whereby cross-pollination is almost inevitable. At the same time the inflorescences are conspicuous, which is accentuated in various ways, either by the florets being outwardly directed, *e.g.*, in *Centaurea*, or by the ligulate character of the corolla becoming exaggerated towards the margin of the capitulum, or in other cases by the development of distinct ray florets or by the presence of an inner series of conspicuous involucral bracts as in *Carlina*.

Further evidence of the success of the family is seen in the efficient fruit-dispersal mechanism occurring in most species. The pappus itself is a highly efficient organ, which is sometimes further improved by the presence of hooks. Distribution by water is also made possible by the imprisonment of air between the hairs of the pappus and by its unwettable nature, thus producing a floating mechanism. Hooked fruits of various kinds also occur, while in a few, sticky glandular hairs are produced on the fruits, as in *Siegesbeckia orientalis* (Fig. 1886), a plant widely distributed in tropical regions the world over. Certain fruits are polymorphic in the same capitulum as is seen in *Calendula officinalis* (Marigold) where the outermost fruits derived from the outer female flowers are much elongated with small spines on the back, while fruits nearer the centre have broad wings inrolled at the margins and fruits at the centre of the capitulum are incurved, often forming a ring, and have narrow involute wings.

FIG. 1886.—*Siegesbeckia orientalis.* Flowering shoots.

The economic importance of the family is considerable and we have already referred to a number of examples. Many contain valuable fatty oils, *e.g.*, Sunflower fruits; others possess ethereal oils and resins. Many are used medicinally, others produce insect powders, *e.g.*, *Chrysanthemum roseum* (Pyrethrum) and *C. carneum*. Colouring matters are obtained from *Carthamus tinctorius* (Safflower), and *Adenostemma tinctorium* is used to make rouge.

Many are used as vegetables and we have already referred to those most commonly used. Innumerable species are grown in gardens and of these many have been altered almost out of recognition as a result of horticultural practices. One has only to consider the variety of shape and colour of the capitula exhibited by Dahlias and Chrysanthemums to recognize the truth of this statement.

We cannot close our account of this family without describing some details of the pollination mechanism, which shows considerable variation in the different tribes. Hermann Müller, many years ago, made an extensive study of this subject and his work has been confirmed and amplified by the later studies of Small.

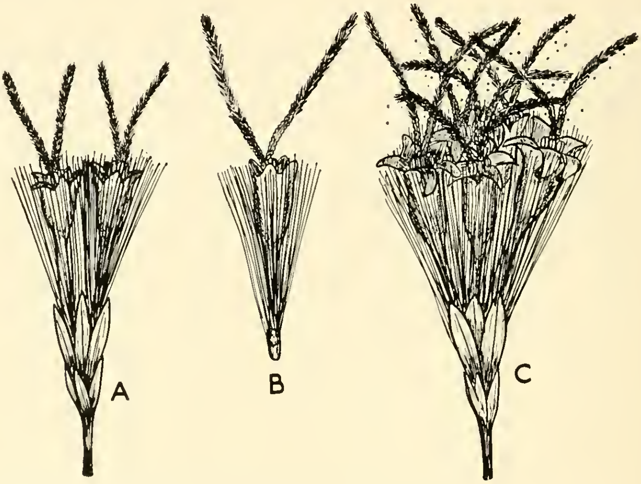


Fig. 1887.—*Eupatorium cannabinum*. Hemp Agrimony. A and C, Reduced capitula with involucres, showing the sweeping hairs which carry up pollen from the anthers. B, Older flower with stigmatic surfaces exposed at the base of the hairy arms of the style. Pollen dropping from the styles, as shown at C, may bring about geitonogamy.

We will select as our first example a member of the tribe Eupatorieae, *e.g.*, *Eupatorium cannabinum* (Fig. 1887) (Hemp Agrimony). Each capitulum usually contains four or five dull-red florets, but since some hundreds of capitula are aggregated into a dense corymb the inflorescence becomes very conspicuous. In the development of the florets the anthers discharge their pollen into the centre of the corolla and it is then pushed upwards by the sweeping hairs developed on the upper portion of the style, which develops late. Thus in the first stage of anthesis the upper part of the style with the sweeping hairs is exposed so that any insect visiting the flower at this stage will be liberally dusted with pollen. In the second stage in anthesis the style elongates further and the receptive stigmatic papillae become exposed above the bell-shaped corolla, so that an insect visiting the flower will now dust off any pollen it has previously acquired on to the papillae. Such an arrangement ensures that if insect visitors have been sufficiently numerous to remove all the pollen from the sweeping hairs, cross-pollination must occur. On the other hand if visits have been infrequent self-pollination must occur as a result of an insect visit. Self-pollination cannot take place in the absence of an insect visit, but geitonogamy undoubtedly occurs, for the stigmatic branches spread out so that they occasionally touch the hairs on adjacent styles. The nectar is secreted from the base of the style and the flowers are visited mainly by butterflies.

In *Petasites fragrans* (Fig. 1888) (Winter Heliotrope) belonging to the tribe Senecioneae, the capitula occur in two forms, quite different from one another in appearance. In the one there are numerous pseudo-hermaphrodite pollen-bearing florets on the disc and a smaller number of female florets in the rays. In the other type the condition is reversed.

FIG. 1888.—*Petasites fragrans.* Winter Heliotrope. A, Female ray floret. The ovary is ruptured and the ovule projects. B, Nectariferous floret from a female capitulum. C, Pseudo - hermaphrodite (male), nectariferous floret from a male capitulum. (*After Knuth.*)

The male florets usually possess nectar and the pollen is swept out of the florets by a columnar style beset with sweeping hairs: the ovary however is vestigial. The corolla is tubular below but expanded above into a bell-shaped structure with four lobes. The female florets are nectarless and possess no stamens, the corolla is tubular and slender while the style is filiform and smooth. The tip of the style branches, the outer surface being beset with fine hairs, the inner surface of the branches with papillae. The pollen grains are white, roundish bodies with long spines adapted to secure adhesion on the stigmatic papillae. The flowers are visited mainly by bees.

In *Petasites hybridus* (Butterbur) the plants are completely unisexual, the male being much the commoner.

Turning to the Astereae we may cite the common Michaelmas Daisy as an example (Fig. 1889). The female ray florets are brightly coloured, either red or blue, while the disc florets are yellow and hermaphrodite. These latter florets have corollas in which the lower portion is contracted and stalklike while the upper portion is expanded into a bell. The pollen is swept out by the lips of the stylar branches which are beset with upwardly projecting sweeping hairs. When the anther cylinder is empty the style projects well above the rest of the inflorescence. At this stage the lips of the styles remain closed together and therefore an insect visiting the flower at this stage will become dusted with pollen. Later the stigma opens and exposes the stigmatic papillae, so that when a flower in this stage is visited by an insect bearing pollen, the grains are distributed on the receptive surface. Automatic self-pollination is also possible on account of pollen left on the stylar hairs. The flowers are visited by various kinds of insects, flies, bees and butterflies, the latter being the most common late in the

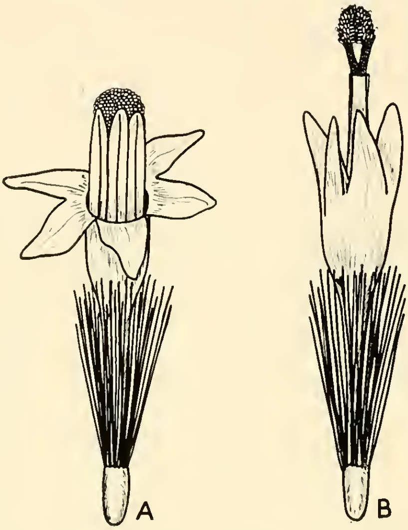


Fig. 1889.—*Aster novi-belgii.* Michaelmas Daisy. A, Pollen mass being extruded from the anther tube by upgrowth of the style. B, Later stage, with emergent style with two stigmatic lobes, each ending in a mass of sweeping hairs to which a few pollen grains still adhere.

autumn, and in October it is not uncommon to see the flowers covered with Tortoiseshell, Red Admiral and Peacock butterflies.

As an example of the pollination mechanism in the tribe Helenieae we may describe the condition in *Chrysanthemum segetum* (Fig. 1890) (Corn Marigold). The diameter of the golden-yellow head in this species is nearly 5 cm., of which about one-third is occupied by the disc. The twelve to sixteen ray florets are female and the stigma projects only slightly from the corolla tube. There are about 300 disc florets each with a corolla tube surmounted by a bell-shaped corolla. In the first stage of anthesis the style, covered with pollen, projects beyond the corolla bell, while later, after the pollen has been distributed, the branches of the style separate to expose the stigmatic papillae. The mechanism therefore in this example is essentially similar to that in *Aster*.

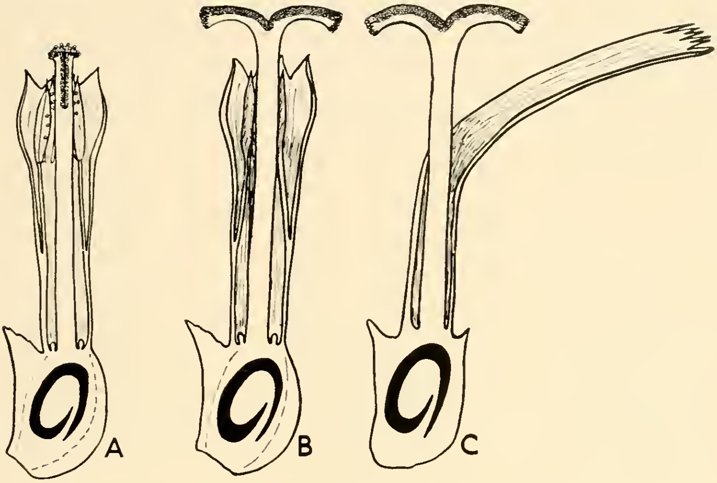


FIG. 1890.—*Chrysanthemum segetum*. Corn Marigold. A, The blunt ends of the stigmatic lobes act like a piston in extruding the pollen. B, Later stage, with stigmatic lobes expanded and receptive. C, Female ray floret.

The pollination mechanism in the tribe Arctotideae is interesting. Small and von Minden investigated this case and found that the style is sensitive to touch. The capitulum consists of about half a dozen rings of male florets which are tubular and in which the style functions only as a pollen presenter, there being no functional ovary. Outside this there is a ring of hermaphrodite tubular florets which may be partly male and partly female, for the fertility varies in different florets. Outside this again are true hermaphrodite florets which can all produce viable seeds. There is one row of ray florets which are ligulate and possess no stamens.

In the first stage in anthesis the style emerges from the tubular corolla. In good growing conditions this takes about five minutes. The upper part of this style is covered on the outside with pollen. If this region is touched it reacts rapidly, turning in the direction of the impact. It soon regains its irritability and will react again within half a minute. In the second stage in anthesis, that is after a day in the male stage, the style is withdrawn completely within the staminal tube. Some of the adhering pollen may be scraped off the style in this movement but the majority remains attached in a ring around the top of the staminal tube. In the case of hermaphrodite flowers the style emerges again the following morning but at this stage it is not sensitive to touch and the forked apex soon expands thereby exposing the stigmatic papillae.

In this case as in many others the ray florets curl over the disc florets as a protection during the night and at the beginning of the fruiting stage.

We shall mention two examples of the Cynareae; the first *Echinops ritro* (Fig. 1891) and the second *Centaurea cyanus*.

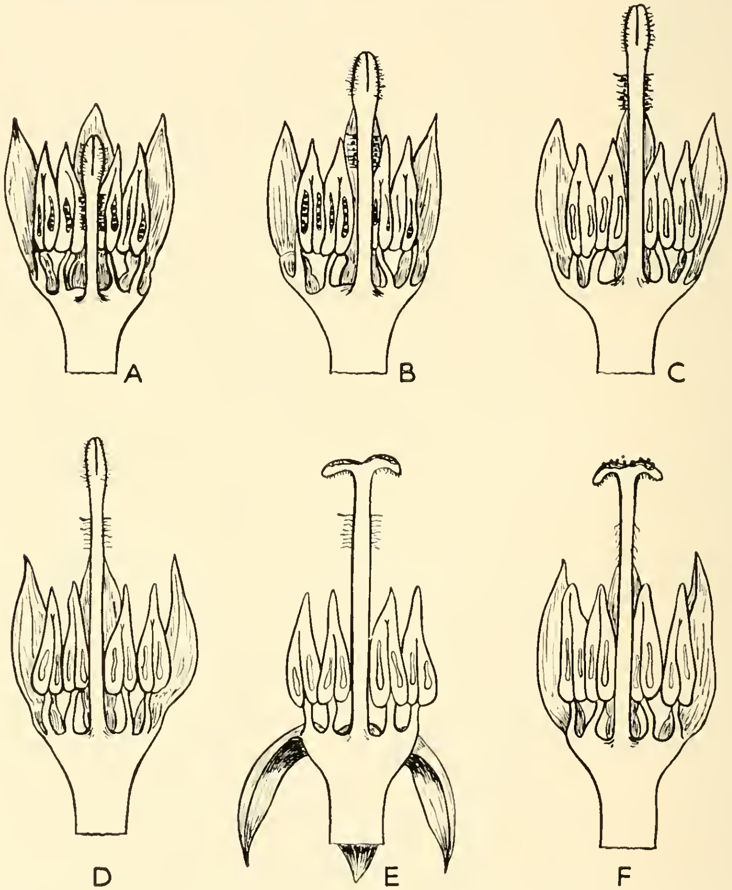


Fig. 1891.—*Echinops ritro.* A to F, Successive stages in anthesis, showing the upgrowth of the style which is provided with two sets of sweeping hairs, one above the other. The stigmatic surfaces remain undeveloped until all pollen has been removed and then expand, as in E and F.

In the first example the heads, which are composed of one-flowered capitula, are about 6 cm. in diameter and the florets develop from the apex of the spherical inflorescences downwards. The corolla of the tubular florets is divided almost to the base into five slender, bright blue lobes which spread out above like a star. The lower portion forms a spherical reservoir for nectar which is partly protected from rain by the hairy margins of the petals. The tip of the style is densely covered with short hairs which push out and hold the pollen grains while a further circle of much longer hairs later removes it from the tubular corolla. At this time the inner surface of the stylar arms is quite undeveloped and it is only several days after the pollen has been discharged that the receptive papillae develop. By this time the pollen has been removed either by insects or by wind and the corolla lobes now bend inwards and surround the style, leaving the stigmas exposed and isolated. It follows therefore that in this case only cross-pollination is possible.

Our second example is *Centaurea cyanus* (Fig. 1892) (Cornflower). In this case the ray florets are neuter, funnel-shaped and radiating while the disc florets are hermaphrodite and tubular. Below the short, broad stylar branches is a ring of sweeping hairs which are directed upwards. The nectar is secreted in the base of the corolla and when the proboscis of a visiting insect is inserted to probe for nectar the filaments of the anthers contract rapidly and the pollen is swept out and carried off by the insect. At this stage only cross-pollination is possible. Later the stigmatic lobes of the style bend back sufficiently to come into contact with pollen adhering to the sweeping hairs, so that self-pollination is now possible. The

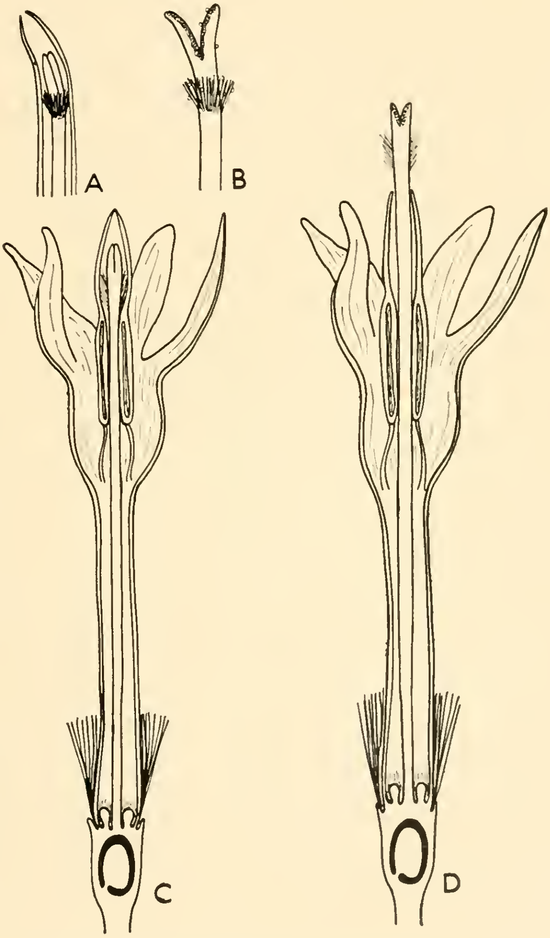


FIG. 1892.—*Centaurea cyanus.* Cornflower. A and B, Details of the sweeping hairs on the style. C, Style still enclosed within the tube formed of the apical extensions of the anthers, in which the pollen collects. D, Style finally emergent. See in text.

irritability of the anther filaments in this case is a contrast to the movement of the style already described in the case of *Arctotis*. Investigations by Juel have shown that irritability of the stamens occurs in a wide range of species included in all the tribes of the family. In a few cases, *e.g.*, *Gerbera*, the pollen is extruded with almost explosive rapidity. Irritability of the style however appears to be restricted to the single tribe Arctotideae.

Our last example of pollination mechanisms is one from the Cichorieae, and we may use *Hieracium umbellatum* (Fig. 1893) as a type. The florets are all yellow and the part of the style projecting from the anther cylinder is completely covered with spinose sweeping hairs, while the inner surface of the stylar branches is beset with stigmatic papillae. If the pollen is removed from the hairs as a result of insect visits then the floret can only be cross-pollinated. If on the other hand the pollen is not removed, self-pollination is effected by the bending back of the stigmatic branches until the papillae come into contact with the pollen on the sweeping hairs. Species of *Hieracium* are visited both by flies and by bees. Occasionally butterflies may also visit them to collect nectar.

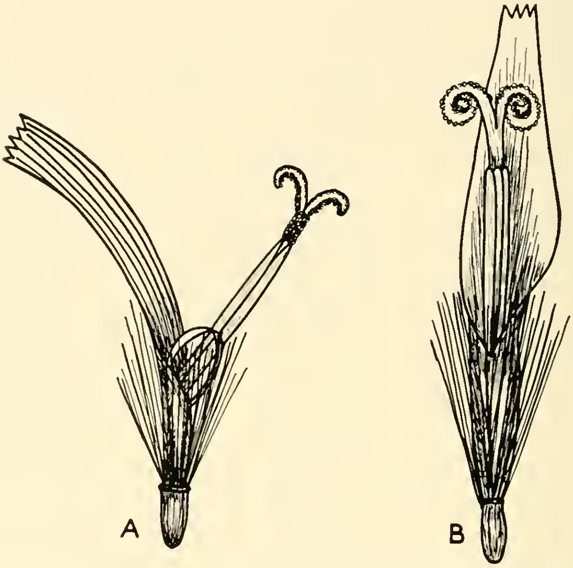


FIG. 1893.—*Hieracium umbellatum*. A, Floret with exserted style showing the spiny zone below the stigmas, which sweeps pollen from the anther tube. B, Stigmas recurved so that they touch the pollen-bearing zone and get self-pollinated. (*After Knuth.*)

In the allied genus *Taraxacum* experiments have shown that if both styles and anthers are removed from hermaphrodite florets they are able to produce viable seeds. The only conclusion which can be drawn, therefore, is that in such species the seeds develop parthenogenetically, and it is to this parthenogenetic propagation of chance hybrids between sub-species that the great multiplicity of apparent species in the genus is due.

CHAPTER XXX

THE ANGIOSPERMAE: MONOCOTYLEDONES

The Monocotyledones are Angiospermae in which only one cotyledon is produced by the embryo. The radicle usually emerges first from the seed and is followed by the cotyledon which surrounds the plumule. In some however the cotyledon remains within the seed and the plumule may then be surrounded by a special plumular sheath. The details of the various types of seed germination occurring in the Monocotyledon have already been described (see Chapter XXVI) and we need not repeat them here.

In the mature plant the leaves are characteristically parallel-veined and the ovate or linear types of leaf are most common. Compound leaves rarely occur. The main stems are often short, for the herbaceous type predominates, and are commonly subterranean, the aerial shoots being only lateral branches. Bulbs, corms or tubers commonly occur as storage organs while fleshy or thin, wiry rhizomes are very frequently met with. This fundamentally herbaceous type may however assume enormous proportions and some herbaceous forms, such as the Banana, reach the size of trees. In contrast to this we have the equally common grass type in which a stiff, slender aerial stem is produced on which is borne a number of long slender leaves. Many of these plants are annuals but others are perennial. This type includes all the cereal crops so essential for human economy.

Aquatic plants, both floating and submerged, are found in considerable numbers while plants inhabiting marshes are equally common.

Shrubs and climbing plants are far less common and are restricted to a few families while the truly arborescent habit is restricted to the Palms and a few genera of the Agavaceae, *e.g.*, *Yucca.*

Anatomically the Monocotyledons show a marked contrast to the Dicotyledons. The primary root rarely persists beyond the seedling stage and is soon replaced by a group of adventitious roots arising from the stem. These roots are structurally simple and do not exhibit secondary thickening. The stem structure is simple and consists of a large number of small, closed, collateral vascular bundles scattered in a ground tissue. No true secondary thickening similar to that in the Dicotyledons ever occurs, but in a few genera a cambium may become differentiated in the outer part of the stem from which additional vascular bundles are formed centripetally. No solid mass of wood tissue is however produced.

The leaves are usually simple, with a sheathing base, and are parallel-veined. Cordate leaves with reticulate venation are characteristic of a number of genera in the families Dioscoreaceae, Araceae, Alismaceae and Smilacaceae, especially in the tropics. The leaf may grow to a very large size. Some of the entire leaves of the Banana may be 8 to 10 ft. long, while in the Palms the leaves may attain enormous size. They consist of a strong, well-developed leaf-sheath, prolonged into a stout petiole and bearing a huge, spreading, palmate or pinnate lamina.

A theory was propounded by de Candolle and later elaborated by Henslow, Arber and others, to the effect that the leaf in Monocotyledons is only a phyllode, corresponding to the base and petiole, or in some cases only to the base, of the leaf in Dicotyledons. On this view there is no true lamina in Monocotyledons. (See Vol. I, p. 997.)

The floral organs are usually arranged in five whorls with three members in each whorl. In more specialized members one or more whorls may be absent and the number of members reduced. A solitary bracteole is characteristic and is situated either in a posterior or rarely in a lateral position.

It is probable that within the Monocotyledons we may trace two series, the one starting with a simple generalized type of flower which gradually becomes elaborated into a highly specialized structure, associated with a very elaborate pollination mechanism. The second is a gradual reduction of the floral parts culminating in the very reduced flower found in the Lemnaceae.

The seed is usually endospermic and sometimes has perisperm as well. In the Orchidaceae, however, there is no endosperm and as the embryos are extremely small the seedling relies on a symbiotic fungus to supply its food requirements during the early stages of development.

The classification of the Monocotyledons varies according to the views of different authorities, but there is a greater degree of uniformity in the methods here than we found in the Dicotyledons. There are several clear and well-defined series, illustrating separate developmental lines, but all showing affinities with one or more of the other groups.

Speculation has naturally been aroused as to whether the Monocotyledons or the Dicotyledons should be regarded as the more primitive. In the light of recent work it is now generally accepted that both groups originated from a common ancestral stock before Tertiary times, but there is little indication among present-day forms of any family in either group from which the opposite group might have arisen. The closest approximation between the groups is shown by the Ranales and the Helobieae, but this does not necessarily mean that the one has arisen from the other.

HELOBIEAE (Alismales)

The Helobieae are Monocotyledons in which the flowers are either hermaphrodite or unisexual, regular and either naked or with a simple or double perianth. There are an indefinite number of stamens occasionally reduced to one. The carpels may also be indefinite or reduced to one. The embryo is large and there is no endosperm.

Most authors are agreed that the Helobieae are undoubtedly primitive, indeed the critical study of numerous examples has led Hutchinson to emphasize that the Butomaceae and Alismaceae, which are here included in the Helobieae, show marked similarities with the Ranunculaceae and may either have been derived from them or at least may have had a common origin. The main difference between the two groups is due, in his opinion, to the fact that the Monocotyledon families have lost the endosperm in the seeds as an adaptation to an aquatic habitat, a view originally proposed many years ago by Henslow.

As treated here the Helobieae are regarded as including the following important families: Alismaceae, Butomaceae, Naiadaceae, Potamogetonaceae, Aponogetonaceae, Hydrocharitaceae and Scheuchzeriaceae. Hutchinson recognizes a considerable number of further families due to splitting up several of the above families. Moreover he does not recognize the Helobieae as an order but has created several separate orders to include the families. His method, though undoubtedly having much to commend it, has not been followed here owing to its complexity.

Of the families mentioned above, we shall consider the Alismaceae in detail, the others we may consider briefly first.

The **Butomaceae** are a small family which, according to Bentham and Hooker, is included in the Alismaceae, but which in the works of Engler and of Hutchinson is elevated to family rank. It only includes some four genera most of which are monotypic. The plants occur either in water or

FIG. 1894.—*Butomus umbellatus.* Flowering Rush. Inflorescence.

in marshes. The inflorescence is a cymose umbel and the flowers are generally trimerous, occasionally dimerous. Generally there is a perianth of two whorls, except in *Butomus* (Fig. 1894). There are from nine to an indefinite number of stamens and from six to an indefinite number of carpels. These are apocarpous with an indefinite number of anatropous ovules scattered over the inner surface of the ovaries. This last point is of particular interest for it is similar to the condition found in the Nymphaeaceae. It has been used as evidence to suggest a common ancestor for both families and as an argument for the equal antiquity of the Dicotyledons and Monocotyledons. Hutchinson points out the close similarity between *Butomus* and *Cabomba*, the latter also having trimerous flowers and being aquatic in habit. He points out that the only fundamental difference between the two is the paired cotyledons in *Cabomba*. Hutchinson considers that too much importance should not be attached to the number of cotyledons among primitive Angiosperms, for he points out that some members of the Ranunculaceae often possess only one cotyledon. He further suggests that his newly constituted Amaryllidaceae may have their origin in the Butomaceae.

The best-known member of the family is *Butomus umbellatus*, the Flowering Rush, which is common in Britain.

The **Naiadaceae** are a small family of submerged aquatic plants rooting in the bottom of ponds containing fresh or brackish water. The slender stems are much branched and the leaves are short and narrow, arising in pairs. The margin of the leaf is spiny and this spine, which may arise either from a single cell or from a group of cells, is considered a specific character. The plants (Fig. 1895) may be monoecious or dioecious and the flowers arise from an outgrowth in the axil of a lower leaf. This lateral outgrowth bifurcates, one half forming the flower and the other an axillary branch at the base of which the flower finally lies. In the male flower there is only a single anther which may contain one to four loculi. It is enveloped in a perianth and a spathe, which arise as outgrowths below the anther, and the perianth ends above it in four close-fitting lips while the spathe is drawn out above into a cylindrical neck. In the female flower the apex of the floral axis bears a single ovary

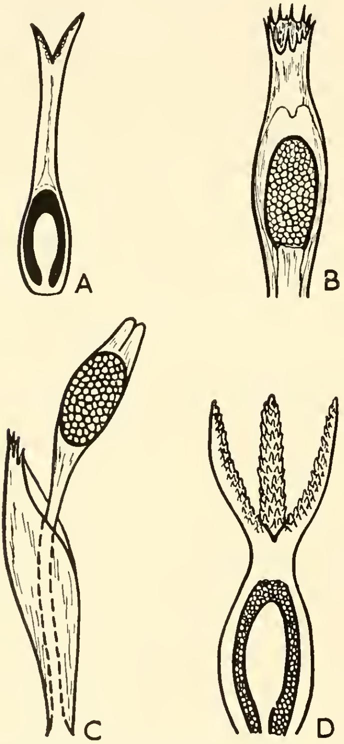


Fig. 1895.—*Naias minor*. A, Female flower. B, Male flower. *N. flexilis*. C, Male flower with elongated pedicel. *N. marina*. D, Female flower. (*After Rendle.*)

containing one basal anatropous ovule. The former terminates in two or three stigmas.

The pollen grains are either spherical or oval and have a single delicate coat. When the anther is ripe the flower stalk elongates, splits open the spathe and the pollen grains are liberated. The pollen is of the same density as water and pollination is said to occur below the surface.

There is only a single genus *Naias*, which contains about thirty-five species, many of which are widely distributed. Two species are now found in Britain, but geological evidence points to the fact that the genus was once more widely distributed and commoner in Britain than it is at the present day.

The **Potamogetonaceae** are a small family of about ten genera which are generally submerged water plants, a few having floating leaves. Several genera are found in sea-water. The stem usually consists of a rhizome anchored by adventitious roots arising at the node. The leaves (Fig. 1896) are produced alternately and consist generally of a broad, entire lamina borne on a long petiole, or they may consist merely of a linear blade. Intravaginal scales occur in the leaf axils. The flowers are either monoecious or dioecious; the floral parts are either dimerous or tetramerous but a perianth is generally absent. In many species the flowers are borne above water. The anthers are sessile and the carpels free with solitary orthotropous or campylotropous ovules. In *Potamogeton* the four anthers bear petaloid outgrowths from the back of the connectives, simulating a perianth. The

FIG. 1896.—*Potamogeton natans.* Flowering shoot.

inflorescence of *Zostera* consists of a linear series of alternating carpels and stamens, the whole being enclosed by the sheathing margins of a leaf.

Special organs of vegetative propagation occur in some species and consist of tuber-bearing runners. Anatomically the plants have the typical structure of aquatics with a well-developed aerenchyma. It has been found that the quantity of sclerenchyma produced varies with the habitat, for plants growing in running water have more mechanical tissue than those found in stagnant water. In marine species the mechanical tissue is well developed and air spaces may be absent.

Pollination in *Potamogeton* (Fig. 1897) is anemophilous and the grains are round, but in other genera, such as *Zostera* (Fig. 1898), the pollen is filamentous and develops into alga-like threads of the same specific gravity as the water. These filaments become entangled in the branching stigmas (Fig. 1899) and pollination is effected. This type of hydrophilous pollination is rare and has been only imperfectly studied.

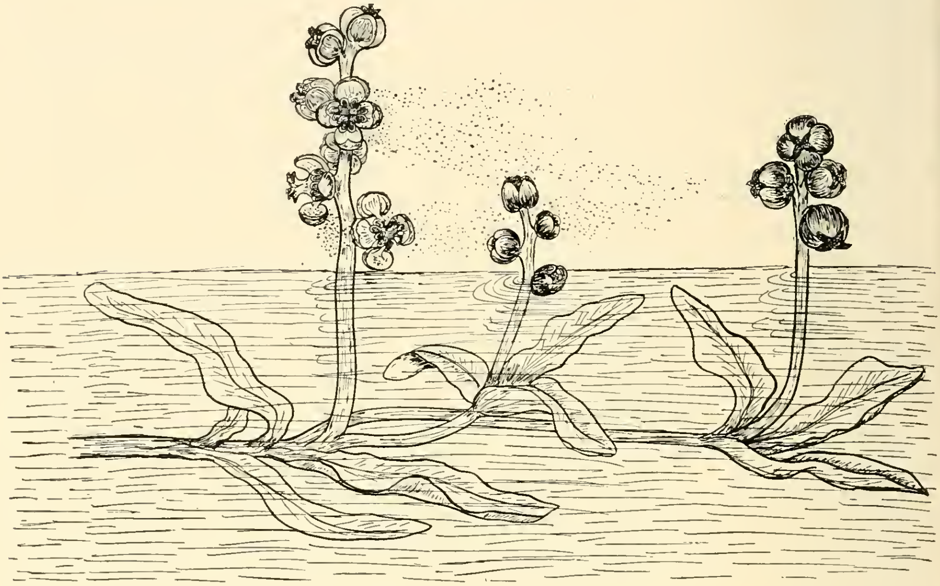


FIG. 1897.—*Potamogeton crispus.* Flowering shoot showing anemophilous pollination. (*After Kerner and Oliver.*)

The family includes a number of genera of which *Potamogeton* is the largest. The species are difficult to separate but over twenty have been recognized in Britain. Among the other genera, *Ruppia* and *Zannichellia*, (Fig. 1900) which are monotypic, and two of the six species of *Zostera* are found in British waters. Other genera occur all over temperate and subtropical regions of both hemispheres.

The **Aponogetonaceae** include the single genus *Aponogeton* with twenty-five species occurring in tropical regions of the Old World and in South Africa (Fig. 1901). They are water plants with sympodial rhizomes

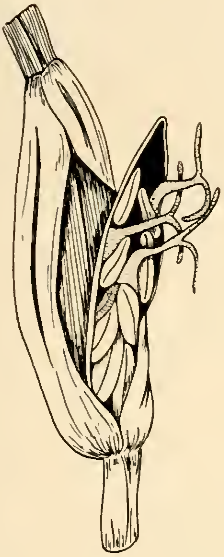


FIG. 1898.—*Zostera nana.* Spathe with spadix emerging. Carpels with two stigmas, stamens of two separate half-anthers. Each stamen and the opposite carpel form one flower. (*After Sowerby.*)

FIG. 1899.—*Zostera marina.* Filamentous pollen grains.

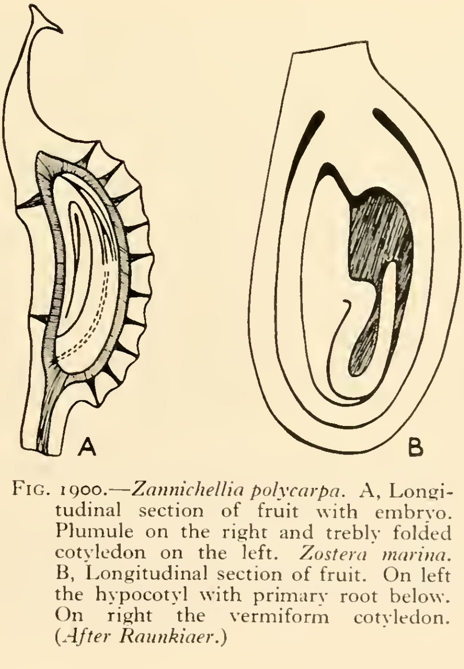


FIG. 1900.—*Zannichellia polycarpa.* A, Longitudinal section of fruit with embryo. Plumule on the right and trebly folded cotyledon on the left. *Zostera marina.* B, Longitudinal section of fruit. On left the hypocotyl with primary root below. On right the vermiform cotyledon. (*After Raunkiaer.*)

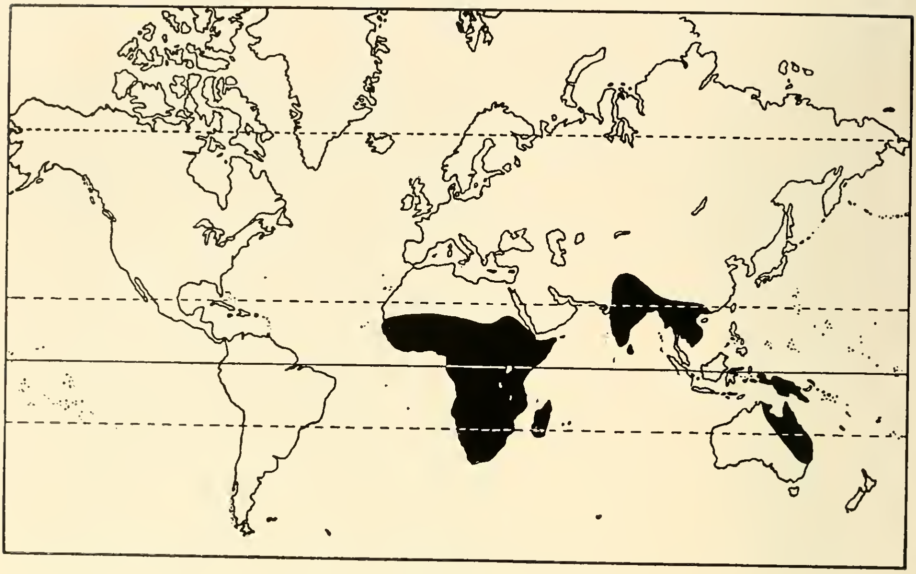


FIG. 1901.—Distribution of *Aponogeton.*

and floating leaves. The flowers arise above the water in spikes which are often branched dichotomously. The perianth consists of one to three segments, there are six or more stamens and three or more free, unilocular carpels with a group of basal ovules. Each flower may be subtended by a conspicuous white bract. *Aponogeton distachyum* (Fig. 1902), the Cape

FIG. 1902.—*Aponogeton distachyum.* Flowering plant.

Pondweed, is often cultivated in ponds in this country. *A. fenestrale*, which used to be placed in a separate genus *Ouvirandra*, has submerged lattice-like leaves with no lamina in the meshes between the veins. It occurs in ponds in dense shade in parts of Madagascar and is sometimes cultivated in greenhouses. (See Vol. I, p. 958, Fig. 944.)

The **Hydrocharitaceae** include a small group of aquatic herbs in which the plants may be either completely submerged, as in *Vallisneria* in which only the flowers come to the surface, or the whole plants may float as in *Hydrocharis*. The family includes some fifty species grouped in fifteen genera. Three genera are found in the sea. Among those which occur in Britain are *Hydrocharis morsus-ranae* (Fig. 1903) (Frogbit), *Stratiotes aloides* (Water Soldier) and *Elodea canadensis* (Water Thyme) which was introduced into this country from America in 1841. It is interesting to note that almost without exception only female plants of *Elodea* occur and reproduction is entirely vegetative, by means of turions, condensed apical shoots which become detached. *Elodea* like *Vallisneria* is pollinated by water. In the former the female flowers are raised to the surface of the water and receive floating pollen which has been shed by detached male flowers. In *Vallisneria spiralis* the female flowers are also elevated to the water surface but the detached male flowers do not shed their pollen but float as a whole on the surface and pollination is effected by the anthers rubbing against the stigmas, bursting and then discharging their pollen (see also p. 1296). In *Hydrocharis* pollination is by insects and in the female flowers nectar-secreting scales are formed at the base of the petals, their structure being remarkably similar to those in the genus *Ranunculus*. In *Stratiotes* the dioecious flowers come above the water only for pollination and submerge again while the fruits ripen.

FIG. 1903.—*Hydrocharis morsus-ranae*. Frogbit. Floating plant.

The **Scheuchzeriaceae** are a small family containing five genera and about twenty species which include herbaceous plants found mainly in marshy places. They bear rushlike leaves often sheathing at the base and large terminal spikes or racemes. The flowers are hermaphrodite, consisting of two whorls of petaloid segments followed by six stamens arranged in two whorls and two trimerous whorls of free or united carpels of which the outer three are sterile. The fertile carpels contain one or two anatropous ovules. A double whorl of carpels is a very rare occurrence in the Angiosperms. The flowers are anemophilous and protogynous. The most important genus is *Triglochin* which is distributed in temperate regions of both the New and the Old World. In Britain there are two species, *T. palustre* which is found in marshy meadows and *T. maritimum* (Fig. 1904) which is stouter and larger and is found in salt marshes. *Scheuchzeria palustris*, a small marsh plant, has been recorded in Britain but is common in the colder parts of Europe.

FIG. 1904.—*Triglochin maritimum.* Flowering plant growing in a salt marsh.

Alismaceae

The members of this family are mostly water or marsh plants, with perennating rhizomes, which are distributed mainly in tropical and temperate regions of the northern hemisphere. The family is of particular interest because of the undoubted general resemblance to the Ranunculaceae. Whether this similarity is due to a true phylogenetic relationship or produced as a result of parallel evolution is a matter not yet easily settled, but we shall later compare some of the characters of the two families.

In the British Flora the family is represented by two well-known plants, *Alisma plantago-aquatica* (Fig. 1905) (Water Plantain) and *Sagittaria sagittifolia* (Arrowhead), while in addition *Elisma natans*, a delicate little European species, is found rarely in British fresh waters. *Damasonium stellatum* (Thrum Wort) is a western Mediterranean plant which is sometimes met with in ditches and ponds in southern England.

The **plants** are rhizomatous with large radicle leaves which may be erect, floating or submerged and are differently shaped according to their position. The veins are parallel with the margins and convergent at the apex, with transverse nerves, often close and parallel. There are small scales in the leaf axils, known as intravaginal scales. Laticiferous tissue may be present.

FIG. 1905.—*Alisma plantago-aquatica.* Water Plantain. Flower, enlarged × 4.

The **inflorescence** is usually much branched, the primary branching being racemose while the secondary branching is cymose. The individual flowers are often whorled.

FIG. 1906.—Floral diagram of Alismaceae.

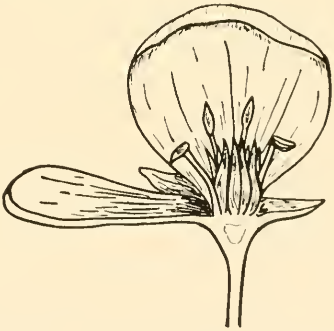


FIG. 1907.—*Alisma plantago-aquatica.* Flower in section showing calyx and corolla.

The **flowers** (Fig. 1906) are hermaphrodite or sometimes monoecious, actinomorphic and possess distinct calyx and corolla (Fig. 1907).

The **calyx** is composed of three sepals which are imbricated in the bud and generally green in colour.

The **corolla** consists of three petals, imbricated in the bud and usually white or violet in colour and often of large size.

The **androecium** is made up of either six or an indefinite number of stamens whose anthers may dehisce either introrsely or extrorsely.

The **gynoecium** is composed of a variable number of carpels, rarely less than six, which are free and developed on a somewhat conical receptacle. Each carpel contains usually a single, or rarely several, anatropous or campylotropous ovules. The style is persistent.

The **fruit** is an etaerio of akenes or of follicles, and hard, woody or leathery in consistency.

The **seed** contains a large horseshoe-shaped embryo, with a long cotyledon and a large hypocotyl ending in a short blunt radicle. The seed is non-endospermic.

The family contains about a dozen genera and includes some fifty species occurring in temperate and tropical regions of the northern hemisphere. The limits of the family have been variously interpreted, more particularly on the question whether the Butomaceae should be included in the Alismaceae, or separated from it.

Anatomically the Alismaceae, as here interpreted, exhibit certain common features of interest, more particularly in the presence, both in the stems and leaves, of an intercellular laticiferous system containing an oil emulsion. In the rhizomes of *Alisma plantago* and in the tubers of *Sagittaria sagittifolia* these laticiferous canals form a network which is closely connected with the vascular bundles. In certain tropical genera the laticiferous system is so extensive in the leaves that it forms bright transparent dots in the green tissue of the blade, always in close association with the vascular bundles.

The stomata are very variable in distribution according to whether the leaf is aerial, floating or submerged, a fact which also affects the distribution of mechanical tissue.

Economically the family is of little importance although the tubers of Arrowhead are a potential source of carbohydrate material. In Germany they are sometimes used to feed pigs, while the ever-careful Chinese cultivate the plant for the sake of the tubers and have produced a variety in which the tubers reach the size of about 3 to 4 in. in diameter. Tubers of the related *S. variabilis* are called Swan Potatoes and are said to be eaten by the American Indians.

The family is not usually subdivided into separate tribes. The following may be cited as the more important genera: *Alisma* with one species found in north temperate regions and Australia; *Sagittaria* with about thirty species occurring mostly in America; *Damasonium* with three species occurring in California, Australia, Tasmania and in Europe; *Elisma* with a single European species; and *Echinodorus*, with twenty species in America and Africa, one of which occurs in Britain.

Pollination mechanisms have only been studied critically in a few instances.

In *Alisma plantago* (Fig. 1908) the flowers are arranged in pyramidal panicles and possess yellow nectar guides at the base of each of the three petals. Nectar is secreted as a series of small drops from a fleshy ring formed by the union of the broadened bases of the six stamen filaments. These filaments are directed obliquely outwards and the anthers dehisce extrorsely. The styles stand erect in the centre of the flowers.

FIG. 1908.—*Alisma.* Flower to illustrate pollination. See in text.

The most frequent visitors are hover flies. These, if they alight on the centre of the flower, are most likely to effect cross-pollination. On the other hand, if they alight on the petal they are more likely to transfer pollen from the anther to the stigma of the same flower. Small bees have also been observed to visit the flowers.

In the other genera the mode of pollination is less certain. Anemophilous pollination may occur in *Sagittaria*, though self-pollination is to a large extent precluded, according to Warnstorf, on account of the monoecious nature of the flowers. In time of floods the flowers of *Elisma natans* remain closed below the water and are pollinated pseudo-cleistogamically.

As has been already pointed out, one of the chief interests in the family is the similarity which it shows to the Ranunculaceae. Hutchinson points out that although the absence of endosperm and the peculiar character of the embryo differentiate them from the Ranunculaceae, there are other features which suggest an affinity between them. He points out that *Ranalisma*, which was discovered by Ridley in a patch of mud between limestone cliffs in Malaya, differs from *Ranunculus* only in the solitary cotyledon and in the absence of endosperm. In this plant on the other hand the carpels are densely aggregated on the receptacle and the leaves are net-veined. Hutchinson therefore would see in *Ranalisma* a possible connecting link between the Ranunculaceae on the one hand and the Alismaceae on the other, and therefore between the Monocotyledons and Dicotyledons and a common ancestral type. It is worth noting moreover that both are herbaceous rather than arboreal.

FARINOSAE (Bromeliales)

The Farinosae are a small order of Monocotyledons in which the plants are herbaceous and sometimes grasslike. The flowers are hermaphrodite or unisexual, usually trimerous, and composed of a perianth of six segments, six stamens in two whorls, or one whorl of three. Carpels three, united.

The ovule is usually solitary and often orthotropous and the endosperm usually mealy in character.

The plants which comprise the order are very various in habit. The Bromeliaceae are essentially xerophytes while the Commelinaceae are tropical and subtropical herbs. The Eriocaulaceae produce flowers in small, terminal capitula, like those of the Compositae among the Dicotyledons.

The order is split up by Hutchinson into four, in accordance with the more important families. None will be considered here in detail and we shall retain the older method and include them together in Engler's order Farinosae. The families which we shall briefly discuss are Commelinaceae, Eriocaulaceae and Bromeliaceae.

The **Commelinaceae** are perennial herbs, bearing leaves with a basal, membranous, closed sheath, covering the young inflorescences. The flowers are usually actinomorphic, rarely zygomorphic, hermaphrodite or rarely polygamous, borne in axillary clusters or in terminal cymes or panicles. The perianth is made up of three sepals and three petals enclosing six stamens, the filaments of which are often hairy. The ovary is trilocular, or sometimes bilocular by suppression, the ovules few and orthotropous. The fruit is a loculicidal capsule. The seeds are large and few in number with a copious endosperm.

The family includes about thirty genera with nearly 400 species of which the best known are *Commelina* and *Tradescantia*. *Commelina*, with about 115 species, is widely distributed in the tropics. *C. coelestis*, with bright blue flowers, is cultivated in gardens. The three inner stamens are sterile, but the filaments contain a sweet juice and are often pierced by bees. *C. benghalensis* has subterranean cleistogamic flowers. The rhizome in some species is edible.

The genus *Tradescantia* contains thirty-five tropical and North American species of which *T. virginica* (Spider Wort) (Fig. 1909) is the best known. It is commonly grown in gardens on account of its bright purple flowers. The stamen hairs are frequently used in the demonstration of cyclosis.

FIG. 1909.—*Tradescantia virginica.* Flower with leafy bracts.

FIG. 1910.—*Eriocaulon septangulare.* The inflorescence stalks bear small capitula of flowers surrounded by an involucre of bracts, as in the Compositae.

The **Eriocaulaceae** are small, perennial herbs with shortened axes and dense tufts of narrow, grasslike, radical leaves from which arise one or more simple, slender scapes bearing more or less spherical capitula of flowers. The individual flowers are minute and unisexual by abortion and the inflorescence is surrounded by an involucre. The perianth is hyaline or membranous, usually sepaloid, and composed of two whorls. Male flowers have four to six stamens; female flowers possess an ovary composed of two or three carpels with one orthotropous, pendulous ovule in each loculus. The fruit is a capsule and the seed is endospermic.

The family contains about 600 species grouped in some nine genera, of which *Eriocaulon*, with some 250 species, is the best known. *E. septangulare* (Fig. 1910) is found in the north-west of Scotland and in west Ireland, though it is really a North American species. The other genera, of which *Paepalanthus*, with 215 species, is the largest, are restricted mainly to tropical South America.

The **Bromeliaceae** are an interesting family of xerophytic and largely epiphytic species, occurring chiefly in the forests of tropical America. The axis bears a rosette of leaves without stalks but with well-developed sheaths which play an essential part in the nutrition of the plant. The sheaths embrace the stem and form a basin or cistern in which water and fragments of rotting leaves, dead insects and the like are collected. Peltate absorption hairs line the inner side of the sheath and through them dissolved substances and in particular nitrogenous material are absorbed.

The leaves are markedly xerophytic in character with a strongly cutinized epidermis and well-developed water-storage tissue. The assimilating tissue is usually restricted to the upper surface. In many the leaf margins bear spines, usually small but in some species of formidable size, those of *Puya chilensis* (Fig. 1911) being used by the natives as fish-hooks. There are often numerous adventitious roots, which in many instances serve only for fixation, secreting an adhesive material to assist in anchoring the plant on its support.

Fig. 1911.—*Puya chilensis.* Plant with inflorescence about seven feet high. Cambridge Botanic Garden.

The flowers are hermaphrodite and trimerous, with an outer sepaloid and inner petaloid perianth, stamens six in number often epipetalous, with introrse anthers, and a gynoecium of three carpels with many anatropous ovules. The fruit is a berry or a capsule, in the latter case the seeds being very light or winged. The embryo is small and immersed in a mealy endosperm.

FIG. 1912.—*Aechmea brasiliensis.* Growing on bare rock in the Jardim Botanico, Rio de Janeiro.

Another genus which may be mentioned is *Aechmea*, with some fifty species which occur in the West Indies and South America (Fig. 1912).

The most important genus is *Ananas*. There are five species including *A. sativus*, the Pineapple, which is largely cultivated in the East and West Indies, Queensland, South Africa and Hawaii. The fruit, which arises from a cluster of stiff leaves, is formed by the post-fertilization enlargement of the axis and bracts of the inflorescence in which the generally sterile fruits become embedded. During development the main axis grows on beyond the fruit and forms a tuft of leaves.

The only other genus which need be mentioned is *Tillandsia*. It contains about 400 species living in tropical America. Most of them are epiphytic, with cisterns similar to those described above, but *T. usneoides*, Spanish Moss (Fig. 1913), forms long festoons of branches

FIG. 1913.—*Tillandsia usneoides.* Spanish Moss. Thread-like stems and leaves hang intertwined in long masses.

with very narrow leaves, giving a superficial resemblance to a lichen. In *Tillandsia* and *Puya* the ovary is superior, though in *Ananas* and *Aechmea* it is inferior.

ZINGIBERALES

The Zingiberales are large perennial herbs with persistent rhizomes and large glabrous leaves with a well-developed sheath, a long stalk and a pinnately veined lamina. The flowers are large and showy, each is hermaphrodite and zygomorphic or asymmetrical. The perianth is in two whorls, either petaloid or separable into calyx and corolla. The stamens are usually five or six in number but often only one is functional, the remainder becoming petaloid. The ovary is composed of three carpels, generally trilocular, with one or many ovules and axile placentation. The seeds, which are sometimes arillate, contain endosperm and are enclosed either in a capsule or a berry.

The plants are tropical or subtropical and are found in swampy forest districts. Several are extremely striking, some are of economic importance and others are cultivated in greenhouses where space permits.

The term Zingiberales, as here used, is due to Hutchinson and replaces the Englerian order Scitamineae. Bentham and Hooker placed all the members in a single family of the latter name. Later writers, including Hutchinson, recognize a number of families of which we shall consider briefly the following: Musaceae, Zingiberaceae, Cannaceae and Marantaceae.

The **Musaceae** are perennial herbs which perennate by underground rhizomes and often attain very large size. The aerial shoot may reach 100 ft. in *Ravenala madagascariensis*, the Traveller's Tree, while in other genera the axis is made up of the long, stiff leaf sheaths, which are rolled round one another and conceal the short stem which finally elongates and bears the inflorescence. The leaves are either radially arranged or are restricted to two rows. They are very large and consist of a strong sheath separated by a petiole from an enormous ovate blade. The blade has a strong midrib from which are given off parallel veins to the margin. The flowers are protected by great spathe-like bracts which are often coloured. The inflorescence may be simple or compound and bears flowers which are often brightly coloured. These flowers are zygomorphic and are either hermaphrodite or may become unisexual due to the abortion of either stamens or pistil. The perianth is petaloid and composed of two series of free, or else more or less coherent parts. The stamens are free, five or rarely six in number. The ovary is inferior and trilocular, containing numerous anatropous ovules. The fruit is a berry or sometimes a loculicidal capsule. The seeds often possess fleshy or hairy arils. The embryo is straight and immersed in mealy perisperm.

The family contains six genera and about 150 species, which are distributed throughout the tropics. Three genera are worthy of mention, *Musa*, *Ravenala* and *Strelitzia*. *Musa* contains about eighty species which may grow to a height of 10 to 20 ft., with false aerial stems arising from a rhizome. The inflorescence emerges from the centre of the column of leaf sheaths and bears numerous flowers in the axils of leathery, often red-coloured bracts. The female flowers are restricted to the basal part of the inflorescence. The sepals and two anterior petals are formed into a tube while the posterior petal is free. There are usually five fertile stamens. The fruit is an elongated berry. *M. sapientum* (Fig. 1914) is the Banana, which is now grown in many parts of the tropics, especially in Central America and the West Indies. *M. paradisiaca* is the Plantain, from which the Banana may have originated. The stalk of *M. ensete* is eaten in Abyssinia, while *M. textilis*, which grows in the Philippine Islands, is cultivated to furnish a useful fibre known as Abaca or Manila Hemp. The dwarf Banana grown in the Canary Islands is *M. cavendishii.*

FIG. 1914.—*Musa sapientum.* Banana. Large pendent inflorescence, the lower part of which is already set with parthenocarpic fruits. The apical part is still in flower, with large caducous bracts. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

The genus *Ravenala* (Fig. 1915) contains only two species which are found in Madagascar and South America. They possess a true aerial stem which bears two ranks of very large leaves giving the plant a fanlike appearance. *R. guyanensis* occurs in America while *R. madagascariensis* is the Traveller's Tree, so called because of the water which collects in the leaf bases and can be used for drinking in cases of necessity. This water is obtained by piercing the leaf base with a knife. The flowers are pollinated by humming-birds. The stamens and style are enclosed by a sheath formed

FIG. 1915.—*Ravenala madagascariensis*. Traveller's Tree. Botanic Gardens, Singapore.

by the paired petals in the young flowers and pressure causes them to separate, releasing the internal organs and thereby scattering the pollen.

In *Strelitzia* there are five South African species, ranging in height up to about 10 ft. or more. The leaves are large and radially arranged and the inflorescences consist of a cincinnus arising in the axil of a great spathe (Fig. 1916). The sepals are free but the lateral petals are united and enclose five fertile stamens. The odd petal is very short and broad. These two anterior petals form a landing-stage for humming-birds which are concerned in pollination. Pressure by the birds causes the free edges of these petals to separate, thus exposing the anthers which come into contact with the under surface of the bird. In a subsequent visit this region will come into contact with the style which projects far beyond the limits of the petals and is therefore the first organ touched. The flowers of *Strelitizia reginae* are coloured blue and orange and are about 6 in. long; hence they are extremely conspicuous objects and are highly valued in cultivation.

FIG. 1916.—*Strelitzia reginae.* Two inflorescences showing flowers emerging from the leafy spathe.

Hutchinson, in his Zingiberales, separates the Musaceae from the Strelitziaceae on the character of the fruit and the arrangement of leaves and bracts. He also includes in this order the Zingiberaceae, Cannaceae and the Marantaceae so that in general terms the Zingiberales are approximately equivalent to the Scitamineae.

The **Zingiberaceae** are perennial herbs growing from underground rhizomes, the form of which varies in the different genera. The leaves are simple, consisting of a sheath, petiole and blade with ligular outgrowths of the sheath. The inflorescence may be simple or compound and the flowers are hermaphrodite and medianly zygomorphic. The perianth consists of two trimerous whorls which are usually interpreted as calyx and corolla. The median posterior stamen of the inner whorl alone is fertile, often with a broad connective. Lateral stamens of the same whorl often unite to form a conspicuous petaloid labellum. Two of the stamens of the outer whorl are sometimes represented as staminodes. The ovary is inferior and trilocular, with axile placentation. The style is slender and lies in a channel in the fertile stamen. The seeds are numerous and generally bear an aril. There is a large development of mealy perisperm with a small straight embryo.

The family contains about 800 species distributed among forty-five genera. They are found in the tropics, especially in Asia. In *Zingiber* the labellum is large and opposite it are the style and the fertile stamen. *Z. officinale* (Fig. 1917) is the Ginger plant, which is always propagated by vegetative methods and like the cultivated Banana is completely sterile. The Ginger of commerce is derived from the rhizome. *Globba* is an Indo-Malayan genus of about eighty species in which there is a short calyx below the corolla tube, from the top of which spring three petals, a large labellum, two staminodes and a slightly petaloid fertile stamen, projecting beyond which is the style. The ovary is unilocular with parietal placentation. The genus *Amomum* contains about 100 species, having flowers produced on scapes from a rhizome. The flowers are protogynous. The Indo-Malayan genus *Elettaria*, with one species (*E. cardamomum*), furnishes the Indian spice-seeds, cardamoms.

FIG. 1917.—*Zingiber officinale.* Ginger. The dried rhizome is used. (*After Schumann.*)

The genus *Curcuma* with fifty-five species is economically important, for the underground tubers of *C. angustifolia* furnish the East Indian Arrowroot, while *C. longa* gives the yellow dye Turmeric, which is obtained from the dried and ground rhizome. *C. zedoaria* yields Zedoary which is used in the East as a perfume and a tonic.

Hedychium (Fig. 1918) is an Asiatic and Madagascan genus of fifty species in which the flower has a long tube at the end of which spring the narrow free parts of the petals and the larger staminodes and labellum. The stigma projects beyond the anther. Several species are cultivated in greenhouses where the brilliant yellow and red flowers borne in large racemes are very conspicuous. (See p. 1193.) Some emit a strong vanilla scent.

The **Cannaceae** are a small family with only the single genus *Canna*, which includes about sixty species found in tropical America. *C. indica* (Fig. 1919) is cosmopolitan and is cultivated as a garden plant. A number of varieties and hybrids are known.

Fig. 1918.—*Hedychium gardnerianum.* Inflorescence.

Fig. 1919.—*Canna indica.* Indian Shot. Inflorescence.

Finally there are the **Marantaceae**, a family with about a dozen genera with about 300 tropical species, occurring in America. They are herbaceous perennials resembling the Zingiberaceae but easily distinguished by a swollen pulvinus at the junction of petiole and leaf blade. The chief genus is *Maranta* with eighteen species, including *M. arundinacea* whose rhizome provides West Indian Arrowroot, which is prepared by grinding and washing the rhizome to set free the storage starch. In the genus *Calathea*, with 130 species in America and the West Indies, *C. allouia* produces tubers which are eaten under the name of Topee Tampo.

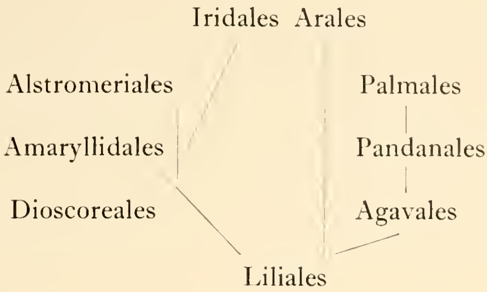
LILIALES

Under the old Englerian term Liliiflorae was included a number of families which are now generally separated as a result of the researches of Hutchinson. He points out that in the course of his study of the families and genera it has become clear that in the past too much attention has been focused upon certain characters to the exclusion of others, with, in his opinion, unfortunate results. In the group of families included by Engler in the Liliiflorae this is particularly true. According to Engler all those plants with actinomorphic flowers possessing a petaloid perianth, six stamens and a *superior* compound ovary are placed in the Liliaceae while those possessing similar characters but with an *inferior* ovary are grouped in the Amaryllidaceae. Hutchinson came to the conclusion that too much importance had been attached to whether the ovary is superior or inferior, with the result that a rather artificial classification had resulted. That the position of the ovary alone need not necessarily be regarded as a family character is well illustrated in the Bromeliaceae, where *Ananas* has an inferior ovary, *Tillandsia* a superior ovary, while the less well-known *Pitcairnia* has an ovary which is intermediate between superior and inferior. If this character of the position of the ovary is treated as of less importance and other characters are made use of in classification, Hutchinson concludes that a more natural arrangement can be achieved. Moreover by splitting up the Liliaceae into several families each containing one of the main groups of the old family a more even distribution of the genera has been achieved. Fundamentally Hutchinson therefore bases his classification on the type of the inflorescence. This rearrangement of the families has necessitated the erection of a number of new orders each of which roughly corresponds to an old family of the Lilliiflorae. Though to some this new arrangement may appear complicated and unnecessarily elaborate it has received very wide appreciation and it is proposed to follow it here, although a number of Hutchinson's new families must of necessity be omitted. Several are represented only by a single genus, some by a single species not well known or not represented in the British Flora. At the same time it must be pointed out that previous textbooks, and more particularly the various British Floras, almost universally follow Bentham and Hooker's method of classification.

The following summary may help to make the relationships clearer:

I. **Liliales**	1. *Liliaceae*
	2. *Trilliaceae*
	3. *Pontederiaceae*
	4. *Smilacaceae*
	5. *Ruscaceae*
II. **Alstroemeriales**	1. *Alstroemeriaceae*
	2. *Philesiaceae*
III. **Arales**	1. *Araceae*
IV. **Amaryllidales**	1. *Amaryllidaceae*
V. **Iridales**	1. *Iridaceae*
VI. **Dioscoreales**	1. *Dioscoreaceae*
VII. **Agavales**	1. *Agavaceae*

The relationships of these orders to one another will be more clearly appreciated from the phylogenetic tree constructed by Hutchinson to illustrate his view on the subject.



Hutchinson considers moreover that his primitive Liliaceous stock may have originated either from the Commelinaceae or the Butomaceae or from both.

The Liliales in the above sense are Monocotyledons in which the flowers are hermaphrodite, actinomorphic or slightly zygomorphic and the perianth mostly petaloid. There are usually six stamens which are inserted opposite the perianth segments. The ovary is superior or semi-inferior, usually with three loculi, and placentation is axile. The fruit is a berry or a capsule and the seed possesses copious endosperm.

The plants are herbs, possessing rhizomes, corms or bulbs, the stem is either leafy or the leaves are clustered at its base or are all radical, rarely they may be replaced by cladodes. They occur very widely in temperate and subtropical parts all over the world.

Hutchinson recognizes six families of which we shall consider only the Liliaceae in detail, but will refer briefly to the Trilliaceae, Smilacaceae, Pontederiaceae and Ruscaceae.

The **Trilliaceae** are a small family erected by Hutchinson to include four genera, of which *Trillium* and *Paris* are the only ones which need concern us here. The genus *Trillium* contains thirty species occurring in Europe, Asia and North America. Most of the species are cultivated under

FIG. 1920.—*Paris quadrifolia*. Solitary terminal flower with large leafy bracts.

the name of Wood Lilies owing to their preference for shady positions. *T. declinatum* and *T. acuminatum* both produce white flowers in April on stalks about 9 in. high, which arise singly from the rhizome. The genus *Paris* contains twenty species, of which *P. quadrifolia* (Fig. 1920) (Herb Paris) is found wild in Britain. The rhizome gives rise to aerial stems with a whorl of four or more net-veined leaves and solitary tetramerous flowers which are protogynous and are pollinated by flies.

The **Pontederiaceae** are a small group of herbaceous water plants which either grow erect in the mud or are free floating. The only important genus is *Eichhornia*, species of which are cultivated in hot-houses in this country. *E. speciosa* (Fig. 1921) has swollen petioles which act as floats and support the plant on the surface of the water. The showy violet or white spikes have earned the plants the name of Water Hyacinths. They constitute very troublesome water weeds because of their rapid vegetative propagation and the ease with which they can be blown about on the

Fig. 1921.—*Eichhornia speciosa.* Water Hyacinth. Floating plants. Brazil.

water, thereby blocking water courses. They are common in Florida and South America and have become naturalized in India, Java and Australia.

The genus *Pontederia* is represented by *P. cordata*, the Pickerel Weed, a hardy garden plant, native of North America.

The family is exceptional in the Liliales in having an irregular corolla. There are six unequal segments in two whorls, the inner posterior segment being enlarged. The ovary is also notable, two of the three carpels being sterile and the third uniovulate.

The **Smilacaceae** differ from the other families of the Liliales in having mostly dioecious flowers and in their climbing habit. The family includes four genera of which *Smilax* itself is the best known. There are over 300 species which are widely distributed in tropical and subtropical parts of the world. They are mostly climbing shrubs with net-veined leaves. At the base of the leaf are a pair of tendrils which have been variously interpreted, though most often as modified stipules (see Volume I, p. 1037). The stems are often beset with curved hooks as a further means of climbing. The flowers are dioecious and are produced in umbels. The dried roots of several species are the source of Sarsaparilla. *S. china* provides the material known as China Root used locally in medicine.

The **Ruscaceae** are another small family in which the plants are either climbers or woody shrubs. The leaves are reduced to scales while axillary branches are modified as cladodes bearing small flowers either on their adaxial surfaces or on their margins. They are restricted to western Europe and the Mediterranean region (Fig. 1922). They differ from the Liliaceae in having united stamens. There are three genera, *Danae*, *Semele* and *Ruscus*. One species of *Semele* is found in the Canary Islands; it is a climbing

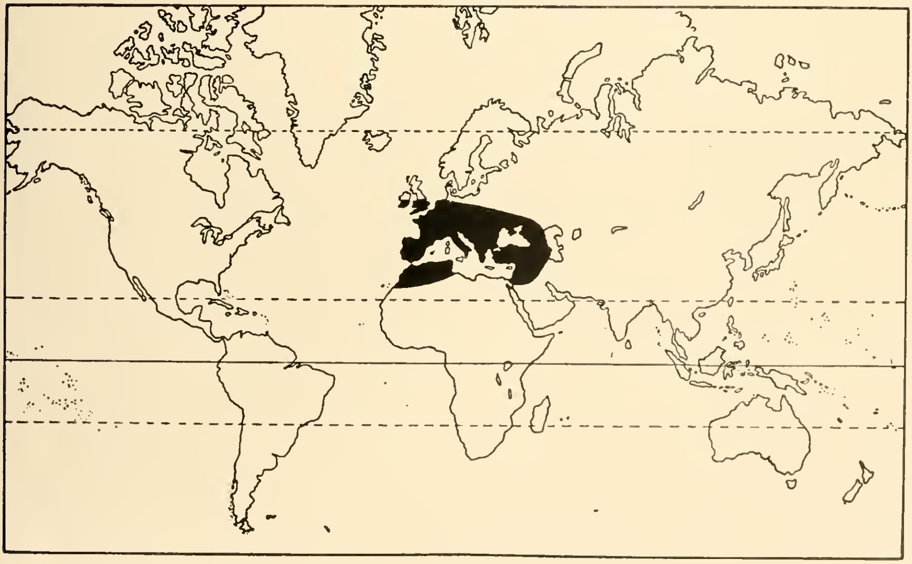


FIG. 1922.—Distribution of *Ruscus*. (*After Hutchinson.*)

shrub bearing little cymes of flowers on the margins of the cladodes. The genus *Ruscus* contains three species of which *R. aculeatus* (Fig. 1923) (Butcher's Broom) is a shrub found wild in Britain. The flowers, which are usually unisexual, are produced on the surface of the cladode and are followed on the female plant by large red berries.

Fig. 1923.—*Ruscus aculeatus*. Butcher's Broom. Shoot with cladodes and berries.

Liliaceae

The members of this family are mostly herbs or rarely soft-wooded shrubs arising from rhizomes, bulbs or corms. They are world-wide in distribution, being found mostly in temperate or subtropical regions. A few are of economic importance, but many are cultivated in gardens on account of their floral beauty. A number are wild in Britain and among these we may mention the following well-known plants: *Polygonatum multiflorum* (Solomon's Seal), *Convallaria majalis* (Lily of the Valley), *Asparagus officinalis* (Asparagus), *Fritillaria meleagris* (Snake's Head), *Tulipa sylvestris* (Wild Tulip), *Ornithogalum umbellatum* (Star of Bethlehem), *Scilla non-scripta* (Bluebell), *Muscari racemosum* (Grape Hyacinth), *Narthecium ossifragum* (Bog Asphodel), *Colchicum autumnale* (Meadow Saffron). Many species of *Lilium* are cultivated and provide some of the finest garden plants.

The **plants** are mostly herbaceous perennials with erect or occasionally climbing stems and arising from rhizomes, bulbs or corms.

The **flowers** (Fig. 1924) are hermaphrodite, rarely unisexual, actinomorphic or slightly zygomorphic. Often large and showy and never produced in umbels.

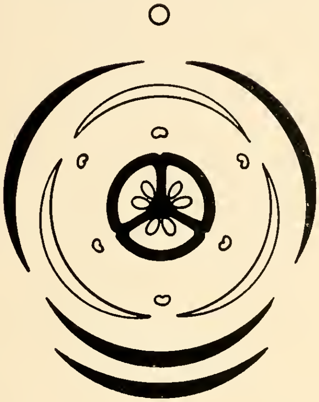


FIG. 1924.—Floral diagram of Liliaceae.

FIG. 1925.—*Scilla campanulata.* Flower in longitudinal section.

The **perianth** (Fig. 1925) may be open or tubular and is composed of six or rarely four segments, usually in two distinct but very similar whorls, imbricated or with the outer whorl valvate in the bud.

The **androecium** consists of six stamens, rarely three or twelve, hypogynous or adnate to, and opposite, the perianth segments. The filaments are free or variously connate. Anthers with two loculi, opening by a longitudinal slit or rarely by a terminal pore.

The **gynoecium** is composed of three united carpels. Ovary superior, rarely adnate to the base of the perianth tube and then semi-inferior; mostly trilocular with axile placentation or rarely unilocular with parietal placentation. Ovules numerous, rarely solitary.

The **fruit** is a capsule, splitting loculicidally or septicidally; sometimes a fleshy berry.

The **seed** is endospermic, containing a straight or curved embryo.

The family includes about 175 genera and about 2,500 species and is therefore one of the largest families of flowering plants.

Anatomically the chief points of interest are the development of sympodial rhizomes and the production of bulbs in which the axis may form a stem bearing leaves and ending either in a single terminal flower, as in the Tulip, or in a raceme as in the majority of the Lilies, or may bear first a number of radical leaves and then form a scape as in the Hyacinth. New bulbs may be formed in the axils of bulb scales, replacing the old bulb which is usually exhausted during the production of the flower, or in other cases bulbils may be formed in the axils of the foliage leaves as in *Lilium bulbiferum.* In *Colchicum* a corm is formed as a swelling at the base of the axis. It persists after the flowers and leaves and bears next year's flowering stem as a lateral shoot in the axil of a scale leaf at its base.

The classification of the family has been worked out by Hutchinson, who proposes provisionally to divide it into twenty-eight tribes. Since this treatment is quite distinct from that employed by previous authors we shall consider it in some detail, omitting only those tribes which contain rare or little-known genera.

I. Rootstock a rhizome, roots fibrous or sometimes tuberous, perennials or rarely annuals

1. *Heloniadeae.* Rhizome short, leaves in radical tufts, flowers in dense spikes or racemes, ebracteate. Perianth segments five, mostly small and white. Stamens six, hypogynous. Ovary trilocular, fruit a capsule with loculicidal dehiscence, seeds tailed at one or both ends. *Helonias*, *Chionographis* and *Chamaelirium.*
2. *Narthecieae.* Rootstock short or a creeping rhizome. Radical leaves crowded, stem leaves short or absent. Flowers in spikes, racemes or cymes, bracteate. Stamens twelve, six or three. Ovary trilocular. Fruit a capsule with loculicidal or septifragal dehiscence. Probably an ancient group with wide discontinuous distribution. *Tofieldia*, *Narthecium*, *Alestris.*

There are four species of *Narthecium* of which *N. ossifragum* (Bog Asphodel) occurs in Britain. It is a typical bog


FIG. 1926.—*Eremurus bungei.* Inflorescence.


FIG. 1927.—*Asphodelus ramosus.* Inflorescence.

plant with spikes of conspicuous yellow flowers which secrete no nectar.

3. *Asphodeleae.* Rootstock a short rhizome, leaves in short basal clusters, or, if on the stem, often reduced. Inflorescence racemose or paniculate, sometimes much elongated. Perianth segments mostly free. Stamens six. Ovary trilocular, fruit a loculicidal capsule. *Eremurus* (Fig. 1926), *Anthericum*, *Eremocrinum*, *Chlorophytum*, *Dasystachys*, *Asphodelus*, *Paradisia*. Several genera are cultivated in gardens, especially *Eremurus*, *Asphodeline* and *Asphodelus* (Fig. 1927).
4. *Kniphofieae.* Rootstock a rhizome, leaves radical, linear but not fleshy. Flowers in terminal racemes or spikes, often pendulous. Perianth segments often united into a tube. Stamens six, hypogynous. Ovary trilocular. Fruit a loculicidal or septifragal capsule.

The only important genus in this tribe is *Kniphofia* (Fig. 1928), which contains some twenty-five species from South and East Africa. Several are cultivated in gardens under the name of Red-hot Pokers. Bees sometimes force their way into the flowers and are unable to return.

FIG. 1928.—*Kniphofia galpini.* Plants with inflorescences. Cambridge Botanic Garden.

5. *Hemerocallideae.* Rootstock a rhizome which may be bulblike. Leaves all basal. Flowers usually racemose or paniculate.

Perianth segments connate into a funnel-shaped tube. Stamens either hypogynous or inserted in the tube. Fruit a loculicidal capsule. *Hosta* (Fig. 1929), *Hemerocallis* (Fig. 1930) and *Leucocrinum*.

FIG. 1929.—*Hosta sieboldiana* (*Funkia*). Inflorescence.

Species of these genera are often cultivated in gardens. In *Funkia*,

FIG. 1930.—*Hemerocallis flava*. Day Lily. Inflorescence.

parthenogenetic embryos are formed in the seeds by outgrowths of the nucellar tissue around the embryo sac. The seeds are winged.

6. *Aloineae.* Rootstock a rhizome, leaves crowded at the base, usually fleshy with marginal prickly teeth. Flowers in terminal spikes, racemes or panicles. Perianth segments equal and connivent or connate into a tube. Fruit either a loculicidal capsule or rarely a berry, seeds often compressed or winged. *Hawthornia*, *Gasteria*, *Aloe* and *Aprica.*

There are about 180 species of *Aloe* (Fig. 1931) in South Africa, especially in the Karroo Desert. They are usually shrubby or arborescent xerophytes. The leaves are very fleshy with a waxy, thick epidermis and the stomata sunken in pits. The juice from the leaves when evaporated gives a bitter drug, aloes. Several species are grown in gardens. The other genera mentioned above are also xerophytic plants occurring in South Africa, but not as a rule reaching a large size.

FIG. 1931.—*Aloe aculeata.* Flowering plant. South Africa. Photograph supplied by courtesy of Dr. Pole Evans.

7. *Convallarieae.* Rootstock a rhizome. Leaves clustered on the rhizome, scape leafless arising at the base or from the axil of a leaf. Flowers racemose or spicate, perianth segments free or united. Stamens eight, inserted at the base of the perianth or on

the tube. Ovary trilocular. Fruit a berry. *Convallaria* and several little-known genera.

Convallaria comprises a single species, *C. majalis* (Fig. 1932) (Lily of the Valley), which is common in north temperate regions, including Britain. It is found chiefly in woods. The flowers are homogamous and pollinate themselves in the absence of insects. They are often cultivated, a large-flowered strain being extensively used for forcing for winter flowering.

8. *Aspidistreae.* Rootstock a rhizome, leaves radical or on a short stem. Flowers solitary or small and in dense bracteate spikes. Perianth trimerous or tetramerous, campanulate or broadly tubular. Stamens six or eight in number, inserted on the perianth tube. Ovary trilocular or tetralocular. Fruit a berry. *Rohdea*, *Aspidistra*.

FIG. 1932.—*Convallaria majalis.* Lily of the Valley. Inflorescence.

FIG. 1933.—*Aspidistra lurida.* Flowers which are borne in the axil of a scale leaf at ground level. On the right, flower in section showing the stigmatic lobes which almost block entrance to the stamens which are attached to the perianth below.

These genera are restricted to eastern Asia. There are five species of *Aspidistra* (Fig. 1933) which are chiefly interesting because of the small brownish flowers, borne at soil level, whose large, flat style forms a lid to the cavity made by the eight perianth segments. Pollination is said to be brought about by small slugs and snails. The one species of *Rohdea* is also pollinated by snails. It is a native of Japan. Aspidistras are commonly grown as pot plants, and in the absence of flowers are sometimes incorrectly assumed to be Ferns.

9. *Polygonateae.* Rootstock a rhizome, stem usually leafy throughout, flowers axillary or in terminal racemes or panicles. Perianth segments four to six, equal; free or united into a tube. Stamens as many as the perianth segments, free or adnate to the perianth. Ovary trilocular. Fruit a berry. *Polygonatum*, *Maianthemum*, *Streptopus* and *Smilacina.*

The first two occur in Britain and in north temperate regions generally. *P. multiflorum* (Fig. 1934) (Solomon's Seal) has a sympodial fleshy rhizome on which the annual shoots leave curious seal-like scars when they die. The flowers are pollinated by bees.

FIG. 1934.—*Polygonatum multiflorum.* Solomon's Seal. Flowering branch.

10. *Uvularieae.* Rootstock a tuberous or creeping rhizome. Stem leafy, sometimes climbing leaves sessile. Flowers terminal, solitary or axillary. Perianth segments free or connate. Stamens six, hypogynous. Anthers sometimes opening by slits or terminal pores. Fruit a loculicidal capsule. *Uvularia*, *Gloriosa*, *Littonia.*

Species of *Uvularia* are sometimes cultivated; there are four species occuring in eastern North America. The genus *Gloriosa* contains five species in the tropics of Asia and Africa. The plants climb by means of the leaves whose tips twine like tendrils. The flowers are pendulous. Several species are cultivated in greenhouses. *Littonia* with four species occurs in South and Central Africa and has a habit similar to *Gloriosa*.

11. *Veratreae.* Rootstock a short erect rhizome or bulb, stem leafy or leaves sub-radical. Inflorescence a raceme, panicle or spike. Perianth segments unequal, free. Stamens six, attached at the base of the perianth segments. Fruit a septicidal capsule. Seeds narrow or winged.

The only genus is *Veratrum* with fifty species in north temperate regions. The rhizome bears a tall leafy stem and racemes, the lower flowers of which are hermaphrodite, while the upper are usually male, caused by abortion of the gynoecium. Some plants are found bearing only male flowers. They are pollinated mainly by flies, nectar being exposed at the thickened base of the perianth segments. *V. album*, which is common in central and southern Europe, is the source of a drug which is sold under the name of White Helleborine Root. *V. nigrum* which is also used medicinally is called Green Helleborine.


FIG. 1935.—*Asparagus officinalis.* Garden Asparagus. Shoot with male flowers. The leaves are replaced by small, needle-like cladodes.

12. *Asparageae.* Rootstock a rhizome. Stem erect or climbing, sometimes woody. Leaves reduced to scales bearing in their axils small, linear cladodes. Flowers hermaphrodite, pedicels articulated near the top (see p. 1142). Perianth segments free. Stamens six, hypogynous and free. Fruit a globose berry, seeds few or solitary.

There is only one genus, *Asparagus*, which is distributed through temperate and tropical regions of the Old World but is absent from America. The genus contains about 300 species, mostly xerophytes. *A. officinalis* (Fig. 1935) occurs rarely in Britain near the sea. The plant is cultivated and the young shoots eaten as a vegetable.

II. Rootstock a bulb or a corm

1. *Tulipeae.* Rootstock a bulb. Stem bearing one or more leaves. Flowers solitary or in a racemose umbellate inflorescence. Perianth segments free, stamens six. Fruit a capsule splitting

loculicidally or rarely septicidally. *Erythronium* (Fig. 1936), *Fritillaria*, *Tulipa* (Fig. 1937), *Lloydia*, *Gagea*, *Lilium*.

FIG. 1936.—*Erythronium tuolumnense*. Two-flowered inflorescence.

The genus *Fritillaria* contains some fifty species distributed in north temperate regions. *F. meleagris* (Fritillary or Snake's

FIG. 1937.—*Tulipa*. Flower of one of the garden hybrids.

Head) is found in Britain. The flowers stand erect in the bud but are pendulous when open. They are protogynous, with nectar concealed at the base of the perianth segments. They are pollinated by humble bees. *F. imperialis* (Crown Imperial) and others are commonly grown in gardens. There are some fifty species of *Tulipa*, found especially on the steppes of central Asia. The seeds are flat and the capsule stands erect, distribution being by a censer mechanism. Many hybrid forms are cultivated in gardens. *T. sylvestris* occurs wild in some southern and eastern counties of England. The genus *Lloydia* is also represented in Britain by *L. serotina* which is found in Snowdonia, the other four species occurring in other alpine parts of the northern hemisphere. The genus *Gagea* is represented in Britain by *G. lutea* (Yellow Star of Bethlehem) and there are some thirty other species in the north temperate regions of the Old World. In some, if pollination fails, bulbils are produced in the axils of the leaves, which when mature drop off and grow into fresh plants.

Fig. 1938.—*Lilium candidum.* Madonna Lily. Inflorescence.

The genus *Lilium* (Fig. 1938) itself contains about sixty species. The bulbs are composed of loosely arranged scales and produce long central stems which bear large flowers in racemes. They are mostly pollinated by butterflies and moths, nectar being secreted from a furrow in each perianth segment. *L. martagon* is pollinated by night-flying Hawkmoths, while *L. bulbiferum* is pollinated by large butterflies. Other species, such as *L. chalcedonicum* and *L. tigrinum*, appear to be self-pollinated though nectar is abundantly secreted from the base of each perianth segment. *L. bulbiferum* is also reproduced by bulbils developed in the leaf axils. In most species with pendulous flowers the capsules when ripe stand upright so that the seeds can only escape when they are shaken. Many species and hybrids of Lilies are in cultivation and some, such as *L. henryi* which grows to 7 ft. and *L.* (*Cardiocrinum*) *giganteum* from the Himalayas, which may reach 12 ft., are extremely striking garden plants (Fig. 1939).

FIG. 1939.—*Lilium* (*Cardiocrinum*) *giganteum*. Flowering plants cultivated in a woodland glade.

2. *Scilleae*. Rootstock a truncated bulb. Leaves usually few and grouped in a cluster at the base of the scapose raceme. Perianth segments free or partly connate. Stamens six, free or rarely united. Ovary trilocular. Fruit a loculicidal capsule. *Scilla*,

Camassia, *Ornithogalum*, *Lachenalia*, *Chionodoxa*, *Hyacinthus*, *Galtonia*, *Muscari* (Fig. 1940).

Fig. 1940.—*Muscari paradoxum*. Dark blue-black flowers.

The genus *Scilla* contains about 100 species distributed in temperate regions. *S. non-scripta* (Fig. 1941) is the Bluebell. In *Camassia* are grouped two North American species from whose bulbs a food, quamash, was prepared by the Indians. There are thirty

Fig. 1941.—*Scilla non-scripta*. Bluebell. Inflorescence.

species of *Hyacinthus* scattered through the Mediterranean region and Africa. From *H. orientalis* have been produced all the cultivated forms now grown in gardens and greenhouses. The British Flora, besides the Bluebell, also includes *S. verna* and *S. autumnalis* and three species of *Ornithogalum* (Star of Bethlehem).

3. *Colchiceae.* Rootstock a corm. Leaves radical, scape below the surface within the leaf sheath, one- to three-flowered, flowers appearing in succession, naked. Perianth segments equal. Stamens six. Ovary trilocular. Fruit a septicidal capsule. *Colchicum, Bulbocodium, Merindera.*

The genus *Colchicum* (Fig. 1942) contains forty-five species which are distributed through Europe, western Asia and North Africa.

FIG. 1942.—*Colchicum speciosum* var. *album.* Flowers appearing before the leaves. Cultivated. Photograph by R. A. Malby.

Reference has already been made to the large corm produced below the soil. In *C. autumnale* the perianth is long and the ovary remains below the soil where it is protected from danger. The flowers are protogynous and are visited by bees. These flowers are developed without leaves in the autumn and the leaves appear the following spring, after which the capsule is brought up above the soil by the elongation of its stalk. Both seed and corm are used medicinally in the preparation of Colchicine. There is only one species of *Bulbocodium*, *B.*

vernum, which is a native of Spain. It is often cultivated in gardens on account of its purple flowers which are produced in February.

4. *Iphigenieae.* Rootstock a bulb or a corm. Stem leafy, leaves narrow but broader around the inflorescence and then coloured. Flowers bracteate. Perianth segments free. Stamens six. Ovary trilocular with numerous ovules. Fruit a loculicidal or septicidal capsule. Seeds sub-globose or angular. *Ornithoglossum* and *Iphigenia.* These and three other genera are all restricted to South Africa.

From this summary of the tribes included in the family it will be seen that more emphasis is placed on the character of the rootstock than has been customary in previous systems. Whether too much importance has been attached to this organ, only time and a more critical study of the species will show, but it is at least refreshing to find more attention is being directed to the structure of the plant as a whole rather than to the floral structure or to those portions normally preserved in a herbarium sheet. It is undoubtedly a fact that in the past systematic Botany has been studied too much in the herbarium and too little in the field. Hutchinson by his field experience in South Africa, a land rich in Liliaceous genera, is well qualified to appreciate the true appearance and growth of the plants he is dealing with, and his conclusions, though revolutionary, cannot be lightly rejected.

ALSTROEMERIALES

The Alstroemeriales are Monocotyledons in which the rootstock is a rhizome with fibrous or tuberous roots. The flowers are showy and are borne in a terminal cluster or raceme. The leaves are alternate, linear or ovate. The perianth consists of six free or partly connate segments, which may all be similar or one may be somewhat dissimilar. There are six stamens which are free or partly connate. The ovary is usually inferior but sometimes superior; trilocular with axile placentation, or unilocular with parietal placentation. The fruit is either a capsule or a berry and the seed is endospermic.

The order is a small one restricted mainly to the southern hemisphere and, according to Hutchinson, comprises three families, Alstroemeriaceae, Petermanniaceae and Philesiaceae. In comparison with other methods of classification the order as here treated contains families made up partly from the old Amaryllidaceae, *e.g.*, Alstroemeriaceae, and from the old Liliaceae, *e.g.*, Philesiaceae. We shall not consider any of the families in detail, but will refer briefly to the first and last. The Petermanniaceae contain a single genus with only one species from New South Wales.

The **Alstroemeriaceae** are characterized by having an inferior ovary and a capsule fruit. There are only two important genera; firstly *Bomarea* with nearly 120 species, occurring in Mexico and central and South America, which are climbers with cymose umbels, and secondly *Alstroemeria* (Fig. 1943) with some fifty South American species. One interesting feature of these plants is the fact that the leaf blade is twisted near the base so that the lower surface becomes uppermost. The capsules split explosively. Many species are cultivated in gardens under the name of Peruvian Lilies. They are mostly red, orange or yellow in colour.

FIG. 1943.—*Alstroemeria aurantiaca.* Inflorescence.

The **Philesiaceae** have superior ovaries and are mostly woody plants or climbers. The fruit is a berry. They are restricted to the southern hemisphere, being found in South America, South Africa and Australia (Fig. 1944). *Lapageria rosea*, in Chile, is a climbing shrub with large

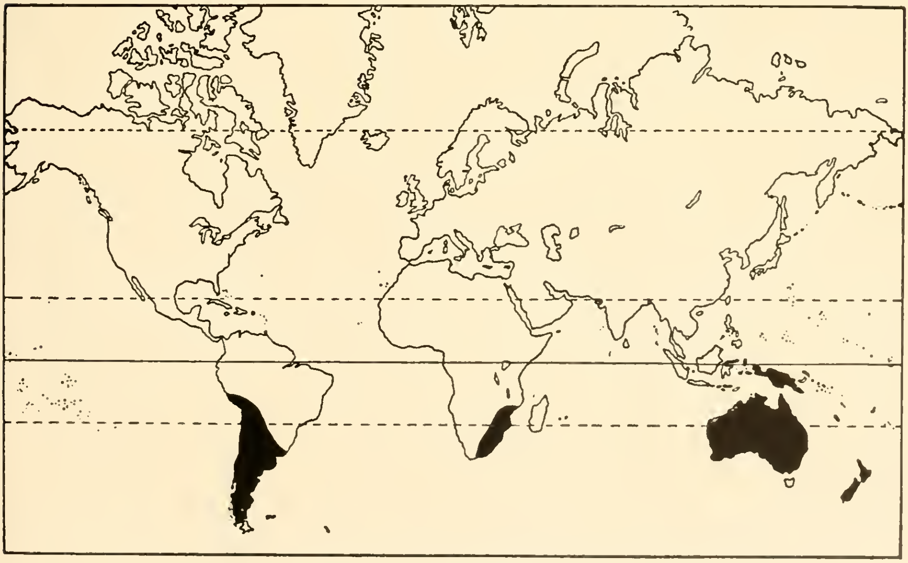


FIG. 1944.—Distribution of Philesiaceae. (*After Hutchinson.*)

flowers and edible fruits, which is sometimes cultivated in southern parts of Britain as a wall climber.

ARALES

The Arales are Monocotyledons in which the flowers are either hermaphrodite or unisexual, consisting of dimerous or trimerous whorls or sometimes reduced to a single stamen and carpel. The ovary is superior. The fruit is a berry with the testa of the seed fleshy and enclosing endosperm in many cases.

The plants are mostly herbs, often of large size, occasionally shrubs, of very variable habit. The leaves are usually radical but if attached to the stem they are arranged alternately. The small flowers are arranged in a spadix or spike, usually subtended by a spathe.

This order, which is due to Hutchinson, includes two families, Araceae, sometimes termed the Aroideae by earlier writers, and the Lemnaceae, the latter containing very greatly reduced floating aquatic plants collectively termed the Duckweeds. Though the Araceae are represented in Britain only by two genera, the family is of sufficient general interest to be considered in detail. The Lemnaceae however are of minor importance except from a morphological standpoint and in that connection they have already been discussed in Volume I. We need therefore only refer to them briefly here.

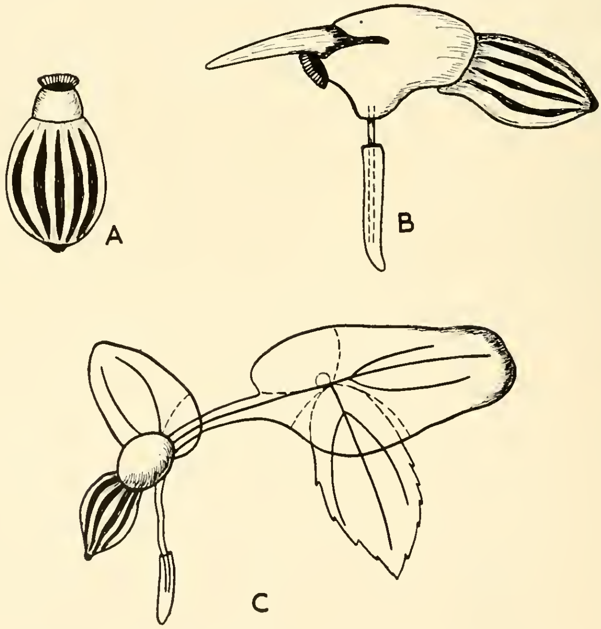


FIG. 1945.—*Lemna trisulca.* A, Germinating seed with operculum being pushed off by the cotyledon. B, Young seedling. Primary root (with cap) and plumule arising from the cotyledon. C, First and second fronds arising from the plumule. (*After Hegelmaier.*)

The **Lemnaceae** are small, floating, fresh-water plants with much reduced dorsiventral " fronds " of lenticular shape and consisting entirely of parenchyma.

There are three genera, *Lemna* (Fig. 1945), *Wolffia* and *Spirodela*, all of which are represented in this country. The genus *Lemna* contains six cosmopolitan species, four of which occur in Britain. *L. polyrrhiza* is the largest, and sometimes produces fronds about 1 cm. in diameter. The roots hang down from the lower surface and have large, conspicuous root-caps which may function as balancing organs to maintain the fronds the right way up. The flowers of the Lemnaceae are reduced to a minimum. In *Spirodela* the flower is composed of a minute spathe enclosing two male flowers, each represented by a single stamen, and one female flower in the form of a one-chambered ovary with one or two ovules. They are probably pollinated by small aquatic insects for they are markedly protandrous.

The genus *Wolffia* (Fig. 1946) contains twelve species and has the distinction of being the smallest of all flowering plants. The largest being about 1·5 mm. in diameter, a dozen flowering specimens could be accommodated on a single frond of *Lemna minor*. Species of the Lemnaceae flower but rarely, propagation being mostly effected by caducous branches which arise at the posterior end of the shoot. In *L. trisulca*, the fronds of which are lanceolate, many branches remain attached, forming extensive compound plants, or they may become detached giving rise to new independent plants which start growth the following spring, while the mother plant sinks to the bottom of the pond.

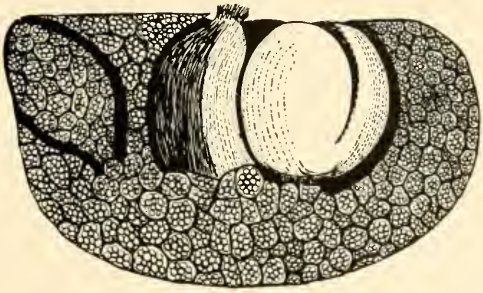


FIG. 1946.—*Wolffia arrhiza*. Vertical section of entire plant. On left, a new frond arising. In central cavity, an anther (left) and a carpel (right). (*After Le Maout and Decaisne*.)

Araceae

The Araceae are a large family occurring most typically in the warmer parts of the world but extending into temperate regions. They are very variable in habit, some having erect or even climbing stems and some having subterranean tubers or rhizomes, while *Pistia* is a floating water-plant.

Only three occur in Britain; one, *Arum maculatum* (Fig. 1947) (Cuckoo Pint), is common in woods and hedges all over the country, while *A. neglectum* is relatively rare. The third, *Acorus calamus* (Sweet Flag), is a rare British water-plant with long sword-like leaves, reproducing generally by vegetative branching of the rhizome. It is thought to have been introduced from India.

Fig. 1947.—*Arum maculatum*. Cuckoo Pint. Spathe cut open showing spadix with zone of bristles, below which is a dark zone of male flowers and a light zone of female flowers. (See also Fig. 1955.)

In other parts of the world, particularly in the tropics of Malaya and Africa, some remarkable types with giant leaves are found, many of which produce enormous flowering spathes which emit highly offensive odours and are pollinated by carrion flies. Only a few are of economic importance.

Hutchinson considers that they have originated from the Liliaceae, through the tribe Aspidistreae. Older writers such as Engler and Rendle relate them to the Palms. There are probably relationships with the Aponogetonaceae.

The **plants** are herbaceous or rarely woody, with watery or milky juice, often producing tubers or elongated rhizomes: many are climbers or epiphytes. The leaves are sometimes solitary, often radical and appearing after the flowers. They are frequently hastate in shape with a membranous sheath at the base.

The **flowers** (Fig. 1948) are small or even minute, hermaphrodite and all alike, or monoecious, arranged in a cylindrical spike called the **spadix.** The males are borne in the upper part of the spadix, with the female flowers below. This spadix is always surrounded by a large bract, the **spathe,** which may be green or brightly coloured.

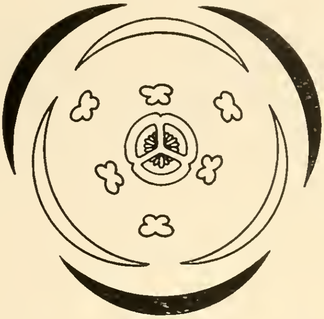


FIG. 1948.—Floral diagram of *Acorus calamus.* Araceae.

The **perianth**, which is present in hermaphrodite flowers, consists of four to six connate segments formed into a truncated cup.

The **androecium** consists of one to six hypogynous stamens, frequently coherent into a synandrium. The anthers open by pores or slits and may be free or united into a single group. Staminodes may be present in female flowers.

The **gynoecium** consists of one or more carpels which may form a unilocular or multilocular ovary, sometimes without a style. The ovules may be one or many and their point of attachment is variable.

The **fruit** is a berry containing one or many seeds.

The **seeds** are mostly endospermic, with a straight embryo lying in the middle of the endosperm. In the absence of endosperm the embryo is curved.

The family contains slightly over 100 genera and about 1,900 species. Though widely distributed in temperate regions its centre of distribution appears to be the tropics of the Old World. Many are climbers or epiphytes, the latter forming an important constituent of the vegetation of the tropical rain forests.

Morphologically the family is interesting, especially the roots, which are all adventitious. Most of the climbing and epiphytic species develop both absorptive roots which grow downwards towards the soil and clasping roots which are sensitive to light but not to gravity and by them the plants become attached to their supports. Other plants may begin life as epiphytes by the germination of the seed on a branch. In this case the seedling may first produce clasping roots to attach it to the branch and then unbranched aerial roots which grow downwards, but may never reach the ground and hang freely in the air. Many of these aerial roots develop a velamen similar to that developed by the aerial roots of Orchids. If they reach the soil they produce underground branches. The stems are normally sympodial, each segment bearing one or more scale leaves before producing a foliage leaf. The axillary shoots are often adnate to the main axis.

The leaves are very variable in form. In some they are narrow with parallel venation. In others they are large, pinnately veined or net-veined and divided into lamina, petiole and sheathing leaf base. In *Monstera* and related genera, holes are produced in the course of development between the lateral veins owing to the cessation of growth over certain small areas. As a result of the holes the leaves may eventually become pinnately dissected. In *Philodendron cuneifolium* the petioles serve as water reservoirs and contain large intercellular spaces lined with mucilage which fill with water after rain.

Latex is present in many genera. It is formed in sacs associated with the phloem both in stems and petioles. The longitudinal arrangement of the latex sacs is more typical of this family than an anastomosing system of canals. Large internal hairs are present in the ground tissue in several genera, such as *Monstera*, projecting into the intercellular spaces.

The classification of the family is variously interpreted. Engler recognizes eight sub-families, while Hutchinson prefers to arrange the genera into eighteen tribes. Since it is only possible here to discuss the genera very briefly we shall follow the simpler Englerian system, though it must be realized that in such a diverse group only a very detailed study of the various genera could produce a truly phylogenetic system.

I. Pothoideae

Land plants without latex. Leaves developed in two ranks or spirally arranged. Flowers usually hermaphrodite. Eleven genera, including *Pothos*, *Anthurium*, *Acorus*.

II. Monsteroideae

Land plants without latex. Flowers hermaphrodite, usually naked. Eleven genera, including *Rhaphidophora*, *Monstera*, *Spathiphyllum* and *Epipremnum*.

III. Calloideae

Land or marsh plants possessing latex. Leaves never sagittate, flowers hermaphrodite or unisexual. Three genera: *Symplocarpus*, *Lysichiton* (Fig. 1949) and *Calla*.

IV. Lasioideae

Land or marsh plants possessing latex. Leaves sagittate. Flowers hermaphrodite or unisexual. Seeds usually without endosperm. Nineteen genera, including *Draconitum*, *Amorphophallus*.

V. Philodendroideae

Land or marsh plants possessing latex. Leaves usually parallel-veined. Flowers unisexual, seeds endospermic. Nineteen genera, including *Philodendron* and *Zantedeschia* (*Richardia*).

Fig. 1949.—*Lysichiton camtschatense.* Flowering plant. Cultivated.

VI. **Colocasioideae**

Land or marsh plants possessing latex. Leaves net-veined, stems mostly tuberous. Flowers unisexual, usually naked. Stamens in synandria. Thirteen genera, including *Remusatia*, *Colocasia*, *Xanthosoma*.

VII. **Aroideae**

Land or marsh plants possessing latex. Leaves net-veined. Stems mostly tuberous. Flowers unisexual, usually naked. Stamens free or in synandria. Twenty-seven genera, including *Spathicarpa*, *Arum*, *Dracunculus*, *Helicodiceros*, *Arisaema*.

VIII. **Pistioideae**

Floating aquatic plants without latex. Flowers unisexual, female flowers solitary, male flowers in whorls. There is only one genus, *Pistia*.

In the Pothoideae we have a number of genera found mostly in the tropics. *Pothos* itself contains about sixty species, all shrubby climbers found in Malaya, while the genus *Anthurium* has over 500 species of American origin, many of which are cultivated in greenhouses (Fig. 1950). There are two species of *Acorus*; *A. gramineus* which occurs in Japan and *A. calamus* which is known wild in Britain under the name of Sweet Flag. Its native home is western Asia, but it has been introduced into many countries for the sake of its sweet odour. It was naturalized in Britain in

FIG. 1950.—*Anthurium scherzerianum.* Yellow spadix with recurved scarlet spathe.

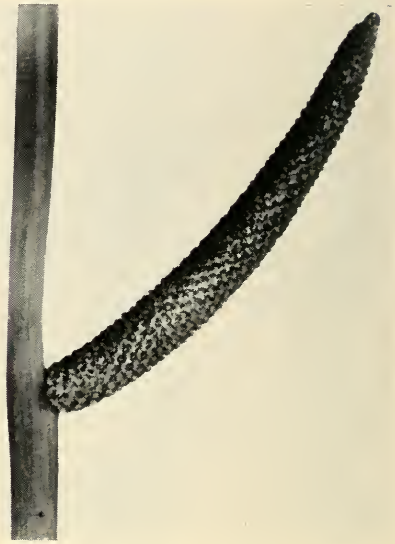


FIG. 1951.—*Acorus calamus.* Sweet Flag. Inflorescence.

FIG. 1952.—*Monstera deliciosa.* Part of a plant with a cluster of infrutescences, which are edible. Photograph supplied by courtesy of the Florida Agricultural Experiment Station.

the seventeenth century (Fig. 1951). In this country it does not bear ripe seeds and reproduces by means of its rhizome. The spadix is about 10 cm. long and 1·5 cm. thick. It is composed of 700 to 800 closely crowded flowers, each consisting of six perianth segments, six stamens and a trilocular ovary. The fruit is a berry. In its native country it is probably pollinated by flies.

In the Monsteroideae we may refer briefly to *Monstera* (Fig. 1952) with thirty American species. They are climbing shrubs with pinnatifid leaves full of holes. It begins life as a climber but soon becomes epiphytic, with aerial roots reaching down to the soil. The flowers are hermaphrodite. The fruiting spikes of *M. deliciosa* are eaten as a fruit.

In the Calloideae, the only species of the genus *Calla*, *C. palustris*, is a marsh plant occurring in central and northern Europe and extending through Siberia. It also occurs in America. The shoots develop in alternate years, bearing firstly long-stalked, roundish leaves with a cordate base. Later a pair of foliage leaves are produced, together with a

FIG. 1953.—*Amorphophallus giganteus*. Inflorescence. Royal Botanic Gardens, Kew. From a photograph in "The Times".

long-stalked, short, cylindrical spadix, subtended by a broad spathe. The inflorescence emits a nauseous odour. The flowers are protogynous. From thirty to fifty stigmas appear in the first stage of anthesis as small whitish, strongly papillose and viscous circles on the ovaries. The lower ones are receptive as soon as the spathe opens. The anthers dehisce only when some of the stigmas have shrivelled. In the first stage they are sessile but later they develop short stalks. Pollination is effected by various insects, particularly small flies, though snails have been observed to feed on the pollen. The ovary is unilocular and from its base there arise from six to nine anatropous ovules.

Belonging to the sub-family Lasioideae is the genus *Amorphophallus* (Fig. 1953) with some ninety species from tropical Asia. Usually the rhizome produces yearly a single leaf up to 10 ft. in length and an inflorescence which may be several feet long. It is made up of male flowers above and female flowers below. It is a dirty red in colour and the foetid smell attracts carrion flies which serve as pollinators. *A. variabilis* is said to be pollinated by snails. The genus *Dracontium* with ten species is similar in structure but occurs in America. In *D. gigas* the leaf may be 15 ft. high; it has a long stem-like petiole and a three-branched lamina.

In the Philodendroideae is included *Zantedeschia*, a small South African genus, species of which are commonly cultivated under the name *Richardia* (Fig. 1954), the Arum Lily. They have thick rhizomes and large sagittate

FIG. 1954.—*Richardia africana*. Arum Lily. Spadix surrounded by the pure white spathe.

leaves. The flower spathes are white or yellow in colour and enclose a yellow spadix.

The most important member of the Colocasioideae is the genus *Colocasia*, which includes *C. antiquorum* whose rhizome is the source of Taro, an important vegetable in the tropics. In the raw state it is poisonous but when boiled it loses its poisonous nature and forms a valuable food. Species of *Alocasia* which are found in tropical Africa are favourite greenhouse plants on account of their variegated leaves.

The Aroideae include the genus *Arum* of which *A. maculatum* (Cuckoo Pint) is wild in Britain, and *A. italicum*, a larger species, occurs rarely in southern counties. The pollination mechanism of the Cuckoo Pint is remarkable. The large spathe which surrounds the inflorescence acts not merely as an attraction, in those species where it is brightly coloured, but also as a protection against wind. In the same way the spadix, which is often contrastingly coloured, also serves for attraction and possibly for protection. Small flies, trying to escape from the wind, congregate in the spathe and crawl downwards into the more sheltered part. They are also attracted by the warmth generated in the spadix as the result of the very rapid respiration of its stored starch. Guided by the spadix they successfully pass below the constriction in the spathe and between the downwardly projecting hairs. Further down they pass another cluster of similar hairs and reach the base of the spathe (Fig. 1955). Unable to find a

FIG. 1955.—*Arum maculatum*. Portion of the spathe cut open to show the flowers. For pollination see in text.

way out they crawl about over the maturing female flowers which, if they have previously visited another flower, they will pollinate in the course of their efforts to escape. As the female flowers mature the lower group of hairs shrivels and the flies can now crawl further up the spadix. Here they come into contact with male flowers whose anthers are just ripening. The upper hairs are still turgid and prevent the flies from escaping and in their struggles to do so they become covered with pollen from the male flowers. Finally, after all the pollen has been discharged, the top cluster of hairs also shrivels and the flies escape. Apparently the flies are unharmed by their temporary imprisonment for often they immediately seek out another spathe and repeat the process, transferring the pollen that covers them to the female flowers as soon as they reach the bottom of the spadix, and the process begins all over again.

The genus contains twelve species which are distributed in central Europe and the Mediterranean. Other interesting genera in this subfamily are *Dracunculus*, with two Mediterranean species, and *Arisaema*, with about 105 species in Asia, Africa and North America. The flowers of this genus are worthy of note. Extra-floral nectaries occur in the angles of the leaf segments and in addition appendages are developed at the ends of the leaf segments which resemble the end of the spathe. Insects creep easily in the direction of the appendages to the nectaries, while others, possibly misled by the similarity of structure, reach the spadix by creeping over the spathe. Eventually they may find their way into the basal part of the spathe and there effect pollination. Some species are said to be pollinated by snails.

The Pistioideae contain the single species *P. stratiotes* (Water Cabbage) which is widely distributed in tropical and subtropical countries. It is a floating water-plant, rarely anchored by its roots and often blown about by the wind. The plant consists of a large rosette of leaves which remain closed at night but open into a horizontal position by day. Stolons grow out from the leaf axils which give rise vegetatively to new plants. The inflorescence is small and monoecious, consisting of a whorl of male flowers above and female flowers below. The male flower has two stamens, the female an ovary produced from a single carpel. There is no perianth. It is generally considered that this plant is a connecting link between the Araceae and the Lemnaceae.

TYPHALES

The Typhales are aquatic or marsh-loving Monocotyledons which develop extensive rhizomes. The leaves are linear, sheathing at the base. The flowers are unisexual, very minute and crowded into clusters or dense spikes. The perianth is either absent or reduced to scales. There are two or more stamens and a unilocular ovary with a single pendulous ovule.

According to Engler the two families Typhaceae and Sparganiaceae should be united with the Pandanaceae and regarded as the simplest of the

Monocotyledons. This was in keeping with the idea of the primitive nature of the Amentiferae among the Dicotyledons. As we have seen, the families included in the latter group are now regarded as reduced types derived from relatively advanced families, this reduction having been brought about by the adoption of anemophilous pollination. It is not surprising to find therefore that the same view is held regarding these families, which are also anemophilous. Hutchinson considers that while the Typhaceae and Sparganiaceae are closely related they bear little relationship to the Pandanaceae. He considers that the former families have orginated by reduction from the Liliaceae, while he thinks that the Pandanaceae are an advanced group, having originated from the Palms, to which they certainly bear a certain resemblance.

Since both the Typhaceae and Sparganiaceae are represented in the British Flora we shall briefly review their more important characters.

Fig. 1956. — *Typha latifolia.* Reed Mace. Inflorescence with staminate flowers above and carpellate flowers below..

Fig. 1957.—*Sparganium simplex.* Flowering shoot.

The **Typhaceae** include the single genus *Typha* with twelve species found widely in tropical and temperate regions. *T. latifolia* (Reed Mace) (Fig. 1956) and *T. angustifolia* occur in ditches, ponds, lakes and river banks in many parts of the world, including Britain. The lower part of the stem is a thick rhizome while the upper part projects high above the water and bears a dense spike divided into two parts. The lower, which is brown in colour, consists of female flowers, while the upper, which is yellow, consists of male flowers. Pollination is by wind. The fruit, which is an akene, is covered by long downy hairs and is wind-distributed.

The **Sparganiaceae** also contain only a single genus, *Sparganium*, with eighteen species living in temperate and colder parts of the northern hemisphere. One species is found in New Zealand. They are aquatic, or marsh-inhabiting herbs, with a creeping, perennial rhizome bearing erect or floating shoots and distichously arranged narrow, entire leaves, sheathing at the base. The flowers are formed in spherical heads, the males usually being produced higher up than the females. The flowers are protogynous and pollination is anemophilous. Five species, including *S. erectum*, *S. simplex* (Fig. 1957) and *S. minimum* occur in Britain and are known collectively as the Bur-reeds. The first two are widely distributed from the Arctic Circle to North Africa and from the Himalayas eastwards to Japan.

AMARYLLIDALES

The Amaryllidales are monocotyledonous herbs with a tunicated bulb or very rarely a rhizome. The leaves are radical and usually linear. The flowers are usually borne in umbellate inflorescences or rarely solitary on a leafless scape and are subtended by an involucre of one or more membranous bracts. There are usually six stamens. The ovary may be superior or inferior and is generally trilocular, bearing numerous ovules with axile placentation. The fruit is either a capsule or a berry.

There is only a single family Amaryllidaceae.

The above description is taken from Hutchinson and represents his new conception of the family, in which the form of the inflorescence rather than the position of the ovary is regarded as the distinguishing feature. The result of this change is, as we have seen, that several sections of the old Liliaceae can now be transferred to the Amaryllidaceae. The most important of these are the Agapantheae and the Allieae. The Agapantheae are regarded as the most primitive group and link the family to the Liliaceae. The Allieae stand as an intermediate group between the Agapantheae and the Amaryllideae.

Though this view of the limits of the Amaryllidaceae is not universally accepted there appears to be so much in favour of Hutchinson's view that we have here followed his suggestions.

Amaryllidaceae

The Amaryllidaceae are a relatively small family which includes a number of common wild and garden plants. Most of them perennate by bulbs and very rarely by a rhizome, though the latter occurs in those genera which may be regarded as more primitive.

Among the best-known examples of the family we may mention the following plants found wild in Britain: Snowdrop (*Galanthus nivalis*), Snowflake (*Leucojum aestivum*), and the Daffodil (*Narcissus pseudonarcissus*). Among garden plants, species of *Amaryllis*, *Crinum*, *Agapanthus* and *Hippeastrum* are grown especially in herbaceous borders. Species of *Allium* (Onion) are used as vegetables.

The **plants** are herbs and usually have a tunicated bulb. The leaves are few in number and generally arise from the bulb. They are more or less linear and have parallel venation with transverse secondary veins.

The **flowers** (Fig. 1958) may be solitary or borne in umbellate inflorescences at the top of a scape. Each flower is hermaphrodite and actinomorphic and is subtended by an involucre of two, or more rarely one, membranous bracts.

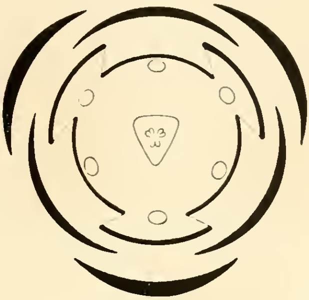


Fig. 1958.—Floral diagram of Amaryllidaceae.

The **perianth** (Fig. 1959) is petaloid and composed of six parts,

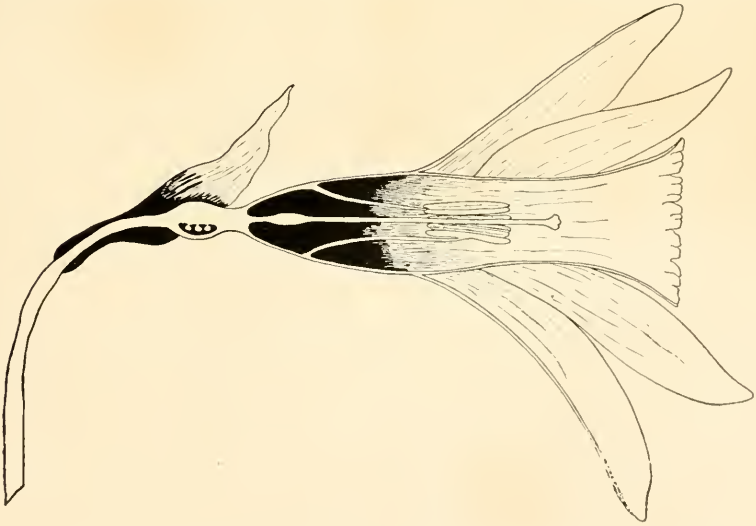


Fig. 1959.—*Narcissus pseudonarcissus*. Daffodil. Flower in longitudinal section, showing perianth segments and elongated corona.

developed in two whorls which may not be equal in size. A corona is often present, and the perianth segments are frequently united into a tube.

The **androecium** consists of six stamens, which are inserted opposite the perianth segments. These stamens are hypogynous, or may be inserted on the tube or at the base of the segments. The filaments are either free or else expanded at the base and connate forming a corona. The anthers are bilocular, introrse and either versatile or basifixed. The lobes open by longitudinal slits.

The **gynoecium** is composed of three carpels and the ovary may be either superior or inferior. Placentation is usually axile. The style is either capitate or trilobed. The ovules are anatropous, arranged superimposed in two rows in each loculus.

The **fruit** is either a capsule or may be fleshy and indehiscent.

The **seeds** are numerous and contain a fleshy endosperm enclosing a small embryo. Sometimes the seeds are angular, compressed or winged.

The family includes about ninety genera and about 1,000 species. They are characteristic of the temperate and warm temperate regions of the world and comparatively few are found in the tropics.

Reference has already been made to the reasons for the adoption of a new set of principles in limiting the Amaryllidaceae. This has led on the one hand to the inclusion within the family of several groups previously regarded as part of the Liliaceae while on the other hand it has resulted in the exclusion of a considerable part of the Amaryllidaceae as conceived by Engler. Of the four sub-families which he recognized, only the first, the Amarylloideae, is now retained, the others are referred to separate families. The following classification of the Amaryllidaceae is taken from Hutchinson's treatment of the family and it should be pointed out that he does not recognize sub-families in his method of classification of the Angiosperms but prefers to group the genera of a family simply in a series of tribes.

1. *Agapantheae.* Rootstock a rhizome, bearing a leafless scape-like stem. The inflorescence is an umbel subtended by two or more involucral bracts. The perianth segments are all similar and united into a tube with six stamens inserted on it. The ovary is superior and the fruit a loculicidal capsule. *Agapanthus* and *Tulbaghia.*

Species of *Agapanthus* occur in South Africa and several are cultivated in gardens. The best known is *A. umbellatus* (African Lily), which bears large umbels of conspicuous blue flowers. It is often grown as a show plant in tubs placed out of doors during the summer months.

2. *Allieae.* Rootstock a bulb or a corm. Stem scapose and leafless, the leaves being all radical and often with long, sheathing bases. The inflorescence is an umbel subtended by an involucre of two or more bracts. The perianth is composed of six, equal, free

segments without a corona. Stamens either six or three with dorsifixed anthers. Ovary superior and the fruit a loculicidal capsule. *Allium*, *Brodiaea* and *Muilla*.

The species are nearly all American except for the genus *Allium* (Fig. 1960) which is widely distributed in the northern hemisphere. This genus contains about 300 species and is the only one which we need consider in detail. *A. ursinum* (Garlic) and *A. schoenoprasum* (Chives) together with six other species are found wild in Britain. *A. cepa*, from which the garden Onion has been derived, is a native of Persia while *A. porrum* has produced the Leek, *A. ascalonicum* the Shallot and *A. fistulosum* the Welsh Onion, which is a native of Siberia and is also known as the Stone Leek.

FIG. 1960.—*Allium ursinum*. Ramsons. Umbellate inflorescences.

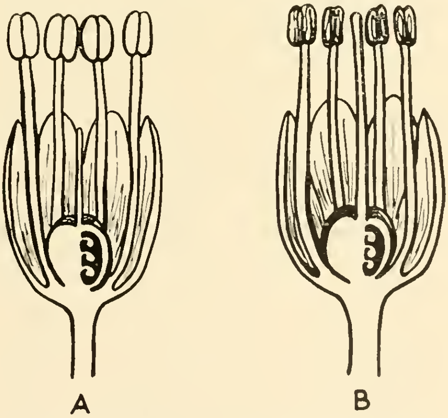


FIG. 1961.—*Allium*. Flowers in vertical section. A, Early male stage, style short. B, Later female stage with style elongated and withered anthers.

In *A. cepa* var. *bulbiferum*, the Tree Onion, the flowers are replaced by bulbils, which when mature drop off and reproduce the plant. In most species the flowers (Fig. 1961) are pollinated by insects and show marked protandry. Nectar is secreted by three double septal glands on the ovary and exudes by canals situated about half-way up. The nectar collects between the base of the ovary and the filaments of the three inner stamens. In *A. ursinum*, for example, the inner stamens dehisce first, followed by the outer three, and during this time the style elongates. Insects probing for nectar therefore touch one side of their bodies against an anther and the other against the style. In this way self-pollination is generally prevented. Later should cross-pollination not occur, self-pollination may be achieved by the bending of the style towards an anther. Humble Bees and Hive Bees have both been observed to visit the flowers. In *A. cepa* the style matures only after the anthers have withered.

3. *Gilliesieae.* Rootstock a tunicated bulb. Leaves radical and linear. Flowers in a terminal umbel with an involucre of two bracts. Perianth segments usually unequal, free or united into a tube. Stamens varying from six to thirteen, the filaments generally connate. Ovary superior and the fruit a loculicidal capsule. *Gilliesia*, *Trichlora* and a number of genera found mainly in Chile. Some species of *Gilliesia* are cultivated as ornamental flowers.
4. *Galantheae.* Rootstock usually bulbous. Stalk rounded bearing a few-flowered fasicle of medium-sized, actinomorphic white flowers. Perianth tube absent, stamens all of equal length. Ovary trilocular with numerous ovules in each loculus.

FIG. 1962.—*Galanthus nivalis.* Snowdrop. Flowers.

Included in this tribe are the closely similar genera *Galanthus* and *Leucojum*. *Galanthus* (Fig. 1962) has six species, occurring in Europe and especially in the Mediterranean region. *G. nivalis* (Fig. 1963) is the Snowdrop. On the inner surface of the inner perianth segments are green grooves secreting nectar. These segments are erect in the bud but become pendulous as the flower opens. The anthers form a downwardly directed cone surrounding the style. Each dehisces by a lance-shaped opening and ends in a brush-like elongation. Against this a visiting insect is sure to strike and become covered with pollen. Since, however, the stigma projects beyond the anther it will be touched first, so that cross-pollination is probable. The flowers are visited by honey bees not only for nectar but also to collect pollen.

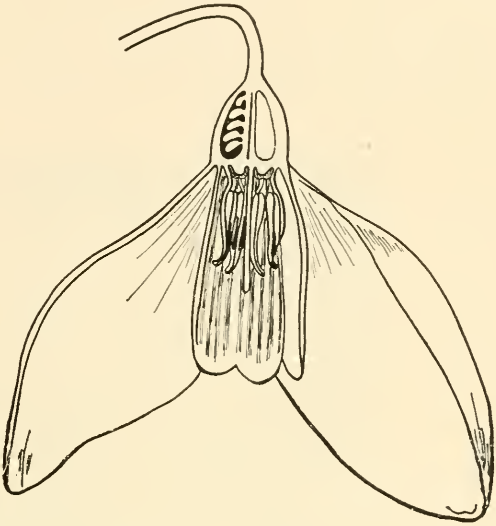


Fig. 1963.—*Galanthus*. Flower in longitudinal section to illustrate pollination. See in text.

Species of *Leucojum* (Snow-flake) (Fig. 1964) occur in southern Europe and are often cultivated in gardens. Two species are rare in Britain.


Fig. 1964.—*Leucojum aestivum*. Flowers.

5. *Amaryllideae.* Rootstock usually bulbous, producing a small umbel of large, brightly-coloured flowers which are usually zygomorphic. Perianth tube absent or short. Ovary trilocular with numerous ovules in each loculus. *Amaryllis* and *Nerine.*

The genera *Amaryllis* and *Nerine* (Fig. 1965) are both found wild in South Africa but are commonly cultivated in this country. *Amaryllis belladonna* is the only species and is found in Cape Colony. It has been extensively cultivated and a number of garden varieties have been produced.

FIG. 1965.—*Nerine flexuosa.* Umbellate inflorescence.

Nerine has a similar distribution but there are some fifteen species. They are also cultivated but are less commonly seen than the previous genus.

6. *Crineae.* Rootstock usually a large bulb. Inflorescence a cluster of many flowers, or occasionally a solitary flower; involucre composed of two bracts. Flowers actinomorphic or zygomorphic. Perianth tube long. Ovary trilocular containing numerous ovules in each loculus. *Crinum*, *Cyrtanthus* and *Ungernia.*

The genus *Crinum* occurs in tropical and subtropical climates, particularly along the coasts. Several species are cultivated. The seeds of *C. asiaticum* have thin, corky coverings and are apparently distributed by water. The ovule has no integuments and the testa is replaced by cork which is developed on the outside of the endosperm. There are sixteen species of the genus *Cyrtanthus* found growing in tropical and southern Africa, several of which are grown as ornamental flowers.

7. *Zephyrantheae.* Rootstock generally a bulb. Flowers actinomorphic and solitary or in biflorous umbels. Perianth tube elongated. Involucre composed of two bracts which may be free or united. Ovary trilocular with numerous ovules in each loculus. *Zephyranthes*, *Haylockia*, *Sternbergia* and *Cooperia.*

None of these genera are of great importance though species of several are grown as ornamental flowers. *Zephyranthes candida* (Peruvian Swamp Lily) is cultivated in the warmer parts of the country on account of its white flowers which resemble a Crocus. *Sternbergia lutea* is supposed to be the "lilies of the field" referred to in the New Testament.

8. *Haemantheae.* Rootstock generally a bulb. Inflorescence an umbel of numerous small or medium-sized flowers, rarely a cluster of few flowers. Flowers actinomorphic, or medianly zygomorphic. Perianth tube short or absent. Ovary trilocular, with one to six ovules in each loculus. Stamens alternately long and short. *Buphane* and *Haemanthus.*

In the genus *Haemanthus* there are about seventy species some of which are in cultivation under the name of Cape Tulips.

9. *Eucharideae.* Rootstock a small bulb. Inflorescence an umbel. Flowers actinomorphic or medianly zygomorphic. Stamens furnished at the base with stipules which are united to those of neighbouring stamens to form a strongly developed corona from whose margin the stamens appear to arise. Ovary trilocular with few ovules in each loculus of which some may abort. Capsule often fleshy. *Pancratium*, *Stenomesson* and *Eucharis.*

The genus *Pancratium* contains twelve species which are found in the Mediterranean region and in tropical Asia. *P. canariense* (Mediterranean Lily) bears white sweet-scented flowers. The plants are not hardy in this country and are propagated by small bulbs. *Stenomesson* has twenty species found in tropical America, while *Eucharis*, with six species in tropical South America, is sometimes cultivated in greenhouses.

10. *Hippeastreae.* Rootstock usually a large bulb. Inflorescence a cluster of many flowers, rarely a solitary flower. Involucre of two free bracts. Flowers actinomorphic or zygomorphic. Corona often reduced to a number of teeth alternating with the stamens, but occasionally forming a complete structure. *Hippeastrum* and *Vagaria.*

Hippeastrum (Fig. 1966) is a large genus with about seventy-five species found in tropical and subtropical America. They produce large, stiff, red flowers and many hybrids are grown in greenhouses in this country. *Vagaria* has one species in Syria.

11. *Narcisseae.* Rootstock usually a bulb bearing linear leaves and solitary or clusters of flowers. Flowers actinomorphic or slightly zygomorphic. Corona more or less developed, arising from the rim of the perianth tube. Stamens alternating long and short and inserted on the perianth tube. Involucre with one bract.

The genus *Narcissus* with about forty species is found in Europe, Asia and the Mediterranean region. Several species are cultivated in gardens, *N. pseudonarcissus* (Daffodil), *N. jonquilla* (Jonquil), *N. poeticus* (Fig. 1967)

(Pheasant Eye Narcissus) and a very large number of hybrid varieties have been produced as garden flowers. In this genus the flowers are feebly protogynous and are visited by Humble Bees and lepidopterous insects in search of nectar, which is secreted in the base of the perianth tube.

Fig. 1966.—*Hippeastrum vittatum.* Cultivated variety.

Fig. 1967.—*Narcissus poeticus.* Hybrid garden variety showing the short corona with deep red edging.

Loeb recognizes several distinct pollination mechanisms represented by different species which we may enumerate below:

1. Humble-bee flowers, in which the corona is large and bell-shaped, the perianth expanded at the end like a funnel and scarcely narrowed by the anthers. This type is shown by *N. odorus* and *N. pseudonarcissus.*

2. Humble-bee flowers, in which the corona is cup-shaped but tolerably deep, the perianth tube narrow and moderately long, the upper anthers projecting from the tube, the lower ones enclosed in it. This type is seen in *N. triandrus.*

3. Lepidopterous flowers, in which the corona is shaped like a flat dish with a crenulate margin, perianth tube long and very much narrowed by the anthers. This is illustrated by *N. poeticus* and *N. biflorus.*

4. Humble-bee and lepidopterous flowers, in which the corona is cup-shaped, perianth tube moderately long, slightly expanded at the top; flowers small and the perianth lobes shorter than the tube. This type is illustrated by *N. primulinus*, *N. tazetta* and *N. polyanthus.*

5. Lepidopterous flowers, in which the corona is shaped like a shallow dish, the perianth tube very long and thin and narrowed still more at the entrance by the anthers. This type may be seen in *N. jonquilla*

Hutchinson recognizes two further tribes of the Amaryllidaceae:

Ixiolirieae and Eustephieae. The first tribe is represented by one genus *Ixiolirion* (Fig. 1968) with only two species: the second contains a number of genera found mostly in the Andes.

FIG. 1968.—*Ixiolirion pallasii.* Flowering shoot.

IRIDALES

The Iridales are monocotyledonous herbs growing from rhizomes or corms, but rarely producing bulbs. The flowers are borne in racemose or cymose inflorescences but never in the form of an umbel. The flowers themselves are usually actinomorphic with a tendency towards a zygomorphic condition. The ovary is always inferior and the stamens are reduced to three. The stylar arms are sometimes petaloid and usually divided. The fruit is a capsule and the seed has abundant endosperm.

The order contains the single family Iridaceae. It has probably been derived from the Liliales or may have come from a stock which gave rise to the Iridaceae and the Liliaceae as two divergent lines. The plants are widely distributed, but their centres of distribution are probably South Africa and South America.

Iridaceae

The family is well known in cultivation in Britain though it is represented in the British Flora only by a few species. The Yellow Flag (*Iris pseudacorus*), Gladdons (*Iris foetidissima*), Autumn Crocus (*Crocus nudi-*

florus) and the rare *Gladiolus illyricus* are almost the only representatives. Species of *Iris*, *Gladiolus*, *Freesia* and *Crocus* are, however, very widely cultivated and at first sight bear only a superficial resemblance to one another.

The family is essentially one which thrives best in a dry climate where there is plenty of sun to ripen the corms or rhizomes and it is for this reason most common in the warmer and drier parts of the southern hemisphere.

The **plants** are mostly perennial herbs growing from a corm or rhizome, occasionally from a bulb. A few are shrubby. The leaves are radical but in a few species there may be cauline leaves in addition.

The **inflorescence** is usually a small cyme or a compound inflorescence of several small cymes. In *Gladiolus* and *Freesia* the lateral cymes are reduced to single flowers each with a bract, thus producing essentially a spike. In some genera the flowers are terminal, as in the *Crocus*.

The **flowers** (Fig. 1969) are hermaphrodite, actinomorphic or sometimes zygomorphic, usually very ornamental and sometimes beautifully mottled or spotted.

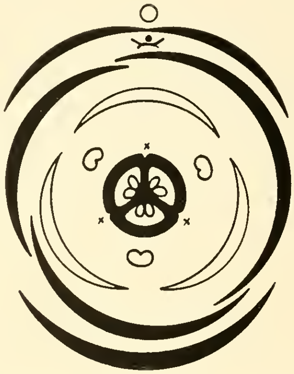


Fig. 1969.—Floral diagram of *Iris pseudacorus* Iridaceae.

The **perianth** (Fig. 1970) is composed of six segments in two whorls, usually petaloid and superior.

The **androecium** consists of three epipetalous stamens which are developed opposite the outer perianth segments. The filaments are free or partly connate. Anthers with two lobes opening extrorsely by longitudinal slits.

The **gynoecium** is tricarpellary and syncarpous. The ovary is inferior, trilocular, with axile placentation or occasionally unilocular with parietal placentation.

The style is slender, three-lobed in the upper part and branched in various ways but in *Iris* it is expanded into three large petaloid lobes. The ovules are usually numerous and anatropous.

The **fruit** is a capsule dehiscing loculicidally by valves, often with a marked circular scar at the top.

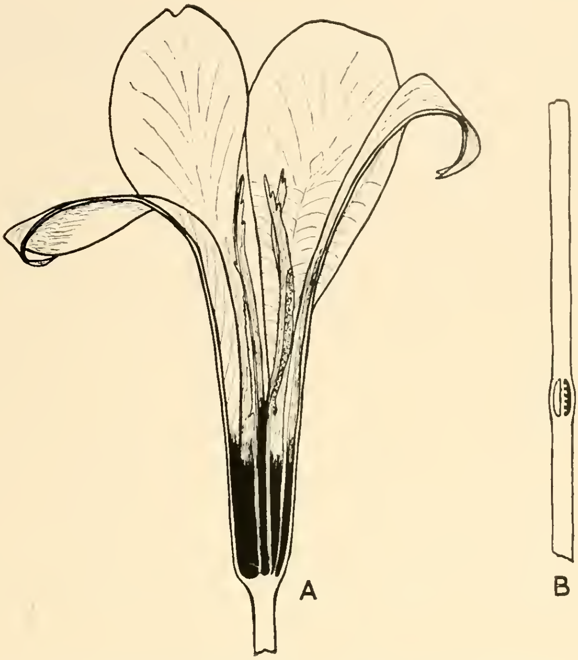


FIG. 1970.—*Iris unguicularis.* A, Flower in longitudinal section with narrow erect styles. B, Downward continuation of the tube to the ovary.

The **seed** possesses copious endosperm in which is enclosed a small embryo.

The family is widely distributed in temperate and tropical regions and includes some sixty genera and over 800 species.

Morphologically the chief interest in the family centres in its organs of vegetative propagation. In the genus *Iris* the majority of the species grow by sympodial rhizomes which are thick and fleshy and develop only just below the surface of the soil. In the Xiphion section, as illustrated by *I. xiphium* itself, a bulb is produced, which bears a stem carrying a few cauline leaves. Corms, derived from the lowermost internode of the stem, are the most common type of rootstock. These corms arise towards the end of the first year in the life of the seedling and thereafter the primary root disappears and is replaced by adventitious roots borne on the corm.

Only in the genera *Aristea*, *Witsenia* and *Klattia* is a shrubby habit developed. In *Witsenia* the stem is branched repeatedly, producing a shrub about 4 ft. high. A curious type of secondary thickening has been described in *Aristea corymbosa* where a cambium is formed in the pericycle which gives rise internally to additional complete vascular bundles embedded in ground tissue while on the outside it produces secondary cortex. At the same time a cork cambium, developed in the cortex, produces external cork and some internal secondary cortex.

In the classification of the family the number and arrangement of the flowers is one of the chief characteristics for distributing the genera. The following is based upon the system proposed by Pax.

I. Crocoideae

Plants small and growing from corms. Flowers terminal with occasionally additional axillary flowers. Spathe one-flowered. Flowers actinomorphic. Perianth segments equal. Leaves linear arranged approximately in two ranks. *Crocus* and *Romulea*.

The genus *Crocus* (Fig. 1971) has about eighty species which are particularly common in the mountains of southern Europe and in western Asia and Asia Minor. Four are naturalized in Britain. The corm is covered with dry scale leaves in whose axils may arise one or more buds, giving rise to new corms on the top of the old. The leaves are dorsiventral and variously grooved on the back. The flowers may be developed in small cymes but are more often terminal and solitary. The flowers close up at night as a result of the lowering of temperature. The perianth is often brightly coloured and the tube is very long, and passes down below the soil. At its base lies the ovary, which is thus protected below the ground.

FIG. 1971.—*Crocus sieberi*. Entire flowering plant with corm.

The flowers are protandrous and are visited by bees, butterflies and moths. Nectar is secreted by the ovary and the anthers dehisce outwards. An insect forcing its way down to the nectar therefore first touches these anthers. A visit later to a more mature flower will ensure cross-pollination owing to the later development of the branched stigma. It is often to be noticed in gardens that birds, especially sparrows, bite off the flowers in large numbers. Whether this is to obtain the nectar is not known but it is remarkable that yellow rather than white or violet flowers generally suffer most in this way.

C. sativa is of economic importance because of the orange-yellow dye which is obtained from the dried stigma and sold as saffron. It is used in flavouring, in colouring dishes and in liqueurs.

The genus *Romulea* includes about fifty species occurring in Europe and especially in the Mediterranean region. Several are in cultivation while *R. columnae* is found rarely in the west of England and the Channel Islands.

II. **Iridoideae**

The rootstock is either a rhizome, or a corm, or a bulb, generally with a leafy stem ending in an inflorescence, the spathes of which are two- to several-flowered. Leaves usually in two rows. Flowers actinomorphic, perianth in two whorls of different form.

Included in this sub-family are about forty-five genera of which the more important are *Iris*, *Moraea*, *Tigridia*, *Sisyrinchium* and *Libertia*.

The largest and most important genus is *Iris*, with about 200 species widely distributed through north temperate regions. Two species, *I. pseudacorus* (Yellow Flag) and *I. foetidissima* (Foetid Iris or Gladdons) (Fig. 1972), occur in Britain, but many other species, varieties and

FIG. 1972.—*Iris foetidissima*. Gladdons.
Flower.

hybrids are commonly cultivated in this country. Most of them grow from sympodial rhizomes which bear sheathing, isobilateral leaves and small cymes of flowers in spathes. The perianth is petaloid, the inner segments erect and the outer three segments usually bending downwards. Opposite to them, and almost resting on them, are the arching petaloid styles, under cover of which are the stamens with their extrorse anthers. Just above the anthers on the outer side of the style is a little flap of tissue whose upper surface is the stigma.

The flowers are pollinated by bees which enter the flowers to reach nectar secreted by the ovary. At their entry they come first into contact with the stigma and there brush off any pollen they may have collected from another flower. As the insect pushes further down it comes into contact with the anther and recovers fresh pollen. Self-pollination is prevented as the insect emerges, by the presence of the stigmatic flap.

The capsule is usually large and opens by a loculicidal split to liberate a large number of seeds which are flat and suitable for wind distribution. Those of *I. foetidissima* and some others are round and brightly coloured, red or orange, with fleshy coats.

The cultivated Irises fall into two main groups; those which possess rhizomes and those which develop from bulbs. Among the former type are recognized the Bearded Iris in which the outer perianth segments (or falls) have a thick band of fine hairs stretching down the middle of the lower half, and the Beardless Iris in which the falls are hairless. The most important species among the Bearded section is *I. germanica* which is the original of many of our Bearded Flag Irises. Many varieties have been

FIG. 1973.—*Iris sibirica.* A garden form with unusually large outer segments. Possibly a hybrid.

produced which form flowering shoots up to 4 ft. in height. The flowers are very beautiful, the falls being of a contrasting colour to the erect or standard petals and to the petaloid styles. *Iris laevigata* is the source of the Japanese Irises which are somewhat similar to the Flag Irises but less hardy. Among the Beardless Irises we have several well-known forms, *e.g.*, *Iris stylosa* (*unguicularis*), with its bright violet flowers which appear about Christmas time, a very popular species. *I. sibirica* (Fig. 1973) is also frequently grown. A number of other hybrid forms have also been produced which have been derived from our British species, *I. pseudacorus* and *I. foetidissima*. Most of them are moisture-loving plants in contrast to the Bearded Flags and *I. stylosa*, which thrive best in dry, limy soils.

Among the bulbous Irises are included the so-called Spanish, Dutch and English Irises. The Spanish Irises have been derived from *I. xiphium*, while the Dutch have apparently come from a specially large, early-flowering strain of Spanish Iris. The English Iris is derived from *I. xiphioides*. In addition to these there are a number of other bulbous species producing flowering shoots less than a foot in height.

The dried rhizome of *I. florentina* smells like violets and is sold as Orris Root. It is used in perfumery and essence of violets is prepared from it.

The genus *Moraea* contains about sixty species which are found mostly in Africa and Australia. Several are cultivated as ornamental flowers. They exhibit the interesting anatomical point that as the ovule ripens the outer integument becomes fleshy.

The genus *Tigridia* contains seven species which are distributed through Central America and Mexico. *T. pavonia* is cultivated under the name of the Tiger Flower. The gorgeously mottled, scarlet and yellow flowers are extremely short-lived and fade after eight to twelve hours.


FIG. 1974.—*Sisyrinchium striatum.* Inflorescence.

The genus *Sisyrinchium* (Fig. 1974) includes about seventy-five species of American origin. They are often cultivated under the name of Rush Lily. They produce dainty flower spikes bearing blue, white or yellow flowers. *S. angustifolium* occurs in Arctic and temperate regions and though really an American species is also found in Galway and in Kerry in Ireland.

The genus *Libertia* contains nine species of which *L. formosa* is often grown in gardens. The genus is interesting because of its distribution. Four species are found in Chile, four in New Zealand and one extends through eastern Australia to the mountains of New Guinea.

III. **Ixioideae**

Rootstock usually a corm with a terminal leafy stem ending in a spicate inflorescence. The spathes are always one-flowered and the flowers themselves are often medianly zygomorphic.

Some eighteen genera are included in this sub-family of which the best known are *Ixia*, *Tritonia*, *Gladiolus* and *Freesia*.

There are about twenty-five species of *Ixia* (Fig. 1975) in South Africa, several of which are in cultivation under the name of Corn Lilies. They produce star-shaped flowers about an inch across on stalks a foot high. The foliage is slender and grasslike. The name *Ixia* means birdlime and refers to the sticky juice possessed by some species.

FIG. 1975.—*Ixia maculata*. Flowers.

The genus *Tritonia* (Fig. 1976) contains about thirty species occurring in South and tropical Africa. Many are cultivated and are grown under the garden name of *Montbretia*. They produce large lax flower-spikes of red, orange or yellow flowers during summer and autumn.

The genus *Antholyza* (Fig. 1977) also occurs in South Africa. It contains some twenty-five species, of which *A. paniculata*, the Giant Montbretia, is often grown in gardens.

Fig. 1976.—*Tritonia crocosmiaeflora.* Garden Montbretia. A hybrid of *T. potsii* and *Crocosmia aurea.*

Fig. 1977.—*Antholyza paniculata.* Flowering plants.

The genus *Gladiolus* (Fig. 1978) is popular with horticulturists and many hybrid varieties have been produced. The genus, which contains about 150 species, occurs in Africa as well as to a lesser extent in Europe and Asia. *G. illyricus* is one of the most northern species and has been found in the New Forest and the Isle of Wight. The flowers are markedly protandrous and are pollinated by humble bees.

Fig. 1978.—*Gladiolus byzantinus*. A Mediterranean species. Cultivated.

Finally we may mention the genus *Freesia*, with three species found in South Africa. Many colour varieties have been produced and are favourite bowl and pot plants, grown in this country under glass for spring decoration.

DIOSCOREALES

The Dioscoreales are a small order of Monocotyledons in which the plants are herbaceous or climbers, growing from a rhizome or a tuber, with leafy shoots and usually alternate leaves, which are either ovate or cordate in shape, with reticulate venation. The flowers are small and either hermaphrodite or unisexual, consisting of a whitish perianth of united segments and either six, or more rarely three, stamens. The ovary is usually inferior, trilocular or occasionally unilocular. The fruit is a capsule bearing endospermic seeds which are often winged. They occur in tropical and warm temperate regions.

This order was made by Hutchinson to include four families, three of them small with hermaphrodite flowers, which need not concern us here, and one, the Dioscoreaceae, with unisexual flowers, which we must describe briefly.

The **Dioscoreaceae** are usually climbers with tuberous rhizomes or thick woody rootstocks. The leaves are alternate and net-veined, often arrow-shaped. The inflorescence is a raceme bearing regular, unisexual flowers, with a perianth of six segments, tubular at the base and enclosing six stamens, three of which may be staminodes. The gynoecium consists of

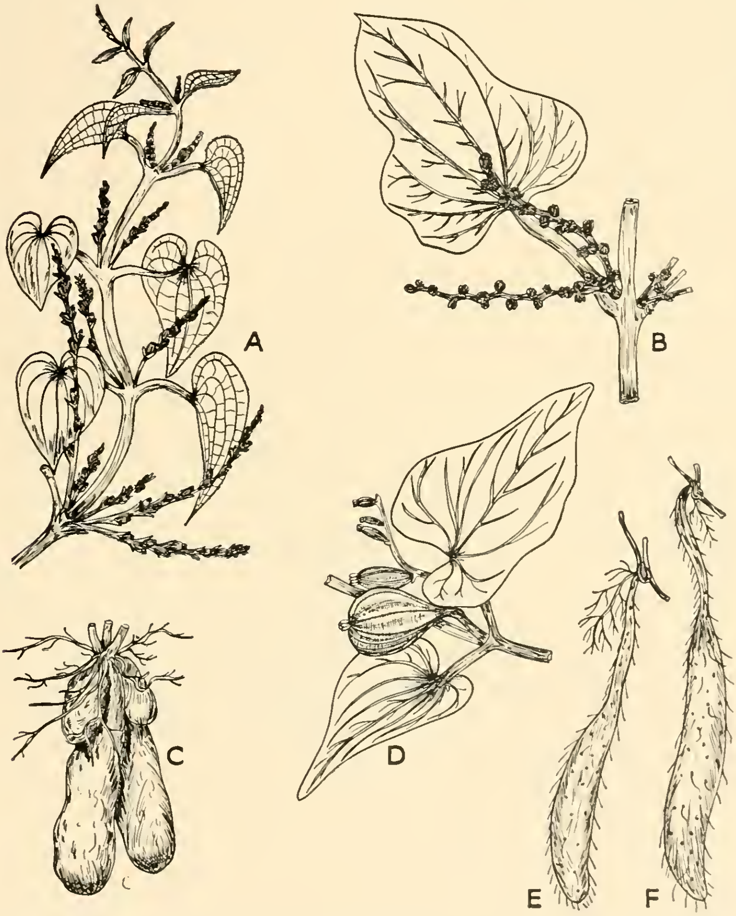


FIG. 1979.—*Dioscorea alata.* A, Flowering shoot. C, Tubers. *Dioscorea batatas.* B, Male inflorescence. D, Female inflorescence. E and F, Tubers. (A, C, E, F *after Bois.* B, D *after Le Maout and Decaisne.*)

three carpels forming a trilocular or rarely a unilocular ovary, with two anatropous ovules in each loculus. The fruit is a capsule, or occasionally a berry, containing seeds with horny endosperm.

The family contains some nine genera and over 200 species. The chief genera are *Dioscorea*, *Testudinaria* and *Tamus*.

The genus *Dioscorea* contains the bulk of the species (Fig. 1979). *D. pyrenaica* is the only European species. The genus has twining annual stems arising from tubers. These tubers vary in their morphology in the different species. In *D. batatas*, the tuber is derived from the hypocotyl and is variously interpreted as a rhizome or a root. In *D. sinuata* the tuber originates from the internodes above the cotyledon, while in *D. villosa* it is a rhizome. The tubers are known collectively as Yams and contain an abundance of starch. They are largely cultivated in tropical countries as a source of food. In cultivation they are propagated by eyes in the same way as potatoes and serve much the same function in diet. Axillary tubers are also found on the main stem.

The genus *Testudinaria* (Fig. 1980) contains two species which grow in South Africa. The tuber is an enormous swelling of the first internode of the stem, which projects above the ground and is covered by a thick layer of cork. Annual, long, thin climbing stems arise, which bear large leaves and small flowers. *T. elephantipes* (Elephant's Foot) is the better known of the two, and is the source of Hottentot Bread.

FIG. 1980.—*Testudinaria elephantipes.* Stem tuber with leafy shoot developed.

The genus *Tamus* contains two European species, one, *T. communis* (Black Bryony), occurring in Britain. They are climbing plants arising from tubers produced by a lateral outgrowth of the first two internodes of the stem. The flowers are small and greenish-white (Fig. 1981) but give rise to bright red berries in autumn.

Fig. 1981*a*.—*Tamus communis*. Black Bryony. Female inflorescence enlarged × 4.

Fig. 1981*b*.—*Tamus communis*. Male inflorescence enlarged × 4.

AGAVALES

The Agavales are a small order of Monocotyledons in which the plants are perennials, with thick woody rhizomes producing stems which may assume the form of a tree. The leaves are usually crowded either at the base or apex of the stem. They are thick, fleshy and sometimes prickly. The flowers are hermaphrodite or unisexual, mostly actinomorphic, produced in much-branched panicles. The perianth segments are similar in shape and consist of two whorls of three parts. There are six stamens, the anthers dehiscing introrsely. The ovary may be superior or inferior with axile or central placentation. The fruit may be capsule or a berry and the seeds contain endosperm.

This order was made by Hutchinson to include two families. Only one, the Agavaceae, need concern us here. It was included in the Amaryllidaceae by Engler.

The **Agavaceae** are tropical or subtropical plants many of which are of economic importance. The family is naturally divisible into five main tribes, the Yucceae, Dracaeneae, Agaveae, Nolineae and the Phormieae.

The Yucceae have woody stems, with crowded leaves which are long and linear. The flowers are produced in racemes or panicles. The perianth segments are free or rarely connate. There are six stamens with introrse anthers, inserted in the base of the perianth. The ovary is trilocular with numerous anatropous ovules forming, when mature, a capsule. The genus *Yucca* (Fig. 1982) (Adam's Needle) contains thirty species distributed in

FIG. 1982.—*Yucca filamentosa.* Developing inflorescence. Cultivated.

Mexico and the southern United States. The stem is short, thick and rarely branched and bears a quantity of long, pointed leaves on its upper part. The flowers are large and are produced at long intervals in very large panicles. The pollination is of peculiar interest and has already been referred to (see p. 1263).

The leaves of *Y. filamentosa* and certain other species furnish an excellent fibre, similar to that produced by other members of the family.

In the Dracaeneae are now included some five genera of which *Dracaena* is the most important. There are forty species in the temperate and tropical regions of the Old World. They are mostly trees. The best known is *D. draco* (Dragon Tree). The largest, on Teneriffe (Fig. 1983), was blown down in 1868. It was 70 ft. high and 45 ft. in girth, and was said by Von Humboldt to be 6,000 years old, but this estimate has been seriously questioned by later observers. The name Dragon Tree is due to a red resin (Dragon's Blood) exuded from the trunk. The genus *Cordyline* with fifteen species has the same general habit as *Dracaena*. Its leaves are sometimes used to provide a fibre. Dragon trees are not uncommonly planted in the south-western parts of Britain.

FIG. 1983.—*Dracaena draco*. The Dragon Tree. Icod. Teneriffe.

The Agaveae have short unbranched stems with crowded leaves which are sometimes fleshy. The flowers are hermaphrodite and produced in large panicles. The plants are monocarpic, and the production of the enormously large inflorescences marks the end of their life. The perianth is developed into a tube enclosing six stamens.

The chief genera of the Agaveae are *Agave*, *Furcraea*, *Beschorneria* and *Doryanthes*. *Agave* (see Fig. 1057) is a large genus with about 250 species occurring in tropical America and the southern United States. The stem is short and stout and at the top is a large mass of long, rather fleshy, stiff leaves generally covered with a wax. Only two or three new leaves are produced each year. The plants live for a long time and may continue to grow for a long period up to 100 years before producing an inflorescence. During this time the plant stores up a vast reserve of food. Finally an inflorescence develops. It is often a gigantic structure, usually a compound panicle, reaching 20 or more feet in height and bearing many flowers. In some plants many, or indeed all, of the flowers may be replaced by bulbils which serve for vegetative propagation. During its formation the rise of sap is so rapid that in Mexico a drink can be readily obtained by cutting off an inflorescence and collecting the sap as it runs out of the cut tissue. As much as 1,000 litres can be gathered from a single plant. This juice is fermented and forms a powerful drink, pulque. The genus *Furcraea* contains twenty species also distributed in tropical America. The plants are similar in appearance to

FIG. 1984.—*Dasylirion hookeri*. Plant with a large stem tuber covered with thick bark, and linear, fibrous leaves.

those of *Agave* but the inflorescences are even larger and have pendent branches. *Beschorneria* is a Mexican genus with ten species while *Doryanthes* with three species occurs in Australia.

In all these genera vegetative propagation commonly occurs by means of suckers from the base of the stem and by the formation of bulbils in place of flowers and is used as a means of rapidly increasing the economic species.

Many of the species of the Agaveae are employed as a source of strong commercial fibres which are prepared from the bundle sheaths in the leaves. Among the more important of these are: *Agave sisalana*, Sisal Hemp; *A. fourcroydes*, Henequen or Yucatan Sisal; *A. funkiana*, Istle or Mexican Fibre; *A. cantala* and *A. americana*, Maguey Hemp; *A. morrisii*, Keratto Fibre; *Furcraea gigantea*, Mauritius Hemp; and *F. cubensis*, Cuban Hemp.

In the Nolineae are included several genera with short woody stems or rhizomes which have long linear, often serrated leaves. Among the better-known genera is *Dasylirion* (Fig. 1984) which is represented by ten species occurring in Mexico and Texas. The plants are xerophytic with large,

FIG. 1985.—*Phormium tenax*. Flax Lily. Flowering plant.

scaly, woody stems. The flowers are dioecious and are borne on large inflorescences. *Nolina* contains twenty-five American species and is interesting because of the large tuberous base of the stem.

In the Phormideae we have plants of smaller stature arising from a rhizome. The leaves are radical and the flowers are hermaphrodite or sometimes unisexual by the abortion of the stamens. The perianth segments are connate. There is only one genus, *Phormium*, with two species in New Zealand. *P. tenax* furnishes New Zealand Flax (Fig. 1985); it is sometimes cultivated in gardens because of its ornamental leaves which somewhat resemble those of an enormous Flag Iris.

The Agavaceae are interesting anatomically on account of the peculiar type of secondary thickening of the stem caused by the activity of a cambium which produces fresh vascular bundles. This type of secondary thickening occurs in *Yucca*, *Dracaena*, *Cordyline* and a few other genera. The leaf anatomy also may show peculiar modifications associated with the xerophytic condition which is especially well shown in *Phormium tenax*.

Besides those already mentioned, many species, especially of *Agave*, are cultivated in the warmer parts of Britain. Particularly fine collections may be seen in the gardens of Tresco Abbey in the Scilly Islands. One of the most striking species is *A. americana*, the Century Plant, whose inflorescence may reach over 20 ft. in height. These plants take many years to flower, for they grow very slowly, but once the magnificent inflorescence has been produced the plant becomes exhausted and dies, though young ones may develop as suckers from its base. Some of the smaller Agaves may flower repeatedly year after year.

PALMALES

The Palmales are Monocotyledons often of large size. The stem is fibrous and ranges from a minute almost vestigial structure to a very tall, woody trunk. A few are climbers. The stem is usually clothed by the persistent bases of the leaves which are often of enormous size. In some species the trunks are armed with large spines formed in many cases from adventitious roots. The leaves may be entire or pinnately divided and the

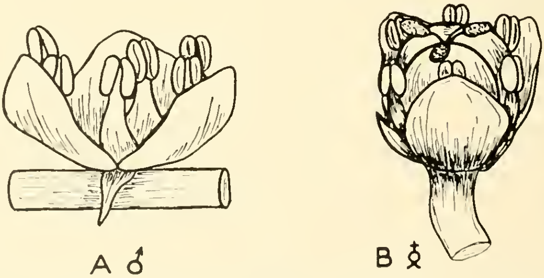


FIG. 1986.—*Chamaerops humilis*. Palmaceae. A, Male flower. B, Hermaphrodite flower. (*After Le Maout and Decaisne*.)

petiole often extends downwards into a fibrous sheath, surrounding the stem.

The flowers (Fig. 1986) are small, actinomorphic and either hermaphrodite or dioecious. They are grouped in panicles, frequently furnished with a large spathe-like bract. The perianth is usually double and encloses six stamens. The ovary is superior and composed of free or united carpels. There is one ovule in each loculus. The fruit is a berry or a drupe and the seeds are endospermic.

The Palmales contain the single family Palmaceae, or as it was formerly called, the Palmae. Owing to the wide distribution of the family in tropical and warm temperate regions and the number of species which are of economic importance, this family requires consideration in some detail.

Palmaceae

The family of the Palms is perhaps the most conspicuous of all in tropical and subtropical climates. Not only are they of great stature and of stately appearance but they are of outstanding economic importance as crop plants. The Date Palm, the Oil Palm and the Coconut Palm are obvious examples, which play a large part in the lives of millions of human beings. The Coconut Palm is one of the most widespread and distinctive of tropical trees and its gracefully curved stems, with their balanced crowns of waving leaves, provide a decorative element in every tropical scene. One or two species of Palms are hardy but only the Nikau Palm (*Rhopalostylis sapida*), in New Zealand, really extends far into temperate regions, reaching 47° S. Latitude.

Palms are light-demanding trees and, contrary to general belief, they are not conspicuous in the jungle, except near the fringes or where openings occur. They prefer a hot and moist environment and some are even semi-aquatic, but a few, such as *Hyphaene thebaica*, in North Africa, have become xerophytic. A few, likewise, *e.g.*, *Calamus*, are climbers.

The **plants** are usually trees, generally with unbranched stems,

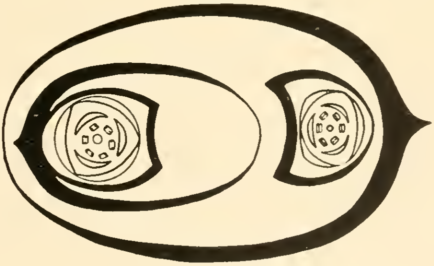


Fig. 1987.—*Raphia ruffia*. Diagram of two male flowers, that on the right being the lower. Flowers enclosed in sheathing bract and bracteoles, coloured black. Each flower has the formula K3, C3, A6. (*After Drude.*)

bearing at the top a crown of large leaves, usually few in number but of great area. Leaf scars or old leaf bases persist even to the foot of the stem.

The **inflorescence** is usually a panicle, sometimes a compound spike, and may be enveloped by a spathe.

The **flowers** (Fig. 1987) are small, actinomorphic, hermaphrodite, monoecious or dioecious and are individually not very conspicuous.

The **calyx** (Fig. 1988) is made up of three sepals, separate or connate, imbricate or open in the bud.

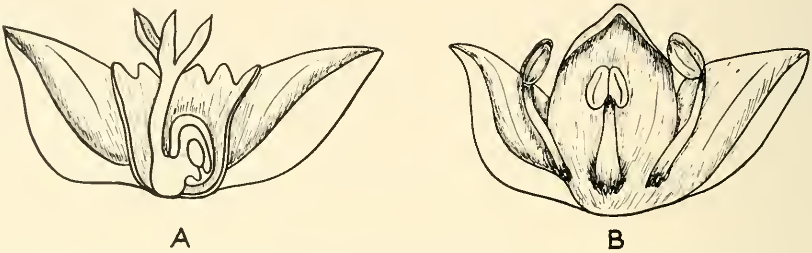


FIG. 1988.—A, *Geonoma wittigiana*. Female flower with corona of fused staminodes. B, *Chamaerops*. Male flower in vertical section. (*After Drude.*)

The **corolla** consists of three petals which are either separate or connate and are valvate in the male flowers or imbricate in the female flowers.

The **androecium** consists usually of six, occasionally numerous, stamens. The anthers possess two loculi and open by longitudinal slits. The pollen is smooth or rarely echinulate.

The **gynoecium** may be absent or rudimentary in male flowers. In the female flowers it may be made up of a number of separate carpels, or three may unite to form an ovary. Each carpel or loculus contains a single pendulous or erect ovule.

The **fruit** is either a berry or a drupe. The epicarp is often fibrous and is sometimes covered by reflex scales.

The **seed** is free or adherent to the endocarp. The embryo is small and is enclosed in a large or small quantity of endosperm.

The family contains about 200 genera and nearly 1,500 species which are widely distributed throughout the tropics. A few occur in warm temperate regions.

Anatomically the Palms show few peculiarities. Despite their size, the stem does not develop secondary thickening, the increase in girth being effected merely by expansion of the apical meristem, producing numbers of vascular bundles and the ground parenchyma which separates them

Every Palm passes through a juvenile phase during which there is very little elongation of the stem, but there is a continuous increase in the diameter of the apical meristem. Only when the full specific diameter has been reached does the stem begin to elongate and thereafter it remains practically columnar.

In a few species an underground rhizome is produced and others only produce a tuberous stem about a foot in height. The Rattan Palms produce such slender stems that they cannot support themselves and the plants live as scramblers hanging over the neighbouring vegetation.

Palm leaves are rarely simple but are usually palmately or pinnately compound, with large sheathing bases. The pinnae are folded where they meet the main rachis, sometimes upwards, **induplicate,** and sometimes downwards, **reduplicate.** These characters are used in classification.

The family is classified as follows:

A. Perianth of six members, enclosing the fruit

I. Coryphoideae

Spadix loosely branched, often a compound panicle. Flowers single or in longitudinal rows, flowering from above downwards. Carpels three; free or loosely united, separating after fertilization. Fruit a berry. Leaves fan-shaped or with induplicate pinnae.

1. *Phoeniceae.* Leaves imparipinnate. Flowers dioecious; gynoecium of three carpels, only one of which usually ripens, forming a berry. Seed deeply furrowed with copious endosperm.

In this tribe is the single genus *Phoenix.* There are twelve species in tropical Asia and Africa. The most important is *P. dactylifera* (Fig. 1989), the Date Palm, which occurs in Africa and south-western Asia. It has a columnar stem, densely covered with old leaf bases. The flowers are dioecious and the Arabs pollinate the female flowers by hanging a spadix of male flowers over the female spadix. The berries (Dates) have a hard endosperm composed of cellulose. The artificial pollination of the Date Palm has been known from ancient times and the ceremony is recorded on Babylonian monuments.

2. *Sabaleae.* The leaves are fan-shaped. Flowers polygamous with three free or slightly united carpels, only one of which usually ripens, forming a berry or a drupe with a thin endocarp. The endosperm is often ruminate. *Chamaerops, Trachycarpus* (Fig. 1990), *Rhapis, Corypha, Livistona, Sabal, Copernicia.*

These genera are widely distributed through the tropics except in tropical and southern Africa. *Chamaerops humilis* (Dwarf Palm) is the only Palm found wild in Europe. Species of *Corypha* are found in Indo-Malaya. In these Palms the gigantic inflorescence terminates the life of the tree. There are six species of which *C. umbraculifera* (see Vol. I, p. 835), the Talipot Palm, is the best known. It grows to a height of 80 ft., chiefly in Ceylon and south India, and the inflorescence may be 40 ft. across. The leaves are used as umbrellas and also for thatching. Using a metal stylus, the leaves can be written upon.

Species of *Sabal* occur in the warmer parts of America and in the West Indies. *S. palmetto* is employed for thatching while the woody stem is also useful. The genus *Copernicia* contains ten species with a similar distri-

FIG. 1989.—*Phoenix dactylifera*. Date Palm. A grove of fruiting trees in California. Photograph by Josef Muench.

FIG. 1990.—*Trachycarpus excelsa.* Bunch of fruits.

bution to the last. *C. cerifera* has its leaves coated with wax which may be removed by shaking. It was formerly used for making gramophone records and for candles. It is known as the Wax or Carnauba Palm, and is a native of Brazil.

Livistona has twenty species distributed between India and Australia.

II. **Borassoideae**

Spadix simple or with a few thick cylindrical branches. Flowers diclinous and dimorphic, invested with bracts, the female much larger than the male. Gynoecium a trilocular ovary forming one-seeded drupes. Leaves fan-shaped, induplicate.

1. *Borasseae.* Characters as in sub-family. *Hyphaene*, *Borassus*, *Lodoicea.*

The genus *Hyphaene*, containing fifteen species, occurs in Africa. It is one of the very few genera in which the stem is branched and practically the only Angiosperm which is dichotomous. *H. thebaica* is the Doum Palm of the Nile valley, whose thick mesocarp has the flavour of gingerbread. There is only one species of *Borassus*, *B. flabelliformis*, the Deleb

Palm. It has been cultivated in Ceylon and India under the name of the Palmyra Palm. It has innumerable uses. Its wood resists salt water, the leaves are used for thatching and for writing material. The leaf base provides a fibre for making brushes. The split leaf is woven into mats. The fruits are eaten roasted, while from the inflorescence a juice can be tapped which is fermented into toddy. This toddy can be converted into sugar (jaggery), alcohol or vinegar. The young seedlings can be eaten or if dried and ground yield a good flour. *Lodoicea* contains a single species *L. sechellarum* (Fig. 1991) which is the Coco de Mer, or double coconut of the Seychelles. The fruit is one of the largest known, averaging about 40 lbs. weight and takes ten years to ripen. It is a bilobed nut with a thick fibrous husk, and was found floating in the Indian Ocean long before the tree was discovered, which accounts for its colloquial name.

FIG. 1991.—*Lodoicea sechellarum.* Coco de Mer or Double Coconut. The fruits are formed on stout offshoots of the main trunk.

III. **Lepidocaryoideae**

Spadix branched. Flowers in cincinni or two-ranked spikes with bracts and bracteoles round them. Gynoecium of three carpels, united into a trilocular ovary covered with scales. Fruit one-seeded. Leaves pinnate or palmate, reduplicate.

1. *Mauritieae.* Leaves always fan-shaped and reduplicate. Only genus *Mauritia.* It contains nine species which are found in America and the West Indies.

They are the South American Fan Palms and are characterized by their pillar-like stems with a dense, leafy crown with large axillary inflorescences. Several of the species furnish wood or fibre and the juice is used in the preparation of wine. The fruits are edible.

2. *Metroxyleae.* Leaves imparipinnate and reduplicate. *Raphia*, *Metroxylon*, and *Calamus.*

The genus *Raphia* contains eight species, mostly in Africa. *R. vinifera* (Fig. 1992) is the West African Wine Palm. *R. taedigera* grows in the lower Amazon region. In *R. ruffia* (Madagascar) roots develop out of the old leaf bases and turn upwards. They are said to function as pneumatophores. There are seven species of *Metroxylon* distributed through the East Indies from Siam to New Guinea. The most important are *M. rumphii* and *M. laeve*, both of which are known as the Sago Palms. They are extensively cultivated in Malaya. They are large trees which die after producing their inflorescences and regenerate from the rhizome. The fruits take three years to ripen. Sago is obtained by cutting down the trees when flowering occurs, and crushing and washing the pith from which the sago is prepared.

FIG. 1992.—*Raphia vinifera.* Fruit.

The genus *Calamus* is a large genus with some 280 species widely distributed in the tropics. They are mostly leaf climbers with thin reedy stems. The mode of climbing is by means of strong, recurved spines, which replace the pinnae on the upper part of the leaf rachis. The stems often grow to enormous lengths of five or six hundred feet. The stripped stems are used in making rattan canes which have many uses, as, for example, chair bottoms, baskets, and even cables.

FIG. 1993.—*Caryota urens.* Toddy Palm in flower. Rio de Janeiro. Cultivated.

IV. **Ceroxyloideae**

Spadix simple or branched. Flowers diclinous and usually dimorphic. When dioecious they are solitary with rudimentary bracts, when monoecious usually in cymes of three flowers, two being male and one female. Carpels three in number. Fruit smooth. Leaves pinnate.

1. *Areceae*. The fruit always a berry.

Included in this tribe are a large number of genera of which the more important are: *Caryota*, *Arenga*, *Areca*, *Oreodoxa*, *Ceroxylon*, *Euterpe* and *Iriartea*.

The genus *Caryota* contains ten Indo-Malayan species with columnar stems. The best known is *C. urens* (Fig. 1993), the Toddy Palm, which is extensively cultivated. It yields palm sugar, sago and Ketul fibre. Fifteen species of *Arenga* occur mainly in Malaya and are similar in appearance to *Caryota*. *A. saccharifera*, the Gomuti Palm, is cultivated for its sugar which is obtained by wounding the young inflorescence and evaporating the sap collected. A variety of sago can be obtained from the pith by washing. White fibre can be made from the leaf sheaths. The genus

Fig. 1994.—*Oreodoxa oleracea*. Cabbage Palm or sometimes Royal Palm. Differs from the true Royal Palm (*O. regia*) in having no swelling in the trunk. Rio de Janeiro. Photograph by "E.N.A."

Areca is also of Indo-Malayan origin. The best known is *A. catechu*, the Betel Nut Palm, which is grown for its nuts, which are really the seeds. They are about the size of damsons and are cut into slices and rolled in a leaf of Betel Pepper (*P. betle*) with a little lime. When chewed it colours the saliva a bright red and acts as a stimulant for digestion. It is now largely cultivated in the Asiatic tropics. *Oreodoxa* (*Roystonea*) is an American genus of six species (Fig. 1994) of which *O. regia*, the Royal Palm, is well known as an ornamental tree. Many tropical cities have one or more avenues planted with this palm. *O. oleracea*, the Cabbage Palm, is used as a vegetable, the young head being cut off and eaten. *Ceroxylon andicolum* from the Andes yields Cera Wax which is secreted from the stem and is used in making candles. *Euterpe edulis* (Fig. 1995), the Assie Palm, possesses edible fruits which when soaked in water provide a much appreciated beverage. The genus *Iriartea* is interesting on account of its aerial roots which somewhat resemble those of *Pandanus*. There are some ten species occurring in South America.

2. *Cocoeae*. The fruit is a drupe. *Elaeis*, *Attalea*, *Cocos*, *Bactris* and *Desmoncus*.

Several of these genera are of economic importance. *Elaeis guineensis* occurs in Africa where it is known as the Oil Palm, because its fruits yield a valuable oil which is used for making margarine and as a thick grease for railway axles.

The genus *Attalea* (Fig. 1996) has thirty South American species some of which extend into the West Indies and Africa. *A. cohune* yields an ivory-like nut while *A. funifera* is the source of Bahia piassava fibre. *Bactris* is also an American genus with over 100 species. *B. minor* has edible fruits and is known as the Peach Palm. *Desmoncus* contains twenty-five species which are reedy palms climbing by hooks similar to those in *Calamus*; they occur in tropical America.

The most important genus is *Cocos* which contains sixty species. By far the best known is *C. nucifera* (Fig. 1997), the Coconut, which is very widely distributed throughout the tropics, especially in the islands of Melanesia where it frequently forms a fringe around the smaller islands. It grows particularly well by the sea and its fruits are adapted for distribution by water. Many an island has received its coconut palm as a result of the nuts washed up on its beach. It is a tall palm with imparipinnate leaves and densely clustered monoecious flowers. The stems are rarely vertical but develop a gradual curve which some think is a phototropic response. The fruits (really drupes) are large and one-seeded. Each consists of a pericarp, the epicarp of which is leathery, while the mesocarp is fibrous and the endocarp very hard, enclosing the seed which is surrounded by a thin testa lined with a white endosperm. In the centre of the seed is a cavity partly filled with a milky fluid. It should be noted that the Coconut as it reaches this country has usually lost the fibrous outer pericarp. The uses of the Coconut are numerous. The leaves are used for thatching and also

Fig. 1995.—*Euterpe edulis.* Group in the Jardim Botanico, Rio de Janeiro.

Fig. 1996.—*Attalea excelsa.* Brazil.

in the making of mats and baskets. The petioles serve for fencing, for broom handles and for many domestic articles. The apex of the stem is edible and is used both as a vegetable and also in the preparation of pickles and preserves. The inflorescence can be tapped to produce a sugary liquid from which toddy can be made. If this fermented drink is distilled a strong spirit known as arrack is produced. Further fermentation yields vinegar. The fruit is particularly valuable. When young it contains a considerable amount of a sweet milky liquid, but this decreases as the nut matures. The endosperm is eaten and a milk is expressed from it, which can be used as a flavouring. By pressure or by boiling coconut oil is obtained. The dried endosperm is known as Copra and is used very largely in the preparation of soaps and margarine. The desiccated endosperm is used in confectionery. The outer fibrous husk contains stout fibres which are used in stuffing and

FIG. 1997.—*Cocos nucifera*. Coconut Palm. Part of a plantation in Tahiti, taken with the sun directly overhead. Photograph by London Electrotype Agency.

for making matting. It is often referred to as Coir. Finally the outer woody part of the stem, known as Porcupine Wood, is used for rafters and in making ornamental furniture.

B. Perianth rudimentary. Fruits in close heads

V. Phytelephantoideae

Male flowers with rudimentary perianth and numerous stamens; female flowers with perianth. Endosperm hard. Leaves pinnate.

There is only a single genus, *Phytelephas*, with four species occurring in America. The fruit is a berry and contains several seeds. The endosperm is composed of a hemicellulose and is very hard (Fig. 1998). It is termed vegetable ivory and is used in turning billiard balls and making buttons.

FIG. 1998.—*Phytelephas macrocarpa.* Vegetable Ivory. Fruit entire and cut in half to show the ivory-like endosperm.

VI. Nipoideae

Male flowers with perianth, containing three stamens; female flowers without perianth. Endocarp woody. Leaves pinnate.

There is only one genus, *Nipa*, with a single tropical species, *N. fruticans* (Fig. 1999). It is a low-growing palm with monoecious inflorescences, which are covered with orange-brown bracts. They spring direct from the underground rhizome. Just before anthesis they become quite warm from the respiration of the young flowers. Indeed these bracts look, feel and smell like a rubber hot-water bottle. The fruits (Fig. 2000) are woody and are combined in a dense head. Each contains a single seed. The plants grow in brackish waters, sometimes forming a fringe in deep mud in which the rhizomes are immersed. The fruits float at first owing to occluded air but later, as the air is dissolved, they sink into the mud. This plant is particularly common along the Asiatic coast from Ceylon to the Philippine Islands. The old leaves are used locally for thatching while the young ones are employed as cigarette paper.

The Palmaceae have left fossil evidence going back as far as Eocene times. In the Oligocene and Miocene periods the Palms apparently extended further north than they do today, for fossil remains are common

Fig. 1999.—*Nipa fruticans.* A thicket growing by a tidal creek in Malaya. The long leaf bases standing up around the plants show where leaves have been cut by natives for thatching ("attap"). Photograph supplied by courtesy of Dr. E. J. H. Corner.

Fig. 2000.—*Nipa fruticans.* Fruit. A sea-washed specimen. Malaya.

in central Europe. In the London Clay at the mouth of the Thames fruits very similar to those of the living *Nipa* have been found.

PANDANALES

The Pandanales are Monocotyledons which are trees or shrubs of Palm-like habit often producing aerial prop-roots. The leaves are closely set in

FIG. 2001.—*Pandanus* sp. Tree in fruit. Jardim Botanico, Rio de Janeiro.

three ranks which form well-marked spirals, probably due to torsion of the stem. The flowers are minute but are produced in large panicles or crowded in spadix-like inflorescences with large spathe-like bracts. They are dioecious. The ovary is superior and the fruits are woody or with a pulpy interior.

The Pandanaceae are the only family. There are three genera, restricted to the tropics of the Old World, and the Pacific Ocean; *Pandanus*, *Freycinetia* and *Sararanga*. Of these the genus *Pandanus* (Fig. 2001), the Screw Pine, is the best known. They are shrubs or trees of striking habit, with straight, slightly branched stems and stiff, long, pointed leaves and large prop-roots. About 180 species have been described. The female flowers are produced in large heads enclosed in spathes. There is no perianth and the one-seeded ovaries are closely coherent. They form a solid mass of fibrous drupes. The plants are of considerable economic importance. The leaves are used in weaving, especially those of *P. tectorius* which is cultivated in Java; the fruits are sometimes eaten, especially those of *P. leram* which is known as the Nicobar Breadfruit; and the pericarp of most species is rich in fibre. Several have sweet-scented flowers or leaves which are used as ornaments in the East. The large quantity of pollen found suggests that the plants may be wind-pollinated, but the warted surface of the grains and the strong smell of the male inflorescence together with the showy bracts make them attractive to insects and suggests that entomophilous pollination may occur. The genus *Freycinetia* contains some fifty species; they are scrambling shrubs occurring from Ceylon to Polynesia. Pollination by bats has been observed in Java. The fruit is a berry. *Sararanga* contains only a single species occurring in the Solomon Islands and New Guinea.

GLUMIFLORAE

The Glumiflorae are Monocotyledons in which the flowers are either small and naked or possess a perianth consisting only of hairs or scales, subtended by scale-like bracts known as **glumes** and forming large, compound, indefinite inflorescences. The stamens are usually three in number arranged in a single whorl. The ovary encloses a single ovule and bears from one to three styles. The fruit is generally a caryopsis or a nut while the seed is endospermic and contains a large embryo.

The plants are mostly annual or perennial herbs with slender stems, elongated internodes, and linear leaves with parallel venation. The leaf is divided into sheath and blade, sometimes with a membranous outgrowth, or **ligule**, at the point of union.

The order as here treated contains three families: Gramineae, Juncaceae and Cyperaceae. Such a method is at variance with the view expressed by Hutchinson in which the three families are included in separate orders each with a single family. Of these families the Juncaceae and Cyperaceae are of comparatively small importance while the Gramineae, which includes all the cereal crops, may be considered as one of the most economically valuable families of Flowering Plants. We shall consider the Gramineae in detail but will first discuss the Juncaceae and the Cyperaceae.

The **Juncaceae** are perennial or annual herbs, very rarely shrublike, often with adventitious roots and producing horizontal or sub-erect rhizomes. The stems are usually leafy only at the base and the leaves are linear or filiform with a sheathing base. The flowers are produced in panicles, corymbs or dense heads. They are often very small and may be hermaphrodite or unisexual. The perianth consists of six segments, in two whorls, which are usually green or reddish in colour. There are either three or six stamens inserted opposite the perianth segments. The ovary is superior and is either trilocular with axile placentation or unilocular with parietal placentation. The fruit is a dry capsule and the seeds are sometimes tailed with a dry arillate appendage. The family is of world-wide distribution mostly in temperate regions. There are seven genera, among which by far the greater number of species is included in the genus *Juncus* (Fig. 2002).

FIG. 2002.—*Juncus effusus*. Common Rush. Inflorescences.

This genus, with about 225 species, occurs all over the world in cool, damp places. Eighteen species or more occur in Britain. They possess sympodial rhizomes bearing one leafy shoot each year and produce cymose heads of small flowers which are protogynous and are pollinated by wind.

Rushes are used in making baskets and chair seats. *J. squarrosus*, which is common in the hill pastures of Britain, is a valuable fodder for sheep. *J. effusus* is chiefly used in the preparation of Split Rush for basket work.

The genus *Luzula* (Wood Rush) has about sixty species, chiefly in the Old World, six of which are found in Britain.

The **Cyperaceae** are a family of world-wide distribution comprising some eighty-five genera and over 2,500 species. They are grasslike herbs with persistent, underground, sympodial rhizomes from which there arise solitary or clustered three-sided shoots. The leaves are formed in three rows and consist of a closed tubular sheath enveloping the stem and a linear blade. They grow chiefly in marshy places though some, like *Carex arenaria*, which forms an important constituent of sand-dune vegetation, inhabit dry soils.

The inflorescence is either a spike or a panicle, bearing numerous spikelets which may each be a small cyme. The individual flower is borne in the axil of a glume and may be either unisexual or hermaphrodite. It is usually naked, or may have a perianth of six or more small scales or hairs. There are three stamens and the gynoecium is composed of three or two carpels. The ovary is unilocular with long feathery stigmas: there is a

Fig. 2003.—*Carex binervis.* Unisexual inflorescences, the two upper ones in each case being staminate, the lower one carpellate, with protruding stigmas.

single anatropous ovule. In the genus *Carex* the female flower is borne in the axil of a second glume, sometimes called the **utricle**, which forms a sac around the ovary. The flowers are pollinated by wind.

The fruit is an akene and the testa is not adherent to the pericarp as it is in the Gramineae.

The members of the family are well represented in the British Flora, the commonest genus being *Carex* (Fig. 2003). This genus has about 900 species occurring in marshes in north and south temperate regions. About sixty species occur in Britain. Among the other genera we may mention *Scirpus* with 200 cosmopolitan species, characteristic of wet moorland, fifteen of which are found in Britain. *S. lacustris* (the Bullrush) is generally used for making matting and chair seats. *Eriophorum* (Fig. 2004) contains fifteen species found on wet moors of north temperate regions. Four occur in Britain and are referred to collectively as Cotton Grass or Cotton Sedge. The perianth consists of bristles which after fertilization grow out into long hairs which serve as a means of distributing the fruits. These hairs are used, especially in Ireland, for stuffing pillows. *Eleocharis* contains ninety cosmopolitan species of which three, including *E. palustris* (Spike Rush), occur in marshes and turfy moors in Britain. *E. tuberosus* produces tubers which are used in eastern Asia as food. Finally we may mention the genus *Cyperus* (Fig. 2005) which includes some 400 tropical and warm temperate species, two of which are found in Britain. *C. papyrus* (Paper Reed) is an African river-side plant with shoots 3 to 12 ft. high from which in ancient times paper was made. The rhizome is edible as are also the tuberous roots of several species, *e.g.*, *C. esculentus*, the Rush Nut, a native of southern Europe. The split or whole stem is also sometimes used in basket-making.

FIG. 2004.—*Eriophorum angustifolium.* Inflorescences with protandrous bisexual flowers. Those on left displaying stamens, those on the right, stigmas.

FIG. 2005.—*Cyperus alternifolius.* Plant growing in a pool with *Eichhornia.* Jardim Botanico, Rio de Janeiro.

Gramineae (Poaceae)

The Gramineae are one of the largest of the families of the Flowering Plants and, next to the Orchidaceae, the largest in the Monocotyledons. Economically it is the most important of all, for the cereals provide the basic food of both man and his domestic animals. The grasses are the most widely distributed of all types of vegetation extending from the tropics to the Arctic. They are among the first colonizers of new ground and form the dominant vegetation of many parts of the world. With the exception of the Bamboos, which are sometimes as tall as trees, the grasses are usually herbaceous, some being annuals though the majority are perennials.

Owing to the popular difficulty in distinguishing the species from one another, the English names are but little used. We may mention however the following common British grasses, as examples.

1. *Grasses common in fields, pastures and wastes places:* Perennial Rye Grass (*Lolium perenne*), Sweet Vernal Grass (*Anthoxanthum odoratum*), Timothy Grass (*Phleum pratense*), Meadow Foxtail (*Alopecurus pratensis*), Yorkshire Fog (*Holcus lanatus*), Couch

Grass (*Agropyron repens*), Brome Grass (*Bromus mollis* and *B. sterilis*), Sheep's Fescue (*Festuca ovina*), Cock's Foot (*Dactylis glomerata*), Dog's Tail (*Cynosurus cristatus*), Quake Grass (*Briza media*), Smooth Meadow Grass (*Poa pratensis*).

2. *Grasses common in marshes and damp places:* Common Reed (*Phragmites communis*), Purple Molinia (*Molinia caerulea*), Flote Grass (*Glyceria fluitans*).
3. *Grasses common in woods:* Millet Grass (*Milium effusum*), Wood Melick (*Melica uniflora*), Wood Poa (*Poa nemoralis*).
4. *Grasses common on moors and heaths:* Common Bent (*Agrostis tenuis*), Mat Grass (*Nardus stricta*).
5. *Grasses found on the sea-shore and dunes:* Marram Grass (*Ammophila arenaria*), Lyme Grass (*Elymus arenarius*), Cord Grass (*Spartina stricta* and *S. townsendii*).

The **plants** are nearly all herbaceous with the exception of the Bamboos. The stems are generally hollow tubes, with enlarged nodes. The leaves are alternate and generally arranged in two opposite orthostichies. They consist of a long sheath, surrounding the stem, and a lamina, which is linear and generally bears a ligule at the base. Many are annuals, but in perennial species vegetative propagation is effected by rhizomes, or by tillering, *i.e.*, axillary branching, at the base of the tuft, the branches often rooting independently.

The **inflorescence** is complex and consists of groups of the individual flowers in spikelets, which are themselves grouped together to form compound inflorescences of various types.

The **spikelet** consists of a short central axis, the **rachilla**, bearing a number of scales closely arranged in two rows. The two basal scales are barren, that is they bear no flowers in their axils, and they are termed the **glumes**. Above the glumes are a number of bracts each subtending a flower. They are called the **outer paleae**. The outer palea or **lemma** sometimes bears a long process called the **awn** or **arista**. The number of flowers in a spikelet varies. There may be from one to five or more perfect flowers, usually the lower ones, while the upper flowers are often incomplete and sterile.

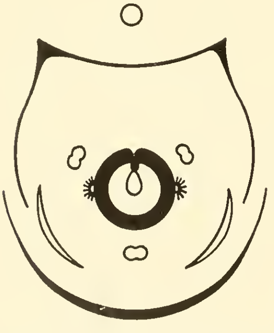


FIG. 2006.—Floral diagram of Gramineae. (*After Eichler.*)

The **flower** (Fig. 2006). The flowers themselves may be either hermaphrodite or unisexual. In the latter condition in some instances, male flowers may be separated from the female flowers and may even be grouped in separate inflorescences, as in *Zea mais*, where the male flowers form a loose, terminal panicle, while the female inflorescences are borne laterally in the axils of the foliage leaves, each consisting of a fleshy spadix sheathed in bracts.

The axis of the flower stands in the axil of the outer palea and bears a scaly bracteole called the **inner palea**, opposite to the **outer palea**. The flower thus lies between the two paleae. There are no sepals or petals. Opposite the inner palea on the outer side of the flower are two small scales termed the **lodicules**. Many consider these to represent the remains of perianth segments which otherwise are entirely suppressed. An alternative view is that they represent a second bifurcated bracteole. The inner palea itself is sometimes bifurcate, which supports this hypothesis. The lodicules are biologically important because they are hygroscopic, and their movements separate the paleae and open the flower at anthesis.

The **androecium** consists typically of three hypogynous stamens corresponding to the outer whorl of the normal monocotyledonous flower. Occasionally, *e.g.*, *Bambusa*, there is an inner, alternating whorl, also of three stamens. Each stamen has a long filament and bears a versatile anther which dehisces extrorsely.

The **gynoecium** is monocarpellary and usually bears two feathery stigmas. It should be noted that these stigmas arise from the carpellary wall and not from the apex and the presence of two is not necessarily an indication of a bicarpellary ovary. The ovary is unilocular and superior, and contains a single, erect, anatropous ovule.

The **fruit** is a caryopsis, *i.e.*, an akene in which the pericarp is adherent to the seed.

The **seed** is endospermic and the embryo lies to one side. It is straight, with a shieldlike appendage, called the **scutellum**, on the side adjacent to the endosperm (see p. 1592). Radicle and plumule are well developed, but the radicle is very short-lived and is soon replaced by adventitious roots.

The family is divided into over 450 genera including, at a conservative estimate, 4,500 species, which are to be found in all regions of the globe. In temperate regions they form the most important constituent of the vegetation covering such vast areas as the prairies and steppes.

Anatomically the grasses show certain peculiarities. The long internodes are usually hollow, due to the failure of the pith to develop, though a transverse diaphragm containing a complex of leaf trace bundles is usually found at the nodes. In many species the upper surface of the leaf is longitudinally ridged. The outer layers of these ridges are composed of sclerenchyma, while the stomata are restricted to the grooves between. In many xerophytic grasses the assimilatory tissue is restricted to the sides of the grooves, and by the shrinkage of a row of large parenchyma cells lying at the base of each groove the whole leaf may be rolled up longitudinally when the air is dry.

Even in grasses not growing under xerophytic conditions the stomata are developed in lines and there are large subsidiary cells. The venation of the leaves is parallel and the vascular bundle is often surrounded by a sclerotic sheath. The young leaves in the bud are usually convolute but in some instances are conduplicate and more or less elliptical or compressed in section.

Pollination is usually brought about by the wind. In fact the grasses are the most important group with wind-pollinated flowers. Many are self-pollinated, but when hermaphrodite the flowers are often protogynous. At anthesis the stamen filaments elongate rapidly and the light versatile anthers discharge a quantity of fine, granular, smooth pollen through a longitudinal slit which is caught by the expanded stigmas of younger flowers.

Most species of Wheat are self-pollinated, while some cultivated races of Barley never open their flowers. Cleistogamic flowers are also known among wild species, *e.g.*, *Triodia decumbens*, *Leersia oryzoides* and *Amphicarpum purshiit.*

In the embryo sac of some species the antipodal cells begin to divide after fertilization forming a many-celled parenchymatous tissue in the lower end of the embryo sac. The embryo sac grows at the expense of the nucellus of which only one or two layers eventually remain and become filled with endosperm. The embryo has a lateral depression above which develops a terminal structure which finally becomes lateral and shield-shaped, producing the scutellum. The plumule is covered by a sheath formed from the borders of a lateral depression which grows up to form a collar known as the **coleoptile**. The radicle is similarly protected by a sheath formed by the edges of a cleft in the scutellum tissue. This is called the **coleorhiza**. Adventitious roots may already appear before the embryo is mature.

The classification of the family has been the subject of considerable study and there is by no means complete agreement as to the number of tribes into which it should be divided nor as to the distribution of the genera among the tribes. The latest and most detailed account is that by Hubbard, published by Hutchinson in his " Families of Flowering Plants". Here we shall follow that treatment but shall mention only the more important of the twenty-seven tribes there described.

I. Pooideae

Spikelets one-to many-flowered, dividing up at maturity above the more or less persistent glumes, or if falling entire, then not two-flowered, with the lower floret male or barren and the upper hermaphrodite, usually laterally compressed or terete.

This is the larger of the two sub-families and is divided by Hubbard into twenty-four tribes, of which the more important are dealt with below. (For the sub-family Panicoideae see p. 2082.)

1. *Bambuseae.* Shrub or treelike, rarely perennial herbs, erect, sometimes climbing and usually woody, bearing leaf sheaths with reduced blades which are flat, linear or oblong-lanceolate with petiolar bases and frequently articulated to the sheath. Spikelets (Fig. 2007) all similar, one- or many-flowered. Glumes usually two but sometimes more, outer paleae awnless, five- or many-nerved. Inner paleae either two-keeled, keelless or suppressed. Lodicules three, rarely more or less. Stamens three, six or more.

Styles mostly two or three. Fruit a nut (*Dendrocalamus*), berry (*Melocanna*) or caryopsis.

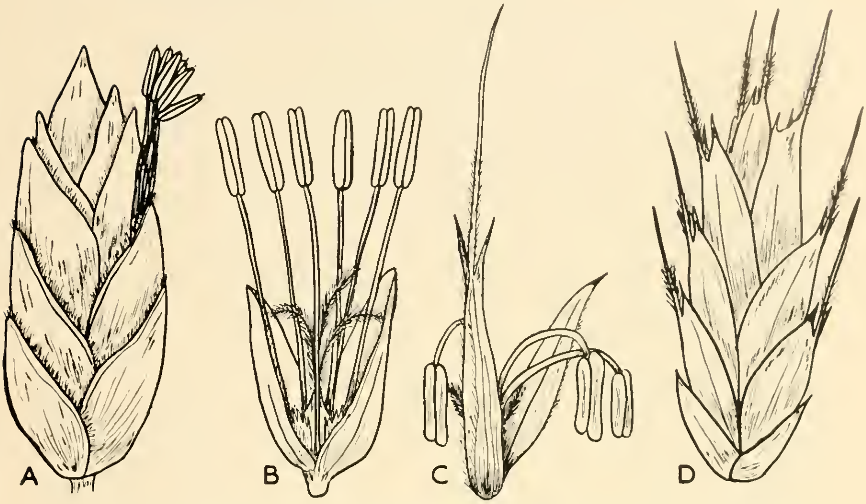


FIG. 2007.—*Bambusa.* A, Spikelet. B, Flower. *Bromus.* C, Flower. D, Spikelet.

This tribe contains about forty-five genera, many of which are of economic importance. The more important are *Arundinaria*, *Bambusa* and *Dendrocalamus.*

The Bamboos usually grow in clumps which continually expand centrifugally by the rhizomes. The rhizomes give off erect, perennial, woody stems which appear at the beginning of the rainy season and grow extremely rapidly. When they have reached their full height the scale leaves fall and the leafy branches spread out. The shoots of *Dendrocalamus giganteus* (Fig. 2008) are said to grow as much as a yard a day. In some species the plants may reach a height of over 100 ft. The economic uses to which the bamboo is put in the tropics are extremely varied, especially in Asia. The stems (Fig. 2009) are hollow except at the nodes and the wood is both elastic and very light and moreover splits very easily. They are used as the main supports of buildings or split to serve as tiles. Bridges are often made of them while they also serve as pipes to conduct water, as water vessels, flower pots, gutters, masts, household utensils and agricultural implements. Fine branches can be split and woven into mats which attached to bamboo poles serve as walls to houses or sails for boats. Split bamboo can be sharpened and used as cutting implements, or pointed as lances or needles. When finely split it can be woven into coarse clothing, mats, blinds, baskets, hats and rope, or made into brushes. The young stems are eaten like asparagus, and the seeds are sometimes used as food.

Bamboos are generally monocarpic. Flowering seasons for certain species recur at irregular intervals, after which all the plants of that species in the area die.

FIG. 2008.—*Dendrocalamus giganteus.* Clump growing in Jardim Botanico, Rio de Janeiro.

In this country bamboos are used chiefly as supports for garden plants, the material being derived from the Far East. During the Second World War when supplies were unavailable, home-grown bamboos were employed. These however have not apparently the durability of the Japanese canes, though the supplies which became available were a testimony to the quantity of bamboos successfully grown, particularly in the west and south-west of the country.

2. *Festuceae.* Annual or perennial herbs with narrow leaf blades. The spikelets are generally all similar, hermaphrodite, two- or

FIG. 2009.—Stems at the base of the clump shown in Fig. 2008.

many-flowered, laterally compressed and arranged in loose or contracted panicles, rarely in racemes or spikes. Glumes persistent, the outer paleae membranous or coriaceous, usually five- to many-nerved, awnless or awned from the middle, or paleae bifid. Lodicules two, rarely three or absent. Stamens three, rarely two or one. Fruit a caryopsis tightly enclosed between inner and outer paleae.

There are some seventy genera included in this tribe, many of which form important fodder grasses of temperate regions. In tropical climates they occur either in forest or mountain regions.

Among the more important genera we may mention *Bromus*, *Festuca*, *Poa*, *Dactylis*, *Cynosurus*, *Briza*, *Glyceria*, *Lolium*, *Melica* and *Sesleria*, all of which are represented in the British Flora. Species of *Festuca*, *Poa*, *Dactylis*, *Cynosurus* and *Lolium* are all valuable fodder grasses.

3. *Hordeeae.* Annual or perennial herbs, leaf sheaths with small auricles at the mouth, blade narrow. Spikelets one- or many-flowered, solitary or in clusters of from two to six flowers, mostly hermaphrodite and sessile. Spikelets alternating on opposite sides of a continuous or jointed rachis, forming solitary spikes or

spike-like racemes. Glumes well developed, outer paleae five- to indefinitely nerved, awnless or awned from the tip. Lodicules two. Stamens three. Styles two. Fruit a caryopsis, free or adhering to the inner or outer palea.

The tribe includes ten genera which are distributed in temperate regions mainly in open grassland. Many are in cultivation.

Among the more important genera are *Agropyron*, *Triticum*, *Hordeum*, *Elymus*, *Secale*. All, except the last, are found in Britain. Of these, *Triticum* (Wheat), *Hordeum* (Barley) and *Secale* (Rye) constitute the most important of the cereals. The modern cultivated varieties have been obtained from wild species found growing mainly in south-western Asia. We shall discuss the question more fully in Volume IV under Economic Botany. Some species of *Agropyron* and *Elymus* make good fodder grasses.

The genus *Lepturus* and several allied genera, which occur in warm temperate regions and along the seashore in the tropics, are placed by Hubbard in a separate tribe, the Lepturaeae.

4. *Arundineae.* Perennials with tall, stout, sometimes woody stems bearing long, flat leaf blades. Spikelets (Fig. 2010) hermaphrodite or unisexual with sexes on different plants, two- to ten-flowered, often arranged in large panicles. Glumes hyaline or membranous, both similar or the lower ones smaller. Outer paleae similar to the glumes, acuminate and either awnless or awned from the tip, one- to five-nerved; enveloped in long hairs arising from the back of the paleae in fertile florets or from the rachilla. Lodicules two. Stamens two or three.

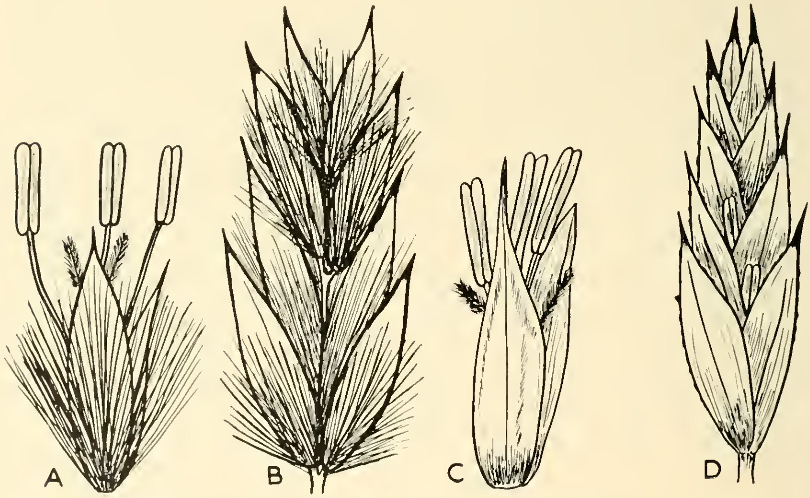


FIG. 2010.—*Phragmites.* A, Flower. B, Spikelet. *Agropyron.* C, Flower. D, Spikelet.

The tribe contains six genera, the most important of which are *Arundo*, *Phragmites* and *Gynerium*. They occur mainly in temperate and tropical regions. The stem of *Arundo donax* is used for making sticks and fishing-rods. *Phragmites communis* (Fig. 2011) is the Common Reed of Britain, where it is often used in thatching roofs. In parts of Europe it grows in great profusion and at the mouth of the Danube it forms great floating fens. The genera *Gynerium* and *Cortaderia* are the Pampas grasses of South America, some of which are grown as ornaments in gardens.

FIG. 2011.—*Phragmites communis.* Common Reed. Inflorescences.

5. *Eragrosteae.* Annual or perennial herbs with narrow leaf blades. Spikelets two- to many-flowered, mostly hermaphrodite, usually laterally compressed, in open or contracted panicles. Glumes usually persistent, membranous or coriaceous, usually shorter than the outer paleae. Outer paleae usually exserted from the glumes or rarely enclosed by them, one- to three-nerved, two- to four-lobed at the tip, awnless or with straight awn from the tip. Lodicules two, stamens two or three. Fruit a caryopsis, loosely or tightly enclosed by inner and outer paleae, sometimes with a free pericarp.

There are about forty genera included in this tribe, most of which are characteristic of tropical regions, extending into the warm temperate zones. *Eragrostis* is the largest genus. It is cosmopolitan with over 150 species. *Eleusine*, with ten species, occurs in the tropics. *E. coracana* is cultivated as a cereal in Ceylon, India and Africa under the name of Ragi or Kurakkan. Other species are used for fodder.

6. *Chlorideae.* Annual or perennial herbs with narrow leaf blades. Spikelets usually laterally compressed, one- or few-flowered, with one hermaphrodite flower with or without imperfect florets above and below it. Spikelets borne in one or two rows on one side of a continuous rachis or solitary or scattered, forming spikes or racemes. Glumes usually persistent. Outer paleae membranous, entire or emarginate or two or three-lobed, awnless or awned, one- to three-nerved with lateral nerves near the margins and often ciliate. Lodicules two, rarely suppressed. Stamens usually three. Fruit a caryopsis enclosed in the inner and outer paleae.

This tribe includes about thirty-five genera mostly inhabiting tropical regions, though some extend into the warm, or even into cool temperate regions. One of the best-known genera is *Spartina.* There are about half a dozen species. *S. stricta* occurs in salt marshes in Britain, while the fully fertile hybrid, *S. townsendii*, of this species with the North American *S. alterniflora* has become an invader and stabilizer of maritime mud flats in southern and western estuaries round Great Britain in recent years. The genus *Cynodon* is represented in Britain by *C. dactylon* which is restricted to sandy parts of the south coast. It is common in all warm countries. Other important genera in this tribe are *Chloris*, *Bouteloua*, *Ctenium* and *Trichloris.* A number of the genera are valuable fodder grasses, while species of *Cynodon* are used as lawn grasses.

7. *Nardeae.* Densely tufted perennials with siliceous leaf bases. Spikelets (Fig. 2012) hermaphrodite and one-flowered, alternate in notches along one side of the continuous rachides of the solitary terminal spikes. Glumes suppressed. Outer paleae acuminate or awned from the tip, three-nerved. Lodicules suppressed. Stamens three, style solitary with a papillose stigma. Fruit a caryopsis, lying free between inner and outer paleae.

There is only a single genus, *Nardus*, with one species, *N. stricta*, which is widely distributed in Europe, northern Asia and in Greenland and Newfoundland. It is found in Britain as the commonest grass of drier grass moors. Although separated by Hubbard in a distinct tribe, the genus *Lygeum* is included here by Arber. There is only one species, *L. spartum*, which occurs in the Mediterranean region and is one of the Esparto grasses.

8. *Aveneae.* Annual or perennial herbs with narrow leaf blades. Spikelets (Fig. 2013) all alike, one- to seven-flowered, with all florets hermaphrodite or only the upper ones barren. The spikelets arranged in open or contracted panicles. Glumes persistent, usually as long as the lowest outer paleae and often as long as the spikelets, membranous with shining margins. Outer paleae with membranous margins, often hyaline and usually five-

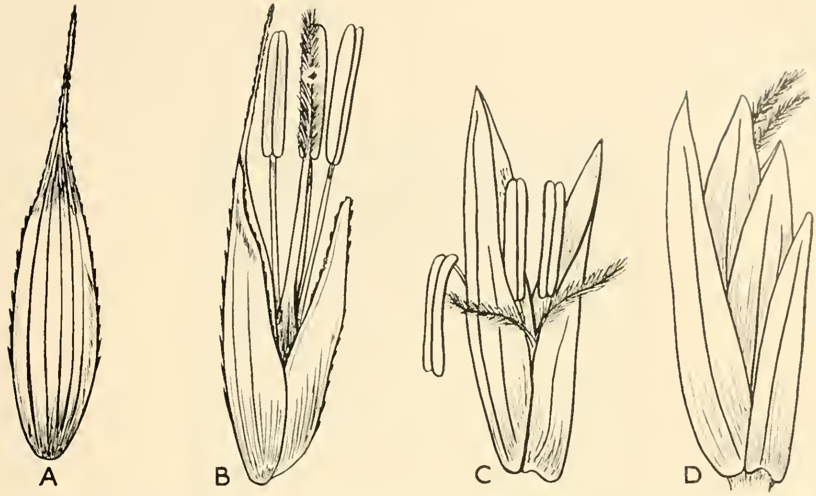


FIG. 2012.—*Nardus.* A, Spikelet. B, Spikelet open showing single flower. *Spartina.* C, Flower. D, Spikelet.

nerved, awnless or awned from the back or from a sinus of the two-lobed tip. The awn is generally geniculate and twisted below the knee. Lodicules two. Stamens three.

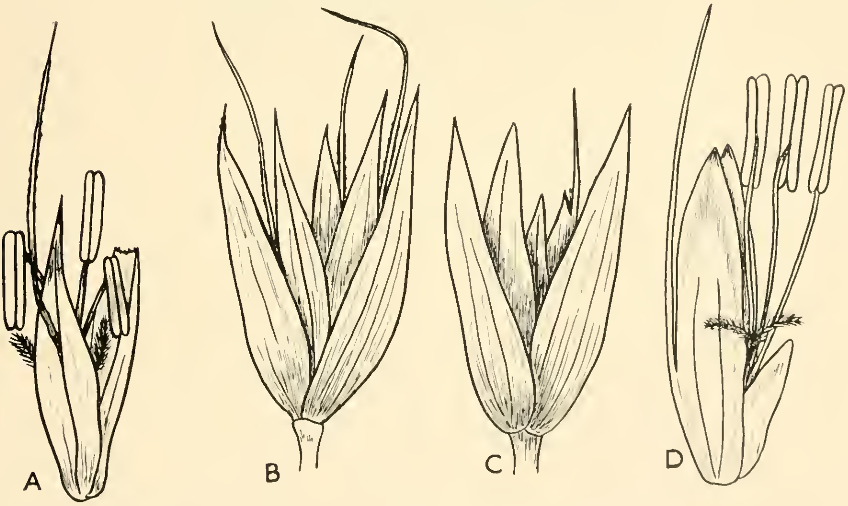


FIG. 2013.—*Avena.* A, Flower. B, Spikelet. *Agrostis.* C, Spikelet. D, Flower.

This tribe contains about thirty-eight genera, including a number of fodder grasses which occur mainly in temperate regions and only in mountainous regions in the tropics. Among the more important genera we may mention *Aira*, *Deschampsia*, *Holcus*, *Arrhenatherum* (Fig. 2014), *Trisetum*, *Avena* and *Koeleria*, all of which occur in Britain. *Avena sativa* is the Oat and will be considered in more detail in Volume IV under Economic

Botany. In *A. sterilis* the awns cross and when wetted they attempt to untwist, thus pressing on one another until they produce a sudden fracture which jerks away the separate fruits.

FIG. 2014.—*Arrhenatherum elatius.* Cluster of two flowered spikelets in anthesis, showing extruded anthers, pendent on their delicate filaments and the feathery stigmas.

9. *Agrosteae.* Annual or perennial herbs, mostly with narrow leaf blades. Spikelets usually all alike and hermaphrodite, one-flowered, small and laterally compressed, borne either in open or contracted or spike-like panicles. Axis of the spikelet disarticulating above the glumes. Glumes usually persistent, as long as the spikelet and enclosing the flower. Outer paleae hyaline or membranous, often thinner than the glumes, mostly three- to five-nerved. Paleae awned or awnless, awns where present arising usually from the back of the entire or two-lobed tip; straight or geniculate. Stamens three, two or one. Fruit a caryopsis, generally enclosed between inner and outer paleae.

Some forty-five genera are included in this tribe, many of which are valuable fodder grasses. They occur mainly in temperate regions or in mountainous regions in the tropics. Among the better-known genera we may mention *Agrostis*, *Calamagrostis*, *Lagurus*, *Polypogon*, *Phleum* and *Alopecurus*. Of these *Agrostis*, with about 130 species, includes *A. alba* (White Bent) which is a valuable pasture grass. This and *Calamagrostis,* with 200 species, are the largest genera.

10. *Stipeae.* Annual or perennial herbs with rough, rigid stems and narrow leaves. Spikelets hermaphrodite, one-flowered, arranged in open or contracted panicles. Axis of the spikelets disarticulating above the glumes. Glumes mostly persistent, one or both longer than the floret. Outer paleae mostly terete with convolute or involute margins, becoming rigid and indurated at maturity; three- to seven-nerved, with nerves close together at the apex. Awned from the centre or from the minutely two-lobed tip. Awn simple or divided into three branches. Lodicules two or three. Stamens three. Fruit a caryopsis, tightly embraced between inner and outer paleae.

The tribe is a small one, containing some eight genera which are distributed mostly in tropical and subtropical regions. Some are found in warm temperate regions. The best-known genera are *Aristida*, *Stipa*, *Oryzopsis* and *Milium*. The genus *Aristida* has about 160 species. *Milium effusum* is known as Millet Grass and occurs in Britain. It must not be confused with true Millets (see p. 2082). The genus *Stipa* (Fig. 2015), with 120 species, occurs mainly under xerophytic conditions. *S. pennata* has leaves which roll inwards when the air is dry. The fruit is awned, the tip of the awn being feathered and hygroscopic. The fruit is thin and sharply pointed with backwardly directed hairs at the tip. The awn twists and untwists with variations in the moisture of the air, and the tip of the fruit, if on soft ground, is driven into it, the feathers by coming into contact with other objects assisting in the process. *S. tenacissima* is the Esparto grass from which paper is extensively made.

FIG. 2015.—*Stipa tenacissima.* Spikelet showing the long, sharply flexed awns, which are hygroscopic. See in text.

11. *Phalarideae.* Annual or perennial herbs with narrow leaf blades. Spikelets (Fig. 2016) all alike, hermaphrodite, mostly strongly compressed laterally; arranged in open or contracted spike-like panicles. They are three-flowered, with the lower two flowers male or barren and the terminal flower hermaphrodite. Glumes persistent, equal, and as long as the spikelet, or the lower or sometimes both shorter than the spikelets. Outer paleae of the two lower flowers longer than those of the third, but sometimes shorter or reduced to small scales; awned or awnless, but terminal paleae always awnless. Lodicules two or absent. Stamens two to six.

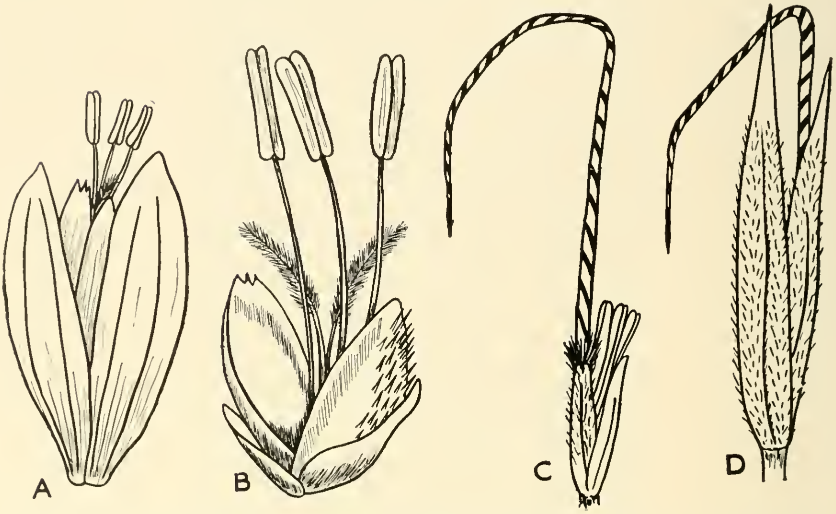


FIG. 2016.—*Phalaris.* A, Spikelet. B, Flower. *Stipa.* C, Flower. D, Spikelet. Showing the twist of the hygroscopic awn.

The tribe includes six genera, of which *Anthoxanthum* and *Phalaris*, both occurring in Britain, are the more important. They form fodder grasses of temperate regions or of mountain grassland in the tropics. Species of *Phalaris* are particularly valuable as fodder, while *P. canariensis* (Canary Grass) is cultivated for its seed which is used to feed cage birds. *Anthoxanthum odoratum* is the Sweet Vernal Grass of Britain. It contains large quantities of coumarin to which the smell of new-mown hay is mainly due.

12. *Oryzeae.* Annual or perennial herbs with narrow or broad leaf blades. Spikelets (Fig. 2017) all alike and hermaphrodite, or dissimilar and unisexual; one- or rarely three-flowered. Glumes very minute, confluent into an annular rim or suppressed. Outer paleae of sterile flowers mostly shorter than those of the fertile florets or often suppressed. Fertile paleae membranous or coriaceous; one- to three-nerved awnless or with a straight awn

arising from the tip. Inner paleae three- to nine-nerved. Stamens usually six, rarely three, two or even one.

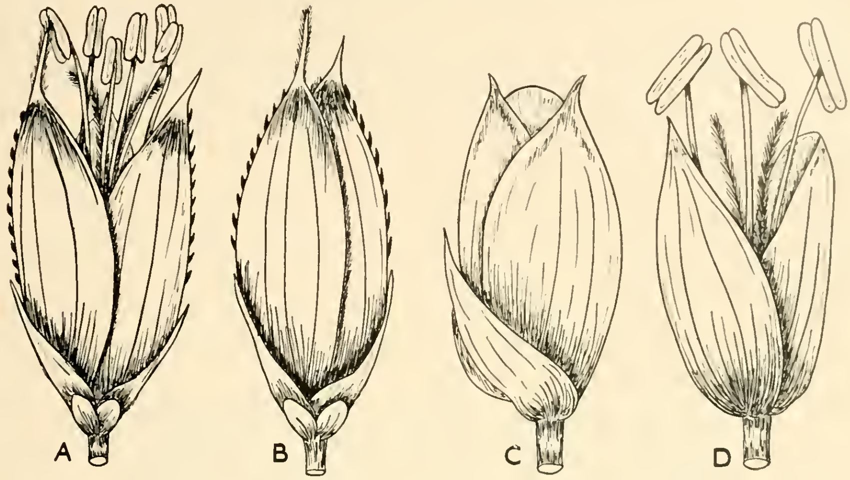


FIG. 2017.—*Oryza.* A, Spikelet open, flower in anthesis. B, Spikelet closed. *Panicum.* C, Spikelet. D, Flower open.

The tribe includes nine genera, which are mainly aquatic grasses of temperate and tropical regions. Among the more important genera are *Leersia*, *Oryza* and *Zizania*. Species of *Oryza*, especially *O. sativa* (Fig. 2018), yield the Rice of commerce, while *Zizania esculenta* is the source of

FIG. 2018.—*Oryza sativa.* Rice. Panicle in fruit.

the Wild Rice used as a cereal by the North American Indians. Rice may be conveniently divided into two kinds according to the conditions of growth: hill rice, which is only cultivated by wild tribes, and swamp rice, which is extensively cultivated in south-eastern Asia, south India, China, Japan, South America and southern Europe. The grain in the husk is known as paddy, hence the term paddy fields which is frequently applied to the flooded, terraced land in which rice is grown.

II. Panicoideae

Spikelets two-flowered, falling entire at maturity, usually with the upper flower fertile and the lower male or barren; in the latter case often reduced to the outer palea; all alike or differing in size, shape and structure; frequently dorsally compressed.

This sub-family includes only three tribes according to Hubbard, but among the genera are a number of great economic importance and we shall refer briefly to each of them.

1. *Paniceae.* Annual or perennial plants with herbaceous or rarely woody stems, bearing linear, lanceolate or ovate leaves. Spikelets usually similar, hermaphrodite or rarely unisexual, usually falling entire at maturity; two-flowered, with the lower flowers male or barren, with or without paleae and the upper hermaphrodite. Spikelets arranged on a continuous rachis forming solitary or scattered spikes, racemes or panicles. Glumes usually membranous, lower usually smaller than the upper. The lower outer palea similar to the upper glume; awnless or with straight, short awn arising from the apex. Lodicules usually two. Stamens generally three in number.

There are about eighty genera included in this tribe, which includes grasses mainly of tropical and warm temperate countries. Many are important fodder grasses of which we may mention the following genera: *Panicum*, *Digitaria*, *Paspalum*, *Pennisetum*. Others contribute cereals of economic importance, among which we should refer to Pearl Millet, *Pennisetum typhoideum*, which is extensively cultivated in India; Common Millet, *Panicum miliaceum*, and Little Millet, *P. miliare*, both of which are cultivated in eastern Europe and in India; and Sanwa Millet, *Echinochloa colona*. The limits of the genera *Panicum* and *Echinochloa* are much disputed and a number of the commercial Millets are now considered to belong to the latter genus. Other species of *Panicum* form important fodder plants, *e.g.*, Guinea Grass (*P. maximum*), Mauritius Grass (*P. motte*), Barnyard Grass (*P. crus-galli*) which is naturalized in parts of Britain, and Crab or Panic Grass (*P. sanguinale*). Many are vegetatively distributed by animals, for the joints of the stem will grow after passing through the alimentary canal.

2. *Andropogoneae.* Annual or perennial herbs frequently with tall stems, bearing linear, lanceolate or ovate leaves. Spikelets usually in pairs, rarely in threes or solitary; one of each pair

sessile, the other pedicelled, those of each pair often dissimilar. Spikelets two-flowered, with the lower flower male or barren, the upper hermaphrodite or female; falling entire at maturity. Glumes more or less rigid and firmer than the outer paleae, the lower always longer than the spikelets. Paleae membranous or hyaline, the upper having a geniculate awn arising from the two-lobed tip. Inner paleae shorter than the outer, frequently the outer or both suppressed. Lodicules usually two. Stamens three, rarely one or two.

There are about eighty genera included in this tribe, which are almost completely confined to tropical and warm temperate regions, where they form an important part of the savannah grasslands. A number are of economic importance. First in importance is the genus *Saccharum* with twelve species, including *S. officinarum* (Sugar Cane) (Fig. 2019), which may be a native of tropical eastern Asia, but has now become so widely cultivated that its origin is lost. There is an underground rhizome, from

FIG. 2019.—*Saccharum officinarum*. Sugar Cane. Photograph supplied by courtesy of the Imperial Institute.

which, year by year, there arise shoots which may grow up to 15 ft., with a thickness of 2 in. The inflorescence is a dense, woolly spike, the first and second glumes of each spikelet being covered with long hairs. Most of the cultivated forms are sterile and are usually propagated vegetatively by means of short pieces of the stem, each bearing a bud. Recently, however, a more vigorous series of races have been grown from seed. The sugar is contained in the soft tissues of the stem (see Volume IV under Economic Botany). Another very important genus is *Sorghum* (Fig. 2020) with fifteen tropical species, many of which have been cultivated as cereals under the names of Guinea Corn, Durra, Kafir Corn, Milo, Brown Corn and Sorgo. The genus *Cymbopogon* contains about sixty species which are characteristic of the savannahs of tropical Africa. Several yield essential aromatic oils such as Lemon Oil, Citronella Oil and Palma-rosa Oil which are used in soaps and in perfumery. Similar oils are also produced by some species of *Andropogon*, which includes about 180 cosmopolitan species. *A. odoratus* is the source of Ginger Oil. The two species of *Vetiveria* which occur in Indo-Malaya possess fragrant roots which are woven into baskets and mats, while the crushed roots are also used to scent water.

Fig. 2020.—*Sorghum vulgare* var. *durra*. Brown dhurra or Indian Millet. Plants with heads of fruits.

3. *Maydeae*. Annual or perennial herbs often with tall stems bearing linear or lanceolate leaves. Spikelets (Fig. 2021) unisexual, dissimilar and awnless. Sexes borne on separate inflorescences or on different parts of the same inflorescence with the male flowers above the female. Male spikelets consisting of two

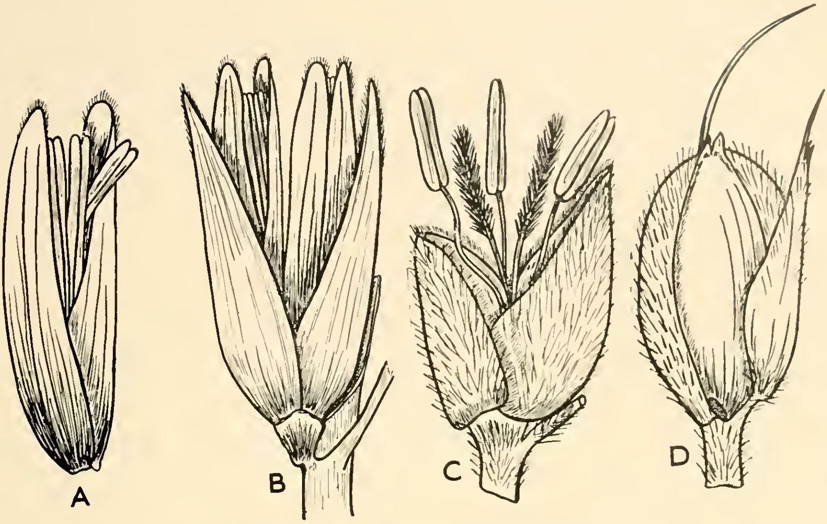


FIG. 2021.—*Zea.* A, Male flower. B, Male spikelet. *Sorghum.* C, Flower. D, Spikelet.

FIG. 2022.—*Zea mais.* Maize. Plant with terminal panicle or "tassel" of male flowers and axillary spike of female flowers still sheathed in its enclosing bracts.

flowers, mostly paired, one sessile, the other or both pedicellate; borne in solitary or panicled spike-like racemes. Glumes membranous to coriaceous, enclosing the flowers. Outer paleae hyaline. Stamens three. The female spikelets are two-flowered with lower flowers barren, solitary or paired, embedded in the hollows of a thickened, pointed rachis or enclosed in the thickened sheath or crowded in rows on a thickened rachis. Outer paleae hyaline.

The tribe contains eight genera which are tropical in origin. The most important genus is *Zea* with the single true species *Z. mais* (Fig. 2022) which is Maize or Indian Corn. Maize is an extremely important cereal, not only of the tropics but of temperate countries, and we shall reserve our discussion of it until Volume IV. The genus *Coix* contains six Indian and Chinese species, including *C. lachryma* (Job's Tears). The inflorescence has a broad, concave bract at the base, enclosing the single female flower. The upper flowers are male. The bract forms the hard covering of the fruit, which is pear-shaped. It has a grey, pearly lustre and is used for ornamentation. The genus is cultivated as food in Burma, and used in medicine in China.

Euchlaena mexicana, which is very similar to Maize, is used as a cereal in Central America, and as a fodder in warm countries, as is also *Chionachne cyathopoda*. This and the preceding tribe may be regarded as showing the highest degree of specialization of the spikelets and of the inflorescence exhibited by the Gramineae and according to Hubbard marks the climax in the evolution of the Panicoideae.

MICROSPERMAE

The Microspermae are monocotyledonous herbs in which the flowers are highly specialized with regard to insect-pollination. Many are saprophytic, while others live as epiphytes. The flowers are cyclic and are based upon a pentacyclic trimerous system; but there is often considerable reduction in the number of parts, especially of the androecium. The perianth is usually composed of two trimerous whorls, the outer whorl being petaloid. The ovary is inferior and composed of three carpels which may form a trilocular or unilocular structure bearing many ovules. The fruit is a capsule and the seeds are very minute with a thin membranous testa and a very small, few-celled embryo, sometimes with a scanty endosperm but often lacking any nutrient tissue and dependent upon an endotrophic fungus for its germination and development.

As here treated the order contains two families, the Burmanniaceae and the Orchidaceae, which are separated chiefly by the fact that in the former the flowers are actinomorphic and the seeds possess endosperm, while in the latter the flowers are zygomorphic and the seed contains no endosperm. Hutchinson separates the families into two distinct orders and splits the Burmanniaceae as defined by Pax into three families. We shall not consider the family in detail here but will mention a few of its more striking features.

The **Burmanniaceae** are a small group of annual or perennial herbs, chiefly saprophytic, which occur in tropical forests. There are about twenty genera described which contain under 100 species (Fig. 2023). The largest genus is *Burmannia* with about twenty species. A few are green herbs inhabiting damp sandy places, but the majority are leafless saprophytes growing on humus on the forest floor. They are usually red, yellow or white in colour, with scale-like leaves, and the stem ends in a raceme or a one-sided cyme. The flowers are actinomorphic and the perianth cup-shaped with all segments alike. A few are zygomorphic due to a great development of the median outer perianth segment. There are usually two whorls of three stamens and the ovary is surmounted by a trifid style. The fruit is a capsule which may split in various ways, sometimes apically. The genus *Thismia* contains about fifteen species which are saprophytes in the tropical forests of South America, Indo-Malaya and Africa (Fig. 2024). The plants are among the most remarkable in the world in appearance as the figure will indicate.

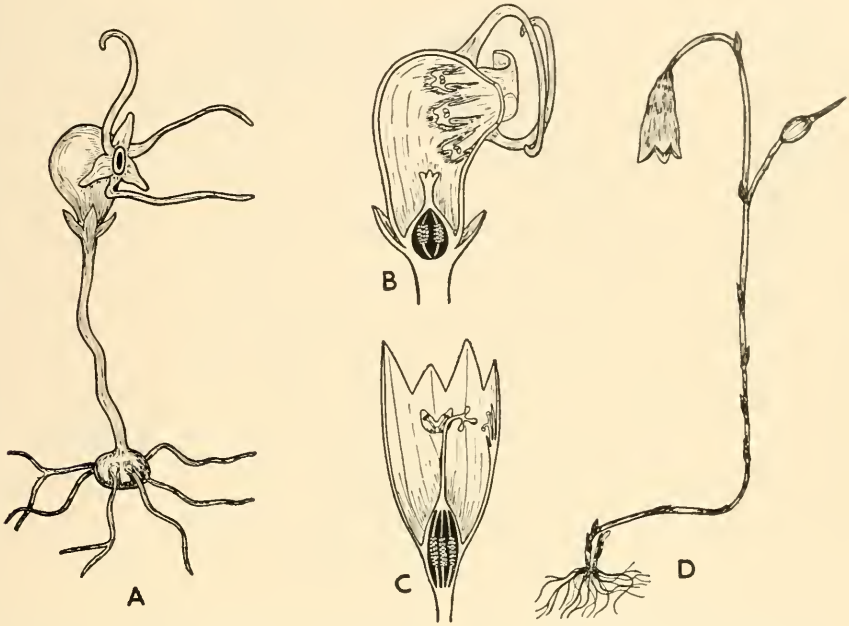


Fig. 2023.—Burmanniaceae. A, *Thismia macabensis*. Flowering plant. B, Flower in section. *Apteria setacea*. C, Flower in section. D, Flowering plant. (*After Engler.*)

It is generally considered that their wide distribution indicates that the family, despite the high degree of specialization, is of ancient origin. The chief centres of distribution are Brazil and Malaya.

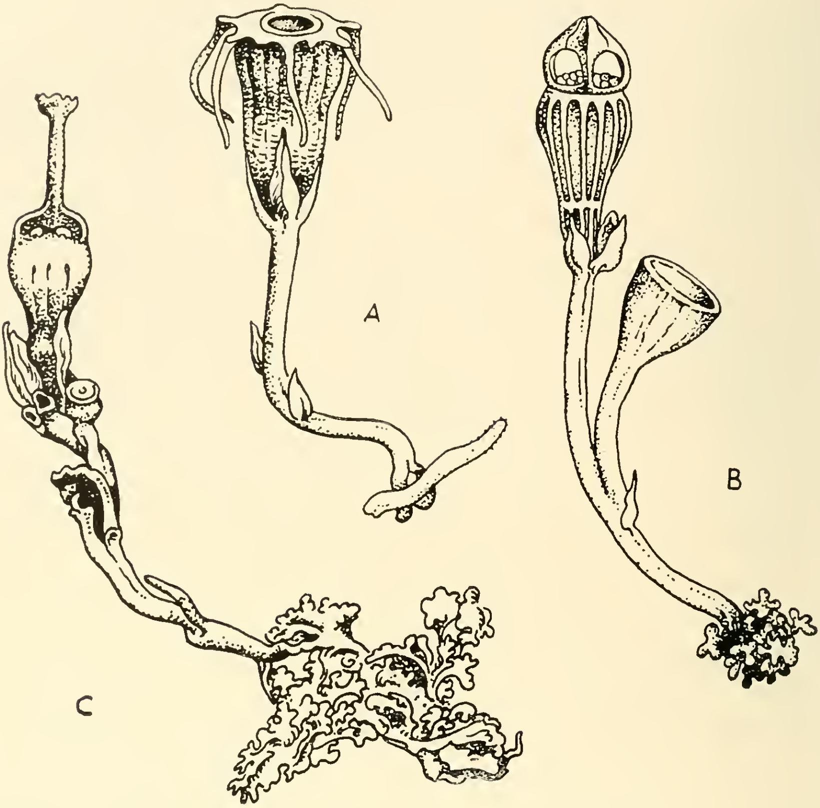


FIG. 2024.—*Thismia aseroe*. A, Flowering shoot arising from the rhizome. *Bagnisia episcopalis*. B, Flowering plant. C, Plant in fruit, showing the lobed underground rhizome. (From " Flora Malesiana ".)

Orchidaceae

The Orchidaceae are a very large family of remarkable plants, indeed it is the largest family of the Angiospermae with about 7,500 species. Some are typical herbaceous land plants, many are epiphytes, while others are saprophytes. Those which live as epiphytes, as well as some of the land forms, are adapted to xerophytic conditions and store up water in thickened leaves, swollen internodes, pseudo-bulbs or in aerial roots.

Epiphytic orchids are very common in the tropics where they develop long aerial roots for the absorption of water while other roots serve as anchorage organs and for the intake of mineral nutrients. The orchids of temperate countries are nearly all terrestrial.

A number of species occur in Britain and while a few are common and widely distributed, many are extremely local in distribution and are only rarely met with. Among the common species we may mention the Early Purple Orchid (*Orchis mascula*) (Fig. 2025), Spotted Orchid (*O. fuchsii*), Marsh Orchid (*O. praetermissa*), Green-winged Orchid (*O. morio*) and Pyramidal Orchid (*Anacamptis pyramidalis*). Several have flowers which bear a superficial resemblance to animals and are called after them. Bee Orchid (*Ophrys apifera*), Butterfly Orchid (*Platanthera bifolia*), Frog Orchid (*Coeloglossum viride*), Fly Orchid (*Ophrys insectifera*) and Spider Orchid (*Ophrys sphegodes*). Several saprophytic orchids also occur in Britain, Bird's-nest Orchid (*Neottia nidus-avis*) and Coral Root (*Corallorhiza trifida*) being the best known. Finally, we may mention Tway-blade (*Listera ovata*), Lady's Tresses Orchid (*Spiranthes spiralis*), White Helleborine (*Cephalanthera damasonium*) and the Lady's Slipper (*Cypripedium calceolus*), found only in Yorkshire and Durham.

FIG. 2025.—*Orchis mascula.* Early Purple Orchid. Inflorescence.

The **plants** are always herbaceous with sympodial stems bearing simple leaves, which may be fleshy. In saprophytic forms the leaves are often reduced to scales. The rootstock may be a rhizome or may consist of tuberous roots, which are sometimes formed into compound structures.

The **inflorescence** is generally racemose and may be a spike, a raceme or a panicle. Occasionally the flowers are solitary.

The **flowers** are often of very beautiful form and colour but occasionally small, colourless or brown and inconspicuous. They are either hermaphrodite or unisexual, always zygomorphic and they show many elaborate modifications of form in relation to special insect visitors; in fact the floral parts are so modified that many of them receive special names (Fig. 2026).

The **perianth** is epigynous, composed of six segments arranged in two whorls of three parts. The outer is calyx-like while the inner forms a corolla; or, in some instances, the outer whorl takes the form of a corolla while the inner may be reduced to a minute size. The segments may be free from one another or may be united in each whorl. Those of the outer whorl are usually imbricated and the median segments of each whorl are different in size, shape and often in colour from the lateral ones, especially that of the inner whorl, which is often much enlarged and modified to form the lip or **labellum.**

FIG. 2026.—Floral diagram of *Orchis mascula.* There is one functional stamen in the outer whorl and two staminodes in the inner whorl. The positions of the missing stamens are indicated by crosses. The flower is represented in its correct morphological relation to the axis, *i.e.*, before resupination. (*After Eichler.*)

The whole perianth (Fig. 2027) is usually twisted through 180° as a result of a torsion produced by the ovary, so that the labellum is placed in the anterior abaxial position. This is called **resupination**. Moreover, the labellum or more rarely the odd sepal may be prolonged backwards into a spur or a sac which may either collect nectar or itself function as a nectar-secreting tissue.

The **androecium** is composed of two trimerous whorls of stamens, which are never all present. There is usually either one or two stamens, united to each other and to an extension of the gynoecium, which together form the **column** (Fig. 2028). The anther or anthers are bilocular and open introrsely by a longitudinal slit. The pollen is granular and generally bound up by elastic threads of viscin into two mealy or waxy masses called **pollinia**. At the lower end the viscin is extended into a columnar organ, the **caudicle**.

The **gynoecium** is composed of three carpels. The ovary is inferior with three parietal placentas and one loculus or very rarely trilocular with axile placentation. The stigma is generally much modified. In *Cypripedium* all three lobes are functional but more often the posterior two only are functional, while the third is sterile and transformed into a small pocket called the **rostellum**, which lies between the anther and the functional stigmas. A portion of the rostellum is modified into a viscid disc, the **viscidium**, to which the caudicles are attached. The ovules are numerous and anatropous, and are exceedingly small.

The **fruit** is a capsule which usually opens by from three to six longitudinal slits.

The **seeds** are very numerous and of microscopic size. They are often elongated at each end or rarely possess wings and the testa itself is extremely thin. At the time of shedding the embryo is undifferentiated, composed only of a few cells and lies freely in the testa, there being no endosperm present.

The family is a large one containing at least 450 genera. They are world

Fig. 2027.—*Orchis mascula.* Flower in profile, showing the twisted ovary, the long spur, the labellum in the anterior position and the stamen under the hood of the two posterior petals. One sepal has been removed.

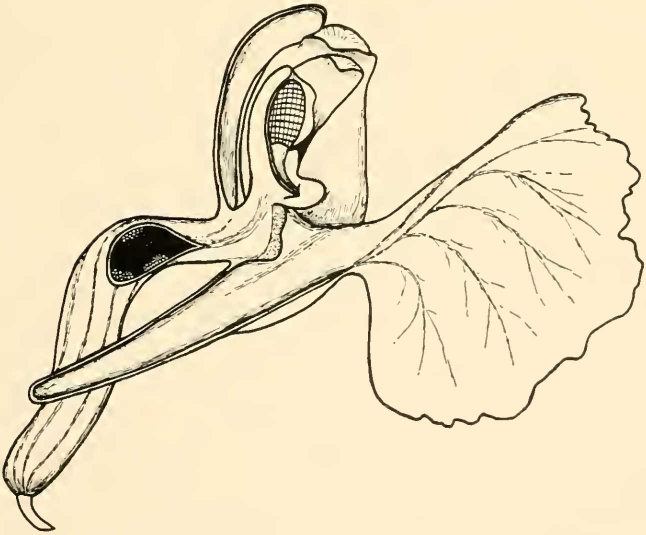


Fig. 2028.—*Orchis mascula.* Flower in vertical section. Above the entrance to the spur stands the stigma (dotted). Above this projects the rostellum and above this is the stamen in section, containing a pollinium, the caudicle from which runs down into the rostellum, the whole forming the " column ". The top of the ovary is cut open obliquely and shows the three parietal placentae with numerous small ovules.

wide in distribution, most common in the tropics and rare in Arctic regions. Those occurring in the tropics are mostly epiphytic while the temperate species are mainly terrestrial.

The Orchid plant may be constructed in several ways. It may be based upon a monopodial construction in which the main axis continues to grow year by year and produces flowers only on lateral branches. Alternatively it may be based upon a sympodial system in which the main axis is composed of annual portions of successive axes, each of which begins with scale leaves and terminates with an inflorescence; alternatively the inflorescences may be produced on lateral axes and the shoot for the current year continues the main axis, stopping short at the end of its growing period, but does not form an inflorescence.

The terrestrial orchids are all sympodial and usually possess a short rhizome, each annual shoot bending up into the leafy branch of the current year. Many form storage organs to tide them over the dormant period of the year. In the majority this takes the form of a thickened internode of the stem, called a **pseudo-bulb**. In many the bud for the next year's growth is laid down at the base of the stem and from it is developed a thick, fleshy, adventitious root which develops into a tuber which provides a food reserve.

The epiphytic orchids are either sympodial or more rarely monopodial. The roots of these orchids consist firstly of clinging roots which are insensitive to gravity but are negatively phototropic. Secondly, there are absorptive roots which may develop between the plant and its support. Such roots may accumulate humus around them and these probably supply nutrient material from the humus which they collect. Thirdly, there are the true aerial roots which hang down in the moist air and are absorptive in function, due to the development of a superficial tissue, the **velamen**, which acts as a sponge and readily absorbs water. The inner tissues are green and apparently form additional photosynthetic tissue. It should be realized that in the tropics the great majority of orchids drop their leaves in the dry season so that under these conditions the aerial roots form the only remaining assimilating tissue. Certain epiphytic orchids which are not provided with pseudo-bulbs persist by the aid of fleshy green leaves. In other respects the vegetative anatomy of the Orchidaceae provides no points of peculiar interest, but reference must be made to the nutrition of the seedling. It has already been pointed out that the seeds are microscopically small, that the embryo (Fig. 2029) at the time of shedding is scarcely developed and that little or no endosperm is present. Under such circumstances it would be virtually impossible for the embryo to survive. In fact, in the absence of the suitable endotrophic fungus it can be shown that death almost inevitably ensues. In the presence of the fungus, however, nutrition is provided for the embryo and its development is made possible. We need not consider here the structural and physiological details for these will be discussed in detail in Volume IV. Nor need we here consider the metabolism of the saprophytic species for here again the problem receives adequate treatment elsewhere. It is, however, important to remember these matters in assessing the high degree of specialization exhibited by the group. When we have described, as we shall do below, the remarkable pollination mechanisms evolved (see also p. 1341), it becomes increasingly clear that the Orchids must be looked on as not only a highly specialized group of plants but as the highest expression of the evolution of the Monocotyledons.

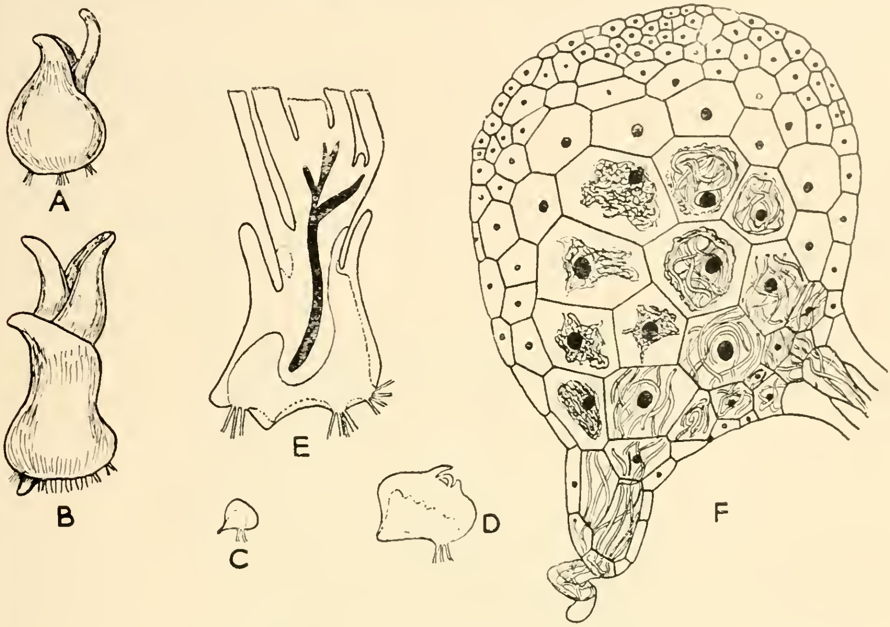


FIG. 2029.—Orchid seedlings. A and B, Development of the first leaves from the tuberous protocorm. C and D, Young protocorms about natural size. E, Section of an older seedling with established plumular growth. Vascular tissue in black. In the above the areas of mycorrhizal infection are indicated by dotted lines. F, Section of a protocorm embryo showing the entry and degeneration of the mycorrhizal fungus. Below is the remains of the embryonal suspensor. On the right, three rhizoidal hairs. (*After* Bernard.)

The classification of the Orchidaceae presents many difficulties, not least being the fact that many species and even genera are very incompletely known. As more facts are gathered the scheme of classification has become modified until taxonomists are increasingly reluctant to formulate any complete scheme. It is not without significance that Hutchinson, though he has subjected the classification of all other families of the Angiosperms to close scrutiny and has made many alterations, asserts that without a lifelong study of this family it would be unwise for him to express any views.

The scheme adopted here is that published by Schlechter in 1926 and is the latest attempt to arrange the tribes in a reasonable classification.

I. Diandrae

There are two stamens representing the two lateral ones of the inner whorl, the third is represented by a large staminode placed posterior to the anthers and more or less covering the stigma. All three stigma lobes are functional, the pollen is granular and not united into masses or distinct pollinia. This group therefore represents those members in which the normal monocotyledonous flower is least modified.

1. *Cypripedieae.* Flowers with well-marked median symmetry and two fertile stamens, the anterior stamen forming a large staminode. The ovary is unilocular or trilocular.

Included in this tribe is the single genus *Cypripedium* (Fig. 2030) containing about thirty species, which by some are separated into several genera. The plants are widely distributed in north temperate zones and in the tropics of Asia and America. The South American species, in which the ovary is trilocular, are often separated into the genus *Selenipedium.* The only British representative is *C. calceolus*, the Lady's Slipper Orchid, now limited in this country to the woods around Durham and north Yorkshire. The so-called slipper is made up of the labellum which plays an important part in the pollination mechanism. In this species (Fig. 2031), the labellum is yellow in colour while the rest of the flower is purple. This colour together with the scent of the nectar attracts small bees, which creep into the inflated labellum, and find there juicy hairs which may secrete nectar. There are three openings which serve as entrances to the cavity of the labellum; two lateral ones, on either side of the column, and a median large opening in front of it. Insects invariably choose this latter entrance.

FIG. 2030.—*Cypripedium* flower. A cultivated variety.

After having eaten the nectar they try to get out again the same way but the walls are strongly arched and they cannot get out that way. Instead they squeeze their way through one of the lateral openings after having crept under the stigma. In doing so they brush one side or other of their body against the soft, viscid anther which forms the side of the lateral opening. When they visit a second flower this pollen is brushed off on the stigma as they creep under it and cross-pollination is ensured. Once again they become smeared with fresh pollen as they creep out of the prison.

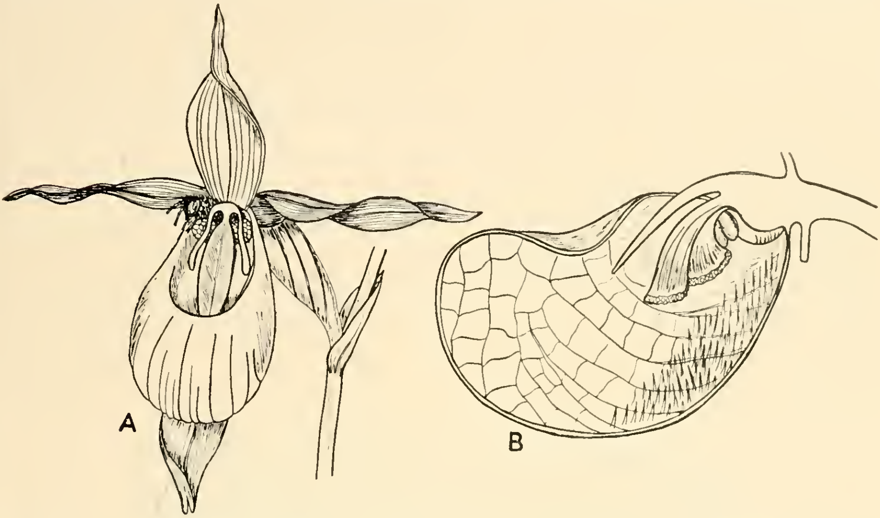


FIG. 2031.—*Cypripedium calceolus.* Lady's Slipper. A, Flower. B, Labellum pouch in section, showing the stigmas in receptive position. In A a bee is shown escaping from a lateral opening of the pouch and pushing past the laterally placed anthers. (*After Kerner and Oliver.*)

Many species of *Cypripedium* are cultivated and a number of extremely beautiful hybrid forms have been produced by orchid-growers.

II. Monandrae

Stamen solitary, representing the abaxial member of the outer whorl. This abaxial member is actually seen in the adaxial position owing to the twisting or resupination of the ovary through 180°. The lateral stamens are completely abortive or are represented only by small staminodes, which are considered to belong to the inner whorl. The pollen united in masses or in pollinia. The two lateral stigmatic lobes are functional, the median, anterior one extending back into a small rostellum placed below and in front of the anther lobes and bearing the viscidia to which the caudicles are attached.

A. Basitonae

Caudicle arising from the base of the pollinium. Anthers erect, or more or less resupinate, very closely adnate to the broad-based column. Never deciduous after flowering. Pollinia always granular.

1. *Ophrydoideae.* Anthers erect. Pollen powdery or granular.

Included in this tribe are the north temperate *Habenaria*, *Platanthera*, *Orchis*, *Aceras*, *Ophrys*, *Herminium* and some forty more, mostly widely distributed.

The genus *Habenaria* contains about 400 species which occur in tropical and temperate regions. Many are highly decorative and have been cultivated in greenhouses. At one time this genus included several British species which were among our most beautiful and remarkable of orchids. Recently these species have been referred to other genera, for the original genus *Habenaria* has now been split up into a number of smaller genera. Among these British species may be mentioned *Leucorchis albida* (*Habenaria albida*), the Small White Habenaria; *Coeloglossum viride* (*H. viridis*), the Frog Orchid; *Platanthera bifolia* (*H. bifolia*), the Butterfly Orchid; *P. chlorantha* (*H. chlorantha*), Large Butterfly Orchid; and *Gymnadenia conopsea* (*H. conopsea*), the Scented Orchid. As will be realized from the English names these orchids are of remarkable form, often with long, narrow perianth segments which together with the essential organs superficially resemble

FIG. 2032.—*Platanthera bifolia.* Butterfly Orchid. Inflorescence.

the animals after which they are named, a resemblance which may be more than merely accidental. We may instance the case of *Platanthera bifolia* which is pollinated by moths (Fig. 2032). The flowers exhale a scent resembling that of a pink and it is particularly strong at night. The spur is long and thin and half-filled with nectar (Fig. 2033), hence it can only be reached by the proboscis of a moth. In probing the flower the pollinia become attached to the head of the insect on either side of the proboscis. As they are withdrawn they turn inwards and downwards by the contraction of the caudicles and cling to the base of the proboscis. When another flower is visited therefore the pollinia come into contact with the stigma and then they burst.

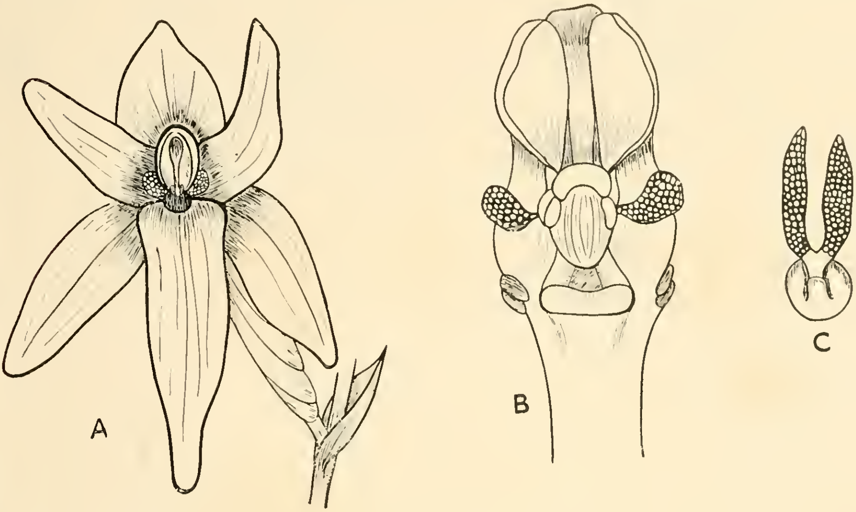


Fig. 2033.—*Platanthera bifolia*. A, Flower showing the column. B, The column. Above, the two half-anthers below which is the rostellum, flanked by two glandular staminodes. Beneath this is the stigma. C, The two pollinia with a common caudicle ending in a retinaculum pad. (*After Knuth.*)

Platanthera chlorantha (Fig. 2034) (the Large Butterfly Orchid) differs considerably from the last in its pollination mechanism. The flowers are strongly fragrant and are greenish-white in colour. The spur is very long, sometimes over 4 cm. in length. The caudicles end in two viscid discs or retinacula, which are not covered by a rostellum. Two small pedicels arise from the backs of the retinacula, to which the caudicles are attached at right angles, the pollinia lying almost horizontally. The retinacula stand in front of the stigmas and attach themselves to the insect's eyes. Then the pedicels rotate so as to lower the pollinia to a position in which they will strike the stigmas in the next flower visited. Darwin suggests that it may be advantageous for the pollinia to become attached to the eyes because adhesion to the hairy parts of the insect's body would be less efficient and the movements of the pollinia, after they became attached, would be less precise if they were adhering to the hairy surface of the body.

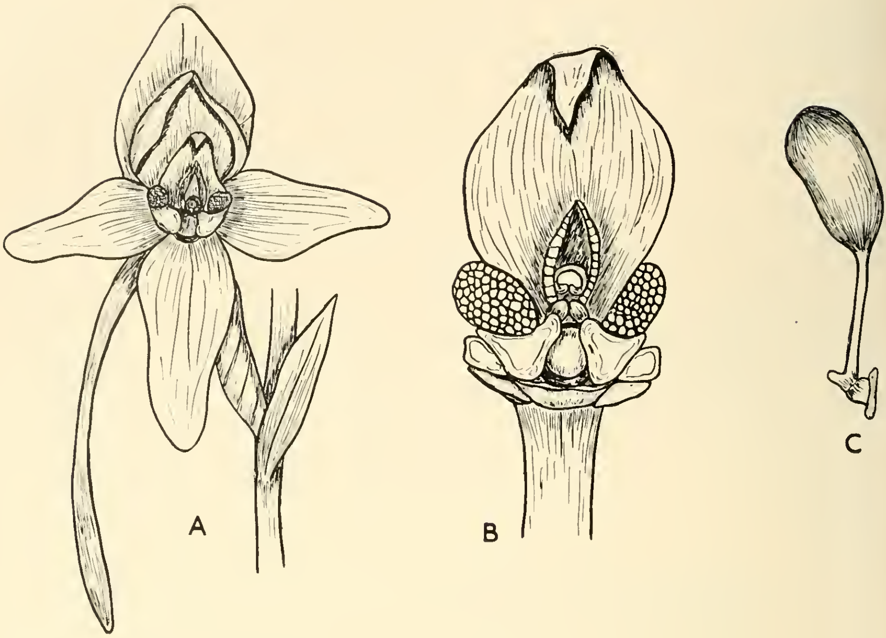


FIG. 2034.—*Platanthera chlorantha.* A, Flower. B, Column showing the two triangular retinacula which attach themselves to the eyes of the insect. C, Pollinium with caudicle and retinaculum. See in text. (A *after Sowerby.* B and C *after Knuth.*)

The genus *Orchis* itself has a relatively large number of British species. Compared, however, with many of the tropical genera it is small, for it contains only about seventy species. They are distributed throughout the northern hemisphere in temperate regions, a dozen of them being found in Britain (see above). The species of this genus are perennials and form one tuber each year. The flowers are produced in dense spikes and the leaves of some species are spotted with brown and purple.

As is usual in the family, the flowers are adapted to insect visits and have received considerable attention in this respect. Darwin in his book on "The Fertilization of Orchids" devotes considerable space to the genus, and students are referred to this book for a more detailed account of the floral structure than can be given here. For our present purpose we may cite one example.

In *Orchis mascula* (Fig. 2035) the flowers are somewhat larger than those of other species and the labellum provides a good alighting place for an insect. The pouch-shaped rostellum projects above the entrance to the nectary so that an insect probing for nectar must inevitably touch it. In so doing it ruptures the membrane of the rostellum and depresses it. This uncovers the retinacula so that one or both the pollinia become implanted on its head. It should be noted (as can be easily ascertained by inserting a pencil in a flower) that the mucilage hardens very rapidly, so that almost as soon as the pollinia have been brought out of the flower they cannot easily be detached from the pencil. As they dry they bend forwards and downwards so that they will impinge on the stigmatic surface of the next flower that the insect visits. Moreover it can be shown that the pollen masses of which the pollinia are composed are attached strongly to one another by a viscid substance so that only a small number are actually detached on the stigmatic surface. In fact many stigmas can be pollinated by the same pollinium as the insect passes from flower to flower.

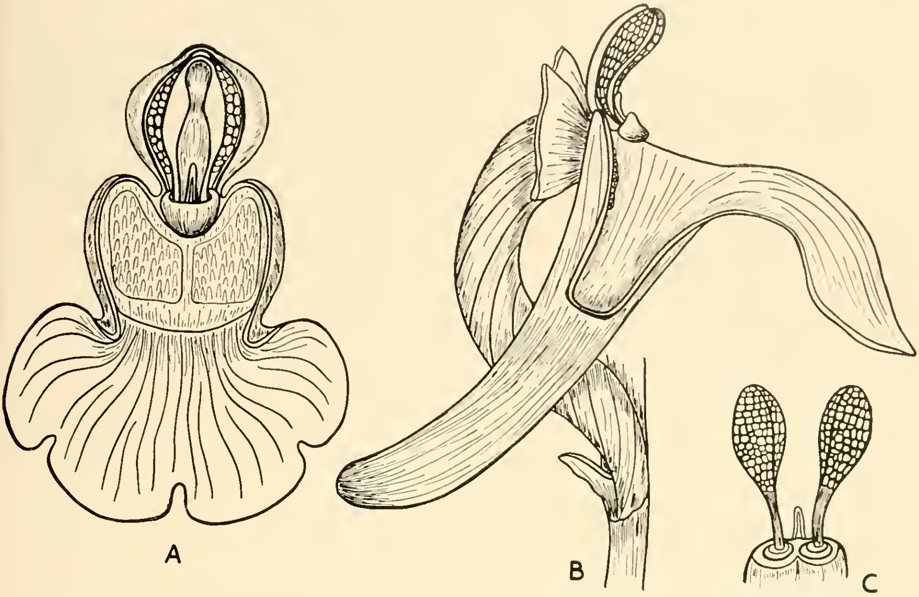


FIG. 2035.—*Orchis mascula.* A, Labellum and column in face view. B, Flower in section showing the caudicles of the pollinia covered by the prominent rostellum which stands over the entrance to the spur. C, Two pollinia attached by their retinacula to the head of an insect. (*After Darwin.*)

The genus *Ophrys* includes some thirty species with a wide geographical distribution in temperate climates. In Britain we have *O. apifera* (Bee Orchid), *O. insectifera* (Fly Orchid) and *O. sphegodes* (Early Spider Orchid). They are terrestrial species whose floral structure is more or less similar to that of *Orchis*, except that there is no spur. In *O. apifera* (Fig. 2036) we have one of the few examples of an orchid which can be self-pollinated, for if the pollinia are not removed by a visiting insect they drop out of the anthers and dangle on their long caudicles in front of the stigma against which they are almost certain to be blown or knocked.

Anacamptis (*A. pyramidalis* in Britain) is another genus closely related to *Orchis*. The flowers are fragrant and nectar is formed at the end of a long spur. There are two round stigmatic surfaces, one at each side of the rostellum. The adhesive foot of the caudicles is saddle-shaped and fits over the proboscis of a visiting insect, to which it and the attached pollinia adhere. As the caudicles dry they bend forward at right angles so that the

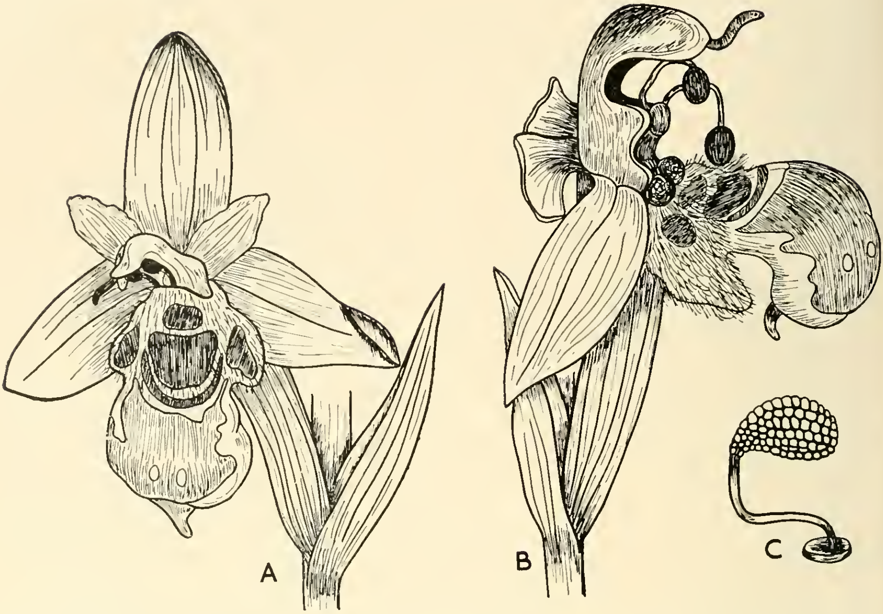


Fig. 2036.—*Ophrys apifera.* A, Flower. B, Pollinia dangling on the elongated caudicles. C, Pollinium with caudicle and retinaculum. (A *after Sowerby.* B *after Darwin.*)

pollinia impinge on the stigmatic surfaces of the next flower visited (Fig. 2037).

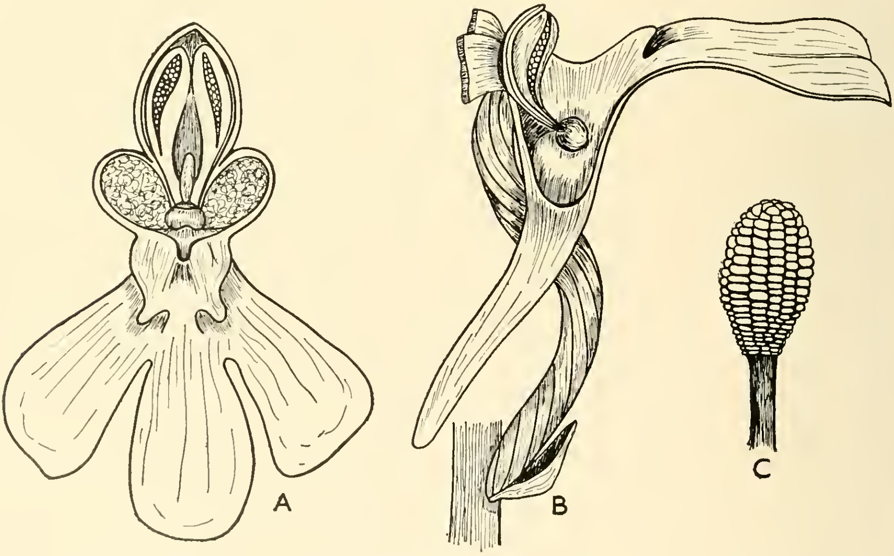


Fig. 2037.—*Anacamptis pyramidalis.* A, Labellum and column in face view, showing the two lateral stigmas and the saddle-shaped rostellum at the base of the anther. B, Flower in section (compare B in Fig. 2035). C, Pollinium and caudicle. (*After Darwin.*)

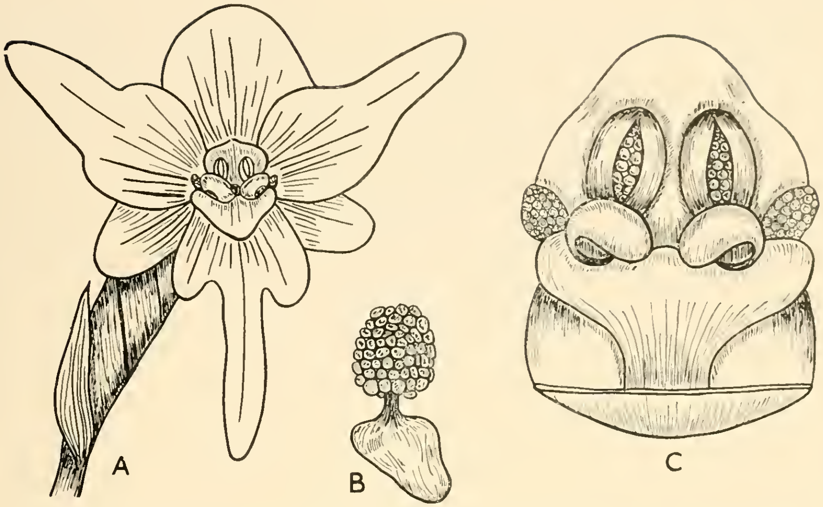


FIG. 2038.—*Herminium monorchis*. A, Flower. B, Pollinium with retinaculum. C, Column showing pollinia in the anther lobes, the large retinacula and the lateral staminodes. (A *after Sowerby*. B and C *after Knuth*.)

Finally, we may refer to the genus *Herminium*. There are eight species in Europe and Asia, of which one, *H. monorchis* (Fig. 2038) (Musk Orchid), is found in Britain. The flowers of this species are small and yellowish-green in colour, with a strong scent of nectar, and are adapted for pollination by very small flies (see p. 1350).

The genus *Aceras* has only one species, *A. anthropophorum* (Man Orchid) (Fig. 2039) which is widely distributed in Europe, especially in the Mediterranean region. It is found locally on the Chalk in Britain.

FIG. 2039.—*Aceras anthropophorum*. Man Orchid. Inflorescence. Box Hill, Surrey.

B. **Acrotonae**

Caudicle arising from the apex of the pollinium. The anthers erect or incumbent, filaments short, slender and generally closely joined to the column, usually deciduous, but if persisting they soon wither.

1. *Polychondreae.* Pollen granular and soft; anthers mostly persistent; inflorescence always terminal.

In this tribe are a large number of genera including the following: *Epipactis*, *Cephalanthera*, *Spiranthes*, *Listera*, *Neottia*, *Goodyera* and *Vanilla*. With the exception of *Vanilla* all these genera are represented in the British Flora. *Vanilla* is a small tropical genus with about thirty species. They are climbers with fleshy leaves. The only important species is *V. planifolia*, which is widely cultivated for its capsules, from which the spice Vanilla is prepared.

The genus *Epipactis* contains ten north temperate species, two of which, *E. helleborine* (Broad Helleborine) and *E. palustris* (Marsh Helleborine), are common in Britain. *Epipactis helleborine* is pollinated by wasps. The flowers are borne horizontally and the outer part of the labellum forms a platform for the insect visitor, the inner part forming a cup containing nectar. The lower part of the stigma is bilobed, with a small, almost globular rostellum projecting above it. It is covered with a viscid cap which can be easily lifted off by pressure from inside and below. The anthers dehisce longitudinally before the flower opens so that the two sessile pollinia are exposed. Their pollen grains are united into small packets by elastic threads, which are joined to cords fastened to the posterior lobes of the cap covering the rostellum. When an insect visits the flower it alights on the front part of the labellum and crawls into the flower. It is prevented from touching the pollinia by the rostellum. As the insect creeps out it lifts the rostellum cap and comes into contact with and removes the pollinia on its head or back. When it visits another flower these pollinia will already be in a position suitable to touch the stigmatic surfaces as the insect enters the flower.

The genus *Cephalanthera* contains ten species, three of which are found in Britain. The flowers are characterized by the complete absence of a rostellum, the pollen germinating *in situ* and fertilizing its own stigma. This is well seen in *C. damasonium* (Fig. 2040) (White Helleborine) in which the pollen is loose and friable, the grains being almost entirely separated from one another with only a very few threads uniting them here and there (Fig. 2041). The anthers dehisce before the flowers open and the pollinia fall on to the upper margin of the stigma which lies below them. In this way automatic self-pollination inevitably takes place. Cross-pollination by means of insects is, however, possible. The labellum is vertical and closes the flower but the anterior part folds down and serves as a platform and the visiting insect scatters the pollen broadcast into the upright flowers. In so doing, it will itself receive a liberal share and when it subsequently visits another flower it may shake off some of this pollen on to the stigma.

FIG. 2040.—*Cephalanthera damasonium.* Inflorescence.

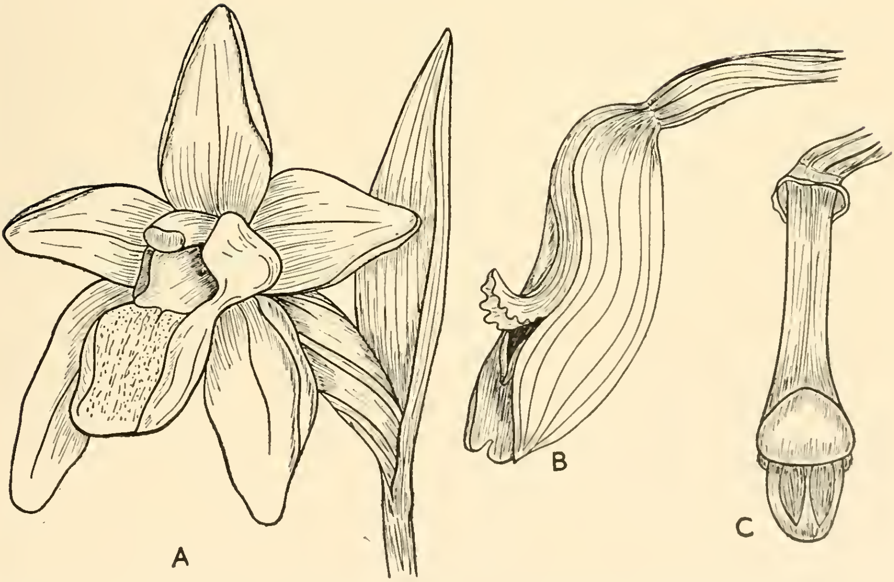


FIG. 2041.—*Cephalanthera damasonium.* A, Flower, artificially expanded to show structure. B, Flower at pollination with only the tip of labellum turned outwards. C, Column with open anther lobes exposing the friable pollen. There is no rostellum and the large stigma partly hides the anther. (B and C in the figure are upside down.) (A *after Sowerby.* B and C *after Darwin.*)

After pollination has taken place the terminal lobe of the labellum becomes erect and once again closes up the flower. The British species of *Cephalanthera* are found chiefly in woods, especially beech woods.

Turning to the next genus in this group, *Listera*, we have two British species. *L. ovata* (Fig. 2042) (Tway-blade) is one of the commoner British orchids found not infrequently in woods. It is not very noticeable, for the flowers are greenish-yellow. The stalk bears only a single pair of rather large ovate leaves. The flowers (Fig. 2043) are rather small; the labellum is forked and the rostellum contains a viscid fluid which is expelled at the slightest touch. This fluid comes into contact with the ends of the pollinia, which when set free from the anthers lie on the concave back of the rostellum. The effect of an insect visit is to bring away one or both pollinia in the viscid drop, which sets hard in a few seconds. Nectar is secreted in a narrow furrow along the upper half of the lip and this is sought after by small crawling insects. As they crawl further in they find themselves under the overhanging crest of the rostellum and should they raise their heads or in any way touch this crest, the explosion of the liquid follows and thereafter the pollinia are cemented firmly on their heads. As the insect flies away the pollinia are withdrawn and when another flower is visited the pollen will be liberally scattered on the stigma. Some twenty species of the genus are recognized, which are widely distributed in north temperate regions. *Listera cordata* is similar but smaller and more northerly in distribution.

FIG. 2042.—*Listera ovata*. Flowering plant.

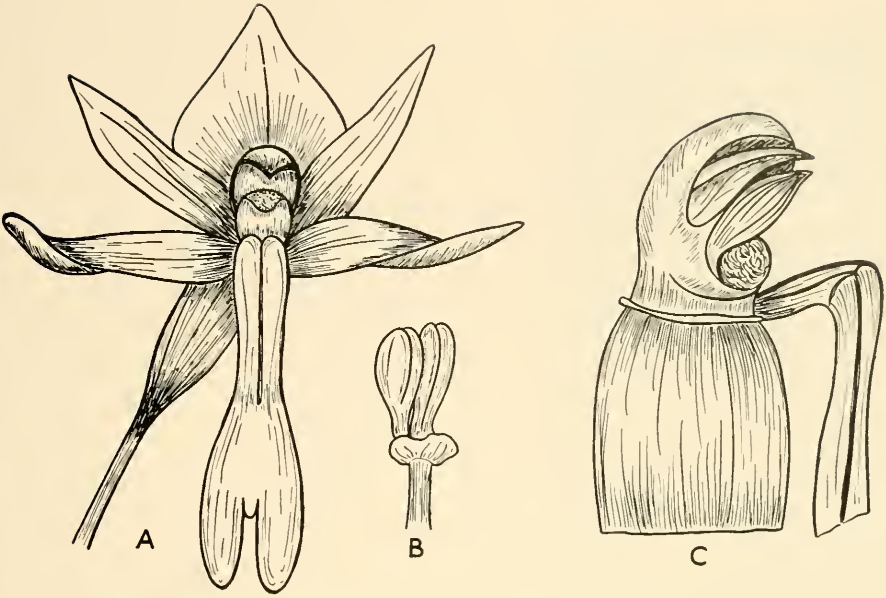


FIG. 2043.—*Listera ovata.* Tway-blade. A, Flower. B, Pollinia. C, Top of ovary with part of the labellum, showing stigma (hatched) above which is the long rostellum; above this the anther lies almost horizontally. (*After Knuth.*)

The next genus we may consider briefly is *Spiranthes* of which some fifty species are recognized. Some are found in Britain, of which *S. spiralis* (Fig. 2044) (Lady's Tresses) is the best known. It is a small plant with a tuberous root from which arise a group of radical leaves and a spirally twisted inflorescence of pale, sweet-scented flowers. *S. romanzoffiana* may be mentioned because of its curious geographical distribution. It is a native of both North America and of Kamchatka, but is also found wild in Ireland, and in the islands of Colonsay and Coll in the Hebrides. It occurs nowhere else in Europe.

Darwin studied the pollination mechanism in this genus. In *S. spiralis* (Fig. 2045) the small, whitish, horizontal flowers possess the scent of hyacinths, which is attractive to insects, and they alight on the reflexed part of the labellum. In the lower part of this structure are two globular nectaries, the nectar from which accumulates in a small receptacle situated below them. The rostellum forms a long, thin, narrow process which is united to the stigmas by two divergent shoulders. The central part of the posterior side of the rostellum forms a receptacle for mucilage. Slight contact causes a longitudinal slit to open in the anterior wall of this receptacle, which gradually extends to the back of the rostellum and exposes the cavity of the anther. Each loculus contains two very crumbly pollinia which are separated above but are united in the middle by elastic threads. The upper part of the anther, pressed against the back of the rostellum, dehisces before the flower opens and the pollinia thus come into contact with the

FIG. 2044.—*Spiranthes spiralis.* Lady's Tresses. Inflorescence enlarged × 2. Plant growing in the lawn outside University College, Cardiff.

back of the mucilage receptacle. The oblique surfaces of the stigma project below the rostellum.

Darwin observed that the flowers were visited by humble bees. The mucilage receptacles with their adherent pollinia cling to their probosces so that eventually only the lateral parts of the rostellum are left. After the flower has been open for a day or two the labellum moves away from the rostellum thus widening the approach to the stigmas. When this has happened a bee with pollinia on it entering the flower will cause pollination to take place. Since this time-interval must elapse before pollination can occur it follows that the pollinia concerned are more likely to be derived from a different plant than from the flowers of the same inflorescence.

The genus *Goodyera* contains about forty species distributed mainly in North America. Species also occur in tropical Asia, in New Caledonia and the Mascarenes. One species, *G. repens*, is found in Britain. Darwin studied the pollination (Fig. 2046) mechanism and found that it was worked by humble bees. The flowers are small and white but only feebly fragrant. The rostellum is square and shieldlike and projects beyond the stigma. On being lightly pressed mucilage is exuded from the projecting surface which is easily displaced upwards. In this process it carries with it a membranous strip to the posterior end of which the pollinia adhere. The anther lobes dehisce while the flower is still in the bud and the pollinia cling with their anterior sides to the back of the rostellum. In this way they are completely exposed. The posterior part of the labellum contains nectar while the anterior part serves as a platform, but owing to the narrowness of the entrance only the proboscis of the insect can be inserted and in search for the nectar it is almost certain to strike against and remove the pollinia. In older flowers the labellum moves away from

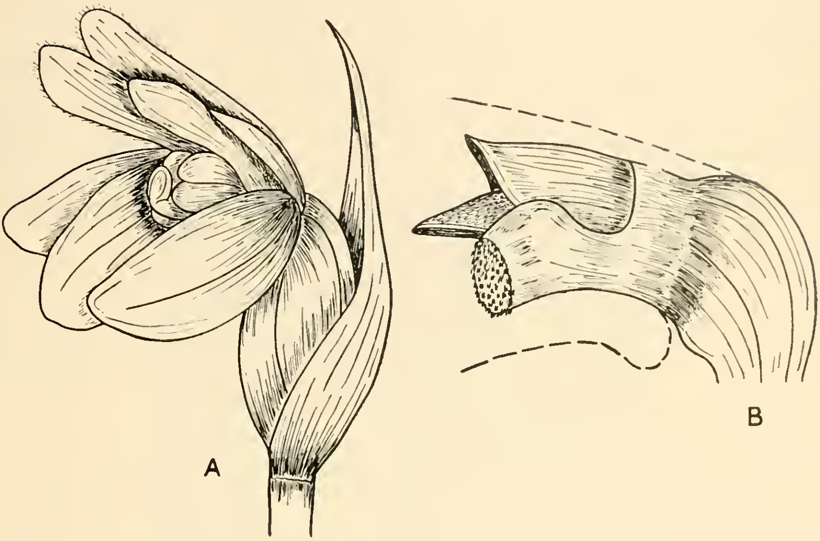


FIG. 2045.—*Spiranthes spiralis.* A, Flower. B, Column, after removal of the perianth. Below, the circular stigma, above which is the pointed rostellum and the closely attached anther. (A *after Sowerby.* B *after Darwin.*)

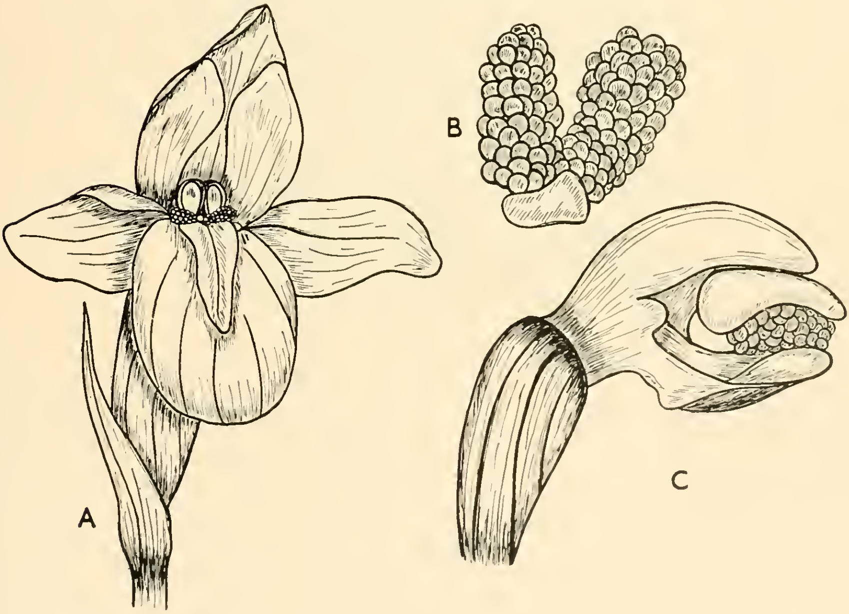


FIG. 2046.—*Goodyera repens.* A, Flower. B, Pollinia. C, Column showing pollinia attached to the back of the rostellum, beneath which is the stigma. (A *after Sowerby.* B and C *after Knuth.*)

the column so that the pollinia carried by an insect may be brought into contact with the stigma.

Our final example of this group is the curious genus *Neottia*. There are only three species in Europe and Asia but one, *N. nidus-avis* (Fig. 2047) (Bird's-nest Orchid), occurs in Britain. It is a leafless saprophyte whose rhizome gives off a large number of branches and roots which become grouped together to form a solid mass resembling an underground bird's nest. It lives by means of a mycorrhizal fungus, upon the humus in the woods, especially in beech woods. Although originally the adventitious roots possess a typical root apex with a root cap, it is stated that at times they may lose the cap and function as stems, producing aerial shoots. The flower (Fig. 2048) spikes are long and the flowers are brownish-yellow in colour. The pollination mechanism is similar to that in *Listera* but the nectar is concealed in the labellum, which forms a shallow bowl, and it is therefore not so exposed as in the Tway-blade. Furthermore the pollinia adhere less firmly. If insects fail to visit the inconspicuous flowers self-

FIG. 2047.—*Neottia nidus-avis.* Inflorescence, in a Surrey wood.

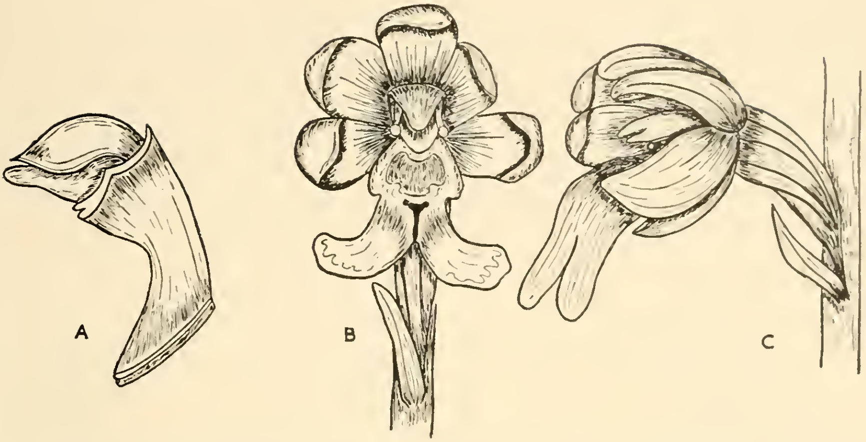


FIG. 2048.—*Neottia nidus-avis.* A, Column. Compare with *Listera*, Fig. 2043. B, Flower, face view showing the nectar trough in the labellum. C, Flower in profile. (A and C *after Fitch.*)

pollination may readily take place by the very crumbling pollen falling automatically upon the stigma.

2. *Kerosphaereae.* The pollinia are hard and waxy or bony in consistency and the anthers are generally deciduous. The inflorescence may be either terminal or lateral.

This is a very large tribe and has been further subdivided into a series of sections:

(i) *Acranthae.* Inflorescence usually terminal or, by abortion of the terminal inflorescence, may be axillary in the uppermost leaves. *Coelogyne*, *Dendrobium*, *Liparis*, *Hammarbya*, *Corallorhiza*, *Epidendrum*, *Cattleya.*

(ii) *Pleuranthae.* Inflorescence usually lateral, arising near the base of the pseudo-bulb or in the axils of the lower leaves or sheaths.

  (*a*) Sympodiales: Plants forming a sympodium in which the stem ends in leaves. *Bulbophyllum*, *Cymbidium*, *Oncidium*, *Maxillaria*, *Odontoglossum*, *Calanthe*, *Phajus.*

  (*b*) Monopodiales: Plants forming a monopodium, stem with indefinite apical growth. *Vanda*, *Angraecum*, *Polyrrhiza*, *Catasetum.*

The great majority of these genera are tropical in distribution and many are epiphytes in the tropical rain forests. Only three species are found in Britain, *e.g.*, *Liparis loeslii* (Two-leaved Liparis), *Hammarbya paludosa* (Bog Orchid) and *Corallorhiza trifida* (Spurless Coral Root). None of them is common. The genera belonging to this tribe, however, produce some of the most spectacular flowers, both in respect to shape and colour as well as in size. They therefore form the basis of most of the hybrid orchids which are cultivated in the hot-houses of orchid specialists both in this country and elsewhere. It is clearly outside the scope of this book to discuss this subject. All we can do is to refer to a few outstanding genera, commenting upon the pollination mechanism where the details have been described.

The genus *Dendrobium* is among the larger genera, with some 750 species distributed throughout the Old World in Asia, Japan, Australia and Polynesia. They are mostly epiphytic and many are in cultivation. Darwin studied the flower of *D. chrysanthum* (Fig. 2049). The rostellum has an upper and a lower surface which are composed of a membrane between which a mass of thick milky-white fluid can be forced out. This mucilage, however, is less viscid than in many other orchids and takes about half a minute to set. The large stigmatic surface lies below the rostellum, while the anterior lip of the anther almost entirely covers its upper surface. The stamen filament is of considerable length but it lies behind the middle of the anther. When the flower is expanded the two pollinia unite into a single mass and lie loosely on the clinandrum, *i.e.*, that portion of the column in which the anther is concealed, which is situated behind the rostellum.

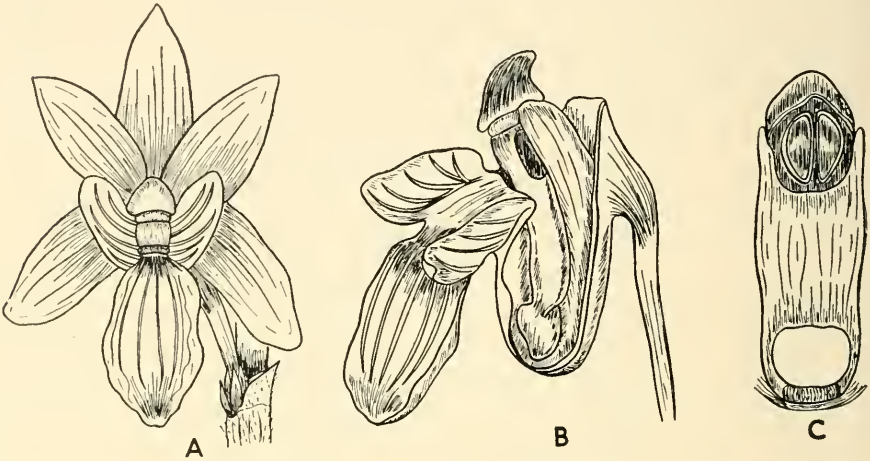


Fig. 2049.—*Dendrobium chrysanthum.* A, Flower. B, Flower in part section, with the side of the labellar pouch cut away to show the column and rostellum, with the anther at the top and the nectary at the base. C, Column, front view, with the two anther cells above partially covering the stigma. The nectary is at the base. (A *after Bateman.* C *after Darwin.*)

The labellum surrounds this central column, leaving an opening in front, while its middle portion is thickened and extends back as far as the top of the stigma. The lower part of the column is developed into a saucer-shaped nectary.

As an insect forces its way to the nectar the elastic labellum will be depressed but the projecting lip of the anther will protect the rostellum from being disturbed. As the insect retreats, however, the lip of the anther will be lifted, thus causing the viscid liquid to be exuded and the pollinia implanted on the insect's back.

Owing to the shape of the clinandrum and the elasticity of the stamen filament, the pollinium always springs forward over the rostellum as soon as the anther is lifted up by a visiting insect. In this way it remains hanging over the stigmatic surface. Should the insect fail to remove the pollinium it seems probable that as the labellum springs back at the insect's emergence, the movement is sufficient to shake the pollinium on to the stigma and thus effect self-pollination.

This elasticity of the filament occurs only in a few species of *Dendrobium*, as far as is known, but in at least one species it has been observed that flower buds which failed to open have later produced fertile capsules, which suggests that some form of self-pollination must have occurred.

Hammarbya paludosa (Fig. 2050) is the only representative of this genus. It is widely distributed in north temperate regions including, as we have mentioned, Britain. The flowers are peculiar in that the ovary is twisted through 360° so that the labellum becomes once again uppermost. The flowers are very small but on examination are found to possess a central column which is more or less triangular. As seen from below two lateral portions of the clinandrum flank and enclose the rostellum, while below is the pocket-like stigmatic surface formed from a fold of the column tissue. Viewed from the back the two anthers lie side by side on the back of the rostellum. As they mature the anthers shrivel leaving the two pollinia exposed. Each pollinium consists of a pair of very thin plates of waxy

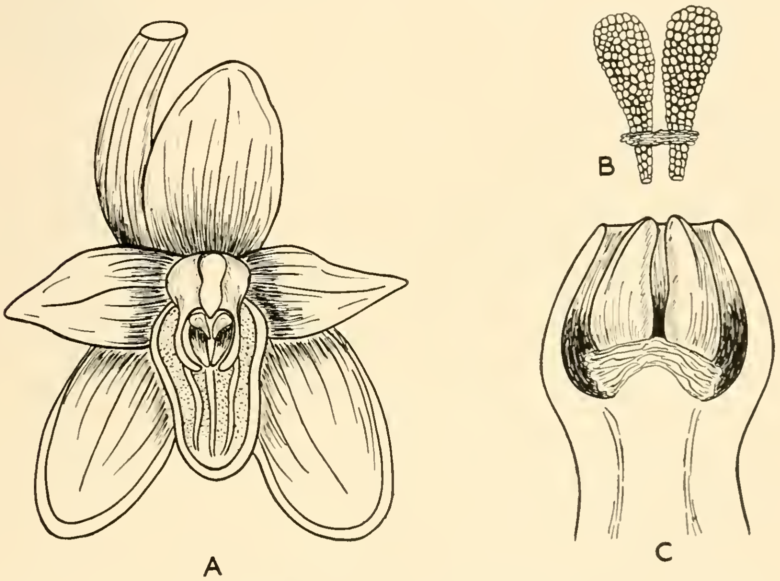


Fig. 2050.—*Hammarbya* (*Malaxis*) *paludosa*. A, Flower, drawn in the normal orchid position with the labellum downwards. In nature the flower is twisted through 360° so that the labellum is upwards. B, The two pollinia. C, Back view of the mature column with the shrivelled remains of the anther exposing the two pollinia. The clinandrum forms a shield around them. (A *after Rendle*. B and C *after Darwin*.)

pollen and as the flowers mature this pollen remains attached only by the top of the rostellum.

An insect visiting the flower inevitably touches with its head the viscid material at the top of the rostellum and as a result withdraws the pollinia when it leaves the flower.

Corallorhiza is a north temperate genus with about fifteen species. They are all saprophytes with much-branched fleshy rhizomes, but unlike *Neottia* develop no roots nor do they produce any scale leaves. In many respects it resembles the monotypic *Epipogium aphyllum* which is also found rarely in Britain. The flowers of *C. trifida* (Fig. 2051) are greenish-yellow in colour with a white labellum and a throat dotted with dark red spots. It is pollinated by small insects which alight on the anterior part of the labellum and creep in to sup the nectar secreted by its posterior part. In doing so, they strike against the projecting rostellum and thereby remove the pollinia, which remain attached to the upper side of the insect and are transferred to another flower.

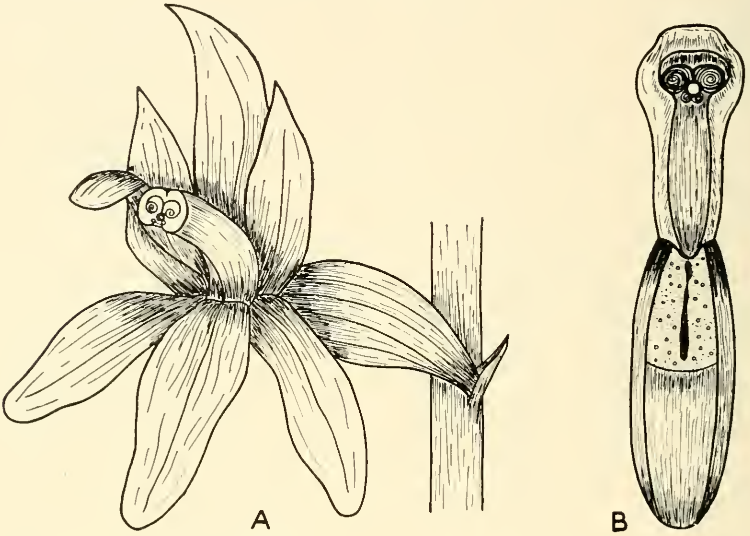


FIG. 2051.—*Corallorhiza trifida.* A, Flower. B, Ovary, partially cut open, bearing the column. Above, the anther showing the two pollinia and the small rostellum, below which is the long, tongue-shaped nectary. (A *after Sowerby.* B *after Knuth.*)

The genus *Cattleya* (Fig. 2052) is well known to orchid-growers, for many species are in cultivation and some are extremely beautiful. They are natives of tropical America. The labellum in this genus encloses the column but is not united to it. From its base a nectary runs down into the ovary. Each anther contains a pair of waxy pollinia, each having a ribbon-like tail formed from a bundle of highly elastic threads to which a number of pollen tetrads are attached. The lips of these caudicles protrude from the anthers which lie on the upper surface of the rostellum. The anther, however, is

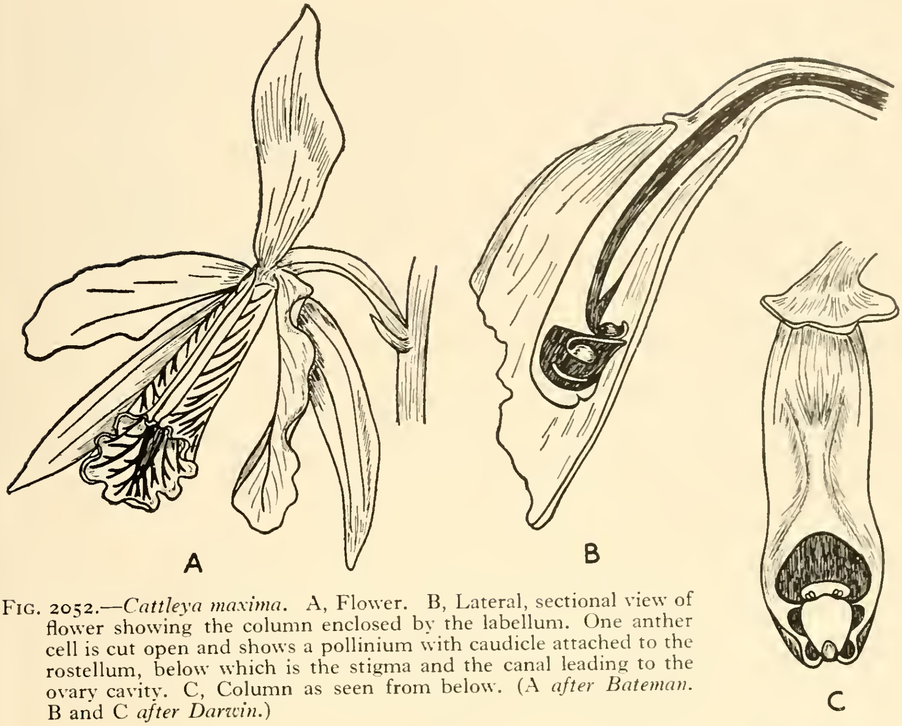


Fig. 2052.—*Cattleya maxima.* A, Flower. B, Lateral, sectional view of flower showing the column enclosed by the labellum. One anther cell is cut open and shows a pollinium with caudicle attached to the rostellum, below which is the stigma and the canal leading to the ovary cavity. C, Column as seen from below. (A *after Bateman.* B and C *after Darwin.*)

kept closed by a spring at its point of attachment on the top of the column. An insect visiting the flower may not, in the first instance, touch the rostellum, but during its retreat from the flower is almost certain to cause the exudation of a viscid fluid from the rostellum and bring out the pollinia on its head. In one species in Trinidad it has been observed that the flowers rarely open, though they produce fertile capsules. In this case the pollen apparently germinates *in situ*, the pollen tubes growing directly down into the ovary. A similar condition has been described occasionally in *Epidendrum*, a large genus with about 400 species occurring in tropical America. Like *Cattleya* many species of *Epidendrum* are in cultivation.

The genus *Calanthe* contains about 120 tropical species and is interesting because about eight pollinia are produced. Darwin studied the case of *C. masuca* (Fig. 2053). Two stigmas are produced as oval pit-like structures lying on either side of the rostellum. There is an oval viscid disc to which are attached eight stalked pollinia which are covered at first by the anther membrane. The labellum is united almost completely to the column leaving a passage to a nectary lying beneath the rostellum. If an insect enters the flower it withdraws on its head the viscid disc with the eight pollinia attached to it which spread out like a fan. They undergo no change in position once they are withdrawn but when the insect thrusts its head into another flower the pollinia are laterally compressed and strike upon the stigmatic surfaces which, as we have seen, lie on either side of the rostellum.

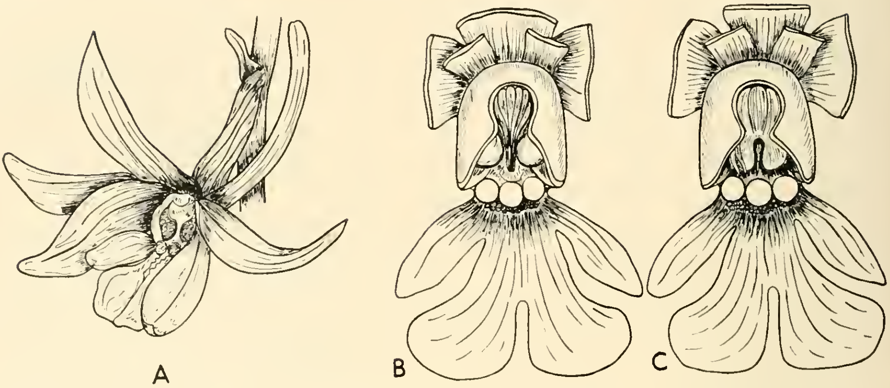


Fig. 2053.—*Calanthe masuca.* A, Flower. B, Flower with perianth removed, except the labellum. Anther case removed to show the eight pollinia within the clinandrum. C, as in B, but pollinia and disc removed showing the notched rostellum. (A *after Bateman.* B and C *after Darwin.*)

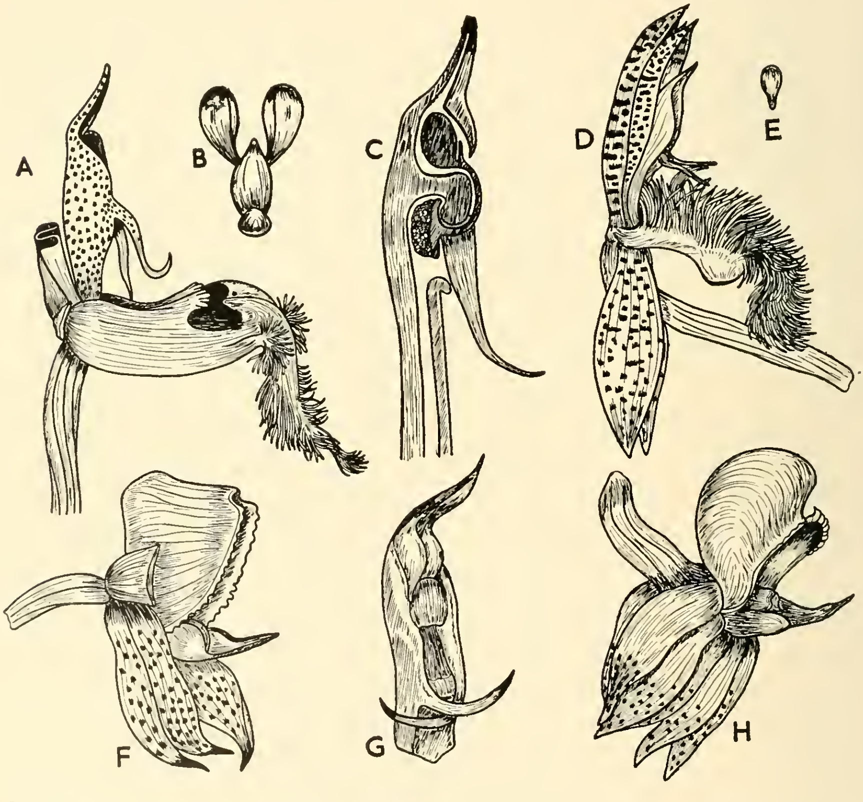


Fig. 2054.—*Catasetum.* A and D, *Myanthus*-form, flowers. In A the perianth has been removed except the labellum. F and H, *Monachanthus*-form (female) flowers. B, Pollinia with strap-like caudicle and retinaculum. C, Column of *Myanthus*-form in section showing the caudicle bent over the rostellum, with retinaculum tucked in below it. G, the above, entire, showing the sensitive arms or antennae. (*Partly after Darwin.*)

Finally, we may refer to the flower structure in the genus *Catasetum* (Fig. 2054). It is an American genus of about forty species. The plants live as epiphytes in the tropical rain forest. The flowers are extremely diverse in form, so different in fact that were they not sometimes found in the same inflorescence, they would undoubtedly be placed in different genera as indeed they originally were. These different forms are moreover usually of different sex (Fig. 2054). In the predominantly male flowers of *C. saccatum* the upper sepal and two upper petals surround and protect the column, the two lower sepals project outwards at right angles. The flower is more or less inclined, with the labellum hanging downwards. In front of the column lies the deep stigmatic chamber and lying above it is the viscid disc. Though termed a stigmatic chamber it is completely sterile and incapable of receiving pollen. Moreover the disc, though of great size, is so placed that it could never come into contact with an insect. Instead, the rostellum is prolonged into a pair of curved tapering horns, referred to as the antennae, which are extremely sensitive. No nectar is secreted but the flowers are conspicuously marked. An insect flying to the flower is almost certain to come into contact with one of these antennae. Should this happen a stimulus is produced which causes the anther covering to split and the pollinia are immediately forcibly ejected a distance easily sufficient for them to become stuck on the insect by their adhesive points.

For long these flowers were regarded as exclusively male and the female flowers were not recognized, though actually they were known under a separate genus *Monachanthus*. The flower is of very different appearance from the male; the pollen sacs are rudimentary and never open, while the antennae are absent. On the other hand the labellum is not as large and the other perianth segments are reflexed. Instead of a large stigmatic cavity there is a narrow cleft beneath the anther just large enough to receive a single pollinium. In addition to these two types, a third has been recognized in which both sexes are represented. This used to be referred to a genus *Myanthus*. It preserves the general form of the male flower so far as the petals and sepals are concerned but the labellum more closely resembles that of the female. Two antennae are present though not as long as those in the male. The stigmatic chamber is of medium size, intermediate between the large one of the male and the small one in the female. Unfortunately no modern work on the pollination of this genus appears to have been done and this description is based upon that of Darwin who was still not wholly satisfied that he was dealing with three forms of the same flower.

Space will not allow us to consider the many and interesting genera which are in cultivation. Among the more important, however, we may mention *Odontoglossum* (Figs. 2055 and 2056), a genus of 100 epiphytic species occurring in the mountains of tropical America; *Maxillaria* (Fig. 2057), with 110 tropical species; *Vanda* (Fig. 2058), with twenty-five Indo-Malayan epiphytes; and *Cymbidium*, with about forty species in Africa and Asia, including Japan.

Possibly there is no more remarkable group of flowering plants, cer-

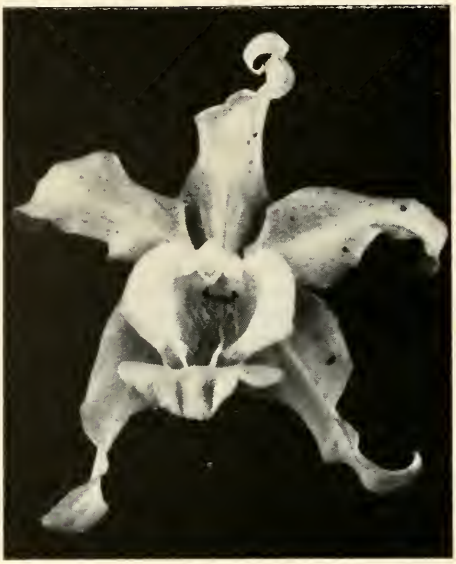


FIG. 2055.—*Odontoglossum.* Flower of a cultivated variety.

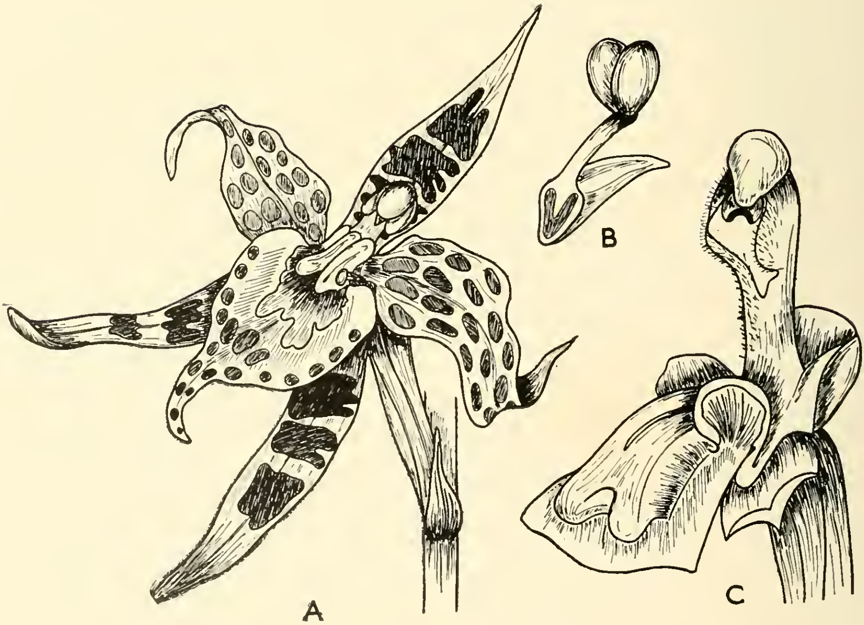


FIG. 2056.—*Odontoglossum cordatum.* A, Flower. B, Pollinia attached to the retinaculum. C, Column with perianth removed showing the anther cap with retinaculum projecting below and the large stigmatic opening. (*After Bateman.*)

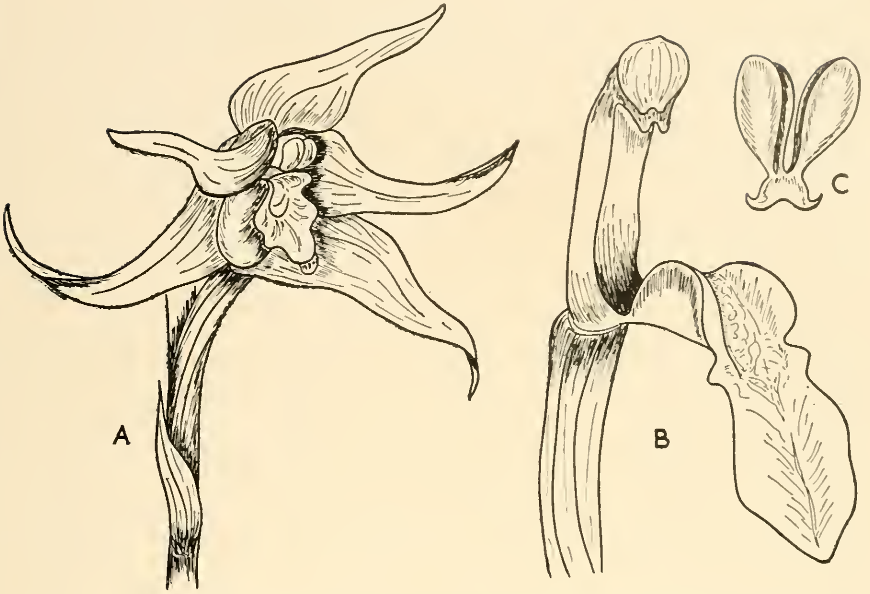


FIG. 2057.—*Maxillaria venusta.* A, Flower. B, Column after removal of perianth. C, Pollinia and retinaculum. (*After Hooker.*)

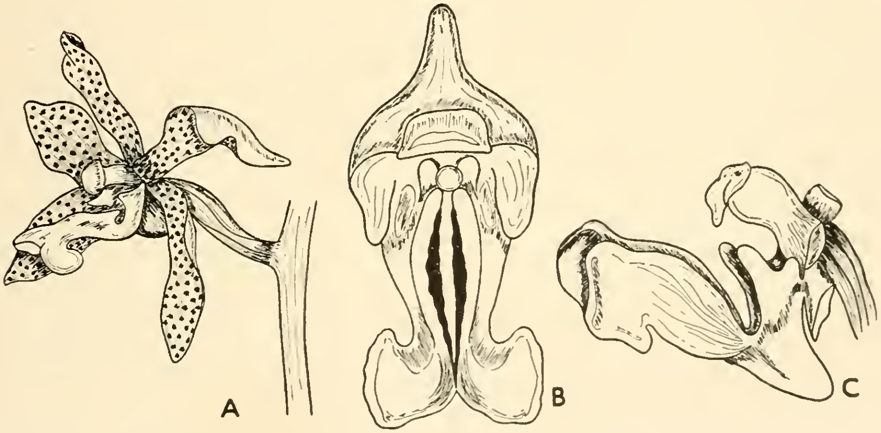


FIG. 2058.—*Vanda bensoni.* A, Flower. B, Column with the large anther covering above and the attached labellum below. C, Column and labellum in side view. (*After Bateman.*)

tainly none which illustrates more closely the interplay between flower and insect in pollination, and a study of the pollination mechanisms in the Orchidaceae brings home, possibly more conclusively than anything else, the belief that these results could only have been produced by the parallel evolution of the flower and the insects which pollinate it.

With this family we must leave the Monocotyledons and also our account of the families of the Angiospermae. Though much ground has been covered a very great deal has been left out. The subject is so vast, in fact, that only a few of the more important aspects could be touched upon. It is not the policy of this book to discuss phylogeny or to enter upon the thorny questions of the relationships of families with one another. From what has been said it is clear that some families are closely related. In many instances, however, the question of relationship is much more problematical and the personal opinions of individuals often outrun definite facts. These are subjects into which we will not enter. They offer food for thought and a student might do worse than reflect upon such matters and attempt to formulate his own ideas.

One thing is clear, however; the Dicotyledons and the Monocotyledons represent two parallel evolutionary series. Whatever their ancestral form may have been, and there are on that subject plenty of theories but few facts, it is obvious that both the great groups have travelled forward side by side. It is not surprising therefore to find a number of parallel adaptations or modifications appearing in the two groups. These must not of course be taken as indicating phylogenetic connections. In fact they serve as a warning to those who would attach too much importance to floral structures as a basis for deducing phylogeny. If two similar organs can be produced by two clearly separate types of organisms, how much reliance can we place on minor similarities as a basis of phylogeny.

The following table prepared by Hutchinson will illustrate some examples of this parallelism.

Dicotyledons	*Monocotyledons*	*Character in common*
Ranunculaceae	Alismaceae	Apocarpous gynoecium
Ceratophyllaceae	Naiadaceae	Aquatic habit
Menispermaceae	Dioscoreaceae	Climbing habit and similar floral structure
Aristolochiaceae	Araceae	Superficial resemblance of perianth and spathe
Balsamaceae	Orchidaceae	Zygomorphic flowers of similar form
Umbelliferae	Amaryllidaceae	Umbelliform inflorescences, usually with inferior ovary
Asclepiadaceae	Orchidaceae	Androecium structure and waxy pollen
Compositae	Eriocaulaceae	Capitulate inflorescence

CHAPTER XXXI

THE CLASSIFICATION OF PLANTS

THE subject of Plant Classification includes three aspects which are distinct in theory, although they necessarily overlap in practice. Firstly, there is **taxonomy**, the " law of order", which is the study of the principles on which classification is, or should be, based. Secondly, **systematics**, which implies the determination of the groupings to be used and their relative positions in a system. Thirdly, **nomenclature**, or the study of the correct naming of the groups employed, according to the generally accepted rules.

All three disciplines have the convergent aim of fixing the names of organisms and of their groups. The identity and the relationships of an organism are embodied in its name and without agreement on this matter every form of botanical enquiry is rendered nugatory. As Linnaeus said: *Pereunt nomina perit et cognitio rerum.* Agreement in nomenclature is still however unrealized and is only being slowly approached through international discussion.

Many debatable problems are involved in classification, ranging from the purely philosophical to the purely historical, and there is no part of biological science in which personal judgment has greater scope or where, in consequence, there is less fixity or agreement. The subject has therefore a powerful appeal to the reflective mind.

To start with, our whole attitude towards classification will depend on how we answer the question whether classification is a subjective, human construction or whether it exists objectively in Nature and we are trying to uncover it. At the one extreme we have the view that classification originates in the human need for simplifying the immense diversity of Nature, by grouping and relating individual objects within a logical framework, to enable our limited powers to cope with them. Classification, thus viewed, is a basic scientific necessity and biological classification is only one aspect of this universal need. Under such a conception classification is an artificial construction, unknown to Nature, and to be formed and judged mainly on the principle of expediency. At the other extreme is the ideal of a perfectly natural system which will express exactly the evolutionary relationships of all organisms, that is to say a truly phylogenetic system which can be discovered through increased knowledge of the processes and the history of evolution. These mutually exclusive views are not often proposed in all their rigour, and even when they are, practical considerations have generally compelled some compromise. For example, those who support the second idea may display a practice which is more logically concordant with the first theory. The result of these inconsistencies has, naturally, been confusing and of late years the need for a philosophical examination of the principles of taxonomy has been felt more and more widely. The outcome of enquiry and discussion has been very helpful in clearing up ideas, though some fundamental differences of opinion have not yet been reconciled, particularly between botanists and zoologists, and it cannot be claimed that anything like finality has been reached. Doubts still exist whether there is, in fact, an ideally perfect classification which may be accepted as an aim of taxonomy and, again, whether phylogeny can ever be fully expressed in classification. If evolution could be represented, as used to be thought, by a " phylogenetic tree " there might be hope of arranging organisms in a corresponding pattern, but attempts to formulate such patterns have not been encouraging and botanical opinion is more inclined to agree with the expressed view that " the phylogenetic order is not so much a tree as a bundle of sticks."

Since one of the primary objects of classification is to produce order, practical convenience cannot be ruled out, and no classification, however ideal scientifically, can be based upon data which are not available. This undeniable necessity of practice, however, conflicts with the fact that organisms may differ, permanently and heritably, in features which can only be ascertained by intensive investigation of the living plants and are therefore only available in a few cases. This is the dilemma which lies at the root of much of the uncertainty and lack of uniformity which pervade the history of classification and are so puzzling to the student and so hampering to the investigator.

The problem is basically a philosophical one and the consideration of it, from this point of view, has only begun, but at least one important conclusion, which bears directly upon our difficulty, may be cited. This is the conclusion that the conflict is not between subjective concepts and objective things or between mind and matter, but that all the units of classification of whatever grade, the **taxa**, to use a general term, *i.e.*, varieties, species, genera, etc., are alike in being mental constructions from sense data. The latter are " real " in a material sense, but the units into which we group these data, whatever their character, are rational constructions of our minds and their nature ultimately depends, therefore, on the ego of the observer, who may prefer purely logical principles, or who may attempt, alternatively, to form his constructions on what he believes to be a " natural " model.

The former was the preference of pre-evolutionary systematists who formed the " artificial " systems which were characteristic of the seventeenth and eighteenth centuries. In these systems logic was the ruling principle and convenient order was the end pursued. They were, in varying degrees, satisfactory for their proposed objects and the most completely logical of them, the Sexual System of Linnaeus, enjoyed wide and prolonged acceptance. Nevertheless, the natural model refused to be ignored. From the beginnings of biological science man had intuitively recognized certain groupings of plants as realities, *e.g.*, Umbelliferae and Compositae, and a logical arrangement which did violence to this feeling was deemed unsuccessful. Linnaeus himself admitted the force of this conception of affinity in proposing the idea of a Natural System. He suggested a list of families, based upon the intuitive feeling of relationship, but left them undefined, because he did not consider that knowledge was at that time sufficient to do this, or in other words, to dress the natural model in logical garments. How far later workers have succeeded in the attempt may be seen by anyone who compares the definitions of families used in various textbooks of Systematic Botany. Of course, the so-called intuitive feeling of affinity among members of a family is not actually a non-rational process, but consists in the summation by the observer of a large number of qualitative sense data, expressed by the term " facies", many of which are either individually minute or so elusive as to escape verbal definition, but which are cumulatively recognized by the observer as a sense-group for which there is a very strong presumption of natural reality. This was, and is, a process of discovery and it stands in complete contrast to the procedure which starts from a logical definition, such as characterized the confessedly artificial systems and which still finds its way, clandestinely, into later and presumptively natural systems. What is true of the recognition of families is true also of the recognition of genera and of species in their differing degrees.

It is often assumed that if we proceed by discovery, we shall, in uncovering natural relationships, uncover at the same time the evolutionary history of the organisms, but this is based upon a misconception. It presupposes that if species A has a character or characters which are believed (as, for example, where evident signs of reduction are present) to be more advanced than the corresponding characters in species B, then species A stands above and is derivable from species B in an evolutionary sense. This procedure arbitrarily assigns predominant importance to certain characters and is essentially the artificial method of classification. It may be unavoidable, it may even be desirable, but it is not a natural or phylogenetic method, for no organism is advanced or primitive in the sum total of its characters. Though it is possible to arrange organisms in a linear series on such partial grounds, it will not represent their true evolutionary status, except with regard to the characters considered.

The difference between the evolutionary progression of characters and the actual descent of the plants bearing them was emphasized by Hayata in 1921 and has been well brought out by Zimmermann in the distinction he has drawn between *Merkmals Phylogenie* and *Sippen Phylogenie.* The former implies the phylogenetic arrangement of homologous structures and is a proper subject-matter of comparative morphology. The latter indicates the grouping of organisms in an order of presumed evolutionary descent. Phylogenetic systematists believe that it is legitimate to proceed from the former to the latter, but this Zimmermann and many other botanists will not admit. To take an example; morphologists may claim that the sympetalous corolla is more advanced than the apopetalous corolla and that it is right to presume that the former condition has been evolved from the latter. The proposition is, of course, a mental concept, but it is drawn from a considerable body of observed data and its truth is highly probable. This is scientifically admissible but it is quite a different thing to translate the proposition into terms of *Sippen Phylogenie* and deduce therefrom that A, which is sympetalous, has been derived from B, which is apopetalous. On the contrary A may be actually less advanced than B in respect of other equally important characters. This statement of the position is perhaps unduly simplified, but it serve to illustrate the fallacy inherent in phylogenetic classification, which seeks to reduce to linear order something which is, in fact, a complex reticulum. The river of evolution has not advanced with the uniform sweep of a tidal wave, but with multitudinous cross-currents and eddies, which logic may analyse but can never simplify without loss of truth.

Classification presents itself differently to the palaeontologists. With all its imperfections the geological record does show a real sequence of organisms in time which is, at any rate in broad outline, an evolutionary succession. It is here that Huxley's dictum that the problem of systematics is that of detecting evolution at work is most clearly true, whatever reservations we may put upon it in the field of living organisms. The relationships which the succession reveals are more important to the palaeontologist than the differences on which systematic distinctions rest. He has to work with only a small part of the data which are available to other biologists and his views on phylogeny are therefore bound to be tentative and alterable. If the classification he uses depends upon his view of the phylogeny of the organism concerned, then every change in ideas about one produces consequent changes in the other, with baffling results in nomenclature. The lineages which are revealed by the succession of fossils in time may be accepted, though never proved, as being genealogical, that is truly phylogenetic. If a classification is to express this it must be " vertical " in its groupings, but there is so much uncertainty in the interpretation of lineages that a " horizontal " classification of contemporary forms is often the only workable method. In spite of the difference in approach the same dilemma reveals itself, the incompatibility of a practically workable classification and of an ideally phylogenetic classification, which demands minute and prolonged study and often inaccessible data.

Nowhere is the cleavage between the two aspects of taxonomy more clearly revealed than in the vexed question of the nature of species. This is not the place to discuss the origination of species, a complex problem which we shall discuss in Volume III, but we must consider here the ideas of the species which underlie taxonomy.

Not only is there no uniformity in the idea of the species, there is not even consistency. Tate Regan defined a species as " a community or number of related communities whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name". Darlington, on the other hand, has defined species as " the minimum permanently isolated groups", adding the rider that the isolation may be of many kinds. It might also be added that the permanency is not absolute. Definitions similar to the latter have been given by several other writers, with a common emphasis on the genetic or reproductive isolation of a group or population as the basic criterion for specific discrimination. Plainly these two definitions are not referring to the same thing. They present the two horns of what we have called the Taxonomic Dilemma.

If both definitions are legitimate, each from its own point of view, then one is forced to recognize that there are really two sorts of species, Museum Species and Natural Species. The museum species are to some extent, at least, conventional. They are the logical species, they are adopted and described upon the evidence of characters which can be readily seen and preserved. They serve an essential purpose, to enable specimens to be named and classified among other specimens to which they show the maximum of resemblance, but they are conceived as subjective entities and they are not necessarily natural units. Museum species are well known and understood and many people think only of them when species are discussed.

Natural species on the other hand are relatively little known and their very existence may be considered disputable in some quarters. They are conceived as being objective entities and they cannot be created by systematists, they have to be discovered. To this end every source of information must be tried; evidence from morphology, anatomy, biochemistry, cytology, genetics and ecology must be sought, and even when all this has been done it is possible that they may bear no recognizable signature, no sure mark by which to know them, so that they remain impalpable, hovering ghostlike behind the screen of the more tangible museum species. Yet they are the ultimate taxonomic units, of which our museum species are only reflections, and until we come to terms of understanding with them the keys to the problem of evolution will not be in our hands.

Although they are so different in conception, the two categories are not necessarily opposed. Museum species are generally based upon morphological characters but this is not so partial as it appears, for morphology is, after all, the expression of inner constitution. Experience has shown in certain cases that extended investigation by other means, *e.g.*, cytology or ecology, which was aimed at disentangling natural species from a museum group, has only served to confirm the majority of the conclusions which had previously been formed on a morphological basis. The criterion that species are groups of individuals which breed only within their own limits may therefore be satisfied in a number of cases by the museum species and to this extent the dilemma is relieved. We may take it that the museum method does frequently delimit the maximum natural species. It fails, however, in delimiting the minimum species, for there are numerous cases in which it is impossible to discriminate natural species by morphological methods. This is most clearly true in some of the lowest groups, especially the Bacteria, where species, or what are called species, rest almost entirely on biochemical tests, by which morphologically identical types may be discriminated. The biochemical exploration of higher plants has only been carried out to a very limited extent, but instances are known of " chemical species " even among the Angiosperms. A good example is *Eucalyptus dives*, the oil of which contains piperitone, cineole and phellandrine. Four types of tree are known, all included in the same morphological species, in which the relative proportions of these constituents are markedly and constantly different, so that collections of the oil are mixed from trees of known types in order to keep the product reasonably uniform. Another similar case is that of *Pinus washoensis* from the western United States, where different trees, morphologically identical, yield oils which are either laevorotatory and contain a large percentage of carene, or dextrorotatory, with carene replaced by β-pinene.

These differences are permanent and are hereditary. The different races are therefore natural species within the terms of Darlington's definition, and if they are assigned to a lower rank it can only be on grounds of convenience.

Opinions differ as to the treatment of such physiological variations in current systematics. Some workers prefer to limit specific rank to types which are morphologically distinct, both among the flowering plants and among the biologic races of the Fungi. Others take a broader view and accord them specific rank. Among the Bacteria, at least, this is almost inevitable.

Cytological " species " are probably common, but they have been uncovered only in a limited number of cases. Such are, for example, polyploid strains within a morphological species, which usually fail to cross with the diploid strains and are thus genetically isolated. Another type arises from inversions of part of a chromosome. The genic combination in the inverted portion is preserved intact because it cannot take part in crossing-over at meiosis and if mutations accumulate in the inversion they may form a basis of major discontinuity within the morphological species. They may not always affect the external form, but, if they cause physiological differences which are differently affected, for instance, by temperature, they may be subject to ecological selection and hence lead to different habitat preferences or a different geographical distribution and thus to genetic isolation. Such hidden specific differences were first found in *Drosophila* and led to the recognition of three cytological species, *D. simulans*, *D. pseudo-obscura* and *D. miranda*, the two latter being intersterile and therefore genetically isolated.

All the above cases come under the general title of " Cryptic Species". Unless some solution to the taxonomic dilemma can be found they are a standing challenge to museum systematists.

To point out these limitations does not imply a criticism of the morphological standpoint nor is it derogatory to the great work done by systematists who have worked from that standpoint. It only shows that, as the origins of species are multifarious, so their distinctions are manifold and not all are large enough to be caught in the morphologist's net. Refinements of morphological method have indeed closed the net considerably in recent years and particularly in the discrimination by biometric methods of closely related species living in the same area. Morphological criteria which would once have been dismissed as trivial have been shown to have decisive value within the limited circles of affinity concerned.

The maximum species, whether conventional or natural, is based not upon individuals but upon populations and is never strictly homogeneous among sexual organisms, or even, though to a lesser extent, among non-sexual or sterile organisms. Every population includes a changeable and changing number of different genotypes, that is to say, genetically differing individuals or groups; which are commonly distinguishable by investigation and often by conventional or " museum " characters. If there exist reproductive barriers, other than mere distance, between the population as a whole and related populations, then, notwithstanding its internal diversity, it forms what we have called a maximum species. It is a statistical concept and calls for analysis into subdivisions according to the degree of variability present. These minor groupings, in their turn, also rest on a statistical basis, though a narrower one, and indeed some degree of variability must be accepted in all our groupings if our analysis is to stop short of the individuals themselves. The kind of subdivisions used and the amount and kind of variability accepted will depend on whether we start from the conventional or from the natural standpoint. Let us compare the outcome of the two methods of approach.

The divisions of the museum species into " sub-species", " variety", " form", etc., are, like the species itself, subjective conceptions which are very difficult to delimit and about their applicability in particular cases systematists often differ. They do not always reflect natural groupings. though they may sometimes do so, and they may conceal, in a subordinate rank, groups which are truly natural species.

The term " **variety** " is generally applied by morphological systematists to plants which show a departure from the norm of the species in some character or characters not directly connected with the influence of the environment, nor affecting the diagnostic characters of the species. Plants in which the variation is the direct result of abnormal conditions of growth are generally classed as " **forms**". The essential point in the use of the term " variety " is that the indicated variation is of stable duration but no questions are asked about its inheritability, genetic constitution or ecological importance. It is a morphological concept. Taxa classed as " forms " are assumed to be unstable and to be subject to change if any alteration occurs in the conditions which have produced them. It scarcely needs to be pointed out that these are artificial groupings and that opinions about individual cases may be modified by new evidence. The variety may prove to be due to environment or, on the other hand, the form may prove to be a stable variation. Two well-known examples are the following: *Plantago coronopus* L. var. *pygmaea* Lange, is a minute plant of dry places with entire, linear leaves. Although classified as a variety it reverts under cultivation to the typical plant of the species and is therefore no more than a form. The second example is *Cytisus scoparius* Link var. *prostratus* Bailey. This was originally classified as a variety, was reduced to a form by several later systematists and has now been shown by Turrill to come true from seed in cultivation and to be therefore a stable variety.

The attempt to distinguish between variety and form rests on the assumption that there are two sorts of morphological characters. They were called " ecad " and " phyad " by Griesbach or " epharmonic " and " filiated " by Vesque. The first category are assumed to be directly related to the environment, the second category to be almost wholly hereditary. Some systematists deny the validity of the distinction and if indeed it cannot be upheld then the separation of variety and form loses its only rational basis.

Jordan in 1864 administered a shock to the classical systematists by his examination of the small Crucifer, *Erophila verna*. He described fifty-three types, later (1873) increased to about 200, all within the same morphological " species", the great majority of which he cultivated and showed that they maintained small but permanent heritable distinctions. This originated the idea of the **microspecies**, or **Jordanon**, as Lotsy called it, in opposition to the **macrospecies**, or **Linneon**. It was the first notable example of the clash between Museum and Natural Taxonomy. Obviously if any considerable percentage of the macrospecies can be dissected in this way, then the macrospecies is only an abstraction and, unless the test of cultivation can be employed, the ground is cut from under the systematists' feet. The problem has stimulated a great deal of theoretical examination of taxonomic principles, but in practice it has been largely met by ignoring it. Winge in 1940 reduced Jordan's types of *Erophila* to four, on cytological grounds, and concluded that the apparent multiplicity of types was due to hybridization and to permutations in the genetic combination of their characters. This certainly simplifies the issue in this case, but many others remain, and basically the principle is the same, whether there are only four types or four hundred, that the morphological macrospecies contains distinct groups, which are permanent and natural units, but which cannot be adequately comprehended by morphological methods, though morphology may, and often does, give evidence of their existence, so that museum microspecies are now an accepted systematic category. The term " **sub-species** " may mean the same thing, or it may in other cases be a transitional assemblage, part of a series between two geographically or ecologically separated groups. It is, once more, a subjective concept.

Natural Species, or as some prefer to call them, Experimental Species, are not all of similar size or of equivalent grade. The causes of discontinuity between them are various, and complete discontinuity is not always achieved at one step. There is an hierarchy of minor groups among them, some of which represent developmental stages, and their discrimination is often a difficult matter involving ecological, genetic and sometimes immunity tests.

If discontinuity is not complete there may occur **Clines**, that is to say, spatial series of intermediates forming gradients between two groups. The extreme forms may be intersterile and yet intermediate forms be capable of interbreeding. The taxonomic status of such intermediates has never been settled.

An attempt was made in 1929 by Turesson to arrange his concepts of the natural units into a hierarchy with the following distinctive names.

The major natural assemblage is known as the **Coenospecies**, which corresponds to the morphological macrospecies and may sometimes, perhaps often, be the same thing. It may be defined as an assemblage of individuals which is genetically isolated from related assemblages and incapable of exchanging genes with them, that is to say incapable of fertile interbreeding. How this genetical isolation arises is another question and does not concern us here; there may be many ways in which it originates. The coenospecies is then the maximum *natural* species as the macrospecies is the maximum *museum* species. Not all macrospecies correspond to coenospecies, as is shown by the frequent occurrence of " interspecific " hybrids between the former. These cases probably fall into the following category.

The coenospecies may be divided into **Ecospecies**, groups which have the same chromosome complement but are separated by ecological or geographical, and usually also morphological, differences. Between themselves these groups are capable of a limited degree of hybridization, but under natural conditions their ecological or geographical differences usually keep them apart. When ecospecies are morphologically distinct they may be equivalent to museum species or sub-species.

In this connection the genus *Vaccinium* is interesting. There are a number of sub-genera, and within each sub-genus there is apparently some hybridization between those species which have the same chromosome number, but not between the diploids and the polyploids. The main evolution of the genus has taken place at the diploid level and these interbreeding diploid species are morphologically distinct, so distinct in fact that they are unhesitatingly called macrospecies by systematists. Viewed from the standpoint of natural species, however, they would only be ranked as ecospecies, because the only barrier to their fusion with one another is that they are ecologically segregated. In *Vaccinium* the coenospecies would correspond to the sub-genus. In other genera a single morphological species may become genetically isolated by some nuclear peculiarity and thus constitute a coenospecies. At the other extreme there are genera among the Gramineae and Orchidaceae in which all the species are capable of being crossed and even bi-generic hybrids are not uncommon. Where the limits of the coenospecies may be in such groups is not clear.

Within each ecospecies may also be found **Ecotypes**, which are genetically distinct groups within the ecospecies, generally showing special ecological preferences for situations to which they may be specially well adapted. These preferences tend to isolate them to some extent, but they are capable, when circumstances permit, of free hybridization with other ecotypes of the same ecospecies.

Conditions of cultivation or a change of climate, for example, may create novel uniformity of habitat which permits hybridization to take place among ecotypes formerly separated by ecological barriers. This has been referred to as " hybridization of the habitat " and it sometimes results in the production of hybrid swarms or the emergence of new, aggressive types by transfer of genes, which may prove to be " weeds in embryo".

Turesson began with the ecotype, which is the only one of the three categories recognizable as an entity in the field. It is supposed to arise in the course of migration of a species-population, by the selective elimination of unfitted types under environmental influences. It is therefore an ecologically " adapted " group. It differs from an *ecad* (in Clements' sense) in that the latter arises through individual plasticity and has no genetical basis, while the ecotype exists because it has a genetical constitution suitable for a particular habitat. The ecad is changeable and unstable but the ecotype maintains its character even under cultivation. Turesson's definition runs as follows: " An ecotype is the product arising as the result of the genotypical response of a species to a particular habitat." He considered it to be akin to the taxonomic variety and some varieties are in fact ecotypes though others may be *topotypes*, that is local populations genetically differentiated from others but not related to ecological differences.

The **Cytospecies**, on the other hand, is an assemblage within the coenospecies which has its own distinct chromosome number and is ecologically or geographically isolated. Cytospecies are only capable of limited hybridization, except in the case of paired species where one of the pair is a polyploid of the other, when they may hybridize freely: *e.g.*, *Viola riviniana* ($n=20$), and *Viola reichenbachiana* ($n=10$).

Many of the morphological species fall into the categories of Ecospecies or Cytospecies, but in many other cases Cytospecies may not be morphologically distinct.

The **Cytotype** is a polyploid component of a cytospecies.

These terms are descriptive only and must not be understood as rigidly defined categories which are mutually exclusive. For example, the cytotype may arise either by spontaneous chromosome doubling (autoploidy) or by a cross between two ecospecies accompanied by chromosome doubling (amphiploidy) which transforms what would otherwise be a sterile cross into a fully fertile and stable type, a potential new coenospecies. Further, the two cytotypes of *Valeriana officinalis*, tetraploid and octoploid respectively, show different ecological preferences and are apparently intersterile. They would appear therefore to be true coenospecies, though they are only distinguishable morphologically by the size of their pollen grains.

A study of the numerous infra-specific groupings which experimentalists have proposed, shows that the species-unit has been as thoroughly pulverized as the atom. Taxonomic species are undoubtedly of very diverse size and composition but in their analysis it would be wise to use a terminology which is free from confusion and to leave the term " species " where we found it, in the museum. For this reason the **deme** of Gilmour and Gregor has much to recommend it. The root " deme ", meaning a population, is non-committal in itself and it can be suitably qualified by prefixes as experimental study may justify. Thus, a *gamodeme* is a freely interbreeding population, an *ecodeme* an ecologically localized population, a *genodeme* a genetically differentiated population, a *cytodeme* a cytologically differentiated population (cytotype) and an *ecogenodeme* would be the equivalent of an ecotype. This kind of system is indefinitely flexible, it makes no inroads upon classical taxonomy and it frees the mind of the investigator to concentrate on the processes of speciation rather than on the delimitation of categories.

Turning now from the analysis of the species as the fundamental unit of taxonomy, what of the relationships of the larger groups? Hayata, the originator of the Dynamic System of Classification, pointed out in 1921 that a natural system must be a network, not a phylogenetic tree, as the affinities of groups depend upon the extent to which they share characters. From this standpoint no groups can be regarded as having a permanently fixed place in a system, since both the outline of the group and its position will depend upon the number of characters taken into consideration. If attention be concentrated upon a few characters, classification will be relatively easy, and this is, in fact, the way in which most of the systems referred to later in this chapter have been built up. However, as we extend our scope of consideration, so will our ideas of relative affinity change and the more numerous the characters used, the more difficult will it become to make any scheme, even in three dimensions, which will express all the relationships involved.

Hayata himself proceeded by grouping around each plant family all the others which showed evidence of characters shared with it. Any one family may thus appear in several groups and the whole pattern is kaleidoscopically changed as we turn from one set of characters to another. This accords very well with the experience of practical systematists in attempting to unravel the tangle of cross-relationships in any group of plants. No fixed system, not even a three-dimensional lattice, can adequately express them all; there is a hyper-dimensional quality about them on which we can only speculate. We need a form of space in which an object can be in a number of different places at the same time. There is, indeed, as Fries said long ago: *quoddam supernaturale in systema naturae.*

All this may be true but it is certainly not practical systematics. We return again to our dilemma and to the old saying, " il faut se borner". A working classification must be to some extent artificial, an abstraction from Nature, founded upon an arbitrary limitation of the criteria included. So long as this is clearly understood and we are not thereby blinded to the wider significance of relationships, the procedure is legitimate and indeed inevitable. To keep our minds clear, however, we must recognize that in systematics there are two distinct aims and two distinct approaches. Linnaeus said that the Natural System was the Alpha and Omega of Systematic Botany and the fashion has grown up of using these two terms to symbolize the two different aspects.

This then is the working solution of the dilemma which has been arrived at, namely to separate Alpha Taxonomy, which is the classical subject, logical and orderly in intent and chiefly morphological in method; a worthy Martha, domestic, even rather urban in outlook; from its younger sister Omega Taxonomy, a Mary in country clothes, with the highest aspirations but with uncombed hair and something of the wildness of Nature still in her heart. Alpha Taxonomy is indispensable. We must wed her and cherish her, while Omega Taxonomy, which promises to unlock for us the secrets of the Natural System, intrigues our romantic imagination. Nor are the two interests incompatible. Alpha leads the way to Omega. As Vavilov has said, the recognition of the Linnean species is the first step in biological knowledge and without that as a foundation the fuller exploration of systematics would not be possible. Linnaeus himself knew this and we may sum up the situation in his own words: "Artificial orders serve to distinguish one plant from another, natural orders serve to teach the nature of plants."

The principle of grouping which has been adopted in the systematic chapters of the present work demands a word of explanation. The tendency of recent classifications of particular groups has been predominantly analytical. This viewpoint may be expressed by the question, " Is there sufficient difference between A and B to justify their separation into different groups?" The replies of the specialist to this question are increasingly in the affirmative, so that a great multiplication of families and orders has consequently taken place. This is to be expected. It is a movement from Alpha towards Omega, but if it obscures and distorts the more practicable Alpha systems it is dangerous and undesirable. On the other hand the writer of a textbook is faced with the pedagogical problem of presenting a synthetic outline, not of a particular group, but of all groups, and he is obliged to react differently. He must keep to the Alpha line. His leading question must be, " What are the largest units which are scientifically permissible? " and he has to approach the classifications of the specialist with this in his mind. The outcome, like all compromises, is naturally open to criticism. The authors are prepared for this in regard to their own particular solution but wish to explain that their attempt to modify the angularities of specialist classifications has been based upon the conviction that it is more important, in the earlier stages of study, to recognize and emphasize similarities, rather than meticulously to discriminate differences.

With the exception of Thallophyta the limits and positions of the main Phyla of the Plant Kingdom are now generally recognized, though the position of the Charophyta is still uncertain. On the other hand, the Thallophyta have proved an unsatisfactory group, and many authorities would discard it altogether. This would be all the more advisable if the tendency to divorce the Fungi from the rest of the Plant Kingdom were to become more widely accepted. It may be desirable therefore to raise the Algae, the Fungi, possibly with the Lichens associated with them, and the Bacteria, each to Phylum rank, equal with the Bryophyta or Pteridophyta. The new names would therefore be: the Phycophyta, the Mycophyta and the Bacteriophyta.

Within these more primitive groups we may expect to find divergences of opinion most strongly expressed, and the methods of classification most variable. In fact, the more critically and extensively a group of organisms is studied, the more various become the methods of classification. The Lichens, which have been studied by comparatively few workers, still retain the same outline classification which was proposed over fifty years ago. On the other hand, because of the activity and number of mycologists, the Fungi have never settled down to any fixed system of classification. Similarly the Bryophyta have a relatively definite system, but the systematic arrangement of the Angiospermae is in a constant state of flux.

LAWS OF BOTANICAL NOMENCLATURE

If the names of plants are to have international value it is necessary that some body of rules should be adopted to govern nomenclature. Moreover, since it is quite possible for the same plant to be described and named by two independent investigators working independently at different times or in different parts of the world, some principle must be adopted to decide which name shall be accepted and which rejected. Again there must be a starting-point in respect of the names to be considered in the case of plants which have been known since ancient times. Bearing in mind that in pre-Linnean times botanical plant names were more like brief Latin descriptions than the binomial Latin names we are familiar with today, it is easily realized that the correct application of old names is often uncertain.

The first attempt to draw up a code of rules was made at the International Congress of Botanists held in Paris in 1867. The application of these rules evoked criticisms and a revision was undertaken at a further congress in Vienna in 1905, which was devoted mainly to this topic. The Rules of Nomenclature formulated at this congress have formed the basis of all subsequent discussions, and, though they have been amended and extended in later congresses, the greater part of the Vienna rules still apply.

The rules themselves are fairly simple in form and are considered binding upon all botanists. They are accompanied by a series of more extensive recommendations, which have not the force of rules and the observance of which is optional. The following excerpts from selected articles of the latest published code, that of 1950, include the rules of most general application.

Article 10. Every individual plant, interspecific hybrids and chimaeras excepted, belongs to a Species, every Species to a Genus, every Genus to a

Family, every Family to an Order, every Order to a Class and every Class to a Division.

Article 12. Where necessary these larger groups may be split up into intermediate groups by putting the prefix *sub* before the name of the group, *i.e.*, sub-Family, sub-Order, etc.

Article 16. Each group with a given circumscription, position and rank can bear only one valid name, the earliest that is in accordance with the Rules of Nomenclature.

Article 19. The name of a taxonomic group has no status under the Rules and no claim to recognition by botanists unless it is validly published.

Article 20. Legitimate botanical nomenclature begins for the different groups of plants at the following dates:

(*a*) Phanerogamia and Pteridophyta—1753 (Linnaeus, " Species Plantarum ", Ed., i).
(*b*) Musci—1801 (Hedwig, " Species Muscorum").
(*c*) Sphagnaceae and Hepaticae—1753 (Linnaeus, " Species Plantarum").
(*d*) Lichenes—1753 (Linnaeus, " Species Plantarum").
(*e*) Fungi (Uredinales, Ustilaginales, Gasteromycetes)—1801 (Persoon, " Synopsis Methodica Fungorum").
(*f*) Fungi (other than those above)—1821–32, Fries (" Systema Mycologicum").
(*g*) Algae—1753 (Linnaeus, " Species Plantarum "), with the exception of the Desmids—1848 (Ralfs, " British Desmidiaceae"), Oedogoniaceae—1900 (Hirn, " Monog. u. Ikonograph. d. Oedogoniaceen ") and certain groups of the Nostocaceae.
(*h*) Myxomycetes—1753 (Linnaeus, " Species Plantarum ").

The starting-point of the nomenclature of the Bacteria, Diatomaceae, Characeae and of some other groups, has not yet been decided. The nomenclature of Fossil Plants begins with the year 1820.

Article 21. To avoid disadvantageous changes in the nomenclature of genera by the strict application of the Rules of Nomenclature and especially of the principle of priority in starting from the dates given in Article 20, the Rules provide a list of names which must be retained as exceptions. These names are by preference those which have come into general use in the fifty years following their publication or which have been used in monographs and important floristic works up to the year 1890. Such names are known as *Nomina Conservanda*.

Article 23. Names of Families are taken from the name of one of their Genera, or from a synonym, and end in *-aceae*. Exceptions. 1. The following names, sanctioned by long usage, are treated as exceptions to the Rule: Palmae, Gramineae, Cruciferae, Leguminosae, Guttiferae, Umbelliferae, Labiatae, Compositae. Botanists are authorized however to use as alternatives the appropriate names ending in *-aceae*. 2. Those who regard the Papilionaceae as constituting an independent family may use that name, although it is not formed in the prescribed manner.

Article 24. Names of sub-Families are taken from the name of one of the genera in the group, with the ending *-oideae.* Similarly for tribes with the ending *-eae* and for sub-tribes with the ending *-inae.*

Article 27. Names of species are binary combinations, consisting of the name of the Genus followed by a single specific epithet. The specific epithet when adjectival in form and not used as a substantive agrees in gender with the generic name.

Article 38. From 1st January 1935 names of new groups of recent plants, the Bacteria excepted, are considered as validly published only when they are accompanied by a Latin diagnosis.

Article 46. For the indication of the name of a group to be accurate and complete and in order that the date may be readily verified it is necessary to cite the author who first published the name in question.

Article 49. When a genus or a group of lower rank is altered in rank but retains its name or epithet, the original author must be cited in parenthesis, followed by the name of the author who effected the alteration. The same holds when a subdivision of a genus, a species or a group of lower rank is transferred to another genus or species with or without alteration of rank.

Article 61. A name of a taxonomic group is illegitimate and must be rejected if it is a later homonym, that is if it duplicates a name previously and validly published for a group of the same rank based on a different type.

Article 69. In cases foreseen (under the Rules) the name or epithet to be rejected is replaced by the oldest legitimate name. If none exists a new name or epithet must be chosen.

Article 74. These Rules can be modified only by competent persons at an International Botanical Congress convened for the express purpose.

The Third International Congress was held in Brussels in 1910 and confirmed the rules proposed by the Vienna Congress. The Fourth International Congress, which should have been held in 1915, was postponed owing to the First World War and was held in Ithaca, U.S.A., in 1926. At this congress no changes in the Rules of Nomenclature were made and it was left to the Fifth International Congress held at Cambridge in 1930 to make further changes.

The Sixth International Congress was held in Amsterdam in 1935 and the Seventh Congress, which should have been held in 1940, was postponed until 1950 in Stockholm, owing to the Second World War.

THE ALGAE

The history of the systematic arrangement of the Algae starts from Linnaeus in 1753, but it is only within the last hundred years that sufficient has been known of the internal structure and methods of reproduction to make an attempt at a natural arrangement possible. The first important contribution to the subject was the publication by Dawson Turner (1808–19) of "The Fuci", an ambitious work in four volumes, containing coloured pictures of many species. His facts were based upon his own observations, made on specimens provided for him by Robert Brown and other botanical travellers, and did much to clarify the knowledge of seaweeds. In the same year that Turner completed his work, Lyngbye published his "Tentamen Hydrophytologiae Danicae" which was another valuable contribution to algology. The first truly comprehensive treatment of the Algae came from the pen of J. G. Agardh and was published serially between 1848 and 1898. This monumental work, entitled "Species, Genera et Ordines Algarum", did for the Algae what Persoon did for the Fungi, and provided the foundation for a general knowledge of the group. In 1843 Kutzing published his "Phycologia Generalis" and later in 1860–1 his "Tabulae Phycologicae", both of which contributed much new material, especially a series of excellent figures. The classic contribution of Thuret and Bornet, "Etudes Phycologiques", appeared in 1878 with very fine illustrations and helped to encourage the microscopic study of the reproductive organs of the Algae, and from that time the study of algology became much more widely undertaken.

The earlier study of the Algae soon revealed similarities between the reproductive organs of certain genera and those of the Fungi. It is not surprising therefore to find that Fungi were regarded as Algae which had lost their chlorophyll. Accordingly, to each of the main groups of Algae were appended certain fungal groups which it was thought had been derived from them. This view was maintained for a considerable time and it was not until well into the twentieth century that the separate derivation of the Fungi and the Algae was generally accepted.

The most extensive systematic work on the Algae was by de Toni, whose "Sylloge Algarum" appeared in a series of volumes published between 1889 and 1924. Unfortunately the phylogenetic study of Algae advanced so much during this long period that the method of classification was already somewhat out of date before the last volume appeared. The work, however, is of great value in that it contains precise descriptions of a great proportion of all the known algal species.

The first system of classification which we must consider in detail is that of Engler and Prantl in the "Natürliche Pflanzenfamilien". Since this system considers the Fungi to be at least in part derived from the Algae, the classification of the two groups is to some extent mixed.

The following is therefore an outline of the classification by Engler published in the "Syllabus der Pflanzenfamilien", seventh edition, 1912:

I. **Schizophyta**
  1. Schizomycetes (*i.e.*, Bacteria)
  2. Schizophyceae (*i.e.*, Blue Green Algae)

II. **Phytosarcodina, Myxothallophyta** or **Myxomycetes**
  1. Acrasiales
  2. Plasmodiophorales
  3. Myxogastres (*i.e.*, Myxomycetales)

III. **Flagellata**
  1. Pantostomatinales
  2. Distomatinales
  3. Protomastigales
  4. Chrysomonadales
  5. Cryptomonadales
  6. Chloromonadales
  7. Euglenales

IV. **Dinoflagellata**

V. **Bacillariophyta**

VI. **Conjugatae**

VII. **Chlorophyceae**
  1. Protococcales
  2. Confervales
  3. Siphonocladiales
  4. Siphonales

VIII. **Charophyta**

IX. **Phaeophyceae**
  1. Phaeosporeae
  2. Cyclosporeae
  3. Dictyotales

X. **Rhodophyceae**
  1. Bangiales
  2. Florideae
    (*a*) Nemalionales
    (*b*) Gigartinales
    (*c*) Rhodymeniales
    (*d*) Cryptonemiales

XI. **Eumycetes** (Fungi)
  1. Phycomycetes
    (*a*) Zygomycetes
    (*b*) Oomycetes
  2. Ascomycetes
    (*a*) Euascales
    (*b*) Laboulbeniales
  3. Basidiomycetes
    α. Hemibasidii
      (*a*) Hemibasidiales
    β. Eubasidii
      (*a*) Protobasidiomycetes
      (*b*) Autobasidiomycetes

In 1904 Oltmanns published his large work on the Algae under the title "Morphologie und Biologie der Algen". This work, which was revised in 1922, was not primarily systematic but he gave an arrangement of the Algae which has had considerable influence. It is reproduced below:

I. **Chrysophyceae**
  1. Chrysomonadales

II. **Heterokontae**
  1. Heterochloradales
  2. Heterococcales
  3. Heterotrichales
  4. Heterosiphonales

III. **Cryptomonadales**

IV. **Euglenaceae**

V. **Dinoglagellata**

VI. **Conjugatae**

VII. **Bacillariaceae**

VIII. **Chlorophyceae**
  1. Volvovales
  2. Protococcales
  3. Ulotrichales
  4. Siphonocladiales
  5. Siphonales

IX. **Charales**

X. **Phaeophyceae**
  1. Ectocarpales
  2. Sphacelariales

X. **Phaeophyceae**—*contd.*
  3. Cutleriales
  4. Laminariales
  5. Tilopteridales
  6. Dictyotales
  7. Fucales

XI. **Bangiales**

XII. **Rhodophyceae** (Florideae)
  1. Nemalionales
  2. Gigartinales
  3. Rhodymeniales
  4. Ceramiales

In 1916 West published his monograph on the Green Algae, with which he included the Myxophyceae (Cyanophyceae), Peridinieae, Bacillarieae (Diatomaceae) and the Chlorophyceae. West never gave a full classification of the Algae as a whole, but his treatment of the Chlorophyceae has had so much influence on the teaching of the group in Britain that an outline of his classification may be given. It was influenced largely by the suggestions put forward by Bohlin in 1901 and Blackman and Tansley in 1902.

CHLOROPHYCEAE

I. **Isokontae**
  1. Protococcales
  2. Siphonales
  3. Siphonocladiales
  4. Ulvales
  5. Schizogoniales
  6. Ulotrichales

II. **Akontae**
  1. Conjugatae

III. **Stephanokontae**
  1. Oedogoniales

IV. **Heterokontae**
  1. Heterococcales
  2. Heterotrichales
  3. Heterosiphonales

Meanwhile in America various modifications of these systems were produced, which may be said to have culminated in the proposals set out by Smith in his " Cryptogamic Botany " published in 1938. Smith elevates the main groups of the Algae to phylum rank and dispenses with the old term Thallophyta. The following is an outline of his proposals:

I. **Chlorophyta**
  α. *Chlorophyceae*
    1. Volvocales
    2. Tetrasporales
    3. Ulotrichales
    4. Ulvales
    5. Schizogoniales
    6. Cladophorales
    7. Oedogoniales
    8. Zygnematales
    9. Chlorococcales
    10. Siphonales
    11. Siphonocladiales
  β. *Charophyceae*

II. **Euglenophyta**
  1. Euglenales
  2. Colaciales

III. **Pyrrophyta**
  α. *Cryptophyceae*
  β. *Desmokontae*
  γ. *Dinophyceae*
    1. Gymnodiniales
    2. Peridiniales
    3. Dinophysidales
    4. Rhizodiniales
    5. Dinocapsales
    6. Dinotrichales
    7. Dinococcales

IV. **Chrysophyta**
  α. *Xanthophyceae*
    1. Heterochloridales
    2. Rhizochloridales
    3. Heterocapsales

  4. Heterotrichales
  5. Heterococcales
  6. Heterosiphonales
- β. *Chrysophyceae*
  1. Chrysomonadales
  2. Rhizochrysidales
  3. Chrysocapsales
  4. Chrysotrichales
  5. Chrysosphaeriales
- γ. *Bacillariophyceae*
  1. Centrales
  2. Pennales

V. **Phaeophyta**
- α. *Isogeneratae*
  1. Ectocarpales
  2. Sphacelariales
  3. Tilopteridales
  4. Cutleriales
  5. Dictyotales
- β. *Heterogeneratae*
  - (i) *Haplostichineae*
    1. Chordariales
    2. Sporochnales
    3. Desmarestiales
  - (ii) *Polystichineae*
    1. Punctariales
    2. Dictyosiphonales
    3. Laminariales
- γ. *Cyclosporeae*
  1. Fucales

VI. **Cyanophyceae**
- α. *Myxophyceae*
  1. Chroococcales
  2. Chamaesiphonales
  3. Hormogonales

VII. **Rhodophyta**
- α. *Rhodophyceae*
  - (i) *Bangioideae*
    1. Bangiales
  - (ii) *Florideae*
    1. Nemalionales
    2. Gelidiales
    3. Cryptonemiales
    4. Gigartinales
    5. Rhodymeniales
    6. Ceramiales

The latest and by far the most comprehensive and authoritative account of the Algae is that published by Fritsch. In a revision of West's " British Freshwater Algae", published in 1927, Fritsch gave some indication of the new ideas on classification which he was maturing, but it was not until 1935, when the first volume of his large work on " The Structure and Reproduction of Algae " appeared, that the import of these new ideas could be appreciated. The first volume deals mainly with the Green Algae while the second, which appeared ten years later, covers the Brown and Red Seaweeds.

It is not possible here to give more than a summary of this elaborate classification and students should consult the original work for a fuller treatment of the subject.

I. **Chlorophyceae** (Isokontae)
1. Volvocales
2. Chlorococcales
3. Ulotrichales
4. Cladophorales
5. Chaetophorales
6. Oedogoniales
7. Conjugales
8. Siphonales
9. Charales

II. **Xanthophyceae** (Heterokontae)
1. Heterochloridales
2. Heterococcales
3. Heterotrichales
4. Heterosiphonales

- III. **Chrysophyceae**
  - 1. Chrysomonadales
  - 2. Chrysosphaerales
  - 3. Chrysotrichales
- IV. **Bacillariophyceae**
- V. **Cryptophyceae**
  - 1. Cryptomonadales
  - 2. Cryptococcales
- VI. **Dinophyceae** (Peridinieae)
  - A. Desmokontae
  - B. Dinokontae
    - 1. Dinoflagellata
    - 2. Dinococcales
    - 3. Dinotrichales
- VII. **Chloromonadineae**
- VIII. **Euglenineae**
- IX. **Phaeophyceae**
  - 1. Ectocarpales
  - 2. Tilopteridales
  - 3. Cutleriales
  - 4. Sporochnales
  - 5. Desmarestiales
  - 6. Laminariales
  - 7. Sphacelariales
  - 8. Dictyotales
  - 9. Fucales
- X. **Rhodophyceae**
  - α. *Bangioideae*
    - 1. Bangiales
  - β. *Florideae*
    - 1. Nemalionales
    - 2. Gelidiales
    - 3. Cryptonemiales
    - 4. Gigartinales
    - 5. Rhodymeniales
    - 6. Ceramiales
- XI. **Myxophyceae** (Cyanophyceae)
  - 1. Chroococcales
  - 2. Chamaesiphonales
  - 3. Pleurocapsales
  - 4. Nostocales
  - 5. Stigonematales

In comparing the various systems in their historical sequence it may be noticed that the differences lie chiefly in the grouping of the orders. The orders themselves have remained fairly constant throughout, although their number has tended to grow somewhat through the separation of parts of the older orders under new names by later authors.

THE FUNGI

In 1801 C. H. Persoon published his "Synopsis Methodica Fungorum", which was the first serious attempt to classify and describe the then known Fungi of the whole world. It was an ambitious task but his references to exotic fungi were so few that his work covers little more than European mycology. The chief value of the work lies in the careful descriptions of those Fungi he includes, which, besides the larger macro-Fungi, embrace many micro-forms. His work is regarded as the starting-point of the nomenclature of the Rusts, Smuts and Gasteromycetes. Persoon arranged the species into Classes, Orders and Families and gave a brief diagnosis of each. The Puff Balls and the Myxomycetes are grouped together because both have closed fruiting bodies, a policy which was adopted by many later writers.

During the next twenty years a number of descriptions were published of collections of Fungi made in various parts of the world and our knowledge of tropical Fungi greatly increased, but no work of general systematic importance appeared till Elias Fries (Fig. 2059) completed his " Systema Mycologicum " between 1821 and 1829. This work was a full account of all the Fungi known to that date and provided a complete classification of the species. His work is taken as the starting-point for nomenclature of all the groups of Fungi not accepted from Persoon's work.

The work of Persoon and Fries offered a natural method of classification of the Fungi during the earliest part of the nineteenth century, indeed Fries expressly sought a natural system, so that the classification of the Fungi was decidedly in advance of the Algae at the same period. In 1837 the French botanist Leveille recognized the Ascomycetes and Basidiomycetes as two main groups and thus signposted the way for future work.

Fig. 2059.—Elias Fries. From Dorffler, " Botaniker Porträts ".

Fig. 2060.—Anton de Bary.

In the years that followed micro-fungi were subjected to increasingly critical study. The work of the brothers Tulasne and of de Bary, the latter particularly, on the Smuts and the Mildews opened up a host of new problems, and with the discovery of many new species led to a reconsideration of classification. De Bary's (Fig. 2060) classical work on the Smuts (1853) and his more general work, " The Comparative Morphology and Biology of the Fungi", published in 1866, presented many new observations, including the discovery of heteroecism, and was the first work to recognize the Phycomycetes as a distinct class.

The year 1882 saw the publication of the first volume of Saccardo's " Sylloge Fungorum Omnium Hucusque Cognitorum", which was carried on by a succession of collaborators almost up to the present time. The counterpart of de Toni's " Sylloge Algarum", its value lies in the precise description of species rather than in the method of classification.

With the growth of the subject monographical works began to appear dealing with the classification of certain groups of Fungi. Among these we may mention the work of Patouillard, who in his "Essai Taxonomique", published in 1900, developed a scheme of classification of the higher Basidiomycetes based on hymenial characters. Mention may also be made of Zopf, whose "Die Pilze", published in 1890, gives the best general account of what was then known of the lower Phycomycetes.

Among the general systematic descriptions of the Fungi which we must consider in some detail, the first is that by Schröter (1897) in the "Pflanzenfamilien" of Engler and Prantl. The outline of this classification is given below:

- I. **Phycomycetes**
  - A. *Oomycetes*
    - (*a*) Sporangieae
      - 1. Hemisporangieae
        - Chytridineae
        - Ancylistineae
      - 2. Eusporangieae
        - Monoblepharidineae
        - Saprolegnineae
    - (*b*) Conidieae
      - Cystopodineae
      - Peronosporineae
  - B. *Zygomycetes*
    - (*a*) Sporangieae
      - Mucorineae
    - (*b*) Conidieae
      - Entomophthorineae
- II. **Eumycetes**
  - A. *Ascomycetes*
    - (*a*) Hemiasceae
      - Protomycetineae
      - Ascoidineae
    - (*b*) Euasceae
      - 1. Protoasceae
        - Saccharomycetineae
        - Endomycetineae
      - 2. Holasceae
      - α. Hymenioasceae
        - x. Gymnocarpeae
          - Taphrineae
          - Helvellineae
        - xx. Hemicleistocarpeae
          - Pezizineae
          - Phacidiineae
        - xxx. Cleistocarpeae
          - Tuberineae
      - β. Plectasceae
        - Gymnoascineae
        - Elaphomycetineae
      - γ. Pyrenoasceae
        - Perisporiineae
        - Sphaeriineae
        - Hysteriineae
        - Laboulbeniineae
  - B. *Basidiomycetes*
    - (*a*) Hemibasidieae
      - Ustilagineae
      - Tilletiineae
    - (*b*) Eubasidieae
      - 1. Protobasidieae
      - α. Phragmobasidieae
        - Uredineae
        - Auricularineae
      - β. Schizobasidieae
        - Tremellineae
        - Dacryomycetineae
      - 2. Holobasidieae
      - α. Hymenobasidieae
        - x. Gymnocarpeae
          - Exobasidiineae
          - Thelephorineae
          - Clavariineae
          - Hydneineae
          - Polyporineae
        - xx. Hemiangiocarpeae
          - Boletineae
          - Agaricineae
          - Phallineae

- xxx. Angiocarpeae
    - Hymenogastrineae
    - Lycoperdineae
    - Nidulariineae
- β. Plectobasidieae
    - Sclerodermineae

III. **Fungi Imperfecti**
1. Sphaeropsidales
2. Melanconiales
3. Hyphomycetes

From it we see that Schröter has accepted the idea that the Phycomycetes are not simply Chlorophyceae which have lost their chlorophyll, as had been previously maintained, but a separate group forming the lowest class of the true Fungi. This system therefore was in advance of that formulated by Lotsy in his " Vorträge über die botanische Stammesgeschichte", the first volume of which appeared in 1907.

Schröter's system maintained its popularity for a considerable time, during which a number of monographical accounts of individual groups of the Fungi appeared. It is unnecessary here to mention more than a few. Among those most noteworthy are Lister's " Mycetozoa " (1894), Massee's " Myxogastres " (1892), " British Fungus Flora " (Hymenomycetes and Ascomycetes) (1892–5), " Mildews, Rusts and Smuts " (1913), Smith's " British Basidiomycetes " (1908), Grove's " British Rust Fungi " (1913), Rea's " British Basidiomycetae " (1922), Coker's " Saprolegniaceae " (1923), " Clavariaceae " (1923) and " Gasteromycetes " (1928), Stevens' " Fungi which cause Plant Disease " (1921) and Cunningham's " Gasteromycetes " (1944).

Systematic mycology was greatly enlarged by these works, but the system of classification was more influenced by the publication in Europe of Rabenhorst's " Kryptogamenflora von Deutschland, Oesterreich und der Schweiz", the fungal volumes of which were published between 1884 and 1918, and the " Kryptogamen Flora der Mark Brandenburg", which appeared between 1909 and 1915 under the editorship of G. Lindau.

In Britain the most important revision of the classification of the Fungi was due to Gwynne Vaughan, who in 1922 published a volume on the " Ascomycetes, Ustilaginales and Uredinales". This was followed in 1927 by a further volume, " The Fungi", by Gwynne Vaughan and Barnes, in which an account of all the groups of the Fungi was included. The following is an outline of the classification adopted in the latter work:

A. **PHYCOMYCETES**

I. **Archimycetes**
1. Chytridiales
2. Ancylistales
3. Protomycetales

II. **Oomycetes**
1. Monoblepharidales
2. Saprolegniales
3. Peronosporales

III. **Zygomycetes**
1. Mucorales
2. Entomophthorales

B. **ASCOMYCETES**

I. **Plectomycetes**
1. Plectascales
2. Erysiphales
3. Exoascales

II. **Discomycetes**
  1. Pezizales
  2. Helvellales
  3. Tuberales
  4. Phacidiales
  5. Hysteriales

III. **Pyrenomycetes**
  1. Hypocreales
  2. Dothideales
  3. Sphaeriales
  4. Laboulbeniales

C. **BASIDIOMYCETES**

I. **Hemibasidiomycetes**
  1. Ustilaginales

II. **Protobasidiomycetes**
  1. Uredinales
  2. Auriculariales
  3. Tremellales

III. **Autobasidiomycetes**
  1. Hymenomycetales
  2. Gasteromycetales

D. **FUNGI IMPERFECTI**
  1. Hyphomycetales
  2. Melanconiales
  3. Sphaeropsidales

Meanwhile Gaumann had published in Switzerland his " Vergleichende Morphologie der Pilze " in 1926. Making use of recent advances in our knowledge of the cytology of the Fungi he was able to show relationships between Fungi hitherto widely separated in systematic position. As a result he considerably altered the method of classification. In 1928 Dodge translated and extensively altered Gaumann's original work in an attempt to make the work more readily available to American readers. This book, " Comparative Morphology of Fungi", is now (1951) regarded as the standard American work and we give below an outline of the classification used therein.

I. **Archimycetes**

II. **Phycomycetes**
  1. Chytridiales
  2. Oomycetales
  3. Zygomycetales

III. **Ascomycetes**
  α. *Hemiascomycetes*
    1. Endomycetales
    2. Taphrinales
  β. *Euascomycetes*
    1. Plectascales
    2. Perisporiales
    3. Myriangiales
    4. Hypocreales
    5. Sphaeriales
    6. Dothideales
    7. Hysteriales
    8. Hemisphaeriales
    9. Phacidiales
    10. Pezizales
    11. Tuberales
    12. Laboulbeniales

IV. **Basidiomycetes**
  1. Polyporales
  2. Agaricales
  3. Gasteromycetes
  4. Tremellales
  5. Cantharellales
  6. Dacryomycetales
  7. Auriculariales
  8. Uredinales
  9. Ustilaginales

V. **Fungi Imperfecti**
  1. Hyphomycetes
  2. Melanconiales
  3. Sphaeropsidales

In regard to the Fungi Imperfecti the authors express the view that, since the classification of the Fungi is based upon the structure of the sexual reproductive organs, which are lacking in the Fungi Imperfecti, any classification of them must be purely artificial. They therefore put forward no new views and follow those laid down in the first edition of Saccardo. The Myxomycetes they exclude from the classification as well as the Acrasiales, a view which was shared by Gwynne Vaughan and Barnes, who excluded the Plasmodiophorales. Later specialists on these groups, however, have shown their striking similarity to the Chytridiales and they are now usually included among the lower Fungi.

In 1930 Fitzpatrick published his " Lower Fungi; Phycomycetes " in which he outlined his ideas of the relationship of the lower Fungi to the rest of the Plant Kingdom. Since this takes into account recent work it is desirable to quote his outline of the Thallophyta:

I. **Myxothallophyta**
  α. *Acrasieae*
  β. *Labyrinthulideae*
  γ. *Myxomycetes*
    1. Exosporeae
    2. Endosporeae
II. **Euthallophyta**
  α. *Bacteria* (Schizomycetes)
  β. *Fungi*
    1. Phycomycetes
    2. Ascomycetes
    3. Basidiomycetes
    4. Fungi Imperfecti
  γ. *Lichenes*
  δ. *Algae*
    1. Cyanophyceae
    2. Chlorophyceae
    3. Phaeophyceae
    4. Rhodophyceae

Though agreeing with Gaumann and Dodge in excluding the Myxomycetes and the Acrasieae from the true Fungi it is interesting to find these groups elevated to such a relatively important position. The Plasmodiophorales here are included in the Chytridiales.

In the same volume of " Cryptogamic Botany " as that containing the Algae, Smith also treats the Fungi. He does not entirely follow Dodge but enlarges the classification of the Fungi still further, incorporating the lower groups referred to above, while at the same time expanding the Phycomycetes to include additional forms. The following is an outline of his method:

I. **Myxothallophyta**
  α. *Myxomycetae*
    1. Endosporeae
    2. Exosporeae
  β. *Phytomyxinae*
    1. Plasmodiophorales
  γ. *Acrasiae.*
    1. Acrasiales
II. **Eumycetae**
  α. *Phycomycetae*
    1. Chytridiales
    2. Blastocladiales
    3. Monoblepharidales
    4. Ancylistales
    5. Saprolegniales
    6. Peronosporales
    7. Mucorales
    8. Entomophthorales
  β. *Ascomycetae*
    1. Aspergillales
    2. Erysiphales
    3. Hysteriales

II. **Eumycetae**—*contd.*
4. Phacidiales
5. Pezizales
6. Tuberales
7. Helvellales
8. Exoascales
9. Hypocreales
10. Sphaeriales
11. Dothideales
12. Laboulbeniales

γ. *Basidiomycetae* *
(i) *Eubasidii*
1. Agaricales
2. Lycoperdales
3. Dacryomycetales
4. Tremellales
5. Auriculariales

(ii) *Hemibasidii*
1. Uredinales
2. Ustilaginales

III. **Fungi Imperfecti**
1. Moniliales
2. Melanconiales
3. Sphaeropsidales
4. Mycelia sterilia

The Second World War interrupted the publication of a work which might have become a standard treatment of the higher Fungi, namely the "Atlas des Champignons de l'Europe", edited by Karina and Pilat. This work which was to have run into a number of volumes was intended to describe and illustrate by photographs all the genera of the higher Fungi. Many changes in nomenclature are introduced but at present the work, which was published in Prague, is too incomplete to judge its final importance.

In 1943 Sparrow published his "Aquatic Phycomycetes", which deals more fully with the question of the relationships of the lower groups, a problem which is likely to continue for a long time to exercise the minds of mycologists, because of its bearing on the origin of the Fungi. Indeed the whole question of the classification of the Fungi is one of the most debatable subjects in plant classification and there is little probability of any major agreement being reached in the near future.

THE BACTERIA

Although the Bacteria were discovered by Leeuwenhoek in the seventeenth century, it was not until the middle of the nineteenth century that they were accepted as plants. Before that they were supposed rather vaguely to belong to the Infusoria, an animal group made up mostly of Protozoa. In 1857 Nageli founded a class of Fungi, the Schizomycetes, or "Splitting Fungi", to include the Bacteria, the characteristics of the class being that the organisms were unicellular and that their reproduction was by simple fission of the cells. Some of the genera still recognized were, however, founded before that date, for example *Bacterium*, *Spirillum* and *Spirochaeta*, which were established by Ehrenberg on the basis of their microscopical appearance. The first attempt to group the genera of Bacteria into families was made by Ferdinand Cohn in 1872, based also on microscopical form.

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* One peculiar point about this system is the apparent lack of any recognition of the Bracket Fungi usually included in the Polyporaceae and placed by many in the Aphyllophorales.

It was not until 1880, when Koch's method of cultivating Bacteria on solid media came into use, that an attempt was made to base a classification on growth characters. Since that time, beginning with Zopf's "Die Spaltpilze", published in 1883, very numerous classifications have been proposed, in the endeavour to combine both sets of characteristics, namely the microscopical form and the growth habit. No finality was reached, but among the treatises produced in the attempt were several of considerable importance, such as those by Lehmann and Neumann, by Alfred Fischer and by Migula. Biochemical criteria were first employed in 1905 by the Winslows and this method was made the foundation of a detailed classification by Orla Jensen in 1909. The investigation of Bacteria was so much in the hands of medical men, to whom classification was only of minor interest, that the nomenclature in the literature became very confused. To remedy this the American Society of Bacteriologists appointed a committee in 1917 to apply the international rules of priority and to evolve a legitimate system. They proposed six orders:

1. Eubacteriales
2. Actinomycetales
3. Chlamydobacteriales
4. Thiobacteriales
5. Myxobacteriales
6. Spirochaetales

since increased to seven by the discovery of the Caulobacteria. Of these orders the first is by far the largest, some of the others containing only a single family. This classification was embodied and developed in successive editions of Bergey's "Determinative Bacteriology" and was generally accepted as authoritative. In the sixth edition it was, however, greatly altered in detail. It is doubtful at present whether the latest arrangement will prove better than the former, though it is an improvement in some respects. The orders adopted are as follows:

1. Eubacteriales
    - (i) Eubacteriineae
    - (ii) Caulobacteriineae
    - (iii) Rhodobacteriineae
2. Actinomycetales
3. Chlamydobacteriales
4. Myxobacteriales
5. Spirochaetales

THE LICHENS

Although interest in the Lichens as a source of dyes may go back as far as Theophrastus, it was not until 1867 that Schwendener announced his theory of their dual nature. Prior to that time attempts to classify the Lichens reflected the inability of the authors to understand their true nature and we need not consider them here.

The first successful attempt to arrange the Lichens in a true natural system is due to Reinke in his "Abhandlungen über die Flechten", published between 1894 and 1896. Though several monographical studies of certain groups of the Lichens followed, it was left to Zahlbrückner in Engler's "Pflanzenfamilien" to compile a complete arrangement of the Lichens along modern lines. His system may be summarized as follows:

I. **Ascolichenes**
  α. *Pyrenocarpeae*
  β. *Gymnocarpeae*
    1. Coniocarpineae
    2. Graphidineae
    3. Cyclocarpineae
II. **Hymenolichenes**

This system has received wide acceptance and was followed by Lorrain Smith in her monograph of the Lichens, published by the British Museum in 1921. The systematics of the Lichens have been further revised in detail by Zahlbrückner in the second edition of Engler's "Pflanzenfamilien", published in 1926, but he has made no fundamental change in his original method.

THE CHAROPHYTA

The Charophyta have had a chequered career so far as their systematic position is concerned, due mainly to the fact that their reproductive organs for long remained a botanical puzzle. The difficulty lies in the marked differences which they exhibit from any other known living types. Early writers grouped the Charophyta either with the genus *Equisetum* or with *Hippuris* on account of their superficial resemblance to these plants. Later the group was variously included in the Naiadaceae, in the Bryophyta, in the Vascular Cryptogams and finally in the Algae.

Strasburger placed them in a separate class of the Thallophyta, while Sachs separated them as a phylum, the Charophyta, equal in rank with the Thallophyta. Modern tendencies have been to transfer them to the Algae. Oltmanns treated them as a separate group of the Algae, equal in rank with the Chlorophyceae, while Fritsch in his later work includes them in the Chlorophyceae.

The most comprehensive treatment of the group was that written by Braun and published in Rabenhorst's "Kryptogamenflora" between 1877 and 1879. The only modern treatment in English is due to Grove and Bullock Webster, who between 1920 and 1924 published two volumes illustrating all the British species under the title of "The British Charophyta". In this they follow the same system of classification as Braun, which we may summarize as follows:

1. *Nitelleae.* Including the genera *Nitella* and *Tolypella.*
2. *Chareae.* Including the genera *Nitellopsis*, *Lamprothamnion* and *Chara.*

Fossil evidence indicates that the group is of great antiquity. It will probably remain a matter of opinion whether the peculiarities of their reproductive organs and their high degree of thallus specialization do, or do not, justify the separation of the Charophyta into a separate phylum.

THE BRYOPHYTA

The main classification of the Bryophyta has presented few difficulties and it is only in detail that the various modern systems differ. Hedwig (Fig. 2061) was the first to propose a general system of classification of the Bryophyta but restricted his detailed study to the Mosses. This method was published in 1801 in his "Species Muscorum". Using the peristome as the most important character, he recognized thirty-five genera of Mosses. This work was followed by that of Brunch, Schimper and Guembel who between 1836 and 1855 published the "Bryologia Europaea". Using vegetative characters to a greater extent than previously, they recognized some 135 genera. With minor modifications this system was adopted by Brotherus in his account of the Mosses in the "Pflanzenfamilien".

FIG. 2061.—Johannes Hedwig. (*After an engraving by Schnorr.*)

Meanwhile work had been done on the classification of the Liverworts, but the first natural system appeared considerably later than that of the Mosses. It was due to Endlicher and appeared in his "Synopsis Hepaticarum", which was published in 1841. This system was followed by most writers up to 1875 when Lindberg published his "Hepaticae in Hibernia lecta" and proposed a different system in which the number of main groups was reduced to three.

In 1893 Schiffner used a somewhat different system in his treatment of the Hepaticae in the "Pflanzenfamilien". The following is a summary of the classification as it appears in Engler's "Syllabus der Pflanzenfamilien":

I. **Hepaticae**
    1. Marchantiales
    2. Anthocerotales
    3. Jungermanniales

II. **Musci**
    1. Sphagnales
    2. Andreaeales
    3. Bryales
        α. Acrocarpi
        β. Pleurocarpi

Cavers in his papers on "The Interrelationships of the Bryophyta", which appeared in the "New Phytologist" in 1911, suggested that the terms Musci and Hepaticae should be dropped and that the Bryophyta should be considered merely as a series of orders. He did this because he thought there was a gradual transition from the one to the other group. His system may be summarized as follows:

1. Sphaerocarpales
2. Marchantiales
3. Jungermanniales
4. Anthocerotales
5. Sphagnales
6. Andreaeales
7. Tetraphidales
8. Polytrichales
9. Buxbaumiales
10. Eubryales

This fusion of the two groups did not find much support among other writers and we find that Dixon in his " Students' Handbook of the British Mosses", and MacVicar in his " Students' Handbook of the British Hepatics", published in 1896 and 1912 respectively, and in the subsequent later editions, retain the separation of the two groups from one another. Their methods of classification, however, follow in the major groups the system laid down by the Engler Syllabus.

Classification is the subject of two articles in the " Manual of Bryology " published in 1932, the one on the Mosses written by Dixon and the other on the Hepaticae contributed by Verdoorn. The outline of these systems is appended below and may be regarded as the most modern system of classification.

I. **Musci**
  α. *Sphagnales*
  β. *Andreaeales*
  γ. *Bryales*
    (i) *Nematodonteae*
      1. Tetraphidales
      2. Calomniales
      3. Buxbaumiales
      4. Polytrichales
    (ii) *Arthrodonteae*
      1. Fissidentales
      2. Grimmiales
      3. Dicranales
      4. Syrropodontales
      5. Pottiales
      6. Encalyptales
      7. Orthotrichales
      8. Funariales
      9. Eubryales
      10. Isobryales
      11. Hookeriales
      12. Hypnobryales

II. **Hepaticae**
  α. *Hepaticales*
      1. Jungermanniales acrogynae
        (*a*) Haplomitreae
        (*b*) Macvicareae
      2. Jungermanniales anacrogynae
      3. Sphaerocarpales
      4. Marchantiales
  β. *Anthocerotales*
      1. Anthocerotales

THE PTERIDOPHYTA

The classification of the Pteridophyta presents problems not encountered in any of the previous groups, due to their greater complexity and diversity of structure. Within the group there are two separate trends of divergence. The first is in regard to the relative size of the foliage and the stem, one line tending towards relatively minute leaves, the other towards leaves of increasing size. The second trend is to the appearance of heterospory in certain groups. These two apparently fundamental features do not, however, show any close correlation and a classification employing the one feature cuts right across one employing the other.

Apart from this, our ever-increasing knowledge of the fossil Pteridophyta and the large number of early types described, which do not fit into the groups of recent forms, make a basis of classification the more difficult to find.

Classifications published before about 1910 can therefore only be considered as applying to present-day genera, for prior to that date our knowledge of fossil Pteridophyta was too imperfect to exercise much influence upon classification.

Historically we may, however, note that Linnaeus in his "Species Plantarum" recognized some 200 species of Ferns and their allies, which he divided among sixteen genera. After this the first general account of the known Ferns was contributed by O. Swartz, who in 1806 described about 700 species in his "Synopsis Filicum". Nineteenth-century writers based their classification mainly on soral characters,* but in 1836 Presl made use of venation and vascular structures in his classification, published in his "Tentamen Pteridographiae". Robert Brown in 1810 laid down four of the families of living Ferns and these were added to by later writers, so that Mettenius in 1857–9 lists seven families out of the twelve recognized by Christensen in 1938. Between 1838 and 1842 W. J. Hooker (Fig. 2062) produced his great work, the "Genera Filicum". This was followed between 1844 and 1864 by the "Species Filicum" and later by the "Synopsis Filicum" (1865–8), the latter being worked out after his death by Baker. In this last work some 2,000 species were described. In 1905–6 Christensen published his "Index Filicum" with about 6,000 species of Ferns and their allies.

FIG. 2062.—Sir William James Hooker.

The classification of the whole of the Pteridophyta set out in Engler's "Syllabus der Pflanzenfamilien" adopted the following system:

1. *Filicales*
    - α. Filicales Leptosporangiatae
        - Eufilicineae
        - Hydropteridineae
    - β. Marattiales
    - γ. Ophioglossales
2. *Sphenophyllales*
3. *Equisetales*
    - α. Euequisetales
    - β. Calamariales

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* Hooker laid down the condition that no character was admissible in the classification of Ferns which could not be observed with a hand lens on an herbarium specimen!

4. *Lycopodiales*
    - α. Lycopodiales Eligulatae
    - β. Lycopodiales Ligulatae
        - Selaginellineae
        - Lepidophytineae
5. *Psilotales*
6. *Isoetales*
7. *Cycadofilices*

Shortly after this had appeared it became known that the members of the Cycadofilices bore seeds, so this group was transferred, with some doubt, to the Gymnospermae. Botanists were not, however, truly happy about this change and we find in 1909 that Lotsy, impressed by the significance of leaf shape and size, adopted the valuable terms Lycopsida, for the types with small leaves, and Pteropsida, for those with relatively large ones. These terms had been introduced by Jeffrey in 1902, but that author did not embody them in a detailed classification. The latter term is applied beyond the limits of the Pteridophyta, as the following scheme will indicate.

A. **Lycopsida**
1. Sphenophyllales
2. Equisetales
3. Psilotales
4. Lycopodiales

B. **Pteropsida**
1. Filicales
2. Cycadofilicales (Pteridospermae)
3. Gymnospermae
4. Angiospermae

In 1910 the first of four volumes on " Fossil Plants " was published by Seward. Though primarily, as the title suggests, concerned with fossils, Seward tried to incorporate the extinct Pteridophytes into the framework of a general classification of the Pteridophyta. The outline of this classification was as follows:

1. Equisetales
2. Sphenophyllales
3. Psilotales
4. Lycopodiales
    - α. Homosporeae
    - β. Heterosporeae
5. Filicales
    - α. Leptosporangiatae
    - β. Marattiales
    - γ. Ophioglossales
    - δ. Hydropterideae

He recognized the Coenopterideae as a group of fossil ferns, which he subdivided into the Botryoptereae and the Zygoptereae, but he did not indicate definitely what he considered to be their relationship with the rest of the Filicales. Meanwhile Scott had also published a volume on Fossil Plants in 1900 in which he gave descriptions of all the then known forms. This work passed through three editions under the title of " Studies in Fossil Botany", the last edition appearing in 1923.

The year 1913 saw the first description of the Rhyniaceae by Kidston and Lang and the subsequent introduction of the Psilophytales as a further class of the Pteridophyta. Meanwhile Campbell, in his book the " Eusporangiatae", and Bower (Fig. 2063), in a series of publications, ending in his great work " The Ferns", which appeared in three volumes between 1923 and 1928, did much to revise the classification of the Filicales on the basis of anatomical and developmental characters. Unfortunately they left the other groups of the Pteridophyta out of consideration and the classification of the phylum remained for some time in a rather confused state.

FIG. 2063.—Frederick Orpen Bower.

In 1927 Hirmer published the first volume of his " Handbuch der Palaeobotanik", in which he considered only the fossil cryptogamic types. Later, in an article in Verdoorn's " Manual of Pteridology " (1938), he gives a more complete classification of the fossil types which conforms fairly closely to that given, in the same work, by Christensen for the living Ferns and by Walton and Alston for the Lycopods.

I. **Psilophytales**

II. **Lycopodiales**
- α. *Eligulatae*
  - (i) Homosporeae
- β. *Ligulatae*
  - (i) Heterosporeae

III. **Psilotales**

IV. **Articulatales**
- α. *Protoarticulatineae*
- β. *Pseudoborniineae*
- γ. *Sphenophyllineae*
- δ. *Equisetineae*

V. **Cladoxylales**

VI. **Filicales**
- α. *Eusporangiatae*
  - 1. Aneurophytineae
  - 2. Coenopteridineae
    - (i) Zygopteroideae
    - (ii) Botryopteroideae
    - (iii) Anachoropteroideae
  - 3. Marattiineae
    - (i) Pecopteroideae
    - (ii) Danaeoideae
  - 4. Ophioglossineae
- β. *Protoleptosporangiatae*
- γ. *Leptosporangiatae*
  - 1. Simpliceae
  - 2. Complicateae

The most authoritative classification of the Ferns based on living forms is that of Christensen in his " Index Filicum", which is summarized in the " Manual of Pteridology " (1938).

I. **Filicales Eusporangiatae**
  1. Ophioglossales
    (*a*) Ophioglossaceae
  2. Marattiales
    (*a*) Angiopteridaceae
    (*b*) Marattiaceae
II. **Filicales Leptosporangiatae**
  1. Filicales
    (*a*) Osmundaceae
    (*b*) Schizaeaceae
    (*c*) Marsileaceae
    (*d*) Gleicheniaceae
    (*e*) Matoniaceae
    (*f*) Hymenophyllaceae
    (*g*) Loxomaceae
    (*h*) Hymenophyllopsidaceae
    (*i*) Plagiogyriaceae
    (*j*) Dicksoniaceae
    (*k*) Cyatheaceae
    (*l*) Polypodiaceae
  2. Salviniales
    (*a*) Salviniaceae
    (*b*) Azollaceae

THE SPERMATOPHYTA

The older classifications did not recognize the Spermatophyta as a distinct phylum, but separated plants into Cryptogamia and Phanerogamia. The former embraced all the groups we have so far mentioned in this chapter while the latter included the Gymnospermae and the Angiospermae. The discovery of the Pteridospermae, as we have seen, opened up a new viewpoint, for it indicated that the separation of the Phanerogamia was not so fundamental as had been previously thought. We find, therefore, that these terms, Cryptogamia and Phanerogamia, became less and less used in modern classification, while the phylum Spermatophyta replaced the latter term and is used to include the three main groups:

1. Pteridospermae
2. Gymnospermae
3. Angiospermae

The more detailed classification of these three sub-phyla can be best treated separately.

THE PTERIDOSPERMAE

The classification of all fossil plants presents special difficulties and the Pteridospermae are in some ways the most difficult group, inasmuch as the limits of the group are still unknown. Fossil plants are often discovered piecemeal and each portion is named and described separately. Only in relatively few cases is enough of the plant known to give us a reasonably clear idea of its general structure. Differences in the mode of preservation add to the obscurity, some parts of plants being known both anatomically and externally, while the majority are only known under one aspect or the other. In the Pteridospermae the production of seeds on the fronds is the only definitive character and a great many fronds are known which are suspected of belonging to the group but have not been found in a fertile state. There are also a number of anatomically preserved stems which show relationships to both the Pteridospermae and the Cycadales and indeed may belong to an evolutionary sequence between those two groups, but it is impossible to say where the line should be drawn or whether these plants belonged, in fact, to either of the groups. The only attempts at classification have been based chiefly on the seed characters and cover therefore, with certainty, only those forms of which the seed structure is known. Seward in his " Fossil Plants " remarks that the practice of classifying fossil plants has been carried to excess. Some sort of grouping is desirable as a matter of convenience no doubt, but it is very definitely Alpha Taxonomy and should not be allowed to create a prejudice in the mind in favour of a genetic relationship which may or may not exist.

Seward distinguished three classes of Pteridospermae:

I. Lyginopterideae
II. Medulloseae
IIA. Steloxyleae

Under these headings are grouped a variety of organs; stems, roots, leaves, seeds, etc., which are believed to be related. This classification, however, can be crossed by another, applying to the seeds only:

1. Lagenostomales (seeds belonging to members of the Lyginopterideae).
2. Trigonocarpales (seeds belonging to members of the Medulloseae).
3. Cardiocarpales (Gymnospermic seeds probably belonging to Cordaitales).

The stem material, showing anatomical characters which are related to Pteridospermae, but with certain cycadean features, Seward placed in the Cycadofilices, divided into the following sub-classes:

1. Megaloxyleae
2. Rhetinangieae
3. Stenomyeleae
4. Cycadoxyleae
5. Calamopityeae
6. Cladoxyleae
7. Protopityeae

The above treatment of Pteridospermae leaves, however, a miscellanea of fronds and seeds which are unclassifiable. In the third edition of his " Studies of Fossil Botany", published six years later than Seward's classification, D. H. Scott employs a different grouping. He does not distinguish between Pteridospermae and Cycadofilices and he distributes the known genera among a series of coequal groups, referred to as " families " although their name endings are those of tribes.

1. Lyginopterideae
2. Rhetinangieae
3. Megaloxyleae
4. Calamopityeae
5. Stenomyeleae
6. Protopityeae
7. Cladoxyleae
8. Medulloseae
9. Aneimiteae
10. Cycadoxyleae

The above groups are all based upon plants of which at least some part of the anatomical structure is known. Side by side with this classification, there must, however, be recognized a number of groups based upon frond impressions alone, some of which are known to have been seed-bearing and were therefore almost certainly Pteridosperms. Others bear no seeds but may bear microsporangia which are not like Fern sporangia. All are, on grounds of resemblance or of cuticular characters, regarded as probable Pteridosperms. Only a few have actually been proved to have been borne by plants of known structure and affinities. These " frond groups " are as follows:

1. Sphenopterideae
2. Pecopterideae
3. Alethopterideae
4. Neuropterideae

They are distinguished on their pinna-form and venation. Arnold, in his " Introduction to Palaeobotany " (1947), uses a simpler and less comprehensive method, grouping the seed-bearing fossils into Lyginopteridaceae, Medullosaceae and Calamopityaceae, to which are added two Mesozoic families of recently recognized Pteridospermae—Peltaspermaceae and Corystospermaceae—which seem to have been related to the Caytoniales. He does not use the families of frond genera mentioned above.

Gothan, in the second edition of the " Pflanzenfamilien " (1926), uses two main families whose structure is fairly well known, under the names Lyginodendraceae and Medullosaceae. Their author maintains that the older name, *Lyginodendron*, was well founded by Williamson and is therefore preferable to the newer *Lyginopteris*, now used by English authors. He also continues to use the older name Cycadofilices for the sub-phylum as a whole.

The genera founded on stem structure he groups as follows:

1. Steloxylaceae
2. Cladoxylaceae
3. Cycadoxylaceae
4. Rhetinangiaceae
5. Megaloxylaceae
6. Calamopityaceae
7. Stenomyelaceae
8. Protopityaceae *

While the frond genera are grouped into formal series thus:

1. Archaeopterides
2. Sphenopterides
3. Pecopterides
4. Alethopterides
5. Callipterides
6. Odontopterides
7. Neuropterides
8. Taeniopterides
9. Glossopterides
10. Megalopterides

* The two Mesozoic families had not been recognized at that date.

Certain broad principles of agreement are observable in these classifications, but it is obvious that the attempt to classify the Pteridospermae should not be pushed too far at present.

THE GYMNOSPERMAE

The early history of the classification of the Gymnospermae is closely bound up with the Angiospermae, for although the class was recognized as distinct by Robert Brown as early as 1827, floristic writers continued to treat them as Dicotyledons even up to the last fifty years. We need only consider the views regarding the separation of the groups within the Gymnospermae as a whole. There is a considerable amount of agreement regarding the various orders, which are mostly well defined. Only in the relative rank assigned to the different groups and in the subdivision of the orders is there much difference of opinion.

In the first edition of the " Pflanzenfamilien " (1889), Eichler treated the Gymnospermae as divided into:

1. Cycadaceae
2. Cordaitaceae
3. Coniferae
    - (i) Pinoideae
        - α. Abietineae
        - β. Cupressineae
    - (ii) Taxoideae
        - α. Podocarpeae
        - β. Taxeae
4. Gnetaceae

Engler, however, in the " Syllabus " to the " Pflanzenfamilien " in 1912, raised these families to ordinal rank and this was adopted in the second edition of the complete work, dated 1926, where Pilger used the following classification:

1. Cycadales
    - (*a*) Cycadaceae
2. Bennettitales
    - (*a*) Bennettitaceae
    - (*b*) Nilssoniaceae
    - (*c*) Caytoniaceae
3. Ginkgoales
    - (*a*) Ginkgoaceae
4. Cordaitales
    - (*a*) Cordaitaceae
    - (*b*) Pityaceae
5. Coniferae
    - (*a*) Taxaceae
    - (*b*) Podocarpaceae
    - (*c*) Araucariaceae
    - (*d*) Cephalotaxaceae
    - (*e*) Pinaceae
    - (*f*) Taxodiaceae
    - (*g*) Cupressaceae
6. Gnetales
    - (*a*) Ephedraceae
    - (*b*) Welwitschiaceae
    - (*c*) Gnetaceae

Seward in reviewing recent types in the fourth volume of his " Fossil

Plants", published in 1919, used a classification of the Coniferales which expressed the views generally held by the last generation of British botanists:

1. Araucarineae
2. Cupressineae
3. Callitrineae
4. Sequoineae
5. Sciadopitineae
6. Abietineae
7. Podocarpineae
8. Phyllocladineae
9. Taxineae

Lotsy, however, in his " Stammesgeschichte", in 1911, divided the Coniferales, on the basis of the supposed simple or compound nature of the female cones, into:

1. Florales
    (*a*) Podocarpineae
    (*b*) Araucarineae
    (*c*) Cupressineae
2. Inflorescentiales
    (*a*) Taxineae
    (*b*) Taxodineae
    (*c*) Abietineae

Coulter and Chamberlain in their " Morphology of Gymnosperms", published in 1917, divided the Coniferales into the following groups:

1. Pinaceae
    (*a*) Abietineae
    (*b*) Taxodineae
    (*c*) Cupressineae
    (*d*) Araucariineae
2. Taxaceae
    (*a*) Podocarpineae
    (*b*) Taxineae

In 1935, when these authors published their " Gymnosperms, Structure and Evolution", the full classification of the sub-phylum had become:

A. **Cycadophytes**
  1. Cycadofilicales
  2. Bennettitales
  3. Cycadales

B. **Coniferophytes**
  1. Cordaitales
  2. Ginkgoales
  3. Coniferales

α Pinares
  (*a*) Abietaceae
  (*b*) Taxodiaceae
  (*c*) Cupressaceae
  (*d*) Araucariaceae

β. Taxares
  (*a*) Podocarpaceae
  (*b*) Taxaceae

The Pinares and Taxares are due to Buchholz, and correspond to the Pinaceae and Taxaceae of Coulter and Chamberlain's earlier system.

Among the recent types the position of the Taxaceae has given rise to most controversy, but there is a considerable amount of support for the view that they should form a separate order, the Taxales, and we have adopted this opinion, in principle, in the text, while leaving open the question of the limits of the proposed order.

With regard to fossil Coniferales, it must be considered that we are still imperfectly informed about the reproductive structures of most of the Mesozoic Conifers. The recent extensive researches of Florin on the epidermal structure of these Mesozoic Conifers has gone a long way to clear up their relationships. If his conclusions are adopted it will become possible to form a tentative system which will include both recent and extinct forms.

THE ANGIOSPERMAE

The classification of Angiospermae presents to the taxonomist by far the greatest problem in systematic Botany. The group is so vast and the variations so great that at first sight it appears virtually impossible to arrange this heterogeneous collection in any satisfactory order. In early times, as we have already pointed out in Chapter III, the study of plants was so closely bound up with their use in medicine that descriptions of plants were necessary and their arrangement in some system was inevitable. All the systems proposed by earlier writers were more or less artificial, that is to say they were based upon the consideration of one character or a small group of characters. Even Linnaeus (Fig. 2064), although he did recognize the imperfection of his sexual system, attempted with its aid to classify flowering plants upon the number and arrangement of the stamens and carpels, without paying any attention to the general characteristics of the plant as a whole. This system contained twenty-four classes and while it did succeed in delimiting certain families quite satisfactorily, it cut right across other families and divorced obviously related plants from one another. Thus the Linnaean Class 15, Tetradynamia, is exactly comparable with our present Cruciferae, and similarly the Compositae fall into his Class 19, Syngenesia. On the other hand his Class 20, Gynandria, contains representatives of both Monocotyledons and Dicotyledons. However, he recognized fully the artificiality of this system and he attempted later to formulate a natural system, in which plants were arranged under sixty-three family headings, in accordance with their general affinities. He did not live to complete this work but his " Fragmenta " provided the foundation for later workers.

FIG. 2064.—Carolus Linnaeus (Carl von Linné). (*After a portrait in the possession of the Linnean Society.*)

The separation of Flowering Plants into Dicotyledons and Monocotyledons, however, goes back before Linnaeus to the work of John Ray (Vol. I, p. 42) who, in his " Historia Plantarum", 1686–1704, divided plants into Herbs and Trees, and subdivided each group as follows:

1. *Herbae*
        A. Imperfectae (Flowerless plants).
        B. Perfectae (Flowering plants).
    Dicotyledones (with two cotyledons).
    Monocotyledones (with one cotyledon).
2. *Arbores*
    Dicotyledones.
    Monocotyledones.

The scheme left by Linnaeus was further elaborated by Bernard de Jussieu and later enlarged, perfected and published by his nephew Antoine Laurent de Jussieu (Fig. 2065) in 1789. This system recognized the importance not only of the cotyledons and the stamens, but also of the petals and carpels. It was in fact the first effort to formulate a natural system. Since many of his one hundred families are still accepted it may be justifiable to outline the main points of the scheme.

Fig. 2065.—Antoine de Jussieu. Copy of a portrait supplied by courtesy of the Wellcome Historical Medical Museum.

Natural Orders	Classes, with Examples
Acotyledones	1 (mainly Cryptogams)
Monocotyledones	
Stamina hypogyna	2 (Aroideae, Typhae, Gramineae)
Stamina perigyna	3 (Palmae, Junci, Lilia, Irides)
Stamina epigyna	4 (Musae, Orchides)
Dicotyledones	
Apetalae	
Stamina epigyna	5 (Aristolochiae)

Natural Orders	Classes, with Examples
Stamina perigyna	6 (Eleagni, Proteae, Lauri, Polygoneae)
Stamina hypogyna	7 (Plantagines, Amaranthi)
Monopetalae	
Corolla hypogyna	8 (Scrophulariae, Solaneae, Gentianeae)
Corolla perigyna	9 (Ericae, Campanulaceae)
Corolla epigyna, antheris connatis	10 (Cichoraceae, etc.)
Corolla epigyna, antheris distinctis	11 (Rubiaceae, Caprifolia)
Polypetalae	
Stamina epigyna	12 (Araliae, Umbelliferae)
Stamina hypogyna	13 (Ranunculaceae, Papaveraceae, Gerania, Malvaceae, Cruciferae)
Stamina perigyna	14 (Saxifragae, Rosaceae, Leguminosae)
Diclines irregulares	15 (Euphorbiae, Urticae, Amentaceae, Coniferae)

Following this step in systematic Botany comes the very important contribution of Augustin Pyrame de Candolle (Fig. 2066) who, in his "Théorie Elémentaire de la Botanique", first published in 1813, gave to the science of comparative morphology its first principles in his theory of symmetry, that is to say the doctrine that the nature of an organism is expressed in the plan by which the positional relations of all its parts is manifested. The uncovering of this plan from beneath the effects of abortion, degeneration and adhesion which obscure it, he conceived to be the rule for the determination of true affinities. All plants, he maintained, have the same physiological functions with slight modifications and therefore the vast diversity of form displayed depends only on diversities in the morpho-

Fig. 2066.—A. P. de Candolle. Photograph supplied by courtesy of the Wellcome Historical Medical Museum.

logical plan. The physiological character of an organ was disregarded as of no importance from the morphological point of view.

De Candolle was influenced by an erroneous view of the processes of stem growth and the two main divisions of his Vasculares were accordingly named Exogenae and Endogenae respectively, the former including the present-day Dicotyledons and Gymnosperms and the latter the Monocotyledons, the stems of which were supposed to increase from within outwards. He also unfortunately included with them the Vascular Cryptogams, a mistake which soon rendered his system obsolete. In the Dicotyledons, however, his subdivisions, Thalamiflorae, Calyciflorae and Corolliflorae, survived up to quite recent times. His ideas were further elaborated and to some extent improved by John Lindley (Vol. I, p. 43), who, in 1830, published his " Introduction to the Natural Orders of Plants". In the " Vegetable Kingdom", published in 1846, the Phanerogams were divided into five classes:

1. Rhizogens—Fructifications springing from a thallus. This included parasitic and non-chlorophyllous plants.
2. Endogens—Monocotyledons with parallel-veined leaves.
3. Dictyogens—Monocotyledons with net-veined leaves.
4. Gymnogens—Seeds naked (Gymnosperms).
5. Exogens—Dicotyledons with seeds enclosed in seed vessels.

Since Lindley's time two great systems of classification have been produced which have commanded world-wide attention. The first is embodied in the " Genera Plantarum " by Bentham (Vol. I, p. 44) and Hooker, published between 1862 and 1883, which elaborated the De Candolle system as applied to the Angiosperms and Gymnosperms and received at once very general acceptance in this country and subsequently in America. The second is the " Natürliche Pflanzenfamilien " by Engler (Fig. 2067) and Prantl, which appeared between 1887 and 1909, and a second edition of which was in process of publication at the beginning of the Second World War in 1939. The Engler system soon attracted attention in America and was to some extent accepted by British botanists. Engler's system was derived essentially from that of A. W. Eichler, which was published in 1883. The system adopted by R. von Wettstein in his valuable " Handbuch der systematischen Botanik ", 1901, follows similar lines to that of Engler, as far as the

FIG. 2067.—Adolf Engler.

Angiosperms are concerned, except that he places the Monocotyledons last.

It is impossible here to consider in detail the scheme of classification adopted in each work. It must however be pointed out that the " Genera Plantarum " was never intended to express a complete phylogenetic picture of classification. It was an attempt to extend and elaborate the ideas of De Jussieu and De Candolle in the light of more recent knowledge. Moreover it was written at a time when the fixity of species was still accepted by many botanists. The Englerian system, on the other hand, did attempt to give a phylogenetic picture and has suffered criticism as a consequence. Moreover the " Natürliche Pflanzenfamilien " was a vast compendium of information, collected and written by a number of separate authors whose views on phylogeny were not necessarily identical.

The most recent treatment of the classification of Flowering Plants on a phylogenetic basis is due to Hutchinson who, in his " Families of Flowering Plants " published in 1926 and 1934, attempted to sift the good in both systems, while at the same time introducing much of his own, derived from a long study of the herbaria at the Royal Botanic Gardens at Kew, and a special knowledge of African plants.

It is mainly upon the question as to what are to be considered the most primitive orders that the three systems differ. Bentham and Hooker started with the polypetalous families and their first order was the Ranales. From the Polypetalae they proceeded to the Gamopetalae and then finally to the Apetalae, ending up with the Gymnosperms, after which they placed the Monocotyledons. It was largely upon the unfortunate separation of the Apetalae, between the Gamopetalae and the Monocotyledons, that the system was criticized by other authorities.

The Englerian system amalgamated the Polypetalae and the Apetalae, while the Monocotyledons take precedence over the Dicotyledons. Thus the catkin-bearing trees are considered to be the most primitive Dicotyledons and they are followed by the polypetalous Ranalean families. Since the " Pflanzenfamilien " appeared, much evidence has accumulated which points to the primitive nature of the Ranalean families, and though the matter is still questioned by some authorities it seems that the weight of opinion now favours the view that the Polypetalae are the most primitive of Angiosperms and hence that we should consider the Dicotyledons as more primitive than the Monocotyledons. All the evidence about phylogeny, however, indicates that evolution has progressed along divergent paths and in regarding the Polypetalae as the most primitive group we certainly must not deduce that the whole of the Dicotyledons are more primitive than the Monocotyledons, but rather that from a primitive dicotyledonous stock both the higher Dicotyledons and also the Monocotyledons may have developed.

In this connection it is recognized that, while fossil evidence indicates that the apetalous families can be traced far back into Tertiary time and are therefore of early origin, they need not of necessity be considered as primitive simply because certain whorls of floral parts are absent. Rather it is thought that these parts, being unnecessary in flowers which rely on wind for pollination, have been reduced and finally in some instances lost. Hence the Apetalae are now regarded by many as reduced rather than primitive families, originating from a polypetalous stock. The Rosales and particularly the Hamamelidaceae have been suggested as a possible origin of some of them, though it is recognized that the group is probably not a natural one and contains families reduced from different ancestral types.

Hutchinson in his treatment further elaborates the system by considering that the primitive polypetalous forms diverged from the start along two separate lines, the one retaining the treelike habit of the ancestral type, the other adopting an herbaceous habit. Thus he separates the Magnoliales as the first order of the arboreal types and retains the Ranales for the related herbaceous families. He considers further that the apetalous families have been derived partly through the Magnoliales and partly through the Ranales.

It is interesting to note that in the course of time the number of recognized orders and families of Flowering Plants has increased, mostly due to rearrangements and to some extent to new discoveries. In the " Genera Plantarum " 200 families are recognized; * in the " Pflanzenfamilien " 280 families are described, while Hutchinson employed 332 families. The same is true of the orders, of which Hutchinson has increased the number very considerably.

Some confusion of ideas has arisen about the implication of the term Order as used by different writers on Angiosperm systematics. Bentham and Hooker use the Linnaean term " Natural Order " for a collection of genera and the term " Cohort " for a group of Natural Orders. Engler and most modern writers adopt the term Family for Natural Order and the term Order to imply the same meaning as Cohort, in accordance with the international Rules.

It is impossible to give in full detail the three main systems of classification now in common use, namely those of Engler, Bentham and Hooker, and Hutchinson. In order, however, that the student may be able to use books employing different systems and more particularly because most British Floras follow Bentham and Hooker, an outline of the three systems is appended.

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* This number includes three families of Gymnospermae—Gnetaceae, Coniferae and Cycadaceae—which were counted as Dicotyledons. English floristic writers following Bentham and Hooker have continued this practice until recent times.

Classification of the Angiospermae according to Engler in the " Syllabus der Pflanzenfamilien "

I. **Monocotyledoneae**
  1. Pandanales
  2. Helobiae
  3. Triuridales
  4. Glumiflorae
  5. Principes
  6. Synanthae
  7. Spathiflorae
  8. Farinosae
  9. Liliiflorae
  10. Scitamineae
  11. Microspermae

II. **Dicotyledoneae**
  α. *Archichlamydeae*
    1. Verticillatae
    2. Piperales
    3. Salicales
    4. Garryales
    5. Myricales
    6. Balanopsidales
    7. Leitneriales
    8. Juglandales
    9. Batidales
    10. Julianales
    11. Fagales
    12. Urticales
    13. Proteales
    14. Santalales
    15. Aristolochiales
    16. Polygonales
    17. Centrospermae
    18. Ranales
    19. Rhoeadales
    20. Sarraceniales
    21. Rosales
    22. Pandales
    23. Geraniales
    24. Sapindales
    25. Rhamnales
    26. Malvales
    27. Parietales
    28. Opuntiales
    29. Myrtiflorae
    30. Umbelliflorae
  β. *Metachlamydeae* (Sympetalae)
    1. Ericales
    2. Primulales
    3. Plumbaginales
    4. Ebenales
    5. Contortae
    6. Tubiflorae
    7. Plantaginales
    8. Rubiales
    9. Cucurbitales
    10. Campanulatae

Classification of the Angiospermae according to the Bentham and Hooker System

- I. **Dicotyledones**
  - α. *Polypetalae*
    - (i) *Thalamiflorae*
      - 1. Ranales
      - 2. Parietales
      - 3. Polygalinae
      - 4. Caryophyllinae
      - 5. Guttiferales
      - 6. Malvales
    - (ii) *Disciflorae*
      - 1. Geraniales
      - 2. Olacales
      - 3. Celastrales
      - 4. Sapindales
    - (iii) *Calyciflorae*
      - 1. Rosales
      - 2. Myrtales
      - 3. Passiflorales
      - 4. Ficoidales
      - 5. Umbellales
  - β. *Gamopetalae*
    - (i) *Inferae*
      - 1. Rubiales
      - 2. Asterales
      - 3. Campanales
    - (ii) *Heteromerae*
      - 1. Ericales
      - 2. Primulales
      - 3. Ebenales
    - (iii) *Bicarpellatae*
      - 1. Gentianales
      - 2. Polemoniales
      - 3. Personales
      - 4. Lamiales
  - γ. *Monochlamydeae*
    - 1. Curvembryeae
    - 2. Multiovulatae Aquaticae
    - 3. Multiovulatae Terrestres
    - 4. Micrembryeae
    - 5. Daphnales
    - 6. Achlamydosporeae
    - 7. Unisexuales
    - 8. Ordines anomala
- II. **Monocotyledones** *
  - 1. Microspermae
  - 2. Epigynae
  - 3. Coronarieae
  - 4. Calycinae
  - 5. Nudiflorae
  - 6. Apocarpae
  - 7. Glumaceae

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* The arrangement of the Monocotyledons is the same as that employed by Eichler but the classification of the Dicotyledons is different.

Classification of the Angiospermae according to Hutchinson in his "Families of Flowering Plants"

I. **Dicotyledones**

α. *Archichlamydeae*

1. Magnoliales
2. Anonales
3. Laurales
4. Ranales
5. Berberidales
6. Aristolochiales
7. Piperales
8. Rhoeadales
9. Loasales
10. Capparidales
11. Cruciales
12. Violales
13. Polygalales
14. Saxifragales
15. Sarraceniales
16. Podostemonales
17. Caryophyllales
18. Polygonales
19. Chenopodiales
20. Geraniales
21. Lythrales
22. Thymelaeales
23. Proteales
24. Dilleniales
25. Coriariales
26. Pittosporales
27. Bixales
28. Tamaricales
29. Passiflorales
30. Cucurbitales
31. Cactales
32. Theales
33. Myrtales
34. Guttiferales
35. Tiliales
36. Malvales
37. Malpighiales
38. Euphorbiales
39. Cunoniales
40. Rosales
41. Leguminosae
42. Hamamelidales
43. Salicales
44. Garryales
45. Leitneriales
46. Myricales
47. Balanospidales
48. Fagales
49. Casuarinales
50. Urticales
51. Celastrales
52. Olacales
53. Santalales
54. Rhamnales
55. Rutales
56. Meliales
57. Sapindales
58. Juglandales
59. Umbelliflorae

β. *Metachlamydeae*

1. Ericales
2. Ebenales
3. Myrsinales
4. Styracales
5. Loganiales
6. Apocynales
7. Rubiales
8. Asterales
9. Gentianales
10. Primulales
11. Plantaginales
12. Campanales
13. Polemoniales
14. Boraginales
15. Solanales
16. Personales
17. Lamiales

II. **Monocotyledones**

α. *Calyciferae*

1. Butomales
2. Alismatales
3. Triuridales
4. Juncaginales
5. Aponogetonales

II. Monocotyledones—*contd.*
    6. Potamogetonales
    7. Najadales
    8. Commelinales
    9. Xyridales
    10. Eriocaulales
    11. Bromeliales
    12. Zingiberales
  β. *Corolliferae*
    1. Liliales
    2. Alstroemeriales
    3. Arales
    4. Typhales
    5. Amaryllidales
    6. Iridales
    7. Dioscoreales
    8. Agavales
    9. Palmales
    10. Pandanales
    11. Cyclanthales
    12. Haemodorales
    13. Burmanniales
    14. Orchidales
  γ. *Glumiflorae*
    1. Juncales
    2. Cyperales
    3. Graminales

THE METHOD OF CLASSIFICATION ADOPTED IN THE PRESENT WORK

In the light of what has been said in this chapter it will be clear that the authors have not had an enviable task in formulating a scheme of classification applicable to a book of this kind. They have from time to time ventured to express their own views on classification of certain groups but to justify these views would involve excursions into phylogeny which they feel should not be intruded into a work dealing with facts rather than with ideas.

The method of classification adopted in this book is, however, stated at appropriate points in this and the preceding volume. Since at this stage the purely systematic portion of the subject has been completed it seems appropriate to close this chapter and Volume II with a synopsis of the classification of plants as followed in this work. For the sake of clarity it includes certain groups which are not considered in detail in the preceding chapters but omits many of the less common or less well-known groups.

In studying such a scheme the student must fortify himself against regarding it as representing more than a working plan. It does represent a view of the relationships of plants but nothing more and in the years to come it will probably be as out of date as some of the schemes we have already quoted in this chapter. But as knowledge grows so the picture becomes clearer; finer details have still to be sketched in, but the general outline of the picture is there and its form can be appreciated. It must be remembered, however, that just as a picture must, in two dimensions, portray a scene which exists in three, so a scheme of classification on paper can only imperfectly illustrate the complexly branched system we believe to represent the course of Evolution. It is the reticulate concept of a Natural or Phylogenetic System of Plant Classification which we must appreciate if we are to understand Nature as we believe she really works.

THE CLASSIFICATION OF PLANTS

I. **Thallophyta**
  A. **Algae**
    (a) *Euglenophyceae*
      1. Euglenales
    (b) *Cryptophyceae*
      1. Cryptomonadales
      2. Cryptococcales
    (c) *Dinophyceae* (Peridineae)
      1. Dinophysiales
      2. Gymnodiniales
      3. Peridiniales
    (d) *Chlorophyceae*
      1. Volvocales
      2. Chlorococcales
      3. Chaetophorales
      4. Ulotrichales
      5. Oedogoniales
      6. Conjugales
      7. Siphonales
      8. Siphonocladiales
    (e) *Xanthophyceae* (Heterokontae)
      1. Heterochloridales
      2. Heterococcales
      3. Heterotrichales
      4. Heterosiphonales
    (f) *Chrysophyceae*
      1. Chrysomonadales
      2. Chrysosphaerales
      3. Chrysotrichales
    (g) *Phaeophyceae*
      1. Ectocarpales
      2. Tilopteridales
      3. Sphacelariales
      4. Cutleriales
      5. Sporochnales
      6. Desmarestiales
      7. Dictyotales
      8. Laminariales
      9. Fucales
    (h) *Bacillariophyceae*
      1. Centrales
      2. Pennales
    (j) *Rhodophyceae*
      1. Bangiales

I. Thallophyta—*contd.*

- 2. Nemalionales
- 3. Gelidiales
- 4. Gigartinales
- 5. Rhodymeniales
- 6. Ceramiales
- 7. Cryptonemiales

(k) *Cyanophyceae* (Myxophyceae)

- 1. Chroococcales
- 2. Chamaesiphonales
- 3. Hormogonales

B. **Fungi**

(a) *Archimycetes*

- 1. Myxomycetales
- 2. Acrasiales
- 3. Plasmodiophorales

(b) *Phycomycetes*

- 1. Chytridiales
- 2. Ancylistales
- 3. Saprolegniales
- 4. Blastocladiales
- 5. Monoblepharidales
- 6. Peronosporales
- 7. Mucorales
- 8. Entomophthorales

(c) *Ascomycetes*

- 1. Plectascales
- 2. Erysiphales
- 3. Exoascales
- 4. Pezizales
- 5. Helvellales
- 6. Phacidiales
- 7. Hysteriales
- 8. Saccharomycetales
- 9. Hypocreales
- 10. Dothideales
- 11. Sphaeriales
- 12. Laboulbeniales

(d) *Basidiomycetes*

- 1. Ustilaginales
- 2. Urediniales
- 3. Auriculariales
- 4. Tremellales
- 5. Calocerales (Dacryomycetales)
- 6. Aphyllophorales

- 7. Agaricales
- 8. Gasteromycetales

(e) *Fungi Imperfecti*
- 1. Hyphomycetales
- 2. Melanconiales
- 3. Sphaeropsidales
- 4. Mycelia sterilia

C. **Bacteria**
- 1. Eubacteriales
- 2. Actinomycetales
- 3. Chlamydobacteriales
- 4. Thiobacteriales
- 5. Myxobacteriales
- 6. Spirochaetales

D. **Lichenes**

(a) *Ascolichenes*
- 1. Gymnocarpeae
- 2. Pyrenocarpeae

(b) *Basidiolichenes* (Hymenolichenes)

II. **Charophyta**
- 1. Charales

III. **Bryophyta**

(a) *Hepaticae*
- 1. Sphaerocarpales
- 2. Jungermanniales
- 3. Marchantiales
- 4. Anthocerotales

(b) *Musci*
- 1. Sphagnales
- 2. Andreaeales
- 3. Bryales

IV. **Pteridophyta**

(a) *Psilopsida*
- 1. Psilophytales
- 2. Cladoxylales
- 3. Psilotales
- 4. Noeggerathiales

(b) *Lycopsida*
- 1. Lycopodiales
- 2. Isoetales

(c) *Sphenopsida* (Articulatae)
- 1. Equisetales
- 2. Sphenophyllales

IV. Pteridophyta—*contd.*

- (d) *Pteropsida*
  - 1. Filicales
    - (i) Eusporangiatae
    - (ii) Leptosporangiatae
    - (iii) Hydropterideae

V. Spermatophyta

- (a) *Pteridospermae*
- (b) *Gymnospermae*
  - 1. Cordaitales
  - 2. Coniferales
    - (i) Araucariineae
    - (ii) Podocarpineae
    - (iii) Abietineae
    - (iv) Taxodineae
    - (v) Cupressineae
  - 3. Taxales
  - 4. Cycadales
  - 5. Bennettitales
  - 6. Caytoniales
  - 7. Ginkgoales
  - 8. Gnetales
- (c) *Angiospermae*

I. DICOTYLEDONES

α. *Archichlamydeae*

- 1. Ranales
- 2. Rhoeadales (Papaverales)
- 3. Rosales
- 4. Saxifragales
- 5. Leguminosae (Viciales)
- 6. Parietales (Violales)
- 7. Cucurbitales
- 8. Guttiferales (Hypericales)
- 9. Cactales
- 10. Aristolochiales
- 11. Sarraceniales
- 12. Centrospermae (Dianthales)
- 13. Proteales
- 14. Polygonales
- 15. Piperales
- 16. Urticales
- 17. Salicales
- 18. Garryales
- 19. Myricales
- 20. Fagales

21. Casuarinales
22. Myrtiflorae (Myrtales)
23. Malvales
24. Sapindales
25. Santalales
26. Rhamnales
27. Geraniales
28. Rutales
29. Euphorbiales
30. Juglandales
31. Umbelliflorae (Daucales)

β. *Metachlamydeae*

1. Ericales
2. Ebenales
3. Primulales
4. Oleales
5. Plantaginales
6. Campanulales
7. Boraginales
8. Plumbaginales
9. Solanales
10. Personales (Scrophulariales)
11. Lamiales
12. Rubiales
13. Asterales

II. MONOCOTYLEDONES

1. Helobiae (Alismales)
2. Farinosae (Bromeliales)
3. Zingiberales
4. Liliales
5. Alstroemeriales
6. Arales
7. Typhales
8. Amaryllidales
9. Iridales
10. Dioscoreales
11. Agavales
12. Palmales
13. Pandanales
14. Glumiflorae (Poales)
15. Microspermae (Orchidales)

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