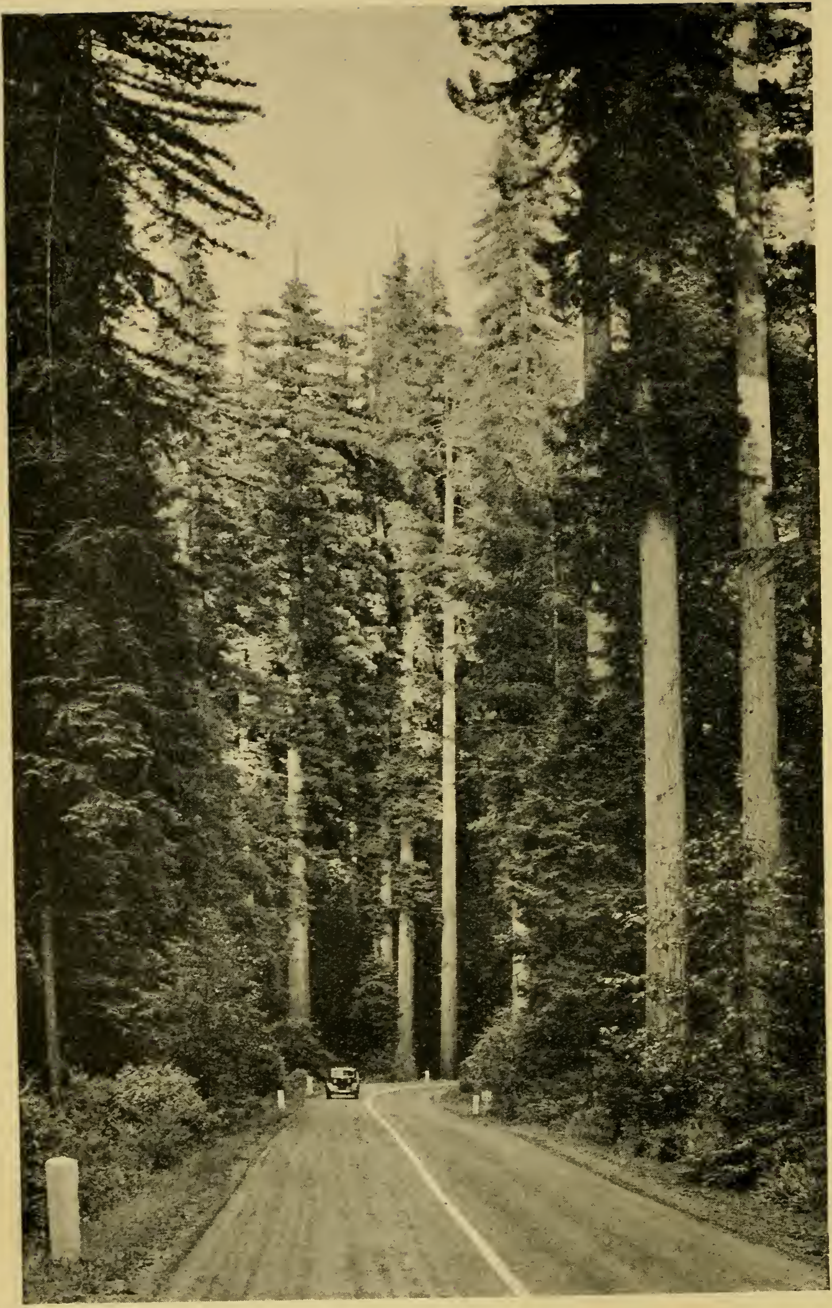
BOTANY OF THE LIVING PLANT



GIANT TREES OF CALIFORNIA

Showing proportionately an approximate limit of size of the plant body. See chapters X. and XXXVI.

BOTANY OF THE LIVING PLANT

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OF THE SECTION ON THE CRYPTOGAMS

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PREFACE TO FOURTH EDITION

A TEXTBOOK of any progressive Science needs to be revised from time to time, if it is to serve the student as it should do. This book, first issued a quarter of a century ago, has been twice revised. In the production of the Third Edition the author gratefully acknowledged the help of Professor Drummond in respect of his new Chapter XXXV., on Heredity and Variation, and of Dr. Bond in the general revision of the parts dealing with Physiology. The exhaustion of that Edition has given the opportunity for another general revision of the Text, together with some additions of fresh matter. In producing this Fourth Edition the author wishes to acknowledge the general help of Professor Wardlaw, and in particular his revision of Chapters XXI. to XXVIII. Both Professor Wardlaw and myself have also made certain other additions, as required. The result of these changes has been to modernise the Text.

F. O. BOWER.

PREFACE TO THIRD EDITION

THE present Volume was framed in 1919 upon the Courses of Elementary Lectures on Botany given in Glasgow University during a long succession of years. Those Courses were progressively re-modelled and developed as time went on, while the elastic limits of a book have allowed the introduction of sundry additions. And so in successive issues the text has expanded. But the main object throughout has been in the first place that of presenting the individual plant as a living, growing, self-nourishing, self-adapting creature, as I always endeavoured to sketch it in the Lecture Room, and to demonstrate it in the Laboratory.

The subject-matter is parcelled out into a series of Essays, each one self-contained. They are designed so as to fit together and form a continuous treatise. The omissions are palpable enough, for no attempt has been made after encyclopedic writing. The material itself is such as will be reckoned elementary. Elementary and fundamental should be held as equivalent terms when applied to those facts and principles upon which the Science itself is built: and it is to these that the available space has been devoted.

The book has not been written in conformity with the schedule of work prescribed by any University or School: nor is it designed to meet the requirements of any specified examination. Its object has been to present a true picture in as simple terms as possible. Proceeding from the known to the unknown, it opens with a description, structural and functional, of familiar Flowering Plants. The consequent inversion of the evolutionary aspect of the Vegetable Kingdom as a whole will probably be criticised. But a definite break has been made at the end of Chapter XIX. Here follows a Chapter on "Evolution, Homoplasy, Homology, and Analogy." It is designed as an introduction to the scientific comparison of Plants. The illustrative material for this is then supplied by the description of a progressive series of forms, starting from some of the simplest and proceeding to those that are more complex. These have been selected in harmony with general opinion as to the trend of evolutionary history. It hardly needs to be said that those selected suggest only the barest and most general outline by means of which the progress of Descent can be sketched. Nevertheless they give a rational foundation, however slender, for the generalisations advanced in Chapters XXXIII. to XXXVI.

In preparing the text of this Third Edition, twenty years after the first and thirteen years after retirement, I have had the advantage of help from younger men actually engaged in teaching. The Chapters relating to Physiology, viz. III., VII.-IX and parts of Chapter XI. and XII., have been amended and largely re-written, and new figures added to them, by Dr. G. Bond, Lecturer on Plant Physiology in the University of Glasgow. Professor M. Drummond of Manchester University has revised the text of the Thallophyta at various points, and has re-written Chapter XXXV., under the title of Sex and Variation. He has also added paragraphs on Vitamins to Appendix II., which deals with Vegetable Food-stuffs. In these amendments we acknowledge valuable suggestions from Dr. F. W. Sansome and Prof. I. M. Heilbron. To all of these I am deeply indebted for their help. I have myself added short statements on the Psilophytales and Equisetales, so as to aid comparison. And finally, I have added in Chapter XXXVI. a condensed statement on "The Relation of Size and Form in Plants". Some may be surprised to find that subject introduced into a current Text-book; holding this to be premature until opinion is more settled than it is at present. Whether or not adherence be given to the views expressed in the Chapter, it seems desirable to raise the topic, (i) as a means of impressing the necessity for uniformity of scale in thought, in measurement, and in illustration, where such questions are discussed; (ii) as pointing the contrast between primary and secondary development; and (iii) as localising the study of primary mouldings in relation to the growing point itself.

More than 200 of the illustrations have been specially prepared for this book. My own original drawings are initialed. Almost an equal number were drawn for the first edition by Professor J. McLean Thompson of Liverpool University, and these are signed by him. Many beautiful French blocks have been borrowed from Figuier's *Vegetable World*, and a considerable number have been taken with permission of the publishers from Strasburger's *Textbook*. By arrangement with the S.P.C.K., many of the excellent drawings of Fungi by the late Professor Marshall Ward are embodied. They are taken from his *Diseases of Plants*, now long out of print. The sources of these illustrations, and of some others not mentioned here by name, are specified in the rubrics, and their use is gratefully acknowledged.

Finally, I wish to thank critics and friends who have, in print or verbally, suggested amendments to the Text: and in particular Dame Helen Gwynne-Vaughan, G.B.E., Professor W. H. Lang, and Dr. S. Williams. But I hold myself fully responsible for the text as it stands.

F. O. BOWER.

Ripon, 1939.

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BOTANY OF THE LIVING PLANT

INTRODUCTION.

The vegetation of any ordinary country-side consists of a vast number of distinct kinds of Plants, large and small, simple and complex. They are mixed up without any apparent system or order. The object of the scientific study of this mixed vegetation is to know as much as possible about the various Plants that compose it. The form of each kind of Plant when fully grown will have to be noted, as well as the way it grows so as to attain that form. The way the Plants nourish themselves is also an important question. And finally we shall enquire how they increase in numbers: for some die off from time to time, and their places are constantly being taken by new Plants.

This study of Plants and of their vital activities cannot be carried out with success by merely examining the mass of Plants all together. They must be taken singly, and examined individually. One can then be compared with another. On the basis of such comparisons we may form opinions as to their probable relationships, and even approach a view regarding their origin. To make such a study methodical and coherent, the Plants recognised must be arranged according to their characters. They must in fact be classified, and the classification should then indicate their natural affinities. In such a *Natural Classification* those which are relatively simple in their structure and mode of life should be placed first, and the most elaborate last.

We may take as an example of a very simple Plant that green powdery growth which is often found on the bark of trees, on wooden rails, and other places, in damp situations. This growth is composed of individual grains which are very numerous, but so small that they are only visible to the naked eye when present in large numbers.

Highly magnified, the powder is seen to consist of single spherical cells, or groups of cells (Fig. 1). Each of these cells is an individual Plant, and it multiplies by division. The results of such repeated divisions may remain for a time coherent, thus forming groups of varying number. But finally they separate, and each single cell can continue its life as a distinct *unicellular organism.* It is called *Pleurococcus Naegelii.* It may be held as taking a low place in the scale of vegetation, and would be classified near to the beginning of our Series.

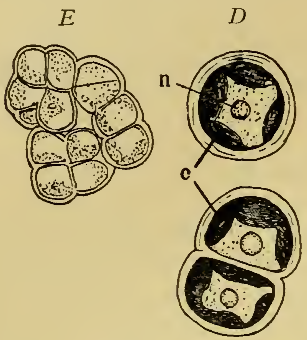

FIG. 1.

Cells of *Pleurococcus Naegelii.* Chod.: D shows cell-structure and division. *n*=nucleus. *c*=chloroplast. (After Fritsch and Salisbury.) E shows packet of cells resulting from division. (After Chodat.)

On the other hand, ordinary herbs, shrubs and trees are examples of more elaborate organisation. Each one of these is composed of various large and complex parts, which are united to form the complete Plant. The several distinct functions which they perform benefit the whole. Such Plants may attain large size, and very complicated structure, as in the case of forest trees (Frontispiece). Each of these Plants is an independent individual. Their increase in number is by *Seeds*, produced through the process of flowering. The production of seed is an involved and elaborate process, as will be seen when it is described in later Chapters. Partly on the ground of their complex structure, and partly because of the elaborate method of their propagation, such *Flowering Plants*, or *Seed-Plants*, are ranked as higher in the scale. Between such extremes as *Pleurococcus* and a Flowering Plant other intermediate types may be ranked according to their structure and their method of increase. And so a Series may be found leading from those which are comparatively simple, by gradual steps, to those which are more elaborate. Such a Series is believed to illustrate roughly, and with some degree of truth, the course which the Evolution of the Vegetable Kingdom has actually followed. The simpler examples are held to represent such types as appeared earlier in the History of Descent, and thus to be more *primitive.* The types which are more complex in structure, and in their method of propagation, are believed to have appeared later in the History of Descent, and are regarded as *derivative.* This agrees essentially with the sequence of fossils embedded in successive

Geological Strata: so that the positive evidence of the Rocks supports, so far as it goes, the grouping of Plants by comparison.

On such grounds as these, Plants may be sorted into five main Divisions, each comprising several Classes. They may be tabulated as follows, while examples are given of familiar Plants, illustrating the sort of living organisms which belong to each Class:

EXAMPLES.	CLASS.	DIVISION.
Seaweeds and Freshwater Weeds	Algae	Thallophytes.
Mushrooms, Mildews, Moulds	Fungi	
Mosses	Musci	Bryophytes.
Liverworts	Hepaticae	
Ferns	Filicales	Pteridophytes.
Club-Mosses	Lycopodiales	
Horse-Tails	Equisetales	
Pines, Firs, Yew	Coniferales	Gymnosperms.
Oak, Sunflower, Potato, Bean	Dicotyledons	Angiosperms.
Grasses, Lilies, Palms	Monocotyledons	

A natural way of studying these would doubtless be to start from the simplest and most primitive, and to proceed to those which are more advanced:—that is, to follow the course which we believe that Evolution has taken. It is, however, easier to begin the study of the Living Plant from those of larger size, which are already familiar objects to everyone, than from minute and unfamiliar organisms, which can only be examined microscopically. It will thus be best for us to take the Higher Flowering Plants first, and to hold over the lower organisms to the end.

One further general statement may be made regarding the Series as thus laid out. It relates to the mode of life of the Plants concerned. Many of the Thallophytes are water-growing Plants, such as Seaweeds, and the Algae of freshwater streams and pools; most of them grow only where abundant moisture is present. The Mosses and Ferns, though they appear as land-living Plants, require external liquid water for completing one essential stage in their life-history: without it they fail. On this ground they may be called the "Amphibians" of the Vegetable Kingdom. But the Seed-Plants are not thus dependent upon external liquid water. The general conclusion follows that Vegetation began in the water, that it spread later to the land, and that it found its climax in the Seed-Bearing Plants of the Present Day. This is the fundamental idea which should underlie all Ecology, that branch of the Science which connotes the study of Plants in relation to their surroundings. The broadest of all ecological conceptions is that Plants were in their ultimate origin aquatic: that they have gradually emancipated themselves from dependence upon an aquatic habitat: and that the highest terms of the series are characteristically Dwellers on Dry Land.

Conclusions like these have been drawn by Zoologists with regard to the Animal Kingdom. Both branches of living things, viz. Animals and Plants, probably originated in the water. Certain of the very simplest Animals and Plants are so alike that it is difficult to draw any line separating at such early stages the one Kingdom from the other. It is therefore concluded that they probably had a common origin, but that in the course of Evolution they diverged. The most distinctive feature which separates them is that of Nutrition. *Plants advanced along the direct line of Self-Nutrition.* They form their own organic food from inorganic materials. These are ultimately Carbon Dioxide and Water, together with Mineral Salts. Their green colouring matter plays an essential part in the process of their nutrition from such simple sources. *Animals*, on the other hand, *advanced along Predatory Lines.* They take their food in more elaborate form as material already organic: that is, either from bodies which are living, or such as have been produced by living organisms. This is seen both in Herbivorous and Carnivorous Animals. Pursuing these divergent lines, both Animals and Plants established themselves upon exposed land-surfaces, and both show in their higher terms abundant evidence of their fitness for living in the surroundings which they have adopted.

Since Animals take their food as organic material—that is, in a sense at second hand, and do not construct it for themselves—it is obvious that at some stage or other they are dependent for it upon the Vegetable Kingdom. This gives Plants a special claim on the attention of Biologists: for *the Green Plant is, in point of fact, the essential source of supply of organised material to all other forms of Life upon the Earth's Surface.*

DIVISION I.

ANGIOSPERMS OR HIGHER FLOWERING PLANTS

CHAPTER I.

SEED. GERMINATION. FORM OF THE ESTABLISHED PLANT.

The Higher Plants are called Seed-Plants, because they bear Seeds. The *Seed* is a detachable part of the parent Plant, which contains the germ of a new individual. When mature, it is usually hard and dry. It can stand drying up without losing its vitality. In this state it may remain dormant for a considerable period, often for years, and may withstand conditions which would be unfavourable for active life, such as extremes of heat and cold. But when the conditions are favourable, the active life of the germ, which has been in a state of suspense in the dry seed, may be resumed. The test of vitality of the seed is whether or not it will germinate when exposed to suitable conditions.

If a dry seed of a Bean, such as may be bought in a seedsman's shop, be dissected, its parts may be easily recognised. But the dissection will be more readily carried out if it be soaked in water for twenty-four hours. The effect of the soaking will be that it will increase in bulk and in weight. The *swelling* is due to the imbibition of water, which is a property of dry vegetable tissues. A distinction must be drawn between such swelling and growth. Swelling by imbibition is a reversible process, and is not a manifestation of life. A dead bean will swell equally with a living one. If either be dried again, it will shrink back to its original bulk. *Growth*, on the other hand, is a result of vital activity. It involves, as we shall see in Chapter IX., p. 139, a redistribution of organic material. This is an irreversible process.

The seed which has once germinated cannot be restored to its original state again. It is the same with all other changes in life : *the prior condition can never be exactly resumed after vital changes have occurred.*

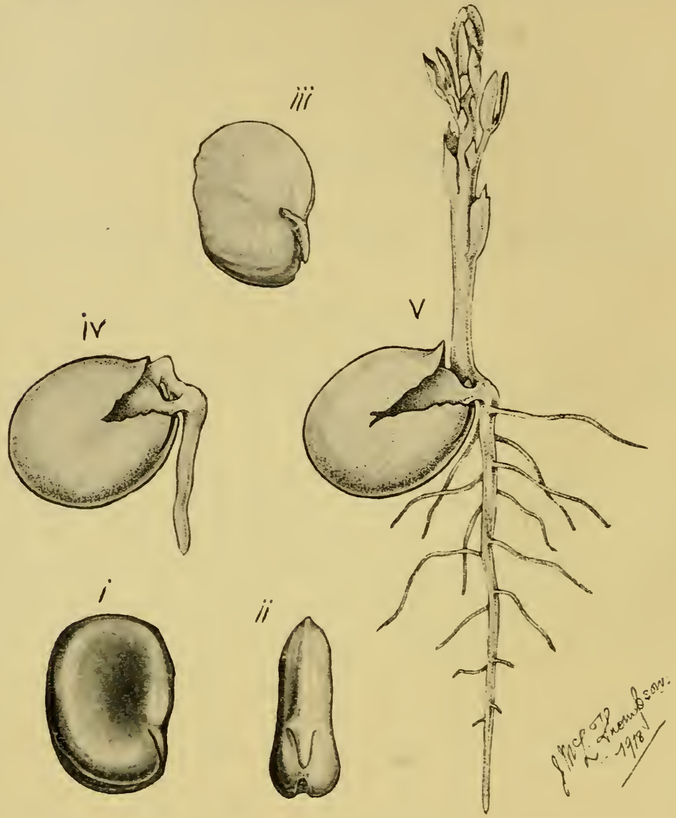

FIG 2.

Common bean (*Vicia Faba*). i. ii., seed covered by seed-coat. iii., germ, with seed-coat and the nearer cotyledon removed. iv. v., successive stages of germination slightly reduced.

The Bean-Seed, as shed by splitting of the Bean pod, appears as a roughly discoid body (Fig. 2). It consists of an *embryo* or germ, protected by an external *Seed-Coat.* On its edge, close to a slight involution of the margin, is an elongated scar, the *hilum*, marking the point of attachment to the parent plant. If the tough brown Seed-Coat be dissected off, the *Germ* or *Embryo* will be disclosed, filling the whole space within. It consists of two large flattened *Seed-Leaves*, or *Cotyledons*, which are attached at the base, right and left, to a curved body which lies between them. Part of this is compressed between the Seed-leaves; it is the *leafy bud* or *plumule*, which is to grow into the shoot of the seedling. Pointing in the opposite direction to this is the *first root* or *radicle*, the conical tip of which is close to one end of the hilum. The parts thus recognised are present in all normal seeds of *Dicotyledons*, which take their name from the *paired Seed-Leaves*. But the form and proportions of the seed and of the germ may vary in different plants, and certain additional tissues may in some cases be present. The Seed-Leaves of the Bean are fleshy in texture, and are stored with materials which serve on germination for the nutrition of the other parts of the germ.

The conditions necessary for the germination of a living seed so constructed are: (i) *the presence of moisture*; (ii) *free access to atmospheric air*; and (iii) *a suitable temperature*. The ordinary conditions of spring-time would meet these requirements, if the seed were buried in an open porous soil. For the soil would be moist, and the air would be free to penetrate its pores; while the rising temperature of the season would meet the third requirement in the case of seeds of temperate climates.

Supposing these conditions to have been fulfilled in the case of a living Bean-Seed, *germination* ensues. The first external change is the rupture of the seed-coat at a point close to the end of the scar. Through this the pale young *root* protrudes, and as it elongates its conical tip at once penetrates vertically downwards into the soil. When the root has attained a length of several inches, a curved *shoot* emerges through the slit between the bases of the two seed-leaves. Clearly this is the result of growth from the leafy bud seen between the cotyledons in the seed. This shoot turns upwards, and soon projects above the level of the soil. *Growth* is thus seen in both parts, the material required for the enlarging tissues being supplied from the fleshy seed-leaves. This is used in building up the enlarged root and shoot. No drying-up will make the root or shoot shrink back to their original size or form, nor can the material drawn from the seed-leaves be by any means replaced. *Such growth is an irreversible process, as is all growth in Plants.*

That the root points downwards and the shoot upwards is not a haphazard result. Experiments with seeds placed in various positions in the soil show that the behaviour of these two parts of the seedling is constant, and suggest that it is a response to some external influence that applies to them all. In this case the influence is Gravity. The subject of external influences will be discussed in detail later (see Chapter IX.). Meanwhile it must suffice to say that an influence such as Gravity, which acts on a living organism so as to produce a change in it, is called a *stimulus*. The effect which the living organism shows is called the *response*. The effect of Gravity upon the growing shoot or root, so as to make the one turn upwards and the other downwards, is an example of *response to stimulus*, *and such a response is one of the essential indications of Life.*

It is familiar to every gardener that, up to a certain point, the higher the temperature the quicker his seedlings appear above ground. But plants vary in their relation to temperature, and that necessary for germination is not the same for them all. Thus most cereals can germinate at a temperature very near to the freezing point, whereas Maize and the Kidney Bean require a minimum temperature of about 9° C. All the functional activities of the Living Plant have such a relation to temperature. The case of germination is merely one example of a general condition of Life. This subject will also be taken up again in Chapter IX.

The root and shoot established on germination are capable of continued growth, which is followed in both cases by the formation of lateral appendages. Thus a *Root-System* and a *Shoot-System* are established, the former being buried in the soil, the latter rising above the level of the soil, and constituting the part of the plant ordinarily seen (Fig. 2, v.). If the soil be carefully washed away from the root-system of a Bean-seedling after the main root has attained about eight inches in length, it will be seen to consist of a *primary*, or *tap-root*, which grows directly downwards and bears horizontal *lateral roots*. The smallest and youngest of these are nearest to the tip of the main root, and the largest and oldest are most remote from it. These may in like manner bear *lateral roots of still higher order*, radiating in all directions. Thus a complex root-system is built up. The extreme tip of each root comes naked out of the soil, and is pellucid and slimy to the touch, so that it readily slides past obstacles as it penetrates the soil. But about three-quarters of an inch back from the tip the particles of soil adhere to the root, showing that from that point backwards a close relation is established between the root and the soil. It will be seen later that this is due to the presence of *numerous minute root-hairs*.

When the shoot of the Bean has grown to the length of about six inches, it will be seen to consist of a central *Stem* terminated by a *bud*. *Leaves*, of which the lowest are pale-coloured scales, are borne laterally on the stem. Passing upwards from the base successively larger leaves are met, each with broad green lobes and a sheathing base. Passing on from these mature leaves, we come to the bud. Dissection of the bud shows that it is composed of a series of successively more minute leaves, very delicate in texture, closely overlapping one another, and all seated on the immature axis. *A bud is thus a compact young shoot, consisting of a short stem overlapped by crowded, immature leaves.*

As the shoot develops, a new bud appears in the axil, or angle of insertion of each leaf upon the stem. Even the cotyledons of the Bean may bear such *axillary buds*. They are constructed like the apical bud, and on development each may repeat the characters of the main shoot. Provision is thus made for multiplication of shoots, so as to form a *branched shoot-system*.

The Bean-Seed itself has throughout germination remained below ground. Its fleshy seed-leaves do not emerge from the seed-coat, but are there gradually emptied of their nutritive store, and finally rot away. Their sole function is storage of food-material for the germ. But in other plants the behaviour is different. A good example is seen in the Charlock. Its seed is nearly spherical, with slightly flattened sides. A lateral scar of attachment (hilum) is seen, as in the Bean, and the seed is covered by a tough leathery seed-coat. Within this is the embryo, with two cotyledons, a bud or plumule, and a first root or radicle. But here the cotyledons are folded sharply in a median plane, giving a compactness to the embryo, which fills the spherical seed (Fig. 3, i. ii.). On germination the seed-coat is burst by the enlarging germ, and the root emerges as before, curving at once downwards (iii.). But here the part of the stem or axis below the seed-leaves grows quickly in length. At first it shows a strong arching curve (iv.). But later this is straightened out, with the consequence that the cotyledons and the bud are carried above ground, still covered by the protecting coat. This soon falls away, and the cotyledons expand, diverging as green leaves, with the bud between them (vi. vii.). The latter elongates as it grows older, forming the leafy shoot. Thus the parts of the seedling of the Charlock are numerically and relatively as in the Bean, and in both cases the food-supply is in the fleshy cotyledons. The difference lies in the fact that in the Bean the active growth is in the region of the axis *above* the insertion of the seed-leaves; in the Charlock it is in the region *below* them. They are thus raised above the soil, and exposed to the light. They expand as green leaves, and help the nutrition. Thus in the Charlock the seed-leaves serve first for storage, and afterwards for carrying out nutrition. It is not an uncommon thing in plants for a part to serve more than one purpose, sometimes simultaneously, sometimes successively.

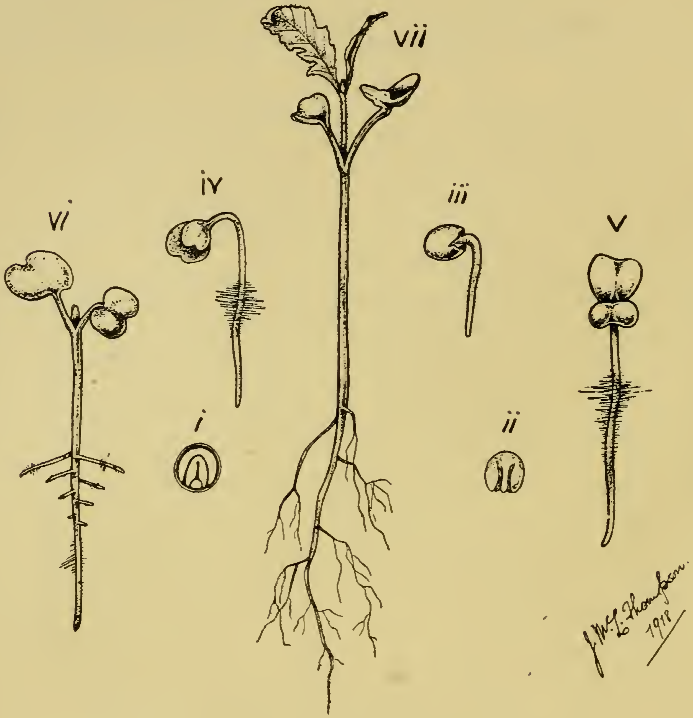

Fig. 3.

Charlock (*Brassica Sinapis*). i. ii., seed with and without seed-coat. iii.-vii., successive stages of germination. Natural size.

A third type of germination may be seen in the Castor-Oil plant (Fig. 4). The seeds are large, and covered by a mottled, brittle seed-coat, which is easily removed, disclosing the semi-transparent contents. These consist of a thin film covering the massive oily *endosperm*, a nutritive store which is not represented in the previous examples. It can easily be split down the middle in the plane in which the seed is flattened (ii. vi.). The germ is then disclosed, having the same number and relation of parts as in the other examples. But here the cotyledons are thin and papery, and the whole germ is immersed in the nutritive endosperm. The chief store of food is thus not in the germ itself, but in the surrounding tissue.

The germination of the Castor-Oil seed corresponds in its external features to that of the Charlock. But here the germ, lying in close contact with the endosperm, extracts the food from it, and absorbs it into itself, while the endosperm gradually shrivels. As the seed-coat is thrown off, the cotyledons turn green and expand. The dry remains of the endosperm may then be seen still for a time adhering to their lower surfaces; but ultimately it falls away. Here the cotyledons act first as suctorial organs, and later expand into nourishing green leaves. The root and shoot thus established may develop further into a root-system and a shoot-system, as in previous cases.

FIG. 4.

Castor oil (*Ricinus communis*). i., seed seen from outside; ii. iii., seen in longitudinal and in transverse section. iv. v., seedling with seed-coat burst but cotyledons still enveloped in endosperm. vi., the same cut longitudinally. vii., hypocotyl straightening, endosperm still adhering to cotyledons. viii., established seedling, with expanded cotyledons and first plumular leaves. (½ natural size.)

The leafy shoot of the Sunflower is produced in a manner very like that of the Castor Oil. But it differs from it and also from its own smooth lower parts in having a harsh roughened surface. This is due to *hairs* of various size. The coarser types of them are seated on conical outgrowths, called *emergences*, often of considerable size. Such surface-growths, or dermal appendages as they are called, are inconstant in occurrence, and irregular in distribution in plants, as compared with the foliar appendages. They vary greatly in character in different plants, and being so inconstant, they are held as less important than the axis and leaf.

Fig. 5.

Diagram suggesting plan of unlimited growth of a Flowering Plant, with multiplication of roots and branches.

Such examples as those now given illustrate some of the differences of proportion, and of function which may occur in seedlings, while the general plan of construction is the same. In each case the result of germination is the establishment of a seedling with its root-system in the soil, and its shoot-system exposed to the air. These regions are directly continuous one with another at the level of the soil. Together they form the living and growing organism. They serve distinct functions, but they co-operate in promoting the general life of the plant.

Each of these two regions of the plant-body once established is capable of indefinite extension (Fig. 5). The radicle continues its apical growth, and can form an unlimited number of lateral roots; these may again repeat the process. In all of them also the root-tip may continue to grow indefinitely. Thus a constantly increasing provision is made for the growing plant as regards mechanical support, and physiologically for the supply of water and salts from the soil. On the other hand, the stem is also gifted with continued apical growth, and it has the power of forming an unlimited succession of leaves, of which the oldest are nearest to the base and the youngest distal, while those at the extreme tip are closely grouped so as to form a terminal bud. Further, in the axil, or angle between the base of each leaf and the stem, a fresh bud may appear, which repeats the chief characters of the terminal bud. Each bud is capable of developing into a lateral branch similar to the main shoot, and so on. The increase in number of shoots or of roots is in fact on a very prolific scale. In herbs, such as the Sunflower, Bean and Castor Oil, this mode of development is not carried far; but still the unlimited possibility exists in the plan of their construction.

It is precisely the same scheme carried out further which gives rise to shrubs and trees. In some of them the development upon this plan may be continued for centuries, and the organism may attain very great size and a high complexity of branching. The result of such continued growth may be very well studied on the twigs and branches of trees in winter, when the leaves have fallen, or in the spring when the winter buds are bursting. For instance, on the Horse Chestnut (Fig. 6), each shoot is terminated by a bud, composed of external bud-scales, which enclose the closely folded foliage leaves awaiting expansion in the succeeding season. The woody stem below is marked by opposite pairs of semicircular scars, where the leaves of the preceding season fell away in autumn. Immediately above each scar an axillary bud may be seen, which is capable of developing into a new branch; but frequently these remain dormant until the distal apex is arrested or destroyed. Some distance down the stem a zone will be found marked transversely by many narrow scars close together. This is the lower limit of the preceding year's growth, and the scars are those left when the bud-scales fell away. Similar zones may be found successively lower down, marking the limits of the increment of growth of earlier years. Each year's growth leaves its record on the outer surface of the branch. Thus, passing

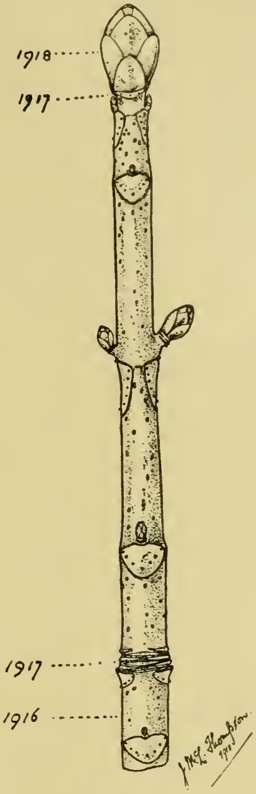

Fig. 6.

Twig of Horse Chestnut in winter, indicating the end of the increment of growth of 1916, the limits of increment of 1917, and the bud to be expanded in 1918, with scars of bud-scales and of foliage leaves, and axillary buds and lenticels. Natural size.

from below upwards along the twig, its annual history can be read, till we arrive finally at the terminal bud, which is already providing for the development of the next year's shoot.

Any Land Plant built upon such a progressive scheme as this requires as it grows additional provision for mechanical support, and for the conduction of water and other supplies from the soil. This is achieved in various ways, as will be seen later. But the most prevalent is the method seen in forest trees, in which the trunk and branches thicken according to the demands of the enlarging body. It is common knowledge how the wood of their trunks is marked internally by annual rings, so called because normally one ring of new tissue is added each year. A similar growth is seen in their roots, both regions showing an automatic increase to meet the growing demands, which are both mechanical and physiological.

The most important factor in determining the conformation of the plant-body in all the Higher Plants is the continued growth at the apex of stem and root. The life of the Higher Plants may be described as *an indefinitely continued embryology*, the increase in the number of parts being in a geometric ratio. In this it differs essentially from that of the Higher Animals, in which the parts of the body are laid down once for all in the initial steps of development, and the body is of a circumscribed and limited type.

But though the body of the Plant is thus theoretically unlimited in its plan, in actual practice limits are imposed. It would be a physical impossibility to develop all the potential parts of so complex a system. Many buds remain dormant. In others seasonal conditions may check or stop apical growth. Various mechanical or physiological injuries may intervene, caused it may be by wind or frost. Animal or fungal attack may destroy many embryonic buds. Consideration must also be given to the physiological drain of flowering. This appears to be effective in the case of herbs, and especially of annuals, as in the Sunflower or Bean. By such influences the theoretically unlimited plan of development is restricted within bounds.

It is upon the scheme laid down in the preceding pages that the body of all the Higher Plants has been constructed. The number and exact position of the leaves may vary, and consequently the number and position of the branches, since these arise from axillary buds. The form and proportion also of the axes and leaves is open to great difference of detail; they are frequently adapted biologically to the conditions under which they live. But these are only minor modifications, which may make the plan more obvious in some cases than in others. Examination of ordinary herbs, shrubs and trees from the point of view suggested here should be practised upon the varied vegetation seen on any country walk. Such observations will show the constancy of the scheme of organisation of the Higher Plants, even in complicated cases. They will also illustrate in what various ways the number, form and proportion of the parts may differ. Thus there comes about that great diversity in appearance shown by the plants that make up ordinary vegetation, though underlying the construction of them all there is still a consistent plan. *The salient feature of this plan of construction of the Higher Plants is the capacity for an indefinite vegetative increase in size and complexity of the individual, which is based upon their "Continued Embryology." This is centred in the Growing Point.*

CHAPTER II.

THE CELLULAR CONSTRUCTION OF THE PLANT.

The apical points of Stem and Root, described in the previous chapter, cannot fail to have attracted attention, by reason of their continued powers of growth and of forming new parts. The perpetual youth of the extreme tips is their leading character. Passing back from these we see parts in successive stages of development up to full maturity. This shows from *external observation* that new parts originate there. To understand how this takes place, a study of the *internal structure* will also be necessary. Such study is called *Anatomy*; in other words, large and solid bodies must be cut into in order that their construction may be made out. Two courses are open for such study. A start may be made from the *mature* parts, such as the fully formed stem, leaf, or root, in which the structure is very complicated. Or the young *embryonic* tip itself may be examined first. Since the construction is much simpler at the tip where the tissues are still young, it will be found best to take this first. Moreover, upon the result of this examination it is possible to base a general idea of the construction of the whole Plant-Body and of all its mature parts.

If an apical bud of a water-plant, such as *Hippuris* or *Elodea*, be dissected under a magnifying power of ten to fifteen diameters, a succession of overlapping leaves will be found, those lying within being constantly smaller than those outside them. The series may be followed inwards till the last are too minute for recognition with the simple lens. In the centre is a projecting cone of soft colourless tissue, with a dome-like ending. This is the *apex of the stem, or growing point* (Fig. 7).

If a median longitudinal section be cut through a bud of *Hippuris* so as to traverse this cone to its extreme tip, it would on microscopic examination show that it is not of uniform texture, like paraffin wax. It is built up of a number of structural units, or *cells*, of more or less cubical form, which are all essentially similar, and are arranged with some degree of regularity (Fig. 8). More highly magnified, they are seen to be all separated from one another by definite, but very thin *cell-walls* (Fig. 9). Each unit comprises a granular mass of material, colourless and semi-liquid in the living state, which is the *cytoplasm.*

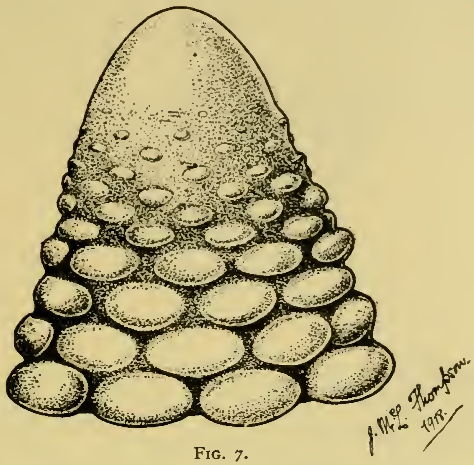

FIG. 7.

External view of the growing point of *Hippuris*, showing the smooth apical cone bearing alternating whorls of lateral leaves, the youngest nearest to the tip. Magnified.

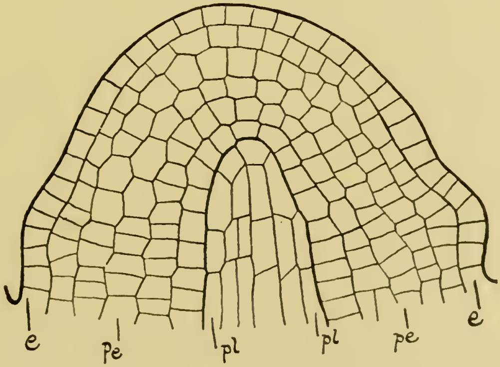

FIG. 8.

Median longitudinal section of the apex of a quite young bud of *Hippuris*. *e*=epidermis. *pe*=periblem. *pl*=plerome. After De Bary. (× 300.)

In a central position in each of them is a more highly refractive, spherical body: this is the *nucleus.* Embedded in the cytoplasm, and often difficult to observe, are other minute roundish bodies, which are colourless: they are the *plastids.* The collective term *protoplasmic body,* or *protoplast,* is applied to all the contents enclosed within the cell-wall. In older tissues the cell-walls are often so conspicuous that the units of construction were called "*cells*" by the earlier observers, from their comparison with the partitioned honeycomb. That name is still retained for them. But it is now fully recognised that *it is the protoplast and not the cell-wall that is the essential part, for it is in it that the active vitality is centred.*

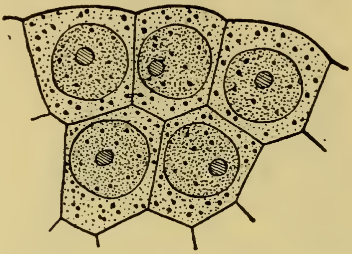

FIG. 9.

Young thin-walled cells from the growing point of *Tradescantia,* each with a relatively large nucleus, containing a highly refractive nucleolus. Many plastids are present in the cytoplasm. After Schimper. (× 800.) The minute size of the cells may be realised by measurement of their diameter as seen in Fig. 9, and division of the results by the magnification as stated: the result is a diam. of about ·02 mm.

INCREASE OF CELLS BY DIVISION.

As the tissues increase with the general growth of the apical region, *the number of cells composing it increases by cell-division.* An examination of the tissues themselves will show how this is carried out. Very frequently cells may be found in the apical cone grouped in pairs, and separated by a very thin wall. These plainly indicate that a division of a pre-existent mother-cell has recently taken place, so as to form two usually equal daughter-cells from one parent cell. The new cell-wall thus formed is inserted at right angles upon the older walls. If the cells always divide into nearly equal halves, and if the new walls are fixed at right angles upon the older walls, the result must necessarily show some degree of regularity in the arrangement of the cells that are formed. In some cases that regularity is very striking. The scheme of construction in the case of the apex of *Hippuris* would be like that shown in Fig. 10, and it is found that in plants at large the young tissues are arranged according to similar schemes. Thus in the young state the axis, and, it may be said more generally, the plant-body throughout, is partitioned up into cells in somewhat the same way as a house is partitioned into rooms. And their arrangement is not at haphazard, but according to laws. *It may be stated generally, as a fact of experience, that the whole of the plant-body, whether young or mature, is made up of such cells, or their derivatives.* This generalisation used to be spoken of as the "cellular theory." But it is now so fully demonstrated that the fact may be enunciated as a positive conclusion. It will be seen later what are the modifications which such cells undergo so as to produce the mature tissues of the plant, which often differ widely in form and structure from the young cells that give rise to them.

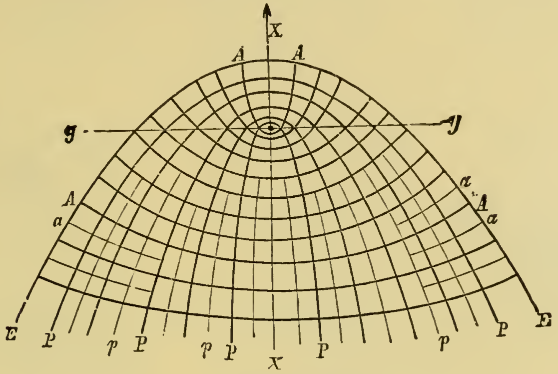

FIG. 10.

Diagram illustrating the plan of arrangement of cell-walls in the apex of the stem of an Angiosperm. XX=axis of construction. EE=external surface. PP=periclinal curves. AA=anticlinal curves. (After Sachs.)

From a comparison of cells in various states of division it is possible to construct a connected history of the process (Fig. 11). The nucleus takes the initiative (i.-iv.). By complex changes, which will be described in detail later, it divides into two exactly equivalent parts, which at first lie in the longer axis of the cell, embedded in the still undivided cytoplasm (v.-vii.). Then a delicate film of cell-wall is formed between them, inserted at right angles to the pre-existent walls, cutting the cell into two nearly equal parts, each containing a nucleus (viii.-ix.). Such simple divisions are called *somatic*, belonging to the *soma* or *plant-body*, to distinguish them from certain divisions which involve further complications connected with the reproductive process. The number of somatic divisions is indefinite, and the numerous cells to which they give rise are while young thin-walled, and all alike.

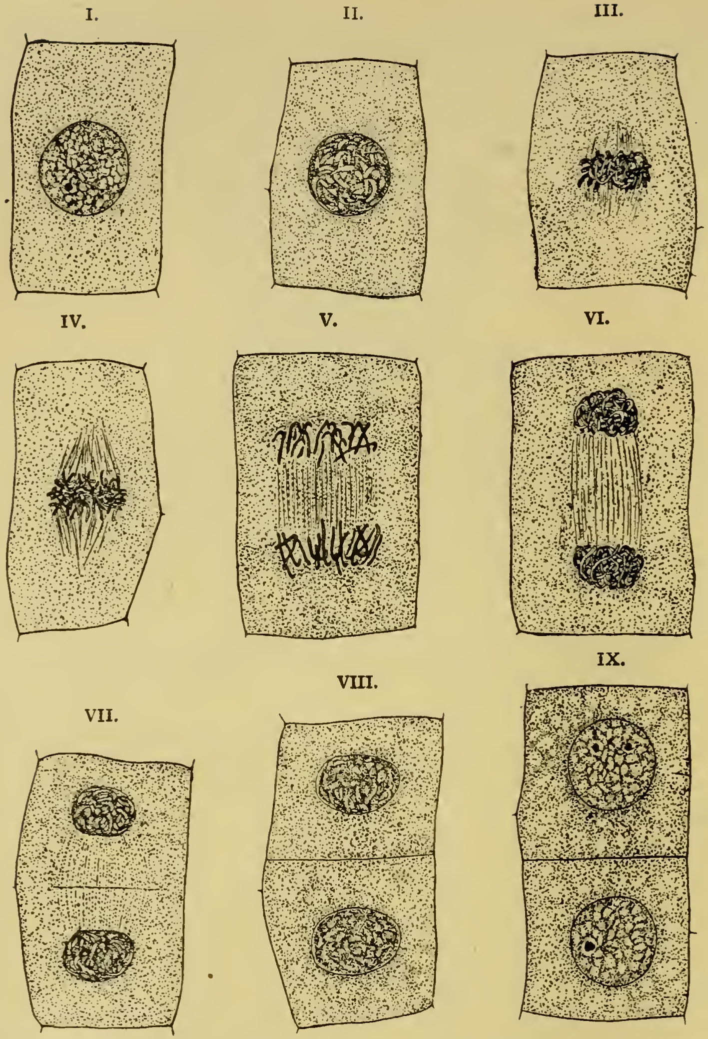

FIG. 11.

I.-IX. Successive stages, drawn from different individual cells of the same root of *Allium cepa* by Dr. J. M. Thompson (× 730). They illustrate the steps in the process of division of a vegetative cell. Such division accounts for the normal increase in number of cells in the "soma," or plant-body: it is therefore called somatic division. Details of behaviour of the nucleus in division will be given later (Chapter XXXV).

The division of the cell being constantly as described, it follows that every cell arises from a pre-existent cell. Every nucleus is derived from a pre-existent nucleus by division, and is never produced *de novo*.

It was formerly believed that plastids also arise only by division, but there is now some doubt whether this is always the case, although their multiplication by division is very common. It is different with the cell-wall. In cell-division it appears as a new film deposited from the protoplasm: while, as we shall see, it may be absent altogether from reproductive cells. It is thus a body of secondary importance, as compared with the more constant constituents of the cell.

Differentiation of Tissues.

Passing in the examination of the longitudinal section of any bud from the growing point downwards, successively older tissues

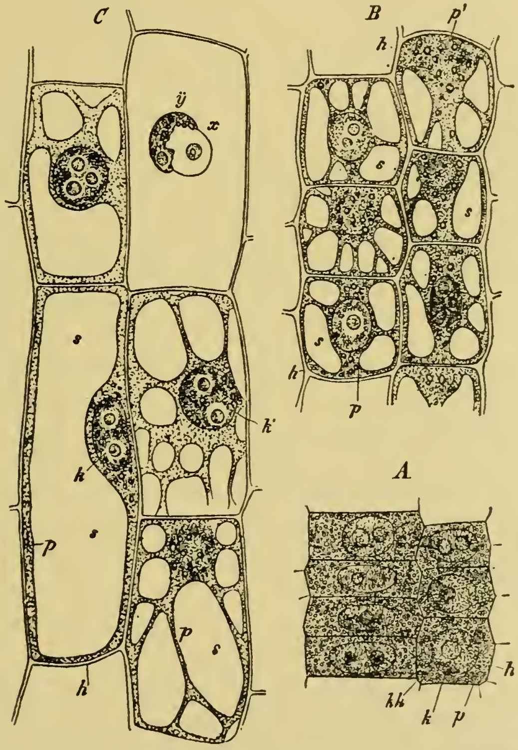

Fig. 12.

Parenchyma-cells from the cortex of the root of *Fritillaria*: longitudinal section (× 550). *A*, very young cells, not yet vacuolated. *B*, older cells with numerous vacuoles containing cell sap, *s*, each surrounded by the protoplasm, *p*. *C*, older cells, with larger vacuoles filled with sap, *s*. The protoplasm (*p*) lines the cell-walls internally, and embeds the nuclei (*k*), which may be suspended centrally, or placed laterally. The large cell to the left has a single large central vacuole, or cell-cavity. (After Sachs.)

are seen, till the mature parts are reached. Various changes appear in the cells. They alter their form and the character of their walls and contents. As a rule the cells enlarge greatly. An important change in the cytoplasm, which is usual in plant-cells, accompanies this growth. It is known as *vacuolisation*, and it may be well illustrated in the cells developing into the pith or cortex of an ordinary stem. Starting from the embryonic state, where the wall is very thin, and the cytoplasm and nucleus fill the whole space enclosed by it (Fig. 12, *A*), the volume begins to increase with age and the wall thickens. But the volume of the cytoplasm does not keep pace with that of the whole cell, and vesicles or drops of clear liquid appear within it.[1] These are called *vacuoles*, and they are filled with vacuole fluid, or *cell-sap*, which is water with certain substances dissolved in it (Fig. 12, *B*). The vacuoles are always completely enclosed in the cytoplasm, which controls them and the substances dissolved in them. The vacuoles may vary in number, size and position, and the position of the nucleus is also inconstant; sometimes it lies laterally in the peripheral cytoplasm; usually it is central. As the vacuoles enlarge they may run together, and finally form a continuous cavity, in the middle of which the nucleus is frequently suspended by radiating threads of cytoplasm (Fig. 12, *C*). A condition is thus arrived at which is characteristic of many cells in the mature state.

Other cells may undergo changes of a much more marked character than this, as they pass from the young to the mature condition. Such changes fit them for performing their several functions in that commonwealth of units of which the mature plant consists. *Division of labour* is characteristic of the mature tissues of all the Higher Plants, and it is the *structural differentiation* of the constituent cells that makes this possible. It will be well here to explain briefly the chief changes which may be traced in the different tissues, as they are developed from the uniform embryonic cells that compose the apical cone.[2]

(1) *Changes in Size and Shape of the Cells.*

Practically all cells grow as they mature, and a simple case in which the change of form is only slight has been seen in Fig. 12 (*A*-*C*).

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[1] It is now known that minute vacuoles are present in embryonic cells.

[2] This analysis of the changes during differentiation finds its proper place here, and forms the natural foundation for any rational study of mature tissues. But it is open to the student to read it either before or after those tissues have been described.

But in the course of their growth cells may also assume various shapes. Usually there is elongation, and the ends become more or less oblique. This naturally follows from the fact that the part of which they are constituent units, such as stem, leaf, or root, itself grows in length. Such changes often involve a readjustment of the cells among themselves by a sliding process, which is specially obvious where the cells become elongated or very wide when mature. They seem then to push the surrounding cells aside, so that the appearance of the mature tissue composed of them may differ strongly from that of the embryonic tissue from which they sprang. Special names used to be applied to all the different characteristic forms which cells might assume. But this is not necessary except in extreme cases; thus the old name *parenchyma* is kept for a tissue of roughly spherical or oblong cells with square ends, while long thick-walled cells with pointed ends are called *fibres* (Fig. 13, i.-v.).

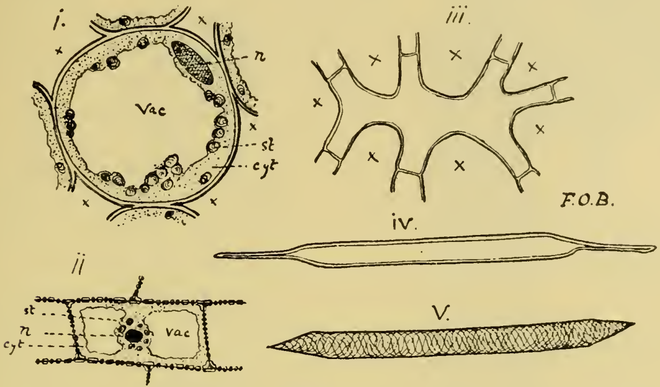

FIG. 13.

Various forms of cells. (i.) cell of the parenchyma from the cortex of the root of a Buttercup, almost spherical; (ii.) oblong cell of the medullary ray of Lime; (iii.) stellate parenchyma of pith of the Rush; (iv.) wood-fibre of the Lime; (v.) fibrous tracheid of Lime.

x=intercellular spaces; *n*=nucleus; *cyt*=cytoplasm; *vac*=vacuole; *st*=starch-grains. (i. ii. iii. × 200; iv. v. × 75.)

(2) *Changes in the Thickness of the Wall: Pits.*

During the growth of the cell the wall is stretched, and like a rubber sheet it would become thinner as it yields, were it not for the deposit of new cell-wall substance by the cytoplasm. In ordinary cell-walls this is effected by *apposition of successive layers* upon the surface of the wall, and so quickly is this carried out that the stretching wall of an enlarging cell actually grows thicker instead of thinner as it stretches. As the limit of size of the mature cell is approached and the stretching ceases, the thickening of the wall may be more rapid, and it is probably this which causes the cessation of growth. The thickening may be continued till in extreme cases a large proportion of the space within the original film of cell-wall is filled up. Often this original wall may be recognised in the mature state as a "middle lamella," where two or more thickened walls adjoin (see Fig. 16, *B*, p. 27). In the mature cells with thick walls the layers of stratification can often be clearly seen (Fig. 14). But the thickening of the walls is seldom uniform. Certain areas are left thin, and a noteworthy feature is that the thin areas in adjoining cells usually correspond. Such thin areas are called *Pits*, and the partitioning wall is called the *pit-membrane*. Pits are of use in facilitating the physiological communication between cells, and practically all mature cells show pits of some sort on their walls (Figs. 15 *B*, 16 *B*).

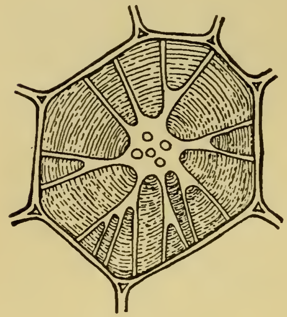

FIG. 14.

Section of a cell of *Hoya carnosa*, with greatly thickened, stratified, and pitted walls. The pits are very narrow, and often branched. (After von Mohl.)

(3) *Changes of Substance of the Cell-walls.*

In the young state the cell-walls are composed of a carbohydrate substance, namely *cellulose*, together with more or less of those pectin-substances which form the basis of fruit-jellies. Such cell-walls are at first yielding and plastic like putty, but they become more resistant and elastic as they grow older. As they become mature the chemical and physical nature of the walls may change. Some walls become *lignified or woody*, and are then mechanically more resistant and harder. Such walls give its character to the wood of tree-trunks. Others become *suberised*, or *corky*, and are then impervious to the passage of water. Bottle-cork consists of masses of dead cells with corky walls. Others may become *gummy*, or *mucilaginous*, and are liable to swell greatly on access of water, which they thus retain. Gum arabic as sold in shops consists of hardened amorphous masses of gum exuded from the stem of certain Acacias. By such changes the cells may become fitted to perform different specific functions in the mature parts.

(4) *Absorption of Cell-wall.*

Though in the young cells the wall completely encloses the protoplasm, it may be partially broken down and absorbed before maturity. This most commonly occurs in those longitudinal rows of cells which are destined to form *vessels*; and usually it affects the transverse, but sometimes also the longitudinal walls. The septa between the cells being thus removed, two or more cells may be thrown together so as to form a continuous tube. Such a tube is called a *Vessel* (Fig. 15). Other cases of absorption of walls may also occur, but that leading to the formation of wood-vessels is the most important, and the most frequent.

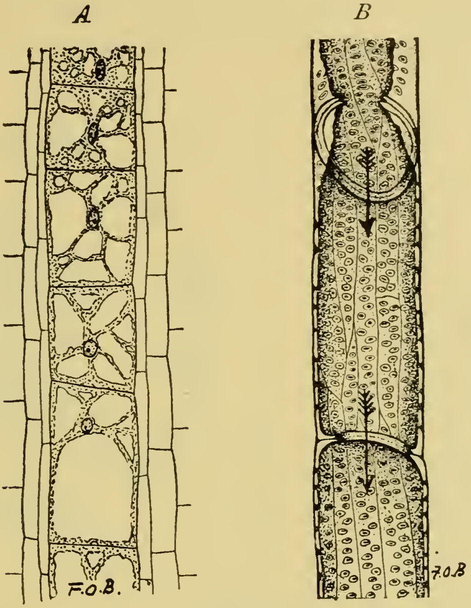

FIG. 15.

A, a longitudinal row of cells from the root of Maize, still with complete septa, nuclei, and cytoplasm, from which a vessel would be formed by absorption of the septa, and disappearance of the protoplasts. *B*, a mature vessel of Sunflower, with thickened and pitted walls and no protoplasmic contents, cut in slightly oblique longitudinal section. The arrows indicate free passage through holes formed by absorption of the septa. The longitudinal lines on the pitted walls show the limits of the adjoining cells. (*A* × 100; *B* × 165.)

(5) *Changes in the Protoplasmic Body of the Cell.*

The common change of *vacuolisation* has already been described. Other changes result in the deposit and removal of contained bodies such as oil-globules, starch-grains, or crystals in the cytoplasm. But the most marked change is the disappearance of the protoplasmic body itself, so that it is not represented in the mature structure. This is found to be the case in the vessels of the wood, in the cells of cork, and in some other tissues (Fig. 15, *B*). Since the vital activities reside in the protoplasm, those tissues where it is absent, consisting only of cell-wall, are no longer actively living, though passively they may still perform functions important in the life of the plant.

(6) *Changes in the Plastids.*

These bodies are minute, and difficult to see in the young cells (Fig. 9). But as the cells mature they may become more numerous by division, and more prominent by their size and colour. In many cells of vegetative parts they turn vivid green, and are called *chloroplasts*, or *chlorophyll-corpuscles* (Fig. 51, p. 76). They are present in myriads in any green leaf, and collectively give the green colour to the parts in which they occur. Other plastids may take red, or yellow colours, as in petals, or in fruits, and they are called *chromoplasts*. Others remain colourless, and are called *leucoplasts*, or *starch-forming corpuscles*, because they are actively functional in the deposit of insoluble grains of starch in tubers, and elsewhere (Fig. 81, p. 124).

By such changes as those described under the headings (1) to (6), the young embryonic cells may be transformed into the various tissues that make up the mature parts. Originally the cells were all alike; as they become mature they are liable to be differentiated and specialised for different functions. It may be held as probable that what is seen in the individual development is a reasonable guide to what actually took place in the evolution of the race. It is probable that plants with little or no differentiation of tissues, that is Cellular Plants such as the Algae, preceded in the history of Evolution the more complex Vascular Plants. These with their higher state of tissue-differentiation constitute the leading feature of the Flora of exposed Land-Surfaces.

Continuity of Protoplasm.

The cells of living tissues all share in a common physiological life, and are in intimate relation to one another. But cell-walls separating adjoining cells do not form complete barriers between their protoplasts. In most mature tissues a *Continuity of Protoplasm* may be demonstrated, from cell to cell. It is established by means of fine *connecting* *threads*. These pass for the most part through those thin areas of pit-membrane, where the distance to be traversed is the shortest. Occasionally they may also extend through the thicker regions of the cell-wall. Examples are shown in Fig. 16, *A*, *B*. The prevalence of Protoplasmic Continuity, now generally demonstrated for the tissues of Plants, forms a structural foundation for their physiological study.

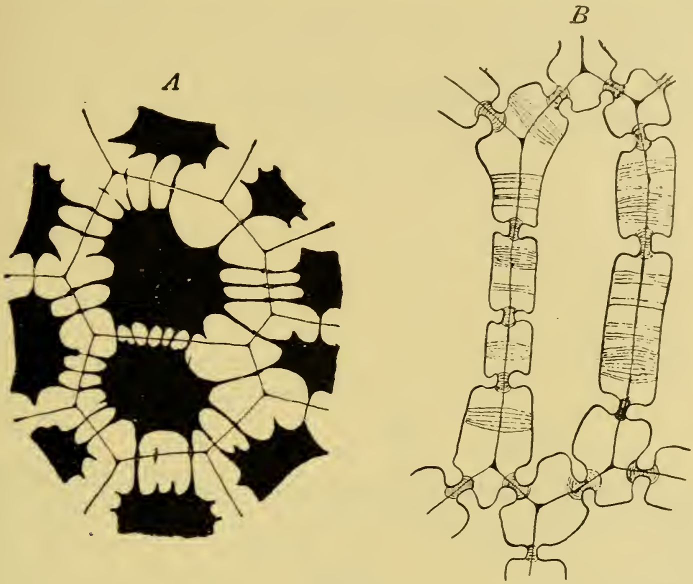

Fig. 16.

Continuity of protoplasm through the walls of plant-cells. *A*. Cells of the pulvinus of *Robinia*, after treatment with sulphuric acid to swell the walls, and staining of the protoplasm with methyl violet. (× 550.)

B. Cell-wall of a single cell of the endosperm of *Lodoicea*, showing the pits and the protoplasmic threads, traversing both the thin pit-membranes and the thickened regions of the wall. (× 400.) (After Gardiner.)

There is reason to believe that the protoplasm is the seat of physiological activity, and since the protoplasm of adjoining cells is connected by threads traversing the cell-walls, whole tracts of tissue will be able to share a common life. This leads us to expect that organs will react as a whole under external stimulus, and that though the cell may appear to be an individual structural unit, still each cell takes its place as a constituent of that physiological commonwealth which we call the Plant-Organism.

While we thus recognise the physiological importance of the continuity of protoplasm through the cell-walls, it should be remembered what circumstance it is that has made it necessary. It is the presence of the cell-wall itself. The encysted state of the cell is a feature of all advanced types of Plant-Organisation. It was probably secondary in origin, and its existence is amply justified by the strength and protection which it affords to the defenceless protoplast. Moreover, it has made possible the building up of large mechanically stable plant-bodies, whether buoyed up in water or supporting themselves in air. The presence of cell-wall may appear to have complicated the problem of physiological interchange by interposing barriers between the protoplasts. But this difficulty has been surmounted by those threads of protoplasm, which traverse the walls, and link up the protoplasts into a *continuous living system.*

CHAPTER III.

THE LIVING CELL.

In order to understand that "continuous living system" of which the plant body consists, it will be necessary to consider in more detail the structure and physiological properties of the cell-units which compose it. As stated in the previous chapter, the mature plant does not consist entirely of living cells, but it is in them that the physiological activities of the plant are concentrated.

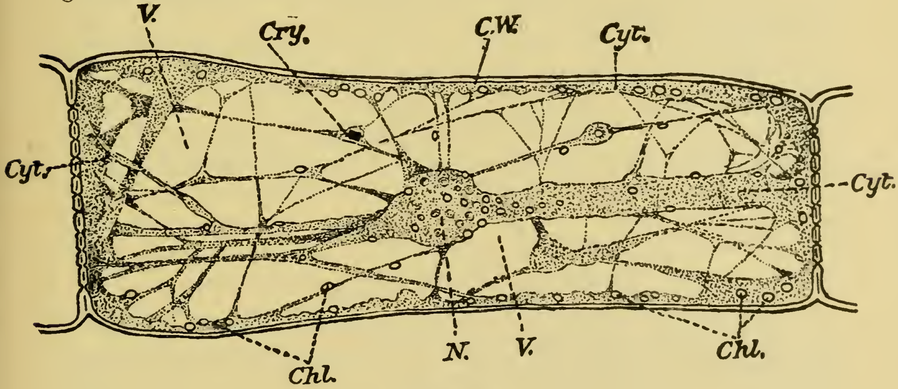

Fig. 17.

Optical longitudinal section of a single cell of a hair of the Cucumber. Externally is the cell-wall (*C.W.*). Its inner surface is lined by a layer of cytoplasm (*cyt.*), surrounding a large vacuole (*V.*). In this the nucleus (*N.*) is suspended centrally by numerous cytoplasmic threads. Movements may be seen in these during vitality, which convey chloroplasts (*chl.*), and even crystals (*cry.*), thus showing active circulation in the living cell. (After Sachs.)

The visible structure of typical living cells has already been described, but the main features will be revised at this point, with the help of Fig. 17, which shows a single cell from one of the coarse hairs that roughen the surface of the shoot of the Cucumber. Externally the cell is limited by a definite *cell-wall* of almost uniform thickness. Its ends are partitioned off from the adjoining cells by transverse septa marked by shallow pits, a condition which is usual for the septa, or party-walls between cells. Protoplasmic connections probably pass through these pits. Each protoplast (p. 18) is thus enclosed by an elastic envelope of cell-wall, composed chiefly of cellulose and normally saturated to a greater or lesser extent with imbibed water. A film of *cytoplasm* lines the whole internal surface of the cell-wall, and thus completely invests the large internal cavity, or *vacuole*, which is filled with watery *cell-sap*. A highly refringent *nucleus* (as a rule more sharply delimited than in the Figure), surrounded by a sheath of granular cytoplasm, is suspended in a central position by threads of cytoplasm, which traverse the vacuole. Their arrangement is irregular, with frequent branchings ; but most of them converge towards the nucleus, which is thus indicated as a functional centre of the whole protoplast. Granules and inclusions of various sorts are seen immersed in the cytoplasm. The largest of these are the plastids, which in this cell are green and are termed *chloroplasts*, but many other smaller bodies are present, including occasional crystals. The nucleus, cytoplasm and plastids are the actual living components of the cell, and collectively form the *protoplast*.

In many living cells the protoplasm exhibits *streaming movements*. It is probable that the movement is initiated in the cytoplasm, the plastids and other cell-inclusions being carried along passively. The plastids may be carried back and forth along the threads that suspend the nucleus, as in the cucumber-hair cell, or along the cytoplasmic lining of the cell.

Properties of the Living Cell.

Of the various properties of the typical living plant-cell, that of effecting *chemical transformation* is one of the most prominent and important. In connection with the nutrition of the plant there proceed within its constituent cells very diverse chemical reactions, complex substances being elaborated from simple raw materials derived from the environment of the plant. Some of these activities are restricted to particular cells in the Higher Plants : thus the process of photosynthesis (see Chapter VIII.) occurs chiefly in the cells of the leaf. Other types of chemical activity are exhibited by all living cells. These chemical activities, involving also transformations of energy, are grouped together under the general term *Metabolism*, and are considered in more detail in Chapter VIII. *Growth* in size and complexity is another feature of the cell, the materials for it being prepared by the metabolic activities mentioned. Finally the living cell is sensitive or *irritable* to certain outside influences which act as *stimuli*. Irritability is most conveniently discussed in relation to whole organs of plants, and is considered in Chapter IX.

In order that the cell may display its full activity, certain conditions must be provided. Suitable *raw materials* must be present before constructive processes and growth can occur, while a source of *energy* must be to hand. For most purposes this energy is derived from the oxidation of sugars previously built up in photosynthesis, and so the presence of *oxygen* is for most cells a necessary condition to normal activity. In the particular constructive process known as photosynthesis, light energy is utilised, and thus *light* must be available for this process to be carried out. The cell structures normally contain a high proportion (over 80 per cent.) of *water* and adequate supplies of this must be available. Its absence leads to death or to a suspension of cell activities, as in dormant seeds where the cells are in a state of desiccation. A *suitable temperature* must be provided, as mentioned in Chapter I. In most plants vital activity is only manifest between 0° C. and about 45° C., with greatest activity prevailing between 25° C. and 35° C. ; exposure of cells to temperatures above or below the former range is liable to result in death (see also Chapter IX.). Vital activity is suspended by exposure of cells to substances such as chloroform or ether, which act as *narcotics*. From the effects of these the cells may subsequently recover, while other substances such as alcohol, or compounds of copper, act as *poisons* and kill the cell.

The operation of some of these factors can conveniently be studied in observations on the protoplasmic streaming, which, as already mentioned, is shown by some cells. The rate of streaming serves as an index of the general activity of the cell. Low temperatures slow down the streaming, higher temperatures accelerate it until a certain temperature (the optimum) is reached, above which the cell is injured and the movements soon cease. Deprival of oxygen or exposure to narcotics or poisons causes the movements to stop.

PROTOPLASM.

All these attributes of the cell—metabolism, growth, irritability—have their genesis in the *protoplasm*. We must therefore enquire why such remarkable properties should reside in the protoplasm.

There is no doubt that chemically and physically protoplasm is very complex indeed, and the study of its nature is attended by great difficulties. Under the microscope the cytoplasmic part of the protoplasm has the appearance of a clear medium with many suspended granules. Experimental evidence shows that protoplasm is usually liquid in nature, though considerably thicker or more viscous than water. In some cases the consistency is more that of a jelly. The nucleus and plastids are somewhat denser parts of it.

Chemical analysis has indicated that protoplasm is a heterogeneous mixture of a great variety of chemical substances, the *Proteins* being present in greatest quantity, both in the nucleus and the cytoplasm (see Chapter VIII.). Associated with them are fats and their derivatives, and mineral salts. All these substances are dissolved or suspended in the water which constitutes over 80 per cent. by weight of protoplasm. The constituents of protoplasm are to a considerable extent in a *colloidal* condition, and some knowledge of the special properties of colloidal substances and solutions is absolutely essential to a consideration, however elementary, of the living cell ; for there is no doubt that it is largely the colloidal nature of its constituents that endows protoplasm with its remarkable powers. The cell-wall and some of the metabolic substances occurring in cells are also colloidal in nature. Graham, in his researches of the middle of last century, divided soluble substances into two classes, as the result of his studies on *dialysis*,—the term applied to the passage of substances in solution through membranes such as parchment. He found that certain substances passed freely through such membranes, and since generally speaking they could also be readily obtained in a crystalline condition he called them *Crystalloids.* As examples we have sugars and soluble salts. Other substances were found not to dialyse, or only very slowly, while a further character was their amorphous nature when dehydrated. These he termed *Colloids.* Many plant and animal products are of this type. As examples gelatin (a protein), agar-agar, gums and starch may be quoted. These substances give a special type of solution in water, known as a *colloidal solution.* In such a solution the substance is present in the form of relatively large particles, either because the molecules are aggregated into groups, or because the individual molecules are very large ; or again because they take into association a number of molecules of water. Such solutions are intermediate between the true solutions given by crystalloids, and suspensions or emulsions. The particles are permanently suspended in the water, they are invisible under the highest powers of the microscope, and will pass through a filter paper, though they cannot pass through the minute pores of parchment, as already mentioned.

In the dry state colloids are often characterised by a high affinity for water, leading to *imbibition* when placed in water. In some cases the colloid dilutes itself so far as to go into solution, as does gelatin. In others the colloid, though imbibing water to a considerable extent, remains in a semi-solid, jelly state. This is the case with the cellulose of the wall. The swelling of dry seeds in water is due to imbibition both by cell-walls and by protoplasmic colloids.

Many colloidal solutions, while liquid at higher temperatures or in greater dilution, set to form a jelly on cooling or on concentration. Gelatin and starch paste are examples. The fact that protoplasm exists sometimes as a liquid, sometimes as a jelly, points to its colloidal nature. *Protoplasm appears to consist of an extremely complex system, in which proteins are present in colloidal solution in an aqueous medium containing also mineral salts and other soluble substances. Associated with the proteins are fats and other constituents, such as the protoplasmic catalysts or enzymes.* They will be considered in Chapter VIII. The surface of colloidal particles, presented to the aqueous medium, is the seat of important phenomena. Crystalloidal substances which may be present in the water tend to accumulate on the surface of the particles by a process known as *adsorption*. This is likely to accelerate any chemical reactions that may occur between different substances adsorbed side by side on colloidal particles; and there is little doubt that the great chemical activity of protoplasm is in part due to this adsorption, especially on to the surface of the protoplasmic catalysts or enzymes.

It is a matter for surprise that many different chemical reactions should be able to proceed at once within the minute confines of a cell. As will be seen later, some of these reactions are known to be restricted to the plastids, and it is often assumed that there is an invisible separation of the protoplasm into further separate areas, each devoted to a particular type of reaction. The nucleus is the bearer of the hereditary characters of a plant, as is described later. It must also play an important part in the other activities of the cell, directing them in such a way that the plant as a whole, in a suitable environment, acquires those morphological and physiological attributes which characterise its race.

Osmotic Phenomena in Plant Cells.

Most free cell-wall surfaces tend to bulge outwards. This is seen even in embryonic cells (Fig. 9), and is a general feature of mature cells of the epidermis (Figs. 22, 47). A tendency to convexity also appears in the free cell-walls of the Cucumber hair (Fig. 17). Such observations are evidence of a feature common in the living cells of plants, namely, the state of *Turgor* (or *Turgescence*), arising from the presence of internal pressure (*Turgor Pressure*) acting equally upon the whole inner surface, and tending to round off the contours of the cell. This state of turgor is due to the *osmotic properties of the cell.*

At this point we may consider an experiment in which the arrangement shown in Fig. 17A is employed. A parchment thimble is initially filled with a solution of sugar and securely attached to a rubber stopper fitted with a long glass tube. The thimble is then immersed in water. Very soon liquid commences to rise in the tube, and if the sugar solution is sufficiently concentrated a column several yards high may be obtained in a day or two. Evidently water is passing from the outer vessel into the sugar solution, and this is leading to the development of a considerable hydrostatic pressure within the thimble. This movement of water through a membrane is known as *Osmosis* and would be produced with a solution of most crystalloidal substances. The motive agent in the movement of the water is what is known as the *Osmotic Pressure* of the sugar solution: the precise nature of osmotic pressure is uncertain, but its existence is connected with the fact that while the molecules of water pass through the membrane rapidly, those of sugar penetrate only slowly. A measure of the osmotic pressure of a given solution is obtained by noting the maximum hydrostatic pressure that is developed when the solution is enclosed in an apparatus of the type shown in Fig. 17A, using a semi-permeable membrane (see below). Such measurements reveal that by osmosis, hydrostatic pressures of considerable magnitude may be set up. Thus the osmotic pressure of a 10 per cent. solution of cane sugar is equal to approximately 8 atmospheres, or 120 pounds per square inch: that is to say, the solution would set up a hydrostatic pressure of this magnitude when enclosed in a suitable apparatus. Osmotic pressure varies with the concentration of a solution, and within limits there is a direct relation between the two values. Osmosis does not occur only from pure water into a solution: if one solution is separated by a membrane from a second solution of greater osmotic pressure, water will pass by osmosis from the first into the second solution, the effective osmotic pressure in this case being the difference between the values for the two solutions.

The parchment membrane used in the experiment described above allows the sugar molecules to diffuse slowly into the outer water; the membrane is to a certain extent *permeable* to the sugar. The concentration and therefore the osmotic pressure of the contents of the thimble thus fall, and some of the water initially taken into the thimble leaks out again. A permanent osmotic retention of water is only possible with a membrane which, while giving free passage to water molecules, denies passage to the molecules of the osmotically active substance. Such a membrane is said to be *semi-permeable* to the solution, and it is only with such membranes that the osmotic pressure of a solution can be determined directly. Copper ferrocyanide forms a well-known artificial membrane which is semi-permeable to solutions of sugar and of various other substances. For purposes of experiment it is usually deposited within the minute pores of a porous pot, which thus gives it rigid support.

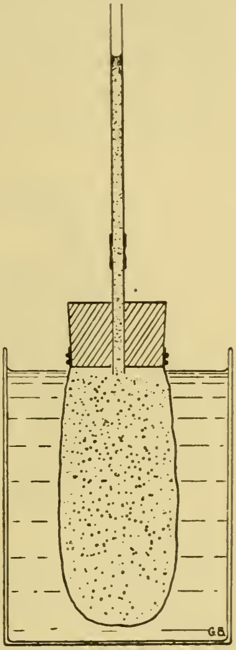

FIG. 17A.

Apparatus for the demonstration of Osmosis. The parchment thimble contains a sugar solution, while the outer vessel is initially filled with water.

The plant cell forms an osmotic system. The cell-sap of the vacuole consists of a solution of osmotically active substances, such as sugars, organic acids and salts, and normally exerts a total osmotic pressure of 5 to 20 atmospheres. This solution is enclosed in the membrane formed by the thin lining of cytoplasm. The cell-wall gives support to the cytoplasmic lining: its presence makes possible the development of a high degree of turgor within the cell. Under normal conditions the plant cell is in a state of inflation or of turgor (p. 34), set up by the osmotic absorption of water. This condition can be removed without harm to the cell by immersion in a solution of potassium nitrate or of cane sugar which is sufficiently concentrated to be of higher osmotic pressure than the cell-sap. Such a solution is said to be *hypertonic* to the sap; one of lower osmotic pressure than the sap would be termed *hypotonic*. For many plant cells a 5 per cent.

solution of potassium nitrate is hypertonic and will withdraw water from the cell-sap. The effect of immersion in such a solution can be most readily observed microscopically in cells which contain a soluble pigment in the cell-sap, giving greater definition to the outlines of the vacuole and of the protoplast. Sections of the Red Beet may be used, or strips of epidermal cells of leaves such as *Cyclamen*, where a red pigment is again present. The initial effect of immersion is a shrinkage of the whole cell as the pressure of the contents on the wall is relaxed (Fig. 18, i. and ii.). In a very short time the protoplast breaks contact with the cell-wall and shrinks to a further extent. The cell is now said to be *plasmolysed* (Fig. 18, iii.). The space between the cell-wall and the protoplast is filled with the nitrate solution, illustrating the fact that the cellulose cell-wall is readily permeable to water and to dissolved, crystalloidal substances. Turning to the cytoplasm, it will be noticed that there is no outward leakage of the red pigment, the colour of which is intensified by the concentration of the sap. *The cytoplasmic lining constitutes a membrane that is in life to some degree semi-permeable to the sap.*

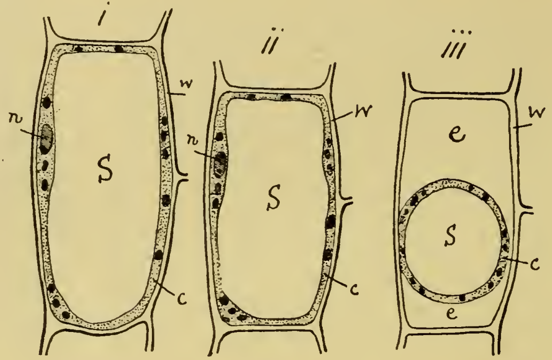

FIG. 18.

Young parenchymatous cell (i.) in the turgid state, (ii. and iii.) successive appearances of cell after immersion in a hypertonic solution of potassium nitrate. *w*=wall; *c*=cytoplasm; *n*=nucleus; *s*=cell-sap; *e*=nitrate solution which has passed through the cell-wall. (After De Vries.)

If plasmolysis be carried out slowly by means of dilute solutions, fine threads of cytoplasm may often be seen to stretch from the cell-wall to the contracted mass (Fig. 19). This indicates under normal conditions of the cell an intimate relation between the two bodies, which is in accordance with the deposit of the cell-wall from the protoplasm. But it is uncertain what relation, if any, these cytoplasmic threads have to the threads that establish protoplasmic continuity through the cell-wall (Chapter II.).

The shrinkage of the protoplast of the plasmolysed cell continues until the sap is concentrated to such a degree that its osmotic pressure becomes equal to that of the external solution: equilibrium is then established, provided that the dissolved substance of the external solution is unable to enter the cell. If it does enter, the osmotic activity of the cell-sap is gradually increased and eventually the protoplast is able to take up water from the outer solution and so to recover its turgor. This recovery or *de-plasmolysis* can in any case be rapidly induced by transferring the cells from the plasmolysing solution into water. The osmotic properties of the cell-sap now result in a rapid intake of water, just as water passed into the parchment thimble in the experiment shown in Fig. 17A. The protoplast swells and soon regains contact with the wall: through continued entrance of water the elastic wall becomes distended. As the wall now exerts a pressure on the expanding protoplast, the capacity of the cell for further absorption of water is thereby curtailed. The effective osmotic pressure conducive to further absorption is clearly the difference between the osmotic pressure of the cell-sap and the inward pressure of the wall. This effective osmotic pressure is distinguished as *Suction Pressure*. As the absorption of water continues a stage

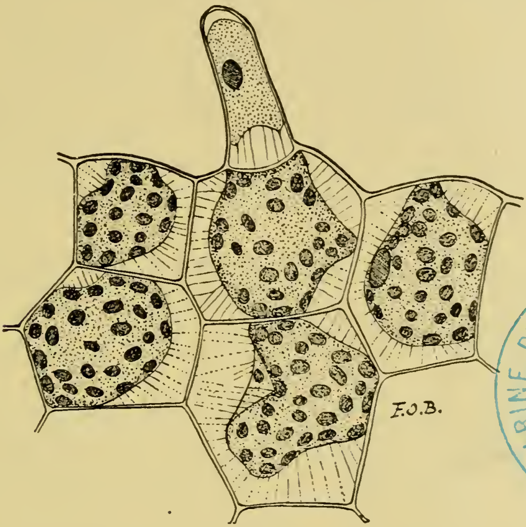

FIG. 19.
Cells from the prothallus of *Nephrodium villosum* after treatment with 3 per cent. solution of common salt (× 550). Drawn as observed about 15 minutes after plasmolysis; the threads are very fine, but appear proportionally thicker in the figure than they actually are.

is eventually reached at which the available osmotic forces are unable to stretch the wall any further. *The suction pressure is now nil, and the cell has no capacity for further absorption of water.* On the other hand the pressure of the cell-contents on the wall—known as the *Turgor Pressure*—is now at its maximum, the whole of the osmotic pressure of the cell-sap being exerted on the wall. The cytoplasmic membrane and the wall of such a turgid cell are in a state of inflation, and may be compared with a blown-up football, the membrane corresponding to the bladder, the cell-wall to the case.

The possible development of turgor pressures of values ranging from 5 to 20 atmospheres within relatively thin-walled cells will naturally occasion some surprise. Actually under normal conditions plant cells are not fully turgid, as is indicated by the swelling usually shown on placing a living tissue in water. Also it should be remembered that most cells are exceedingly small, and what would be impossible in a larger structure may be quite possible in a smaller (Chapter X.).

By command of such high osmotic forces as those above quoted, upon which the growth of the cells depends, the organs of plants are able to overcome considerable resistances (Chapter IX.). Thus the root forces its way into the soil, while the shoots of plants occasionally lift asphalt or flagged pavements. The turgor of the individual cells also gives such degree of firmness and rigidity as is seen in sappy and herbaceous plants, which they lose on wilting or withering or on plasmolysis (Chapter X). Like the football or the pneumatic tyre they are rigid when distended, but flaccid and limp when the pressure falls. In pneumatic tyres it is a pressure of compressible gas that gives the mechanical effect: in the plant cell it is a turgor caused by an accumulation of incompressible liquid. But in both cases the mechanical effectiveness depends upon the resistance of the elastic outer cover.

The Living Cell and Dissolved Substances.

It is frequently stated that the cytoplasmic lining of the cell is semi-permeable to the cell-sap solution. It is, however, obvious that the mineral salts of the sap must have entered the cell from without, and unless the cell contains chloroplasts any sugars that are present must also have passed from another cell into the one in question. In fact the physiology of the plant requires that there shall be free diffusion of dissolved substances from one living cell to another. It seems that the cytoplasm must be appreciably permeable to salts, sugars, amino acids and such crystalloidal substances, although under experimental conditions the degree of this permeability appears to be lower than one would expect. It is possible that movement from cell to cell of substances in solution also occurs through the cytoplasmic connections already mentioned.

Experiments show that some classes of substances penetrate the cell very quickly, as is the case for example with alcohol (poisonous in higher concentrations), urea and other organic compounds. There has been much speculation as to why some substances are able to pass the cell-membrane more easily than others. There is some evidence that membranes, both natural and artificial, act as molecular sieves, allowing smaller molecules to pass through, but holding up larger ones ; though this theory only accounts for some of the facts.

If a cell is killed the cytoplasmic membrane immediately becomes very much more permeable to dissolved substances, its organisation having been destroyed. Thus, while Beet cells are in life semi-permeable to the red pigment of the sap, if the cells are killed, by heat or by exposure to chloroform, the red pigment quickly begins to diffuse out of the cells into the external liquid in which they may be lying.

In some cases the entrance of dissolved substances into a cell proceeds according to the laws of ordinary diffusion, continuing until the concentrations inside and outside the cell are equal in respect of a particular substance. This holds for various organic compounds. If the substance is being constantly used up in one way or another inside the cell, or is passing into neighbouring cells, equality of concentration may never be reached, and entrance will continue indefinitely. A similar consideration applies to the entrance of inorganic salts, and of the ions produced by their dissociation: but with these entrance may continue even after the state of equal concentration has been reached. This is a fact of great importance in connection with the absorption of mineral salts by the root-hairs from the very dilute soil-solution (Chapter VII.). It is clear that here forces over and above those productive of ordinary diffusion are operative, though their nature is still problematical.

CHAPTER IV.

THE TISSUES OF THE STEM.

THE *mature tissues* of a Plant are not homogeneous as they are in the apical bud. At first they are all soft. But as they pass over to the mature condition, while certain tissues retain their relatively thin-walls, others become indurated, forming strands which are mechanically resistant. This is illustrated in a familiar way in the shoots of garden vegetables. If these are allowed to mature too far they become stringy, owing to the development of toughened strands. Where the succulent tissues preponderate the harder strands form isolated threads embedded in the softer tissues. In other cases they may be fused into larger tracts, and this is especially so as they grow older. They thus form in tree trunks and twigs of woody plants a cylindrical core, from which smaller strands extend outwards into the leaves and branches. The mature Shoot, with its constituent axis and leaves, is thus composed of a relatively firm skeleton, consisting of the *Vascular* and *Fibrous System* : this is embedded in the softer *Ground-Tissue* ; and the whole is covered on the outside by a continuous skin of the *Epidermis*. The first of these serves for *conduction*, and gives *mechanical strength* : the second carries on the functions of *nutrition* and *storage* : while the epidermal system may give *external protection*.

In order to obtain a more exact idea of the general construction of the shoot of a Flowering Plant either the firmer strands may be dissected out by hand, or their position may be studied by means of sections. It is only in large and herbaceous plants that the former method is effective ; but it is well to carry it out in some such plant as the Sunflower, for this gives a better understanding of the results obtained by sections. By either method it is possible to trace the course and connections of the strands through the softer tissues, and so to construct the vascular skeleton of the shoot. Such a skeleton is shown for *Clematis* in Fig. 20. Here the leaves are arranged in pairs, and from each leaf three vascular strands pass into the stem. Each strand curves downwards before reaching the centre of the stem, and after taking a straight downward course to the level of the next pair of leaves it forks. The two shanks are then inserted right and left upon the strands that enter there. If a transverse section be cut at any point between the pairs of leaves, the section shows six main strands arranged in a ring, with smaller strands between them (Fig. 21). A very simple connected system of vascular strands is thus formed, and it illustrates the arrangement usual for them in the shoots of Dicotyledons. There are differences in the number of the strands entering from each leaf in various examples. In some there is only one strand, in others more. The

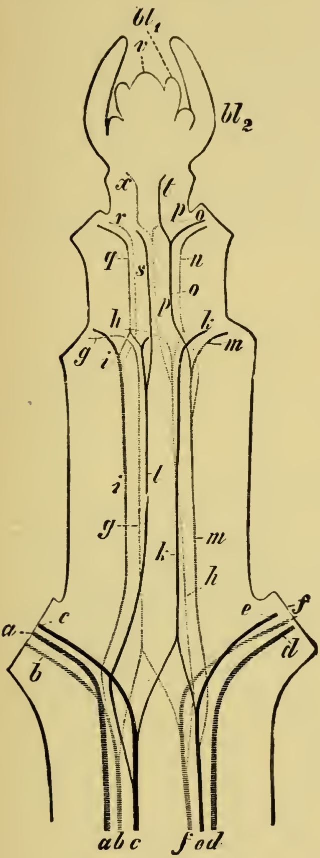

FIG. 20.

Clematis viticella. End of a branch which has been made transparent by the removal of the superficial tissues and treatment with caustic potash. The emerging strands have been slightly displaced by gentle pressure. The two uppermost pairs of young leaves (bl^1, bl^2) are still without leaf-traces; *v*, apical cone. (S. after Naegeli.)

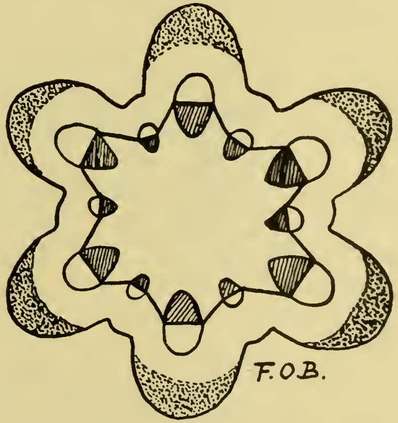

FIG. 21.

Transverse section of an internode of a stem of *Clematis*, showing a ring of six larger and six smaller vascular strands, surrounding the central pith, and covered externally by the thick cortex. In the adjoining skeleton it is only the six larger strands that are represented. The collenchyma massed at the projecting angles is dotted. (× 15.)

arrangement of the leaves on the stem may also vary, as well as the distance through which the strands keep a separate course down the stem. Such differences will naturally alter the number and relations of the strands. But as they all regularly take the curved course in the way shown in *Clematis*, the vascular strands will appear in all ordinary Dicotyledons to be arranged in a circle in the transverse section. Within that circle lies the central column of *pith*. Outside it is a more or less broad band of *cortex*, and externally is the *epidermis*. The pith and cortex thus embed the vascular system, and are sometimes called collectively the *ground-tissue*. It is in herbaceous Dicotyledons that these tissues are most easily studied, such as the Bean, Sunflower, or Potato.

STEMS OF HERBACEOUS DICOTYLEDONS.

The superficial layers of the stem in herbaceous Dicotyledons show well-marked characters, and are relatively simple in construction (Fig. 22). Starting from the outside, the *epidermis* appears as a single superficial layer of living cells, each with its lining of cytoplasm. The outer wall of each cell is thickened, and covered externally by a thin film of *cuticle*, which, being highly impervious to water, controls the loss by evaporation. The epidermis thus forms a skin protective both mechanically and physiologically. It is, however,

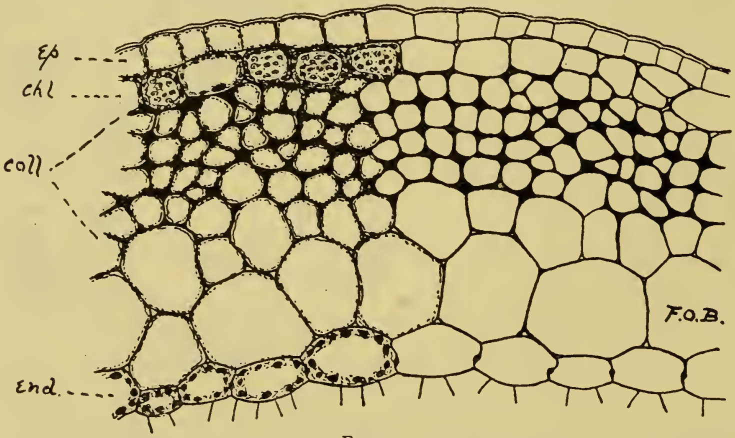

FIG. 22.

Superficial tissues of the stem of Potato as seen in transverse section. (× 100.) *ep*=epidermis; *chl*=outermost layer of the cortex containing chlorophyll corpuscles. *coll*=collenchyma; *end*=endodermis with starch-grains. The protoplasmic contents of the cells are omitted on the right, so as to make the cell-walls appear more prominent.

interrupted here and there by breathing pores, or *stomata* ; but none of these happen to have been traversed in the section drawn. They serve for ventilation of the tissues, and will be described later (compare Figs. 47, 48, 51).

Beneath the epidermis is a band of *cortex*, limited internally by the *endodermis*, which is the innermost layer of its cells. They are easily recognised while young by the *starch-grains* which they contain (dark blue with Iodine solution). The outermost layer of the cortex consists of thin-walled cells containing green *chloroplasts*, while triangular spaces occur where their walls meet. It is chiefly this layer that gives the green colour to the stem. Beneath it lies a broad band of cells with their cellulose walls thickened at their angles, which gives them added strength. It is called *collenchyma*, and it passes over gradually to an inner, thin-walled cortex, with cells of larger size, and triangular *intercellular spaces*. These spaces are formed by splitting of the cell-walls as they pass from the young to the mature stage, at the angles where they meet. Since in life they are filled with gases they form a connected *ventilating system*, which communicates with the outer air through the stomata. The cells of the cortex are all living cells, each with its protoplasmic lining. Gaseous interchange is thus provided for them by the connected system of air-channels. But this communication is cut off inwards, or at least restricted, by the layer of the *endodermis*, in which the cells fit closely together, and form a barrier between the outer tissues and those which lie within. They are thin-walled, and in addition to the starch which they contain while young, they are characterised by a band of corky substance on each radial wall, which being thrown into folds as the wall shrinks on death of the cell, gives the appearance of a *dark dot*. The endodermis is actually the innermost layer of the cortex, and it delimits the tissues that lie within. The whole aggregate of these may be styled the *central cylinder*, or more briefly the *stele*.

The cortex is a variable tissue. The Potato gives an example of the bulk and character that is usual for herbaceous stems, in which the stele is relatively large and the cortex narrow. In young woody stems the stele is smaller in proportion at first, and the cortex usually broader, as it is in *Clematis* (Fig. 21). Aquatic plants have a contracted stele, and the cortex is more bulky still, with large intercellular spaces ; as in *Hippuris*, or the Pond Weeds. On the other hand, in some Monocotyledons, and especially in the Grasses, it may be extremely narrow, so that the stele takes up nearly the whole transverse area (Fig. 29). It may also vary in constitution. Sometimes it consists wholly of soft green parenchyma, as in *Hippuris :* or this tissue may be associated in various ways with strengthening collenchyma : or sometimes it may be hard and woody, as it is in the haulms of Grasses. It may also contain occasional tissues, such as resin-passages (Sunflower, Ivy, Pine), or milk-vessels and cells (Dandelion and Spurge, see p. 54). But however variable, it is constantly present between the epidermis and the stele.

The stele *comprises the ring of vascular strands, together with the tissues that envelop them, and the central column of pith.* The *pith* is a bulky mass of thin-walled parenchyma, its living cells resembling those of the inner cortex. Similar tissue may extend between the vascular strands outwards to the endodermis. A single strand of the stem of the Figwort thus isolated is shown in transverse section in Fig. 23. It is typical of an herbaceous Dicotyledon. The endodermis (*e*), indicated by its starch-grains, defines the inner limit of the cortex. The *vascular strand* is roughly oval in section, but it is not strictly circumscribed. It consists of two main regions which differ in structure and in function. A softer region,

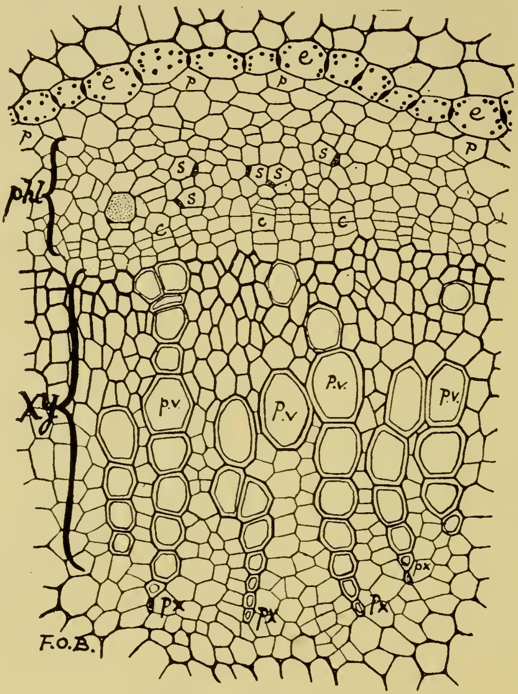

Fig. 23.

Transverse section of a vascular strand of *Scrophularia nodosa*. *e*=endodermis. *p*=pericycle. *phl*=phloem. *s*=sieve-tubes. *c*=cambium. *xy*=xylem. *p.v.*= pitted vessel. *px*=protoxylem. (× 150.)

which lies peripherally, is called the *phloem*, or *bast* (*phl*); a firmer region, which lies next the pith, is called the *xylem* or *wood* (*xy*). Between them are very thin-walled cells showing active division; this is the *cambium* (*c*). The transition between this and the wood appears sudden in the drawing; but the radial rows in which the cambial cells are arranged may be traced inwards into the wood, and also outwards into the bast, showing that all the tissues are structurally related.

The most marked constituents of the *xylem* or *wood* are radial rows of *tracheae*, or *vessels* which are elements with thick woody walls. The smallest are nearest to the pith; these are the *protoxylem* (*px*), or first-formed tracheae of the wood. The larger tracheae are *pitted vessels* (*p.v.*), and the transition from one to the other is gradual. There is no protoplasm in any of these, but they are embedded in tissue of which at least some cells retain it, and are thus alive. Near to the protoxylem the tissue is thin-walled, but towards the cambium it is thick-walled and woody, so that here the xylem forms a firm and coherent mass. The *phloem* or *bast* has no woody walls, but is soft, with cellulose walls and protoplasmic contents. The most marked constituents are the rather wide *sieve-tubes* (*s*), which are embedded in thin-walled parenchyma. A layer of more or less definite cells, called the *pericycle* (*p, p*) adjoins the endodermis internally.

A very incomplete idea is obtained by seeing the tissues only in transverse section. It is like seeing the ground plan of a building without the "elevation." The tissues must also be examined in longitudinal section, so that each unit is followed throughout its length, and the character of its lateral walls disclosed. If a longitudinal section be taken in a radial plane through the stem of the Figwort, so as to cut through the middle of a vascular strand like that in Fig. 23, its appearance would be as in Fig. 24. To the right are the external tissues, and the pith to the left. Starting from the *epidermis* (*epid*) its cells are oblong, with their outer walls thickened and cuticularised. A *stoma* has been cut through longitudinally (arrow). Below is a thin-walled *cortex*, with intercellular spaces. There is no collenchyma here, and the cortex is a narrow band. It is limited internally by the closely-fitting oblong cells of the *endodermis* (*endod*), with numerous starch-grains, which marks off the cortex from the stele. The *vascular tissue* shows up as a compact strand of more elongated elements, the phloem being thin-walled, and the xylem thick-walled and woody. The *sieve-tubes* are now seen to be long cylinders, traversed here and there by oblique septa of beaded appearance. These are the *sieve-plates* which are perforated, while the cytoplasm that lines the tubes is collected in a mass above each plate. The tubes are embedded in long prismatic cells of the phloem-parenchyma, and in this stem no bast-fibres are present.

The *cambium* consists of long, very narrow cells, with thin walls and dense protoplasm. In each radial row of them the cells are as a rule of the same length, showing that they are the result of division of a single parent cell.

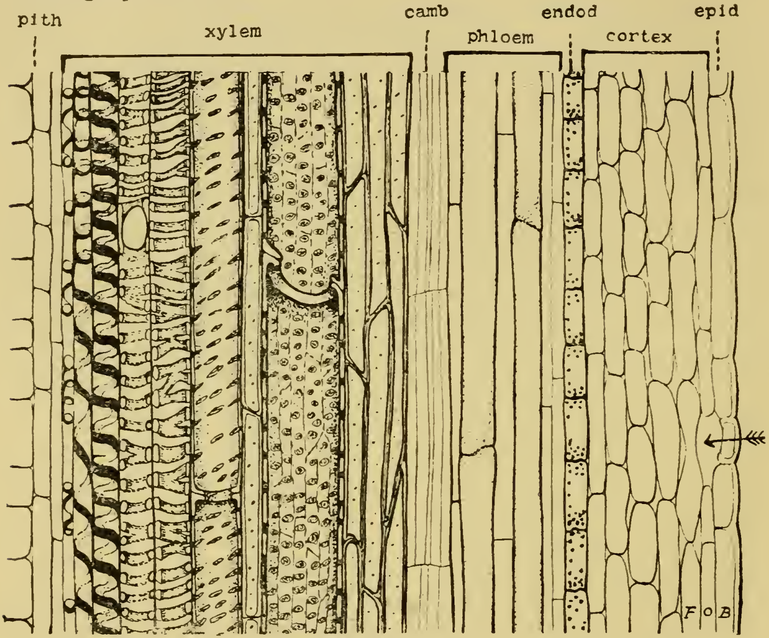

FIG. 24.

Median longitudinal section through a vascular strand of *Scrophularia nodosa*, similar to that shown in Fig. 23. The arrow indicates the pore of a stoma, and points towards the centre of the stem. (× 150)

The *xylem* is more varied in structure, and if the section happened to have followed one of those radial series of vessels seen in the transverse section, its appearance would be as shown in Fig. 24. Starting inwards from the cambium, a series of *fibrous tracheides* would be met. They are elongated and pointed, with thick lignified walls bearing small pits. They surround and embed a larger *pitted vessel*, which appears as a wide tube without any protoplasmic contents, and is limited by a thick, pitted, woody wall. About half-way down the section it is marked by a ring; this indicates where an oblique septum divided two of those cells from the fusion of which the vessel was derived. That septum was in fact occupied by a large round pit, of which the margin remains as the ring, while the thin pit-membrane has been absorbed. Further inwards the vessels are successively smaller, and show very characteristic markings. In this particular case there is first another pitted vessel, but narrower, with the pits arranged with some spiral indication. In the inner vessels complete *spiral* bands of thickening are coiled within the thin wall. In the successive vessels nearer the pith the spirals are more loosely coiled, till finally there is no continuous spiral, but a series of more or less regular rings (*annular vessels*). Such vessels are characteristic of *protoxylem*, and they abut directly on the parenchymatous pith.

The structure of the protoxylem is a consequence of the earliest vessels being developed while the stem is still growing in length. While the thickening is being deposited upon their walls they are being constantly stretched, and those earliest formed will be stretched most. The annular thickening appears in these. The closer spirals of those formed later show that they have been stretched less. Finally, where the stretching has been slight, the spirals run together laterally, leaving only irregular pits between them. The thickening rings and spirals are effective in keeping the cavity of the vessels open against the pressure of the surrounding cells. On the other hand, a sufficient area of thin pit-membrane is necessary to allow of the exit of water from the vessels to them.

Stems of Aquatic and Climbing Plants.

The plan of construction of the vascular bundle of *Scrophularia* is that *general for Angiosperms.* The bundles, however, vary greatly in size and composition in different types, and this is closely related to the needs of the plants in question. A marked variant is seen in aquatic plants, where the need of water-supply is not pressing. There the woody tissue is reduced sometimes to the vanishing point (*Elodea*); in less extreme cases the stele is contracted, and the individuality of the vascular strands is not maintained (*Hippuris*). In plants with a climbing habit, on the other hand, the vascular strands are isolated, with bands of soft parenchyma between them, while the wood-vessels are large, and the phloem plentiful. A case in point is seen in the Cucumber (Fig. 25). Here, though the vessels are few, their radial rows can be traced, with the protoxylem directed centrally. A few vessels of enormous size associated with pitted tracheides replace the more numerous vessels of herbaceous stems. The most marked modification is in the phloem, which is much more plentiful. A large mass of it with numerous large sieve-tubes is seen in the normal position; but additional sieve-tubes are present also on the side adjoining the pith. Cambial activity is evident between the xylem and the outer phloem, and a few divisions are also seen between the xylem and the medullary phloem.

The stems of climbing plants, and especially of the Cucumber and Vine, have been habitually used to demonstrate the structure of *sieve-tubes*, because there they are specially large. In Figs. 25, 26 the

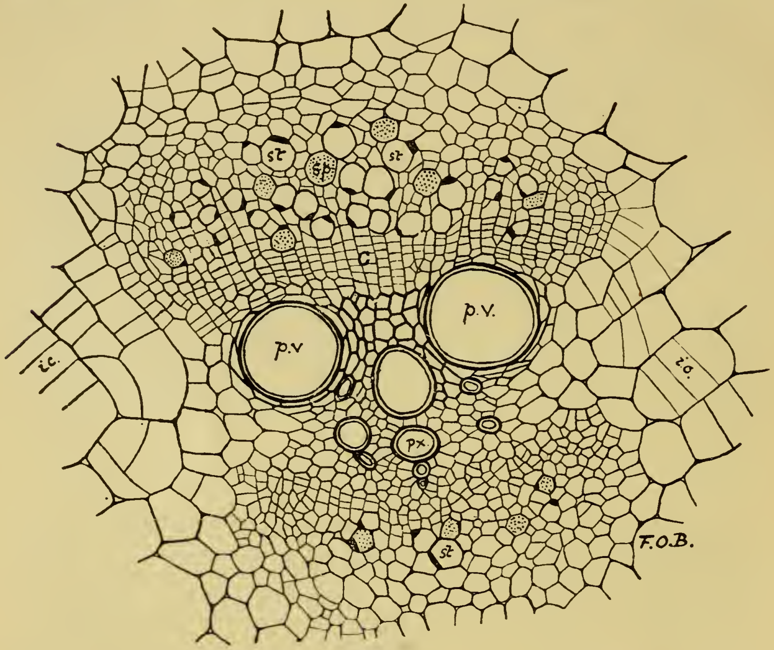

Fig. 25.

Transverse section of a vascular strand of the Cucumber, showing plentiful phloem both on peripheral and central sides of the xylem (bicollateral). The vessels of the xylem are few, but very large. *st*=sieve-tubes. *p.v.*=pitted vessels. *px*=protoxylem. *c*=fascicular cambium. *ic*=interfascicular cambium. (× 75.)

sieve-tubes appear nearly circular in transverse section; they are limited by a cellulose wall, and a cytoplasmic lining invests the wall during life. This readily contracts from the wall when the tissues are cut across, and the internal pressure relieved. That is the state in which they are usually observed. Associated with each is a small *companion-cell*, often triangular in transverse section, and with dense nucleated cytoplasm. Where a sieve-plate is included in the section it will present a surface perforated by dot-like pores. The contents are densely aggregated round the plate. Under a high power, when treated with solvents that remove the contents, and stained, the structure of the perforated cellulose wall is well seen (Fig. 26). Longitudinal sections show that the tubes are partitioned at intervals by transverse or oblique septa, each of which bears a sieve-plate that occupies its whole area (Fig. 27) The cytoplasm contracted in the preparation appears as a thick cord which widens out so as to cover the sieve-area, with which it is closely related. There are no nuclei in mature sieve-tubes. In fine sections suitably stained the continuity of the cytoplasm by threads traversing the pores can be easily seen. But another way of demonstrating the continuity is by treatment with sulphuric acid which destroys the cell-wall, while the more resistant cytoplasm retains its outline (Fig. 27, *D*).

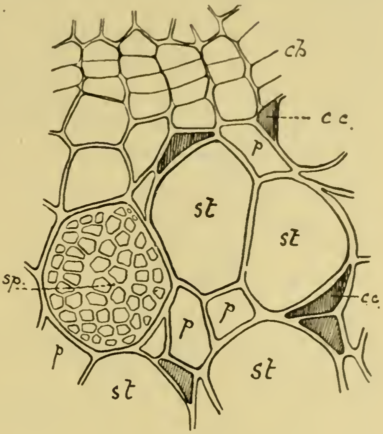

FIG. 26.

Phloem and cambium (*cb*) of Cucumber (× 200). *c.c.* = companion cells. *st* = sieve-tubes cut through between the sieve-plates. *sp* = sieve-plate in surface view. *p* = phloem parenchyma. F.O.B.

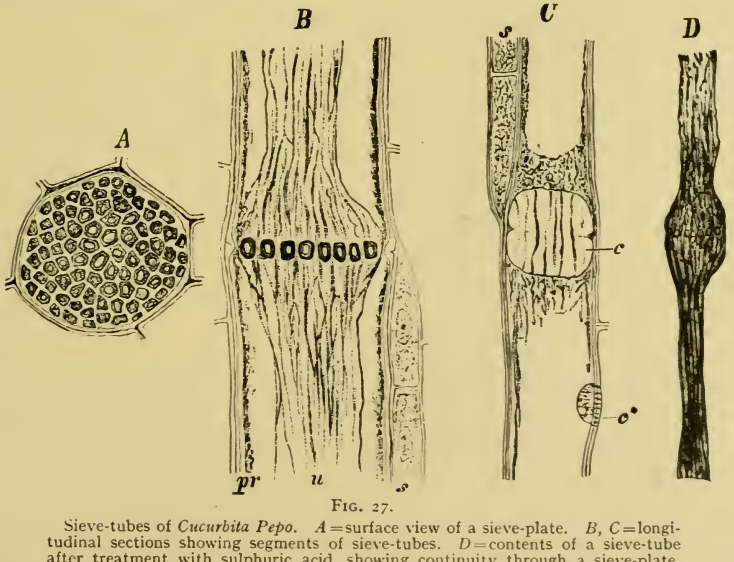

FIG. 27.

Sieve-tubes of *Cucurbita Pepo*. *A* = surface view of a sieve-plate. *B*, *C* = longitudinal sections showing segments of sieve-tubes. *D* = contents of a sieve-tube after treatment with sulphuric acid, showing continuity through a sieve-plate. *s* = companion cells. *u* = mucilaginous contents. *pr* = peripheral cytoplasm. *c* = callus plate. *c** = small lateral sieve-pit, with callus plate. (× 540.) After Strasburger.

As a tube grows older a mass of *callus* substance is formed around the cellulose framework (Fig. 27, *A*), embedding it and extending into its pores, so that finally they may be quite closed. In most plants a tube which has been thus closed does not resume its function (*e.g.* Cucumber) (Fig. 27, *C*). But in some cases (*e.g.* Vine) the autumn-formed callus, which is a readily soluble carbohydrate, may be re-absorbed in the spring, and the sieve-tube resumes its activity. There is considerable evidence that the transfer of metabolic materials, such as sugars and amino acids, from one part of the plant body to another takes place through the sieve-tubes (see Chapter VIII.). The function of the nucleated companion-cells, which show great constancy of occurrence, is still unknown.

The sieve-tubes are sometimes called bast-vessels because of the analogy in development and structure between them and the vessels of the wood. In both cases a number of cells fuse to form the vessel. In the wood-vessel the walls separating these cells are occupied by one or more large pits. As the walls thicken with woody deposits these thin pit-membranes break down, while the original protoplasm is absorbed. The cavities of the cells thus coalesce into a continuous tube, which is filled in life by sap, with or without bubbles of gas. They serve as open channels of transit for water with substances in solution. But the distance through which they are continuous as open tubes is usually limited to a few centimeters, though sometimes considerably greater.

Similarly the sieve-tubes originate from a number of cells usually attached end to end. The terminal walls bear the sieve-plates, each plate is thickened in a reticulate manner, and the meshes are styled sieve-fields, which are actually individual pits. Each of these is stopped when young by a pit-membrane which is perforated by fine threads. These perforated membranes are then completely absorbed, so that a thick rope of protoplasm replaces the fine threads. Thus technically speaking the sieve-tube also is a cell-fusion. But at maturity its walls still consist of cellulose ; the protoplasts lose the nuclei they originally contained, and the tube is filled with a vacuolated column of non-nucleated cytoplasm, which is continuous through the open pores of the sieve. The analogy of their development with that of the wood-vessels is close, but the contents and the function are different.

Stems of Monocotyledons.

In the Monocotyledons both the arrangement and the structure of the vascular strands may differ from that in the Dicotyledons, though the general plan is essentially the same. The cortex in Monocotyledons is reduced, and the stele is distended, containing isolated vascular bundles, but no cambium. The vascular strands are sometimes disposed in a simple ring round a central pith, as in *Tamus* or *Schoenus* (Fig. 28). In other cases their regularity is disturbed, the largest of them lying isolated towards the centre, as in *Molinia* (Fig. 119, p. 185). But in sections of Palms, Maize, and Sugar-Cane such strands appear more numerous, and they are seen to be scattered throughout the pithless stele (Fig. 29). This is a consequence of the

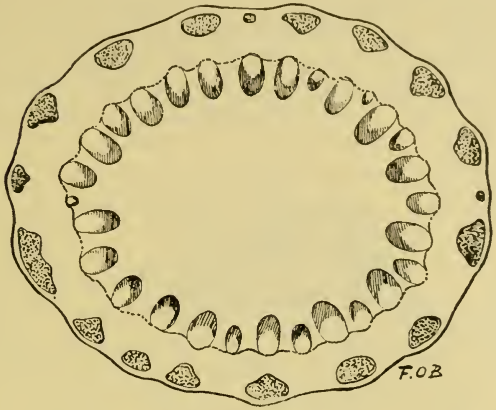

FIG. 28.

Young shaft of *Schoenus nigricans* cut transversely: centrally is the pith, surrounded by an irregular ring of vascular bundles. The dotted patches near the periphery are mechanical tissue. (× 35.)

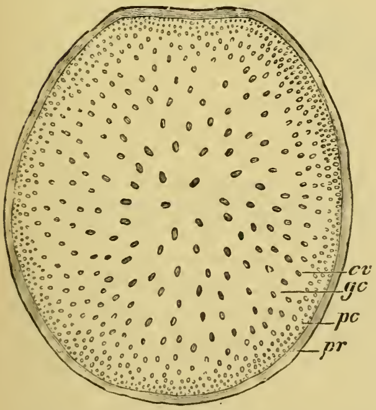

FIG. 29.

Transverse section of an internode of *Zea Mais*. *pr*=primary cortex. *pc*=pericycle. *cv*=vascular bundles. *gc*=conjunctive parenchyma (× 2.) (After Strasburger.)

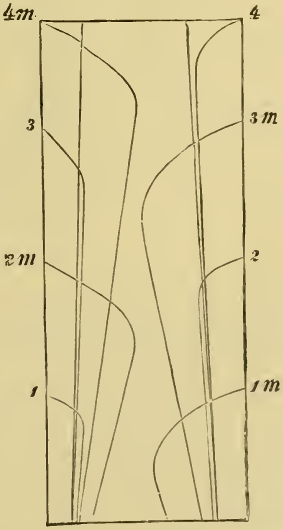

FIG. 30.

Diagram showing the course of the vascular bundles of the "Palm type" of Monocotyledons. The numbers indicate the succession of the alternating leaves. *m* = median bundle. (After De Bary.) (From Strasburger.)

fact that each of the largest strands on entering the stem from the leaf slants sharply inwards, but short of the centre it curves again outwards, and gradually approaches the periphery. There it fuses with other strands. As the strand is thickest in the middle of this course, the consequence is that the strands appear fewest and largest at the centre, and smaller but more numerous near to the periphery (Fig. 29). Thus the difference between the arrangement of the strands in Dicotyledons and Monocotyledons is not fundamental. As a matter of fact the one type graduates by intermediate steps into the other.

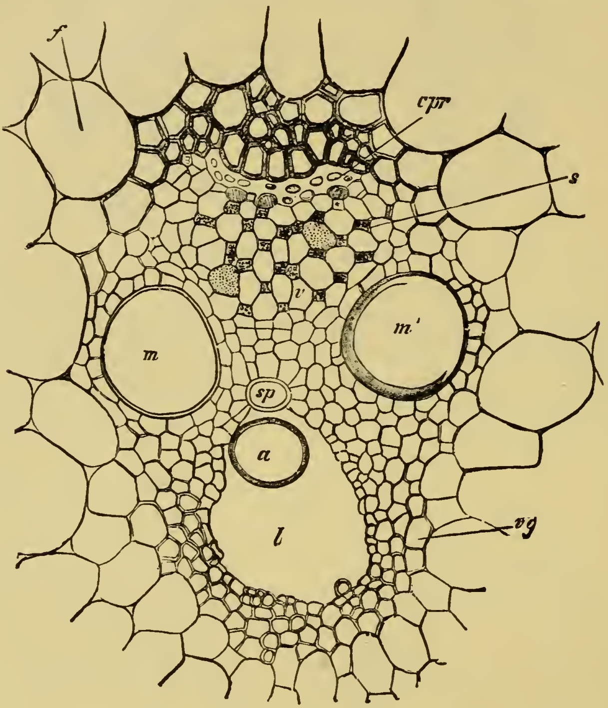

FIG. 31.

Transverse section of a vascular strand from the internode of *Zea Mais*. *a*=annular tracheid. *sp*=spiral tracheid. *m*, *m'*=vessels with bordered pits. *v*=sieve-tubes. *s*=companion cells. *cpr*=compressed first tissues of phloem. *l*=intercellular space. *vg*=sclerotic sheath. *f*=conjunctive parenchyma. (× 180.) (After Strasburger.)

Similarly the structure of the strand itself is on the same plan in both, the most conspicuous difference being the absence of cambium in the Monocotyledons. One of the larger strands towards the centre of the stem of Maize shows features usual in them (Fig. 31). It is embedded in thin-walled conjunctive parenchyma of the stele, and is surrounded by an indefinite sheath of sclerotic fibres. It consists of xylem directed as in the Dicotyledons to the centre of the stem, and phloem towards the periphery. The xylem is represented by two or three annular or spiral vessels of the protoxylem (*a*, *sp*.), adjoining a large air-space (*l*), and two large pitted vessels (*m*, *m*′), with a bridge of fibrous tracheides coupling them together. The number of these vessels may vary, especially near to the nodes. Together they form a **V**-shaped group, and the phloem is fitted between the limbs of the **V**. It consists entirely of sieve-tubes (*v*), and associated companion-cells (*s*).

Vascular bundles in which the xylem and phloem run alongside one another, as in the stems of Dicotyledons and Monocotyledons, are called *collateral*. The xylem is usually directed centrally, and the phloem peripherally in the stem. The case of the Cucumber, where extra phloem adjoins the protoxylem, is described as *bicollateral* (Fig. 25). When a cambium is present the bundle is described as *open* (Figs. 23, 25), when cambium is absent it is *closed* (Fig. 31).

The uniformity of the cylindrical structure of the stems of Flowering Plants is very striking. The reason for it is to be found in the fact that it satisfactorily meets the requirements. The stem has at once to serve for the physiological transfer of material, and for the mechanical support of the leaves and branches. The cylindrical form, or even the hollow cylinder serves these purposes well. A parallel may be drawn with bones. The marrow-cavity corresponds mechanically to the pith of the stem, while in either case the harder tissue forms an external cylinder. In the case of Birds, however, the bones may be hollow, as in a Grass-haulm. The result in either case is high mechanical strength combined with lightness (see Chapter X.).

In addition to the tissues thus described, which are generally distributed in the stems of land-living plants, there are others of occasional occurrence. These are often characteristic of certain families of plants. The most important of them are the laticiferous tissues, and various glandular, secretory, and excretory cells or groups of cells, containing crystals, essential oils, and other bodies. The *laticiferous tissues* consist of continuous tubes widely spread through the parts of the plants that contain them, and filled with a milky white, or sometimes red or yellow juice, called *latex*, which exudes whenever the tissues are cut, or otherwise damaged. This latex coagulates on exposure to the air, or on addition of certain chemicals. Rubber is prepared from such coagulated latex, the foundation of the coagulum and of Rubber being the complex hydrocarbon, Caoutchouc. Laticiferous tissue exists in two different types. In the first the tubes result from the fusion of many distinct nucleated cells, by the absorption of their septa : while the contents which have previously assumed the character of the secretion flow together, though their nuclei may still persist (Fig. 32, *B*). New branches may also be formed which anastomose freely, so that a dense network of tubes results. This type of *latex-vessel* is found in the Chicoriaceae, Campanulaceae and Papaveraceae, and they are found also in *Manihot* and *Hevea* (the chief rubber-yielding tree), among the Euphorbiaceae. The other type, occurring in most of the Euphorbiaceae, the Urticaceae and Apocynaceae, consists of *much-branched cells which do not fuse.* They may be recognised in the young embryo : they grow with the growth of the various tissues, branching frequently, and thrusting their ends between the cells of other tissues. They contain the milky latex and numerous nuclei, which divide actively near to the growing tips of the tubes.

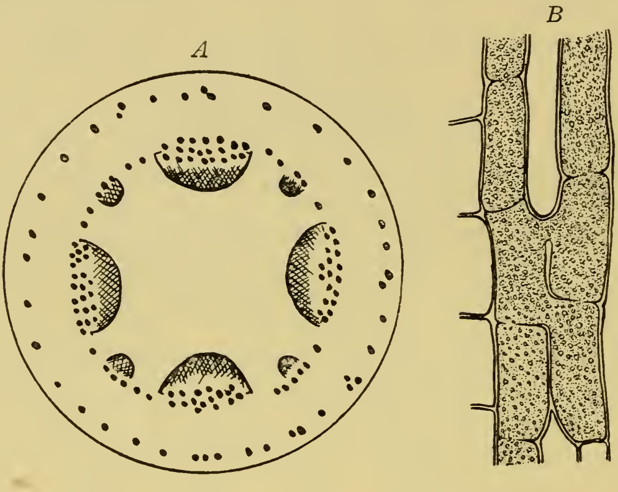

FIG. 32.

A.—Diagrammatic section of the hypocotyl of *Tragopogon*, showing the position of the latex-vessels relatively to the other tissues.

B.—Latex-vessels from a longitudinal section of a cotyledon of *Tragopogon*, showing the absorption of the cell-walls in progress. (After Scott.)

The function of the latex-tubes is uncertain. They have been regarded as storage elements or as a channel for transport of organic materials through the plant. Their contents include proteins and carbohydrates, caoutchouc and resin. It is uncertain to what extent these materials can be again used by the plant. The structure of the latex-tubes, and their close relation to the mesophyll of the leaf and to the phloem of the vascular strands (Fig. 32, *A*), lend some support to the suggestion that the tubes are connected with transport.

Calcium oxalate is found as solitary crystals laid aside in cells scattered through the tissues of many plants (Figs. 34, 47). But it may also take the form of numerous long acicular crystals, or *raphides*, which lie parallel to one another in special cells (Fig. 33). The whole bundle is often enveloped in mucilage which, swelling on any perforation of the cell from without, ejects the crystals. Being sharply pointed they are found to serve as a protection to the plants in which they occur against gnawing by snails, and other animals. They are chiefly seen in the Monocotyledons.

Secretory cells or cell-fusions containing essential oils are characteristic of certain families. For instance, those borne on the glandular hairs of the Labiatae, which are the source of their aromatic scents: or the sunken cysts seen in the Rutaceae: those in the rind of the Orange are good examples of these bodies.

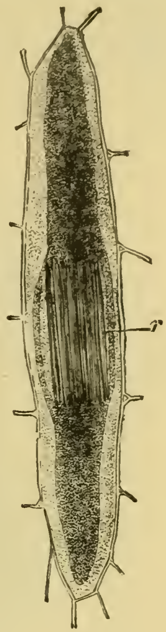

FIG. 33.

Cell of the cortex of *Dracæna rubra*, filled with mucilaginous matter and containing a bundle of raphides, *r*. (× 160.) (After Strasburger.)

WOODY STEMS OF DICOTYLEDONS.

The apical bud is potentially capable of unlimited growth and production of new leaves; the bud in the axil of each leaf may also grow into a branch similarly endowed. Correlated with these developments the mechanical and conducting tissues of the shoot are augmented by radial growth. This is particularly evident in plants which continue growing for a number of years, and thus attain large size. In them the increase in girth takes place by *secondary growth*, through the activity of the tissue called the *Cambium*. Cambium is also present in herbaceous Dicotyledons, but it is specially active in enlarging the trunks and branches of shrubs and trees. From the bulky column formed by its activity the superficial tissues may be peeled off, separating with special ease in the spring. The line of easy rupture is the *cambium* itself, and the reason why it splits so easily is that in the spring it is actively growing, and its cells are then thin-walled and weak. It will be necessary first to examine this tissue in detail, since it produces such important changes.

In herbaceous stems of Dicotyledons, such as the Sunflower, Figwort, or Cucumber (Figs. 23, 25), the cambium is seen between the wood and bast of the vascular strands. In woody stems it occupies a similar position, as in the Elm (Fig. 34). The difference is only one of the proportion of the tissues, and of the activity of the cambium. Where the strands are separate, as in herbaceous stems, the cambial activity may be seen to bridge over the spaces between the strands, thus completing the cambial ring. The cambium then forms a complete cylinder. The parts within the strands are called *fascicular*, and those between them *inter-fascicular cambium* (*i.c.* Fig. 25). In woody stems where the strands are closely grouped, this distinction is not so obvious.

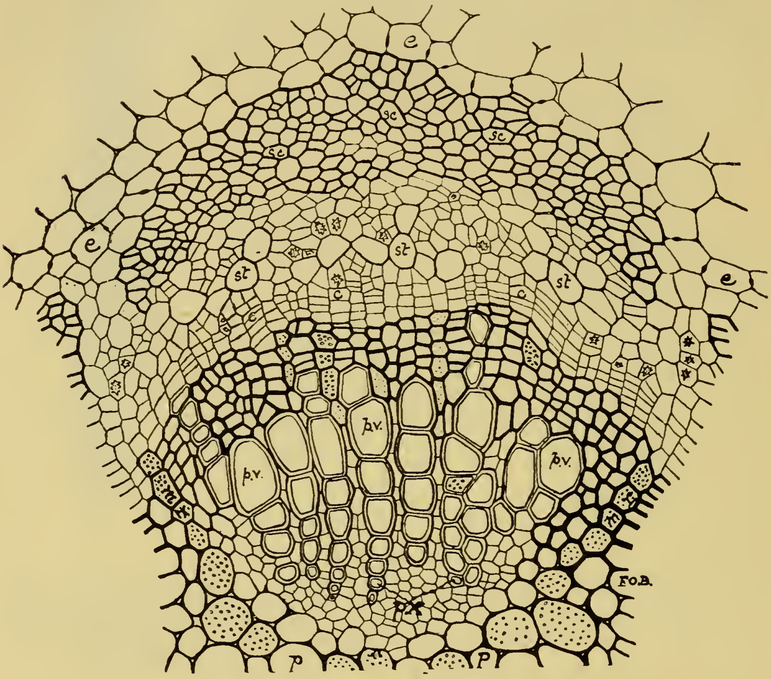

Fig. 34.

Transverse section of a single vascular strand from the young stem of the Elm. *ee*=endodermis. *sc*=sclerotic pericycle. *st*=sieve-tubes. *cc*=cambium. *p.v.*=pitted vessels. *px*=protoxylem. *mr*=medullary rays. *P*=pith. (× 150.)

The cambium is recognised by the repeated division of its thin-walled cells by tangential walls, so that *radial rows of cells* are produced. As there is no limit to the repeated divisions, a great increase of the tissues may be the result. The clearest evidence of division is in the centre of each radial row, and it has been concluded from careful comparison of many such rows that in each of them there is an ultimate *initial-cell*, which retains its identity, giving off on the one side cells formative of wood, and on the other cells formative of bast. This has been styled Sanio's law of cambial division (Fig. 35).

In transverse section each cambium cell appears oblong, with the broader sides facing inwards and outwards, while the narrower run radially (Figs. 25, 26, 35). If a section be taken longitudinally through the cambium in a tangential plane, the cells appear with pointed ends interlocked one with another (Fig. 36). If a radial section be taken, so as to follow one of the radial rows, the individual cells will appear long and narrow, with square ends (Fig. 24).

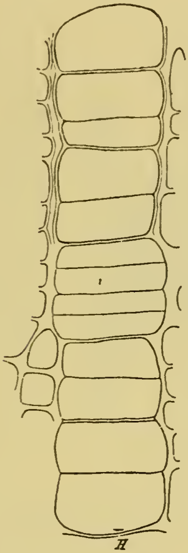

Fig. 35.

Cross section through a radial row of cambial zone in *Pinus sylvestris*, after Sanio. (× 400.) H = side next the wood. i = the conjectural initial cell. (From De Bary.)

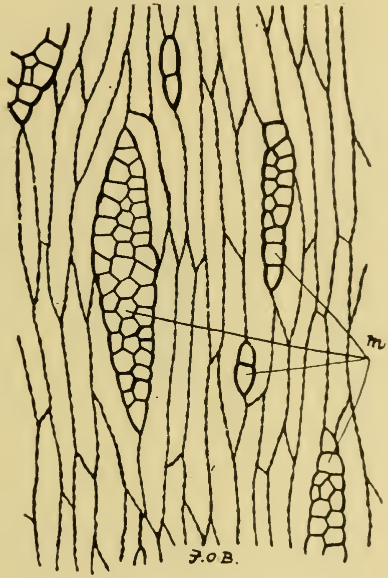

Fig. 36.

Tangential section through the cambium of the Elm, showing the elongated form of the prismatic cambium cells. m = the groups of cambial cells forming medullary rays. (× 100.)

Putting together the results of these three sections, the form of the cell as a solid body would be flattened prismatic; it is placed with its pointed ends directed up and down, and its broader faces inwards and outwards. The cells have very thin walls, and plentiful cytoplasm, with a large nucleus. In fact they show the characters of embryonic tissue. The cells given off from the initial cell, after further division pass over gradually to the mature state, forming additions to the tissues already present. Those which lie internally are added to the wood, those externally are added to the bast outside the ring. If this process be continued, the structure of the stem will become like that shown in Fig. 37, *C*.

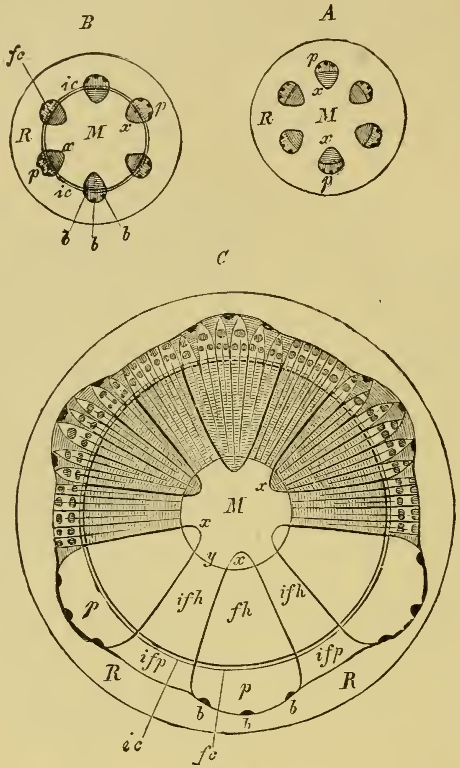

Fig. 37.

Diagrams of secondary thickening in stem of Dicotyledon, based on transverse sections of the hypocotyl of *Ricinus*. *A* represents the stem before origin of interfascicular cambium. *B*, same after it has been formed. *C*, after it has produced internally a broad ring of secondary wood, and externally a narrower ring of secondary phloem. *R* = primary cortex. *M* = pith. *p* = phloem. *x* = primary xylem. *b* = bast fibres at periphery of phloem. *fc* = fascicular cambium. *ic* = interfascicular cambium. *fh* = wood of primary bundle. *ifh* = wood developed from interfascicular cambium. *ifp* = phloem developed from interfascicular cambium. By the intercalation of the secondary tissues the primary bast, *b*, *b*, *b*, is removed some distance from the primary wood *x*, *x*. In *C* the principal medullary rays extend the whole distance through the ring, the secondary rays only part of that distance. (After Sachs.)

Three different results accrue from the growth of the vascular column, viz. increased power of *conduction*, of *storage*, and of *mechanical resistance*. Three different types of tissue are involved, and though differing in detail, all of these are to be found as a rule both in the internal woody column and in the external band of bast. The tissues in question are, the *vessel for conduction*, the *parenchymatous* *cell for storage* and other functions, and the *fibrous cell for mechanical resistance.* The forms of these various products of the cambial cells, as seen in the stem of the Lime, are shown all to the same scale in Fig. 38, i.-x.

When a large *vessel* of the wood is being formed, cambial cells in a longitudinal row widen greatly, pushing aside the adjoining cells. The lateral walls become thickened, and usually pitted, but the end walls are absorbed, and the protoplasm disappears. Thus they become tubes for transit of the sap that fills them. As they have lost their protoplasm they are dead elements. Smaller vessels develop similarly, but with less disturbance of the neighbouring cells (iv. v.). When *wood-fibres* are being formed the cambial cells elongate, and their pointed ends bore their way upwards and downwards, with a sliding readjustment among themselves. As considerable tracts of cells may develop thus alike, and as the cells themselves take a more or less sinuous course, they become interlocked, almost like the strands of a rope. At the same time their walls become greatly thickened, and woody, and their protoplasm disappears. Their function is thus not vital but mechanical (vi. vii.). When *wood-parenchyma* is being formed

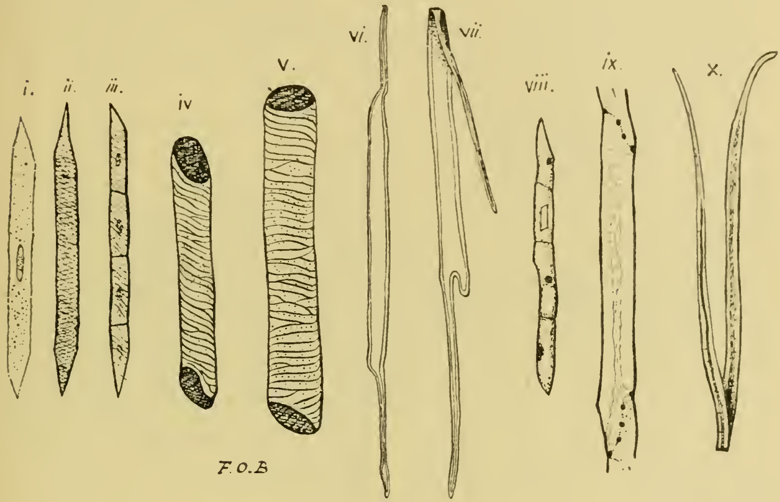

FIG. 38.

Cambium cell of the Lime, and its various products in the secondary wood and secondary bast, all drawn to the same scale, and seen in tangential section. i.= nucleated cambium cell. ii.=fibrous tracheid. iii.=group of cells of wood-parenchyma. iv. v.=single lengths of vessels, the oblique terminal walls having been absorbed. vi. vii.=wood fibres, bent to save space in the figure. viii.=group of bast-parenchyma. ix.=single length of sieve-tube, with oblique terminal walls perforated. x.=bast fibre bent to save space in the figure. (× 75.)

the cambial cells widen and undergo divisions, transverse and sometimes longitudinal, into a number of square or oblong cells. Their walls become thick, woody, and pitted, but the cells retain their cytoplasm and nucleus. They are living cells, and are often stored with starch (iii.). Analogous changes occur in the maturing of tissues of the phloem. When *sieve-tubes* are being formed one or more sieve-plates appear on the oblique terminal walls of the cambial cells; the cytoplasm is continuous through these, and they act as bast-vessels for transit of plastic materials (ix.). The formation and function of *bast-fibres*, if present, and of *bast-parenchyma*, corresponds in essentials to that of the fibres and parenchyma of the secondary wood (viii. x.).

One other component of the vascular column remains to be described, viz. the *medullary ray*. The name is derived from the fact that in transverse section radial lines of tissue, which look structurally like the medulla or pith, run part or the whole way from the cambium inwards through the wood, and are also continued outwards through the bast. Such rays are narrow plates of tissue, and though they extend far in a radial direction, they are continued only a short distance up or down (Fig. 39). They are composed of brick-shaped cells with their longer axis horizontal; these cells often have thick pitted walls, and many of them retain their protoplasm and nucleus. They link up with the parenchyma of wood and bast, forming a connected system of living tissue extending inwards and outwards from the cambium (Figs. 40 and 41). The rays appear as bright streaks in the mature wood, and are the *silver grain* of carpenters. Two types of rays may be distinguished: *primary rays*, which intervene between the original vascular strands, and extend the whole way from cortex to pith; and *secondary rays*, which are initiated subsequently in the cambium, as the stem increases in bulk. These extend only part way through the vascular ring. The tissue of the rays is derived from special cambial cells, which are readily recognised in transverse sections by the fact that they are not so narrow radially as the cells of the ordinary cambium (Fig. 41). The form of the rays, and of the cells composing them, should also be observed in tangential sections (Fig. 36), in which it may be seen that minute triangular intercellular spaces occur where three cell-walls meet. Thus a ventilation-system extends through the rays inwards into the vascular trunk. Examined in radial longitudinal sections it is apparent that the rays are, as their name implies, narrow plates of tissue extending far radially, but only a short distance vertically (Fig. 39). They serve as means of ventilation, and of interchange of materials in a radial direction through the vascular column.

The complete ring of cambium is capable of indefinite activity of growth and cell-division. Cells produced on its inner margin develop as wood-vessels, wood-fibres, or wood-parenchyma by changes such as those above described, and they form additions to the *internal column of wood.* Cells produced on the outer margin of the cambial zone develop as sieve-tubes, bast-fibres, or bast-parenchyma, by changes such as those above described, and they form additions to the *external zone of phloem or bast.* The internal additions are the more active, so that the woody column grows more rapidly than the bast. This is suggested by Fig. 37, *C*, and the proportions are actually shown for the Lime in Fig. 40. The relations of the wood and bast to the cambium, and that irregularity of arrangement of the several constituents which is usual for Dicotyledons, are suggested in detail in Fig. 41. The chief bulk of the wood and bast consists of tissue-elements elongated in a vertical direction. This structure would make radial interchange a difficulty were it not for the fact that the medullary rays penetrate radially inwards and outwards

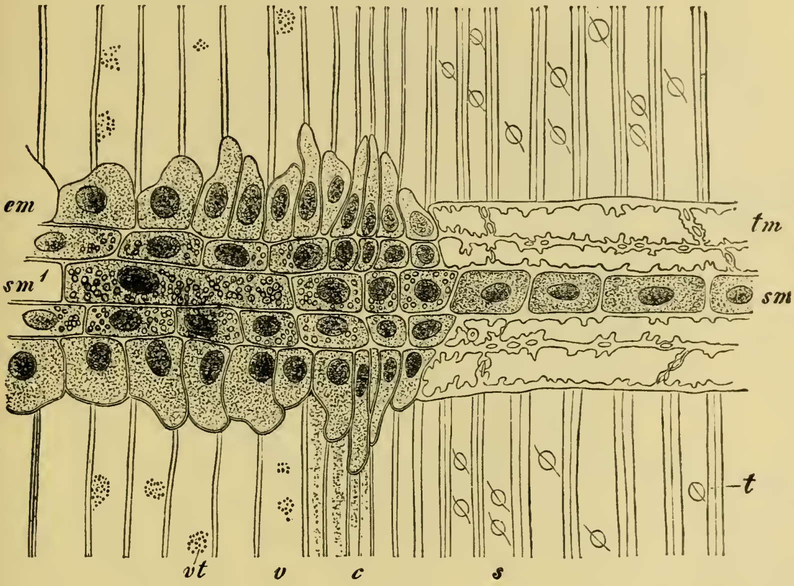

FIG. 39.

Medullary rays of the Pine (*em*, *tm*, *sm*), seen in a radial section through the cambial region (*c*). Phloem to the left, xylem to the right. (× 240.) Strasburger.

from the cambium, and thus facilitate radial communication. *All the arrangements in the woody trunk are such as to admit of development being indefinitely continued.* The woody column increases by successive additions from without: the bast by additions from within. The former presents no mechanical difficulties: but the continued addition of tissue from within will tend to stretch the outer-lying layers of the bast, cortex, and epidermis. The effect of this is seen in the Lime, where the medullary rays widen in the phloem into broad parenchymatous masses, which intervene between the wedges of bast. Thus the stretching of the outer layers is indirectly provided for (Figs. 40, 41. *M.R.*). But in other trees the difficulty may be overcome in other ways (see p. 65).

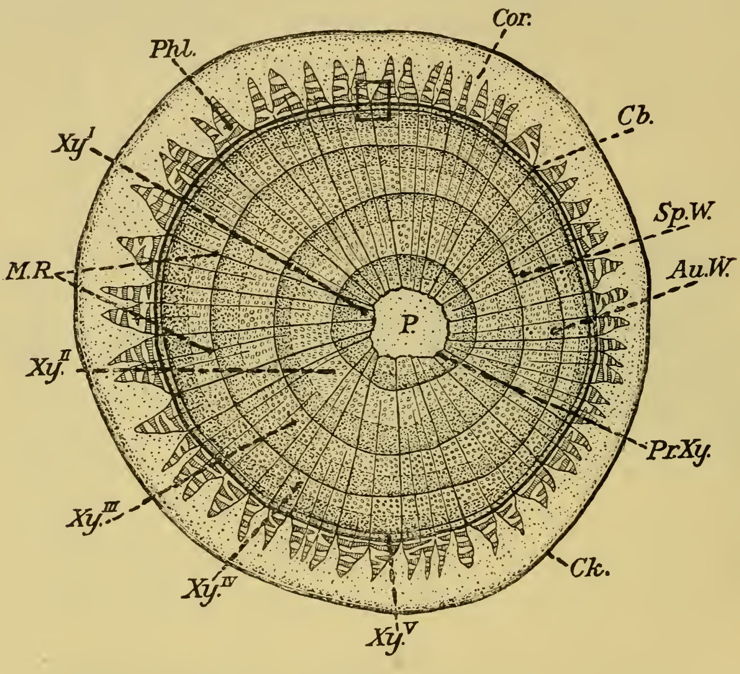

FIG. 40.

Transverse section of stem of Lime, cut in the spring of its fifth year. Drawn by Dr. Thompson. *P*=pith. *$Xy.^{I}$-$Xy.^{V}$* xylem of first to fifth season. *M.R.*= medullary ray. *Sp.W.*=spring wood. *Au.W.*=autumn wood. *Phl.*=phloem. *Cb.*=cambium. *Cor.*=cortex. *Ck.*=cork. (× 12.) The small outlined square of tissue is represented on higher scale in Fig. 41.

In temperate climates the activity of the cambium is interrupted each winter. This leaves its mark on the woody column in the form of *annual rings*, each of which represents the increment of growth of one year. Consequently it is possible by counting them to estimate the age of the trunk (Fig. 40). The reason why these rings are recognisable is that the wood formed in the spring has larger and more numerous vessels and on the average thinner walls than that formed as the season advances. The physiological advantage of this may be that the arrangement ensures an increase in the water-conducting tissues in spring, called for by the new leaves; but in the later part of the season, when nutrition is high, more material is spent in thickening the walls, thus adding to the mechanical strength. The result of continued development of a woody trunk in the manner described is to give a column constructed after the plan shown in Fig. 42, where the relation of the annual rings and medullary rays is clearly seen.

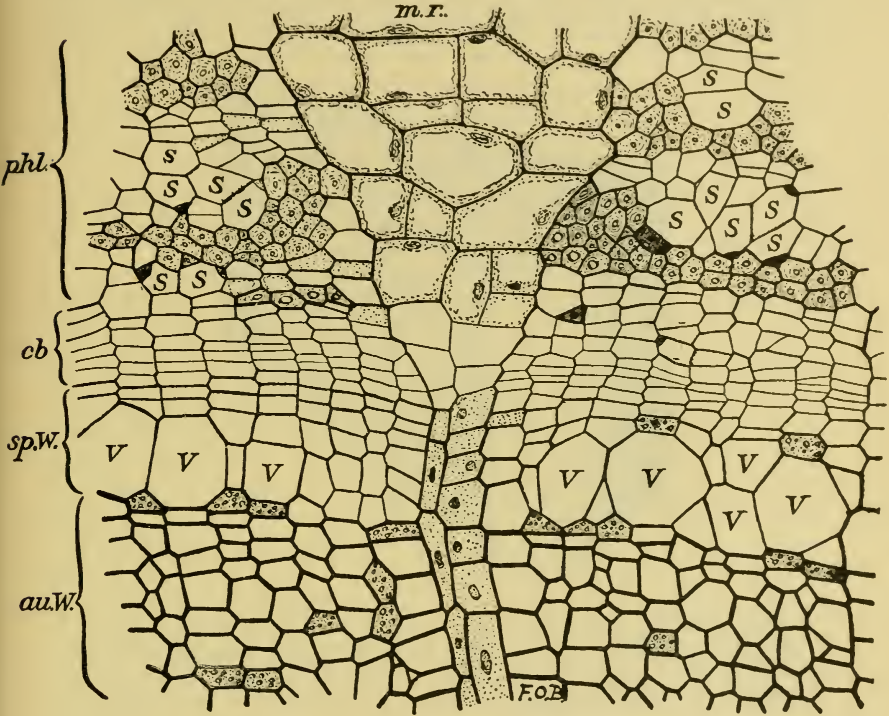

FIG. 41.

The tissues in the small outlined square in Fig. 40, magnified 200. *au.W* = autumn wood of fourth season. *sp.W* = spring wood of fifth season. *cb* = cambium. *phl.* = phloem. *m.r.* = medullary ray. *V*, *V* = vessels of wood. *S* = sieve-tubes.

As trunks grow old the colour and quality of the central wood changes in many trees, but not in all. It becomes darker in colour, and harder, and it is distinguished as *heart-wood*. It is prized by joiners for its strength and durability, as distinct from the more superficial *sap-wood*, which is paler in colour, softer in texture, and more liable to the attacks of vermin, or fungi, when used in joinery. The change from sap-wood to heart-wood follows on the death of the wood-parenchyma and medullary rays. The sap-wood, as its name implies, is functional for conveyance of sap and for storage. The heart-wood being dead serves only the purpose of mechanical support. It is, however, liable to be attacked by certain fungi in the living tree, which bring about its decay. Trees hollowed by such means, though mechanically weakened, retain their external sap-wood and cambium, and so possess in the more superficial tissues all that is otherwise necessary for normal life.

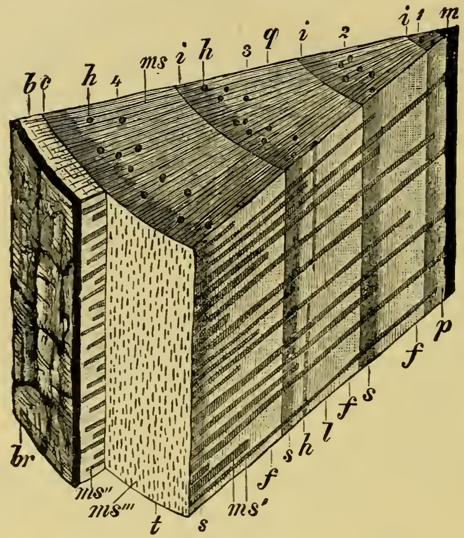

FIG. 42.

Wedge cut out of a four-year-old stem of Pine, in winter. Though the Pine is a Gymnosperm, the construction of its trunk is on the same plan as that seen in Angiosperms. *q*=transverse view; *l*=radial view; *t*=tangential view. *f*=spring, *s*=autumn wood. *m*=medulla. *p*=protoxylem. *h*, *h*=resin-passages. 1, 2, 3, 4=successive annual rings. *ms*=medullary ray in transverse, *ms'*, *ms''*, in radial, *ms'''*, in tangential view. *c*=cambium. *b*=bast. *br*=bark. (× 6.) Strasburger.

The occurrence and proportion, as well as the mutual arrangement of the component tissues are variable in different stems. It is this that gives the characteristic qualities to their wood and bast. Thin walls, and relatively few fibres result in soft wood, as in the Lime. Thicker walls, and numerous fibres grouped in solid masses give a hard wood, like that of the Oak or Laburnum. Fibres may be absent from the bast, as in the Currant; or they may be present in large numbers, forming irregular masses, as in the Lime, which gives the "bast" for tying up garden plants. The grouping among themselves of the several tissues composing the wood and bast appears at first sight confused. To secure conduction, mechanical strength, and storage it is necessary that each of the tissues that meets these needs must be continuous in order to be effective. There is no general or regular rule of their arrangement for all stems. The complex problem is solved by different trunks in different ways. A careful microscopic analysis of the masses of wood and bast is necessary for the understanding of any individual case. But such analysis shows, for instance in the wood, that the three tissue-types form each their own connected system, though all are fused together into the woody column. The clearest example of this is found in the medullary rays, which are intimately related to the parenchyma of wood and bast, and thread together these apparently isolated tracts radially, so as to form a connected living system of storage-cells, which finds its inner limit at the barrier of the dead heart-wood.

The growing vascular column is covered externally as it expands by the cortex and epidermis. These must necessarily yield in some way to the increase within. Sometimes they simply stretch, and this is usual in most stems for a time. But as a rule the epidermis and some of the cortex dries, and peels off, owing to the formation of *cork*. The nature and function of a corky tissue is that it forms an impervious barrier to the passage of water. As bottle-cork it is used for this purpose. In the plant a layer of cork, wherever formed, will cut off any tissues outside it from physiological interchange with the tissues within. The first layer may be succeeded by other layers formed more deeply, and cutting off successive bands of deeper tissue. The layers may encroach into the phloem, from which successively the outermost, that is the effete layers, would thus be cut off by an impervious barrier from the active tissues within. All tissues lying outside the innermost cork-layer are called collectively *Bark*, which is consequently a dead tissue, including it may be epidermis, cortex and phloem. As the stem continues to grow, the bark being dead does not keep pace with it, but splits into fissures, or peels off in scales. Thus the characteristic appearance of the fissured trunks of the Oak or Elm may arise, or the scaly surface of the boles of the Scots Pine or Sycamore. The thick masses of bark in old stems give also mechanical protection, while they form a non-conducting barrier against excessive heat, as witnessed by the survival of Australian Eucalypts after forest fires.

Cork may originate from the epidermis (Apple, *Sorbus*), but more commonly from the outer cortex, often from the layer immediately below the epidermis (Elm, Birch, Figs. 43, 44). Divisions appear by walls parallel to the outer surface, and are repeated so that from each parent-cell a row of cells is produced. A certain cell in each row remains narrow and thin-walled, and it continues to grow and divide, acting as a cambium-cell. The cells thrown off from it on the inner side take the characters of additional cortex ; those on the outer side enlarge, their cell-contents are absorbed, and their thin walls are changed to impervious cork (Fig. 44 : parts right and left of the drawing). As the cells fit closely without intercellular spaces, they form a complete protective covering. Partly owing to the growth in bulk within, but chiefly because the cork cuts it off from the living tissues, the epidermis soon dries up, splits, and peels away.

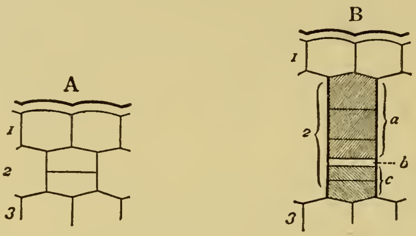

FIG. 43.

Diagrams illustrating successive steps in the formation of cork in the cells (2) directly below the epidermis (1). *A* shows the first division. *B* shows the state after repeated divisions, resulting in a radial row of cells. Of these the outer (*a*) are cork ; the innermost (*c*) are phelloderm, which adds to the cortex. (*b*) represents the cork-cambium.

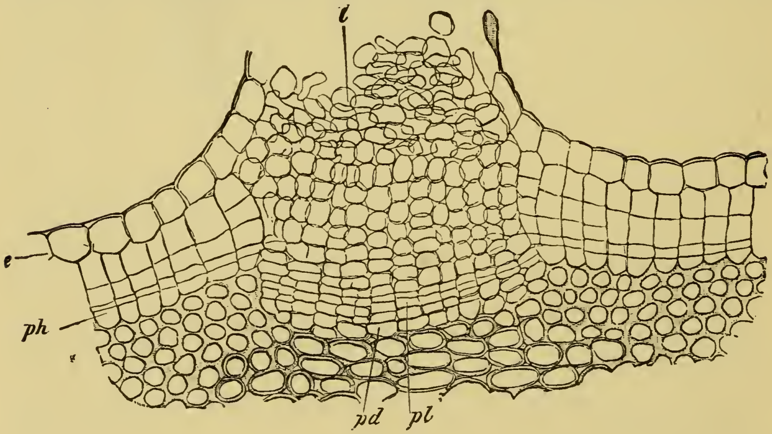

FIG. 44.

Transverse section of the stem of Elder, traversing a lenticel. *e*=epidermis. *ph*=phellogen, or cork cambium. *l*=spongy cells filling the lenticel. *pl*=phellogen of the lenticel. *pd*=cork, or phelloderm. (× 90.) Strasburger.

The covering of cork having its cells closely fitting together is not only impervious to water, but also to gases. Thus the living tissues would be cut off entirely from the outer air, were it not for interruptions of the continuity here and there. These are called *lenticels*, and they may be seen with the naked eye on most stems, as brownish, slightly swollen spots (Fig. 6, p. 13). A lens shows that here the epidermis is split, and that powdery tissue lies within. Microscopically it is seen that in place of the closely fitting cork-cells those of the lenticel are rounded, with intercellular spaces, so that the tissue is spongy, and allows ventilation into the cortex (Fig. 44, *l.*). The lenticels remain for years, and may grow to a large size, as may be seen on the surface of many woody trunks, where they often determine the position of the fissures of the bark. The brown crumbling spaces in bad bottle-corks are the lenticels, which traverse the otherwise impervious cork of the Cork-Oak.

The stem of a Dicotyledon showing secondary thickening as thus described is mechanically a stable structure. Its form is that of a cone with its base at the level of the ground. There it often widens out into a broad "stool," which helps to give it stability. Many large trees of the tropics form radiating buttresses at their base, which are still more effective. The stems of Monocotyledons are constructed differently. Most of them do not increase in bulk at the extreme base; but developing stronger above than below, assume the form of an inverted cone, with its apex at the level of the soil. This unstable structure is propped up by roots, which act like oblique struts; this may be very clearly seen in large plants of the Maize, or of the Screw Pine. In many large Palms, however, the base of the stem distends with age. This is due to a general expansion of the conjunctive parenchyma, which may be accompanied by the formation of additional deeply-seated vascular strands. In some few Monocotyledons, however, as in *Dracaena*, there is a cambial increase. It arises in the pericycle, outside the primary bundles, and it forms new vascular strands which are closed, and embedded in a sclerotic parenchyma. Physiologically the result is the same as in Dicotyledons, but it arises in a different manner (see Chap. XXXVI, p. 590).

Those who have followed the foregoing description of the woody Dicotyledons will see how admirably the trunk meets the requirements. Their shoot-system is constructed on a scheme of indefinite expansion, consequent on continued apical growth and branching. The demands that will be made upon the trunk and branches are well illustrated by any Sycamore or Beech tree exposed to a wind in early summer, after the leaves are expanded and the tree is in full flower. The strain of the wind-pressure is transferred from the leaves to the twigs, and from them downwards to the branches, and finally to the cylindrical trunk. It culminates towards the base, where there is the greatest leverage. The butt must stand firm from whatever quarter the wind may blow. It cannot yield as the branches can without loosening its hold on the ground. Actually it is here that the trunk is thickest. As it tapers upwards it becomes more pliant, and yields to the wind: but a condition of successful resistance is the perfect recovery of trunk, branches, and twigs when the wind falls. The *mechanical effectiveness* of the tissues within the several parts is demonstrated by any tree that stands erect and unbroken after a wind.

It is a familiar fact that a detached twig soon wilts by evaporation, and more quickly in a wind than in still air. It requires water in order to recover. In a tree exposed to the wind the young shoots normally retain their firmness. During the wind they will have been exposed to more than normal loss by evaporation, but still they are firm, showing that they have been supplied with sufficient water to make good their loss. The trunk, and the distributing agency of its branches and twigs have carried out their *water-conducting function.* Clearly the water-conducting system meets the requirements.

The rapid production of leaves and flowers in early summer is in itself evidence of the *storage capacity* of the trunk and branches. The material required for their formation is gained previously. The rapid development in the spring depends upon its transfer from the storage tissues in the trunk and branches to the buds that were dormant during the winter. Thus the tree demonstrates by results obvious to any observer the efficiency of the tissues of the trunk and branches for mechanical resistance, water-conveyance, and the storage and transfer of materials. Not only this, but also the method of thickening of the stem is such that it meets the growing demands of the enlarging plant. Finally, the adjustment of the surface tissues to the increasing bulk is peculiarly effective. Not only does the development of cork, and of that heterogeneous covering of bark, give protection to the surface of the increasing stem, but it provides for the removal of effete tissue. The old phloem, with its cells charged with tannin, crystals of calcium oxalate, and many other substances no longer required, together with old and collapsed sieve-tubes, would be a useless burden to the stem. It is cut off by cork, and shed with the decay of the outer layers of bark. The trunk that shows such features as these is highly organised indeed. It is characteristic of those plants which are recognised as the most advanced, viz. the Seed-Bearing Plants, and particularly the Dicotyledons.

CHAPTER V.

THE LEAF.

Everyone knows roughly what is meant by the term Leaf. It is commonly a flat, stalked structure, which exposes a large area of green tissue to the light and air, usually in a more or less horizontal plane; and in a great many of our native plants it falls off in the autumn by detachment at the base of the leaf-stalk. But this general conception of the leaf is not of universal application, and it does not define the leaf in a scientific sense. The essential features of the leaf are not found in its form or direction, or in its detachment in autumn, for all of these are liable to vary. *The features that are constant for leaves, and so define them morphologically are, that they arise as lateral outgrowths from the apical cone, that they spring from the superficial and underlying tissues, and appear in acropetal succession; also that they do not repeat the characters of the shoot itself.* It follows from their origin that their tissues are continuous at the base with the tissues of the axis. The conceptions of axis and leaf are correlative: the axis is a spindle bearing leaves, and the leaf is a lateral appendage upon the axis. Axis and leaves together constitute the *Shoot*. This conclusion holds notwithstanding that both stem and leaf may vary greatly in form and proportion. Particularly the leaf is variable in outline: it may have a stalk or *petiole*, which bears the blade or *lamina* at its end: or there may be no stalk, and the blade is then seated directly upon the axis. Further, the blade itself shows the greatest variety in outline; it may be a simple flat expansion (entire), or it may be cut up in various ways into parts (pinnae), and these may be again subdivided. We need not follow this further than to recognise the fact that the outline of the leaf varies greatly. It may even show differences in the individual, as is seen on comparing the bud-scales and foliage leaves of any ordinary plant with those leaves of the floral region which, however diverse in appearance, are all none the less leaves (see Figs. 260-264, pp. 349-351).

The leaf differs habitually from the stem in its symmetry, though this difference does not apply to all cases, and cannot be held as in itself distinctive of the one from the other. The *stem* is usually *radial* in symmetry, being developed equally all round. But the *leaf* is as a rule a flattened organ, showing what is described as *dorsiventral* symmetry, and having more or less clearly defined surfaces. In most leaves one face is turned upwards to the sky, and the other downwards; but this is by no means constant. It is important for clearness of description to distinguish these two faces by some more constant character than that of direction up or down. The most constant is their relation to the axis which bears the leaf. One of the faces is directed in the young bud towards the axis which bears it; it is therefore defined as the *ad-axial*, though as it is usually directed upwards it is often called the *upper* surface. The other faces away from the axis in the bud, and is defined as the *ab-axial*, and as it is usually directed downwards it is styled the *lower*. But the terms "upper" and "lower" are merely descriptive of the positions that are usual: they are not scientific definitions as the others are. The Common Garlic shows how necessary this precision is, for in most of its leaves, by a twist of the leaf-stalk, the adaxial face is turned downwards.

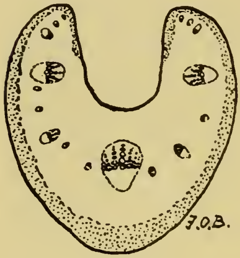

Fig. 45.
Transverse section of the petiole of the Sunflower. (× 6.)

Since the tissues of the leaf are continuous at the base with those of the stem, the constitution of the *petiole* may be expected to resemble that of the stem. But its form is more or less flattened or channelled on the upper (ad-axial) surface. This is in accordance with the mechanical requirements; for it has to support the weight of the blade, and hold it with some degree of firmness in its horizontal position. The necessary strength is secured by a form which in transverse section would appear semicircular, or semilunar, as it is in such a leaf as the Sunflower (Fig. 45). In this case it is traversed by three large vascular strands, which with some smaller strands are arranged in a semicircle. The surrounding tissues are essentially like those of the young stem, but there is no stelar tract defined by a general endodermis; here each strand is surrounded by its own sheath. The *xylem* of each strand as it curves out from the stem is directed *upwards* (ad-axial), and the *phloem downwards* (ab-axial), and these relative positions are regularly maintained throughout the leaf (Figs. 20, 47). The petiole appears to be structurally little more than a means of junction between the axis and the blade. Its presence brings two advantages: that the blade is carried some distance outwards from the stem, and thus the probability of one leaf overshadowing another is avoided; and secondly, the narrow petiole allows the blade to yield to the pressure of wind, instead of rigidly resisting it.

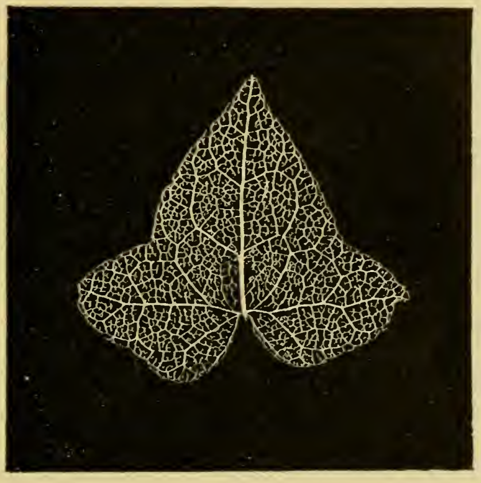

Fig. 46.
Skeleton of the lamina of Ivy. Natural size.

It is the blade, or lamina, which is the distinctive feature of the foliage leaf. As shown in such common types as the Sunflower, Dahlia, Cabbage, or Sycamore, the blade consists of a skeleton or framework of thickened and mechanically firm ribs, which support an expanse of relatively thin and delicate tissues. A prominent mid-rib runs up continuously from the leaf-stalk to the tip of the blade, and branch-ribs of successively smaller size pass off from it towards the margin. On removing the softer tissues by reagents, the vascular system can be demonstrated as a leaf-skeleton (Fig. 46). It is then seen that vascular strands of the midrib and of the stronger lateral ribs, give off thinner lateral branches; that smaller branch-veins pass off from these, and with further ramifications and many fusions form a fine network traversing the thinner areas of the blade. Such a *reticulate venation* is characteristic of the leaves of Dicotyledons. In Monocotyledons the main veins run *parallel* to one another, but still they are connected laterally by transverse branches. Thus the vascular system, of which the leading function is conduction, is very effectively placed for carrying out its purpose: for it is connected below with the conducting system of the stem, and it spreads throughout the blade, and reaches to its extreme tip and margin.

A superficial examination gives only a very imperfect idea of the structure of this important part of the plant. Transverse sections through the thin *lamina* so as to traverse one of the ribs transversely, reveal the characteristic structure upon which the functional activity of the foliage leaf depends (Fig. 47). The upper (ad-axial) face is easily distinguished from the lower (ab-axial) by the fact that the larger veins project strongly from the latter surface. Where the vein is traversed it shows on a reduced scale the same construction as the petiole, and like it the ribs are often strengthened by collenchymatous tissue, as is seen in the Aspen. Here again the xylem of the vascular bundle is directed towards the upper (ad-axial) face, and the phloem towards the lower (ab-axial). The tissues which compose the thinner expanse of the lamina bear definite relations to these opposed surfaces, and to the incidence of light upon that which faces upwards. They will be described, starting from the upper (ad-axial) face, as they might

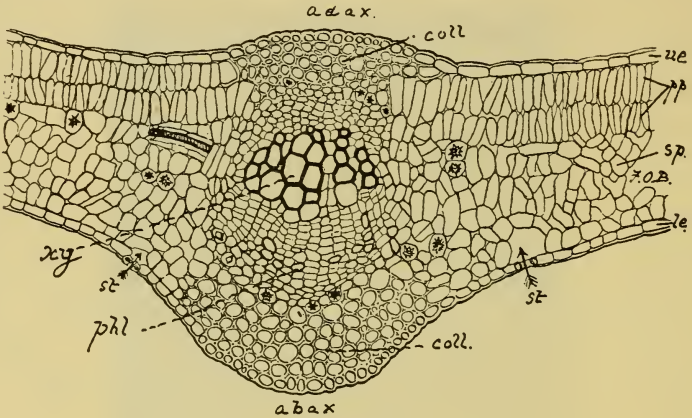

FIG. 47.

Transverse section of the midrib of the leaf of Aspen (*Populus tremula*), extending to the thinner expanse of the blade right and left. *ue*=upper epidermis. *le*=lower epidermis. *pp*=palisade parenchyma. *sp*=spongy parenchyma. *coll*=collenchyma. *xy*=xylem. *phl*=phloem. *st*=stoma. Note numerous crystals of calcium oxalate. *adax*=adaxial or upper, *abax*=abaxial or lower leaf-surface. (× 75.)

be seen in the leaf of the Aspen, or as shown more in detail in the Privet (Fig. 48).

The upper surface is covered by a continuous layer of *epidermis*, composed of oblong cells with their outer wall thickened and cuticularised, better seen in Fig. 52, p. 77. The lower surface is similarly covered by epidermis, but the continuity of its cells is here and there interrupted by pores (*stomata*), which allow communication between the outer air and the intercellular spaces within. Between these two epidermal layers lies the tissue of the *mesophyll*. Towards the upper surface its cells are arranged with some degree of regularity, frequently in two layers. The cells of these layers are of oblong form, and stand parallel with one another, the ends of the outermost layer abutting on the epidermis. From their form and arrangement they are called the *palisade-parenchyma*. Towards the lower surface the cells are less regular in form and arrangement, and as the intercellular spaces are very large and numerous this tissue is described as the *spongy parenchyma*. The whole mesophyll is composed of thin-walled cells, with living cytoplasmic lining, a nucleus, and very numerous discoid, green *Chloroplasts*. To these is due the full green colour of the leaf. The *intercellular spaces*, so conspicuous in the spongy parenchyma, are continuous though of smaller size between the palisade-cells, and they connect with the stomata. A specially large space is usually present opposite the pore of each stoma. The whole mesophyll

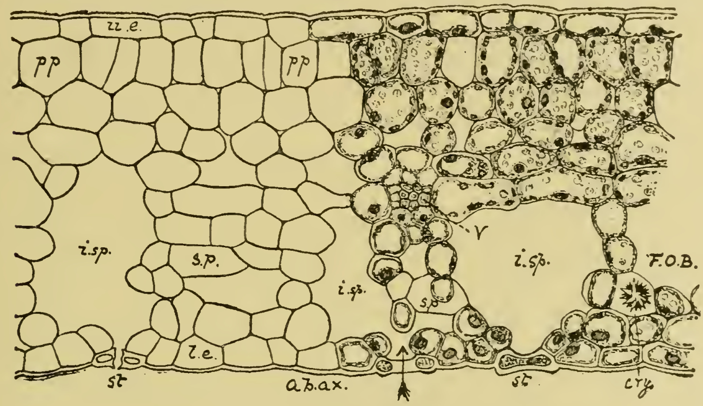

FIG. 48.

Transverse section of lamina of Privet (*Ligustrum vulgare*). *ab.ax.* = the abaxial or lower surface. The protoplasts are omitted on the left-hand side. *u.e.* = upper epidermis. *l.e.* = lower epidermis. *i.sp.* = intercellular space. *v* = vascular strand. *st* = stoma. *pp* = palisade parenchyma. *s.p.* = spongy parenchyma. *cry* = crystal. (× 75.) The palisade parenchyma is poorly developed in the section of this shade-loving leaf. Compare Fig. 47.

is thus permeated by a ventilating system of air-channels, which may communicate through the pores of the stomata with the air outside.

Most foliage leaves have such a structure as that described. But the leaf-blade of different plants fluctuates almost as much in the details of its internal construction as it does in its outline : this may even be seen in some degree in those of the same individual plant. Leaves may vary in thickness from the delicate, almost filmy leaf of shade-loving plants, to the leathery texture of those exposed to the sun in dry climates. The leaves may be smooth in surface, as is usual in water-plants, or covered with rough hairs like the Sunflower, or with a dense woolly protection like the Alpine Edelweiss. Internally they may have only a single layer of palisade parenchyma, as in most shaded leaves ; or two, which is common in leaves exposed to the full sun ; or more. They may be strengthened by mechanically effective tissue, often placed just below the upper epidermis (hypoderma), as in the leathery Cherry-Laurel: or distended by water-storage cells, usually occupying the middle of the leaf, as in the succulent Stonecrop, or Aloe. Notwithstanding such differences as these, and many others, their construction is as a rule based upon the same essential scheme as that described.

The leaf is the chief organ of nutrition in green plants. An essential point of structure to this end is the perforation of the epidermis by the stomatal pores, for this gives the opportunity of gaseous interchange between the intercellular spaces and the outer air. *Stomata* occur here and there in the epidermis of the stem and petiole, and even upon the various parts of the flower. But it is on the surfaces of the leaf-blade that they are found in the greatest numbers. Sometimes, as in the Sunflower and many herbaceous plants, they are present on both sides of the blade ; but frequently they are fewer on the upper epidermis, or even absent, as in many woody plants. They are often very minute, especially in the Dicotyledons, so that large numbers, usually 100 to 300, may be counted on each square millimetre of surface. The following table gives the result of countings per sq. mm. on the leaves named :

	Upper.	Lower.
Lilac	100	150
Oak	0	346
Apple	0	246
Water Lily	460	0 (submerged).
Wheat	47	52

Examined microscopically in surface view the epidermis of a Dicotyledon appears as a film of tabular cells, often with sinuous outline (Fig. 49). The stomata form part of the epidermal layer, but their cells differ in form from the rest. Each stoma is composed of two *guard-cells* attached by their ends, so that between them there is a *pore* that may be either open or closed. In a microscopic preparation of a living epidermis taken on a sunny day, and mounted in water, the pores, governed by the still living cells, will be seen to be widely open, as they are represented to be in the drawing of the leaf of *Tropaeolum*. Access is thus readily given to the intercellular spaces within. Fig. 49 further shows the mesophyll visible through the transparent epidermis. The palisade-cells are here seen end-on; and it is more apparent than in transverse section how well ventilated this tissue actually is. Almost all its cells touch another cell laterally; but in all of them a very considerable proportion of the wall-surface is freely exposed to the gases contained in the intercellular spaces. These spaces are specially large in the

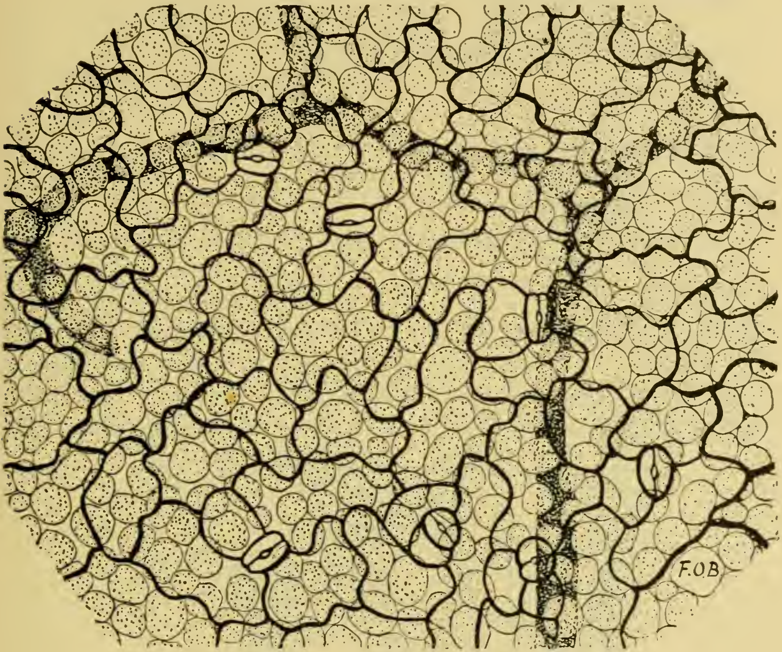

FIG. 49.

Part of the lamina of *Tropaeolum*, seen as a transparency, in surface view from above; showing the sinuous outline of the epidermal cells, with stomata. Below the epidermis the palisade-cells are seen end-on, with large intercellular spaces, especially below the stomata. The vascular veins are more deeply shaded. (× 175.)

neighbourhood of the stomata. Lastly, part of the vascular network is shown dimly in a still lower plane. The strands lie between the palisade and the spongy parenchyma, and the conducting system is thus in near relation to the bases of the oblong palisade cells.

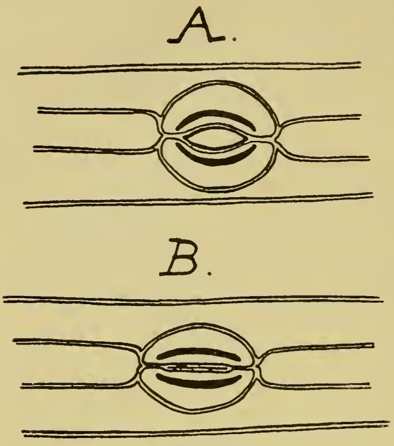

Fig. 50.

Drawings from the same Stoma of *Narcissus*, in surface view. *A*, in the open; *B*, in the closed state. F. O. B. (× 250.)

In the Dicotyledons the stomata are relatively small, and irregular in their orientation. They are shown in section in Figs. 47, 48, and in surface view in Fig. 49. In Monocotyledons they are usually larger, and their orientation regular. The large stoma of *Narcissus* serves as an example (Fig. 50, *A*). Its guard-cells have a characteristic outline, each with a projecting ridge on its oblique outer and inner walls. The stoma is here slightly sunk below the outer surface of the leaf (Fig. 51). The level of the stoma relatively to the leaf-surface varies in different types according to their habitat. In plants of temperate climates

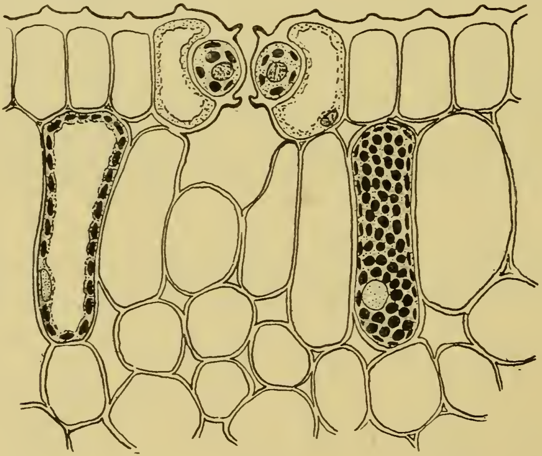

Fig. 51.

Stoma of *Narcissus* in transverse section, showing its relation to the adjoining epidermal cells and to the mesophyll below. Two of the cells of this tissue are drawn in detail, that to the right as seen in surface view from without; that to the left in optical section. The chloroplasts are black. (× 300.) F. O. B.

it sometimes projects, or lies about level with the general surface. But in plants of dry climates it is apt to be sunk inwards. This is seen in slight degree in *Narcissus* (Fig. 51), but more distinctly in *Aloe* (Fig. 52), a succulent plant with strongly cuticularised epidermis. The stomata themselves are of the same type as *Narcissus*, but seated at the bottom of deep pits. A more extreme case is seen

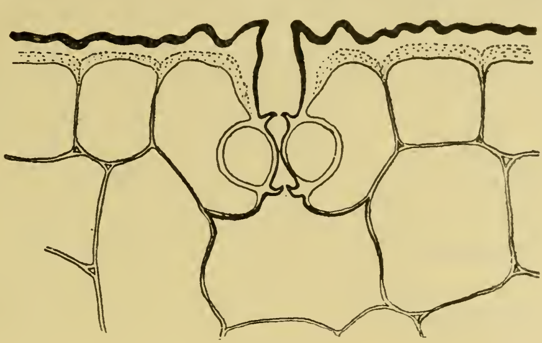

FIG. 52.

Stoma of *Aloe* depressed below the well-developed epidermis. The thick cuticle is shown black. (× 300.) F. O. B.

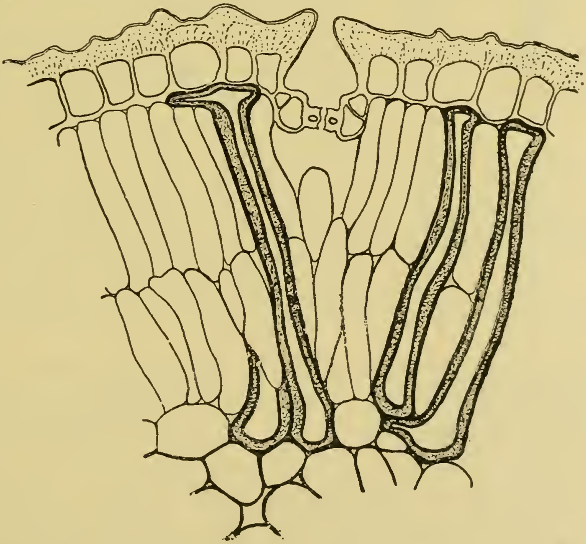

FIG. 53.

Part of a transverse section of the xerophytic leaf of *Hakea*, showing a stoma greatly depressed below the well-developed, and cuticularised epidermis, which is propped out by thick-walled sclerotic cells. (× 150.) F. O. B.

in *Hakea* (Fig. 53). Additional control over evaporation of water is gained by this means (Chapter XI.).

Seeing that the epidermis serves for protection, and for regulating the ventilation of the leaf, both functions of a secondary character, it seems clear that the mesophyll is the tissue of prime importance. The cells of the palisade-parenchyma are oblong in form, and each is bounded by a thin cellulose wall, which is rounded off at the angles so as to provide the intercellular spaces (Fig. 51). The cell-wall is lined internally by a film of cytoplasm, within which is a large vacuole filled with sap. The nucleus may be suspended in the middle of the cell, but more frequently it is embedded laterally in the cytoplasm. The most marked features of these cells are the *chlorophyll-corpuscles*, or *chloroplasts*, which are discoid in form and of a full green colour. They are always embedded in the cytoplasm, and are as a rule so placed that one flattened side faces to the cell-wall, the other to the central vacuole. The cells of the spongy-parenchyma resemble the palisade cells in all essential points except in their form, which is very irregular, and in the fact that their chloroplasts are fewer (Fig. 48).

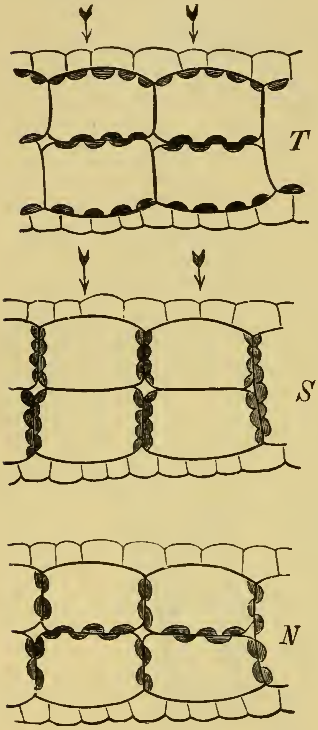

Fig. 54.

Varying positions taken by chlorophyll grains in the cells of *Lemna trisulca* under illumination of different intensity. *T*, in diffuse daylight. *S*, in direct sunlight. *N*, at night. The arrows indicate the direction of the light. (After Stahl.)

As the cytoplasm has been seen to be capable of movement, it can alter the position of the chloroplasts embedded in it. Apart from any other disturbing cause, they collect at the cell-surfaces adjoining the intercellular spaces. Their movements are regulated by external conditions, of which one is the aeration of the cell. Another, and apparently a stronger influence is light. In diffused light they place themselves so as to present their flattened surfaces to the incident rays (*T*, Fig. 54); in intense sunlight they present their edges, and so protect themselves from its harmful effects (*S*, Fig. 54).

The origin of the chloroplasts is primarily from the plastids of the embryonic cells, which enlarge and assume a green colour. These plastids multiply by fission, and it is easy to see that the chloroplasts do the same. Comparison of a number of them shows some with an elongated form, others with a median constriction, and others again grouped in pairs as though resulting from a recent fission (see Fig. 76, *B*, p. 115): but it is doubtful whether it can be said that plastids in general arise only by fission of pre-existing plastids.

The structure of the palisade-parenchyma, with its oblong cells, is admirably suited to accommodate large numbers of the chloroplasts, which thus present for the most part their edges to the light incident upon the upper surface of the leaf. The cells of the spongy parenchyma, with their irregular form, are less specially fitted for this, and usually they contain fewer chloroplasts than those of the palisade. They are also less important in that they get most of their light at second hand, that is, after it has passed through the palisade tissue. About midway between the upper and lower epidermis the smaller vascular strands of the reticulum may be found traversing the mesophyll, and in intimate relation with it (Figs. 47-49). They vary in complexity from considerable bundles downwards, to a minimum size where the xylem may be represented by a single tracheid. The sieve-tubes stop short before this point is reached; but certain richly protoplasmic cells, like large companion cells, extend further than they towards the vein-endings. Each strand is surrounded by a parenchymatous sheath, the cells of which are in contact with the cells of the mesophyll. Thus the conducting system penetrates and thoroughly permeates the green tissues of the lamina.

The characteristic function of nutrition carried on by the leaf is discussed more fully in Chapter VIII. Here it may be stated simply that in the presence of light the cells containing the green pigment (chlorophyll) build up new organic compounds from carbon dioxide obtained from the atmosphere, and water. The process is known as *Photosynthesis*; it is of fundamental importance to the plant.

In the leaves of many plants the period of this activity is limited by the season, and autumn with its lowering temperatures and shortening days leads to the *fall of the leaf*. At the base of the petiole a band of corky tissue is formed in a transverse plane. Immediately above it the cells become rounded off by increase of the intercellular spaces. This is called the *absciss layer*, because the line of fracture is determined by the weakness of its cells, and it is here that the leaf falls away. *The scar is covered by the layer of protective cork*, while the vessels and sieve-tubes running up to its surface are constricted by the pressure of the adjoining cells (Figs. 6, 55). Thus the fall of the leaf causes no open exposure of the living tissues liable to attack by intrusive organisms. Prior to the fall of the leaf its tissues are depleted of all useful materials, which are transferred down the petiole to the axis. This is accompanied by changes in the cell-contents which give the varied autumnal tints. What falls away is then little more than an empty shell. Its removal leads to a great reduction of the exposed surface of the plant, with the result that there is less loss from evaporation, and less resistance to the winter winds. As a whole the plant enters a dormant condition in autumn, partly determined by the climatic conditions, partly by the absence of those organs which play so active a part in its vegetation. But the fall of the leaf is not an inherent feature in any group of plants, nor does the absciss layer form any constant limit between leaf and stem. For example, the British Oak (*Quercus robur*) is *deciduous*, that is, it drops its leaves in autumn ; but the Holm Oak (*Quercus Ilex*), which is a native of the Mediterranean region, remains *evergreen*. The common Cherry (*Prunus cerasus*) drops its leaves in autumn ; but the Cherry Laurel (*Prunus lauro-cerasus*) is evergreen. Thus though the leaf-fall is a very striking feature of many trees and shrubs in temperate climates, it is really nothing more than a seasonal, and often a specific, adaptation. In many woody plants it does not occur at any regular intervals, while in most herbaceous plants, and especially in annuals such as the Sunflower or Bean, the whole shoot simultaneously ceases its vegetative activity, leaf and axis remaining connected till they rot.

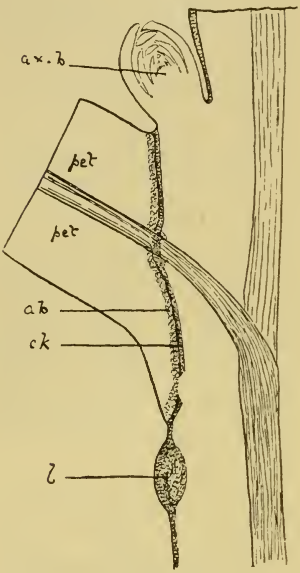

FIG. 55.

Vertical section through the base of a petiole (*pet*) of a Horse-chestnut at its junction with the axis, showing the absciss layer (*ab*) with cork (*ck*) beneath it. (*l*) = a lenticel. When the leaf falls the scar is protected, and the axillary bud (*ax. b*) is left attached. F. O. B. (× 10.)

From the description which has been given of the structure of the leaf it will be seen how well that organ is fitted for carrying out the duty of nutrition, while exposed to the ordinary climatic conditions. In the first place a broad expanse of green tissue suitably orientated makes for a maximum interception of light. In terms of photosynthetic activity the larger this area the better. Since the active cells are those of the mesophyll, it is essential that their thin cellulose walls, saturated with water, shall be exposed for aeration. If simply and directly exposed to the atmospheric air they would quickly dry up and shrivel, but they are protected on either side by the epidermis, which is a continuous layer covered by the impervious cuticle. Access to the atmosphere is still maintained, though under control, through the numerous stomata: by means of the intercellular spaces that permeate the mesophyll it is extended onwards to the individual cells. The epidermis also gives mechanical strength. The mesophyll with its thin walls and spongy texture would by itself be too weak to maintain its form, and resist the impact of winds. It is bound together by the firmer epidermis. The thin expanse of the blade is further stiffened by the framework of the midrib and veins. (Fig. 46.) These illustrate in modified form the same methods of mechanical strengthening as the stem itself. (Figs. 45, 47.) Often the blade is strengthened also by a marginal band of hardened tissue, which acts like a hem. Lastly, the whole lamina is attached to the leaf-stalk, which, though sufficiently rigid to support it, will yet yield to the impact of wind, and so avoid mechanical damage.

On the other hand the conducting system is continuous from the axis outwards through the leaf-stalk, and on through the midrib and veins to the ultimate branchlets which ramify throughout the mesophyll. Thus there is efficient provision for the transit of water from the axis to the remotest points of the lamina, and conversely materials may also be transmitted backwards from these to the leaf-base and into the axis. Such transit does actually take place, the first through the woody tract of the vascular strand, the other through the bast. In short, a foliage leaf is fundamentally a structure with adequate provision for mechanical strength, and for the transit of materials backwards or forwards between the axis and its distal points, which is secured by its conducting system: at the same time it exposes a large area of green tissue to the light, and affords to each cell ready access to the atmospheric air.

CHAPTER VI.

STRUCTURE OF THE ROOT.

THE origin of the primary, or tap-root from the radicle of the embryo, the development of the root-system from it, and the relation of that system to the shoot in the normal Flowering Plant have been described in Chapter I. Its fixation in the soil by means of its root-hairs has also been noted. The details of its structure will now be examined, so that the facts may serve as an introduction to the study of the functions which the root has to perform.

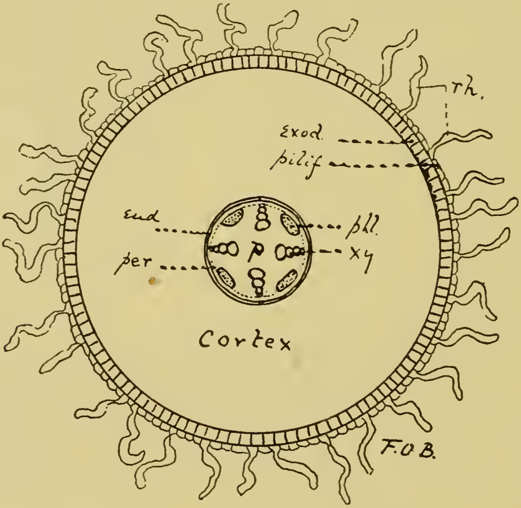

FIG. 56.

Diagram illustrating the arrangement of tissues in the transverse section of a root. *rh*=root-hairs. *exod*=exodermis. *pilif*=piliferous layer. *end*=endodermis. *per*=pericycle. *xy*=xylem. *phl*=phloem. *p*=pith.

The root is typically cylindrical, and accordingly its transverse section will be circular. The general arrangement of the tissues, exposed in a section cut about two or three inches behind the apex of any ordinary root, is more regular than that usual in stems. It is shown diagrammatically for a thin root, such as that of a Pea seedling, in Fig. 56. There is a superficial covering which may be held as corresponding to the *epidermis*. Within it lies the *cortex*, and centrally the *stele*. But here the cortex is relatively bulky, while the stelar column is much more contracted than is usual in stems. This disposition of the tissues is typical for roots at large.

The superficial layer consists of an unbroken series of thin-walled cells, without any cuticle upon their outer walls. It is called the *piliferous layer* because many of its cells are extended outwards as *root-hairs* (Figs. 57, 60). Below the piliferous layer comes the bulky tissue of the cortex, of which the outermost and the innermost layers are sharply defined, while the massive band of tissue between them consists in the young root of a featureless, thin-walled parenchyma with intercellular spaces. The outermost layer, lying directly below the piliferous layer, and with its cells alternating with these, is called the *exodermis*. Its cells fit closely together, and they show a sharply defined corky band upon their radial walls, which often extends with age to the other walls (Fig. 57). This throws the control of the passage of water upon the protoplasts of the living cells so long as the root is young. The exodermis is thus a living physiological barrier, as is also the innermost layer, which is called the *endodermis*. Its cells also are in close lateral relation one to another, while the radial walls have a corky band which serves a similar purpose (Figs. 58, 59). The cortex thus composed forms the larger part of the area of transverse section, and it may be regarded as a water-reservoir round the stele, controlled both on its outer and its inner surfaces by the protoplasm of living cells.

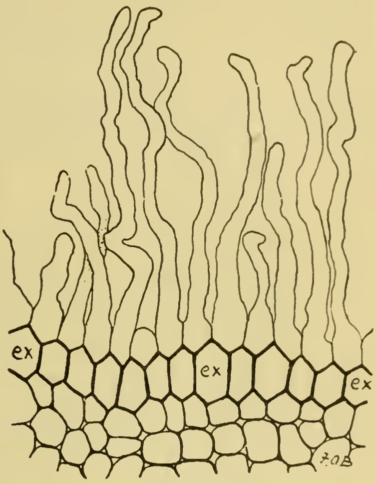

FIG. 57.
External tissues of the root of *Ruscus*, showing each cell of the piliferous layer grown out into a root-hair. *ex*=exodermis. The section shown was probably taken above the absorbing region. (× 100.)

The most prominent tissues of the stelar column are certain well-defined strands of xylem and phloem. In small roots like those of the Cress or Onion there may be only two of each of these ; and the strands may meet at the centre, there being no pith at all. In larger roots of Dicotyledons there are usually more of them, four or five being common numbers (Fig. 59). But the number is not constant in roots of the same species, or even of the same individual. In Monocotyledons the number is usually larger still, and it may run to a very high figure in roots of Palms, or Screw Pines. In such roots a pith is present, and it may be of considerable bulk. A typical structure of the stele for a simple Monocotyledon is seen in the root of the Sweet Rush, *Acorus* (Fig. 58). The cortex and endodermis surround the stele itself, of which the superficial layer is the thin-walled *pericycle*, here a very regular row of cells. There are seven groups of xylem, and seven of phloem alternating with them. Each group of xylem is composed of smaller vessels of the *protoxylem* (*pr.xy*), which are directed to the periphery, while successively larger, pitted vessels (*p.v.*) constitute the later-formed *metaxylem*. The alternating groups

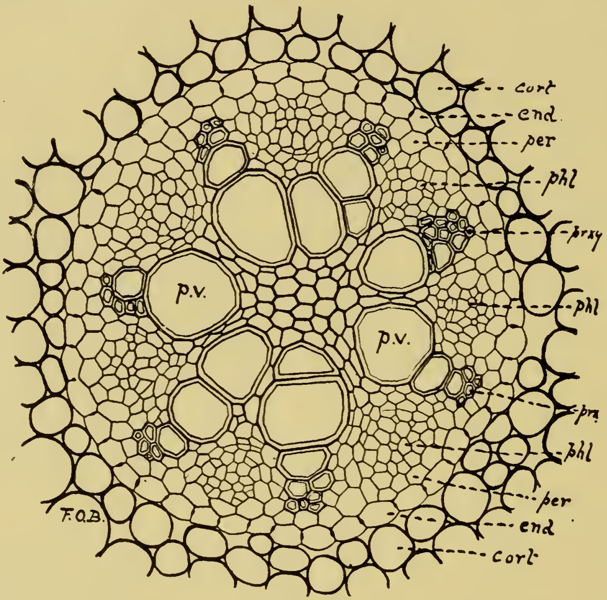

Fig. 58.

Transverse section of the stele of the root of *Acorus*—a Monocotyledon. *cort*=cortex. *end*=endodermis. *per*=pericycle. *phl*=phloem. *prxy*=protoxylem. *p.v.*=pitted vessel. (× 150.)

of phloem are not strongly developed, and the whole is compacted by cells of the *conjunctive parenchyma*, which fill up the interspaces and extend to the centre. Here its cells instead of forming a soft pith become sclerotic with age, so that the lignified tissues are all welded together into a central, mechanically resistant strand.

Internally to the phloem cell-divisions may be seen at several points in the Fig. 58. These are in the position where in other roots a cambial activity arises. Here, however, as in Monocotyledons generally, the divisions proceed no further. It will also be noticed that the intercellular spaces in the cortex are large. *Acorus* is a swamp-growing plant, and the tissues of water-plants are characterised by large intercellular spaces.

The arrangement of the vascular tissues thus seen in roots, with the xylem and phloem alternating on different radii, is described as *radial*. It is in sharp contrast to the *collateral* arrangement characteristic of stems, where the xylem and phloem are upon the same radius, the phloem being outermost. Moreover, while in stems the protoxylem is directed centrally, in roots it is peripheral in position. Evidence of the centripetal succession of development can easily be seen in sections of young roots. Fig. 59 shows such a section from

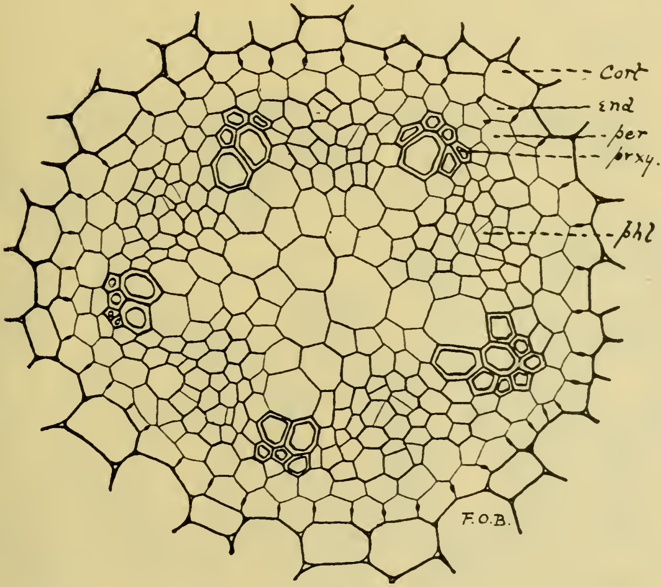

FIG. 59.

Transverse section of the stele of a young root of *Ranunculus*, showing the central metaxylem not yet developed. Lettering as before. (× 200.)

the Buttercup, which has five protoxylem groups, a number not uncommon for Dicotyledons. But of these only the protoxylem vessels are as yet developed; the vessels of the metaxylem are still thin-walled, but they extend to the centre of the pithless root, and they form a solid star of xylem when mature.

Since the arrangement of the vascular tissues is radial in the root, but collateral in the stem, it is obvious that a readjustment must take place where the one passes into the other. The change is effected in seedlings in various ways, at or near to the level of the soil. The xylem-masses rotate upon their axes, and this is combined with splittings and fusions of the strands in some cases, so that the peripheral protoxylem of the root becomes central in the stem and the xylem-masses range themselves internally to the phloem-masses. Thus without break of the continuity of the conducting tracts, the characteristic structure of the root passes upwards into that of the stem.

In order that the root may absorb water from the soil, a close relation with the soil must be established. This is effected by the root-hair.

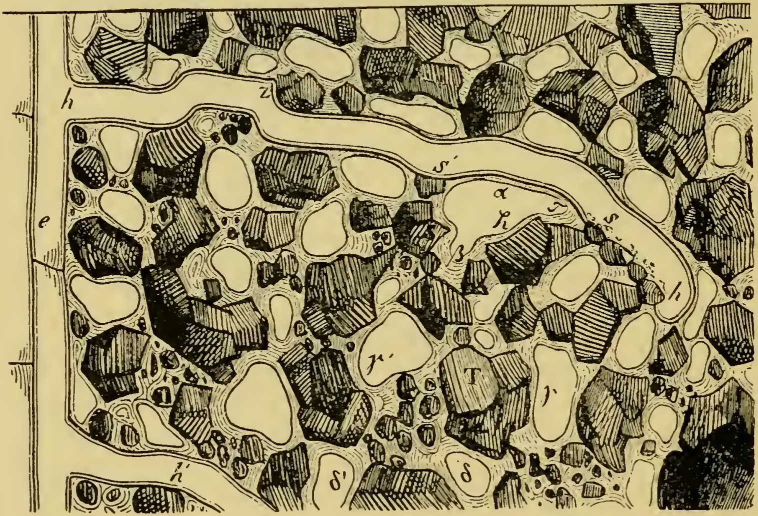

Fig. 60.

Representation of root-hairs in the soil. *e*=piliferous layer of the root. *h*, *h'*=root-hairs grown out from its cells, and adjusting their growth to the solid fragments of the soil. Each of these is covered by a film of water, which is shaded; while the clear spaces indicate the air-cavities in the porous soil. (After Sachs.)

The parent cell is usually oblong in form, and from a point about the middle or upper end of its outer face the hair arises as a cylindrical process, which penetrates between the particles of the soil. It adjusts its form to the spaces between them, while the nucleus passes out into the growing hair, and the delicate cell-wall is lined by a thin film of cytoplasm surrounding a central vacuole. A gummy softening of the wall near the distal end leads to a most intimate connection with any solid particle. The state of the root-hair in the soil is suggested by Fig. 60. As the water in the soil is held in the form of surface films covering the several particles, the root can by its hairs tap those films, however thin they may be in a dry soil. It is important further to realise how numerous these root-hairs are. It has been estimated that over two hundred of them may be borne on one square millimetre of surface of the root of a Pea, while in other plants, for instance the Maize, the number may be still higher. The effect of this is greatly to increase the possible absorptive surface of the root.

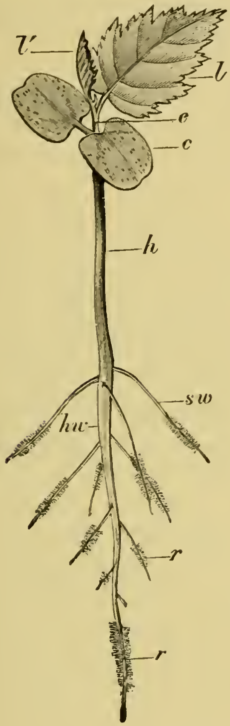

FIG. 61.

Seedling of *Carpinus Betulus*. *h*=hypocotyl. *c*=cotyledons. *hw*=main-root. *sw*=lateral roots. *r*=root-hairs. *e*=epicotyl. *l*=foliage leaf. Natural size. Strasburger.

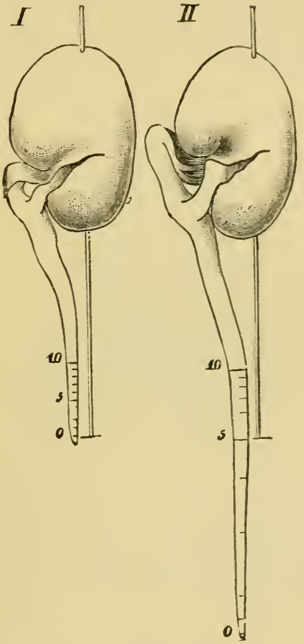

FIG. 62.

Localisation of growth near to the root-tip of *Vicia Faba*. In I. the root-tip has been marked with 10 zones by lines 1 mm. apart. In II. the same root after 22 hours. The lines nearest the tip are now most separated owing to the growth having been there most active. (After Sachs, from Strasburger.)

The hairs arise in acropetal order. Individually they are functional only for a short time, as is seen from the fact that though active at a short distance backwards from the growing root-tip, at a further distance from the apex they may have already shrivelled away, so that the older part of the root no longer preserves its intimate relation to the soil. Thus as the root-system extends, it taps an ever enlarging area of the soil, while it is actively absorbent only at the outer limit of the area invaded (Fig. 61).

As soon as any part of the root is anchored in the soil by its outgrowing hairs, it could not possibly increase in length without tearing them away from their hold. But of this there is no sign. It follows, therefore, that the growth in length of the root must be restricted to the region beyond the youngest root-hairs. It may be demonstrated that the growth is thus restricted, and that the most rapid growth is close to the tip, by making marks with Indian ink at equal distances upon the outside of a growing root. The root should then be kept in condition as near as may be to the normal. After a period of twenty-four hours, if the distance between the marks be compared with the original scale, it will be seen that the two do not tally. It will easily be seen where the greatest elongation has been (Fig. 62). The most rapid growth in an average root is about 5 mm. from the tip. It diminishes gradually from that point in both directions, and ceases at about 10 mms. from the tip. This restriction of the growth in length to a short region behind the tip is characteristic of roots, and is in sharp contrast to what is seen in ordinary stems. In them the growth in length may be spread sometimes over a length of several decimetres.

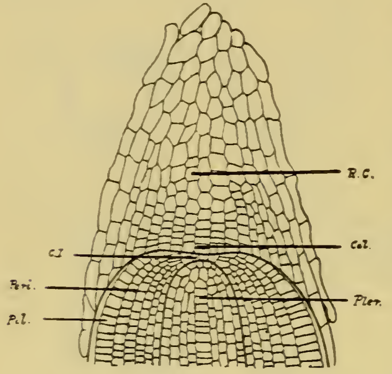

FIG. 63.

Root-tip of Barley, cut in median longitudinal section, and placed apex upwards. *R.C*=root-cap. *cal*=calyptrogen layer, which renews the tissue of the cap. *CI*=common initials for piliferous layer (*Pil*) and the periblem (*Peri*). *Pler*=central cylinder of plerome, giving rise to the stele. (× 110.) (After Janczewski.)

A consequence of the growth of the region beyond the anchoring root-hairs is that the root-tip itself is forced forward. As in the stem, so in the root the apical tissue is embryonic, and of delicate texture. Nevertheless this delicate root-tip is driven through the soil, forcing aside the solid particles in its course. A study of its structure explains how injury to the apex is avoided. External observation shows that the conical apex itself is semi-transparent and slimy to the touch. By this sliminess it readily slides past obstacles, losing occasionally some superficial cells in the process. But the structure of the root-tip as seen in section explains the protection better ; it is well shown for the common Barley in Fig. 63. The actual growing point is protected by a calyptra, or *root-cap*. The superficial piliferous layer as it approaches the apex, curves inwards, though still preserving its identity. Outside it lies a cap of tissue (*R.C.*), which though thick at the actual tip, gradually thins off as it spreads backwards. Its superficial cells are only loosely attached. Their walls, being gummy and swollen with the water in the soil, are easily rubbed away. But the loss is made good by growth and cell-division arising from the innermost cells just outside the incurved piliferous layer. Internally the central stele continues up to the apex, ending in a rounded dome. At that point a single layer of cells intervenes between it and the root-cap. This layer gives rise by successive divisions to the piliferous layer and the cortex. There are thus in this type, which is common for Monocotyledons, *three definite strata* at the apex of the root, and each gives rise to a tissue which takes special characters as it matures.

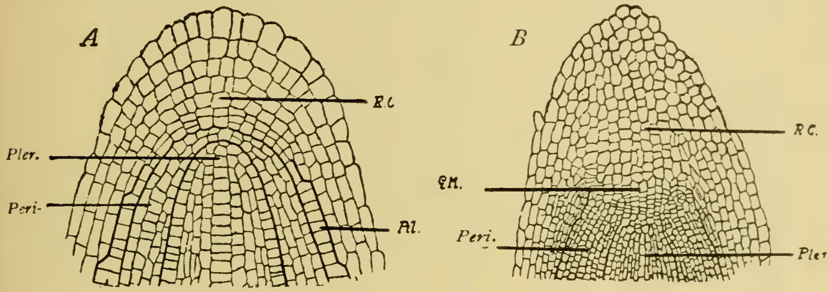

FIG. 64.

A=Root-tip of Buckwheat (× 120). *B*=root-tip of Pea (× 60). *R.C*=root-cap. *Pil*=piliferous layer. *Peri*=periblem. *Pler*=plerome. *GM*=the general meristem in the Pea from which the different tissues are gradually derived. (After Janczewski.)

The stratification of the growing point of roots is not always on the plan described, though that is the usual type in Monocotyledons. In Dicotyledons various conditions are seen, of which two examples may be given. The most common is that seen in the Sunflower and Buckwheat (Fig. 64, *A*), where the stele is as before a distinct column ending in a definite dome. The cortex is also a distinct tissue covering it, but reduced to a single layer at the extreme tip. The piliferous layer has a joint origin with the root-cap, by periclinal divisions of cells just outside the tip of the cortex. The chief difference is that the piliferous layer is distinct in origin from the cortex, while in the Barley they were seen to have a common origin. A second type is illustrated by the Pea and other Leguminosae. (Fig. 64, *B*.) Here the stele, cortex, piliferous layer, and root-cap all originate from a common mass of meristem, which occupies the apex, and segregates gradually into the several tissues as the cells mature. Such facts show that no theory of "germinal layers" can have any general application in the development of the plant-body.

The normal increase in number of roots is by the formation of lateral rootlets, which originate from deeply-seated tissues, and force their way out of the parent root. Such an origin is described as *endogenous*, and is in contrast to the *exogenous* origin of leaves, where the surface-tissue remains continuous over the new growth. The lateral root springs from the cells of the pericycle, usually at a point opposite to one of the protoxylem-groups. If the parent root be cut longitudinally through the point where a lateral rootlet is being formed, the cells of the pericycle opposite the protoxylem will be found in active division (Fig. 65, *a*). Later the tissues thus formed give rise to the central stele (*pler.*), the cortex (*cort.*), piliferous layer (*pilif.*), and root-cap (*calyp.*), of the

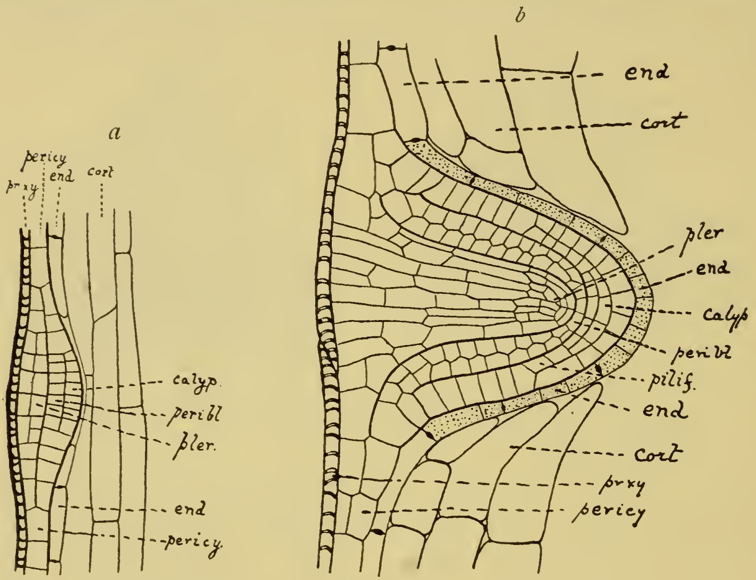

Fig. 65.

Origin of a lateral root from the pericycle, as seen in longitudinal section of *Reseda*. In (*a*) the pericycle has divided by periclinal walls to form four layers to which the tissues named are referable; the endodermis has yielded. In (*b*) the formative tissues are clearly recognised. The endodermis (*end*) has developed as a digestive sac. (× 100.) (After Van Tieghem.)

lateral root (Fig. 65, *b*). By reason of its deep-seated origin the tissues of the lateral root are intimately connected with the tissues of the main root. At its tip it pierces the cortex of the parent root by a process of digestion, through the activity of cells of the endodermis (*end.*), though in some cases cells of the cortex also act in the same way. They form a glandular *digestive sac* which softens the cells outside, so that they yield to the growing rootlet within. The substances of the digested cells are absorbed by the rootlet as it forces its way out from the parent.

The details of division of cells in the formation of a rootlet vary in different cases. It is here illustrated for the type usual in Dicotyledons. The cells of the pericycle divide by periclinal walls, so as to form several layers, and by anticlinal walls, so that each layer consists of numerous cells. The innermost layer forms the plerome of the young root, giving rise to its central stele (*pler.*). The next outer layer is the periblem, giving rise to the cortex (*peribl.*) ; while the third outermost layer gives rise on the one hand to the root-cap (*calyp.*), and on the other to the piliferous layer (*pilif.*) ; the two having a joint origin, as already explained in the case of the Buckwheat. The consequences of this mode of origin are that the vascular tissues of the rootlet connect directly with the vascular tissues of the main root. This is essential to the effective transfer of materials. But the cortex, piliferous layer, and root-cap of the lateral root are all distinct in origin from those of the parent. Physiologically this discontinuity is not a matter of importance.

The individual root thus growing indefinitely at its apex, and bearing an increasing number of lateral roots, is subject to increasing demands upon it, as a means of transit from the distal absorbing region to its attachment at the base of the plant. In Monocotyledons (Fig. 58), and in some Dicotyledons (Fig. 59) there is no special development of tissues to meet this, but there is usually an increase in the number of adventitious roots, as in Palms, Maize, Onion, etc. In most Dicotyledons, and especially in those that are woody, there is a process of *secondary thickening by means of a cambium*, analogous to that seen in their stems. Cell-divisions appear in the conjunctive parenchyma lying internally to the several groups of phloem (Fig. 66, *a*). Arcs of cambial activity are thus formed, which soon spread to the tissue of the pericycle lying peripherally to the protoxylem (Fig. 66, *b*). The several arcs are thus linked together to a continuous band, in the form of a corrugated cylinder. As in the stem, this cambium produces secondary wood internally, and secondary bast externally, to an indefinite degree. But at first the cells lying peripherally to the protoxylem form only parenchyma, so that a broad medullary ray appears externally to each group of the primary wood. In the secondary wood additional medullary rays and annual rings may

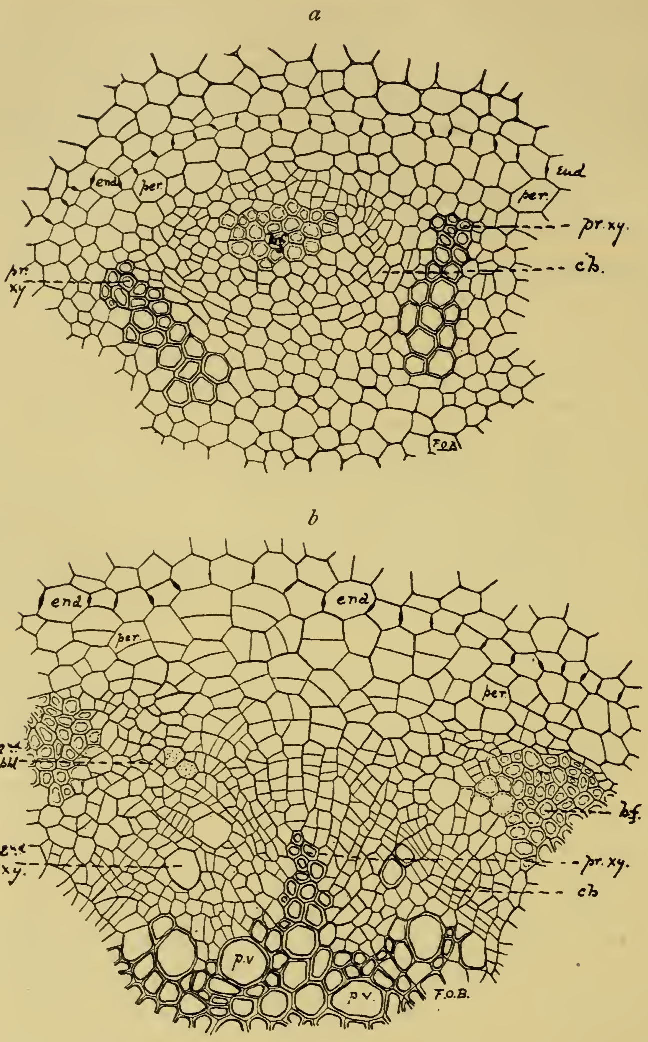

Fig. 66.

a, *b*, Successively older sections of the root of the Bean (*Vicia Faba*), showing the beginning of cambial activity. In (*a*) divisions appear (*cb*) in the conjunctive parenchyma internally to the phloem, but the pericycle (*per*) is quiescent. In (*b*) the cambium has already formed xylem internally (*2nd xy*), and phloem externally (*2nd phl*), and cell division has spread to the pericycle, and is continuous outside the protoxylem (*pr.xy*). (× 100.)

appear, as in the stem. Consequently an old root of a Dicotyledon acquires a structure very like that of an old stem (Fig. 67). The difference may be often observed even in old roots by looking for the primary wood. If the protoxylem is central the section has come from a stem; if it is peripheral relatively to the rest of the primary wood, then the section has come from the primary region of the root.

As the distal part of a young root grows older the root-hairs upon it shrivel. In Monocotyledons, and in some Dicotyledons the cortex is retained; but as it grows old its cells lose their turgor, and the cortex shrinks. In bulbous Monocotyledons, and in some Dicotyledons the whole root then shortens, anchoring the plant firmly in the ground, while evidence of the shrinkage is seen in transverse wrinkles on its surface. In most woody Dicotyledons the bulky cortex itself collapses and finally peels off. This is due to the formation of a band of cork, which originates from the pericycle, and cuts off the outer-lying tissues from physiological connection with those within, so that they perish (Fig. 67, *C*). Since the cortex makes up a very large proportion of the whole bulk of the root, the consequence in such cases is that at first the root appears to become thinner as it grows older. But as a matter of fact the central stele has meanwhile been increasing in bulk, and it is protected externally by the band of cork which originates from the pericycle. Since this cork may be further

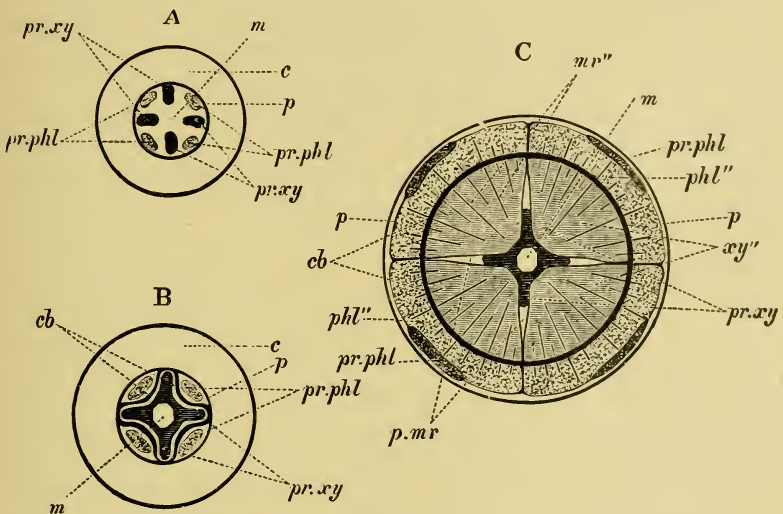

FIG. 67.

Diagram A shows arrangement of tissues in a young root of a Dicotyledon before cambial activity begins. B. the same when cambium can be clearly recognised. C. after secondary thickening has progressed. *c*=cortex, present in A and B, but in C it has been thrown off. *pr.phl*=primary phloem. *phl''*=secondary phloem. *pr.xy*=primary xylem. *xy''*=secondary xylem. *p.mr*=primary medullary ray. *mr''*=secondary medullary ray. *m*=pith. F.O.B. Compare Fig. 37, p. 58.

developed as in stems, the old root is covered by a band of bark not unlike that of a woody stem.

The stem, leaf, and root, as seen in ordinary Flowering Plants, have now been described. In subsequent chapters the Plant-Body can therefore be considered as a connected whole, and some idea gained of its physiological position as a concrete living organism. Normally, with its root in the soil and its shoot in the air, it acts as a sort of intermediary between the two regions in which it lives. One phase of the Botanical interest would be to see how the Plant plays off the one medium against the other, drawing meanwhile its nourishment from both. Another phase is to follow the material abstracted and to see how it is used in Life, and how on the disorganisation of the Plant after Death that material is finally restored to its original source. Vegetation may thus be looked upon as an active factor in that interchange and circulation of material which is constantly taking place at the surface of the Earth's crust.

CHAPTER VII.

THE WATER-RELATION.

If you neglect to water plants grown in pot culture in the greenhouse the plants will wither : if the withering has not gone too far the plant may recover after watering ; but if the neglect has been too prolonged the plant will die. These facts are familiar to everyone who has experience of indoor cultivation of plants ; and though the problem of water-supply may perhaps be less obvious in plants growing naturally in the open, it is no less a grave one for them also.

In discussing the relation of plants to water it is necessary in the first place to realise how high is the proportion of water contained in ordinary plants. If a block of wood be cut out from the trunk of a living tree, and weighed, and after drying out thoroughly at 100° C., it be weighed again, it would be found to have lost about half its weight. Thus water forms about half of the weight of so solid a tissue as the wood in the normal living state. In succulent tissues of the leaves or young stems, or in the tissues of herbaceous plants, the proportion is much larger. In the case of the fresh Cabbage it amounts to about 92 per cent., and in the Lettuce, as cut fresh for a salad, to about 95 per cent. Thus only about 5 per cent. of a crisp Lettuce consists of the substance of protoplasm, and cell-walls. The living plant may then be regarded as a structural framework retaining within it a very high water-content. The water exists there in various forms. A large part of it appears as *liquid water*, filling the vacuoles of cells, or in the cavities of the vessels, and it can be seen as such microscopically. But a considerable proportion of it is absorbed into the substance of the protoplasm or the cell-walls and starch-grains, as *water of imbibition*, upon which their swollen condition depends. Some may be present as "*water of constitution*," entering more intimately into relation with the substances of which the plant body is composed.

The significance of water to the plant is manifold. It is the medium in which the protoplasm conducts its chemical reactions and it is actually used up in a number of chemical operations, *e.g.* in photosynthesis ; it is the solvent through which all materials enter the plant cell from its environment, and thus they pass from point to point in the plant : finally, its accumulation at an early stage under pressure within the cells leads to their enlargement, and subsequently gives firmness to them and to the organs that they compose.

It is clear that an active plant will require constant supplies of water for its chemical operations, and to meet the needs of new tissues. But over and above the small amount of water required for these purposes, a very much greater quantity is needed to make good the loss incurred by the evaporation of water (or *Transpiration*) from the aerial organs.

Absorption of Water by the Plant.

Land-plants rely on the soil for their water supply. But the absorption of water is mainly restricted to the younger parts of the root system, and especially to the regions bearing root-hairs. The structure and distribution of these hairs have been described in the previous chapter, where it was pointed out that their presence increases the absorptive area of the root very considerably, while the hairs make intimate contact with particles of the soil (Fig. 60), facilitating absorption of water present as films round those particles. Each root-hair-cell forms an osmotic system, as described for plant-cells in general in Chapter III. ; the cell-sap normally has an osmotic pressure of 5 atmospheres or more, so that the hairs are in a position to carry out osmotic absorption of water under suitable conditions.

The soil in which the root system develops is a complex mixture of materials, organic and inorganic, holding within it water to a greater or lesser degree. No soil in the open is ever actually dry, and normally the amount of water contained is considerable. Soil-water is of different types. Thus we may recognise as *gravitational* water that which is only present in badly-drained soils, or after rain. Of the water retained by a well-drained soil, some is held by *capillarity* in the minute channels between the particles, or in the form of films round the particles ; while some is held by *imbibition* in the colloidal constituents of the soil, such as *clay* and *humus*. Humus, using the term in a broad sense, is the decaying organic matter of the soil, derived from previous generations of plants. Leaf-mould is a type of humus. It is important to realise that the soil-water is mobile, and tends to distribute itself uniformly through a mass of soil, so that if water is drawn off at any point in the soil there will be a certain compensatory flow of water towards that point. The consequence of this will be that a root can to some extent draw on the whole reservoir of water which the soil in its neighbourhood contains. Dissolved in the soil-water are small quantities of salts such as nitrates, carbonates, phosphates and sulphates of sodium, potassium, calcium, etc., the total concentration being usually less than 0·1 per cent.

The study of soils is a science in itself. Only a few general features can be mentioned here. The constituents of a soil fall into several groups. The first group includes those which together form the general framework of the soil. This is composed firstly of the coarser particles of sand and gravel, consisting for the most part of pure silica: secondly, of finer particles forming clay, which consists of silica combined with oxides of iron, aluminium, and other metals. There is no sharp line to be drawn between the former and the latter, and the name "silt" is sometimes applied with varying meaning to material that is intermediate between them, while the name "loam" is used for soils containing more fine clay than sand. These components of the soil all owe their origin to the weathering of rocks of inorganic origin.

A second group of soil-constituents includes those derived ultimately from organic life. The most important is calcium carbonate, produced by the weathering of chalk and limestone; this is a regular constituent of loams. It has important effects on the condition of soils, preventing sourness, and making a heavy clay soil more workable. Lime (calcium oxide) has a similar effect. Another substance of this type is calcium phosphate, which is partly of organic origin, but partly derived from the decay of rock.

A third group consists of those organic substances collectively called *humus* (see above), which represent the intermediate products of the decay of plants which have previously grown on the soil. As these die their leaves and other parts are carried down by earth-worms into the soil, and there the materials which compose them are gradually broken down into simpler compounds. This is largely the result of the activities of the micro-organisms of the soil (see below). These simple compounds are then available for absorption by existing plants. There is thus a circulation of material between the soil and the vegetation which it carries: food is extracted from it, but restoration of the substances is made on the decomposition of the plant-body.

Any ordinary soil contains water in more or less quantity, and being porous, it may be permeated by atmospheric gases. The supply of water comes from rain, or from the sub-soil. It is diminished by evaporation and by drainage, and the water-content of the soil at any moment represents the balance between gain and loss, being liable to constant change. The constitution of the soil, and the nature of its surface are factors which affect it. For instance, sand retains water less than clay: a fine surface broken by rake or hoe checks evaporation. About 60 to 70 per cent. of the volume of an arable soil is made up of soil-constituents as above detailed, and about 30 to 40 per cent. is accounted for by spaces between the soil particles, occupied by air (which may be somewhat different in composition from atmospheric air) and by water. In badly drained soils the spaces are largely occupied by water, and aeration is correspondingly reduced. The soil-water carries in solution small quantities of any constituent of the soil that is soluble. Examples of materials commonly found in solution in the soil are mentioned above.

Besides the plants rooted in it, the soil houses a vast population of other organisms. Earthworms are constantly at work burrowing through the soil, passing large volumes of it through their alimentary canal, and voiding it at the surface as worm-castings. They bring up material from the lower layers to the surface, and conversely they draw down into their burrows leaves and other decaying parts, thus serving as tillers of the soil. Many other animals are also present, such as wire-worms, eel-worms, etc. There are also multitudes of microscopic forms of life, such as the Protozoa, Fungi and Bacteria. The latter play a very important role in the decay of organic materials in the soil, and in other ways by the varied chemical changes which they bring about (see Chapters VIII. and XXVIII.).

The root-hair in exercising its function of absorbing water has to face a certain resistance from the soil. This arises from the physical forces of capillarity and imbibition, and from the slight osmotic activity which the soil-water, with its salts in solution, possesses. The magnitude of this last factor is unusually high in salt-marshes and other sea-side situations, where the salt-content of the soil may be considerable. But the fact that plants usually manage to keep that condition of turgor, on which their firmness and mechanical rigidity largely depend, indicates that the absorptive forces of root-hairs are adequate to overcome these resistances to a requisite extent (see Chapter X.). It is probable that plants utilise chiefly the capillary water, since the colloidal particles of soil cling very tenaciously to their imbibed water, and the absorptive forces of the root-hairs may be inadequate to overcome these forces of imbibition. Reference has been made to the osmotic pressure of the root-hairs. The actual proportion of this osmotic force that is available for absorption at any moment depends on the degree to which the root-hairs are removed from complete turgor. It was pointed out in Chapter III. how a fully turgid cell has no absorptive capacity (or Suction Pressure), while this capacity is at its maximum in a plasmolysed cell. Only if there is a steady movement of water out of the root-hairs into the interior of the root will absorption by the root-hairs continue, for otherwise complete turgor would soon be reached and absorption cease.

This brings us to the first section of the route which most of the water absorbed by the root-hairs pursues through the plant, in the so-called *Transpiration Stream*. The water passes laterally from the root-hairs across the cortex of the root, through the endodermis and pericycle and into the xylem vessels (Fig. 68). Until the xylem is reached the water passes through living cells, each cell forming the usual osmotic unit. As in the case of the root-hairs, so with these inner cells, if there were not a constant movement of water from the innermost living cells into the xylem vessels, all the living cells would soon become fully turgid, and a static condition would be reached. The fact that a constant movement of the type mentioned does exist results in the maintenance of an absorptive capacity in those inner living cells. These in consequence take up water osmotically from the cells lying next outside them, a process which extends outwards until the root-hairs and soil are reached. A lateral flow of water from the soil through the living cells of the root is thus maintained till it reaches the xylem. The movement of water from the innermost living cells into the xylem will be reserved for later consideration. At this point we leave it in its journey through the plant, and go on to study the course of events above soil-level.

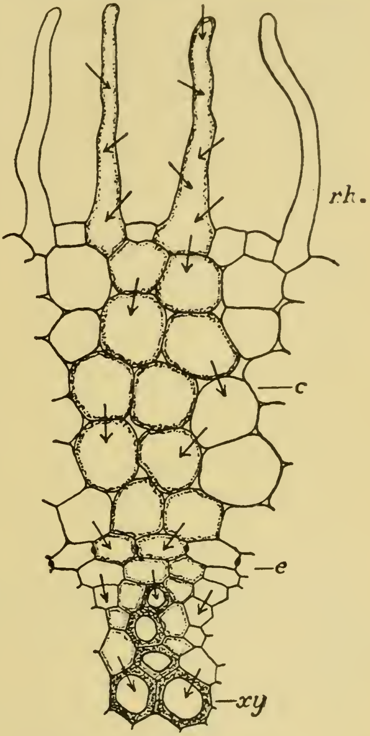

FIG. 68.

Part of a transverse section of a Pea root to show the direction of movement of water (see arrows). The root-hairs were proportionally longer than they appear in the drawing. The cell-contents are shown in some cases, diagrammatically. *r.h.*=root-hair; *c*=cortex; *e*=endodermis; *xy*=xylem. (× 133.) (With acknowledgments to Priestley.)

TRANSPIRATION.

We have seen in previous chapters how the leaves and young stems of the plant are covered by a protective *cuticle*, which is highly impervious to water. The cuticle is, however, interrupted by the very numerous *stomata*. Within the organs, and connected with the stomata, we find a ramifying system of air-spaces, which ventilate the internal tissues. They are thus brought indirectly into communication with the atmosphere, making possible that exchange of carbon dioxide and oxygen which the functions of photosynthesis and respiration require. It is clearly possible that there will be loss of water by evaporation from the tissues so ventilated, just as clothes hung out in the open-air dry by evaporation.

Experiment confirms that from the aerial organs of plants, especially the leaves, there is an extensive evaporation of water, to which the term *Transpiration* is applied. If leafy shoots are placed under a bell-jar, a deposit of condensed water-vapour soon appears on its inner surface. Further, if pieces of dry cobalt chloride paper be fixed on the surface of a suitable leaf and protected from the atmosphere, a rapid change of colour from blue to pink will indicate the liberation of water-vapour from the leaf-tissues. The actual evaporation is generally held to occur from the cell-walls of the mesophyll, which contain imbibed water, into the atmosphere of the air-spaces : thence the water-vapour diffuses through the stomata into the outer air. The path can be traced in Figs. 48 and 49. There is also some transpiration through the cuticle of leaf and stem ; but that the greater part is through the stomata is indicated by an experiment in which pieces of cobalt chloride paper are placed on both surfaces of a leaf showing stomata on the abaxial surface only. The change in colour is found to occur considerably more rapidly in the lower piece of test-paper than in the upper. Alternatively two similar leaves may be taken and a thin film of vaseline smeared on the adaxial surface of one, and on the abaxial surface of the other ; here again leaves with stomata on the lower surface only are to be used. It will be found by weighing that the first leaf loses water by transpiration much more quickly than the second, in which the stomata are covered up.

We thus realise that transpiration is for the most part an unavoidable result of aeration of the tissues. In times of water-shortage transpiration may be a definite disadvantage to the plant, and it has been remarked that more plants perish or are retarded in growth through lack of water than from any other cause. Many plants, especially those inhabiting dry situations (the so-called *Xerophytes*, see Chapter XI.), display structural modifications tending to reduce transpiration in times of drought. To a plant, however, that is well supplied with water, it is probable that transpiration has certain advantages. In the first place, evaporation has a cooling effect which may prevent harmful overheating of the leaf especially when exposed to strong sunshine. Secondly, the flow of water up the plant that is initiated by transpiration, probably accelerates the movement of mineral salts from the roots to the upper part of the plant (see also p. 110). The fact that there is a subsidiary mechanism which tends to provide for a current of water through the plant in the absence of transpiration suggests that the maintenance of such a current is of importance to the plant (see Root Pressure, p. 108).

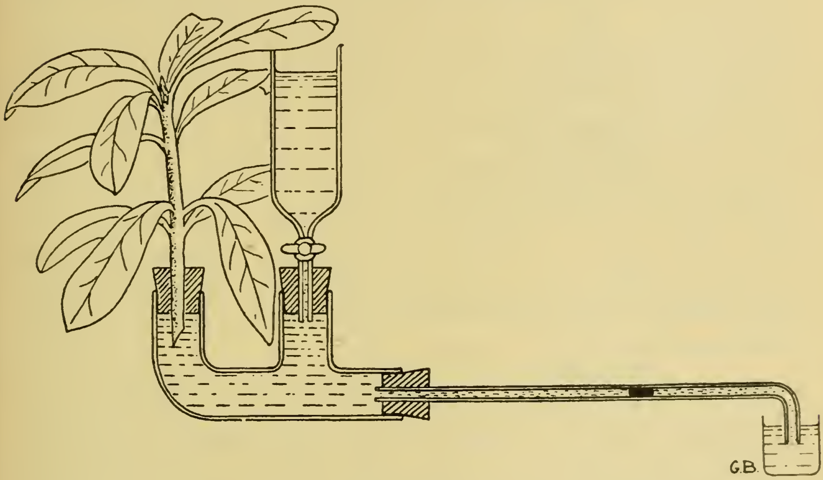

Fig. 69.

Potometer of the Ganong pattern. When necessary the air-bubble (shown in black) can be driven back to the right-hand end of the capillary tube by admitting water from the funnel.

The actual amount of water lost in transpiration may be considerable. For example it has been estimated that a Birch tree may lose as much as 600 lbs. of water during a hot dry day. Measurements of transpiration can conveniently be made on plants growing in pots. The pot and soil must be carefully sealed up in metal shells roofed over with sheet rubber so that evaporation can occur only from the plant. The whole arrangement is weighed at intervals and the loss in weight during a period represents the transpiration. An instrument called the *potometer* is frequently used in experiments on transpiration, though what is thus measured is actually the rate of *absorption* of water by the cut shoot fixed into the apparatus (see Fig. 69). The whole apparatus being initially filled with water, absorption by the cut end of the shoot will cause a movement of water from the small beaker on the right into the bent and graduated capillary tube. An air-bubble is introduced into this tube by raising its end out of the water in the beaker for a few moments. The number of graduations subsequently traversed by the bubble in a certain time gives an indication of the rate of absorption, and since normally absorption is approximately equal to transpiration, we have here an indirect method of measuring transpiration.

With the potometer it can be shown that exposure of the shoot to a current of air from an electric fan increases transpiration. Exposure of the shoot to specially dried air also increases transpiration, while exposure to a very moist atmosphere decreases it. These results we should expect from experience of ordinary evaporation; but the further observation that transpiration at night is very much less than in the daytime would not have been entirely expected. This result may be in part due to differences of temperature: but it is also referable to the influence of the *stomata*. Some information concerning these structures was given in Chapter V., where it was pointed out that the stomatal guard-cells are adjustable, so that the pore can be either open or closed. Generally speaking the stomata open in light and close in darkness, the difference being due to a greater turgor prevailing in the guard-cells in the presence of light than in its absence. When turgor is high the guard-cells tend to curve apart, and the pore opens: but when turgor falls the cells tend to relax into the straight position, and the pore closes (Fig. 70). The changes of turgor are due to alterations in the amount of osmotically active sugars in the sap of the guard-cells. These, unlike the other epidermal cells, regularly contain chloroplasts, and in the presence of light sugars will presumably be produced by photosynthesis: in saying this we anticipate information to be given in Chapter VIII. It is now believed that a production of sugars,

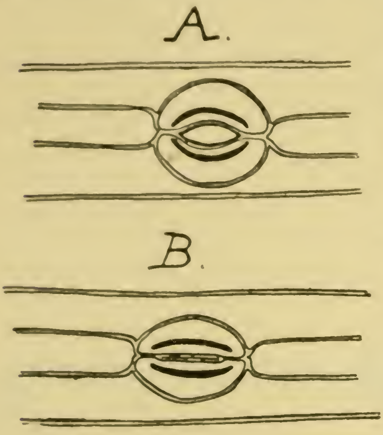

Fig. 70.

Stoma of *Narcissus*, in surface view. *A*, in the open; *B*, in the closed state. (× 250.) F. O. B.

more important to the action of the stoma, is as follows. Observation shows that in darkness abundant starch grains are present in the chloroplasts of the guard-cells. When light falls on the leaf, these starch grains disappear owing to their conversion to sugar, probably through enzymic action. The increase in sugar content of the guard-cells thus produced leads to an intake of water from the neighbouring epidermal cells: for these have as a rule no chloroplasts and no starch reserves, and experience no increase in sugar content when exposed to light. This intake of water and consequent increased turgor in the guard-cells produces the opening, as described. Observation indicates that when the light fails in the evening the sugars in the cell-sap of the guard-cells are largely converted back into starch, with a resultant fall in turgor and closure of the pore. So that the effect of light intensity on stomatal aperture is due to its exertion of a close control on the starch-sugar balance of the guard-cells, though at present it is somewhat uncertain how this control arises. That the opening of the stoma depends on turgor is readily proved by treating a living preparation from a leaf, showing open stomata, with a 5 per cent. solution of common salt. The osmotic withdrawal of water and loss of turgor quickly results in closure of the stomata, the guard-cells ultimately becoming plasmolysed.

The mechanics of stomatal movement are complex, and are bound up with the structure of the guard-cells. While the latter varies a good deal, the chief features are these. The two guard-cells, attached at their ends, are usually curved, the wall facing the pore being shorter than that in contact with the adjoining cells. The inner and outer slopes of the face next the pore bear each a projecting ridge (Fig. 71). The open stoma, with its tense cells, requires more room than the closed stoma. That room has to be gained by forcing the adjoining cells aside. Where the cell-walls are thick, special thin areas of cell-wall are found which are effective as joints or hinges, allowing the cells to adjust themselves mutually when the pore opens. It is the increase in turgor, produced as explained above, acting on cells of the form and structure of the guard-cells, that makes the pore open in the presence of light. The internal pressure being equal over the whole internal surface, since the convex wall presents a larger area, it will stretch more than the concave wall when turgor increases; this would in itself produce a greater curvature and opening of the pore, even if the walls were all of the same thickness. But they are not. The ridges of thickened cell-wall on the outer and inner faces of each guard-cell make the average thickness of the wall greater on the side next the pore. This will accentuate the curvature of the cells when the turgor rises. A further effect of the increased turgor will be to make the section of the cell-cavity approach as nearly as possible to the circular. This too will result in withdrawing the projecting surfaces where the guard-cells meet when closed. All these factors act together in opening the stoma.

It may be noted here that the stomata provide for a surprisingly rapid interchange of gases and vapours between the leaf tissues and the atmosphere. This is partly because of their huge numbers (p. 74), but also for the less obvious reason that far more diffusion *per unit area* takes place through a very small pore, such as a stoma, than through a pore of larger dimensions. This principle can be illustrated by reference to experiments on the diffusion of water vapour through perforated metal discs securely fixed to the tops of glass specimen-jars containing water. The evaporation through the various discs can be followed by noting the loss in weight of the jars. In a particular experiment the evaporation from a jar covered by a disc with a single hole one centimeter in diameter was compared with that from a second jar in which the disc bore four smaller holes equal in combined area to that of the single pore in the first jar. The evaporation from the second jar was considerably greater than that from the first. Thus subdivision of pores gives them greater efficiency as channels of diffusion. The efficiency of microscopic pores like those of stomata is therefore very high.

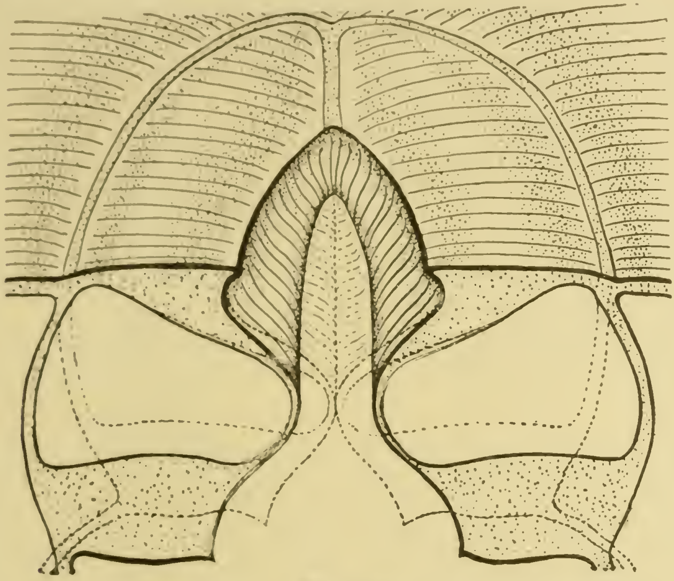

FIG. 71.

Diagram representing a stoma in median section, and also in surface-view. The continuous lines show the position of its guard cells in the open state ; the dotted lines show their position in the closed state.

The closure of the stomata at night, together with the fact that the rest of the epidermis is roofed-over by the cuticle, through which water can pass to a limited extent only, results in the avoidance of unnecessary loss of water by transpiration during a period when there is little need for gaseous exchange with the atmosphere. It was formerly believed that the stomata exercised a close control over the transpiration from the leaf during the whole day and adjusted it in accordance with the available supply of water. It was supposed that if transpiration tended to exceed supply, the turgor of all the leaf cells including the guard-cells would tend to fall, leading to reduced stomatal opening and to a check to transpiration. Experiment has indicated, however, that frequently a very considerable reduction in stomatal aperture must occur before transpiration is itself reduced, the reason being that when the stomata are wide open their diffusive capacity may not be fully utilised. Transpiration at such times is under the control of other factors, such as atmospheric conditions or the water supply at the seat of the process (see below). When, however, transpiration is so excessive as to produce visible loss of leaf turgor, as shown by flagging or *wilting*, the stomata usually tend to close completely and leaf moisture is thus conserved. Independently of any stomatal regulation, transpiration does tend to keep step with the supply of water to some extent : for if the latter becomes inadequate the cell-walls in the leaf become somewhat drier, and evaporation is correspondingly reduced.

Ascent of Water through the Plant.

Since in our climate leaves usually present a turgid appearance, except perhaps on a hot summer's day, it is obvious that the water lost by transpiration from them is continuously replaced. The replacement is effected by an upward transport of water absorbed by the root from the soil. This current of water, flowing through the plant from the root hairs to the leaves, is known as the *Transpiration Stream.* Experiment proves that the stream of water ascends the plant through the vessels and tracheides of the xylem, a tissue which forms a continuous system through root, stem and leaf ; moreover, its elaborate system of pitting gives the impression of its being adapted for aiding the conduction of liquid. If plants or cut shoots are stood in dye solutions until signs of the dye are seen in the upper parts of the shoots, sections then taken from the stem will show that the xylem tissues alone are stained. The water of the transpiration stream thus indicated contains small quantities of mineral salts, and of organic substances, and the contents of the xylem elements are for this reason sometimes referred to as *sap.*

It has been mentioned that 600 lbs. of water may be evaporated from the leaves of a tree in the course of one day. Clearly, very considerable forces will be needed to raise water so quickly from the soil to the leaves against the force of gravity and to overcome internal resistances ; the same consideration applies in lesser degree to smaller plants. The nature of the forces operating to this end in the plant has been the subject of much discussion, and although in the *Cohesion Theory* a fairly satisfactory explanation is now forthcoming, there is admittedly much still to be elucidated.

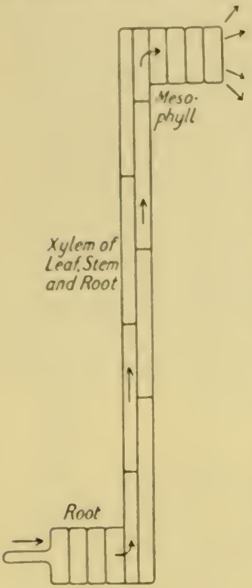

Fig. 72.

Diagram showing the path of the Transpiration Stream through the plant. (After Walter, from Strasburger, modified.)

In the region where transpiration occurs the cell-walls bordering on the air-spaces lose water by transpiration. It may be assumed that the walls imbibe a corresponding amount of water from the protoplasts which they enclose, creating in each protoplast an increased osmotic suction which leads it to absorb water from a neighbouring cell. This cell in turn absorbs water from a third cell, the process being repeated until we arrive at a cell which is in contact with a tracheide or vessel of one of the fine leaf-veins. This cell takes water from the xylem element (Fig. 72).

At this point reference must be made to the *Cohesion* of water. Because of its liquid nature, the water under experiment must be supported in a rigid envelope before this property can be demonstrated. Fig. 73 shows a suitable arrangement. Before being sealed, the curved glass tube (actually about one metre in length) is partly filled with water, which is then boiled so as to wet the sides of the tube thoroughly and to expel the air. The tube is then sealed-off. If it has been properly set up, the tube can be brought by careful tilting into the position shown, with the water hanging in the long arm. The film of water in contact with the glass clings to it, while the rest of the water retains its continuity as the result of its cohesive powers. The cohesion is due to the mutual attraction between the molecules of water, and the weight of the column of water is insufficient to pull the molecules apart. Other experiments have proved that very high tensions are necessary to break down the cohesion of such a column of water.

In consequence of its cohesion, a column of water could be pulled up the tube supporting it if suction were to be applied to the top of the column; just as a vertical steel rod can be lifted by its upper end. In the plant, the vessels of the xylem provide a series of rigid tubes, through which continuous columns or threads of water may stretch from the leaves down to the roots. While it is true that individual vessels are of limited length only, yet the walls separating one vessel from its neighbours are thoroughly permeated with water, and this provides for continuity of the water columns. When, as described above, the leaf-cell abstracts water from the xylem of the vein, the abstracted molecules draw up more behind them by cohesion. It is suggested that the wholesale abstraction of water from the leaf-veins during transpiration pulls the water of the transpiration stream up the trunk or stem. That at least is how the Cohesion Theory explains the ascent of the water. *Summarising, we may say that the ascent of the water is regarded as being mainly initiated by an osmotic suction arising in the leaf-cells as the result of transpiration, and this pulls the water up by virtue of the cohesive properties of water enclosed in rigid tubes.*

There is considerable evidence in favour of this theory. Calculation shows that the leaf-cells, with an osmotic pressure of 10 to 20 atmospheres, are in a position to exert an osmotic suction sufficient to account for the ascent of the transpiration stream to the top of the tallest tree, while the cohesive power of water is ample to withstand the resulting tension. The theory implies that the water in the vessels is in a state of tension, not of pressure as would be the case if the water were being forced up from below. A simple experiment confirms this. If a seedling is placed with its roots and lower part of the stem in eosin solution, and a cut be made across the stem below the level of the dye, it will be observed that the eosin ascends the plant very quickly, and in less than a minute may appear in the veins of the leaf. Evidently the opening of the conducting strands by cutting relieves a state of tension and leads to a rapid absorption of the dye.

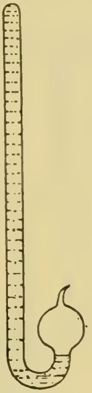

FIG. 73. Experiment to show cohesion of water. (After Dixon.)

The Cohesion Theory requires the existence of continuous columns of water stretching right through the plant. These must be free of air-bubbles, since the presence of bubbles would destroy cohesion in the columns of water, discontinuity thus developing by the expansion of the bubbles as soon as the columns are subject to tension. It has been remarked that, in point of fact, the water-columns within the vessels often include air-bubbles: but the upholders of the Cohesion Theory maintain that the contents are free from bubbles in a sufficient proportion of the vessels to provide the necessary degree of continuity: moreover, that the effect of the air-bubbles is only local.

Any tension in the xylem vessels will spread downwards into the roots, and will there promote the flow of water into the xylem from the adjacent living cells. This will activate the osmotic chain which stretches across the cortex, and continued absorption of water from the soil will ensue (see Fig. 72, also p. 99).

It appears, however, that there is another mechanism capable of inducing movement of water into the vessels of the root and up through the plant. This is suggested by the phenomena of *Exudation* and of *Root Pressure.* If a plant is severed a few inches above the soil on a warm day, and the cut surface immediately examined with a lens, it will appear dry. A drop of water placed upon it will at first be absorbed, but in a short time it will be found that water emerges from the cut surface, issuing from the region of the vessels. The stump is said to "bleed," and may do so very extensively. Thus a vine has been observed to exude an average of 500 c.c. of liquid per day over a period of several weeks. As might be expected the exudate is not pure water, but contains small quantities of mineral and of organic matter. Occasionally the latter is more abundant, as in the Sugar Maple, where the exudate from incisions made into the trunk in spring, before the leaves are fully formed, may contain 3 per cent. of sugars. The use of apparatus similar to that illustrated in Fig. 74 shows that a considerable pressure

FIG. 74.

Arrangement for demonstrating root pressure. The tube *g* is fitted on the cut stem *s*. Water is absorbed by the roots and forced into the tube, and the pressure can be measured in terms of the height of a mercury column (*Q*), which it is able to raise. (After Strasburger.)

(*Root Pressure*) may be developed in exudation from a root system, amounting in some cases to 1 atmosphere or more: it is possible that in the intact, uninjured plant Root Pressure may reach considerably higher magnitudes.

A phenomenon that is probably due to Root Pressure is to be seen in plants that are provided with water glands. Drops of water issue from the leaves of such plants when conditions are unfavourable to transpiration, though still favouring absorption, as during a warm night (Fig. 74 A). The water exuded in this way from the leaves of Grasses at night is often mistaken for dew. It frequently contains salts in solution, and these may form an obvious incrustation round the water gland, as for example in various Saxifrages. The deposit here is largely calcium carbonate. Exudation from leaves is very common in tropical rain-forests, where the humid atmosphere depresses transpiration.

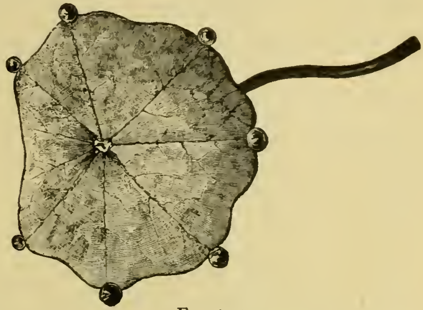

FIG. 74 A.
Exudation of water from the margin of the leaf of *Tropaeolum*, through water stomata which are permanently open. (After Strasburger.)

It appears then that a mechanism is present in the roots of plants which forces water up through the plant when transpiration is not operating, as is the case at night or in a decapitated plant. One suggestion is that special osmotic arrangements cause the innermost living cells to pump water into the xylem (see Figs. 68 and 72). The endodermis, with its radial walls made impermeable to water by the strip of corky material previously mentioned, may play an important part in preventing the water which is accumulated under pressure in the xylem vessels from leaking out of the stele along the cell-walls, and perhaps eventually finding its way back to the soil. *The Root Pressure mechanism may co-operate with that contemplated by the Cohesion Theory in raising the transpiration stream when transpiration is in progress.* On the other hand, in many experiments only feeble Root Pressure has been detected, while it is known that during active transpiration the contents of the xylem are in a state of tension rather than of pressure. Hence the opinion has for some time been prevalent that Root Pressure plays only a minor part in promoting the upward stream. Probably the significance of Root Pressure in the plant has not yet been properly evaluated. Lastly, there has all along been a school of botanists who have held that the living cells that lie along the course of the transpiration stream, both in the root and in the stem, play a more important part in raising water than the upholders of the Cohesion Theory would ascribe to them.

ABSORPTION OF SALTS FROM THE SOIL.

Water is not the only substance derived from the soil. The root-hairs also absorb a variety of inorganic salts that are present in solution in the soil-water (p. 97). Analysis of plants reveals that in addition to carbon (derived from atmospheric carbon dioxide) hydrogen and oxygen (derived from water), a great variety of elements may be detected within the tissues. Those most commonly present are nitrogen, potassium, sodium, calcium, magnesium, iron, phosphorus, sulphur, silicon, chlorine, manganese, aluminium, zinc and boron. All these elements are derived from the soil, and are absorbed by the plant in the form of salts.

Information concerning the absorption of dissolved substances by plant cells in general has been given on pp. 38-39. The extent of absorption of a particular salt or ion by a plant is affected by its concentration in the soil and by the permeability of the root-hairs towards it : also by the rate at which it passes from the root-hairs into the other parts of the plant, and by the operation of factors not properly understood and referred to on p. 39. The entrance of salts into the root-hairs is a process essentially independent of the entry of water. It could continue in the absence of the latter process, while conversely the mere presence of a particular salt in the soil-water does not necessarily mean that the salt will pass into the root-hairs along with any water that is being absorbed. It seems probable, however, that the movement of water will hasten the absorption of salts to which the root-hair is permeable, as well as the subsequent transport of the salts to the xylem of the root. There is fairly general agreement that the salts are carried up to the aerial organs of the plant in the transpiration stream, as already mentioned. The structure of the endodermis necessitates that all materials diffusing through this layer should pass through the protoplasts, wall-diffusion being prevented by the corky strips on the radial walls (p. 83). Thus only materials to which the protoplasts are permeable can penetrate into the inner part of the root and undergo transport to the other parts of the plant.

Of the elements listed above only seven are usually regarded as being essential to plant development, namely, nitrogen, phosphorus, sulphur, potassium, calcium, magnesium and iron. This view is based on experiments in which advantage is taken of the fact that most plants will grow with their roots in aqueous solutions instead of in soil. Any desired combination of salts can be supplied in solution to the roots, and the effect on growth studied. The usual arrangement is shown in Fig. 75. A solution containing the above seven elements in suitable form usually results in satisfactory growth. Knop's culture solution is often employed in these experiments, and is made up as follows: calcium nitrate, 1·0 gm.; potassium nitrate, potassium di-hydrogen phosphate and magnesium sulphate, 0·2 gm. each; ferric chloride, a trace; distilled water, 1 litre. By suitable adjustments of this formula, modified culture solutions can be prepared

FIG. 75.

Water Cultures of Barley. The plants in the left-hand jar had been grown in a solution containing all the essential elements. Certain elements were omitted from the other jars, as labelled. The glass tubes allow of aeration of the solutions. Photo. G. B. (× ⅛.)

from which particular elements have been omitted. Thus instead of magnesium sulphate, potassium sulphate could be added, giving a magnesium-free solution. The growth of a plant in such a solution could then be studied, and by this procedure it is found that omission of any of the seven elements mentioned prevents proper growth (see Fig. 75). In addition to these elements it now appears that certain others, for example boron and manganese, must be accessible, to some plants at least, in order to secure proper growth. These elements are only needed in minute quantity, and it is probable that they are present in sufficient amount as impurities in ordinary water cultures.

These various elements must be supplied in particular forms before they can be appreciably utilised by the plant. Thus sulphur and phosphorus must be in the form of sulphate and phosphate respectively, while nitrogen is most suitable in the form of nitrate, or of ammonium salts.

Though the reasons why the elements mentioned should be essential to plant development scarcely fall to be considered at this point, it may be mentioned that nitrogen, sulphur and phosphorus are required for protein synthesis, while magnesium is a constituent of the chlorophyll molecule. The absence of iron also interferes with chlorophyll formation and leads to a condition of *chlorosis*, in which the leaves have a sickly yellow colour. The reason of this may be that iron acts as a catalyst in the building up of the complex molecule of chlorophyll. Iron and its compounds may also serve as catalysts in the cell in other connections, while the same applies to potassium. Calcium is essential since it is a constituent of the pectic bodies which, as mentioned on p. 24, enter into the composition of the cell-wall, particularly of the middle lamella. The application within the plant of elements such as boron is at present uncertain. In addition to these uses of elements derived from the soil, it is certain that inorganic salts and ions figure in the actual make-up of protoplasm (Chapter III), and in regulating its activity.

THE SOIL AND PLANT DISTRIBUTION.

The essential materials required from the soil are much the same for all plants. It is, however, a matter of common observation in the field and in the garden that a soil which favours certain plant species is unfavourable to others. Some plants require more of a particular raw material than do others. This applies especially to water, and the water-content of the soil, which depends on the climate, on the make-up of the soil and on topographical conditions, is a very important factor in plant distribution. Requirements also vary with regard to mineral nutrients. Thus some plants, such as the Nettle (*Urtica dioica*), appear to have a high nitrogen requirement and flourish best in the vicinity of dwellings or in other positions where organic nitrogen and nitrates are relatively abundant. Among cultivated plants the potato has a high potassium, and swedes and turnips a high phosphorus requirement. The distribution of plants is markedly affected by the presence in the soil of lime or other compounds of calcium. Some plants, such as Sheep's Sorrel (*Rumex acetosella*), Heather

(*Calluna vulgaris*) and Bog Moss (*Sphagnum*), thrive best under a deficiency of lime, and regularly inhabit such soils. Other plants, such as Dog's Mercury (*Mercurialis perennis*), are lime-loving. It is not so much that the calcium requirements of plants varies, but rather that lime is the chief basic substance of the soil, and its presence affects the properties of the soil very considerably, especially the soil-reaction. Some plants prefer an acid soil, others a neutral or slightly alkaline one. Plants are also liable to be affected by the presence of non-essential salts such as sodium chloride. Most plants are unable to make satisfactory growth in a soil, such as that of a salt-marsh or other maritime area, in which sodium chloride is relatively abundant, because of the harmful effect of the salt. The group of plants known as Halophytes (Chapter XI.) are, however, able to thrive in such places, and their development is actually improved by the presence of the salt. Enough has been said to indicate the complexity of the relationship between the plant and the soil, the number of factors that come into play, and the degree to which soil factors affect the distribution of plants.

CHAPTER VIII.

SYNTHESIS, STORAGE AND BREAKDOWN.

LIVING cells and the plants which they compose are characterised by a remarkable chemical activity. They promote a great variety of chemical transformations which collectively constitute the *Metabolism* of the plant. We shall consider first the constructive phases of plant metabolism. One of the most important properties of the green plant is its ability, when supplied with a few simple raw materials, to elaborate or *synthesise* within its cells a great variety of organic substances which are utilised in the further growth of the plant, and in other activities. The raw materials, comprising carbon dioxide, water and mineral salts, are said to undergo *assimilation* into the substance of the plant. In a study of the synthetic activities of the plant the process of *Photosynthesis*, in which sugars are elaborated from carbon dioxide and water, occupies a very prominent position and will now be considered.

PHOTOSYNTHESIS.

As the term implies, photosynthesis is a constructive process in which the presence of light is a necessary condition. It is of twofold importance to the plant, for not only is it an essential step in the manufacture of carbohydrates for incorporation into new cell-walls and into new proteins, but it is also a process whereby light-energy derived from the sun is fixed and stored in the plant for future use. This fixation of solar energy occurs because the green plant is equipped with a mechanism for conducting the synthesis of sugars from carbon dioxide and water, an energy-consuming reaction, at the expense of the energy of sunlight. The amount of energy utilised, expressed in terms of heat units, is indicated in the following equation which sums up the process of photosynthesis.

$$6CO_2 + 6H_2O + 674{,}000 \text{ calories} = C_6H_{12}O_6 + 6O_2$$

That is, the synthesis of a gramme-molecule (180 gm.) of sugar requires the equivalent of 674,000 calories of heat-energy. It will be seen from this equation that photosynthesis consists of the formation of sugar from carbon dioxide and water, energy being utilised and oxygen liberated.

Fig. 76.

A. Chloroplasts in cells of the leaf of ***Funaria***, showing small starch-grains included in them. *B* shows stages of division of the chloroplasts. *f* shows the included starch-grains after the plastid has swollen in water. (After Sachs.)

The green pigment of plants, *Chlorophyll*, is a key substance in photosynthesis. The pigment is located in special protoplasmic bodies, the *Chloroplasts*, which are restricted to those organs of the plant that are exposed to light: they are especially abundant in the mesophyll of the leaf, which is the chief organ of photosynthesis. Experiment proves that only those parts of the plant that contain chlorophyll can carry on photosynthesis. To confirm this, variegated leaves may be used, and it can be shown that only the green parts of the leaf can conduct photosynthesis. In order to detect the occurrence of photosynthesis one method is to test for the presence of the end-products. Sugars themselves are not so easily detected as the higher carbohydrate *Starch*, which in many plants is very quickly formed from the initially-produced sugars. A plant with variegated leaves is exposed to sunlight for several hours, at the end of which time a leaf is to be detached, and the outlines of the yellow and green parts noted. The leaf is dipped in boiling water and then immersed in methylated spirit, which is heated over a water-bath until all the green pigment has been extracted. The leaf is then softened by immersion in hot water and placed in iodine solution. It will be found that the areas of the leaf which were originally green now take on a blue-black colour, due to the presence of starch within the tissues, while the non-green parts show no such coloration. A microscopic examination of the leaf would show that the starch is actually deposited within the chloroplasts (Fig. 76), while other experiments indicate that the oxygen of photosynthesis is liberated from the chloroplasts (see later). We may therefore conclude that *photosynthesis is restricted to green parts of the plant and that it proceeds on or in the chloroplasts.*

The chemical and physical properties of chlorophyll have been closely scrutinised. Chlorophyll is a complex substance built up from the elements carbon, hydrogen, oxygen, nitrogen and magnesium: and it is interesting to notice that it is related chemically to Haemoglobin, the red blood-pigment of mammals. The necessity of *iron* for chlorophyll formation, as already mentioned, may be due to that substance acting as a catalyst in the building-up of the complex molecule of the pigment. Chlorophyll can be extracted from the leaf by alcohol or other organic solvents, and if such an extract is examined through a spectroscope it will be found that of the various colours which make up sunlight, certain red rays are strongly absorbed by the pigment, and the blue-violet rays slightly less strongly, while the intervening green and yellow rays mostly pass through unabsorbed (see Fig. 77). The green leaf itself has similar absorptive properties. Various experiments, some of which are mentioned below, indicate that if plants are exposed to light of different colours, photosynthesis is most rapid in the red and (at least according to some investigators) also in the blue-violet rays: *i.e.* the same rays that are absorbed by chlorophyll. From this it may be concluded that *chlorophyll absorbs the particular light-rays the energy of which is used in photosynthesis.*

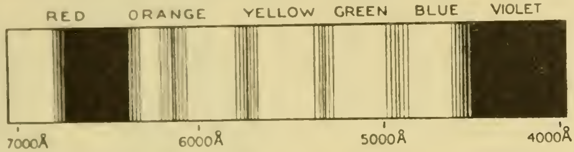

FIG. 77.

Absorption Spectrum of an ether-solution of Chlorophyll (actually the *a* form). The black and shaded regions are respectively those in which the light rays are completely or partially absorbed. The wave-lengths in Ångström units are shown below. (Re-drawn from Willstätter and Stoll, 1918.)

It should be mentioned that two slightly different forms of chlorophyll (*a* and *b*) are always present in the chloroplasts, the significance of this being unknown. Accompanying the green pigments are two yellow pigments, *Carotin* and *Xanthophyll*, whose function in the chloroplasts is also uncertain. It may be noted that the carotin of plants is of great importance to animal nutrition, since it is from that substance that Vitamin A is produced in the animal body. These yellow pigments also occur separately from chlorophyll in yellow and red flowers and fruits and other organs, for example the carrot.

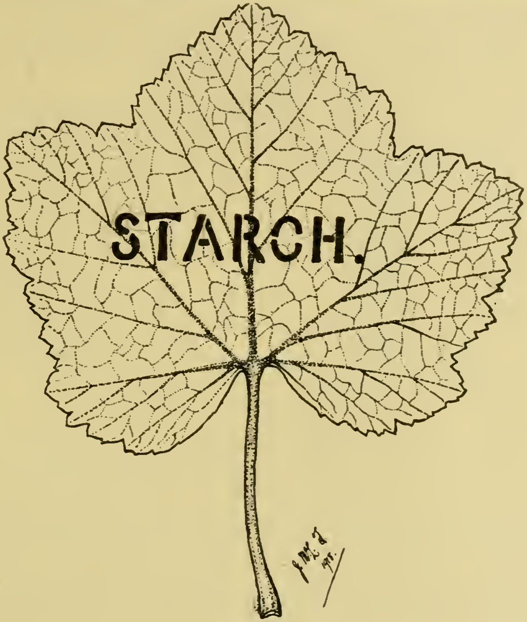

Fig. 78.
Results of experiment to show that Photosynthesis only proceeds in parts of the plant that are exposed to light. See Text.

Since light-energy is utilised in photosynthesis, it is not to be expected that the process should continue in plants or parts of plants that are deprived of light. If a potted plant is placed in darkness, application of the iodine test will show that the amount of starch present in the leaves gradually decreases until a negative result is finally obtained. This usually requires from twenty-four to forty-eight hours. The explanation is that the starch originally present has been used up for respiration (see p. 133), or transported in soluble form to other parts of the plant: and owing to the absence of light no new starch has been photosynthesised. If the plant is returned to light, starch formation is resumed. If, in a particular leaf, light is allowed to fall only on certain parts of the leaf, starch formation will be quite restricted to those parts. To effect a demonstration of this a stencil may be prepared from a piece of opaque material, such as tinfoil, and fixed to the upper surface of a starch-free leaf. After several hours exposure of the leaf to light, application of the iodine test will show that only the areas that were exposed to light will take on the blue-black colour, indicating that photosynthesis has been limited to these parts (Fig. 78). Clearly the effect of light is local: the light rays can be used in photosynthesis only by those parts that are actually illuminated.

The land plant depends on the atmosphere for the carbon dioxide used in photosynthesis. This is indicated by an experiment in which a stream of air, previously freed of carbon dioxide, is passed through a bell-jar which is sealed to a glass plate and contains a number of leaves with their stalks in water. The leaves should be initially starch-free (see p. 117). Although the bell-jar is placed in a good light, a subsequent test will show that under these conditions no photosynthesis occurs. Alternatively, normal air may be passed over illuminated leaves and the issuing air shown to contain less carbon dioxide than it did originally.

Carbon dioxide is present in the atmosphere to the extent of 3 volumes per 10,000 volumes of air. This is an average figure and may be departed from at certain times and places. Thus in the neighbourhood of extensive vegetation the carbon dioxide-content of the atmosphere may during the middle of the day be appreciably below the figure mentioned, owing to photosynthesis. Again, there is a constant evolution of carbon dioxide from the soil, due to the respiration of soil organisms, and the proportion of the gas present in the atmosphere near the soil is liable to be considerably above the average figure. The average figure is kept constant because the various processes affecting it, photosynthesis and plant respiration being the chief, are in equilibrium. The amount of carbon dioxide available to the plant appears at first sight to be very small, though it must be remembered that if molecules of the gas are absorbed at any point their places are taken by others diffusing from neighbouring regions of the atmosphere. It is, however, known that the photosynthetic process is often hindered by the low proportion of carbon dioxide that is present in the atmosphere (see p. 119).

In order to reach the actual site of photosynthesis, the molecules of carbon dioxide must first diffuse through the stomatal pores (Fig. 79), these being usually open in daytime, to which period photosynthesis is naturally restricted by considerations of lighting. Gases or vapours can be absorbed or evolved by the leaf tissues through the stomata with surprising rapidity (see p. 104), and it is quite certain that the fact that the carbon dioxide has to diffuse through the stomata in no way restricts photosynthesis, provided the stomata are appreciably open. The gas then diffuses through the continuous system of air-channels that permeates the leaf. According to the general view, the carbon dioxide next becomes dissolved in water present in the cell-walls bounding the air-spaces, and subsequently diffuses in solution into the cytoplasm of the cells, where the chloroplasts are situated (Fig. 79). So long as the gas continues to be used up in photosynthesis by the chloroplasts, there will be a constant inward flow of further carbon dioxide from the external atmosphere, because of the tendency of a gas to diffuse from a region of higher concentration to one of lower. In the case of submerged water-plants the carbon dioxide present in the water round about the plant is that utilised in photosynthesis. The carbon dioxide enters these plants in solution rather than in the gaseous form: it should be remembered, however, that in land-plants also entrance into the actual cells can only be effected in solution.

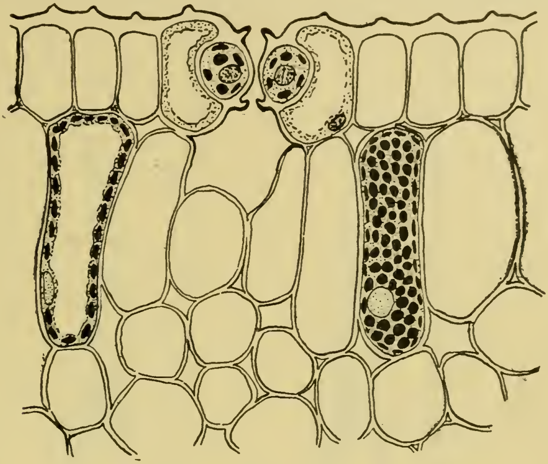

FIG. 79.

Part of leaf of *Narcissus* in transverse section. Two of the cells of the mesophyll are drawn in in detail: that to the right as seen in surface view from without; that to the left in optical section. The chloroplasts are shown black. (× 300.) F. O. B.

There is no doubt that the rate of photosynthesis is under natural conditions frequently restricted by the low carbon dioxide-content of the atmosphere, which can be termed the *limiting factor* at such times. Experiment shows that the rate of photosynthesis can be accelerated by increasing the supply of carbon dioxide. The growth of the plant is consequently benefited, and experiments in greenhouses have proved that by enrichment of the air with additional carbon dioxide the yield of tomato and other crops can be very materially increased, though so far there has been no extensive application of this knowledge to practical operations. Ultimately a point is reached at which the gas begins to exert a harmful effect on the plants, though previous to this it may be observed that continued addition of carbon dioxide produces little further benefit; probably some other factor such as light intensity is inadequate to support higher rates of photosynthesis, and *it* now becomes the limiting factor.

It is by virtue of the *evolution of oxygen* during photosynthesis that plants can be said to "improve the air" in the presence of light, a property which was noticed many years ago. The oxygen that is produced in photosynthesis diffuses from the chloroplasts through the cytoplasm and cell-walls and thence in the gaseous form through the air-spaces of the leaf, and finally emerges into the atmosphere, apart from that utilised in respiration (see p. 133). The production of the gas is most easily demonstrated in water-plants. If a cut shoot of Canadian Pond Weed (*Elodea*) lying in water is exposed to bright sunlight, a continuous stream of bubbles may be seen to escape from the cut end of the shoot, especially if the water has previously been enriched with extra carbon dioxide. The temperature also must be favourable. The gas can be collected by the arrangement shown in Fig. 80, and tests will show that the gas contains a high proportion of

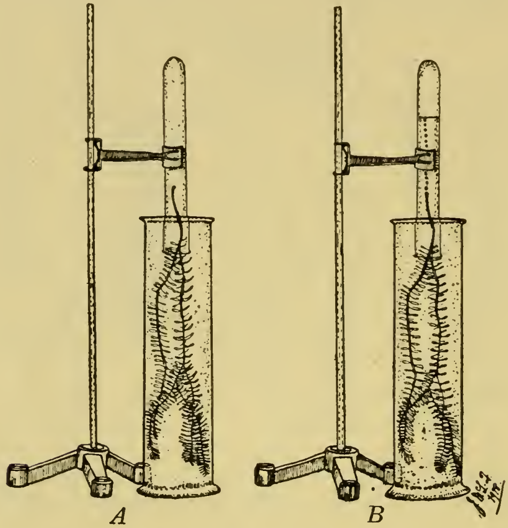

FIG. 80.

Arrangement for showing that oxygen is given off in Photosynthesis. *A*, before exposure to light, the tube is filled with water. *B*, after exposure for some time. A large volume of discharged gas has collected in the tube. (After Noll.)

oxygen, produced by photosynthesis. Some of the oxygen so produced diffuses away from the plant in solution, but owing to the low solubility of the gas in water it accumulates under pressure in the gaseous form inside the intercellular spaces and escapes from any cut surface. The rate of production of bubbles gives a rough index of the rate of photosynthesis, and experiment would show that the bubbling slows down if the light-intensity be considerably reduced, and would stop if water free of carbon dioxide were to be supplied to the plant. Or again the method could be employed to compare the rates of photosynthesis in light of different colours, and to demonstrate the fact that up to a point increase in temperature hastens photosynthesis, if other factors are favourable. Another method, chiefly perhaps of historical interest, for demonstrating the liberation of oxygen involves the use of certain bacteria which show movements only if supplied with oxygen. If a filament of *Spirogyra* (a simple water-plant, see pp. 372-3) is mounted in water containing the bacteria, and air excluded, the movement of the bacteria continues in the vicinity of the plant, provided it be exposed to light. The production of oxygen is thus indicated. A special tendency has been detected for the bacteria to accumulate near the chloroplasts. Other experiments involving the use of methods of gas analysis show that *the volume of oxygen produced in a given time by photosynthesis is equal to that of the carbon dioxide absorbed.*

It is impossible to attempt here any detailed consideration of the chemical changes that may be involved in the building-up of sugars from carbon dioxide and water. There is no doubt that the synthesis involves a number of intermediate reactions, and though actually we have little information about these, it has often been supposed that first the substance formaldehyde is produced according to the equation:

$$CO_2 + H_2O = H \cdot CHO + O_2$$

and that six molecules of the aldehyde then become united together to give sugar:

$$6H \cdot CHO = C_6H_{12}O_6.$$

This latter reaction is easily effected in the test tube by subjecting formaldehyde to the action of alkalies. Each of these steps may itself involve a series of intermediate reactions. The evidence in favour of the formaldehyde theory is rather slender, and indirect rather than direct in nature; but it should be realised that the investigation of the chemistry of photosynthesis is beset with great difficulties. There are two obvious lines of attack, namely, to test for the presence of formaldehyde in green cells during photosynthesis, and to try to obtain sugar synthesis in the plant starting from artificially supplied formaldehyde rather than from carbon dioxide: neither has yielded conclusive results. Other investigators have attempted to obtain a photochemical synthesis of carbohydrates from carbon dioxide and water in artificial systems where the chemistry of the process could be more easily studied. Extracted chlorophyll has been introduced into some of these systems. While some investigators claim to have obtained a synthesis of sugars under such conditions, all such claims have been subject to strong criticism, and so far this line of investigation has not assisted very much in the elucidation of photosynthesis in the plant.

It is generally believed that the rôle of chlorophyll is not limited to the absorption of light-energy, and to the application of that energy to the photosynthetic system; but that the pigment also participates, possibly in the capacity of a catalyst, in the chemical changes of photosynthesis. One well-known theory assigns a function of this type to the pigment in connection with the formation of the formaldehyde, which is believed to be an intermediate product in photosynthesis.

Application of analytical methods to leaves shows that sugars are the first products of photosynthesis, as already stated. It is probable that the simpler sugars, Glucose and Fructose, are those actually formed first (see next section). In many plants the initially-formed sugars are to a considerable extent converted quickly into Starch, which acts as a temporary reserve substance. But in a number of plants, as for example many Monocotyledons, no starch is formed and the sugar accumulates as such.

Estimates of the rates of carbohydrate-synthesis under natural conditions have yielded very variable results: but in order to give a rough idea of the extent of photosynthesis, it may be mentioned that Sachs concluded from his measurements that as much as 25 grammes of carbohydrate may be formed within a square metre of Sunflower leaf during a summer's day. The carbohydrate of the leaf would be mostly in the form of starch, and if this quantity of starch is weighed out on scales it will be seen to be of very considerable bulk; in forming that amount of starch the leaf would deprive 50 cubic metres of normal atmospheric air of its carbon dioxide.

In this consideration of photosynthesis we have looked at the process from the standpoint of the plant itself: the process is also of profound significance to the animal kingdom, a matter which is considered at the end of this chapter.

Chemosynthesis—Certain bacteria are able to synthesise organic carbon-compounds from carbon dioxide and water without the assistance either of light or of chlorophyll by a process known as chemosynthesis. An example is provided by the nitrifying bacteria (p. 452). The necessary energy for the synthesis is obtained chemically by the oxidation of environmental materials. Certain other bacteria contain a green pigment related to chlorophyll and carry on a photosynthetic process resembling to some extent that of higher plants.

CARBOHYDRATES.

In the preceding section we have chiefly considered the synthesis of one type of carbohydrate—the sugars. From these there arises within the plant a whole range of more complex carbohydrates, by processes independent of light or chlorophyll : these may occur in any part of the plant. Carbohydrates figure very prominently in plant metabolism, and this is a convenient point at which to review them. They will be considered in order of increasing complexity. It will be noticed that carbohydrates are all compounds of carbon, hydrogen and oxygen, in which there are twice as many hydrogen atoms as there are of oxygen. In treating of them frequent reference will be made to Enzymes : a later section of the present Chapter will be devoted to a special consideration of these highly important protoplasmic catalysts (p. 128). The carbohydrates may be grouped as follows :

(1) *Monosaccharides.*—Most of these have the molecular formula $C_6H_{12}O_6$; and the most important examples in the plant are Glucose (Grape Sugar) and Fructose. It has been mentioned that the initial product of photosynthesis consists probably of one or both of these sugars, and they are very common in plant-cells, both of the leaf and of other parts. The plant-cell is able to convert one into the other, though no enzyme promoting the conversion is known.

(2) *Disaccharides.*—These have the molecular formula $C_{12}H_{22}O_{11}$ and like the first class are sugars. The molecule of a disaccharide is built up by the combination of two monosaccharide molecules with the elimination of a molecule of water. The most important example, Sucrose (Cane Sugar), prepared commercially from plant sources (Sugar Cane or Sugar Beet), is built up by combination of glucose and fructose in the manner mentioned, a combination which is probably accelerated in the plant by the enzyme Invertase. It can easily be demonstrated that this enzyme at other times accelerates the decomposition of sucrose into glucose and fructose. Sucrose and these two monosaccharides are together the commonest sugars of the plant. Another disaccharide, Maltose (Malt Sugar), has also been detected in plants in small quantity. It is produced by the action of the enzyme Diastase on starch, but in the plant the maltose is quickly converted by the enzyme Maltase into glucose, from which maltose is built up.

(3) *Polysaccharides.*

These are complex substances built up by the combination of many molecules of monosaccharide sugars, again with elimination of water ; the empirical formula for most of them is $(C_6H_{10}O_5)_n$. The molecular weights of the polysaccharides are not definitely known. Unlike the sugars, the polysaccharides are tasteless, colloidal substances.

Starch is a common polysaccharide in plants, and is built up from many associated glucose molecules. It forms a reserve substance, either of a temporary nature, as in the chloroplasts of the leaf—where its presence in connection with photosynthesis has been noted: or of a more permanent nature, as in storage organs of many kinds. It is almost always deposited in the form of grains within plastids, either the chloroplasts of green organs, or the corresponding but colourless *leucoplasts* of non-green organs (Figs. 81, 85, *A-E*). The presence within plant tissues of an enzyme, Diastase, which promotes the decomposition of starch into maltose, can easily be demonstrated, and it is generally assumed that the same enzyme at other times builds up starch from maltose. This enzyme appears to be located in the plastids. Starch grains show a characteristic stratification, which is related to their growth by apposition (Fig. 82), while the blue-black coloration with iodine is also distinctive. They may be simple or compound, and are larger in storage organs than in the leaf.

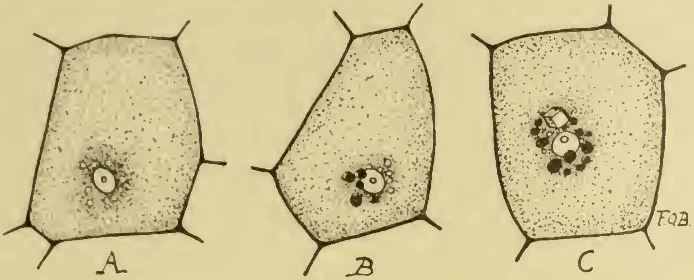

FIG. 81.

Cells of young Potato. *A*, with minute leucoplasts surrounding the nucleus. *B* shows some of these already forming starch, stained darkly with iodine. *C* shows further starch-formation, and one cubical protein crystal. (× 220.)

Inulin is another reserve polysaccharide, built up from fructose, and differing further from starch in its restricted occurrence in plants, and by its existence in a state of colloidal solution in the cell-sap. It is present in large quantity in the storage organs of members of the Compositæ, *e.g. Dahlia* roots and Artichoke tubers.

Cellulose is the substance from which the walls of plant-cells, especially of young cells, are largely built up, and is thus of structural rather than of nutritional importance. The cellulose is deposited by the protoplast. Its molecule is larger than that of starch, but it again is built up from a large number of glucose molecules, presumably under the influence of enzymes. An enzyme system capable of converting cellulose to glucose has been detected in a few of the lower plants. Cellulose is a colloidal substance with a strong attraction for water; hence the cell-wall usually contains a high proportion of imbibed water. Later the original cellulose may become impregnated with other substances such as Lignin (in xylem, and particularly in fibrous elements), giving increased mechanical strength: or Cutin and Suberin, in epidermal and cork cells, to which they give impermeability to water (see p. 24).

A somewhat different substance known as *Reserve Cellulose* occurs in certain seeds (Lupin, Date) : and the cell-walls are in consequence much thickened (Fig. 83). As its name implies, this substance is of nutritional rather than structural significance. During germination it is converted into sugars under the influence of an enzyme Cytase.

Fats, although not carbohydrates, may be considered here. Fatty substances may figure in the make-up of protoplasm, as already mentioned, and so be present in any living cell. It is in seeds and fruits that fats are best known and most abundant, forming in many cases the chief non-nitrogenous reserve substance. This for example is the case in the seeds of the Castor-oil plant (*Ricinus*) and in various nuts,—Brazil, Walnut and Hazel (see Appendix B). The fats exist in the form of globules in the cytoplasm : they contain the elements carbon, hydrogen and oxygen, and are organic salts produced by reaction between fatty acids and glycerine, a basic substance. There is no doubt that fats arise from sugars within the plant cell, though the steps in the transformation are obscure. It is believed that fatty acids and glycerine are separately formed from sugars, and the two then react together. During the germination of fatty seeds a reverse change occurs, the fats being reconverted into sugars. The well-known enzyme *Lipase* effects the formation of fats from fatty acids and glycerine, and under other conditions it promotes the reverse reaction.

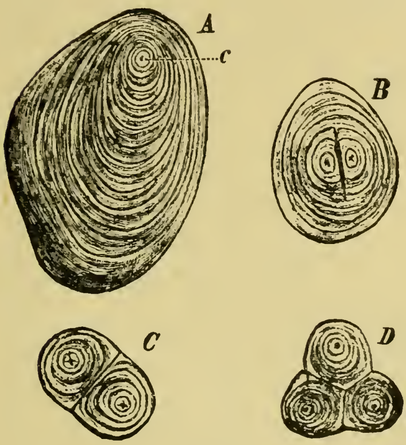

FIG. 82.
Starch grains from the Potato. *A*. simple ; *B*, half compound ; *C*, *D*, compound grains. *c*, organic centre, or nucleus of formation. (× 540.) (After Strasburger.)

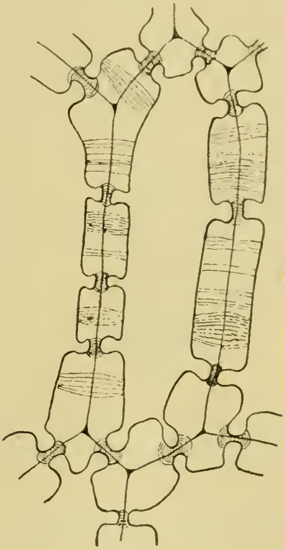

FIG. 83.
Cell-wall of a single cell of the endosperm of *Lodoicea*, consisting of reserve cellulose which forms the thickened regions of the wall. (× 400.) (After Gardiner.)

PROTEINS AND PROTEIN SYNTHESIS.

Proteins and carbohydrates are the most important constituents of the plant body, though there is in addition a great range of substances of other types. As we saw in Chapter III., the especial importance of proteins lies in the fact that the living substance, protoplasm, is largely made up from them. Chemical analysis shows that proteins and their derivatives may account for as much as 60 per cent. of the dry weight of protoplasm.

The protein molecule contains the elements carbon, hydrogen, oxygen, nitrogen and sulphur (the latter in very small proportion). It is an exceedingly complex structure with a molecular weight running into many thousands. A great many different proteins have been detected in plants, and each plant contains a variety of them. They are all built up in the main from *Amino-acids.* These are organic acids containing the amino group, $-NH_2$. Glycine, Aspartic Acid, Tryptophane and Cystine may be named as examples. Some of these amino-acids are themselves quite complex, but it is probable that several hundreds of amino-acid molecules are required for the formation of a single protein molecule. Certain proteins, distinguished as *Nucleo*-proteins, contain phosphorus in addition to the above elements. The nuclear structures of the cell are believed to consist largely of these. As mentioned in Chapter III., proteins give colloidal solutions, and it is doubtless in this state that proteins are present in the protoplasm.

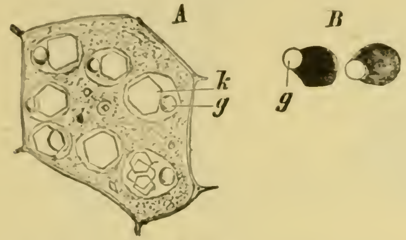

FIG. 84.

A, cell from the endosperm of *Ricinus* in water, which causes the outer coat of the aleurone grains to swell. *B*, isolated aleurone grains in oil. *k* = albumen crystals. *g* = globoid. (× 540.) (After Strasburger.)

In addition to the protoplasmic proteins there are also *reserve* proteins, regularly present in seeds and other storage organs either in a crystalline form (Fig. 81), or in the form of grains, known as *Aleurone* grains. These may be quite complex in structure, as for example in the Castor Oil seed (Fig. 84). Here the aleurone grain contains within an outer coat of protein a protein crystal, and a so-called globoid consisting of protein associated with inorganic groups. Enzymes that are capable of resolving proteins into their constituent amino-acids are present in plant tissues: this process occurs extensively during germination. Information regarding these protein-splitting enzymes is as yet rather incomplete: for the present purpose it will suffice to refer to them collectively as the *Proteases*.

For the *synthesis of proteins* in the plant a supply of *nitrogen* is required. We must therefore consider the sources from which nitrogen is secured for this purpose. The typical plant is dependent for its nitrogen supplies on combined forms of the element, absorbed from the soil, and is incapable of utilising the free nitrogen of the atmosphere. Water culture experiments of the type described on p. 111 lead to the conclusion that plants are incapable of making appreciable growth if no compound of nitrogen is supplied to them. Further, experiments show that for the majority of plants nitrates, ammonium salts, and to a lesser extent nitrites, are the most suitable sources of nitrogen ; and there is no doubt that it is in these forms, especially the first two, that the plant obtains its nitrogen from the soil. Soluble organic forms of nitrogen also occur in soils, and may be used to some extent. The supply in the soil of soluble nitrogen-compounds is maintained as the result of a constant circulation of nitrogen between the plant world, the soil, and the atmosphere. There is also a somewhat similar circulation of carbon. After the death of a plant (or animal) the materials of which it is composed become eventually added to the soil, and under the influence of bacteria and fungi they pass through processes of decay. The nitrogen present in the proteins is restored to the form of nitrate as the result of a series of transformations described in detail on p. 452, though some absorption by plants may occur before the nitrate stage is reached. An important part is played by those soil bacteria (*Azotobacter*, *Clostridium* and *Bacillus radicicola*) that possess the special faculty, denied to the great majority of organisms, of utilising or "fixing" atmospheric nitrogen. The second of these is discussed on the page quoted, while the third, which lives symbiotically with certain higher plants, is considered in Chapter XII. The activities of these organisms result in an enrichment of the soil as regards nitrogen, though this is counterbalanced by other factors which lead to a loss of combined nitrogen.

The nitrates or other nitrogen-compounds are absorbed by the root hairs, and are probably transported through the plant by the transpiration stream along with other salts, of which sulphates and phosphates are also needed for protein synthesis. While the synthesis of sugars is dependent on light and on the presence of chlorophyll, and therefore confined to aerial and green tissues, protein synthesis is essentially independent of light, and can probably take place in any living cell in the presence of suitable raw materials. It is likely, however, that the leaf cells are the most important sites of protein synthesis, since it is here that sugars are most abundant. We have little definite information with regard to the intermediate stages in the synthesis of proteins within the plant, though it can be assumed that the process consists essentially in the interaction of nitrogenous compounds with the sugars of photosynthesis or their derivatives. A common view has been that by interaction of ammonia, derived from the inorganic nitrogen absorbed from the soil, with organic acids arising from sugars, a whole range of amino-acids is produced in the plant. These acids may then become linked up to form protein under the influence of the enzymes mentioned above,—the proteases,—which at other times catalyse the splitting of proteins. This view is, however, rendered rather uncertain by experimental evidence which indicates that substances known as *Amides* (especially Asparagine) may figure prominently in protein synthesis. Energy is required for the synthesis of proteins. In this case the energy is not derived directly from the sun's rays, but only indirectly through the process of respiration as discussed below (p. 133).

ENZYMES.

A number of *enzymes* have already been mentioned. These agents play a most important part in plant metabolism, since they enable the protoplasm to carry out at high speed chemical transformations which otherwise would not occur at all, or only very slowly. Enzymes are in many respects comparable to the *Catalysts* of chemistry, and they are in effect *protoplasmic catalysts*. As an example of ordinary catalysis we have the very rapid combination of hydrogen and oxygen to form water in the presence of finely divided platinum, the latter acting as a catalyst. The combination of the gases is extremely slow in its absence. An important feature of catalysis, including enzymic catalysis, is that the catalyst remains unchanged at the end of the reaction and can be used over and over again.

The chemical nature of enzymes is uncertain, though it is agreed that they are complex substances, probably present in a colloidal form in the cell. It is to this colloidal nature, and the resulting high adsorptive capacity, that the catalytic properties of enzymes are in part attributed (Chapter III.). It was formerly believed that they were proteins, though examination of the relatively pure preparations of enzymes that have been obtained in later years has not in every case confirmed this belief. It is, however, very difficult to prepare enzymes free from contamination with other cell-contents. Enzymes may be extracted from plant tissues with water or other solvents after the cells have been disrupted by pounding, or the cell-membranes rendered more permeable by pre-treatment with alcohol, or by freezing. For example, a crude extract containing the enzyme diastase can be prepared from germinating cereal grains by mashing the grains in water and standing the mixture aside for a time. Experiment shows that the extract is able to effect the conversion of starch into sugar, so that evidently *an enzyme may retain its activity after separation from the plant.* Extracts so prepared contain a mixture of enzymes in additions to other cell-contents, and special methods have to be adopted in order to isolate a particular enzyme.

The following is a list of the better known enzymes of the plant, together with the reactions which they characteristically catalyse outside the plant :—

Invertase	catalyses	Sucrose → Glucose + Fructose.
Diastase	,,	Starch → Maltose.
Maltase	,,	Maltose → Glucose.
Lipase	,,	Fats → Fatty acids + Glycerine.
Proteases	,,	Proteins → Amino-acids.
Zymase	,,	Sugars → carbon dioxide + Alcohol.

Every plant cell almost certainly contains all these enzymes and others not mentioned here.

Many of the reactions proceeding within the plant are *reversible*, that is they may proceed in either direction. For example during the daytime starch is formed in the chloroplasts of the leaf from sugars, while at night the starch is converted back into sugars. Under the conditions usually obtaining in experiments with enzymes outside the plant, it is the breaking-down actions (presented in the above table) that are most manifest: but in certain cases it has been shown that the opposite, that is a building-up or synthetic property, is also possessed by enzymes. It is assumed that this finding applies to all enzymes concerned with reversible reactions. Circumstances prevailing within the cell will decide the predominating activity of such an enzyme at any moment, the relative concentration of substances concerned in the reaction being especially important. Thus in a reaction $A \rightleftarrows B$, if substance A is considerably in excess of B, the reaction will proceed chiefly from left to right. As the concentration of *B* increases the right to left action commences and finally a state of equilibrium is reached. If, however, *B* is removed as fast as it is formed, or if it is converted into an insoluble and chemically inactive substance, the left to right action will continue to predominate.

The period of germination of seeds or of renewal of growth of other resting organs is one characterised by intense enzyme activity. The reserve substances (starch, protein, fats, reserve-cellulose, etc.) of the resting organ are mostly insoluble and indiffusible. Before being transferred from the region of storage to the growing points, they are converted into soluble diffusible forms. This *mobilisation* of reserves is promoted by appropriate enzymes, each acting in a downgrade fashion as indicated in the above list. Fig. 85, 1-4, illustrates the process of solution of starch grains under the influence of diastase during germination of barley.

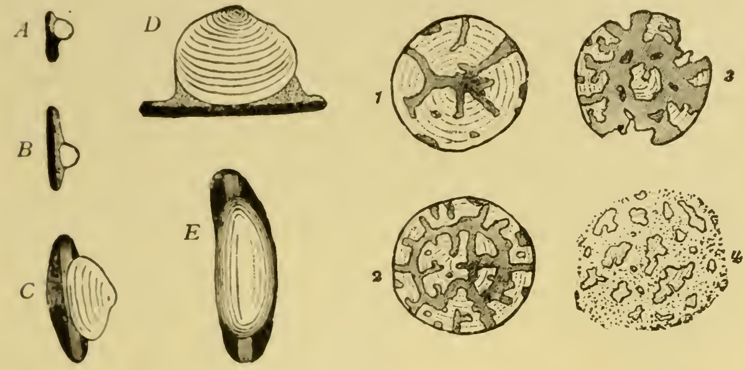

Fig. 85.

A-E, Leucoplasts from tuber of *Phajus*, showing various stages of development of starch grains. 1-4, Various stages of the corrosion of starch-grains in germinating Barley. (After Strasburger.)

Translocation and Storage.

The division of labour between the different organs of the higher plant requires that there shall be a constant movement of metabolic materials from point to point within the plant, to which the term *Translocation* is applied. The chief directions of translocation are: (*a*) from the leaves to actively growing parts, (*b*) from the leaves to storage organs, and (*c*) from regions of storage to actively growing parts. In addition we have the upward movement of salts from the roots to the aerial parts of the plant, to which the term translocation is sometimes extended. This has already been discussed in Chapter VII.

The leaf is the organ in which the synthesis of carbohydrates and probably of proteins is chiefly located, and provision must be made for the conveyance of these manufactured materials from the leaves to the apices of root and shoot, or to regions where there is cambial activity. Further, the rate of synthesis of materials in the leaf is usually in excess of that demanded by current growth. The balance of material is deposited in various parts of the plant in the form of carbohydrate (starch, sugar, inulin, reserve cellulose), fat, or protein and may serve for future use. Any parenchymatous tissue may serve for storage. For instance, in trees which lose their leaves in autumn and form a new suit of them in the spring, the material for these is prepared in the previous season, and stored in the medullary rays, wood parenchyma, and cortex of the trunk and branches. But in many cases, especially in herbaceous plants, storage is effected in parts which may become greatly distended, as in the turnip, carrot, and potato (see also Chapter XI.). Seeds habitually contain stored material, the product of the activity of the parent plant. They meet the needs of the seedling in the early stages of growth. *Storage*, in one form or another, is then a common phenomenon in plants. It involves the translocation of the materials from the point of production, usually the leaves, to the point of storage.

The translocation of manufactured materials out of the leaf to regions of growth and storage proceeds constantly, but is most easily detected when the leaf is in darkness. Synthetic processes are then stopped or slowed down. Suitable tests show that both the carbohydrates and protein of the leaf decrease in amount overnight, chiefly as the result of translocation. Thus, application of the iodine test will show that the starch content of the leaves of a given plant is much less in the morning than in the previous evening, while if the plant is kept in darkness for a further period all the starch will disappear.

At a later date the reserve substances stored in the various tissues mentioned above will be required for growth and undergo translocation, as already noted. *At all times materials to be translocated must be brought into a soluble form*, i.e. *they must be mobilised.* Materials undergoing translocation are mostly crystalloidal in nature, though there may also be some movement of colloidal materials. There is evidence that sucrose is the usual form in which carbohydrates are translocated, while nitrogenous compounds may move as amino-acids, or as amides.

It is now held by most authorities that longitudinal translocation of metabolic materials in the plant is chiefly through the sieve-tubes of the phloem, except for the upward passage of inorganic salts, which in all probability occurs with the transpiration stream in the xylem (see Chapter VII.). The structure of the sieve-tubes (see p. 48) appears to facilitate a lengthwise flow of materials through them, inasmuch as they are elongated and the cross-walls are perforated to form the sieve-plates, permitting of free movement of material from one tube to the next. Further, the contents of sieve-tubes are rich in carbohydrates and nitrogenous substances. More direct evidence is furnished by ringing experiments. It can be shown that the removal over a short zone of a leafy stem of the tissues external to the cambium interferes with the downward translocation of materials from the leaves; as indicated by reduced growth of the parts of the plant below the ring, and by accumulation of carbohydrates and nitrogenous compounds above the ring. A tree is usually killed if its trunk is ringed, because the ring interrupts the flow of food substances from the leaves to the roots, which are in consequence gradually starved. The result of ringing cuttings is illustrated in Fig. 86. The production of the roots *above* the ring is at least partly due to the arrest of the flow of nutritive materials which diffuse from the upper part of the cutting to the region of root-initiation. Corresponding results have been obtained in connection with the upward movement of organic materials through the stem, such as occurs in a deciduous tree in spring, when reserves stored in the trunk are transported up to the opening buds. These ringing experiments indicate that the conveyance of organic materials is effected not in the xylem but in some more external tissue: and the considerations already mentioned point to the conclusion that the phloem is the tissue in question. This view has received

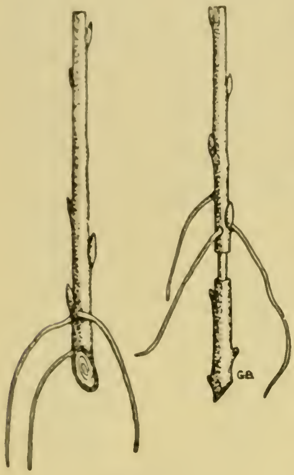

FIG. 86.

Lower parts of Willow cuttings which had been induced to form adventitious roots by standing in water. The right-hand cutting was initially "ringed" shortly above the base. Note the effect on the position of root-production. (× ⅔.)

confirmation in more critical experiments, which have revealed a close correspondence between the daily fluctuations in the concentration of carbohydrates and nitrogenous substances in the leaf-cells, and those in the sieve-tubes of the stem below the leafy zone.

The movement of soluble materials through the sieve-tubes is not a matter of simple diffusion, although it has certain resemblances to a process of that type: such as the fact that often, though not always, translocation occurs from regions of higher concentration of a particular substance to those of lower. But the rate of translocation is greatly in excess of that which could be accounted for by diffusion alone. One suggestion is that passage of material through the sieve-tubes is hastened by a circulation of the protoplasm. But this phenomenon, though fairly common in plants, is not regularly observed in sieve-tubes. Another suggestion calls in the aid of osmotic forces. At present, however, we have no definite information of the forces productive of translocation.

Though the sieve-tubes provide the main channels for translocation, it is clear that since relatively few cells are in direct contact with those elements, translocation from one organ to another must involve in both organs a cell-to-cell movement of materials in tissues other than the phloem. It has been suggested that materials in solution may pass rapidly from cell to cell through the finer protoplasmic connections (see p. 26), as they are known to do through the larger protoplasmic connections traversing the sieve-plates.

Respiration.

A living organism requires a constant supply of energy. The most obvious way in which energy may be used in a plant is in the various chemical syntheses; in the particular instance of photosynthesis the energy of light from the sun's rays can be utilised directly, but for the rest, and for other vital activities, an internal source of energy is necessary. The readiest source of energy available for the ordinary purposes of men is by the combustion of fuel, such as coal or wood: that is, its oxidation, the ultimate products being carbon dioxide and water. The latent energy of the fuel is converted on combustion into kinetic energy. This supplies the motor impulse for engines of various kinds. In a somewhat similar way there proceeds, within the cells of the living plant or animal, what may be described as a slow physiological combustion of materials, yielding chemical energy for the cell-processes. The term *Respiration* is applied to any such energy-releasing processes in plants, some type of which is carried on in every living cell.

The type of respiration normal for the great majority of plants consists in the oxidation of sugars to carbon dioxide and water; it may be summarised by the equation:

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O + 674{,}000 \text{ calories.}$$

A considerable amount of energy is evidently produced by the combustion of sugar: it is equal to that required for the building-up of sugars (see p. 114). The process represented by the above equation is in effect that of photosynthesis reversed, though the intermediate stages are very different, as we shall see later. The sugars oxidised in respiration have been previously manufactured in the plant by photosynthesis. Since the sugar molecules are broken down in the process, we may see in respiration a phase of metabolism which is *destructive* in nature, as compared with the *constructive* phases which we have so far considered. In photosynthesis the plant stores up potential chemical energy within the sugar molecules, while it is able by means of the respiratory process to release that energy as required and at any point in the plant body.

The equation indicates that respiration in the plant, as in the animal, is attended by the absorption of oxygen, which is obtained from the atmosphere (or from photosynthesis) and by the evolution of carbon dioxide. While in the animal there may be mechanical inhalation and exhalation of the gases involved the respiratory interchange in the higher land-plants depends on simple gaseous diffusion between the atmosphere and the air spaces of the tissues, in aerial organs *via* the stomata and lenticels. In roots oxygen enters dissolved in the water which the root absorbs, while the carbon dioxide produced in respiration escapes from the roots in solution. Similar considerations apply to submerged aquatic plants.

The evolution of carbon dioxide by plants is most readily demonstrated in the case of germinating seeds or of flowers, in which respiration is specially active; while photosynthesis, which tends to mask respiration, is absent. If a stream of air, from which the carbon dioxide initially present has been removed by passage through caustic soda, is drawn through a flask containing such respiring material, and then through a further flask containing lime-water, a copious precipitate will soon be formed in the latter. The evolution of carbon dioxide is thus demonstrated.

By a suitable elaboration of this arrangement the amount of carbon dioxide evolved could be determined and an index of the rate of respiration so obtained. It could be shown that respiration quickens with increasing temperature until levels are reached at which the cell-structure is adversely affected ; also that actively-growing material such as germinating seeds respire more quickly than mature or dormant parts of plants. This observation is indicative of a close connection between respiration and growth. If by any treatment respiration is checked, growth is correspondingly depressed. Practical advantage of this has been taken in the storage of fruit and vegetables. By storing these in an atmosphere which is initially rich in carbon dioxide, respiration is reduced, the development and over-ripening of the material is slowed down, while the growth of micro-organisms is likewise discouraged.

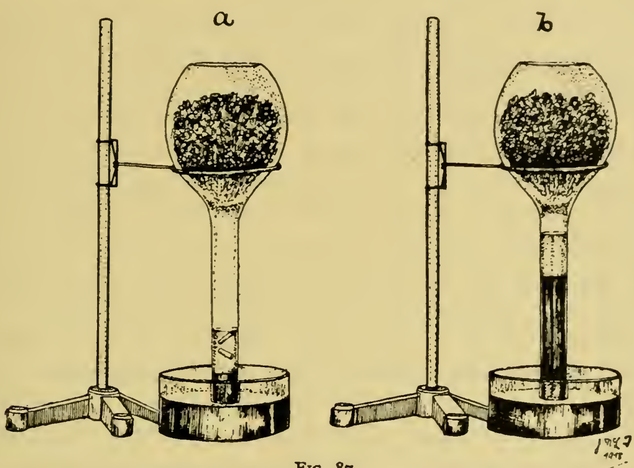

Fig. 87.
Arrangement for demonstrating gaseous interchange in Respiration. *a*, shows an earlier stage of the experiment ; *b*, a later stage. See Text.

Another instructive experiment dealing with the respiratory interchange of plants is shown in Fig. 87. A quantity of flower-buds or of germinating seeds is placed in a long-necked flask, which is then fixed with the neck projecting downwards into a dish of mercury. A strong solution of caustic potash is then floated above the mercury in the neck. The potash serves to absorb the carbon dioxide which we have seen to be produced by the respiring material. At the same time the mercury is observed to rise up the neck of the flask (see Fig. 87, *b*), indicating that some part of the original atmosphere of the flask has been absorbed by the respiring material. Actually it is the oxygen that is so absorbed, as is indicated by the observation that the mercury continues to rise until the volume of the gas within the flask has been reduced by about one-fifth.

In photosynthetic cells such as those of the leaf, the breakdown of sugars goes on side by side with their synthesis, though only a small proportion of the sugars manufactured in photosynthesis is consumed in the respiration of the leaf. One result of this predominance of photosynthesis is that in green organs such as leaves, *when exposed to light*, the gaseous interchange of photosynthesis, which as we have seen consists in the *absorption* of carbon dioxide and *evolution* of oxygen, masks that of respiration and is alone in evidence. In order to demonstrate the latter process in such organs light must be excluded, photosynthesis being thereby prevented while respiration continues, since it is independent of light.

If we refer back to the equation for respiration we see that the volume of oxygen absorbed should be equal to that of carbon dioxide produced; so that the so-called *Respiratory Quotient*, that is the ratio of carbon dioxide given off to oxygen absorbed, should equal unity. Experiments show that this is usually approximately true. There are exceptions, one being provided during the germination of seeds with fatty food reserves, the fats providing the initial fuel for respiration. Here a greater volume of oxygen is absorbed than of carbon dioxide produced, giving a quotient of less than unity (frequently in the region of 0·6). The probable explanation is that a preliminary to respiration proper is here the conversion of the fats to sugars. Oxygen is needed for this, over and above that subsequently required for the oxidation of the sugars. Conversely the volume of carbon dioxide evolved may exceed that of oxygen absorbed ; carbon dioxide may even be produced without any absorption of oxygen. This type of respiration is displayed by plants when they are deprived of oxygen. It is known as *Anaerobic Respiration*, as distinct from the normal or *Aerobic Respiration* carried on in air, such as we have so far been considering.

Anaerobic respiration can be demonstrated by passing a few germinating peas up into an inverted test-tube completely filled with mercury and supported in a dish also containing mercury. After some hours gas will be found to have accumulated over the mercury, and will continue to increase in amount for several days. On testing the gas it will be recognised as carbon dioxide. In this type of respiration sugar is again consumed, though here the products are carbon dioxide and ethyl alcohol. There is in fact evidence that *in this anaerobic respiration of higher plants we have a process very similar to the well-known alcoholic fermentation promoted by the fungus Yeast.* Higher plants do not, however, live very long if they are deprived of oxygen, probably because the alcohol produced is poisonous to their tissues, or because the energy liberated by anaerobic respiration is insufficient to maintain life.

There is no doubt that the respiratory processes are very complex and involve a chain of intermediate reactions, many of which are those of catalysis activated by enzymes or other protoplasmic agents present in the cell. This conclusion is forced upon us by consideration of the fact that in the laboratory carbohydrates are relatively difficult of oxidation. It is widely believed that in normal aerobic respiration there are two chief phases, only the second of which actually requires atmospheric oxygen. In the first phase the sugars are thought to be broken down to simpler compounds, possibly through the agency of the enzyme *zymase* which is present in higher plants, though known best in yeast. This first phase is considered to be common to both normal aerobic respiration and to that of the anaerobic type. If oxygen is present the products of the first phase are believed to be oxidised with the final production of carbon dioxide and water. In this oxidative phase enzymes known as *oxidases* and *dehydrases* are thought to play a part. If on the other hand oxygen is absent, the degradation of the sugar is less complete, and the products of the first phase are converted to alcohol and carbon dioxide. By this scheme normal and anaerobic respiration are linked up and regarded as alternative developments of a common initial phase. Yeast differs from higher plants in that it continues to exhibit the anaerobic form of respiration even when oxygen is present.

Some of the respiratory energy of the plant is evolved as heat, as may be shown if steps are taken to prevent loss of the heat by radiation. Thus germinating seeds if enclosed in a thermos flask, with precautions to prevent bacterial growths, will show an appreciable rise in temperature. The amount of heat so produced in plant tissues is small, and under normal conditions is quickly lost by radiation, so that body heat is not a characteristic of plants. The temperature of plant-organs, at least in darkness, is much the same as that of the surrounding atmosphere.

Concluding Remarks.

In this study of metabolism we have seen how the green plant utilises simple materials from its environment and from them elaborates carbohydrates, proteins, and other complex substances. This ability to make use of entirely inorganic materials for purposes of assimilation is practically limited to the green plant. As mentioned in the Introduction the activities of the plant in this way are of fundamental importance to animals, as well as to non-green plants; such organisms being dependent for their food on the organic materials synthesised by the green plant. Animals can utilise organic food only, and the food of an animal is always derived, directly or indirectly, from plants. An herbivorous animal feeds directly on plant materials. While a carnivorous animal feeds on other animals, the latter will probably be herbivorous in diet. And thus the so-called "*food-chains*" are established which always terminate in the green plant. This holds not only on land but also in the sea, where minute plants such as the Diatoms are the ultimate source of the food of all marine animal organisms.

In animals food is used partly for purposes of body-building, in which connection the Vitamins, essentially of plant origin, are of recently-discovered importance; also as a source of energy for vital activities. The energy which an animal obtains by respiratory oxidation of food materials is derived from the sun, and was originally fixed by some plant, in the process of photosynthesis. Thus the whole organic world depends on the sun for the energy which its vital processes require; all this energy is originally trapped by green plants in photosynthesis. The future may, however, see some reduction in the dependence of the animal kingdom on plants; for means may be devised for synthesising food materials without the co-operation of the plant.

In addition to the energy which we consume physiologically, the vast supply of energy which modern civilisation requires is largely vegetable in origin. Materials such as wood, coal, peat and probably petroleum have been ultimately derived from plants, and the energy liberated from their combustion was originally fixed in photosynthesis. Thus we return into present currency balances of the sun's energy stored in the Earth's crust from an earlier age.

These general remarks are, however, a digression from the study of the plant. Returning to the green plant itself, its constructive metabolism provides new material. This is required in the first instance for the nourishment and growth of its several parts: that is for the *maintenance of the individual.* But secondly, it is required for the increase in number of individuals. The *propagation of the race* can only be carried out when sufficient material is at hand from which to form new germs.

CHAPTER IX.

GROWTH, IRRITABILITY AND MOVEMENT.

In the preceding chapter we considered the processes of synthesis in which raw materials derived from the environment are built up within the plant into substances such as sugars and various organic nitrogenous compounds. Except for the proportion that is consumed in respiration, these products of synthesis are ultimately utilised in the formation of new tissues, leading to the *growth* of the plant. We have now to consider various aspects of growth processes in the plant and of associated phenomena. This includes a study of the sensitiveness or *irritability* which growing organs of the plant exhibit towards certain directive influences to which they are exposed during their development. And it will lead to a general consideration of phenomena of *movement* in plants.

I. Growth.

Growth is one of the most conspicuous features of Life. Its most obvious sign is increase in Size. But as applied to a living organism the term means something more than mere enlargement. It involves change and transfer of materials which cannot by any means be restored to their original state. Nor is it merely that the existing plants or parts of them enlarge as seen from without: for additional organs are successively developed, so that growth of the plant commonly leads to an increasing complexity of form, and also of internal structure.

1. *Germination.*

In entering on the study of Growth it will be convenient to consider it as it is seen in Flowering Plants, and to trace it from the germination of the seed (see Chapter I.). The external conditions recognised as conducing to germination of the dormant seed are:

(*a*) The presence of *moisture*, which causes swelling, and the passage from that state of desiccation which its tissues show in the dormant seed. The mobilisation of the food reserves soon follows (see Chapter VIII.).

(*b*) Access to *air*: actually it is the oxygen component that is needed for respiration.

(*c*) *Temperature* within the range to which vital activity is restricted.

While in a majority of cases *light* is without effect, in some seeds germination is retarded or even prevented by the incidence of light, while in others light has a beneficial effect. The retarding effect obtains in the seeds of some Phloxes, the beneficial one in seeds of Mistletoe (*Viscum album*), Tobacco and Purple Loosestrife (*Lythrum salicaria*). The full explanation of these effects is not yet available.

It does not follow that germination will always occur when the external conditions are favourable. The seed may continue to show dormancy as the result of the operation of some internal factor. Seeds of many species are incapable of germinating immediately after liberation from the parent plant. This may be because the embryo is immature at the time of separation from the parent, as it is in the seeds of the Lesser Celandine (*Ranunculus ficaria*), Marsh Marigold (*Caltha palustris*), the Ash (*Fraxinus excelsior*), and perhaps the Sycamore (*Acer pseudoplatanus*). When the seeds of such plants are placed under suitable conditions for germination, the development of the embryo is completed, but germination is arrested until that stage is reached. In the Sycamore and Ash germination may be held up in this way for months, and so tide over the winter. In a number of other cases the testa has properties which for a certain time prevent germination. It may show a high degree of impermeability towards water, so that no absorption proceeds even if the seeds are submerged. This is the case in seeds of many members of the Leguminosae, as for example Gorse (*Ulex europaeus*), Clover (*Trifolium* spp.) and Sweet Pea (*Lathyrus odoratus*). The testa gradually becomes permeable to water, but germination may be delayed for months or even years; there is, however, great variation in this respect among the seeds from a single plant. The advantage of this may be that the germination of the seeds produced by a parent plant is spread over several months or years: the chance of some of the seedlings finding favourable conditions for their development is thereby increased. By chipping the impermeable testas of these seeds prompt swelling and germination can be secured. In other cases the seed coat is at first relatively impermeable to oxygen and carbon dioxide, respiration and hence germination being impeded: in other cases the seed coat restrains the sprouting of the embryo for a time mechanically.

The period over which seeds retain their capacity for germination, though denied conditions suitable for it,—that is their *viability*,—

varies very considerably. Seeds of Willow (*Salix*s pp.) lose it a few days after liberation from the parent plant; those of a number of other native trees lose their viability a few months after shedding. But records are available of the long survival by seeds of periods of enforced dormancy. Thus those of a leguminous species, taken from a dried herbarium specimen, were still capable of germination though known to be over 150 years old. Examples are also known of seeds having lain dormant buried deep in the soil for very long periods. When grassland, which has at some previous period been arable, is again ploughed up, a crop of characteristic weed-plants of arable land may be obtained in the first season. There is evidence that the seeds producing these plants have lain dormant at low levels in the soil for periods up to fifty years. It is possible that the dormancy here is due to the high concentration of carbon dioxide present at low levels in the soil. This will arrest their respiration, and hence their growth (see p. 334).

2. *The Vegetative Phase of Growth.*

(*a*) *General Features.*

Germination having been effected, the young plant enters upon a period of growth in which the plant body characteristic of the species is built up. The particular form assumed by a plant is the result of the interaction of external conditions of growth with the internal hereditary factors (Chapter XXXV.).

Growth is initiated in the meristematic regions of the plant, where new cells are formed. *Meristems* are found at the apices of shoots and roots, and also in the form of cambium, often present in older parts of the plant. In a meristematic cell new protoplasm is elaborated, and this is usually accompanied by an increase in the size of the cell. In due course division of the nucleus and protoplasm occurs, and with the laying down of a new wall two daughter cells are formed. The meristematic regions are characterised by the constant repetition of these events. The influences that induce the continued activity of the meristems are but little understood: there is, however, evidence that cambial activity in the stem is induced by an activating substance diffusing from apical regions (p. 150). The formation of new protoplasm and of cell-walls in the meristematic regions necessitates a supply of organic materials such as amino-acids, amides and sugars. These are transferred to the growing points from the leaves, where they are originally manufactured; or from storage organs (p. 130). The total mass of the meristematic cells at the apex of a root or shoot remains relatively constant because the cells on the side of the meristem remote from the apex are successively ceasing to divide, and pass into the phase of enlargement. Much the same applies to cambial activity. In an organ of limited growth, such as a leaf, all the cells soon pass into the later phases of development.

On entering the phase of enlargement the newly-formed cells undergo a very considerable increase in size, due not so much to further elaboration of protoplasm within them, as to *the intake of water.* It is to this that most of the increase in size of the growing plant is due. This enlargement of new cells, with the attendant formation of vacuoles, has already been described on pp. 21-22, though the mechanism was not there considered. It was formerly believed that cell-enlargement was due to an increase in osmotic pressure of the cell-sap. This might be produced by the conversion of insoluble into soluble, crystalloidal substances, *e.g.* starch might be converted to sugar. Experiment has, however, failed to reveal evidence of such increase. It is now believed that the intake of water is due rather to an increase in the plastic extensibility of the walls of the newly-formed cells, although presumably there is a production of additional osmotic substances while the stretching is in progress, so as to counterbalance the tendency to dilution caused by the absorption of water. During the stretching of the cells additional layers of cellulose are deposited on the walls, resulting in an increase in thickness rather than the decrease which would otherwise follow. The final arrest of the stretching may be due to the continued strengthening of the walls in this manner. The stretching of the cell-wall during growth is permanent: plasmolysis of the mature cell does not result in the shrinkage of the cell-walls to the dimensions which they possessed in the newly-formed stage.

A considerable interval may elapse between the emergence of cells from the meristematic phase and their enlargement. Instances of this are seen in the resting buds of trees. By meristematic activity the various parts of the shoot for the forthcoming year are laid down within the buds during the summer and autumn: only in the subsequent spring do the cells undergo enlargement, causing the unfolding of the buds.

In roots and stems the enlargement of cells is chiefly a matter of elongation. This follows with some regularity on the emergence of the cells from the meristematic phase, so that behind the growing points of root and shoot is a region of cell-elongation, which is also the region in which the extension of the organ itself chiefly occurs. These growth zones can be located by marking on a young shoot or a root a series of initially equidistant dots of Indian ink (Figs. 88, 89). After a day or so the distances between the dots are re-measured, and the amount of elongative growth in this way is ascertained for different parts of the organ. In the shoot the greatest elongation will be shown in a region considerably below the tip, while it gradually diminishes, on the one hand towards the tip and on the other downwards, until a point is reached where growth has ceased (Fig. 88). This demonstration at once accounts for the general contour shown by growing shoots. In the apical bud the leaves are closely grouped because the axis has not yet extended to its full dimensions. The length of the internodes (or intervals between the leaves) increases downwards till their growth is complete, and their full length has been attained. Below that point the stem has become rigid, owing to general thickening of the cell-walls as they mature. In roots the cells enter on the phase of elongation with less delay and complete it more rapidly than in stems: with the result that the region of most active growth is more compact. It is localised within a few millimetres of the tip of the root (see Fig. 89, also p. 88). This proximity of the zone of growth to the apex may facilitate the penetration of the soil by the root: if it were further back, bending of the apical part might follow,

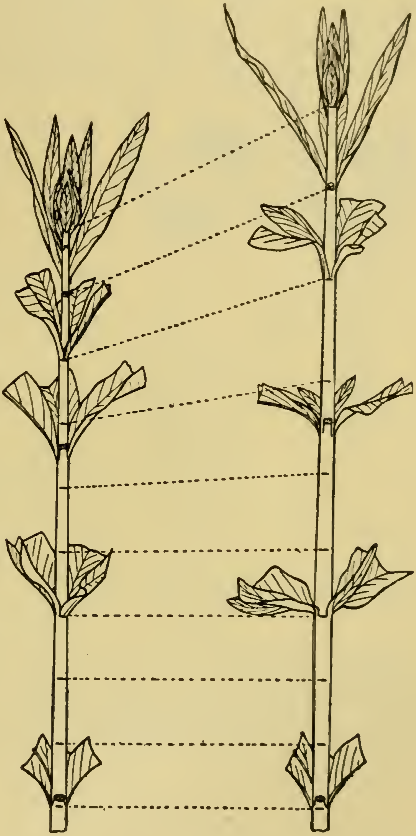

Fig. 88.

The left-hand figure shows a growing shoot at the beginning, the right hand-figure at the end of the period of observation. See Text. (After Errera.)

just as a long nail tends to bend when it is being driven into hard wood. It will be seen later that the elongation of the cells of shoot and root is subject to control by the apical tissues.

The elongation of cells in the zone of most active growth of a stem or a root is liable to be proceeding, at any moment, at varying rates on different sides of the organ. In this event the apical part of the organ will tend to curve away from the side of greatest growth. If the tendency towards most rapid elongation moves regularly round the stem, the tip will exhibit a revolving movement, and will pursue a spiral course through space. The shoot-apices of many plants do exhibit such a revolving movement or *circumnutation*, as was first discovered by Darwin. But the movements are not readily discernible owing to their slowness and small amplitude. Darwin devised a method of magnifying the movements and of projecting a record of them on to a plane surface (Fig. 90). It will be seen that the movements are slow and somewhat irregular, although there is a rough revolution round a central point. These nutatory movements are of much greater amplitude and have special significance in the shoots of twining plants, and in the tendrils of climbers (pp. 215, 216). Nutatory movements are also found in roots.

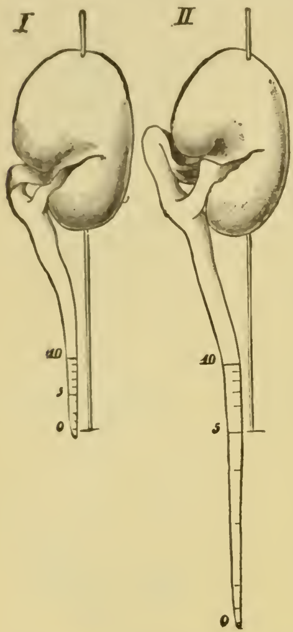

Fig. 89.

Localisation of growth near to the root-tip of *Vicia Faba*. In I. the root tip has been marked with 10 zones 1 mm. apart. In II. the same root after 22 hours. The lines nearer to the tip are now most separated owing to the growth having been most active there. (After Sachs, from Strasburger.)

During the enlargement of the cells, or subsequent to it, structural differentiation sets in: this leads to the production of vascular elements from some cells, photosynthetic tissue from others; and so on, according to their position within the growing organ (Chapter II.). This marks the last stage in the formation of the cell: when completed the cell is mature and normally it does not exhibit further growth.

(*b*) *Measurement of Growth.*

There are several attributes of the growing plant, or plant-organ, that can be made the basis of observation when an estimate of growth is required. Thus we can measure increase in linear dimensions, in volume, or in weight: the impression that is gained of the growth of a plant or organ is, however, liable to vary according to the particular index of growth that is adopted. The growth of a root or a stem is usually measured by noting the increase in length over a given time. For this purpose the *horizontal microscope*, of which different patterns are available, may be employed, or one may use the *auxanometer*, in which the growth is magnified by means of levers or pulleys for the purpose of measurement. If the growth of the plant as a whole is required it is usual to observe the increase in its weight. A special value as a growth-index has been placed on the *dry weight* of the plant, *i.e.* the weight of matter remaining after the water originally present has been driven off by drying the plant tissues in an oven. What this method measures is the net amount of environmental material that has been incorporated into the actual substance of the plant, irrespective of whether this has been used for growth or deposited as a storage material. The determination of dry weight involves killing a plant, so that consecutive observations cannot be made on a single plant: a series of similar plants must be available when growth is to be measured in this way.

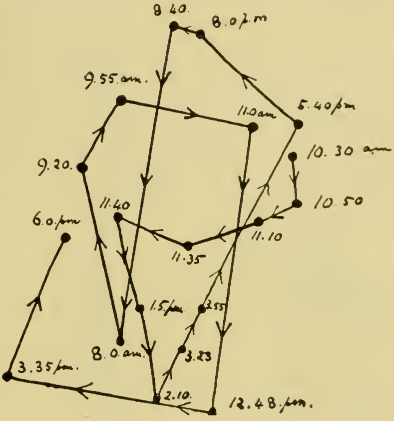

Fig. 90.

Record of circumnutation in a seedling made by Malins Smith. Note that the direction was reversed before 8.0 a.m. in this record.

(*c*) *Factors affecting Growth.*

Since in its growth the plant utilises the products of its assimilatory processes, such as the synthesis of carbohydrate and of protein, it is obvious that factors affecting those processes may also affect growth. Thus growth will be hindered if adequate supplies of raw materials such as carbon dioxide, water and nutrient salts are not to hand: experiments indicating the importance of nutrient salts have been described on p. 111. Light must also be present if autotrophic growth is to occur, while oxygen is required for respiration. Some of these factors have specific effect on growth, and these have now to be considered, while in addition other factors, not so far mentioned, also affect growth.

Light.

Since light is necessary for photosynthesis, in which essential materials for growth are prepared, it is obvious that there can be no growth of the autotrophic plant in the absence of light unless supplies of necessary organic materials are available. Given such supplies growth will occur. Thus the root system is normally able to develop in darkness because it draws supplies of organic materials from the aerial organs, which are exposed to light: while growth of both root and shoot may be obtained in darkness from such structures as seeds, tubers, or rhizomes, etc., where reserve substances are present, provided other conditions are suitable. The growth so obtained may however be of a very different type from that in light, making it clear that light has a direct effect on growth. This statement applies chiefly to the shoot, the growth of roots being usually but little affected by the presence of light. The shoot grown in darkness is distinctly abnormal in appearance, and is said to be *etiolated.* The result of etiolation varies a good deal, but in many species stem-elongation is much more rapid than in illuminated shoots, so that the etiolated shoot becomes very tall, an effect which is due to a greater elongation of the cells rather than to more rapid cell-division. Differentiation of the tissues is incomplete in the etiolated stem, while the growth of the leaves, or more precisely of the leaf blades, is arrested (Fig. 91). Chlorophyll formation is inhibited, the shoot having a white or yellow colour.

FIG. 91.
Normal (left) and etiolated plants of Broad Bean (*Vicia Faba*). (× ¼.)

The appearance of an etiolated shoot suggests that in addition to its nutritive effect, light has a direct effect on the growth of the shoot: it controls the growth of the stem, induces leaf development, and promotes internal differentiation. To some extent the light may operate through its effect on the growth-regulating substances of the shoot (see p. 148). In addition the reduced elongation of the stem may be associated with a general decrease in cell-turgor which results from the occurrence of more rapid transpiration in the presence of light. Experiment shows that the blue and violet constituents of white light are the most effective in this connection: for instance, a plant grown in red light is almost as markedly etiolated as one grown in darkness.

Although growth in the usual sense of the term is obtained *in darkness* in the examples quoted above, yet the plant as a whole is steadily *decreasing* in dry weight, since respiration is not counter-balanced by assimilation of fresh material. The dry weight of those parts of the etiolated plant that are actually developing—the root and shoot—would, however, show some increase, since food will be drafted into them from the storage tissue.

It is the want of sufficient light for normal development that makes plants in crowded greenhouses and dwelling rooms grow "leggy," with unduly lengthened stems and leaf-stalks. Crowding of field crops has a like effect, and often leads to the "laying" of corn under heavy wind and rain before harvest, the plants being top heavy and their stems weak. The apparent stimulating effect of darkness on stem elongation has the advantage to the plant that the young shoots of seeds or other organs sprouting underground grow rapidly up through the soil, and are able to enter on photosynthesis earlier than would otherwise be the case. In consequence of the controlling effect of light, the rate of elongation of shoots is more rapid during the night than in the daytime, provided the temperature is not too low: while the short stature and rosette form of alpine plants is partly due to the high light-intensity to which such plants are exposed.

Temperature.

It has previously been remarked that vital activity in general, which includes growth, is only possible within a certain range of temperature, which for many plants is approximately 0° to 45° C.; though there is considerable variation in this respect. Species from temperate regions have lower temperature requirements for their growth than those from the tropics. Alpine and arctic plants have still lower requirements. It is a common fact of experience that in temperate climates a rise of temperature from the normal accelerates growth, if other conditions are favourable. In order to force plants on, the gardener grows them in hot-houses, or in frames slightly warmed by fermentative changes in rotting manure upon which frames are placed. The rise of temperature in spring and early summer is a leading factor in the stimulation of growth at that season, while conversely the fall of temperature in autumn is at least a contributary cause of the period of dormancy in vegetation at large which then sets in. The high temperatures prevailing in tropical regions, combined with the generally favourable conditions, result in very rapid growth: thus shoots of the Giant Bamboo may grow in length over a foot a day, a rapidity which can be followed by careful observation with a hand lens.

Exposure to temperatures in the region of 0° C. results in growth and other vital activities being arrested, but it does not necessarily kill plants; nevertheless, in many plants, such as Tomato, Potato or *Dahlia*, fatal results may follow. In such cases, though there may be a direct effect of the low temperature on the protoplasm, it is the formation of ice in the tissues that contributes to the death of the plant. The ice forms in the intercellular spaces and leads to the withdrawal of water from the vacuoles and protoplasm of the cells. The protoplasm is killed by such dehydration, probably because its proteins become coagulated. In addition, the development of ice within the tissues may cause mechanical injury. By suitable treatment many plants can be "hardened," and are then able to withstand exposure to moderately low temperatures without injury. Some plants, especially those inhabiting polar regions, are so constituted that they can withstand exposure to very low temperatures, in some cases as low as $-50°$ C., without being killed. The full explanation of this ability to withstand low temperatures is unknown. Exposure of plant organs to low temperatures results in the conversion of any starch that may be present into sugars: the sweetening of frosted potatoes is an example of this. Experiment shows that in the presence of sugars, proteins are less easily coagulated by freezing than otherwise. Also, hardy plants or organs tend to be relatively low in water content: less ice can therefore be produced, while of the water that is present an unusual proportion may be bound up as water of imbibition in colloidal substances, and not readily subject to freezing.

Water.

Cell-enlargement is dependent on an adequate supply of water. For normal growth the plant must have access to such a supply: the plant will otherwise be stunted owing to the failure of the cells to attain their normal size.

Internal Regulation of Growth. Plant Hormones.

An obvious feature in the growth of a plant is that there is co-ordination of the growth of its various parts, which is adjusted in the interests of the organism as a whole. As a result the plant body is well-balanced and forms an efficient physiological system. This co-ordination, or *correlation* of growth arises from the exercise of influence of different parts mutually upon one another. Its existence is frequently more obvious when a part of a plant is removed, and the effect of the removal on the rest of the plant is studied. Thus, though many of the buds on trees and shrubs normally remain dormant, if the upper growth is severely pruned or defoliated through the action of some pest, the dormant buds may resume growth. For this reason regular trimming of a hedge results in denser growth below. In herbaceous plants, such as the Broad Bean or Chrysanthemum, if the terminal bud is removed, one or more of the lateral buds, which previously had remained dormant, will become active, and continue the growth of the shoot. In these examples it would appear that the growth of the dormant buds is arrested through the exertion of some influence by existing parts. Not all correlative influences are inhibitive. Thus the buds on a cutting (p. 248) have been shown to exert a promoting effect on the formation of roots at the base: while in the spring developing buds on trees stimulate cambial activity in the branches bearing them. It might be suggested that the dormancy of lateral buds was simply due to inadequacy of food materials for their development. Experiments have made it clear that this nutritive factor is not the only one, and the present tendency is towards the view that correlation within the plant is to a large extent due to the operation of specific chemical *growth regulators*, an idea which Sachs advanced many years ago. These substances are produced in one part of a

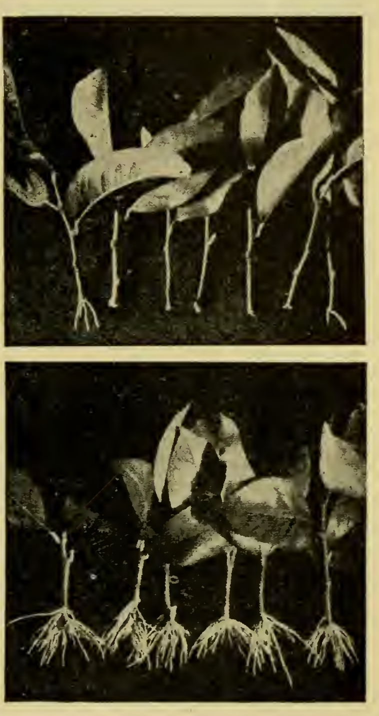

FIG. 92.

Lemon cuttings, the lower ones initially treated at the base with a very dilute solution of a substance promoting root-formation, the upper ones untreated. Photographed 2½ weeks after the cuttings were taken. (From Cooper, after Thimann and Went, 1937.)

plant and undergo transference to some other part, the growth of which is in consequence modified. Such substances are now termed *Plant Hormones*, since they correspond to those products of the animal organism to which the term *Hormone* was originally applied. For example, there is evidence that the dormancy of lateral buds is due to the production within the terminal bud and young leaves of a hormone which passes down the stem and inhibits lateral bud development. A similar explanation is now forthcoming for the promoting effect of buds on cambial activity and root formation. Chemical substances have been discovered which simulate the effect of the natural hormones. By supplying such substances to the plant a particular effect may be obtained more rapidly than would normally be the case. Thus the formation of roots on stem-cuttings can frequently be hastened by preliminary treatment with a variety of chemicals (see Fig. 92).

The particular instance of hormone-action in plants that has been most investigated still remains to be considered. Experiments suggest that the stretching of cells in the zone of cell-elongation in shoots (pp. 142-3) is markedly affected by a hormone which is chiefly produced by the tissues at the tip of the shoot, and then diffuses back to the region of cell-elongation. A similar state of affairs may exist in roots. These effects are of special importance in connection with the tropic curvatures of shoots and roots (see p. 153). So far most of the work on this particular hormone-effect has been carried out on the young shoot or sprout of seedlings of Oat or other Grass, since it provides very convenient material for experiment. Actually it is the outer cylindrical sheath, or *coleoptile*, of the shoot that is used in these experiments. This sheath encloses the developing foliage leaves. The actual formation of the cells of the coleoptile is completed at an early stage, and the subsequent growth of the organ, which occurs chiefly in the basal and central zones, is due simply to cell-elongation. The coleoptile is an organ of limited growth and is soon split open by the development of the leaves.

Experiment shows that if the extreme tip of the organ is amputated, the growth of the coleoptile rapidly diminishes to a very low level. That this effect is not merely due to injury is suggested by the observation that if the tip is immediately replaced in position after amputation the reducing effect on growth is much less than in the absence of the tip. It appears then that the tip in some way promotes the elongation of cells in the lower part of the organ, and there is convincing evidence that a *growth-promoting hormone* is secreted by the tip. For instance, a number of coleoptile tips may be placed on a thin sheet of agar-jelly for a time. If small blocks of the agar are then prepared and placed on decapitated coleoptiles, the growth of these will be much stimulated ; evidently as the result of the diffusion of some substance out of the agar into the organ. If the blocks are placed asymmetrically on the coleoptile a curvature away from the side below the agar block will develop (see Fig. 93). A considerable amount of information about the chemical nature of this growth-promoting hormone, which is known as *Auxin*, has been obtained, and a number of other substances, natural and synthetic, have been found to stimulate the growth of the coleoptile much like Auxin itself. The manner in which cell-elongation is affected is not yet clear, though there is evidence that the hormone increases the plasticity of the cell-walls (see p. 142). Similar experiments to those described for the coleoptile have been carried out with shoots of some dicotyledonous plants with like results : thus the stem apex appears to produce a hormone which promotes cell-elongation in lower regions of the stem.

FIG. 93.

Curvatures in decapitated Oat coleoptiles resulting from the application of agar blocks containing a substance of similar action to Auxin. The first leaf was partly pulled out of the coleoptile at the commencement of the experiment, and in each plant it is seen projecting beyond the top of the amputated coleoptile. (From Thimann and Went, 1937.)

The position with regard to cell-elongation in the root is rather obscure. Parallel experiments to those described above suggest that root elongation is somewhat *accelerated* by amputation of the tip, and that auxin and other substances which promote the growth of shoots retard that of roots. The explanation of these observations must await further investigation.

3. *Physiological Aspects of Reproduction.*

So far we have considered chiefly the vegetative phase of the growth of plants, in which the plant body, consisting of root and shoot systems, is built up. At the same time, many of the remarks in the preceding section apply to growth processes as a whole. Sooner or later in the growth and development of the higher plant reproductive structures are produced, first the flowers and from these the fruits and seeds. The manner of development and the structure of these organs are considered in later Chapters: at present we are primarily concerned with the study of the factors that induce the formation of reproductive organs. In the case of annual and biennial plants the origination of reproductive structures happens but once in the life-cycle, and after their formation the plant dies. There is some connection between the events, for if flowering and fruiting are prevented the life of an annual plant can often be prolonged considerably. In perennial plants, however, there is normally an annual production of flowers, though the first flowering may not occur until the plant has attained a considerable age. Thus the first flowering in the oak may be delayed until the tree is forty years old.

Much attention has been paid to the study of the conditions that affect flowering and fruiting. Illumination is again important.

Flowering frequently tends to be arrested in plants growing in poor light, as for example in honeysuckle and other plants growing in the shade of trees, though some plants flower freely in such positions. The pioneer experiments of Klebs in this field of investigation led him to the belief that flowering is favoured by a preponderance of carbohydrates within the tissues, especially in comparison with nitrogenous substances. Defective light will tend, through its effect on photosynthesis, to prevent this condition. An excess of nitrogenous manure will also have the same result, and it has frequently been observed to lead to vigorous vegetative growth, but to poor reproduction. In the presence of abundant reserve food flowering may, however, occur in darkness, as in the case of some bulbous plants.

The length of daily illumination is also an important factor in determining the time of flower formation under natural conditions: by artificially adjusting this the time of flowering can in some cases be controlled, though a number of plants are relatively insensitive to day-length. In some plants, of the so-called *short-day* type, flowering can be hastened by exposure to artificially shortened days. Examples are Dahlias, Chrysanthemums, and the Runner Bean. Such plants tend in these latitudes to produce their flowers in the shorter days of autumn: but by exposing Dahlias to shortened days from the time they were planted, flowering has been secured in July instead of September. In *long-day* plants flowering can be hastened by exposure to lengthened days, using artificial light for the purpose. Cereals are examples of this type, and they normally produce their flowers in the summer months. Exposure of these plants to shortened days tends to suppress flowering. These effects of the length of daily illumination are not yet understood, but they have considerable practical importance: thus in introducing a new crop into a particular region, the influence of length of day upon flowering and fruiting must be considered, and those varieties selected which are best fitted to local conditions in this respect.

Temperature may also affect reproduction. It has been found that exposure of a plant to low temperature during germination may hasten the onset of flowering. This has been applied practically, and is described as *vernalisation.* A similar effect is seen in biennials, such as the turnip, which tends to flower in the first year if exposed to frost.

4. *Periodicity in Growth.*

The plant exhibits frequent changes in its growth activities. Thus during the course of the yearly growth-season the phase of vegetative activity is succeeded by one in which reproductive structures are formed. In the autumn, or earlier in some plants, growth tends to cease: the leaves and other aerial organs may be lost, and a phase of dormancy opens. In annuals the death of the plant occurs at this stage, the race being carried on by the seeds, which themselves exhibit dormancy. It is these and many other types of rhythmic change in its activities that justify the statement that *periodicity* is a characteristic feature of the growth of the plant.

It would appear at first sight that many of these periodic changes could be ascribed without much hesitation to the direct effect of obvious climatic factors. Closer examination reveals a more complex condition : more obscure environmental or internal factors are then discovered to be involved. It has been pointed out that the dormancy of some seeds during the winter is due, not solely to the unfavourable external conditions, but also to internal factors (p. 140). Again the onset of dormancy in shrubs and trees in autumn, often accompanied by leaf-fall, might be ascribed to the direct effect of unfavourable climatic conditions of autumn and winter. But protection of the plant from the unfavourable weather will not prevent leaf-fall, and will not induce the dormant buds to grow out. Several months must elapse before the buds can be induced to open by merely exposing them to a favourable temperature, though more drastic treatment may "force" the buds into activity. Thus buds of lilac and of other shrubs can be induced to open by immersion of the plant in a warm bath of water in the region of 30° C., or by exposure to ether vapour. Continuous illumination from an artificial source has been seen to break down the dormancy of buds of the beech. The dormancy of potato tubers can be broken by treatment with certain chemicals, a method which has been used in countries where the climate permits of successive crops of potatoes in one season.

II. Irritability and Movement in Plants.

The organs of plants normally show definite orientation. Main stems grow vertically upwards, main roots vertically downwards : leaves occupy a horizontal or oblique position, while the lateral branches of shoot and root usually grow out obliquely. These positions are those in which the respective functions of the organs are most efficiently performed, and the assumption of them is due to the sensitiveness or *irritability* of plant organs towards certain directional influences. Gravity is the chief of them, though the direction of incident illumination is also very important for the shoot. These influences act as *stimuli* to the organs of the plant, which during their growth assume a definite orientation with regard to the direction of their impact. When the organs of the plant become displaced from their customary orientation, or when the direction of one of these stimuli is changed, then as the result of curvatures and torsions which soon appear, the organs or the younger parts of them tend to resume their normal relation to the stimulus. In such circumstances a type of *movement* of plant organs is exhibited. In adjusting the orientation of its organs with regard to directional stimuli the plant exhibits *Tropic* responses, or *Tropisms*. The response to the force of gravity is termed *Geotropism*, that to the direction of light, *Phototropism*. These phenomena will now be considered in more detail.

1. *Geotropism*.

That the upward growth of the main stem and the downward growth of the main root are due to the influence of gravity might be deduced from the consideration that gravity is the only directional influence of general operation that could be involved. Confirmation of that inference is provided by experiments with Knight's wheel (see p. 155). The root, growing towards the source of the gravity stimulus, is said to be *positively geotropic*, while the main shoot, growing upwards and away from the centre of the earth, is *negatively geotropic*: organs such as lateral shoots and roots and many leaves which place themselves in oblique or transverse positions are *plagiogeotropic*. The assumption of a strictly transverse position with regard to the direction of gravity is sometimes distinguished by the special term *diageotropism*. Stolons, runners and some rhizomes and leaves provide examples of this. An organ may exhibit different types of geotropism in the course of its development. Thus in seedlings the upper part of the plumule, or of the hypocotyl in epigean types, is frequently bent over and points downwards, becoming upright after emerging from the soil (Chapter I.). This is, at least in part, due to changed geotropic response. An advantage to the seedling following from this is that the terminal bud is less liable to be damaged by being dragged through the soil than by being pushed. The upper part of the peduncle of the Poppy is also positively geotropic before flowering and points downwards, but during flowering and fruit-production the upright posture is gradually assumed. Some flowering axes become positively geotropic as the fruits ripen. This is the case in the Monkey-nut (*Arachis*), where the fruits are as a result pushed downwards into the soil.

If the organs of a plant are displaced from their normal orientation, in which a state of equilibrium exists with regard to gravity, then geotropic curvatures may be exhibited. Thus if a seedling is fixed horizontally or obliquely in a moist atmosphere, in the course of a few hours curvatures will develop and will gradually bring the apical parts of the root and stem back into the normal orientation (Fig. 94).

These geotropic curvatures appear in the zones of cell-elongation (p. 143). They are due to the setting up of different rates of growth on the upper and lower sides of the horizontal or oblique organ. In a horizontally-placed stem growth becomes greater on the under side of the organ than on the upper, while the opposite obtains in the root. But it is only the apical part of the root or shoot that is restored to its normal orientation: generally speaking the older and basal part is incapable of longitudinal growth, and shows no change of orientation. Geotropic curvatures may also occur in plagiogeotropic organs when they are displaced.

The length of time required for the development of a visible geotropic curvature in a horizontally-placed root or shoot (known as the *reaction time*) varies greatly according to the material and the conditions. In some cases a reaction time as low as fifteen minutes is obtained, though values of one hour or longer are more usual. The organ need not, however, be in the position of stimulation for the whole of this period, but only for a part of it; the necessary time for effective stimulation being known as the *presentation time*.

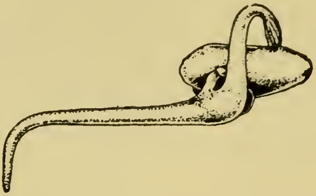

Fig. 94.

Seedling of Bean; after having been germinated, and the radicle had grown downwards and plumule upwards, its position was changed so that they were horizontal. The figure shows its recovery, the root having curved downwards, and the plumule upwards. The former is positively the latter negatively geotropic. (Dr. J. M. Thompson.)

It is possible to prevent the usual geotropic curvatures of roots or shoots fixed in a horizontal position, by arranging for them to be slowly but continuously turned about their long axes. For this purpose the rotating Klinostat is used, and finds frequent employment in experiments on geotropism. In a root or shoot that is thus revolved round a horizontal axis, that region of the organ which at one moment is lowermost will in a short time be uppermost. Any tendency to react to gravity which developed in the first position would be cancelled by an equal but opposite tendency in the second, and so on all round the organ, which therefore continues to grow horizontally unless some other factor intervenes. A forerunner of the Klinostat was the device known as Knight's wheel, used in experiments carried out at the beginning of last century. Knight fastened seedlings to the rim of a wheel which was rapidly rotated in a vertical plane, a considerable centrifugal force being in this way set up. Gravity was eliminated for the same reason as in the Klinostat: but it was found that the direction of growth of the organs was now controlled by the centrifugal force. The shoots grew towards the centre of the wheel, the roots away from it. The fact that centrifugal force was able to control the orientation of plant-organs in these experiments confirms the view that under normal conditions gravity is the determining influence, since centrifugal force resembles gravitational force in that *both will cause internal pressures within the cells.*

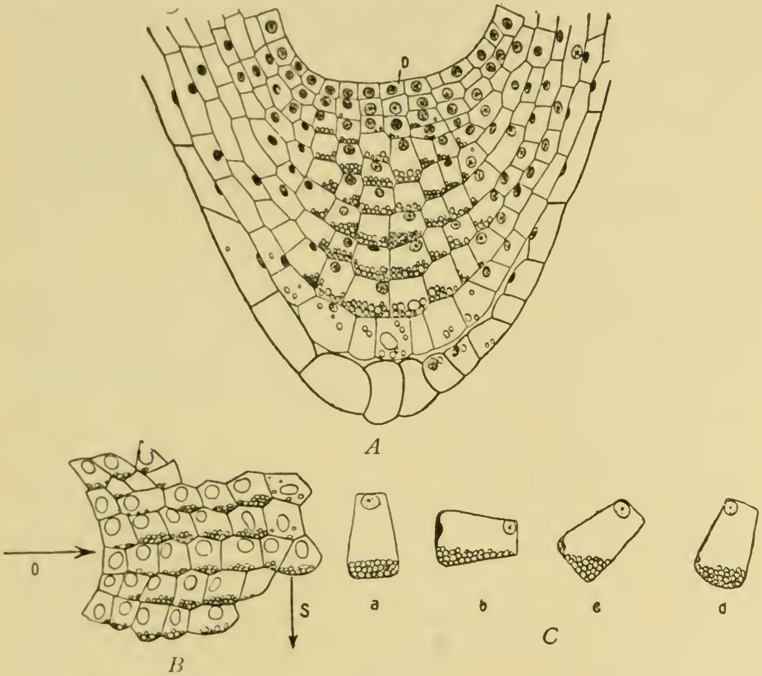

FIG. 95.

A. Median longitudinal section of the root cap of ***Roripa amphibia***, showing starch-grains settled to that side of the cells which was lowermost. *D*=dermatocalyptrogen.

B. Tissue of root-cap of ***Helianthus annuus*** after 24 hours in a horizontal position. Arrow (*O*) shows axis of root. (*S*) shows direction of gravity.

C. Diagrammatic representation of the statolith cells of the root-cap of ***Pisum sativum***. *a*, at rest ; *b*, 30 minutes in horizontal position ; *c*, *d*, cells fixed in intermediate positions.

(After Nemec.)

One well-known theory suggests that the sensitiveness to gravity is confined to certain special cells which contain relatively heavy cell-inclusions, free to move in the cell : these will therefore tend to lie against the physically lower wall. These inclusions are termed *statoliths* and it is suggested that they normally consist of starch grains. It is certainly the case that many plant-organs include cells containing starch grains which are free to move in the cytoplasm, though generally speaking their position is fixed. In roots such cells are usually present in the root-cap (Fig. 95), while in stems they are often present in the starch-sheath in the younger part of the stem. When a root or a stem is displaced from its normal position and placed, say horizontally, the statoliths under the influence of gravity move until they lie against the wall which is now lowermost (Fig. 95, *B*, *C*). They will then be pressing on a part of the cytoplasm that is not customary : the theory suggests that this unusual pressure activates some mechanism which results in growth being altered in such a way as to produce a curvature. This curvature ultimately results in the statoliths returning to their normal position.

Though the statolith theory of gravity-perception is not universally accepted, there is considerable evidence in its favour. Experiment shows that *in roots the sensitiveness to gravity is largely confined to the tip*, i.e. *to the region where the statoliths are present*. The remaining part of the root, even the zone of cell-elongation where the geotropic curvatures are effected, is relatively insensitive. That this is so is suggested by the observation that a root which has been decapitated can be placed horizontally without any resulting curvature, although the zone in which curvature would be expected has not been removed. It might be suggested that this was merely due to the injury involved in decapitation, but the fact that the ability to execute curvatures is restored if the tip is replaced in position by means of a drop of water or a thin layer of gelatin is against this view. In the coleoptile of cereals the position is similar to that in the root : the statoliths occur in the apex and sensitiveness to gravity is chiefly resident there. In stems the apical part is in general again the most sensitive, though there is not the same degree of localisation of sensitiveness as in the root. This is in agreement with the occurrence of the statoliths, which are distributed through the younger part of the stem.

Much attention has recently been paid to the importance of hormones in the production of geotropic curvatures. Evidence has been obtained that the development of a curvature follows on a re-distribution of the growth-controlling hormone, which, as we have seen (p. 150), diffuses back from the apices of coleoptiles, of shoots and probably of roots, to the zones of cell-elongation. Under normal conditions the hormone arrives at the zone of elongation equally distributed all round the organ : when the organ is placed in an unusual position with respect to gravity the movement of hormone appears to be in some way so affected that more arrives on the lower than on the upper side of the growing zone. Since the hormone is growth-promoting in the stem and coleoptile, and growth-retarding in the root, an upward curvature is the result in the former, a downward in the latter. According to this explanation the importance of the apex in geotropic curvatures is that it is the source of the growth-controlling hormone. The significance of the statoliths in these events is uncertain.

It has been remarked that geotropic curvatures in general are only shown by young still-growing parts of plant organs, the mature parts being relatively incapable of curving. An exception to this statement is provided by the stem (haulm) of cereal Grasses, in the lower part of which curvatures may be developed. The nodes of these shoots, which are really the swollen bases of leaf-sheaths, retain the power of growth. When the shoot is placed in a horizontal or oblique position the nodes resume growth on the *under sides*, with the result that the upper part of the shoot again becomes erect (Fig. 96). In this way cereal plants which have been "layed" by wind and rain stand up again if they are not too old. Similar responses are to be seen in the Carnation.

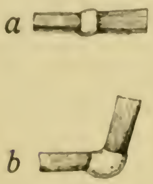

FIG. 96.
Geotropic curvatures in haulms of cereals. *a*, original appearance of a node of a haulm brought into a horizontal position. *b*, shows how by elongation of cells on the lower side of the node the part of the haulm situated above the node has been raised.

So far as leaves are concerned, the curvature of the upper part of the stem brings the younger leaves back into their normal position with regard to gravity. Leaves on older parts have an independent capacity for adjusting their position by means of curvatures and torsions of the leaf stalk. In pulvinoid leaves, which will be considered later, these occur especially at the pulvini.

2. *Phototropism.*

By Phototropism is meant the capacity of plant-organs to orientate themselves in definite relation to the direction from which light falls on them. Stems tend to orientate themselves so that they point towards the source of light, and are said to be *positively phototropic*. With overhead illumination the stem grows vertically: lateral illumination frequently results in curvature (Fig. 97). The curvature that develops in such a laterally illuminated stem is again due to differential growth, the cells in the zone of elongation that are away from the light tending to elongate more rapidly than those on the more brightly illuminated side. The result is that the apical part of the stem is moved over until it is directed towards the source of light. Before such curvature can develop, the tendency of the shoot to remain upright as a result of its geotropism has to be overcome: the position which is finally assumed is the resultant of the operation of the two tropisms. The same applies to other phototropic responses.

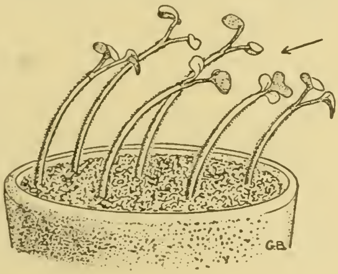

FIG. 97.
Phototropic curvatures in the hypocotyls of Mustard (*Sinapis*) seedlings illuminated from the side. (× ½.)

Although earth-roots in general show no phototropic response, those of some plants, such as Mustard (*Sinapis*), show *negative phototropism*, *i.e.* growth away from the source of light. As in geotropism, we see that here again the phototropic response of these roots is the converse of that characterising stems, a fact for which there is as yet no agreed explanation. The aerial roots of Ivy and the tendrils of Virginian Creeper (*Ampelopsis*) are also negatively phototropic, a property of obvious significance in relation to their function (see also p. 217).

Leaves are on the whole *diaphototropic*, placing themselves so that their upper surface is presented at right angles to the incident light, a position which secures a maximum incidence of light on the leaf, and is obviously a very suitable one for photosynthesis. Under natural conditions of growth, light usually falls on the leaves of a plant from a variety of angles: it is the direction from which the *most* light comes that determines the position which the individual leaves take up during their development. Phototropic responses of leaves are usually prominent in plants grown in dwelling rooms or against a wall. The adjustments of leaf-position in response to the direction of light are mostly due to growth-curvatures and torsions of the petiole. In the case of plants growing in tropical or other regions where they are exposed to very intense sunlight, leaves may take up a quite different position, one in which the incidence of light, especially of the strongest midday rays, is minimised. Some examples of this are given later in the section on Xerophytes. A further well-known instance is provided by the so-called Compass plants, of which the European *Lactuca scariola* is an example. When this plant is growing in a position subject to strong sunlight, the leaves, though actually produced spirally on the stem, twist until they all come to lie in a vertical plane running North and South, *i.e.* in the position in which they will be least exposed to the hot midday sunlight. In this way overheating of the leaves and excessive transpiration may be avoided.

As in geotropic responses, the type of phototropic response exhibited by a particular organ may vary during its development. Thus the flower stalks of Ivy-leaved Toadflax (*Linaria*) are positively phototropic during flowering, but subsequently turn away from the light, with the result that the fruits tend to be deposited in the crannies of some wall on which the plant usually grows. Experiment has also revealed that the type of phototropic curvature exhibited by an organ may vary with the strength of the light-stimulus. Thus although positive phototropism is usually obtained with the coleoptile of cereals, yet under certain conditions of light intensity and period of stimulation negative curvatures have been obtained.

To a certain extent the law of "quantity of stimulus" applies to phototropic responses. The result of brief exposure to a strong unilateral light may be the same as that of a longer exposure to a weaker light. The length of exposure that is required to produce a subsequent curvature (*i.e.* the presentation time) thus depends on the intensity of light that is used. Similar considerations actually apply to geotropism.

As in geotropic curvatures, so in those of phototropism there is evidence that hormone re-distribution is involved. For the most part this is provided by experiments on the coleoptile, where there is a similar localisation of sensitiveness and curvature as is encountered in that organ with regard to gravity. If the tip is covered by an opaque hood, and thus screened from light, the organ becomes much less sensitive to lateral illumination, although the zone where curvature would normally occur is exposed to the light. It thus appears that the one-sided light acts more on the apex than directly on the actual growing cells. Experiments suggest that there is in the laterally-illuminated tip a re-distribution of auxin, more accumulating on the shaded side. This inequality is transmitted down to the growth zone and is manifested there in a positive curvature, since the hormone is growth-promoting (in this connection see Fig. 93). There may, however, be in addition a direct, growth-retarding effect of the light on the growing cells. Similar considerations apply to the phototropic responses of stem structures in general.

3. *Other Tropisms.*

In addition to gravity and light, certain other factors exert directive influences on the growth of plant organs. Roots are frequently sensitive to the distribution of moisture in the rooting medium, and curve in their growth towards the region of greater moisture-content, exhibiting the property known as *Hydrotropism*. This particular tropism has not been very intensively investigated, and there is some doubt as to the degree to which it is developed by roots in general. The blocking of field drains by the invading roots of neighbouring trees is probably an example of hydrotropism. *Aerotropism*, as a result of which an organ is sensitive to the distribution of gases, especially of oxygen, has been detected in roots, which tend to grow towards a higher concentration of oxygen, as is perhaps seen in "pot-bound" root-systems. Pollen tubes, which grow away from a source of oxygen, behave in the opposite fashion (Fig. 97 A). *Chemotropism*, or sensitiveness to the distribution of chemical substances in the vicinity, is especially important in fungi (see Chapter XXIV.), since as a result their hyphae grow towards sources of food material: in the higher plants it is exhibited by roots. *Hapto-*

tropism, or curvature in response to contact, is best known in tendrils (p. 216). Contact of the tendril with a solid object causes growth on the side away from the point of contact to be considerably accelerated, with the result that the object, provided it is of suitable dimensions, tends to become entwined by the tendril.

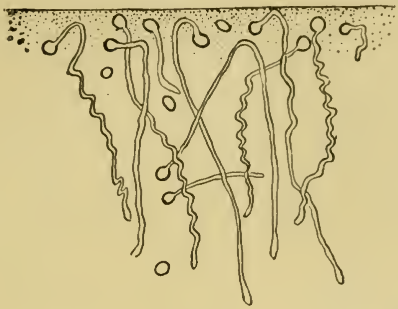

FIG. 97 A.
Pollen-grains germinated in a nutritive medium under a cover glass, of which the margin is shown. The tubes curve away from the margin, that is, away from the supply of oxygen. (After Molisch.)

4. *Nastic Movements.*

So far we have studied the effect on plant organs of directional stimuli such as gravity, line of incident light, unequal distribution of water and so on. Many plant organs in addition display a sensitiveness towards non-directional and uniformly distributed stimuli such as variations in light intensity and temperature, or mechanical shock, and show change of orientation or movement under the influence of such stimuli. In these cases the new orientation is determined not by the stimulus, as in tropic responses, but by the structure of the plant. Such responses are said to be of the *Nastic* type. Whereas tropic movements are due to growth changes and are therefore confined to growing organs, nastic movements are mostly, though not always, due to changes of turgor. Such changes can occur in mature parts, provided that mechanically the organ is suited for bending. They are frequently more rapid and striking than tropic movements, though of less importance biologically.

The opening and closing movements shown by many flowers and by some foliage leaves are examples of nastic responses. They usually occur in the morning and evening, the evening movements being commonly termed "sleep movements." It so happens that the opening and closing of flowers are due to growth changes in the petals or perianth members, rather than to turgor changes. For example, the opening and closing of Crocus and Tulip flowers are due to differential growth on the inner and outer surfaces of the perianth members, temperature being the controlling factor. A fall in temperature induces closure of the flower, while a rise results in opening. In other plants, such as Dandelion, changes in light intensity are more important than those of temperature. The closure of flowers at night or in wet weather serves to protect the inner floral organs from damage by low temperatures or by rain. In some plants, such as the Night Scented Stock (*Matthiola*), the flowers open at night and close in the daytime, which suggests an adaptation to pollination by moths.

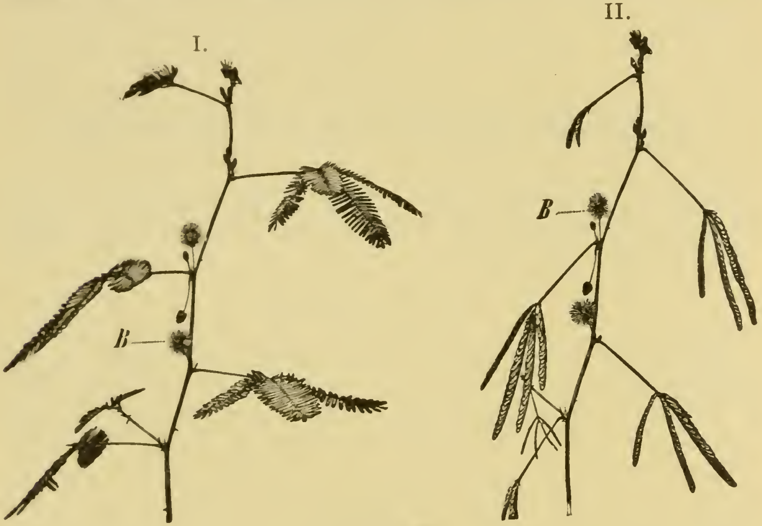

Fig. 98.

Shoot of *Mimosa pudica*. I. with leaves in the normal day-position. II. in the night-position assumed at dusk, or after stimulation. B = inflorescences. (After Strasburger.)

Sleep movements of foliage leaves are to be seen, for example, in Clover, Wood-sorrel and *Mimosa*, all of which have compound leaves. In the daytime the leaves are open and the leaflets occupy a horizontal position, but with the approach of night the leaves close up. In Clover this is the result of the leaflets rising, while in Wood-sorrel they droop. In *Mimosa* the pairs of leaflets fold their upper surfaces together, and the pinnae converge, while the petiole falls into a pendant position (Fig. 98). These movements are made possible by the presence of structures (*pulvini*) which act like hinges or joints at the base of each leaflet in Clover and Wood-sorrel, while in *Mimosa* they are also present at the base of the pinnae and of the leaf stalk. Externally the pulvini can be recognised as swollen, dark green regions, while internally the vascular tissues are found to be contracted to a compact central strand, surrounded by a broad cortical band of parenchyma which forms the motor tissue. The movements of the leaves are brought about by differential changes of turgor in the motor tissues on the upper and lower sides of the pulvini, induced chiefly by changes in light intensity. An increase in turgor on one side will lead to an expansion of that half of the pulvinus, a decrease to a contraction. A corresponding movement of the leaflet or other part governed by the pulvinus will follow.

The point which leads to *Mimosa* being commonly called the *Sensitive Plant* is that in response to mechanical shock the leaves rapidly assume the same appearance as they take up more gradually in the evening (Fig. 98). The disturbance of walking roughly through a patch of *Mimosa pudica* results in a broad track of completely transformed vegetation: it must, however, be admitted that the value of this sensitiveness to the plant is far from obvious. If the stimulus be applied gently, steps in the leaf movement can be observed. A soft touch at the sensitive lower surface of the hinge at the base of the petiole makes the whole leaf fall, and the response may then be extended outwards to the pinnae and successive pinnules. Or if the distal pair of pinnules be pinched, or stimulated with the hot head of an extinguished match, the stimulus received distally will extend downwards. The leaflets will fold in successive pairs, and finally the leaf will fall. If the stimulus be sufficiently strong its effect may extend along the stem to other leaves. It thus appears that the state of excitation set up at the point of stimulation may be conducted through the plant.

The method of conveyance of excitation through the plant is still the subject of investigation. It has been found that if a stem of *Mimosa* is cut right across and the two parts then joined together by a glass tube filled with water, application of a stimulus below the interruption will result in closure of leaves above it. The inference from such experiments is that a chemical substance of hormone-type is produced at the point of stimulation, and that it is conducted through the plant, affecting the pulvini in turn as they are reached. The path of conduction of the stimulus is still in doubt. An earlier suggestion was that the conduction of excitation is effected in a mechanical fashion as a wave of pressure running through peculiar elongated elements that are present in the phloem of *Mimosa*, in addition to the sieve tubes. It was suggested that the pressure waves are set up as the result of the movement in the pulvinus where the stimulus was first received, and pass on through the elements mentioned: much as a wave of pressure can be sent through a rubber tube filled with water. If one observer pinches one end of it, a second observer can feel the wave at the other end of the tube.

As in the sleep movements of *Mimosa*, so in the shock movement, changes of turgor in the pulvini are responsible. On stimulation the cells of one side of the motor tissue suddenly lose the power to retain the water of their vacuoles, with the result that the water filters out into the intercellular spaces and that side of the pulvinus shrinks. Thus in the main pulvinus these events occur at the under side on stimulation, with the result that the petiole falls (Fig. 98, II.).

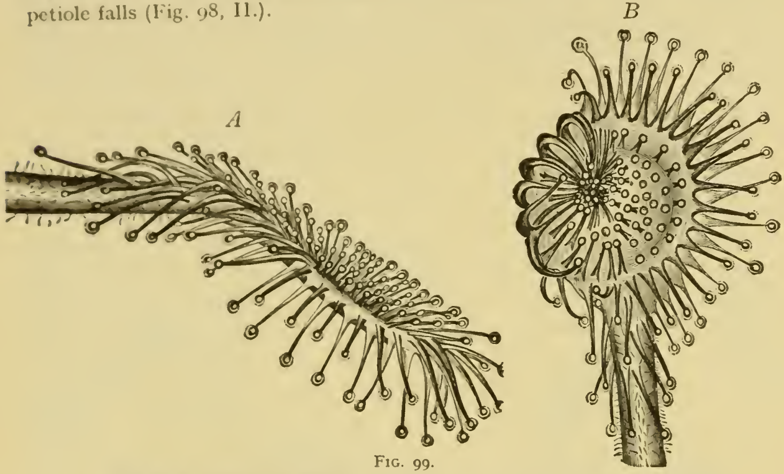

Fig. 99.

Leaves of *Drosera rotundifolia*; enlarged. *A*, in the receptive state before stimulation. *B*, after stimulation, viewed from above, with tentacles partly incurved. (After Darwin.)

Other striking nastic movements are those of Carnivorous Plants (see also Chapter XII.). In Sundew (*Drosera*) the spathulate leaves bear numerous radiating tentacles, each terminating in a spherical gland, which secretes a viscid juice containing protein-splitting enzymes (Fig. 99, *A*). This acts like bird-lime, detaining any small insect that touches it. The tentacles are sensitive to contact and to the presence of chemical substances, especially those containing nitrogen, such as ammonium salts or proteins. When such stimuli are applied the tentacles, as the result of unequal growth, begin to close inwards, sometimes within a few minutes after application of the stimulus (Fig. 99, *B*). An insect that is responsible for stimulating the tentacles thus becomes enveloped by them, and undergoes digestion by the enzymic liquid which they secrete. In another native carnivorous plant, the Butterwort (*Pinguicula*), the presence of insects leads to an inrolling of the leaf margins, again tending to envelop the insects, and to hasten their digestion by a secretion from glandular hairs on the upper surface. The movements of the Venus Fly Trap (*Dionaea*), an American plant, are very striking. Each of the rosette of leaves of the plant bears at its distal end a two-flapped mechanism, like the covers of a book, mobile along the median line as a hinge (Fig. 100). The flaps are furnished with marginal spines, while three sensitive bristles rise erect from the upper surface of each. Under favourable conditions, a touch on any of these six bristles results in the immediate closure of the flaps, with interlocking of the marginal spines. Any insect touching them would be captured within the trap; and as the inner leaf-surfaces are furnished with secreting glands, digestion follows, with the usual absorption of the soluble products of digestion. The movement is due to combined turgor and growth changes.

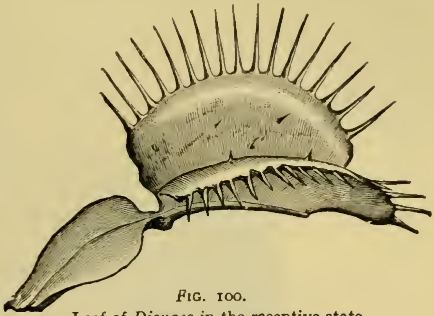

Fig. 100.
Leaf of *Dionaea* in the receptive state. (After Darwin.) (× 4.)

Fig. 101.
Fruits of *Cardamine hirsuta*. The uppermost are unripe. Those below them are ripe, and the carpellary walls, splitting away from below, curve so quickly as to throw the seeds forcibly outwards.

5. *Hygroscopic Movements.*

All the instances of movement in plants that we have so far considered, whether tropic or nastic, depend on changes of growth or turgor, and therefore involve living cells. There is, however, another class of movements in plants which stand in no direct relation to living cells, and which are physical rather than physiological in nature. These movements can take place in dead plant organs and are due to changes in water content of the tissues, in combination with special structural features. Such hygroscopic movements are seen in the dehiscence of many fruits, and are often due to tensions set up through unequal contraction of different layers of the wall of the fruit as it dries. The tensions ultimately lead to the rupture of the fruit, and in the sudden relaxation the seeds may be thrown out and scattered. An instance of this is provided by the native Hairy Bitter-Cress (Fig. 101), but a more notable one is the Sand Box Tree (*Hura crepitans*), a native of tropical

America. The fruit of this plant explodes with a report like a pistol-shot, and throws the large seeds out to a distance of many yards (Fig. 102). These and other explosive fruits will be considered again on p. 324. Mention may also be made of the hygroscopic awns of the grass *Stipa*, through the twisting movements of which the seed tends to be pushed into the soil; and also of the movements of the peristome teeth of Mosses. An example of a rather different type of hygroscopic movement is seen in the dehiscence of the Fern sporangium, which depends on changes in volume of the water present in the cavities of specialised cells of the annulus (Fig. 103). When exposed to a dry atmosphere these cells gradually lose the water with which the cell-cavities are filled. The diminishing mass of water within each cell retains its continuity because of the cohesive properties of water, and also continues to adhere to the cell walls: the latter therefore suffer a deformation and the annulus as a whole curves backwards (Fig. 103, *A*, *C*). A point is ultimately reached at which the continuity of the water within the cells is broken. The cells immediately resume their normal shape and the annulus recovers with a sudden jerk (Fig. 103, *B*, *D*), throwing out the spores. The rolling and unrolling of certain Grass leaves (p. 188) is also due to changes in volume of the water present in special cells.

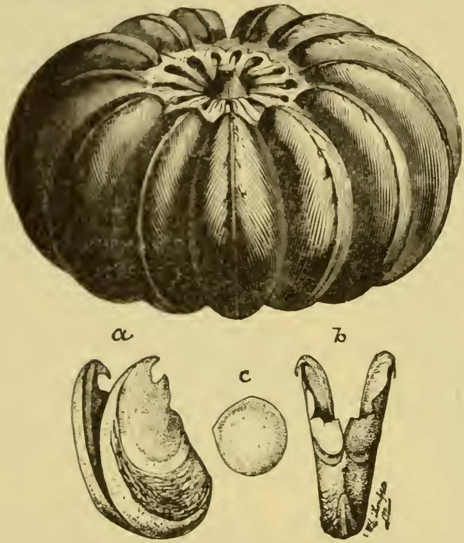

FIG. 102.

Whole fruit of *Hura crepitans*, before rupture of its woody carpels. (After Le Maout.) *a*, *b*, single carpels after the explosion, showing each coccus with gaping halves. The rupture happens suddenly, each coccus taking a wider shape; the cocci and seeds are thus thrown asunder. *c* = a single large seed. The tree is native in Tropical America.

It is evident from what has been said in the latter part of this Chapter that the several organs of the plant exhibit a wide variety of movements and curvatures. The plant as a whole is, however, fixed in position, a feature of difference from the animal which is to be associated with their divergent methods of securing nutrition. The animal goes in search of its food: while the raw materials which the plant requires for its nutrition reach it by processes of diffusion. Such movements as are exhibited by the individual organs of the plant involve a quite different mechanism from that in animals. With the exception of the hygroscopic movements, they are all dependent on variations of the osmotic turgor of living cells or of the resistance of cell-walls; it is structurally impossible that the mechanical effects of the movements should exceed, as they mostly fall short of, the limit of the pressure of the protoplast upon the containing walls. Such movements of the plant-body are brought about in an essentially different way from those positive contractions of muscle-fibres, which are the source of movement in the animal body. In this, as in so many other features, the two kingdoms show evidence of their initial divergence. However parallel their behaviour may appear to be, when fully analysed it becomes apparent that it is analogy, rather than any closer correspondence, that holds between them. For we do not find either that contractile muscular fibres exist, or any specialised nerve-system in the body of the plant. Such movements as plants show, and even the conveyance of stimuli, are brought about without them.

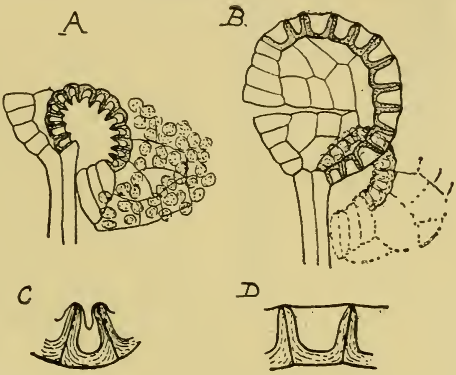

FIG. 103.

Fern sporangia: *A*, with the cells of the annulus darkly shaded, and curved strongly backwards by drying of its cells. *B*, the annulus after its sudden recovery, while the previous position is shown in dotted lines. *C* shows in detail cells of the annulus in *A*, and *D* shows similar cells in the state seen in *B*. See Chapter XXXI.

Two other types of movement are encountered within the plant kingdom. *Locomotion* is displayed by some Algae (Chapters XXI.–XXII.) and by ciliated reproductive cells, such as the sperm of the Fern (Chapter XXXI.). *Movement of cell contents* also is common in plants. It usually takes the form of protoplasmic streaming (Chapter III.).

CHAPTER X.

THE MECHANICAL CONSTRUCTION OF THE PLANT-BODY.

The texture of any normally growing Plant is relatively firm and elastic, so that it keeps its form, and after yielding to pressure tends to recover. Even young shoots show this ; but it is a much more prominent feature in older plants. Woody trunks, large leaf-stalks of Palms, and old roots consist of hard masses of resistant tissue. They also may yield to the pressure of the wind, and they recover very perfectly after it is over. But if the limit of elastic recovery is passed, any part, young or old, may be so damaged that it is of no further use to the plant. A trunk may be shattered, a limb or a leaf may be severed, and so lost ; or soft cells may be crushed between harder tissues, as may be seen in any leaf-blade roughly folded at too sharp an angle. To minimise such risks it is necessary that plants shall be mechanically constructed so as to resist those stresses and strains which are likely to befall them in their ordinary course of life.

Individual plants often attain large size. The Brown Tangles of the colder oceans, such as *Macrocystis*, may be several hundred feet in length, and are among the largest of living organisms. Their leathery body is anchored to rocks, and buoyed up by sea-water, though exposed to its currents and waves. To maintain the form and attachment of so large a plant offers a quite considerable mechanical problem, which is shared by other water-plants in proportion to their size. But the requirements in the case of aerial plants are much more exacting, for they are not buoyed up by a medium of high specific gravity. They must be stiff and firm of texture. Forest trees grow upwards to a height sometimes of 300 feet or more, and there hold aloft the dead weight of branches, leaves, and fruits. Not only must this be done in still air, but they must also be ready to resist successfully the impact of winds. In large plants this presents a serious engineering problem, and especially so in view of the fact that perfect elastic recovery after the wind-pressure ceases is a condition of its successful solution. A similar mechanical problem varying with the size, presents itself in relation to every living plant that grows in the air. *The solution of such problems is based upon the fact that the cells forming the plant-body are encysted.* The necessary firmness which they show depends, in one way or another, upon the fact that a cell-wall surrounds each soft and slimy protoplast.

There is reason to believe that the evolution of multicellular plants started from simple unicellular beginnings. Those primitive creatures, the Flagellates, of which *Euglena* is an example, may be regarded as illustrating at the present day the sort of organisms from which the evolution of the higher forms may have started. *Euglena* shows two phases in its life: an active phase of motion, in which the plant exists as a primordial cell, that is, as a protoplast without a cell-wall. (Fig. 104, *A*, *B*, *C*.) But there is also a second quiescent phase, in which the protoplast is encysted, that is, surrounded by a cell-wall. (Fig. 104, *D*, *E*.) It is probably from some such source as this that the evolution of the plant-body of all the higher forms originated. For the encysted state of *Euglena* corresponds structurally and mechanically to that of the cells composing the ordinary tissues of plants; and it has been seen that the whole plant-body, however complicated, is built up of such encysted cells or their derivatives (Chapter II.). But the primordial phase is still represented in sexual propagation. The cells directly involved in that process, even in Flowering Plants, are primordial cells, and in many of the lower forms they are still capable of movement in water, like the active *Euglena*. The primordial protoplast has the advantage of free movement, but it is mechanically weak. Its soft slimy consistency may suffice for small unicellular organisms; but it would be quite impossible to construct large plants from such cells without some means of mechanical strengthening, especially if they are to live in air.

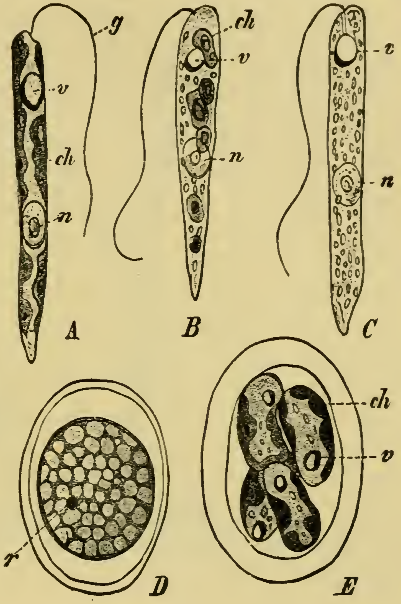

FIG. 104.

Euglena gracilis. A Flagellate, showing in *A*, *B*, *C*, the motile condition, without cell-wall. *D*, is a resting cyst, with cell-wall. *E*, shows a cyst germinating. (Highly magnified.) (After Strasburger.)

It is on the basis of the encysted state, strengthened and protected by cell-wall, that large plant-bodies have been made possible. But the mechanical advantage conferred by the cell-wall has been gained at the sacrifice of mobility. Moreover, the mechanical framework offers an obstacle to physiological activity, and this may sometimes be a serious difficulty. *The method of construction of the plant-body is thus a compromise between the need for mechanical strength, and for the carrying out of the vital processes.* That the result is in favour of the plant is shown by the success which vegetation has achieved.

Whether *economy of material* is actually as important in plants as it is in the construction of bridges or ships by the engineer, such a principle is undoubtedly manifested in the construction of many plants. In both cases the less material that is used the lighter the structure will be. In the plant the material used has to be gained through photosynthesis. Where the formation of a large vegetative system is involved it must be mechanically strong enough to maintain its form. Our chief interest will lie in seeing how plants use their materials so as to be mechanically effective. It will be found that the methods of its use run parallel to those adopted by man to gain similar results. In plants there are two distinct methods of securing mechanical resistance together with economy. One is through *turgor of the cells*, the other is by the formation of *specific mechanical tissues*. The former plays the chief part while the tissues are young, the latter is effective in the mature parts of the organism. But in their action they are not distinct from one another. Both may be effective in the same part, and at the same time. For the dependence on turgor gradually passes over to dependence on the specific mechanical tissues, as the shoot develops and its requirements become greater.

RIGIDITY AS BASED ON TURGOR.

The fact that *living cells are normally turgescent* has already been discussed in Chapter III. The firmness and rigidity of the tense cell was there compared with the condition of an inflated football, or of a pneumatic tyre. The elastic cellulose wall corresponds to the outer cover, and the protoplast to the bladder, or to the inner tube. The withered or plasmolysed cell loses its power of mechanical resistance like a punctured tyre, or a deflated football. This condition holds for every normally living encysted cell while young, whether isolated as in some Algae, or forming a unit of some larger structure.

In the evolution of the higher forms from simpler organisms it might appear that the simplest way of extending the plant-body would be to enlarge the single cell as a non-septate sac. The best of this simple but ineffective method has been made by the Algal family of the Siphonales. But it is only under favourable conditions that it can succeed, for it is a method of construction with obvious limitations. Unless buoyed up by water it is unsuitable except in the case of small organisms. Some relatively small members of the Siphonales, such as *Protosiphon* or *Vaucheria*, live in damp situations exposed to the air. But all the larger forms are submerged, and live usually in still lagoons or pools. In *Valonia ventricosa*, which is a sea-weed, the form of the sac is simply spherical, or pear-shaped, and may be an inch or more in diameter. But in other genera it is more elaborate in form, and may extend to a foot or so in length. Some mimic curiously the creeping shoots of aerial plants ; for instance *Bryopsis* and *Caulerpa* (Fig. 105). Many other of the larger forms, however, grow with numerous branches matted together, giving mutual support (*Codium*), or even cemented together into a solid mass by deposits of lime (*Halimeda*). Such structural modifications as these show that the non-septate sac is too weak a method of construction for practical

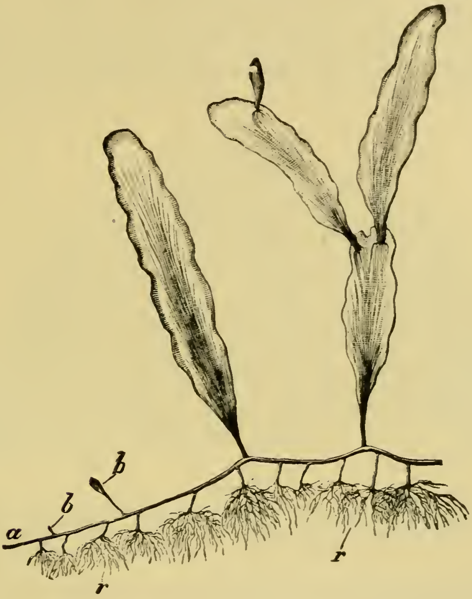

FIG. 105.

Caulerpa prolifera. *a*, growing apex. *b*, young thallus-lobes. *r*=zhizoids. Notwithstanding its elaborate form this plant is a single non-septate sac. (½ Nat. size.) (After Strasburger.)

use. It has only been adopted by a few organisms, the chief of which are certain Algae living in still water, a medium of nearly the same specific gravity as themselves. Thus buoyed up the action of gravity upon them is minimised.

If a spherical rubber balloon be filled with water so as to be turgescent, it keeps its form so long as it is submerged. But if it be lifted out into the air it changes its form according to the support, and the larger it is in proportion to the firmness of its skin the greater will be the deformation. A very large one with a weak skin will burst. These simple facts are in accordance with a general principle which rules for similar structures of various size. Their strength increases as the square of their dimensions, their weight as the cube of their dimensions. So long as the structure rests in a still medium, of its own approximate specific gravity, no mechanical difficulty need arise. But in a medium of less specific gravity the demand for rigidity rises in a higher ratio than the dimensions of the structure. The result of this applied to plants is that a method of construction which suffices for small organisms, consisting largely of water, and exposed to the air, will not suffice for those of larger dimensions. The mechanical demand on the turgor and strength of the cell-wall in order to maintain form rises in a more rapid *ratio* than the size. *Here it may be noted that all large land-growing plants are septate* ; also that land-growing Siphonales are small, and the larger ones are all aquatic. In the case of the non-septate cell of large dimensions exposed in the air, the wall would have to be of such thickness in order to maintain the form of the organism under the influence of gravity, as to be on the one hand wasteful of material, while on the other it would present a formidable obstacle to physiological transit. Such thickening is seen in the large species of *Valonia* and *Caulerpa*, even though they grow submerged. In both of these genera the cell-wall is considerably thickened ; but in the latter additional firmness is secured for the otherwise feeble structure by numerous cellulose rods, which stretch across the internal cavity and act as ties (Fig. 106). In other

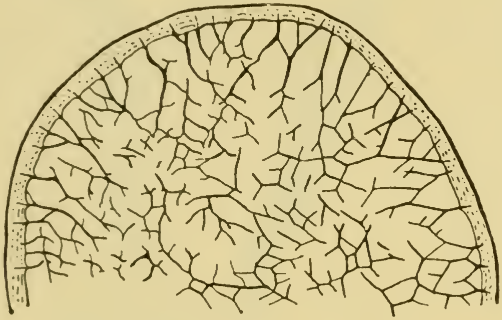

FIG. 106.

Part of a transverse section of *Caulerpa*, showing the thick outer wall, and the reticulate rods of cellulose, which act as ties, and give added rigidity. F. O. B. (× 50.)

large types some accessory means of strengthening has to be adopted, such as matting the branches together as in *Codium* and *Penicillus* : or cementing them together with lime as in *Halimeda*. These are to be regarded as concessions to the mechanical imperfection of the non-septate construction.

Cases of non-septate tissues exist in the body of some of the higher plants, but as they are embedded in other tissues they are not exposed to mechanical demands. Examples are seen in the latex-cells and vessels, as in the Euphorbiaceae and Cichoriaceae (Fig. 32, p. 54) ; and in the young embryo-sacs of the Flowering Plants. (See p. 295.)

All ordinary plants of large size are septate. This is specially necessary where they live exposed in the air, and are thus subjected to greater strains than if floating in water. In the embryonic region the cells are seen to divide into equal parts, each newer cell-wall being inserted at right angles on the older walls. This leads to a cell-net the exact detail of which depends upon the external form of the part (Fig. 107). The disposition of the walls is from the first such as to give added mechanical strength, together with other advantages. But in the young cell the walls are extremely thin, and are composed of pliant material. In the young shoot the mechanical strength is almost entirely dependent on the turgor of the individual cells. When they are tense their walls do not act as mere props or stays, as do the floors or partitions of a house ; but the turgor gives individual rigidity to each cell, and through them collectively to the whole part which they construct. A high mechanical effect is thus gained in a succulent structure with extreme economy of material. This may be illustrated by the case of the Lettuce. We have seen that a crisp

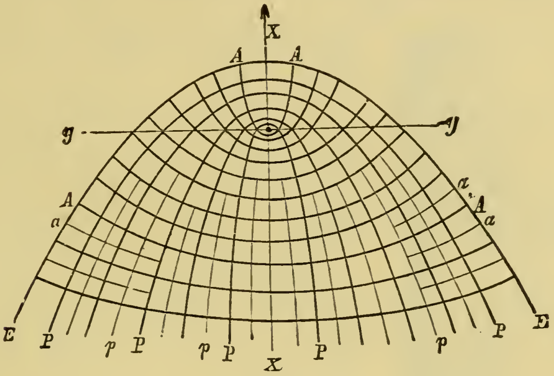

FIG. 107.

Diagram illustrating the plan of arrangement of cell-walls in the apex of the stem of an Angiosperm. XX = axis of construction. EE = external surface. PP = periclinal curves. AA = anticlinal curves. (After Sachs.)

Lettuce suitable for a salad gives by weight 95 per cent. of water, and only 5 per cent. of organic material for cell-walls and protoplasts. Such a structure is in fact a very slight organic framework containing water. The mechanical effectiveness of the internal turgor of the cells, and the insufficiency of the mere partitioning of a young or succulent part is shown by comparing a crisp fresh leaf with one which has withered, or has been plasmolysed.

There is, however, another factor which increases the mechanical effectiveness of succulent parts in the young state, viz. the *mutual tensions of tissues.* If a fresh young stem of Sunflower or Elder, or any extending part of an herbaceous plant, be slit longitudinally into quarters, these take strong curves. The outer surface of each quarter becomes concave, the inner faces of each quarter convex. The curves become more marked after the cut stem has been steeped in water. These curves show that the relations of the tissues in the living stem are not passive. (Fig. 108, *2a*, *2b*.) That the phenomenon is one of turgor of the cells may be shown by allowing the slit stem to wither, or by plasmolysing it with a salt solution, when the curves disappear, and the parts become limp. On the other hand, if the several tissues be completely separated from a measured length of a fresh stem, and be themselves measured after separation, the column of pith will be found to have elongated, and the outer tissues to have contracted. To bring them back to their original state the pith would have to be compressed and the outer tissues stretched. (Fig. 108, 1.) This is in fact their condition in the growing stem. The pith tends to elongate, but is held back by the outer and firmer tissues, which are thus kept tense. The relation of the inner and outer tissues is then analogous to that of the protoplast and wall in the turgescent cell, and the mechanical effect is the same. *It is thus seen that the firmness of succulent stems is due in large degree not only to the turgor of the individual cells, but also to the mutual tensions of their tissues.* Similar relations also hold for the tissues of leaves and roots, but these need not be described in detail.

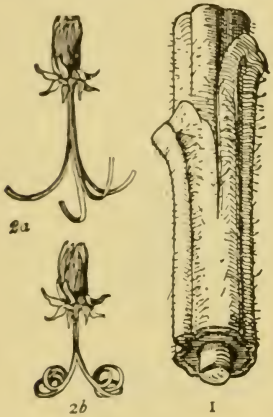

FIG. 108.

1, Shoot of Sunflower with pith separated by a cork-borer from the outer tissues. *2a*, split stem of Dandelion. *2b*, after immersion in water. (After Strasburger.)

Rigidity as based on Specific Mechanical Tissues.

Such methods serve to give the necessary mechanical strength to young parts. But as the tissues grow older, their walls become thickened. They are then less susceptible to turgor, as they are also more resistant to growth. Moreover, in the older parts the mechanical demand for support increases with the increasing burden of leaves and branches. These demands are met by *specific mechanical tissues*, fitted by their thickened walls to offer greater resistance. Though the effect of turgor is characteristic of young plants, and that of the specific mechanical tissues of the mature, there is no definite limit between the action of each. Dependence on the one merges gradually with age into dependence on the other, and in the growing part both sources of support may be effective at the same time.

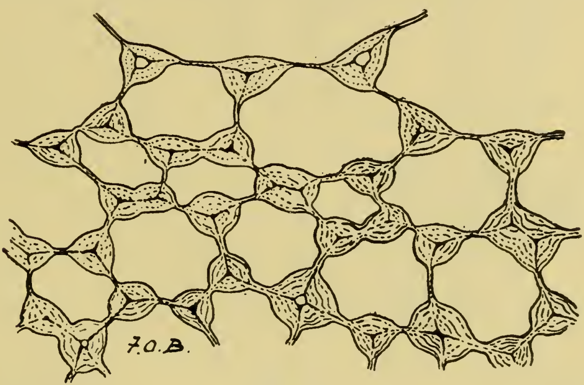

Fig. 109.

Collenchyma from the stem of the Potato, seen in transverse section. The walls only are shown. (× 300.)

There are two types of specific mechanical tissue, (*a*) *Collenchyma*, which is found in growing herbaceous stems and leaves ; and (*b*) *Sclerenchyma*, which is characteristic of more mature parts. *Collenchyma* consists of cells which retain their living protoplasts, and thus remain physiologically active, while chloroplasts are frequent in its cells. These cells usually have the form of 4-6-sided prisms, with transverse or oblique ends, and are sometimes transversely partitioned. The cell-walls are composed of *cellulose*, which is swollen in life with water. They are thicker at the angles of the prisms than at their flattened sides, where the thinner membrane allows of ready physiological interchange. This gives the tissue, when seen in transverse section, the appearance shown in Fig. 109. It is thus a tissue which, though mechanically effective, is not fully specialised for giving strength. The cells do not offer rigid resistance to elongation, but they themselves grow with the growth of the part they support, offering a persistent though plastic resistance. The position of the collenchyma is usually peripheral, closely below the epidermis. This gives it its full mechanical effect. In fluted stems it is usually massed at the projecting ridges, and between them it is often interrupted by thin-walled green tissue of the cortex. (Fig. 110.) Functionally it takes an intermediate place in the individual development between the state dependent upon turgor and the full rigidity of the mature state. The resistance which it offers to elongation is one of the chief factors in producing the mutual tensions of tissues above described in the succulent elongating stem.

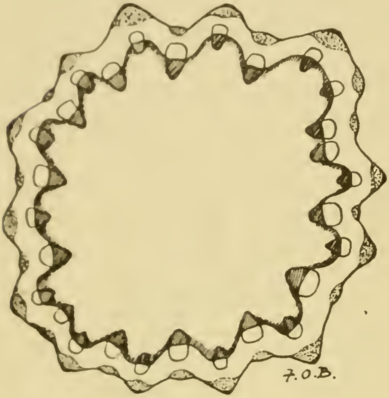

FIG. 110.

Flowering stem of *Astrantia* in transverse section. (× 10.) The collenchyma is dotted.

The *Sclerenchyma* is, however, the more important specific mechanical tissue. Its effectiveness depends partly upon its own characteristics, partly upon its distribution. It consists of cells with thickened walls, which are usually but not always lignified. When mature its protoplasts are no longer functionally active, and may be represented only by vestigial remains. It is then practically a dead tissue. The form of the cells varies. Sometimes they are cubical or oblong with square ends, and may be isolated, or disposed in groups. Such *stone-cells*, or *sclereids*, give a hard gritty texture to the parts where they occur, as in the bark or pith of various woody plants. The gritty nature of the fruit of the Pear is due to nests of such stone-cells. But frequently the sclerotic cells are elongated, and variously branched, as in the sclereids of the leaf of Tea, or unbranched with flattened ends, as in the leaf of *Hakea* (Fig. 111). Such cells are commonly isolated. They stiffen the parts where they occur by the resistance which their thickened walls offer to compression. The form, structure, and function of the sclereids of *Hakea*, which prop out the firm epidermis and thus give the leaf its remarkable stiffness, may be compared with that of the hollow steel columns used for supporting shop-fronts.

A more frequent, and mechanically a more effective type of strengthening cell is seen in the *elongated sclerenchyma-fibre*. Such cells are commonly associated in masses, often forming strands which run continuously for long distances. These strands of the Flax supply the material for linen, of the Jute for sacking, of Hemp, New Zealand Flax, etc., materials for cordage, while similar strands of the Coco-Nut, and other Palms are worked up into mats, brushes, etc. In the plant they frequently accompany the vascular strands, and are often associated with the phloem as *bast-fibres*, or with the xylem as *wood-fibres* (compare Fig. 38). But there is no necessary association with vascular tissues, and the sclerenchyma is often quite independent of them. The mechanical cells themselves are elongated, with ends pointed and sides flattened, so that they fit closely together. (Fig. 112, *A*, *B*.) The cells of Hemp are about 100 times as long as broad, in linen the proportion is about 200 to 1 ; in the extreme case of the Rhea fibre (*Boehmeria*) the length has been estimated at 1500 times the breadth. The lignified walls may be so thickened that the cell-cavity is obliterated. They are thus practically rods of resistant material.

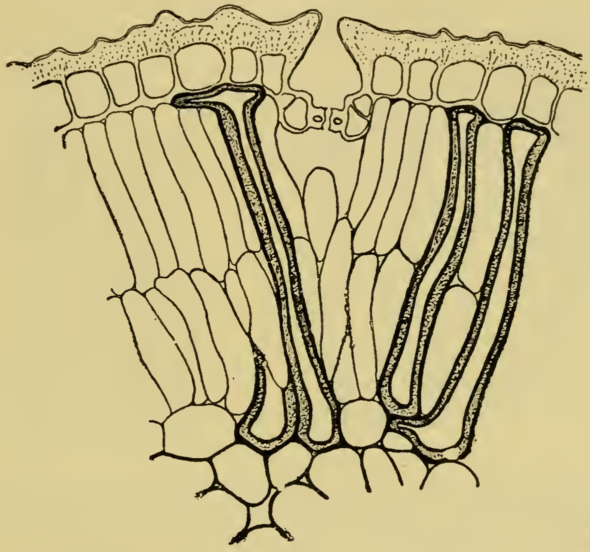

FIG. 111.

Part of a transverse section of the xerophytic leaf of *Hakea*, showing a stoma greatly depressed below the well-developed epidermis, which is propped out by thick-walled sclerotic cells. (× 150.) F. O. B.

Each develops from a single embryonic, or cambial cell. As it elongates, its pointed ends slide between those of other fibrous cells, taking a sinuous course. The result is that the cells of the strand interlock, and when a longitudinal stress[1] is applied, the resistant rods press laterally upon one another, so that the greater the stress the more closely are they united. Mechanically such strands act like solid metal wires.

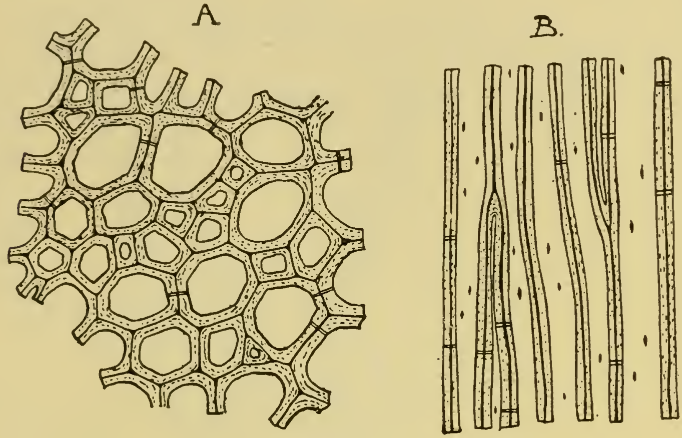

FIG. 112

A, Transverse section of sclerenchyma of stem of Sunflower. The larger sections show cells cut through the middle of the fibre, the smaller near to the pointed end. *B*, the same in longitudinal section, showing the pointed ends of the cells. Small pits are present, in surface view, and in section. F. O. B. (× 300.)

Characteristic features of the resistance of plant-fibres, as contrasted with those of certain metal wires of similar transverse section, show how different is the behaviour of the two under stress.

NAME.	Limit of Elasticity in Kg. per sq. mm.	Breaking stress in Kg. per sq. mm.	Elongation at limit of Elasticity per 1000 units of length.
Dasylirion - - -	17.8	21.6	13.3
New Zealand Flax - -	20	25	13
Hyacinth - - -	12.3	16.3	50
Garlic - - - -	14.7	17.6	38
Nolina - - - -	25	. .	14.5
Silver Wire - - -	11	29	. .
Wrought Iron - - -	13.13	40.9	0.67
Steel - - - - -	24.6	82	1.20

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[1] *Stress and strain.* When a force is applied to a piece of material, the material is said to be under *stress.* In mechanical construction those portions intended to be under *pull* are called *ties*, and those under *push*, *struts*. Ties are

The first column shows the maximum burden per unit of transverse section of the fibrous strand, or of the metal wire respectively, under which the *limit of elastic recovery* is not overstepped. The fibre of *Nolina* (25) is actually superior to steel (24.6). Other fibres compare favourably with silver and wrought iron. The second column shows the burden per unit of transverse section which causes rupture ; that is, it states the *limit of tenacity.* It is seen that in this metals are distinctly superior. But the table brings out a very important feature of plant-fibres, that their limits of elastic recovery and of tenacity are very nearly coincident, while those of metals are widely apart. *Metals are ductile, fibres are not.* The importance of this in the plant-body lies in the provision thus made for *perfect recovery after strain.* Great breaking strength would be of no value if the plant subjected to the strain were permanently deformed.[1] The third column shows the *elongation* which the strand or wire suffers *at the limit of elastic recovery*, stated in terms of units of length per 1000 of the strand as a whole. Here the difference between the fibres and the wires is strongly marked, the fibres yielding in much higher degree than the metal wires. This again meets the requirements of a plant exposed to forces, such as wind. For *the tissues while resisting the force very efficiently, yield to it, but recover very perfectly when the force is removed.*

In late years metal straps have been used largely in concrete construction, reinforcing the concrete in which they are embedded. Ordinary herbaceous plants are constructed on the same principle. The sclerotic strands correspond to the metal straps, the surrounding parenchyma with its turgescent cells corresponds mechanically to the concrete. The office of the latter in either case is to keep the resistant straps in place, while the straps resist the tensions which would produce loss of form. In the reinforced concrete a high degree of

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said to be under *tensile stress* when pulled, and struts under *compressive stress* when pushed. The term *strain* is used to signify the change of length or other dimensions or the change of form which occurs in a material under stress.

[1] Collenchyma is, however, exceptional. While its absolute strength is little inferior to that of bast fibres, its limit of elasticity is much lower : and it is thus liable to permanent elongation. But this is an advantage in growing stems in which it usually occurs ; for it offers no rigid barrier to growth, while it is sufficiently resistant to meet sudden stresses. It is like the Second Chamber in the Constitution of a State, which resists a new initiative ; but if the initiative be continuously pressed, it yields. Meantime stability is maintained.

rigidity is necessary, or the concrete would crack. But in the plant-body, with its elastic cells and tenacious fibres, a considerable change of form is allowable in yielding to the stress without permanent injury following. The herbaceous plant thus has a distinct superiority over any building of reinforced concrete, for the embedding medium is itself elastic. The conditions are most nearly matched by the covers of certain motor tyres, where resistance must be coupled with elasticity, and fibre is embedded in the rubber.

In the economical use of material the *disposition of the specific mechanical tissues* is important, both on grounds of lightness of the structure, and the physiological expense of the substance used. The problem of obtaining the best mechanical effect with the least expenditure varies with the requirements to be met. *The girder principle*, which has been adopted by engineers as a means of securing a high degree of mechanical efficiency with economy of material, is frequently illustrated in the construction of plants. It is even seen in plants of the Coal Period, such as *Cordaites*, which lived ages before the origin of man. The common type is the double-strap girder, which gives in transverse section the figure (I). If a girder of such construction be fixed in the position indicated by the figure, and loaded in the middle while it is supported at the ends, there will be a tendency to curvature which will compress the upper strap or flange, while the lower strap will suffer tension. The resistance to these stresses will depend upon the two straps being held rigidly in their relative positions by the connecting plate. The material will be most economically used if it be concentrated in the form of the upper and lower straps at the regions of greatest strain. The connecting plate may even be replaced in " latticed girders " by a system of connecting ties, which follow the lines of greatest stress. The wider the upper and lower straps are apart, consistent with their being held rigidly in place, the better the result will be. The principle is illustrated by the use of girders, or simple combinations of them, in the construction of bridges, floors, and shop-fronts. More complicated arrangements giving columnar construction are seen in lattice-signal-posts, and large gasometer-frames. The latter offer close analogies with certain types of stem-construction in plants.

In plants girder-construction depends upon differences of mechanical resistance of tissues. An illustration of a simple case is given in Fig. 113 from the leaf of *Cyperus*. On either side of the vascular strand there is a band of thick-walled resistant woody sclerenchyma. Each is close to the upper and lower surfaces respectively, indeed three cells of the lower epidermis are themselves sclerotic. These bands represent the upper and lower straps of the girder, while the less resistant vascular strand represents the connecting plate. The girder is kept in place by the softer tissues, but especially by the firm layers of epidermis.

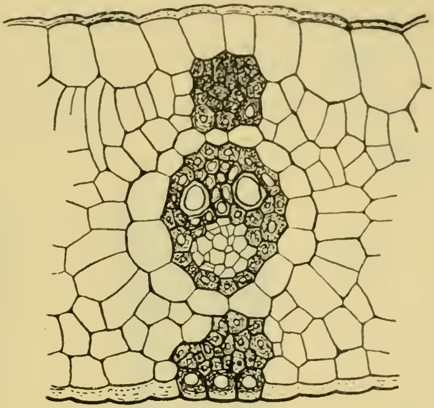

FIG. 113.
Transverse section through a leaf of *Cyperus*, showing a vascular strand with a strand of resistant sclerenchyma above and below, constituting a girder. (× 300.) F. O. B.

The requirements that are most commonly illustrated in plants fall under three heads, which are typified by parts of normally growing plants, though they are subject to great variety with the varying form of the plant-body:

(*a*) Columnar requirement, as in an upright stem.

(*b*) Stiffening of flattened surfaces, as in the leaf-blade, and protection of the margins against tearing.

(*c*) Rope-requirement, as in roots of upright plants exposed to wind.

(*a*) THE COLUMNAR REQUIREMENT.

The *columnar requirement*, for support of the growing dead-weight of branches, leaves, and fruits, is met in large Dicotyledons chiefly by the woody column, which grows in proportion to the growing need for support. It is cylindrical, so as to meet all winds equally. It is composed of mixed xylem-tissues, with continuous woody walls. The most important of these mechanically are the wood-fibres, and the resistant quality of the wood is roughly in proportion to their preponderance. But all the tissues,—vessels, wood-parenchyma, and medullary rays,—contribute in varying degree to the mechanical effect. This is enhanced as the central tissues die, and are converted into heart-wood. The method of construction is that of the solid column, now acknowledged by engineers to be not the most economical of material. But in Dicotyledons the retention of this rather primitive method is to be explained as a compromise, the success of which is evidence of its fitness to meet the circumstances. For the living part of the growing trunk affords in addition to mechanical strength, room also for storage, and a means of transmission of materials.

In the stems of Palms, where a large terminal tuft of leaves has to be supported at a great height against winds, the mechanically effective tissues are massed towards the periphery, while the central regions are softer. This may be compared with the hollow metal column filled with concrete, which has the effect of preventing the metal skin from "buckling." On a smaller scale this construction is found also in the stems of pithed Rushes and Sedges, and in many herbaceous Dicotyledons. It is only a step from such arrangements to that seen in the Bamboo, or on a smaller scale in the haulm of Grasses; and in some Dicotyledons, such as the Umbelliferae. Here the thin-walled pith present in the young state breaks away, leaving a central cavity surrounded by a cylinder of firmer tissue. In this case the comparison is with the hollow column so largely used in metal construction by man. But it is liable to "buckle," as has been found in the masts and

FIG. 114.

Stem of Bamboo including one node at its upper end. In *A* it is seen from outside, with transverse scar of the leaf-insertion, and the circular scar of its axillary branch. In *B* it is cut so as to show the hollow, and the septum which gives added strength. (Reduced to ½.)

spars of racing yachts, in which internal ties of metal have been used to meet that risk. In the haulms of Grasses, and conspicuously in the large Bamboos, hard woody septa at the level of the leaf-insertions serve the same purpose (Fig. 114). Without these it would not be possible for hollow stems to uphold the huge head of leaves, sometimes one hundred feet above ground, against all winds, as the Giant Bamboos are able to do.

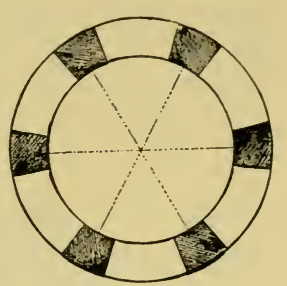

Fig. 115.
Diagram of crossed girders. See Text.

The hollow cylindrical stem of a Bamboo, or of a straw of wheat, may be imagined as corresponding to a series of crossed girders (Fig. 115), with the straps or flanges all fused laterally, so as to form a firm peripheral band. The effective material is placed as far as possible from the centre. The straps being fused laterally, the connecting plate or web of the individual girders can be dispensed with, and the stem is accordingly hollow. But in many cases, and especially in young stems of Dicotyledons, the relation of the structure to girder-construction is more plainly seen, since in them the straps of mechanical tissue are not fused laterally. This gives reality to the conception. Thus, in the stem of *Astrantia*, or more clearly in *Clematis* or *Lamium*, the bands of mechanical tissue are isolated, and alternate with softer tissues which keep them in their position (Figs. 116, 117). In *Astrantia*, the resolution of the whole arrangement into a girder-construction is less obvious because

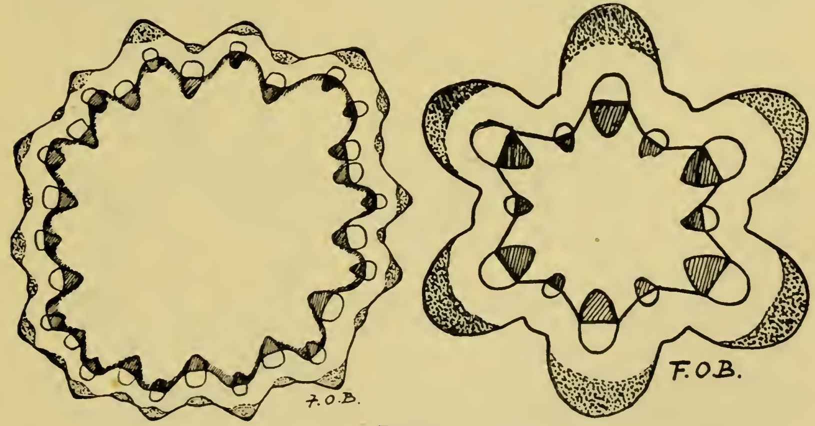

Fig. 116.

Flowering stem of *Astrantia* in transverse section. (× 10.) The collenchyma is dotted.

Transverse section of an internode of a stem of *Clematis*, showing a ring of six larger and six smaller vascular strands, surrounding the central pith, and covered externally by the thick cortex, with six projecting bands of collenchyma. (× 15.)

of the large number of the strands, and their slight irregularities; and this is common in herbaceous Dicotyledons. But in the case of *Clematis* only three crossed girders enter into the construction, so that the method appears clearer: and still more so in *Lamium*, where there are only two. There are other points of wide application illustrated in these cases. The stems are fluted, with projecting angles, and one strap of mechanical tissue is seated in each. This gives added strength on the principal of the fluted column, the depth of each girder being thereby increased. The second point is that one of the stronger vascular strands is opposite each of the mechanically strengthened ridges, so that the construction of the stem, as it grows older and the vascular strands become mechanically more effective, resembles that of a number of peripheral girders disposed in a ring. This method is seen in the frames supporting large gasometers. The central tissue may even be replaced by a cavity filled with air, which gives added point to the comparison. The simpler construction of the stem in *Lamium* may be compared mechanically with that of a lattice signal post. In it four bands of metal occupy the four angles, and are kept in place by a lattice work of thin straps, while the centre is hollow. So in *Lamium* (Fig. 117), the projecting angles contain the chief mechanical tissue. The softer tissues hold them in place, while there is a central pith-cavity. It is immaterial exactly how the mechanical arrangements are analysed in such stems as these quoted. The point is that the girder principle can be recognised in them all, with strengthening strands isolated and peripheral. But in Dicotyledons these arrangements are apt to be lost sight of as the stems grow older, owing to secondary thickening, and the development of the vascular ring into the central column of wood (p. 58, etc.). The stem thus assumes at last the type of the solid column. In large tropical trees a further mechanical device is often seen at the base. By unequal thickening broad flanges are produced, which radiate outwards, and act in support like the buttresses of a Gothic tower. The final result of such development might be compared with the outline of the greatly widened base of the Eiffel Tower.

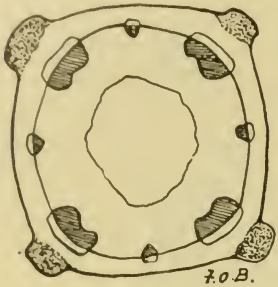

FIG. 117.

Transverse section of stem of *Lamium*, showing projecting angles of collenchyma (dotted), opposite four larger vascular strands: an arrangement equivalent to two crossed girders. (× 14.)

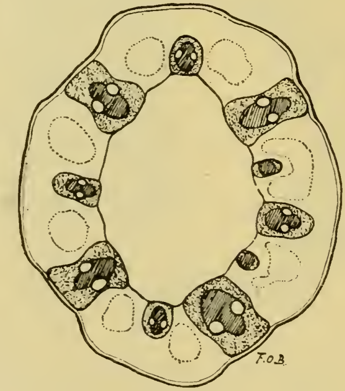

FIG. 118.

Transverse section of the shaft of *Scirpus* (*Eleocharis*) *caespitosus*, showing four large girders, with smaller and less perfect girders between them. Centrally is a large cavity. The dotted areas indicate thin-walled water-storage tissue. (× 62.)

Similar principles hold also for the stems of Monocotyledons; but the circumstance that their closed vascular strands are usually scattered over the transverse section tends to complicate their scheme of construction (p. 51). On the other hand the absence of cambial thickening makes its recognition in the mature stem easier. Commonly the sclerotic tissue accompanies each vascular strand, as bands following its course, or even as a sheath encircling it (Fig. 113). Such an arrangement is in itself comparable with a girder, and occasionally, where there is a ring of vascular strands thus invested, the construction is simply a circle of sub-epidermal girders, as in *Scirpus* (*Eleocharis*) *caespitosus* (Fig. 118). Sometimes the sclerotic bands may be quite separate from the vascular strands, though usually opposite to the strongest of them, as in *Schoenus nigricans* (compare Fig. 28, p. 51). These simple arrangements are very like those seen in the Dicotyledons. But in most Monocotyledons the vascular strands are scattered over the transverse section, and this introduces a good deal of variety of detail. Where the vascular strands are thus scattered, and the mechanical construction more complicated, the sclerotic bands may be fused together laterally in various ways. A continuous sclerotic ring may thus be formed, and the vascular strands be embedded in it, with or without flanges projecting from it (Fig. 119). Such structure developed on a larger scale, and with more general fusion of the sclerotic tissues, leads to the condition seen in the large Bamboos and Palms.

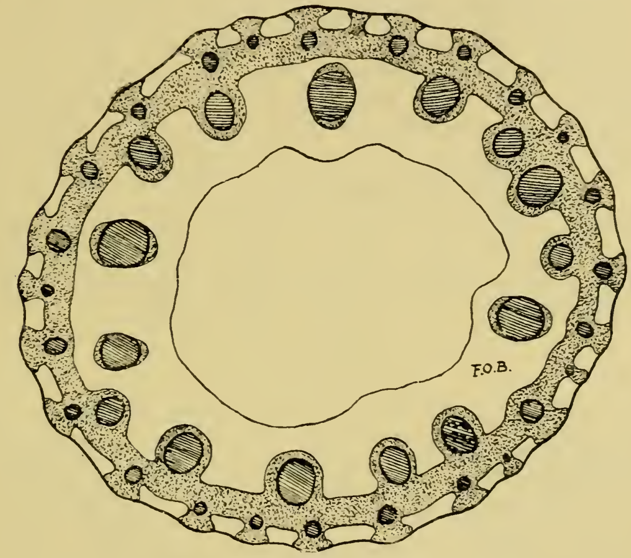

FIG. 119.

Transverse section of the flowering shaft of *Molinia coerulea*. Centrally is a large cavity. Thin-walled tissue is left clear: sclerotic tissue is dotted, vascular strands cross-hatched. The peripheral vascular strands are embedded in a continuous ring of mechanical tissue. (× 40.)

The case of *Molinia coerulea* proves how effective this mechanical strengthening actually is. The structure of the haulm is shown in transverse section in Fig. 119. At its base it is about $\frac{1}{16}$ of an inch in diameter, but it is there supported in some degree by its sheathing leaves. It may grow in favourable cases to a length of 30 inches before bearing its inflorescence. Thus the length of the stem is to its diameter as about 500 to 1, and still it can uphold the inflorescence at its distal end, together with the weight of the fruit when ripe. This extreme proportion of length to diameter suffices for a small Grass; but it cannot be maintained indefinitely for larger structures. For the weight of a structure varies as the cube of its dimensions, while the strength varies only as the square. There must be then a limit of size beyond which it becomes impossible for a certain type of structure to be maintained. For instance, according to the proportion of the *Molinia* stem, a ten-foot fishing rod should only be ¼ inch in diameter at the butt; but it is thicker than that. A striking case is seen in the Giant Bamboos. Ewart quotes one 60 metres high, and 40 cms. in diameter at the base. That is a proportion of only about 150 to 1. For a plant of that size these dimensions have been calculated as about the limit possible, though the proportions are less striking than those of the smaller *Molinia*. There is in point of fact a size-limit for any plan of plant-construction based upon a certain quality and use of material: beyond this limit the stem will either bend or break. In the Bamboo, which approaches the limit, the extreme top does bend in a graceful curve; as it does also in the haulms of most Grasses, which like *Molinia* approach the limit of mechanical resistance from their actual dimensions, structure and materials.

(*b*) Stiffening and Protection of Flattened Surfaces.

The mechanical problems affecting the dorsiventral leaf differ from those of the radially constructed stem. The end to be gained is the largest possible expanse of blade, with the least possible risk from winds, and the employment of the least possible material. The elastic petiole allows the blade as a whole to yield before the wind. In the extreme case of the Aspen, where the least breath causes a shiver of the leaves, the petiole is laterally compressed so as to be very flexible. But in most leaves it is stiffer, and semilunar in section, with the convex side downwards, an arrangement which secures efficient support for the blade, while still permitting some freedom of movement (Fig. 45, p. 70). Another feature of mechanical importance is the cutting of the larger leaves into segments, so that while the aggregate area may still be considerable, no unduly large surface is exposed to the wind. The risks of a large leaf-area are two: first, that of folding into so sharp a curve as to crush the soft mesophyll between the firmer layers of epidermis; and second, that of tearing from the margin inwards. The former is met by the vascular venation, which is often accompanied by sclerotic strands, and by enlargement of the surrounding tissues so as to form strong ribs. The latter danger is met by arched venation, which is often aided by marginal deposits of sclerenchyma. The whole blade is held together by the upper and lower layers of epidermis, which, having a thickened outer wall, form a firm skin over the softer mesophyll within. Sometimes the mesophyll may be itself sclerotic in places, as it is in many Monocotyledons.

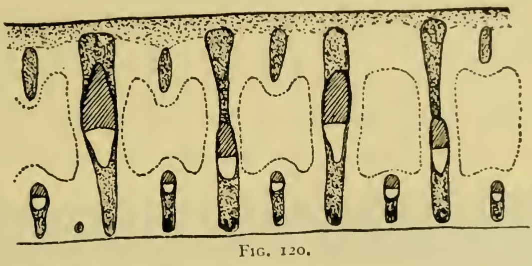

FIG. 120.

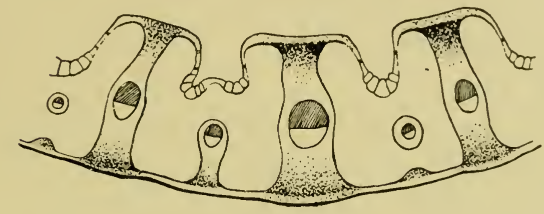

FIG. 121.

FIG. 122.

FIG. 120. Transverse section of the leaf of *Phormium tenax*, New Zealand Flax. FIG. 121. ditto, *Elymus arenarius*. FIG. 122. ditto, *Deschampsia caespitosa*. (× 20.) Thin-walled tissue left clear: mechanical tissue dotted; xylem cross-hatched. Aqueous cells in Figs. 121, 122 indicated diagrammatically. In Fig. 120, aqueous areas are outlined with dots. The involutions in Figs. 121, 122 appear in positions opposite to the aqueous areas in Fig. 120. (F.O.B.)

The structural stiffening of the flattened blade against folding is best illustrated in the leaves of Monocotyledons, for there the parallel venation makes the transverse section appear simpler. All the main veins are then cut at right-angles, and in simple cases each may present an appearance as in Fig. 113, p. 181, of *Cyperus*. Sclerotic strands follow the veins on either side, forming with each a girder, as above explained. Since these girders run parallel, and are held in place by the firm upper and lower epidermis, the construction of the whole is on the same principle as that of a lattice-girder railway-bridge, in which also a high degree of rigidity is required, together with economy of material. In some, as in the old Charing Cross railway-bridge, the tracks run between the girders, that space being left vacant in the construction. In many leaves of Monocotyledons the corresponding space between the girders is occupied by mechanically ineffective mesophyll, while in some there are large thin-walled cells for water-storage (Fig. 120). It thus appears that the requisite stiffness of Monocotyledon-leaves is gained by means very similar to those employed by engineers to obtain like results in bridges. But irregularities are frequent, especially in thick leaves. The girders may be incomplete, or the sclerotic bands may be fused laterally. But still the girder-principle may be recognised as underlying such deviations.

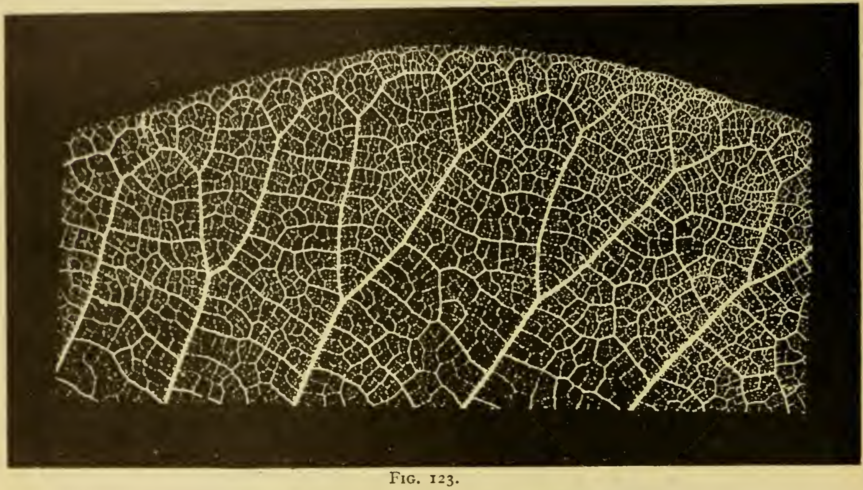

FIG. 123.

Photograph of the skeleton of a Dicotyledon leaf, showing reticulation with successive intra-marginal arches. (Natural size.)

The most interesting variants are those seen in xerophilous grass-leaves, which curl automatically so as to check transpiration. Native examples are seen in the Sheep's Fescue, the Marram, Lyme, and Tussock Grasses (Figs. 120-122). Their mechanism shows a reduction of the mesophyll with a corresponding involution of the surface between the girders, while the latter are specially deep. The upper leaf-surface is thus marked by parallel grooves, the aqueous cells at the bottom of each furrow being large and thin-walled. The lower side of the leaf is sclerotic, so as to maintain its outline, while the upper is liable to shrink with drought. Such shrinkage draws the margins together. The sloping faces of the grooves, which bear the stomata, meet, and transpiration is checked. Access of water, on the other hand, swells the aqueous cells, and the leaf flattens out again.

The Monocotyledon leaf, with its parallel venation, is usually secure from marginal tearing. A prominent exception is seen in the Banana, where the huge leaf seldom appears perfect in plants grown in the open. It has a midrib from which the veins run out parallel towards the margin, on the plan of a feather. These leaves are readily slit to ribbons by the wind, from the margin inwards, since there is no sufficient marginal protection. In most Palms a similar subdivision of the leaf is carried out during development, by the plants themselves. Certain tissue-tracts dry up, cutting the blade into segments, and giving the appearance when mature of a true pinnation. For smaller leaves tearing from the margin is still a risk, and there are structural arrangements which prevent it. The commonest is the curving of the veins into intramarginal arches (Fig. 123). Several series of these of successively smaller size towards the margin, effectually check tearing. The most dangerous spots are naturally the indentations in toothed or deeply cut leaves. These are often protected by small "gussets" of indurated tissue at the base of each sinus. Good examples are seen in Ferns, as in the genus *Asplenium* (Fig. 124); or a special strongly arched vein may run across the point of deepest indentation; while not uncommonly a patch of sclerotic cells may be fused with it at the point of danger (Fig. 125). This is often continued along the margin as a sclerotic band, which serves, like the hem of a handkerchief, to prevent a marginal tearing. Similar hems are found in many ordinary leaves, but conspicuously in xerophilous plants. Good examples are seen in the Date Palm, and in the Gum Trees. The

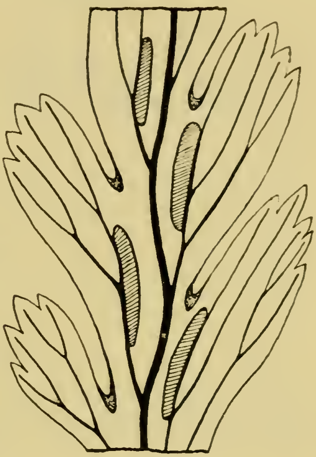

FIG. 124.

Part of leaf of *Asplenium horridum*, showing "gussets" dotted, at the base of indentations. (Slightly enlarged.) F.O.B.

marginal stiffening becomes actually aggressive in spinous leaves, such as the Holly, Barberry, and Gorse. A particular instance of a like sclerotic development that serves a peaceful end is seen in the Sand Sedge. It burrows with its creeping rhizome through the sand. The apical bud has its successive scale-leaves developed to a point, tipped with hard sclerenchyma, by means of which it passes through soft objects like a brad-awl. These are a few examples of the mechanical adaptability of the leaves of Flowering Plants.

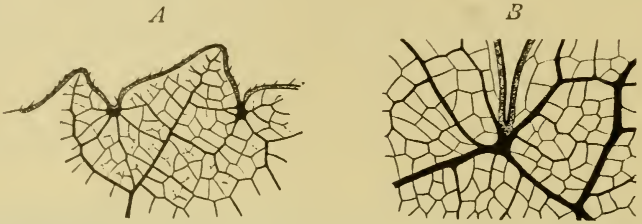

FIG. 125.

"Gussets" at margins of the indentations of leaves (*A*) of the Elm, (*B*) of the Sycamore, showing their relation to the vascular network, and to the mechanically strengthened margin. (× 14.) F. O. B.

(*c*) THE ROPE-REQUIREMENT.

Those parts of the plant, such as roots or rhizomes, which hold it upright in the soil against the impact of winds are subject to longitudinal tension, as on a rope or string. In cordage, in order to resist such tension, the fibres are twisted together so as to be grouped in as small a transverse area as possible. This method secures the even distribution of the stress over them all. A similar condensation of the mechanical tissues, but without the twisting, is usual in roots. Their stele is small compared with the whole transverse section, and it is frequently pithless. But often the xylem stops short of the centre, which is then occupied by sclerotic tissue. This links up the xylem, so as to form with it a resistant central cord (compare Fig. 58, of *Acorus*). In larger roots a pith may be present, surrounded by a dense ring of mechanically effective tissue composed in the same way (Fig. 126). But still the

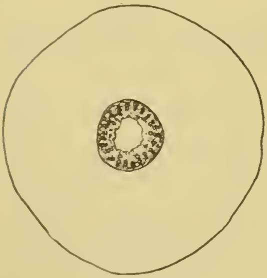

FIG. 126.

Transverse section of root of *Ruscus* showing large proportion of cortex to the contracted and pithed stele. (× 12.) F.O.B.

stele is compact as compared with that of the axis. Underground rhizomes show a similar construction. Their stele is contracted, and their cortex widened, as is seen in the Marram Grass, and still more clearly in the Sand Sedge, where the cortex is very weak and lacunar, while the stele is compactly cemented together with sclerotic tissue, so as to form a solid core (Fig. 127, *A*). This is in sharp contrast to the aerial stems of most Sedges (Fig. 127, *B*). Stems supporting heavy, pendent fruits show a like structure ; also submerged and some climbing stems, all of which are liable to longitudinal tension. The similar modification of plants of such various habit, when subjected to the same mechanical demand, indicates that the rope-like concentration is adaptive.

Fig. 127.

Sections of stems of two Sedges. *A*, Rhizome of *Carex arenaria* with mechanical tissue condensed centrally, as resistant to the rope-requirement. (× 14.) *B*, *Carex vulgaris*, aerial stem constructed to meet the columnar requirement. (× 25.)

The problem for strut-roots, such as are seen at the base of the stem of the Maize, is a mixed one ; for the roots on the windward side of the plant suffer longitudinal tension, while those on the lee side act as oblique struts, and are subject to columnar pressure. The structural requirements are thus opposed. The mechanical tissues in such roots are found to form two systems (Fig. 128). The stele is compact, and cemented together in a hollow ring, which is, however, wider than in the underground roots. It is suited to resist longitudinal tension, but is not highly specialised to meet it. The cortex is, however, sclerotic, the thickening being greatest at the periphery. This is suited to meet the columnar

Fig. 128.

Transverse section of strut-root of *Zea Mais*. The mechanical tissue of the cortex is dotted. (× 12.) F.O.B.

requirement. Thus the mixed problem is solved by a structure that serves both purposes.

Such cases as those quoted in the last paragraphs confirm the view which follows inevitably from the study of the distribution of the mechanical tissues generally in plants, viz. that those methods are adaptive, and have been acquired in the course of Descent in accordance with the requirements. The structure is as a rule hereditary, though the conditions to which the developing parts are exposed may have an influence in determining the quantity of sclerotic tissue formed in the individual part. There is reason to believe that the forces acting on the developing part serve as stimuli, increasing or even causing the formation of the mechanical tissue. This is in accordance with the well known fact that those tendrils of climbers which grasp a support develop much more strongly, and are able to bear a greater load than those which do not. In the large woody climbers of the tropics the difference is often very marked, the fixed tendril developing as a large woody structure.

While such observations are in themselves interesting in their bearing on the quantity of the mechanical tissue present, they do not explain the origin of the methods of its distribution. The degree of parallelism which those methods show to the methods of modern engineers in using their stone, steel, and concrete, is remarkable. While we admire the efficiency of the result in either case, and especially the economy of material made possible by such methods, it is to be borne in mind that the priority of initiative undoubtedly lies with the Plant. For many of the methods represented by ancient types of vegetation have been adopted by man only within the last few decades. Nor is there evidence that engineers ever took, as well they might have done, any suggestion from the study of the engineering methods of Plants. What we see in the two cases is accordingly a result of *parallel, or homoplastic development.* Similar results have been acquired independently along two quite distinct lines of evolution. In the one case the results have followed from human calculation and experiment, in the other they are described as "adaptive." But it is still an open question how the mechanically effective structures seen in plants, and produced during development, are causally related to the requirements of the adult state.

CHAPTER XI.

MODIFICATIONS OF FORM IN THE VEGETATIVE SYSTEM OF THE HIGHER PLANTS.

It has been seen that the primary construction of the Higher Plants is according to a general and uniform plan (p. 14). But the scheme may be worked out in detail in very different ways. Either the root or the shoot, or both, may vary in form and proportion in different plants. Such differences are clearly related to the conditions under which the plants grow. Since it is possible in very many cases to see that the particular form taken is suitable for successful life under corresponding particular conditions, such forms are described as being *specialised*, or *adapted* to them. Those special modifications of form which lead to success are described as *adaptations*, and will be so grouped here: though with the same reservation as to causality as that expressed at the close of the preceding chapter with reference to internal structure.

Plants may be recognised as being thus adapted to the *medium* in which they grow; as, for instance, in water or in air: to other *physical conditions*, such as the action of gravity, or the direction of light: to the *climate* to which they are exposed, hot or cold, dry or moist, equable or with marked seasons, quiescent or stormy: or to the *soil* which provides them with requisite supplies: or they may show special features which enable them to take advantage of other surrounding circumstances. Prominent examples of this are seen in plants which *straggle* or *climb* over others; or in those which, by taking to some irregular form of nutrition, derive advantage from their neighbours as *parasites*, or in other ways. Such modifications of form according to circumstance often lead to difficulties in recognition of the category of parts to which the modified organs rightly belong. A stem or even a root may carry out photosynthesis. A leaf may be effective only for climbing, or for protection. It becomes therefore necessary to observe some order and method in the study of parts so variable. The classification of parts of the Plant will be taken up in Chapter XX.: meanwhile a few examples illustrating the adaptability of the plant will be described in the present chapter. But it would be impossible in such a book as this to treat so wide a subject exhaustively. It must suffice to refer to the *Natural History of Plants*, by Kerner and Oliver (Blackie & Son, 1895, 4 vols.), where many adaptive features of plants are described and illustrated; or for the consequences of adaptation as shown in the distribution of British Plants to *Types of British Vegetation*, by Tansley (Camb. Univ. Press).

BIOLOGY OF SEASON AND OF DURATION.

If we attempt to sketch a general, that is a non-specialised type of Flowering Plant, it would have a cylindrical upright stem, bearing leaves with petiole and lamina radiating out on all sides of it, and with axillary branches repeating the characters of the main shoot. Its root-system would consist of a tap-root and lateral roots of successive orders, all fibrous. A young Sycamore or Apple-tree would answer this general description. Further, it seems probable that the perennial state was prevalent, or even constant among early Vascular Plants. For it is seen almost exclusively in living Pteridophytes and Gymnosperms, and it is characteristic of the early fossils. So that in this respect, as also in their general form, an Apple or a Sycamore may be held as representing a type of vegetative construction usual for early Flowering Plants.

In one marked feature, however, the Sycamore and the Apple are certainly adaptive. Both are *deciduous*, that is they drop their leaves in autumn, as do most of our British trees and shrubs. *Leaf-fall* is clearly related to season. It brings the biological advantage of reducing the transpiring area at the time of low temperature, when the activity of the roots in the cold soil declines. It is in fact a provision against what may be called *physiological drought*, for the roots in the cold soil in winter are unable to make up for any great loss of water by transpiration. But many familiar plants retain their leaves during the winter, as "evergreens." They are mostly shrubs with leathery leaves, and many of them have been introduced from southern lands, such as the Rhododendron and Cherry-Laurel, from the Levant; but Holly, and Yew, and Ivy are native evergreens.

The evergreen state is more common in plants of lands where the seasons are equable, and it is probably a primitive state, while the deciduous habit has been acquired in species that have spread to regions with marked seasons. On the other hand, in hotter climates than our own, a dry and hot season may also be tided over by many plants by a fall of their leaves, and a new suit of leaves is usually formed after the commencement of the rains. The physiological advantage is similar to that of our autumn leaf-fall at home. Protection against drought is gained. But the drought thus met in the tropics is a real lack of water in hot weather. In very hot dry seasons our own trees sometimes drop their leaves in the same way. Thus by a simple modification plants can limit their transpiring area temporarily. However prominent the fall of the leaf in autumn may appear to be, it is not a fundamental feature, but only a special adaptation to season.

The *annual habit* may similarly be regarded as an accommodation to seasonal change. The seed is more resistant to extremes of temperature and drought than the growing plant. If then the vegetative development, from germination to flowering and fruiting, can all be completed within one growing season, an adverse period can be safely passed as seed, and the species will survive. Practically this has proved more effective in temperate than in tropical climates, as is shown by the prevalence of annuals in the temperate Flora. On the other hand, annuals are few in forest areas, which are less favourable to their growth than open ground. It is worthy of note that the Arctic and Alpine Floras consist almost entirely of perennials. This is easily understood, since the vegetative season is there too short for the completion both of vegetation and propagation. The fact is illustrated by the Alpine Flora of the Scottish Hills, which is distinctively Arctic in its character.

PERENNATION AND STORAGE.

Perennation, that is the maintenance of the individual from year to year, presents no difficulties where the seasons are equable, as in many tropical areas: here perennials, growing steadily on from year to year, form a leading element in the Flora. But in temperate regions, with their strongly marked seasons, various adaptations of the vegetative shoot besides that of leaf-fall may be seen, especially in herbaceous plants, for tiding over the winter. They are associated with the *storage of material*, which is thus carried over from one season to the next (Chapter VIII.). The simplest case is that of biennial plants, such as the Evening Primrose and Foxglove ; or, among cultivated plants, the Turnip, Carrot, Beet-root, or Onion. These in their first year store their surplus nutriment in the vegetative organs at the base of the plant, and use it up in flowering and fruiting in the following year, after which the plant dies. Extreme cases of this method, where the vegetative period may extend over several years, and is terminated by flowering, fruiting, and death of the individual, are seen in certain Bamboos, in *Agave*, and conspicuously in the large Palm, *Corypha*. This plant, after years of vegetative growth, flowers with an inflorescence thirty or forty feet in height, fruits profusely, and dies.

FIG. 129.
Perennial stock of *Iris*. *a*, *b*, *c*, successive yearly growths. (After Figuier.)

On the other hand, if the flowering be not profuse the perennation may go on indefinitely, as in ordinary bulbs and herbaceous plants. Each year a surplus of food-material is laid aside in underground parts. In autumn the aerial parts may die away, but the stock remains dormant and usually buried underground. Its store is thus protected from the rigours of winter, till in spring fresh shoots develop similar to those of the previous year. Most of these plants form their foliage leaves first, and they have the advantage of developing more rapidly than in germination, as they can draw on the store already in hand in the stock. But some flower at once, even before their vegetative leaves are fully formed, as in the Christmas Rose (*Helleborus*), the Crocus, and Snowdrop.

For the disposal of their store a slight distension of the tissues is often sufficient in these herbaceous perennials. This is seen in the Iris (Fig. 129), where the short stock grows onwards from year to year, bearing fresh leaves each season and axillary buds, and storing each year's surplus in the massive stem. In other cases the various parts may be considerably changed in their proportions. Thus the roots of the *Dahlia* are swollen to hold inulin (Fig. 130), and root-storage is also seen in the native Orchids, in *Ranunculus Ficaria*, and in *Spiraea Filipendula*. But it is more frequently the stem, or rhizome as it is called when underground, that is distended for storage. The familiar corm of the *Crocus* is the base of an upright stem of the previous season's growth, which is swollen for storage. The store is depleted in the spring by the development of leaves and a terminal flower upon a new axillary bud. The foliage leaves on that axillary bud serve to nourish it as the season progresses, and its distended base then remains

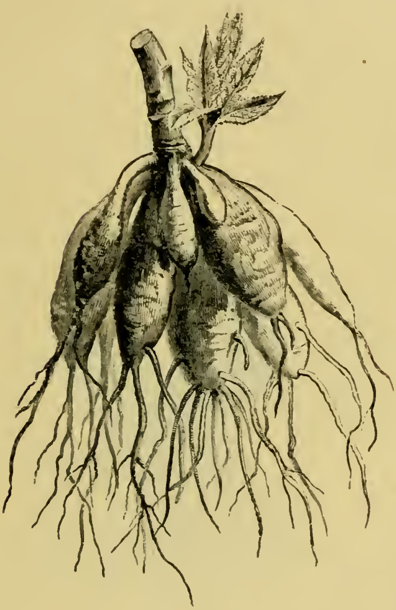

FIG. 130.
Tuberous roots of the *Dahlia*. (After Figuier.)

FIG. 131.
Corm, or storage stem of *Crocus*. (After Figuier.)

as the swollen corm for the succeeding season. The membranous bases of its withered leaves cover the corm externally, while their axillary buds may provide additional corms. The perennation is thus carried out by a sympodial series of storage-corms (Fig. 131). Similar distended axes are found in many other perennials, *e.g.* the Tuberous Buttercup (*Ranunculus bulbosus*), and the Pig-Nut (*Conopodium denudatum*). In other cases the storage is in lateral branches borne in large numbers, as in the Potato and Jerusalem Artichoke.

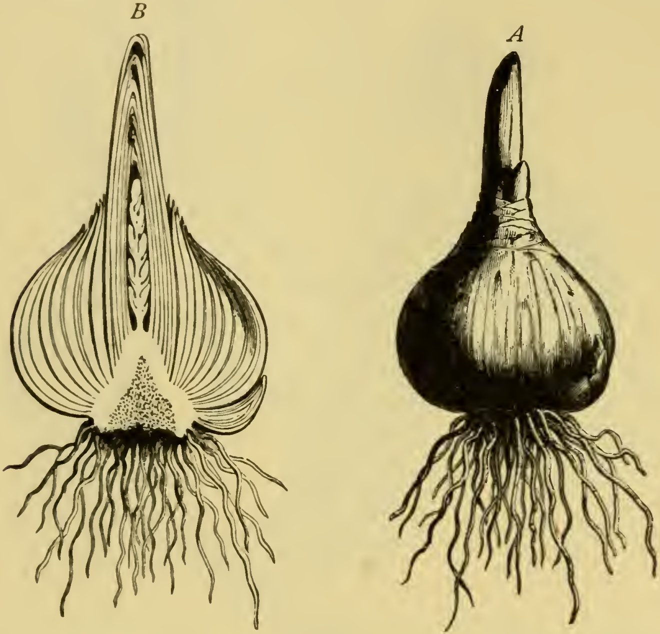

FIG. 132.
Bulb of the Hyacinth. *A*, seen externally; *B*, in median section. (After Figuier.)

These will be considered later in relation to vegetative propagation, to which such developments readily lead. The bulb, as in the Hyacinth, Snowdrop, or Lily, is similarly an upright, abbreviated, perennial shoot, with its growth interrupted by dormant periods. Its biology corresponds to that of the corm; but here the chief storage region is not the axis, which remains small and broadly conical, but the bases of the leaves. The whole bulb is in fact a perennating bud, the apex of which terminates in a flower, or inflorescence, while the growth is then continued by one or more leafy buds formed in the axils of the storage leaves (Fig. 132). The plants quoted are sufficiently distinct from one another to show that they are all cases of independent adaptation, though the method of their perennation is essentially the same in each.

Such arrangements are biologically suited to life under strongly marked seasons. The plant starts the active season of each year with a sufficient store of nutrition already in hand to support rapid flowering. In the remainder of the active season the store for the next year is acquired by the expanded foliage leaves, and laid aside in the ripening bulb. The bulb-dealer is understood to sell fully ripened bulbs : flower-buds are already present in them, and only wait to expand. The purchaser simply offers the conditions for active growth, and for the transfer of the store to the flowering region. But to ensure a repetition of the flowering in the next year he must fully ripen the bulb again as before. This is often difficult, or impossible in the case of room-culture, or in towns. Hence the dealer has a safe and continued market, based on the ignorance, or the lack of opportunity of the public. The professional bulb-grower secures normal perennation, with seasonal flowering ; the purchaser is apt to forget that its continued success depends on nutrition being maintained till the green leaves shrivel, and functional activity ceases for the year. This dormant state, in which the bulb or corm is bought, is itself an accommodation to seasonal drought. The bulb-habit is widely spread, but it is specially characteristic of countries like Southern Europe and the Cape, with a moist spring, but a dry and hot summer.

Symmetry, and its Modifications.

The Root-System, developing in the soil, finds a medium in which the conditions of temperature and moisture are relatively constant; but its form is liable to be strongly influenced by the texture of the soil. Growing roots yield readily to the mechanical resistance thus offered by any large obstacle. But if the roots develop in water, or if the texture of the soil be fine and uniform, as it is in prepared garden soil, the root-system develops with a regular symmetry. When, as in Dicotyledons, there is a definite tap-root, this grows vertically downwards, and the lateral roots radiate from it equally in all directions. Except for the effects of mechanical resistance, the root-system of ordinary plants shows little departure from this regular symmetry, while the individual root is typically cylindrical. It is different where, as in epiphytes, the roots are aerial. Thus those Orchids, which normally grow perched on the branches of trees, but are cultivated in hanging baskets or on cork, often have roots of a flattened form, which follow closely the surface to which they become attached. Occasionally they may even become green, and act as effective organs of Photosynthesis. But these are exceptional cases. Speaking generally the root of Flowering Plants retains its uniform cylindrical outline, and the whole *root-system* is built up as *regularly or radially symmetrical.* This fact may rightly be related to the uniformity of its usual surroundings.

The Shoot, on the other hand, is exposed to much more varied conditions than the root. It may be developed in water, still or moving; or if developed in air, it may be subjected to various degrees of lighting and moisture, and to winds from any quarter, as well as to the various incidence of gravity. It is possible to trace, in the different forms of the shoot which we see, a relation to and fitness for its surroundings. It would be strange if the shoot, which is so adaptable individually as we have seen it to be (Chapter IX.), should not show variety of conformation in the race, seeing that its surroundings are so diverse. It may not be possible to correlate all its forms directly, or even indirectly with circumstance. The difficult question of the actual method, by which such adaptive features as we recognise may have been produced in Descent, must be also left aside. But we may agree to accept as results of adaptation those features which harmonise with the surroundings: and from this point of view the shoot and its parts may be studied comparatively.

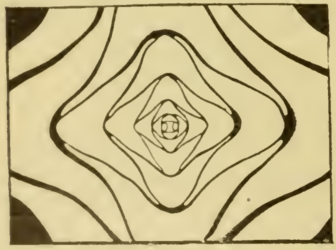

Fig. 133.
Transverse section through the apical bud of *Epilobium angustifolium*, L., showing a symmetrical 2 × 2, or decussate system. (After Church.)

An ordinary *upright shoot* develops as a rule with *radial symmetry*, that is equally all round the central axis. The axis being cylindrical meets equally the impact of all winds, and its leaves radiate out from it as a centre, occupying a circular area whose radius is the length of the mature leaf. This type is probably a primitive one, and is very general. But it may be worked out variously in detail as regards the arrangement of the leaves, as well as in their form, so as to secure an approximately equal exposure of all the leaves to the incidence of light. It is obviously undesirable that one leaf shall overshadow another, and it is interesting to observe the various ways in which this may be avoided.

Following on the paired seed-leaves, the plumular leaves of Dicotyledons are often paired also, and at right angles to the prior pair (*decussate arrangement*). This arrangement may be maintained through life, as it is in the Dead-Nettle, Willow-herb (Fig. 133), Lilac, Horse-Chestnut, or Sycamore. The upright shoot of the Sycamore is a good example of the way in which the circular area round the axis is put to the best use by leaves arranged on a decussate plan. Each successive pair fits into the gap between those of the preceding pair. But if the internodes were short, as they are in the young state, the higher would overshadow the next pair but one of lower leaves. This difficulty is met by the lower pair having longer petioles, so that their blades are carried out beyond those of the leaves immediately above them, forming a compact "*leaf-mosaic*" (Fig. 134).

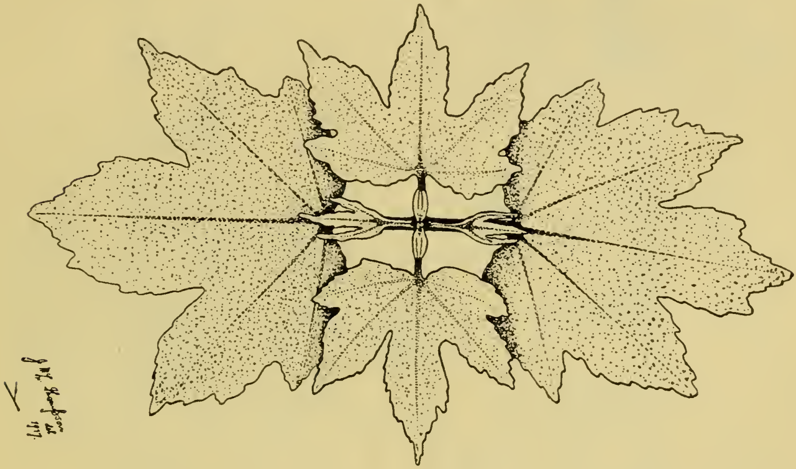

FIG. 134.

Young leafy shoot of Sycamore seen from above: showing how with very little overlapping the leaf-blades form a mosaic. The spaces unoccupied centrally will be filled as the younger leaves expand.

The decussate is the simplest of the *cyclic* or *whorled* arrangements, where two or more leaves are seated at the same level. But in other cases the number of the leaves at the same level may be not two only, but three, four, or more. As in the decussate plan the leaves of each succeeding whorl alternate as a rule with those of the preceding, so that they occupy the spaces between them, an arrangement that is very convenient in the packing of the crowded parts into small compass in the bud. A transition to higher numbers in the cycle may be seen in the individual plant. Thus in *Fuchsia*, which has usually decussate leaves, a very strong shoot may bear alternating whorls of three. In *Lysimachia vulgaris*, and in the Privet, a like variability is common. It is styled *meristic variation*, and probably one factor in producing it is the size of the apical cone, which, when large proportionally to the leaf-primordia, can accommodate a larger number of young leaves at the same level. Such variations are common in the floral region, where cyclic arrangements prevail. (Compare Floral Diagrams in Appendix A.)

But in most Dicotyledons, and very generally in Monocotyledons, the arrangement of the leaves is *alternate*; that is, they are seated singly, each at a different level upon the axis. The arrangement is often such that an ascending spiral line may be drawn round the mature stem so as to thread together the bases of them all. Such arrangements are therefore described as *spiral*. That the cyclic and spiral modes of arrangement are not essentially distinct from one another is shown by the fact that both may appear successively in the same plant. For instance, in the Sunflower, the seedling starts with paired cotyledons, followed by decussate leaves of the plumule (Fig. 135, A), which arrangement may be maintained for a time (C); but sooner or later irregularities appear (B), leading to an alternate arrangement (D), which becomes more complex in the upper vegetative region (E), and culminates in the very complex structure of the flowering head (Fig. 135, F). It will be unnecessary for us to trace

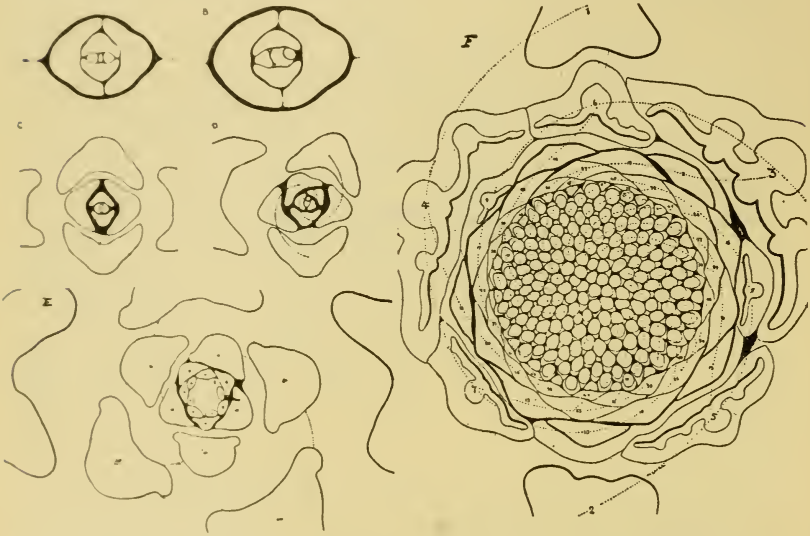

FIG. 135.

A-F. Ground-plans of buds of Sunflower of different ages: but these drawings are not uniform in scale. See Text. (After Church.)

these successive stages out into detail, though they are found to follow certain definite methods. The point is that from a cyclic beginning a spiral disposition is arrived at. As the individual plant develops and its apex expands, the complexity of the arrangement of its appendages increases. The individual life of the Sunflower illustrates a relation that is usual, viz. that complex spiral arrangements are found where a widened axis develops with short internodes, and where the crowded primordia of leaves are of relatively small size. Such spirals occur either in the vegetative or the floral region. Very beautiful examples are seen in the vegetative shoots of *Araucaria excelsa* of various size (Fig. 136). A biological consequence is that with very numerous leaves each obtains a maximum exposure to light incident from above. Moreover, since the branching is axillary in the flowering plants, the position of the branches themselves will

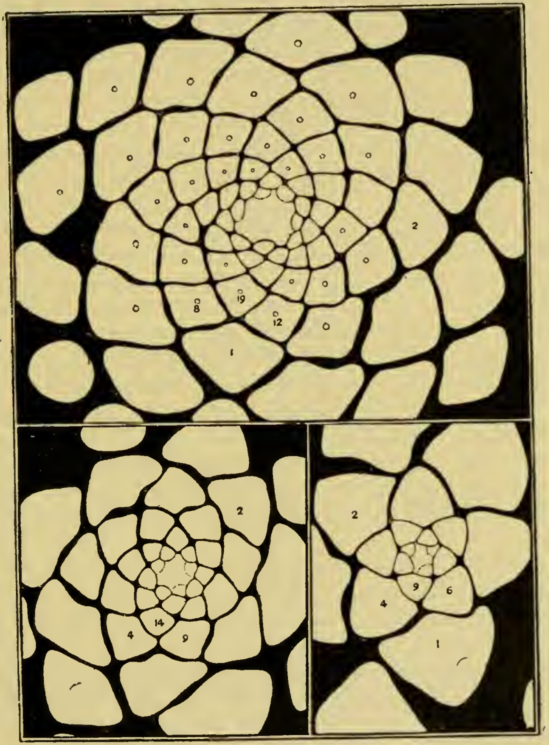

FIG. 136.

Transverse sections through the apical buds of branches of *Araucaria excelsa* of different sizes. (After Church.) The uppermost is of a branch of the first degree (7+11): the lower, left, a branch of the second degree (5+8): the lower, right, one of the third degree (3+5).

follow the arrangement of the leaves. This still further defines the external form of the mature organism.

Very striking phenomena of spiral leaf-arrangement are afforded by many plant-shoots. This is the after-effect of rhythmic sequence in leaf-formation and is seen most clearly in transverse sections at the level of the bud-apex, as in Fig. 136. Such patterns present systems of intersecting curves, which may be expressed numerically; the spiral effect being due to the fact that the numbers as counted in different directions, left or right, are unequal, as, for instance, 7 : 11, 5 : 8, 3 : 5. When the numbers are equal the system is whorled.

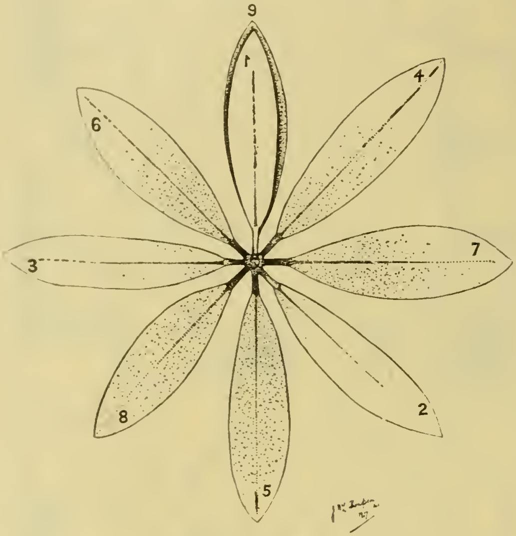

FIG. 137.

Accurate drawing of a shoot of *Rhododendron*, seen from above. The successive leaves are numbered, and it is seen that the ninth is covered by the first, while an imaginary spiral including all their bases successively, will have encircled the stem thrice. That is, the angle of divergence between any two successive leaves is $\frac{3}{8}$. (Reduced to ½.)

The fact that the numbers commonly observed at the shoot-apex, or residual in older constructions, are in the great majority of cases successive numerals of the Fibonacci ratio-series, 1 : 2 : 3 : 5 : 8 : 13, etc. (other ratios being exceptional), has been taken to imply that the arrangement, as also working out in terms of angular divergence of successive members as the Fibonacci angle of approximately 137½, gives the optimum effect in distributing the leaf-laminae to incident light (Wiesner); but though the mechanism may be effective in such a direction it does not necessarily follow that this is the causal factor of the phenomenon (Church).

The different types of spiral seen in the mature shoot may be designated according to the angle between the median planes of the successive leaves. This is called the *angle of divergence*, and it may be expressed as a fraction of the complete circle. It is found that in many plants, and even in whole families, certain angles are constant in the mature shoot. This gives a comparative, or even a systematic value to their observation. For example, in the Grasses, and in *Iris*, the angle of divergence is $\frac{1}{2}$, that is, the leaves are alternately on opposite sides of the stem, the third being above the first: they thus constitute two longitudinal rows. In the Sedges, *Veratrum*, and other Monocotyledons the angle is $\frac{1}{3}$, the fourth leaf being above the first, and their arrangement being in three longitudinal rows. In the Rosaceae and many other Dicotyledons a common angle of divergence is $\frac{2}{5}$ths, and the leaves are arranged in five rows. Consequently the sixth leaf will be directly above the first, while the imaginary spiral threading their bases together will have passed twice round the axis before reaching it. Other more complex arrangements are expressed by divergences of $\frac{3}{8}$ (*Rhododendron*) (Fig. 137), and $\frac{5}{13}$ (*Dracaena*), etc. These higher divergences go along with shorter internodes, and compact grouping of the leaves; while their overlapping is avoided by the spiral arrangement.

Various theories have been propounded to account for these facts. The old spiral theory assumed an inherent tendency to spiral organisation in plants, and, deductively, attempts were made to read spiral construction into all shoots. Subsequently a theory of contact-pressures was suggested, according to which the spirals resulted from mechanical arrangement of the leaf-primordia upon the axis, comparable to those of marbles in a flat frame. But though such pressures may in certain cases have an effect upon the arrangement of the parts as they mature, they do not explain the initial steps. For when the primordia first appear they are not in contact with one another. In point of fact the exact position of the primordia of leaves upon the axis, and their initial arrangement relative to one another, can at present only be referred to inner causes as yet unknown; such as localisation of hormone within the growing point (see Chapter XXXVI.).

Some plants develop with *bilateral symmetry*, having anterior and posterior, or right and left sides, which are alike. The flattened shoots of the Prickly Pear, or of *Phyllocactus*, are examples, also certain Mosses (*Fissidens*). But the headquarters of this type of symmetry, which is uncommon in Flowering Plants, is in the Marine Algae, and a good example is seen in the common Bladder Wrack (*Fucus*, Fig. 280, p. 379).

Dorsiventrality.

While radial symmetry is the rule in upright shoots, those in which the axis is oblique or horizontal usually diverge from the radial in more or less degree. They show an obvious relation to the direction of gravity, light, etc., developing differently on the sides directed upwards and downwards. Such developments are styled *dorsiventral*. Sometimes the effect appears only in the later development of the axes or appendages; but in more pronounced cases the initial arrangement of the leaves is itself dorsiventral.

Examples of the former are seen in the lateral branches of many trees, and conspicuously in many Conifers, such as the Spruce.

While the main axis of the "Christmas Tree" is upright and radial, the lateral branches appear flattened. This is due partly to the fact that the lateral branches of higher order have been developed from buds seated right and left on the main branches; partly to the curvature of the leaves upwards. Nevertheless the construction of these dorsiventral branches is essentially radial. If the terminal bud of the main stem be removed, one or more of the lateral buds, which would normally grow into flattened lateral branches, will grow upwards and take its place. With the vertical position, it regains its radial symmetry. Very much the same may be seen in the Sycamore, or the Horse Chestnut, both of which retain the radial structure of the leading shoot. Their lateral branches are slightly dorsiventral, but they do not modify the symmetry of the lateral branches so much as the Spruce.

Fig. 138.

Strongly dorsiventral branch of Lime, seen from above. Its leaves form a compact leaf-mosaic. (Reduced to $\frac{1}{3}$.)

On the other hand, the upright radial shoot, or leader, in many trees may itself become dorsiventral as growth proceeds, while the lateral branches are conspicuously so. Consequently the whole tree when full grown will be made up of flattened shoots, the lateral branches spreading out like fans. (Fig. 138.) In the Elm, Beech, and Lime this change of the leading shoot comes early. Their seedlings are radially constructed. In the Elm and Beech the dorsiventral structure, with alternate distichous leaves (in place of the decussate arrangement) appears in the second year of the seedling, and continues from then onwards. But though the whole tree is thus built up of dorsiventral shoots, these may form collectively a radial crown, as in the Elm. Such examples of the transition from radial to dorsiventral symmetry are carried out in each individual plant. They indicate that the radial is the more primitive state, and the dorsiventral derivative.

In many herbaceous plants the dorsiventral habit is more pronounced than in trees. The whole shoot may take a creeping horizontal position, or a climbing habit by lateral attachment, as in the Ivy. The lopsidedness then becomes marked, and different degrees of it may be noted. Thus in the creeping rhizome of *Carex*, while the leaves show the 1-3rd divergence, the axillary bud of some downward-directed leaf, frequently the fourth, alone is developed. The apex of the main shoot then turns upwards, while the axillary bud grows on, continuing the false-axis (sympodium). Thus the individual shoot

FIG. 139.
Successive sympodial shoots of *Carex*. Each shoot is of radial construction, but the whole system is dorsiventral. (After Figuier.)

is radially constructed, but the sympodial system is dorsiventral. (Fig. 139.) In other cases the mature shoot may be itself dorsiventral, though that condition is only acquired in the course of the individual development, and is not shown by the apical bud. This is seen in the rhizomes of *Acorus*, where the apical bud shows a bilateral symmetry, with alternate leaves. But in the mature rhizome the two rows are shifted to the upper surface, giving a dorsiventral condition, with roots arising from the lower surface. In other cases again, and conspicuously in Ferns, the dorsiventrality is fixed already at the growing point, and is not the mere result of any subsequent displacement of parts. This is seen in the Common Polypody, which has from the first distichous leaves placed obliquely on the upper surface of the rhizome, while roots only arise on the lower side. This arrangement is already apparent at the growing point (Fig. 140). Such examples show various steps in the impress of dorsiventrality on the vegetative shoot.

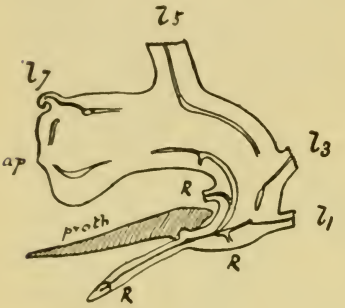

Fig. 140.

Polypodium vulgare. (× 6.) Median section through prothallus and embryo, showing one series only of the distichous leaves l_1, l_3, l_5, l_7. *R*=roots. *ap*=apex of axis. The young shoot becomes inverted, growing backwards over the prothallus. (F.O.B.)

Lopsidedness may also appear in the inflorescence of many flowering plants, e.g. in many grasses, such as *Dactylis*. But, as we shall see later, it is in the flower that dorsiventrality becomes most marked, and of great biological importance. In all cases among the Higher Plants the dorsiventral is probably a condition which has been derivative from a primitive radial state.

Plant Communities.

It is thus seen that Climate and other conditions of life are frequently related to special modifications in the plant, which meet special needs. As the conditions will be substantially similar for all plants which grow in a district or specific area, they may collectively take characters which they share in common. Thus they form characteristic *Communities*. The water-relation more than anything else determines such adaptations. Where the climate or conditions are dry, so that water must be carefully conserved, the plants so adapted are termed *Xerophytes*. Where water is abundant, or the vegetation is actually submerged, the plants specially developed under such conditions are termed *Hydrophytes.* Where the water is brackish or salt, plants assume the characters of *Halophytes.* But where the conditions as regards temperature and water-supply are not extreme, though there may be marked seasons, the vegetation would be described as consisting of *Mesophytes.* Such groupings cannot be drawn with definiteness. They must be held as generally descriptive rather than mutually exclusive. In point of fact the communities overlap and graduate one into another. Naturally the distinctive characters impressed upon each community are best illustrated by extreme types.

FIG. 141.
Succulent stem and flowers of a Cactus. (After Figuier.)

Xerophyte Vegetation is characterised by various features which have the effect, individually or collectively, of controlling transpiration, and thus making the best of a limited water-supply. The leaf-area is reduced, and its texture is often fleshy, so as to serve for water-storage, as in the Stonecrop, Aloe, or Onion. In other cases leaf-reduction may go along with a corresponding distension of the stem, which becomes green, and takes over the function of photosynthesis. This is seen in the tropical Euphorbias, and Cactaceae:

the former especially on the dry areas of the Old, the latter of the New World (Fig. 141). In some cases the stem swells to an almost spherical form, by which means the greatest possible proportion of bulk to surface is attained. By virtue of the water stored up within its tissues a cactus plant can live for several months without any external supply of water. A spiny or thorny character is common in Xerophytes (Fig. 141), and is a marked feature in dry districts such as the veldt of South Africa. A consequence of this is protection against the attack of herbivorous animals. Many Xerophytes possess extensive and deep root-systems (*e.g. Welwitschia*); moreover, their root-hairs are characterised by high osmotic pressures and this allows them to dehydrate the soil more thoroughly than is usual in Mesophytes.

Along with these features go various other structural modifications. Thickened epidermal walls and cuticle are common (Fig. 142), and this together with a free development of mechanical tissue frequently gives the leaves a leathery texture. Hairiness is common. The stomata are frequently sunk in deep pits (Figs. 52, 142) in which a pocket of moist air collects and is likely to impede diffusion through the pore. Hairs have a like effect on evaporation from the cuticle. Protection of stomata is also achieved in other types by the lengthwise rolling of the leaf in such a way that the stomata lie

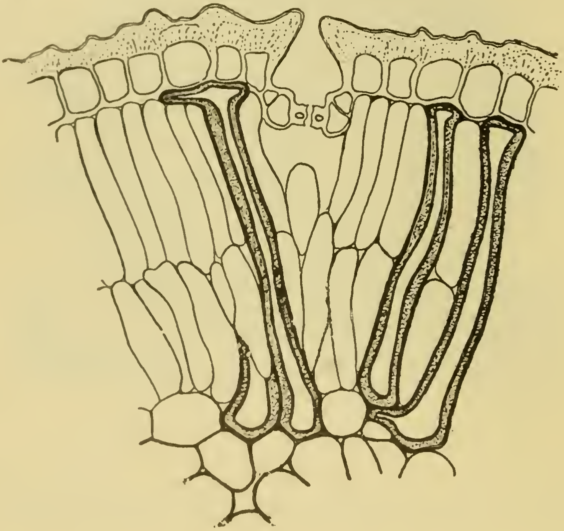

FIG. 142.

Part of a transverse section of the xerophytic leaf of *Hakea*, showing a stoma greatly depressed below the well-developed epidermis, which has greatly thickened outer walls, covered by a thick, continuous cuticle. (× 150.) F. O. B.

on the inner surface. The rolling may be permanent as in *Empetrum* and members of the Heath family, or may only appear during dry spells, as in various Grasses (p. 188). In some Xerophytes the leaves occupy a vertical rather than a horizontal plane, due to a bending of the petiole, as in certain species of Eucalyptus. The incidence of the sun's rays on the leaf is thereby much reduced. A similar feature is commonly found in those plants in which the leaves are replaced by flattened stems or petioles. Butcher's Broom (*Ruscus*) and certain Acacias are examples of these (Fig. 259, p. 344).

Recent experimental work has revealed that when water is available some Xerophytes show a surprisingly extensive loss of water by transpiration, perhaps related to the need for rapid photosynthesis and growth during the infrequent wet spells. They cannot as a class be said to show low transpiration at all times. During dry periods, however, the possession of heavy cuticle, of hairs and of protected stomata which may remain closed, doubtless tends to reduce transpiration. A further property of Xerophytes is the ability of their protoplasm to withstand desiccation to an unusual extent.

Modifications like those shown by xerophytes are seen also in other plants where water-supply is for other reasons difficult, as it is in those which live attached to the branches or trunks of other plants (*Epiphytes*). Since they have no direct access to the soil, they must receive and store the water from rainfall, or condense it from a moist atmosphere. This is the condition of many tropical Orchids and Bromeliads. In the latter a special surface-protection is afforded by scurfy peltate hairs, while others serve for absorption of water.

Again, in Arctic and Alpine plants many xerophytic characters are presented, such as deep rooting, leaf-reduction, succulence, waxy surface, or hairy coverings. These are probably related to the condition of *physiological drought* caused by the prevailing low temperature of the soil, which checks the activity of root-absorption: while the shoot, in clear weather and in a wind, may be exposed to conditions which would stimulate transpiration to a dangerous degree. The same applies to the temporary reduction of leaf-area of deciduous trees in winter (see p. 194).

Halophytes living on the sea-shore, or in salt-marshes, also show characters similar to xerophytes, such as reduced leaves and succulence (*Salicornia*), and development of spines (*Salsola*). To explain this it has been assumed that halophytes experience physiological drought because of the high osmotic pressure of the saline soil solution. Experimental investigation has not supported this theory, for halophytes transpire freely and appear to have no difficulty in securing water, while despite their succulence they cannot withstand drought. Their resemblance to xerophytes may be an apparent one only.

On the other hand, *Hydrophytes*, which grow in wet situations or actually submerged, are independent of the risks of water-supply. Their leaves are often finely divided, giving a large proportion of surface to bulk, as in the water Buttercups. They are mostly perennials. The Water-Lily (*Nymphaea*) will serve as a good example. Its thick stock is rooted in the mud and bears floating leaves, with broad but thin lamina and smooth surface. Stomata are absent from the submerged parts, but are present on the exposed upper surface (see p. 74). The shoot has little mechanical or woody tissue, but contains large air-spaces which give buoyancy. The air-spaces also allow of the storage of carbon dioxide or oxygen, and of gaseous diffusion from point to point within the plant. The texture of such plants is limp. Their parts dry up quickly in the air, owing to deficient cuticular protection. These characters, which are common in the Hydrophytes, are in sharp contrast with those of xerophyte types.

The *Mesophyte vegetation* remains to be considered. Excepting in the higher temperature, and the greater intensity of lighting of the latter, the Temperate Zones and the Tropics are alike in presenting conditions very favourable to growth, so long as extremes of season and of water-supply are excluded. In the low lands of the temperate zones and of the tropics, many areas exist where vegetation is easy. Here, when supplied with seed produced by prolific methods, the soil becomes covered with a dense investment of herbage or of woody plants, in which the potential individuals are more numerous than the ground can carry. Over-population is the character of the sward of any field, as it is habitually of natural woods and forests. Two points emerge from the contemplation of such native or natural growth. One is that plants of very diverse outline and construction may thrive, mixed indiscriminately together. The normal types of Monocotyledons and of Dicotyledons seem to succeed equally well side by side. This indicates that under such conditions there is little need for specialised development. The second is that the overpopulation leads to *competition for space and light*. Evidence of this is found in the commonness of stunted plants, crowded out by the stronger. Any area of densely overgrown ground in a lowland field or wood shows in a convincing way how important access to sunlight really is. The plants engage, in fact, in a race for the light, and the tallest plants win. It is upon this fact that the most striking adaptive feature of the Mesophytic and Tropic vegetation is based, viz. the *Climbing Habit*.

The Climbing Habit.

The biological advantage gained by the climbing habit is that the plant which adopts it reaches the light with a minimum expenditure upon its stem. A plant standing alone has to form a strong supporting column. To do this requires a considerable expenditure of material on tissues which are of little physiological use beyond giving mechanical support. If then such support can be attained in some other way, so much material will be gained. That the expenditure is really saved by climbing plants is seen from their anatomy; for their stems show vessels relatively few and large, few other tissues of the wood, and in herbaceous types, though cambium may be present, there is an absence of tissue-masses formed by cambial thickening. There is, however, a well-developed phloem, which in some cases is duplicated on the side next the pith. The vascular strands thus constructed contain little fibrous tissue, and are usually isolated one from another by intervening tracts of soft parenchyma (compare Fig. 25, p. 48). The result is that climbing stems are relatively weak and flexible, while their leaves, flowers, and fruits may be large. These facts demonstrate their dependence upon attachment to some stronger support.

The *methods of climbing* are various, and they are assumed by representatives of many distinct families; not uncommonly by isolated species in a genus that does not climb as a rule. But in some families of plants many genera and species are climbers, as in the Leguminosae, Sapindaceae, and Bignoniaceae. The habit is much more frequent in Dicotyledons than in Monocotyledons. Several Ferns have also adopted a very successful climbing habit. This widespread and often isolated occurrence of climbing, as well as the variety of the methods involved, suggests that the habit has been acquired along many distinct lines of Descent. Instances of marked homoplasy are numerous. While climbing is common in our native Flora, it is most frequent here in herbaceous plants, such as Vetches, Convolvulus, or Hop. They may be annuals, like the Black Bindweed; or perennials with an underground root-stock, like the Hop, or Black and White Bryony. Some few are woody, as the Honeysuckle, and Clematis and Ivy. While this is less common in temperate Floras, it becomes a very marked feature of Tropical Forests. There the huge woody "lianes" develop their leafy shoots high up amid the branches of the lofty canopy of trees, while their flexible but woody stems hang down like ropes, connecting the shoot above with the root-system in the soil. But such climbers of large size do not differ essentially in their methods from the smaller climbers of Temperate zones.

The methods of climbing may be ranged under three heads: (1) *straggling*, (2) *prehensile*, and (3) *adhesive climbing*. The first of these is the least specialised. It is successfully practised at home by Cleavers (*Galium aparine*), and in the south by the Wild Madder (*Rubia peregrina*), herbaceous plants which thread their way through undergrowth or hedge, supporting themselves partly by stiff whorls of leaves expanding at right angles to the axis, partly by hooked prickles borne chiefly on the projecting angles of stem and leaves.

In the Tropics the *straggling method* gives very successful support to larger woody plants. (Fig. 143, i.-vii.) In many cases widely spreading branches in the axils of decussate leaves are an important aid, as in a species of *Lantana*, which was introduced into Ceylon as a decorative plant. It has taken possession of large tracts of abandoned coffee-land, favoured partly by

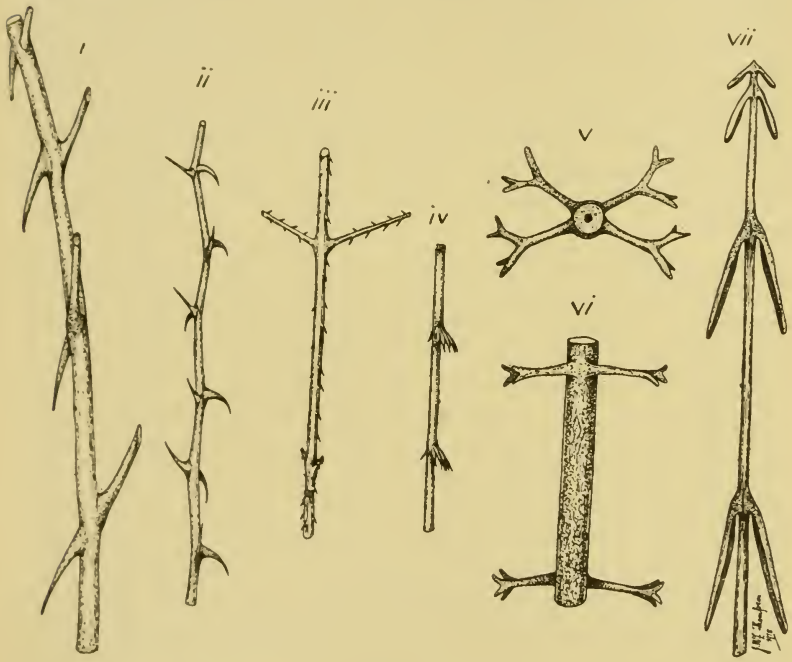

Fig. 143.

Various woody stragglers collected in Ceylon, showing various parts reflexed for support. (i.) axillary shoots of *Sageretia*; (ii.) stipules of *Zizyphus*; (iii.) prickles of *Lantana*; (iv.) prickles of *Calamus*; (v. vi.) axillary branched shoots of *Carissa*; (vii.) reflexed pinnae of *Desmonchus*.

its straggling habit, partly by the spread of its pulpy fruits by birds. The widely spreading branches bear hooked prickles on their projecting angles, which are effective in aiding support (iii). In other cases hooks that help the straggling are produced from other parts. The climbing Rattan Palms of the genus *Calamus* bear them on the concave side of the whip-like leaf-apices, or of the axillary buds; for it is sometimes the one, sometimes the other, which serves in this genus as the climbing organ (iv.). In the Jujube (*Zizyphus*) there are woody stipules to the leaves which are borne by the curved, whip-like branches. Of these stipules the one that is downwardly-directed of each pair is sharply reflexed, while the other points forwards (ii.). A parallel is seen in *Sageretia*, but in this case it is the axillary buds that are effective, for the lower of each pair forms a recurved hook, while the upper develops upwards as a leafy shoot. (i.) The mechanical effect is exactly the same as in the Jujube, but the parts used are different. In the Palm *Desmonchus*, it is the distal pinnae that are reflexed, and act almost like the flukes of a patent anchor (vii.). A very similar mechanical effect is shown by the reflexed axillary branches of *Carissa* (v. vi.). Such examples illustrate in what varied ways straggling may be made an effective method of support. They involve such diverse parts as emergences, stipules, pinnae, and axillary branches. In fact any part of the shoot-system may be used. The instances come from most diverse families of Dicotyledons and Monocotyledons.

FIG. 144.

Twining stems. *A*, Sinistrorse shoot of *Pharbitis*. *B*, Dextrorse shoot of *Myrsiphyllum*. (After Strasburger.)

Climbing by *prehensile methods* has gained more attention than straggling, because it is so well represented in the Native Flora, and because the advantages which it brings are so obvious. The attachment to the support may be by a twining stem, as in the Hop, Scarlet Runner, or *Convolvulus*; or by tendrils of various sorts, and by prehensile leaves. The twining of a stem is partly due to the execution of circumnutatory movements by the apical part of the stem, the sweep of the nutatory spiral being greatly increased by the horizontal or oblique orientation which the upper part of the stem assumes. If the stem comes in contact with an upright support of suitable thickness it laps round it with a continuous spiral course upwards. There is evidence that the twining is to some extent a geotropic response of a special type. There is here little morphological change beyond an elongation of the internodes, and frequently a delay in the development of the leaves till their support is assured. Such climbers may be *dextrorse*, following the hands of a watch (Hop), or *sinistrorse*, showing the reverse, which is more common, as in *Convolvulus* or *Phaseolus* (Fig. 144). There is here little or no contact stimulus, the twining being a nutatory and geotropic phenomenon.

But *tendrils* grasp their support as a consequence of contact-stimulus, which reacts by disturbing the growth while young. The tendril is a cylindrical whip-like organ, usually with a hooked tip. Its sensitiveness is sometimes localised along a definite line. During growth it shows movements of circumnutation: if it then comes in contact with a support, inequality of growth causes the tendril to lap round it. (Fig. 145.) Its morphological origin may be various. In the Garden Pea, Vetch, and *Cobaea* it obviously represents the distal region of the leaf, including several pinnae; or it may be the excurrent tip of the lamina, as in *Gloriosa*; or extended parts of the lower region of the leaf may be prehensile, while the lamina or pinnae develop normally after the lower region has grasped the support, as in *Corydalis*, *Clematis*, and *Solanum jasminoides*; or lateral "stipular" structures may be represented by tendrils, as in *Smilax*; or again, the tendril may be referable to a whole shoot, as

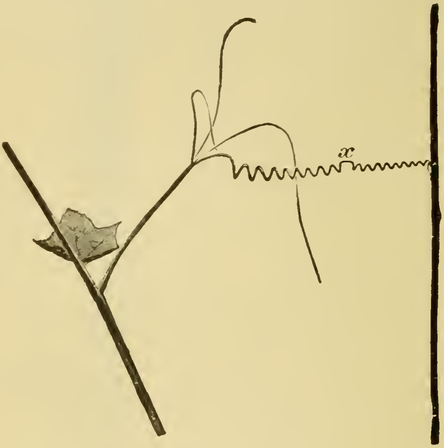

Fig. 145.
Portion of stem of *Sicyos*, a Cucurbit, with tendril attached to support. x=point of reversal of the coiling of the tendril. See Text. (After Strasburger.)

in the Grape-Vine; and probably a like interpretation may be applied to those of the Passion Flower and the Cucurbits. Thus various parts of the shoot, or the whole of one, may in different cases develop as structures called tendrils, and act as prehensile organs.

Once they are attached, tendrils strengthen their tissues. As growth ceases, the part between the distal attachment and the base is usually thrown into spiral curves; and as both ends are fixed, these are necessarily equal in number in reverse directions. The elastic tissues of the spirally coiled tendril act like a spring in resisting wind, and recover when the pressure is relieved (Fig. 145).

Adhesive Climbers attach themselves by application of some part of their surface very closely to the surface of the support, following its minute irregularities. The result is that they are affixed so closely that they will often break before quitting hold. *Roots* require little adaptation to this function. The Ivy is a native type of a number of plants of other lands, often large and woody, which attach themselves in this way to tree-trunks, rocks, etc. Such roots of attachment are "adventitious," that is, they are formed not from the root-system, but at points on the shoot, which are usually determined by the external conditions. The roots sometimes lap round the support, with a prehensile action, as in many of the large Aroids.

The familiar case of the Virginia Creeper (*Ampelopsis*) is morphologically identical with its relative the Grape-Vine, but the tendrils are attached by *adhesive discs.* The tips of the branched tendril move away from the light, and this leads to contact with the support: a rock, wall, or tree-trunk. After contact each tip widens into a disc, which at first secretes an adhesive cement. This together with its very close application to the inequalities of surface gives a firm attachment. Subsequently the tissues harden, and the tendril may assume spiral curves, which give a spring-like resistance (Fig. 146).

Fig. 146.
Climbing shoot of *Ampelopsis Veitchii.* The tendrils (*R*) have attached their adhesive discs to the wall-surface behind them. (After Strasburger.)

Correlation of Growth.

The examples of external adaptation thus selected show that the Vegetative System of the Higher Plants is liable to various modifications of form and appearance, and that these often have definite relation to the surroundings under which the plant grows. But such modifications are subject to *the limiting principle of Correlation.* Correlation of Growth involves the fact that where one part is developed larger than usual another part is liable to be correspondingly reduced. This applies especially to the shoot, and it may be illustrated by many familiar examples. The succulent stem of a *Cactus* (Fig. 141, p. 209), distended for water storage, bears correlatively small leaves. The same is seen in the swollen tuber of the Potato, with its correlatively reduced scale-leaves (Fig. 147). An extreme and peculiar case is that of *Welwitschia*, where two enormous plumular leaves increase in size through a long term of years, but the main axis which produced them is an enlarging stump, bearing no further leaves upon it.

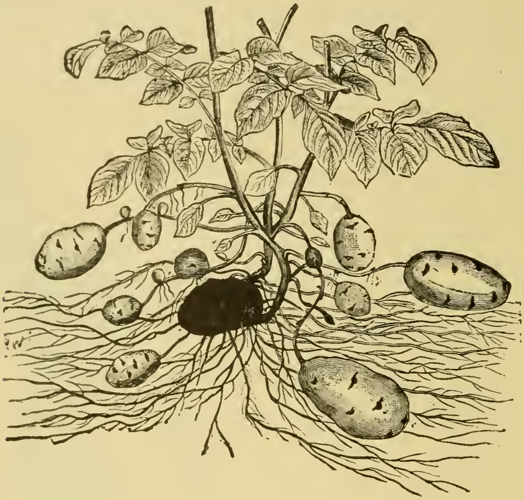

Fig. 147.

Lower parts of a Potato plant, *Solanum tuberosum*. The swollen tuberous stems bear correlatively small scale-leaves. (After Baillon, from Strasburger.)

Correlation applies not only between leaf and axis, but also between the various parts of the leaf. Thus in the young Broad Bean, and still more clearly in the genus *Bauhinia*, the two basal pinnae develop to a large size, while the distal part of the leaf is represented only by a minute apical spur between them. In *Lathyrus aphaca* it is the stipules which become large foliar expansions, while the lamina itself is linear (Fig. 148). In such cases, which might be multiplied indefinitely, *extra development of one part is accompanied by the correlative reduction of another, as compared with normal examples.* But there is no exact numerical *ratio* that can be put upon the proportions. They suggest in general terms, rather than with any exactness, that the excessive expenditure from the total amount of available material on one part leaves a deficiency for others. There is no doubt that this principle of correlation has a very wide application in determining the adult proportions of parts in plants.

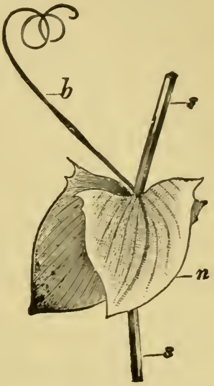

FIG. 148.

Lathyrus Aphaca. *s*, stem; *n*, stipules; *b*, leaf-tendril. (½ size.) (After Strasburger.)

Correlation is neither a cause nor an explanation of adaptability, which remains a quite independent problem. It is important to see clearly what is meant when the word "adaptation" is used. It has been used by some biologists to indicate *those special modifications of the plant which arise in relation to the environment.* In another view all plant structures are to be regarded as the expression of the specific hereditary substance during growth and development under a certain set of conditions. The structures so developed may, or may not, be adaptations. Other things being equal, those structures which are advantageous to the plant will tend to be perpetuated by the process of natural selection. Thus although many modifications in plant structure appear to be closely adapted to the environment it is not necessary to say that they actually arose in relation to that environment. The advantage which certain features confer upon the plants that show them often appears obvious enough. But it should be realised that their recognition as adaptations is no more than an assumption: it is rarely well founded. This applies to many of the peculiarities of form discussed in this chapter. They have been grouped under the heading of adaptations for convenience. The study of "adaptation" is an attractive phase of biology. But it has led to much facile or even sentimental writing, which has in it little of the scientific spirit, and still less of true scientific method.

CHAPTER XII.

IRREGULAR NUTRITION.

So far the plant has been regarded as a self-supporting organism. Starting from the seed with its small supply of food, it has been seen to have the power of acquiring, from the soil and through photosynthesis, the material necessary for its development. The great majority of plants have this ability. They build up their substance by assimilation of simple inorganic materials derived from the environment. (See Chap. VIII., p. 147.) To such a type of nutrition, dependent on inorganic raw materials, the term *Autotrophic* is applied.

While the typical plant thus depends on an autotrophic nutrition, a number of plants have not the ability to assimilate purely inorganic materials: hence they must have at their disposal a supply of organic substances before growth is possible. The nutrition of these plants is said to be *irregular* or *Heterotrophic*. Some plants are wholly dependent on irregular nutrition, others are only partially dependent on it. Organic food can only be derived from some other organism, living or dead. If this food is taken from a living organism, plant or animal, this organism is called the *Host*, while the dependent organism is called a *Parasite* upon it. Sometimes the dependent organism feeds not upon the living host, but upon the dead body, or upon the products of its decay. Such a dependent is called a *Saprophyte*. Parasitic and saprophytic plants frequently show marked modifications of form, usually regarded as results of reduction. There is no sharp line that can be drawn between these two conditions of parasitism and saprophytism, for sometimes the parasite causes death but continues to feed upon the corpse, and so is first a parasite and afterwards a saprophyte. A peculiar place is taken in this respect by the *Carnivorous* plants which digest small animals. They capture the living animal, but feed upon its dead body. Lastly, there is a condition known as *Symbiosis*, where two organisms exist together in special association: this may be regarded as a kind of parasitism in which the parasite is held in check, and a state of balance arises.

There is one fact which is common to all these irregular methods of nutrition. *Contact with the source of supply* is necessary for the establishment of any of these dependent conditions. The circumstances of a crowded vegetation naturally favour this. The matted roots of any sod give the opportunity for *root-parasitism*, such as is seen in the Yellow Rattle; the close contact of climbing plants with their support offers facilities for *stem-parasitism*, as in the Dodder. The various types of Algae attached to the submerged surfaces of water-plants, or it may be actually growing in the intercellular spaces of aerial parts, are common examples of close contact. This state has probably led on from mere association to that physiological dependence which is seen in certain Fungi. The decaying remains of a crowded vegetation persist for a long time as *humus* or *leaf-mould*, which itself supplies the most common source for saprophytic nourishment. Whether the frequency of these phenomena is to be explained by the advantage which the dependent organism gains by securing its nourishment "ready-made," or whether there is another explanation, cannot be decided on the evidence so far available.

Irregular nutrition is not restricted to any one Family or Group of Plants, but it has become the leading character of some of them. The *Fungi* are the chief examples of it. But as they are very highly specialised in this relation, while the fossil history shows that irregular nutrition was established very early in them, they will be held over for special study in later chapters (Chaps. XXIV. to XXVIII.). For the present, the illustrations will be taken from the Flowering Plants. Some families of them appear to be specially prone to physiological dependence. For instance, the Loranthaceae, and Orobancheae. In other cases isolated genera have adopted the habit; for instance, the Dodder among the Convolvulaceae, or *Cassytha* among the Laurels. Such facts lead to the conclusion that *irregular nutrition among Flowering Plants is a relatively late and sporadic departure from the state of nutrition characteristic of the Green Plant.*

PARTIAL PARASITES.

Certain plants which have adopted a parasitic habit still retain their chlorophyll, though their colour is apt to be yellowish rather than the full green. They are thus able to carry on photosynthesis, and to produce at least part of their own nourishment. They are only partial parasites. This state is seen in the Loranthaceae, with the familiar example of the Mistletoe (*Viscum*), a plant which grows fixed on the branches of various trees. It occurs occasionally on the Oak, on which it was in early days recognised as the mysterious "Golden Bough." Other native green parasites are the Eyebright (*Euphrasia officinalis*), and the Yellow Rattle (*Rhinanthus Crista-galli*), while *Cassytha*, a very omnivorous parasite of the tropics, has also a green colour.

These plants are all fixed by means of *haustoria* or *suckers* upon the host-plant in such a way that the tissues of the one come into close relation with the tissues of the other. In the case of Eyebright and Yellow Rattle there are suckers upon the roots, and they penetrate the roots of the grasses with which the plant grows. The close juxtaposition of the roots in the sod offers a ready opportunity for the parasite (Fig. 149). The effect of the parasitism upon the Grasses in a meadow is such that patches infested by Yellow Rattle can often be recognised from a distance by the poverty of their growth. In *Cassytha* the suckers arise from the shoot, and the close vegetation of the tropical undergrowth gives the necessary contact at many points. In the case of Mistletoe, and of its near relative *Loranthus*, the opportunity for parasitic attachment arises from the fact that their fruits are viscid ; in fact Bird-Lime is derived from them. The berries are eaten by birds which reject the sticky seeds, leaving them attached to the twigs on which they perched. Here the seeds germinate, and

FIG. 149.

Root of Louse-wort (*Pedicularis*), which like Eyebright and Yellow-Rattle, is fixed by suckers upon the roots of the host, here represented black. (After Maybrook.)

a sucker penetrates the living tissues of the host. In *Viscum* a suctorial system spreads from the original centre within the tissues of the host, penetrating along the region of the cambium. But in *Loranthus* the shoot of the parasite creeps along the outside of the host, and puts in suckers at intervals (Fig. 150).

All these green parasites establish a relation with the conducting system of the host, especially with its xylem. Water with its dissolved salts is then drawn off from the transpiration stream. In the root-parasites this supply is additional to what they can themselves absorb. But in those attached to the shoot their whole supply is thus obtained. It is uncertain whether or in what degree organic supplies may also be abstracted. In any case the presence of chlorophyll shows that these green parasites are not wholly dependent upon their host, but can themselves carry on photosynthesis. Some at least of the root-parasites can grow quite well without the parasitic connection, though this is naturally impossible in shoot-parasites such as Mistletoe, where normal roots are absent.

FIG. 150.
Loranthus parasitic externally upon a branch of an Alligator Pear, by means of haustoria penetrating its tissues at intervals. Ceylon. (¼ natural size.)

COMPLETE PARASITES.

In these, though the plant may show various colours, the green of chlorophyll is almost absent, and it is evident that the parasite leads a heterotrophic existence at the expense of the host. A familiar example is the Dodder (*Cuscuta*), a genus represented in the British Flora by three species. It belongs to the Convolvulaceae, and shares with *Convolvulus* the twining habit (Fig. 151). Clover fields are sometimes attacked by one of these Dodders (*Cuscuta trifolii*), and the infected patches can be seen from a distance by the reddish colour of the parasite and the stunted growth of the clover upon which it preys. Examination shows the Dodder to have cylindrical stems, which twine closely round the host plant, and are attached by numerous suckers along the surface of contact. Though the seedling germinates in the soil, the parasite after making its attachment to the host, loses its hold on the soil. It thus becomes entirely dependent on the host for its supply of water and soluble salts. Since it has little or no chlorophyll, it is also dependent on the host for its organic supply. It is in fact a complete parasite.

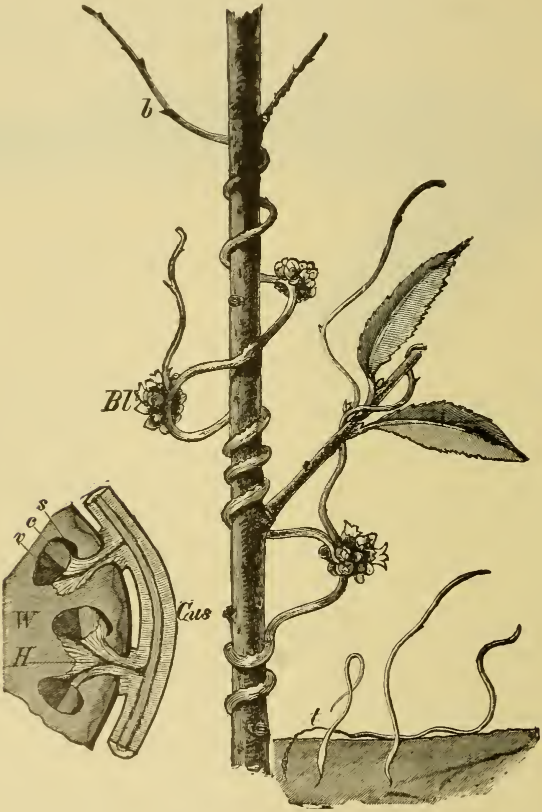

Fig. 151.

Cuscuta europaea, on the right germinating seedlings. In the middle a plant of *Cuscuta* parasitic on Willow: *b*, reduced leaves of the floral region; *Bl*, flowers. On the left cross-section of the host, showing haustoria, *H*, in intimate contact with the vascular strands. (After Strasburger.)

A marked feature is the absence of foliage leaves in the vegetative region of the Dodder. There are not even any cotyledons on the embryo. This is to be connected with the parasitic nutrition; there is no self-nutritive function in the parasite, and the leaves which would normally carry it on are not developed. *Such reduction of the vegetative system is usual in complete parasites.* But this reduction does not apply to the floral region. The flowers of the Dodder, which are produced in dense heads, arise each in the axil of a bract, and structurally they show the characteristic features of the Convolvulaceae. From these facts the conclusion seems justified that Dodder is a type related to *Convolvulus*, and that the twining habit has led to its parasitism. Whereas *Convolvulus* is dependent by twining only for mechanical support, Dodder has gone a step further and has become dependent upon its host for its complete physiological support also. Further, as it is an isolated parasitic genus, and its flowers are like those of *Convolvulus*, though on a smaller scale, it appears probable that its parasitic habit has been acquired relatively late in its evolution.

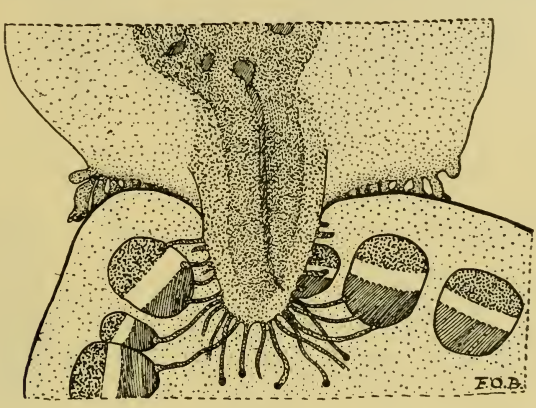

FIG. 152.

Cuscuta europaea. Section vertically through a sucker, which projects from the stem of the Dodder, shown above in the drawing, into the stem of the host. See Text. (× 35.)

The attachment of the Dodder to its host is by means of suckers, which probably represent highly modified roots. The details of the connection appear to be variable in different species, and perhaps on different hosts. In specimens of *Cuscuta europaea* the facts appear strongly to support their root-character (Fig. 152). First an adhesive disc projects from the stem of the parasite, and becomes closely appressed to the surface of the host, attaching itself by rhizoid-like hairs. Endogenous tissues then burst through like a root, and penetrate the tissues of the host. The superficial cells of the penetrating sucker then grow out into tubes of varying length. Some of these apply themselves to the wood, others to the bast, others to the pith and cortex, thus tapping both storage and conducting tissues. Where the sucker impinges upon a vascular strand a continuous xylem-connection may be established; in the phloem also a close relation of the sieve-tubes of the parasite with those of the host has been shown.

Fig. 153.
Median section of a young plant of *Orobanche* seated upon the root of its host. (After Hovelacque.) (× 20.)

The Broomrape (*Orobanche*), and the Toothwort (*Lathraea*) are further examples of parasites with complete physiological dependence. Both of these are root-parasites, with attachment to the host by haustoria, which penetrate the tissues. The Toothwort which infests the roots of Hazel is classified in the Scrophulariaceae, close to the Eyebright and Yellow Rattle, which are themselves partial root-parasites. But it differs from them in having become entirely dependent physiologically upon its host. The leaves are still represented on the underground shoot, and their curiously reduced and altered form gives rise to the name of Tooth-Wort. But the flowering shoot rises above ground, displaying flowers with structure characteristic of the Family.

The Broom-rapes (*Orobanche*), which attack various plants, woody or herbaceous, are closely related to *Lathraea*. They show a greater modification of the shoot, which attaches itself on germination to the root of the host, developing a brown tuberous body, without leaves, and shut off from the light. By means of a sucker it burrows with a broad surface into the root of the host plant, and establishes a close relation with its conducting tissues (Fig. 153). The flowering shoot with its brownish leaves rises above ground, bearing numerous flowers. Their structure shows that it is a form related to the Toothwort, but its vegetative system is still more reduced, leaves being absent from the base of the tuber. This reduction runs parallel to but distinct from that seen in *Convolvulus* and Dodder. The two sequences provide a good example of *homoplasy*, or parallel development, and show that parasitism may originate separately in distinct families, though the steps of the consequent modification may be alike.

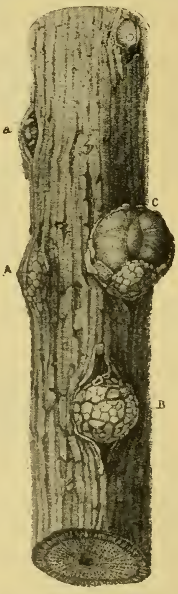

Fig. 154.
Flower-buds of *Rafflesia* bursting their way out from the root of *Cissus*. (After Robert Brown.) Much reduced.

An example of a still further reduction of the vegetative system of a complete parasite is seen in *Rafflesia*, which grows enclosed within the tissues of its host. It infests the stems and roots of *Cissus*, traversing the tissues with branched filaments of cells, which provide no semblance of stem, leaf, or root. The vegetative system is, in fact, reduced to the level seen in filamentous Fungi. But when flowering follows, large buds are formed deep down in the tissue of the host. These burst through, and develop as flowers (Fig. 154). In *Rafflesia Arnoldi* each flower is thirty inches across when full blown, and has a very peculiar and complex structure (Fig. 155).

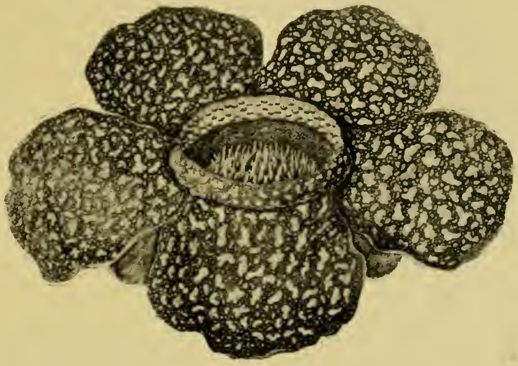

FIG. 155.
Flower of *Rafflesia Arnoldi*. Much reduced. (After Robert Brown.)

It thus appears that while in parasites the vegetative system shows reduction, which may at times reach an extreme as in *Rafflesia*, the flower may nevertheless be disproportionately large and elaborate, and produce very numerous seeds. Biologically their number may be held as an offset to the risk of not finding the proper host on germination.

MYCORRHIZA.

The roots or other underground organs of many flowering plants regularly grow in close association with the filaments (or *hyphae*) of a fungus: the term *Mycorrhiza* is applied to this association. There is evidence that at least in some cases of mycorrhiza the higher plant gains organic food and so displays an irregular nutrition. The mycorrhizal association has usually been regarded as an example of *Symbiosis* (or " living together ") from which both higher plant and fungus derive benefit, but at present we are not in a position to assess with any certainty the extent of such benefit. Probably any advantage accruing to the higher plant is connected with the special saprophytic faculty which the fungal partner has of absorbing organic materials from the decaying vegetable matter of the soil. Some of these materials, or derivatives of them, may become transferred from the fungus to the higher plant with which it is associated in the mycorrhiza. Indeed in those higher plants described as *Complete*

Saprophytes (see later) there appears to be complete dependence on organic food derived from the fungus of the mycorrhiza.

Two types of mycorrhiza are recognised. In the first the fungus lives outside the root tissues of the plant with which it is associated; this is described as *ectotrophic*, and it regularly occurs in many trees, *e.g.* Beech, Oak and Pine; also in some herbaceous plants. In the second type the fungus penetrates into the cortical cells of the root of the higher plant, and this is styled *endotrophic* mycorrhiza. This type is found in the Heaths and Orchids. But the two types of mycorrhiza are linked by intermediate conditions, and in many examples of so-called ectotrophic mycorrhiza there is some degree of penetration into the cells.

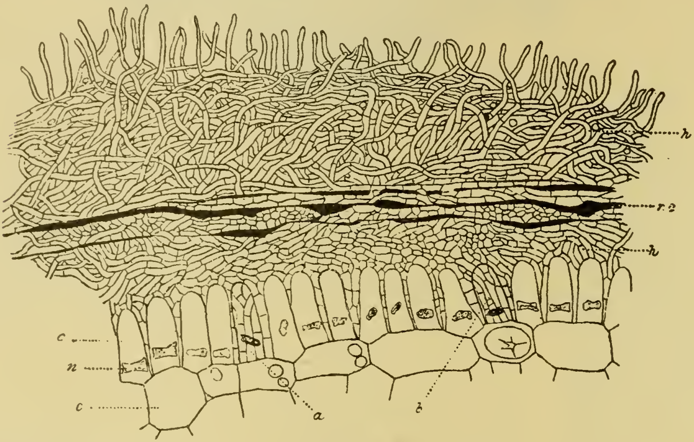

Fig. 156.

Part of the superficial tissue of a root of *Sarcodes*, covered by a felt of fungal hyphae (*h*), in which the dark lines (*r, c*) are cast-off layers of the root-cap. The outermost layer of cells of the cortex (*c*) is covered by a piliferous layer (*e*), but the root-hairs are replaced by conical cells between which the fungal hyphae have forced their way. (After Oliver.) Greatly magnified.

(*a*) *Ectotrophic Mycorrhiza.*

Externally roots showing typical ectotrophic mycorrhiza appear wrapped round by a covering of fungal origin and are short and thick, and repeatedly branched. Sections show that the roots are covered by a thick felt of matted fungal threads which usually envelop the apical part of the root completely. The development of the dense mantle of fungus may be due to the excretion from the root surface of a substance favourable to fungal growth. Fig. 156 shows part of a section through the root of *Sarcodes*, a native of N. America, with ectotrophic mycorrhiza. The fungal mantle is seen closely investing the superficial cells of the root, and forcing them apart; but still they appear healthy and active. The fungal filaments do not as a rule penetrate the cells themselves, so that the investment is morphologically external. It is, however, so complete when fully developed that the surface of the root has no direct contact with the soil, and must take its supplies through the medium of the fungus. The hyphae at the outer surface grow out into absorptive filaments that take the place of the root-hairs. In this particular type the root-cap is shed off in layers, which are held in the fungal mantle. Like the native *Monotropa* (Bird's Nest) growing in Fir and Beech woods, and developing ectotrophic mycorrhiza, *Sarcodes* is a complete saprophyte and shows, as with the complete parasites, a reduced vegetative system including an almost complete lack of chlorophyll (Fig. 157). The only visible source of nutrition of these plants is from the abundant decaying vegetable matter (humus) of the woodland soils in which they live, presumably through the intermediary of the fungus. These higher plants would thus appear to be saprophytes at second-hand.

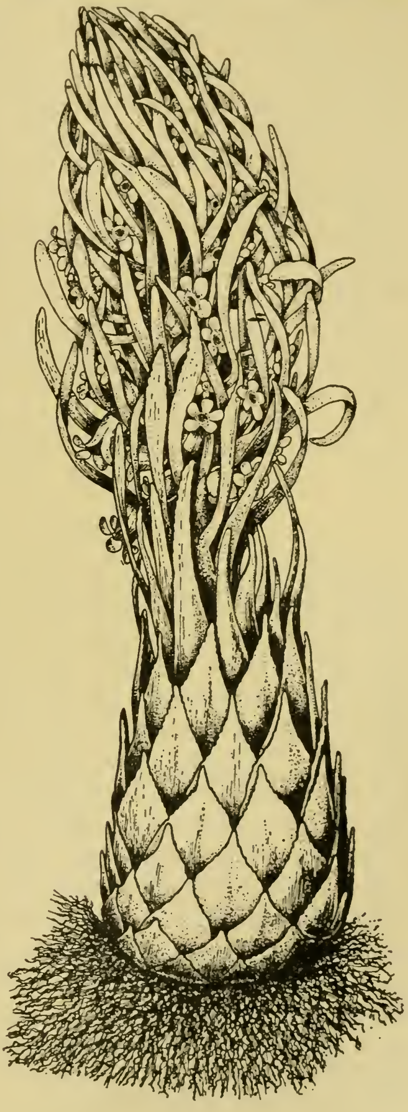

Fig. 157.

Whole plant of *Sarcodes*, showing the mycorrhizic root-system, from which arises a bulky flesh-coloured shoot, with broad sheathing scales below, and a terminal inflorescence with prominent bracts. Reduced. (After Oliver.)

The toadstools of various types which are commonly found in woods are the spore-bearing parts of fungi which otherwise grow below soil level (p. 439), and it has been shown that it is these same fungi that participate in the mycorrhiza of the roots of trees. A good deal of work has been carried out with a view to determining the importance of ectotrophic mycorrhiza to trees, chiefly in connection with afforestation schemes. There is evidence that in some types of soil the tree does not flourish unless the mycorrhizal association is properly developed, though the explanation of this is not yet clear. Benefit to the tree might arise as already mentioned by absorption of organic food derived by the fungus from the humus of the soil, and subsequently transferred to the tree. A further suggestion is that the fungus may supply water and mineral salts more rapidly than the tree could absorb these for itself.

Whether the fungus gains much from the association with the higher plant is uncertain, especially where the latter is of the completely saprophyte class, such as *Monotropa* or *Sarcodes*; but there is evidence that in some cases the fungi of tree-mycorrhiza develop unsatisfactorily apart from their normal associate.

(*b*) *Endotrophic Mycorrhiza.*

In this type of mycorrhiza the fungal filaments penetrate and inhabit the cells of the higher plant and come into intimate relation with their protoplasts, though normally these do not appear to be adversely affected. Besides the Orchids and Heaths endotrophic mycorrhiza is present in many other flowering plants and in some lower plants, for example in *Lycopods*, and certain Liverworts. As with the ectotrophic type, most of the plants with endotrophic mycorrhiza are normal in appearance; but some, such as the Bird's Nest Orchid (*Neottia*), are almost devoid of chlorophyll and are classed as complete saprophytes, being obviously of irregular nutrition.

Special attention has been given to the endotrophic mycorrhiza of the Heath family and of the Orchids. The fungus concerned in the mycorrhiza of the common Heather (*Calluna*) has been identified as a species of the fungal genus *Phoma*. The fungus enters the fine young roots of the Heather in spring, from the soil, and is to be found within the cortical cells, these internal hyphae being connected with others growing on and near the surface of the root (Fig. 158). The existence of the fungal filaments within the cells of the root is of limited duration, for during the summer and autumn the filaments undergo what appears to be a process of *digestion* under the influence of enzymes of the Heather plant. While this digestive process, which has been compared with phagocytosis in animals, is perhaps to be regarded as a method of keeping the fungus in check, its products may be of use to the plant as nutrient substances. A proportion of these food substances may have been originally derived from the Heather itself but some part may have been obtained by the fungus from the humus of the soil, and by digestion this is placed at the disposal of the plant. In addition this particular fungus may, like the root-nodule organism, have the faculty of fixing atmospheric nitrogen (see p. 235). Any nitrogen so fixed would be transferred to the host by digestion. There is no evidence that food materials obtained from the fungus are essential to the existence of the adult Heather plant, though it is possible that the plant is thereby enabled to thrive better in the rather unfavourable habitats which it frequents. Some experiments have indicated that the association with the fungus is beneficial or even essential to the proper development of seedling Heathers, but this point is not finally settled. A special feature of the mycorrhiza of Heather is that the fungus is not confined to the roots, but is to be found also in the aerial organs.

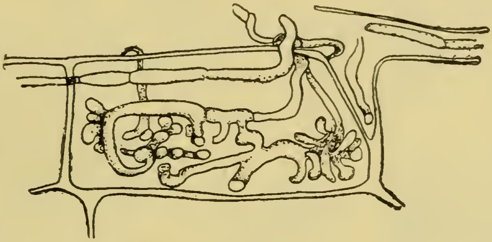

FIG. 158.
A single superficial cell of the young root of Common Heather (*Calluna vulgaris*) showing the endotrophic fungus, and its penetration of the cell-walls. (After Rayner.) (× 1500.)

In the Orchids, we find that while the majority are green and normal in appearance, a number are complete saprophytes and show the usual reduced vegetative system. The mycorrhizal fungus, known as *Rhizoctonia*, inhabits the cortical cells of Orchid roots, and frequently of the tubers that characterise many Orchids. These internal hyphae are connected up to a certain extent with other hyphae growing in the soil. In some of the infected cells the fungus soon undergoes digestion, as in Heather; while in others, termed *Host* cells, the fungus persists unharmed, at least for a considerable period (Fig. 159). These two types of cell (digestive and host) may be very regularly arranged, a well-known example being provided in the root of *Neottia*. Here again the digestive process may result in the transference of food materials from the fungus to the higher plant. There is no evidence that in the *green* Orchids the adult plant is actually dependent on any such additional food: but the position is different with those Orchids classed as complete saprophytes, of which *Corallorhiza* (Coral-root) and *Neottia* (Bird's Nest Orchid) are native examples. The former grows in Pine woods with its freely branched rhizome embedded in rich humous soil. The rhizome produces scale-leaves but no roots, while the aerial part of the plant is a simple scape bearing only colourless scales and at the top a raceme of small pale flowers. The tissues of the rhizome are freely infected with mycorrhizal fungus. *Neottia* also grows in woods, and if the plant is dug up the underground portion, which has some imagined resemblance to a bird's nest, is found to consist of fleshy roots crowded upon a short central rhizome which also bears scale leaves. The plant throws up an aerial stem bearing only scale-leaves and flowers, all being of a pale brown colour (Fig. 160). Rhizome and root are freely infected with fungus. Both these plants, being

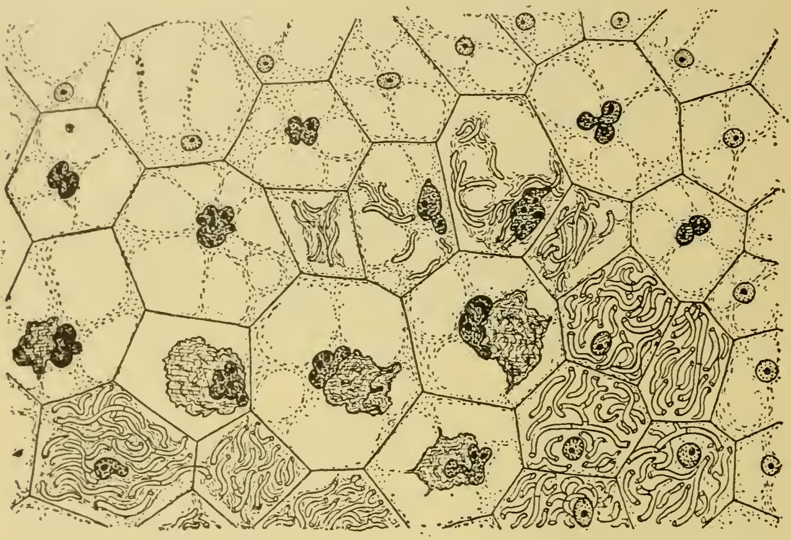

Fig. 159.

Section through the mycorrhizal region of the tuber of the Orchid, *Phalaenopsis*. At the top of the figure are normal cells of the host; at its lower limit are cells crowded with fungal filaments, but still retaining their nuclei. Between these zones are cells in which the fungal filaments have undergone digestion. An amorphous mass, or "clump," of undigested material remains, while the nuclei are lobed. (After Bernard.) (× 98.)

almost devoid of chlorophyll, are, like *Monotropa* and *Sarcodes*, obviously incapable of normal plant nutrition. The general view, which is not entirely satisfactory, is that during the course of evolution the plants have come to rely chiefly on organic food secured from the mycorrhizal fungus; and this in turn derives its supply from the abundant humus of the soil which these plants inhabit.

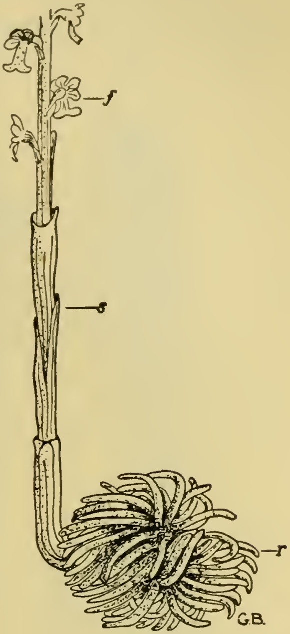

FIG. 160.

Lower part of a plant of *Neottia nidus-avis*, showing the dense mass of roots springing from a central rhizome, which is concealed by the roots. *s*=scale-leaf. *f*=flower. *r*=root. (× ⅜.)

It is, however, probable that in the seedling stage all Orchids, green or saprophytic, are to some extent dependent on assistance derived from the mycorrhizal fungus. Observation shows that in the presence of the fungus, infection of the Orchid seedling frequently occurs at a very early stage (Fig. 161). The difficulty of securing germination of Orchid seeds in horticultural practice is well known. Experiment has shown that usually Orchid seeds will not develop under sterile conditions. Inoculation with the fungus is followed by normal germination (Fig. 162). The explanation may be that the Orchid seed requires a stimulus before germination will take place; the stimulating substance, and additional food, may be provided by the fungus. The nutritional aspect is supported by experiments which show that if Orchid seeds are provided with organic food such as sugars, normal development will proceed *in the absence of the fungus.* Both of these observations have been put to practical application in horticulture, and Orchid plants can be raised (*a*) by sowing seeds on special soil infected with the mycorrhizal fungus, or (*b*) by feeding the seedlings with organic materials. The

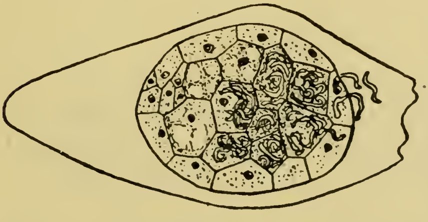

FIG. 161.

Seed of *Neottia* infected by fungus at a very early stage in germination. The outer line represents the testa. (After Bernard.) (× 100.)

second method has been termed *Asymbiotic* germination, and is the more successful.

It seems probable that in the association called endotrophic mycorrhiza the initiative comes from the fungus, by an essentially parasitic attack from the soil into the tissues of the host plant. By digestion the intrusive fungus may be kept under control, while incidentally the higher plant gains materials which may be of value for its own nutrition. The same view can be taken of ectotrophic mycorrhiza,

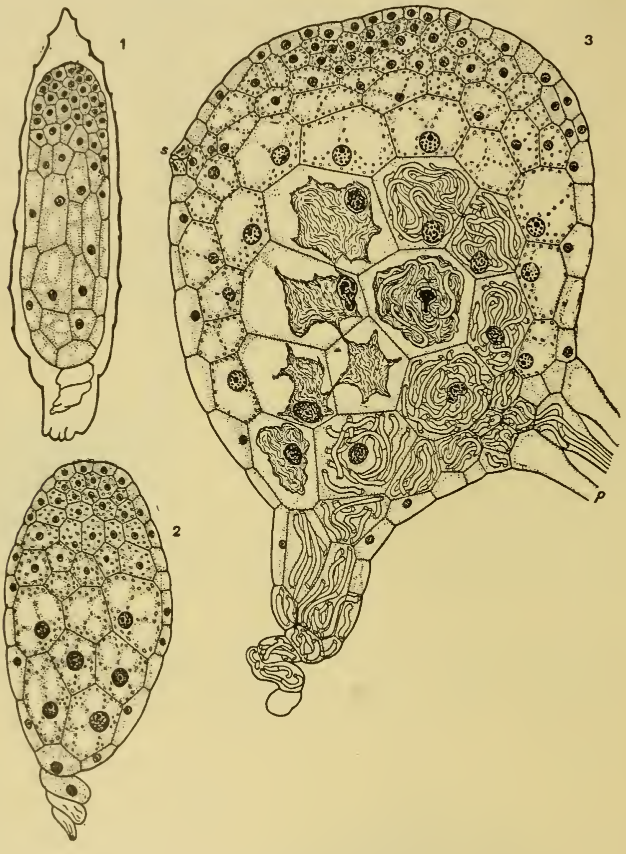

Fig. 162.

Germination of the orchid *Odontoglossum*. All sections are median longitudinal. (1) a seed; (2) shows the extent of development after three months under germinating conditions in the *absence* of the fungus; (3) shows the development obtained in a similar period in the *presence* of the fungus. From this tuberous structure the root and shoot later arise. Note the heavy infection and signs of digestion. *p*=absorbing hairs (through which infection occurs). *s*=stoma. (× 100.) (From Bernard, *Ann. Sci. Nat.*)

where, however, the parasitism is of a milder type. The two organisms, the fungus and the higher plant, essentially antagonistic to each other, may be looked upon as being in a state of balance; and that this leads to a prolonged symbiotic existence together, from which both may gain advantage. In the above treatment the possible benefit to the higher plant has received most attention, but the fungus probably gains at least a favourable environment, and some food materials from the higher plant.

The symbiotic condition presented in mycorrhiza occupies a middle position between two extremes. The one is that of *mortal disease*, where one organism of an association causes the ultimate death of the other. The other extreme is that of *immunity*, where though two organisms may be in relation, the one has no power over the other. There is evidence that under conditions unfavourable to the development of the higher plant the state of balance in the mycorrhiza may be upset, and that the fungus develops more pronounced parasitic tendencies.

Root-Nodule Plants.

Plants of the family Leguminosae (which include Peas, Beans, Clovers and Lupins) are regularly characterised by the presence of *nodules* on their roots. The nodules yield another example of Symbiosis, in this instance between a flowering plant and a *bacterium*. The lower organism is again perhaps best regarded as being essentially parasitic in nature. It inhabits the cells not of the root itself, as in endotrophic mycorrhiza, but of those special structures, the nodules, which arise on the roots and which may be compared with other swellings produced on plants by the presence of a foreign organism, *e.g.* galls.

Fig. 163.
Root of *Vicia Faba*, with numerous root nodules. Reduced. (After Strasburger.)

The nodules may be either spherical or cylindrical, simple or branched, according to the particular plant concerned, and they are present on main and lateral roots (Fig. 163). The nodule consists of a central mass of enlarged cells, crowded with bacteria which do not, however, destroy the nucleus or other parts of the host cell (Fig. 164, 1, 2). Vascular strands traverse the outer tissues of the nodule and connect up with the stele of the root, while the presence

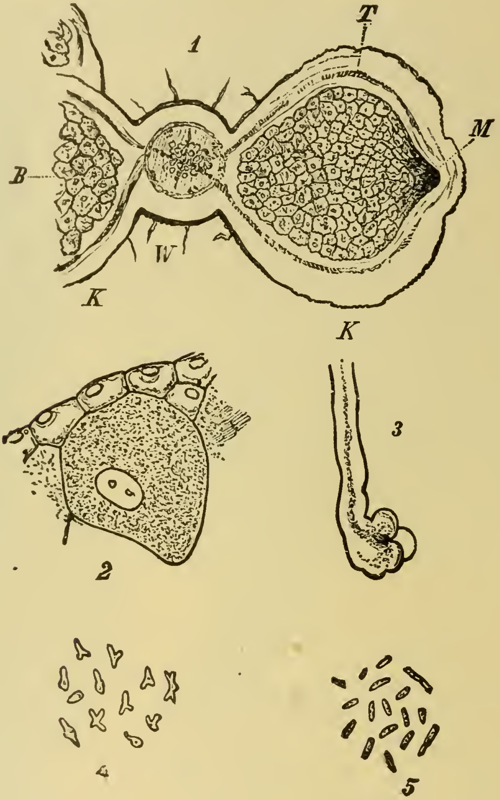

Fig. 164.

1. Young Nodules (*K*) on a root (*W*) of *Vicia Faba*. *B*=large-celled tissue filled with masses of Bacteria. *M*=meristem. *T*=tracheids. (× 60.) 2, a cell infected with Bacteria, and smaller non-infected cells. (× 320.) 3, an infected root-hair. (× 320.) 4, Bacteroids. 5, unaltered Bacilli. (× 1200.) (After Strasburger.)

of a meristem at the apex of the nodule provides for its continued growth. The bacterium (known as *Bacillus radicicola*) exists in the soil in a motile condition and penetrates the root-hairs of suitable leguminous plants. Inside the root-hair the bacterium multiplies very rapidly, and in the form of an "infection thread" advances along the hair (Fig. 164, 3), penetrating a group of cortical cells, which begin to divide, and the nodule is thus originated. The bacteria leave the infection thread and by continued multiplication eventually fill the cells of the developing nodule, though they are restricted to its tissues and do not infect any other part of the plant. The bacteria within the nodule-cells have at first a spherical or rod form, but eventually most of them pass into an enlarged, frequently forked condition, known as the *Bacteroid* form (Fig. 164, 4, 5). The formation of nodules usually begins during the first few weeks of development of a young leguminous plant, and the nodules persist in an annual until the close of the life-cycle of the plant approaches, when their tissues decay.

FIG. 165.

Plants of Soya Bean (*Glycine*) growing in nitrogen-free sand. Those on the left bore root-nodules, those on the right were free of nodules. Photo. G. B. ($\times \frac{1}{9}$.)

Unlike the great majority of plants, nodulated leguminous plants are able to make good growth in rooting media free of nitrate or other nitrogenous compounds, although other necessary salts are provided: a result *which indicates their ability to utilise atmospheric nitrogen in protein synthesis.* On the other hand, if the medium is initially sterilised and if other precautions are taken to prevent infection and nodulation, the leguminous plant develops signs of starvation and makes poor growth (Fig. 165). Evidently it is the presence of the bacterium which enables nitrogen fixation to proceed in nodulated plants, and there is general agreement that the bacterium itself effects the fixation within the nodules, though the chemical stages in the process are at present uncertain. In some way the nitrogenous products of fixation are transferred from the bacterium to the surrounding cytoplasm of the nodule cells, perhaps by a digestion of bacteria under the influence of plant enzymes, or through excretion of nitrogenous compounds by the bacteria. There is a steady passage of these products of fixation from the nodules into the rest of the plant, to its great advantage, especially when the soil is deficient in nitrogen. No doubt the bacteria appropriate to their own use certain carbohydrate materials from the plant. The environment provided by the nodule cells of the Leguminosae seems to be particularly favourable to the process of nitrogen-fixation, for although the bacterium can readily be grown on a variety of prepared nutrient media, there is as yet no satisfactory evidence that appreciable fixation of nitrogen proceeds under such conditions.

The significance to the organic world in general of this fixation of nitrogen by *B. radicicola* in association with a leguminous plant has already been stressed. After the completion of the life-cycle of the plant the nitrogen fixed during its development is added to the soil, and in due course it becomes available for uptake by plants in general. We have here a process whereby soil fertility is maintained. In agriculture the manurial effect of leguminous crops such as clover and lupins has been known for centuries. It is, however, possible that leguminous plants confer benefit not only on *future* generations of other plants, in the manner explained, but also on *contemporary* plants of other families that may be growing in the vicinity. For there is evidence that at least under some conditions there is a leakage from the nodules into the soil of nitrogenous compounds, available for absorption by other neighbouring plants.

It is frequently advantageous in agricultural practice to inoculate the seeds of a leguminous crop with the correct bacterium, in order to ensure plentiful nodule-formation. This is especially the case when a new crop is being introduced into a district, since the correct bacterium may not be present in the soil. It should be mentioned that a number of different races of the nodule bacterium exist, each capable of infecting only a limited number of different leguminous species.

It has been established that the red colour which the central tissue of the nodule usually shows is due to haemoglobin.

Root nodules are not entirely restricted to the family Leguminosae, but are also found for example on the Alder tree, Bog Myrtle, Sea Buckthorn, and a few other plants. The infecting organisms here are different from that in leguminous types, but they also possess the faculty of nitrogen fixation.

CARNIVOROUS PLANTS.

The predatory methods of Carnivorous Plants have been considered from the point of view of the reception of stimulus, and the consequent movements, in Chapter IX. Another aspect of them is in respect of nutrition. The plants which show this peculiar habit grow under conditions where the supply of combined nitrogen is difficult, such as in peaty or humous soil, where the native *Pinguicula* and *Drosera* are habitually found. Venus' Fly Trap and *Sarracenia* grow on boggy moors in America, while *Nepenthes* is an epiphyte. In such positions nitrates and other salts would naturally be deficient. On the other hand, all of these plants contain chlorophyll, and can thus construct carbohydrate for themselves. In point of fact the carnivorous habit is not essential to their existence, though experimentally it is found that a moderate supply of animal food is beneficial.

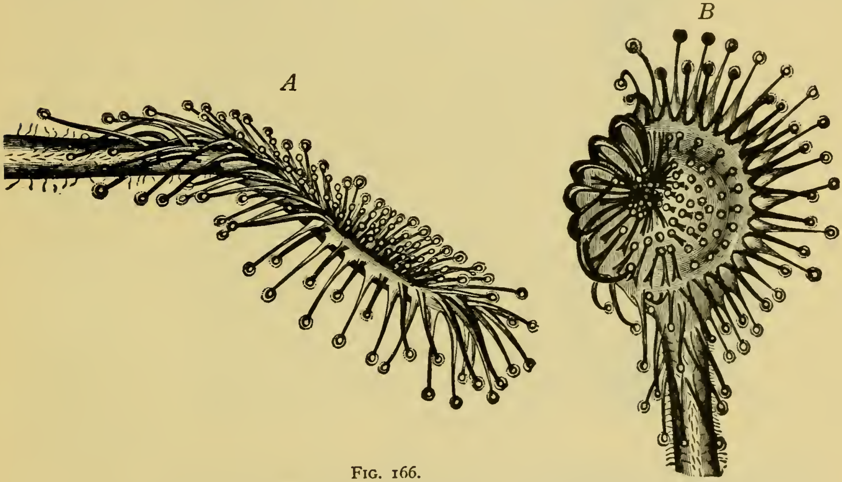

FIG. 166.

Leaves of *Drosera rotundifolia*: enlarged. *A*, in the receptive state before stimulation. *B*, after stimulation, viewed from above, with tentacles partly incurved. (After Darwin.)

Apart from the mere mechanism of capture, which is very various, the physiological treatment of the prize is fairly uniform. Its success depends upon secretion of digestive juices from certain localised, glandular cells. This has been studied very thoroughly in the Sundew (*Drosera*), in which the mechanism of capture has already been described (p. 164). The secretion which plays so important a part is produced by the glandular head of the tentacle, which receives its vascular supply through a strand traversing its stalk (Fig. 166). The digestive fluid is exuded by the epithelium that covers the surface of the gland. On contact with an insect, or with a small piece of nitrogenous matter, such as a cube of white-of-egg, the gland is stimulated to greater secretion. A proteolytic enzyme, which breaks down the complex protein to simpler soluble substances, is given out, and the secretion takes an acid reaction. The emission of the enzyme and of the acid is, as in the gastric secretion of the animal stomach, dependent upon the absorption of nitrogenous matter from the stimulating body: a piece of indigestible matter produces less secretion and without proteolytic powers. The body of the insect, or the cube of white-of-egg, enveloped in the secretion, is slowly digested, and the dissolved material, together with the secretion itself, absorbed into the cells of the leaf. In the white-of-egg the rounding of the edges of the cube can easily be followed. All that remains of an insect when digestion is complete are the insoluble chitinous parts. The process of digestion in the Butterwort and Venus' Fly Trap is essentially the same as in Sundew. The difference lies in the varying perfection of the mechanism.

FIG. 167.
Pitcher of *Nepenthes*, with part of the wall removed to show the fluid (*F*) secreted by the glands borne on the inner surface. (½ natural size.) (After Strasburger.)

In *Nepenthes* the pitcher-shaped leaves are effective traps for luring small animals into the fluid that partly fills each pendent urn (Fig. 167). In Botanic Gardens these are often choked by the partially digested remains of ants, cockroaches, and other victims. There is no motile mechanism that catches them, but only a static trap. The pitcher's lip slopes inwards, and is cartilaginous and smooth, with secreting glands at its inner rim. Insects attracted by the secretion into a dangerous position on the smooth sloping surface lose their footing and fall into the pitcher, from which, owing to the absence of foothold on the converging walls, there is no escape. Death and digestion follow.

The secretion within the pitcher is exuded by numerous large, button-shaped glands upon its inner surface. Each is covered on its upper side by a downward drooping hood, which effectually prevents its use as a step in climbing up out of the fluid. The presence of an insect in the base of the pitcher stimulates the glands to secrete digestive enzymes which convert the proteins of the insect body into soluble compounds suitable for absorption by the cells of the pitcher. Somewhat similar pitchers are present in *Sarracenia* and *Cephalotus*, though no secretion of enzymes has been demonstrated in them.

FIG. 167 A.

Bladder of *Utricularia vulgaris* in front view. The semi-circular entrance is seen, closed by the lid, which is attached to the rim along the top and part-way down the sides. Four bristles project from the base of the lid. Attached to the rim of the entrance are the antennae and other hairs. (× 33.) (From Skutch, *New Phyt.*)

The trapping arrangements in the Bladderwort (*Utricularia*), a native aquatic insectivorous plant, are quite different (Fig. 167 A). The numerous minute bladders, replacing leaf-segments, are normally filled with water, and are "set" as the result of an osmotic withdrawal of water from the interior of the bladder by glands on the inner side of the wall. The bladder-walls are in this way drawn in and brought into a state of tension. If now an aquatic animal touches the bristles which project from the lid of the bladder and so opens the lid, the tension is released and the walls spring back to their original shape, producing an inrush of water which sweeps the animal into the bladder. There is no escape since the lid cannot open outwards. Death and decay eventually occur and the products are absorbed by the plant.

The extraordinary forms and mechanisms thus seen in carnivorous plants seem to accentuate the importance for them of the gain which follows on this accessory nutrition. Yet all of these plants can live without it, while a surfeit of animal food may be experimentally shown to be harmful to them. These plants stand out as some of the strangest results of special adaptation, and strike the observer as showing a grotesque disproportion between the end gained and the means adopted to secure it.

Thus many plants, and often those in which we should least expect it, have other methods of nutrition than the autotrophic process. The degree of dependence upon irregular methods varies greatly. The habit is not restricted to any one family or group of plants. It has been seen that sometimes single species or genera, sometimes whole families, are affected. These phenomena are chiefly found in advanced families such as Leguminosae, Orchids, Heaths, or Orobancheae, rather than in those held to be primitive. All these facts taken together lead to the conclusion that *irregular nutrition among Flowering Plants is secondary.* Its methods have been adopted individually, and comparatively late in Descent, by organisms of which the ancestors were autophytes. Moreover it has not started along any single line of Descent, but along many. In this, as in so many special adaptations, homoplasy, or parallel development, is frequently illustrated. The advance has been along lines of opportunism. Close crowding has encouraged it. Use has been made of such circumstances as offered in order to achieve the end of the plant's existence. *That end is not merely the maintenance of the individual, but the propagation of the race by new germs.* The case of *Rafflesia* illustrates this in a striking though extreme manner (Figs. 154, 155). The vegetative system is reduced, in accordance with its parasitism, to the level of fungal hyphae. But its flower is of enormous size, complex in structure, and results in a great output of seeds, each containing a new germ (*ovula numerosissima*, as Robert Brown called them). The nutritive system, though reduced, is still effective for nourishing this flower. Thus the propagation of the race takes precedence over the vegetative development. This is the ultimate lesson taught by the study of irregular nutrition, and by the morphological degradation of the vegetative system, which so often follows on its successful practice. *Propagation is the real end. Vegetative development is only a means to that end.* The whole vegetative system may be regarded as a physiological scaffold, while the mechanism of propagation is the substantive building which is erected by means of it.

CHAPTER XIII.

VEGETATIVE PROPAGATION.

In the life of any organism there are two chief phases, which are not always distinct from one another, and may overlap. The one secures the maintenance of the individual, the other increases the number of individuals. Thus far the former only has been followed. It has been seen how the Plant is established on germination, and developed as an organism which can maintain itself. It is able, moreover, to acquire material in excess of its immediate needs. This is in itself a necessary condition of increase in number, for there must be at least a sufficiency of material for forming the new germ or germs. But it is not possible to put any measure on the amount of material required to be at hand before increase takes place. An unusually early propagation in a Seed-Plant is seen in the Potato, where the seedling may form a tuber from the axillary bud of each cotyledon (Fig. 168).

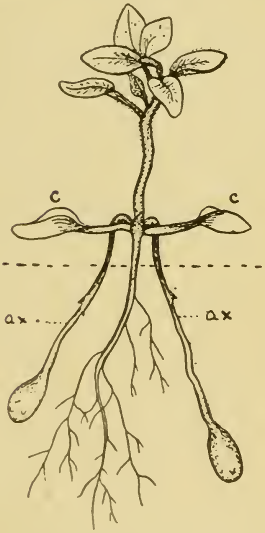

Fig. 168.
Seedling of the Potato, showing how the buds (*ax*) in axils of the cotyledons (*c*) develop as tubers. (After Percival.)

There are two methods of increase. One is by *Vegetative Propagation*, which consists simply in separation of a part of the plant-body as a being physiologically independent of the parent. During its early development that part is nourished by the parent. The separation may finally be completed by the death of the parent, as in the Potato ; or it may be the result of rupture or death of the tissue connecting it with the parent, as in the bulbils of the Orange Lily. It is the separation that defines the new individual. *In origin it was a part of the parent plant, the characters of which it retains and repeats.* The process may be simply described as *budding* ; or more specifically as *somatic budding*, as it involves the detachment of some part of the *soma*, or plant-body.

The other method is by *sexual reproduction*, which involves the fusion of two *sexual cells, or gametes*, to form a new cell, the *Zygote*. This is also the starting point of a new individual. The two gametes are more or less distinct from one another in origin and character. The offspring shows features derived from both of the parent gametes. But it differs in some degree from either of them. The process is not then a mere act of repetition, as the budding is. On the contrary, *Sexual Reproduction may be a source of something different from either parent, though it shares the qualities of both* (see Chapter XXXV.).

Vegetative propagation is a very wide-spread means of increase both of wild plants and of those in cultivation, and there is considerable variety of detail in the way in which it is carried out. In Flowering Plants it consists in the independent establishment of buds. Such buds may be produced in the normal sequence, as *axillary buds* ; or they may be produced out of the normal sequence, as *adventitious buds*. Examples of each will first be taken from plants growing naturally, and later it will be seen how the cultivator in the exercise of his art makes use of these, or actually induces their production artificially.

The propagation by *buds formed in the normal sequence* sometimes involves no modification of the shoot, and is so simple a process that it can hardly be distinguished from ordinary normal growth. An example is seen in the Canadian Water-Weed (*Elodea*). The shoot produces axillary buds which grow into long branches. Either mechanical rupture, or progressive decay from below, may sever the physiological connection, and the branch becomes a new individual. *Elodea* shows also the indefinite degree to which this vegetative propagation may extend ; for since the plant was introduced into Britain about the middle of the nineteenth century, it has spread throughout the waterways, notwithstanding that only the female plant was introduced ; and, being dioecious, it does not propagate here by seed. This simplest of all methods of vegetative increase in numbers is very common. Ordinary perennials, such as Grasses and Sedges, give abundant examples of it.

In other plants some slight modification of the axillary buds may be seen, giving biological advantages. For instance, there may be an elongation of the basal internodes, leading not only to vegetative increase, but also to a wide extension of the area occupied. A "runner" is thus formed, and the bud is carried out to a distance from the parent plant. It there roots in the soil without competing with the parent. This is seen in the Strawberry (Fig. 169), the Silver-Weed, the Bugle, and many other creeping herbs. In other cases storage, either in the axis or the leaves of the bud, gives it an additional advantage at the start, especially in plants subjected to seasonal change. Such buds may be produced above ground, as in the bulbils of the Lily or Onion; but more frequently they are buried, as in the Potato (see Fig. 147, p. 218), or Artichoke. Perennation as well as increase in numbers is secured by such measures as these. Sometimes the parent survives, as in *Saxifraga granulata*, or *Scrophularia nodosa*; in other cases it dies, as in the Potato and Jerusalem Artichoke. In the latter cases, since each tuber is borne on an elongated stalk and can grow into a new plant, both spread and increase are secured, as well as perennation. It will be unnecessary to illustrate further the manifold varieties of detail shown in vegetative propagation by means of buds produced in the normal sequence. In nature a very large proportion of individual plants may be traced as having been produced in this way. But it is more common in herbaceous than in woody plants.

Fig. 169.

Strawberry Plant, bearing axillary buds developed as runners, with long internodes which may branch and root at their distal ends. (Reduced to ½.)

Adventitious buds, that is, buds formed in positions where buds are not normally present, serve the same end, but they are less frequent. The case most commonly quoted is that of *Bryophyllum*, one of the House-Leek family, whose fleshy leaves may be induced to form buds in the notches of the leaf-margin, by pegging them down on moist soil (Fig. 170). These buds root themselves in the soil, and as the leaf decays they remain as substantive plants. A similar case occurs in the familiar Cuckoo Flower (*Cardamine pratensis*). In old plants the radical leaves lie along the surface of the soil, and buds are formed on the upper surface, usually at the forking of the veins. In *Malaxis paludosa*, a small native swamp Orchid, minute buds appear at the tips of the leaves. Frequently the adventitious bud-formation appears under some stress of circumstances. But this is most evident in those cases where they appear upon roots. For instance, if a Poplar or an Elm be cut down, the root-system is left still alive in the soil. It contains a large supply of plastic material, which it uses in the formation of buds. They originate without order from the region of the cambium, and rise above ground as "suckers" (Fig. 171). Fruit trees, such as plums, if severely pruned, also produce similar suckers. These are familiar objects in the vegetable garden, where plums are trained against a wall and pruned. Such adventitious developments are clearly related to a check of the aerial shoot, and may be held to be a method of recovery from it.

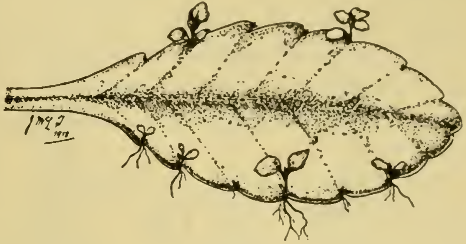

FIG. 170.
Leaf of *Bryophyllum* after culture on moist soil, with adventitious buds borne at its margins.

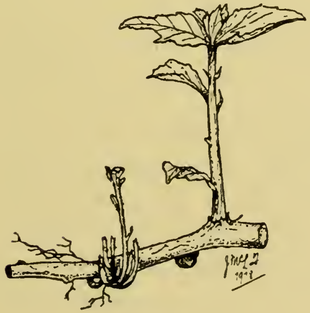

FIG. 171.
Root of *Populus alba*, bearing adventitious buds, which come above ground as suckers. (Reduced.)

A special interest attaches to the fact that vegetative propagation is common among alpine plants. In them vegetative buds easily detached replace flower buds. This is seen in *Polygonum viviparum*, where the lower part of the inflorescence bears as a rule bulbils only, while a variable number of flowers occupy its distal end. The rare *Saxifraga cernua* seldom flowers in Britain, but usually bears bulbils instead. Certain Grasses frequently show this state, *e.g. Poa alpina*, *Deschampsia caespitosa*, and particularly the mountain variety of the Sheep's Fescue (*Festuca ovina*, var. *vivipara*). Such developments may be held as a response to stress of circumstances. The short season and alpine conditions being unfavourable for flowering and fruiting so as to set seed, the formation of vegetative buds gives a greater certainty of survival. Any advantage that follows from sexual propagation is sacrificed to attain that certainty.

Such examples suggest how various are the ways in which Flowering Plants propagate by budding. It is, however, rare among Gymnosperms. In lower forms, such as Ferns, Horse-tails, and Club-mosses, it is common. Among the most prolific of all plants in this way are the Mosses, some of which are practically unknown in fruit. Finally in the Algae, and especially in the Fungi vegetative propagation is conspicuous as a source of increase. This raises the question whether this method might not suffice for all practical purposes. Cases are known among cultivated Flowering Plants where it is continued indefinitely. The cultivated Banana and the Pineapple are seedless. The Sugar Cane rarely flowers. The Jerusalem Artichoke has been grown regularly in British gardens for two centuries from tubers. There appears in fact to be no definite limit to repetition of increase by budding. It has always been favoured by horticulturalists for the good reason that the qualities of the strain or variety are as a rule retained, while in propagation by seed those qualities are liable to be modified or lost. *It is the weakness, as it is also the strength, of somatic budding that there is as a rule repetition rather than evolutionary change.*

This repetition is exactly what the horticulturalist requires when dealing with special strains of cultivated plants. His methods depend on the maintenance of the desired strain through buds produced in normal sequence, or adventitiously induced. *Cuttings* and *slips* are merely parts of the shoot of the parent plant bearing one or more normal buds. They are kept under circumstances to promote root-formation, which takes place best if the cut be made just below a node. The shoots must be selected of the right age and condition to secure success (see also pp. 149-150). Greater certainty follows on *layering*, in which the shoot is not separated from the parent, but pegged down in the soil, with or without a notch or ring, cut so as to check the downward flow of plastic material (p. 132). This promotes root-formation, after which the shoot may be detached (Fig. 172).

This method is used for rapid production of established plants in the case of currants, vines, and various fruiting stocks. But some plants are refractory and difficult to root. In such cases the stem below the shoot it is desired to establish may be nicked with a knife, and packed with wet moss or soil. Roots may then be formed, after which the shoot may be severed.

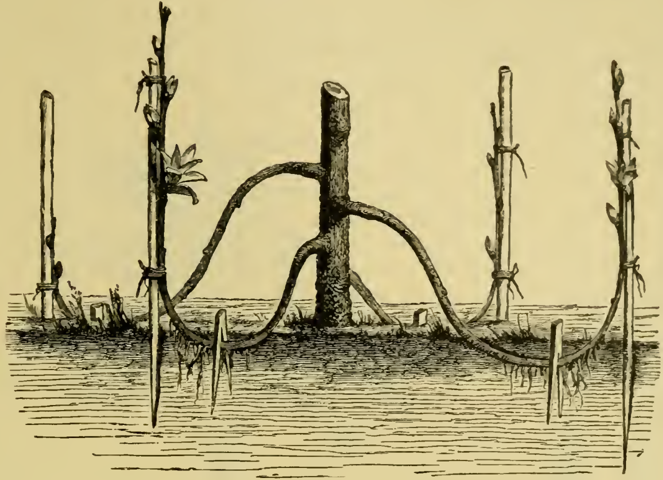

Fig. 172.
Propagation by layering. (After Figuier.)

Budding and *grafting* are methods commonly used for woody plants, but latterly they have been employed also with success in succulent plants. These processes consist in the insertion of a single bud, or of a shoot bearing a number of buds, not in the soil, but upon the corresponding tissues of some related plant. In the case of *shield budding*, which is largely practised in the propagation of varieties of roses, a bud is removed from the plant which it is desired to propagate, together with an area of superficial tissues separated at the cambium layer. A surface for its reception is

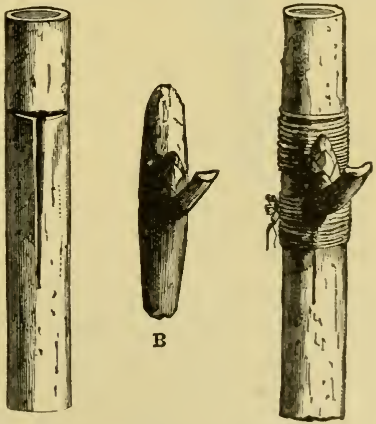

Fig. 173.
Method of shield-budding or cushion-grafting. (After Figuier.)

prepared by a T-shaped cut into the tissues of the stock that is to receive it, and the tissues down to the cambium are separated from the woody column (Fig. 173). The cambium-layer of the shield is placed in contact with the wood, and the whole is bound up with bast and wax to exclude air and intrusive fungi. The two living tissues form each a callus: the two unite, and their junction is such that the woody column of the stock provides the transpiration stream to the alien bud. *Grafting* is essentially the same process; but a woody shoot with a number of buds is removed, and inserted upon a correspondingly cut surface of the stock, so that the active cambial tissues of both shall be in contact (Fig. 174). *Inarching* or *approach-grafting* is similar, but has the advantage of both plants remaining rooted till the union is complete (Fig. 175). After the bud or graft has fully united with the stock its own root is cut away. Meanwhile the head of the stock having been removed, the graft or bud takes its place.

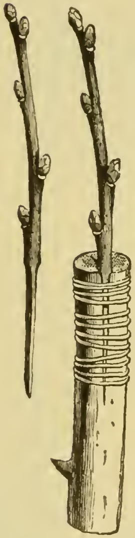

FIG. 174.
Cleft-grafting.
(After Figuier.)

FIG. 175.
Approach-grafting or inarching. (After Figuier.)

The bud or graft retains its original qualities. But according to the vigour of the stock it may mature earlier in the season, and fruit more profusely than upon its own root. Besides such advantages, time is also saved. For it is much quicker to insert a graft or bud upon an established stock than to raise an equally strong plant from a cutting.

The graft, or bud, or *scion*, as it is often called, need not necessarily be of the same species as the stock upon which it is placed. For instance, the Peach may be grafted on a Plum stock, the Apple on the Pear, the Pear on the Quince, or the Medlar on the Hawthorn. But the affinity must be close, such as within the Natural Order. The stock often influences the scion, though the latter retains its essential characters. The size, age of coming into fruit, or the period of maturing of the fruit may be affected ; but such changes are ascribed rather to the nutritional capacity of the stock than to any more profound cause. On the other hand, a more intimate association of the characters of the stock and of the scion is occasionally set up. Reputed *Graft-Hybrids* exist, which appear to share the characters of stock and scion. The most notable of these is *Cytisus Adami*, of which the parental forms are stated to have been the common yellow Laburnum and *Cytisus purpureus*, the latter having been inserted on the former. The plant which resulted has been widely propagated. It shows usually purple flowers, but certain branches " throw-back " to the common yellow form.

Others have also been raised artificially; the most notable of these were from grafts between *Solanum nigrum*, the black Nightshade, and *S. Lycopersicum*, the Tomato. A wedge or saddle-graft is made, and after the tissues have united the graft is cut through transversely : this causes a callus to be formed with numerous buds. Most of these show only the characters of the stock, or of the scion: but some show those characters intermingled. For instance, the shoot might be almost equally divided so that one side of it is Nightshade the other Tomato. Such monstrous forms are called " *chimaeras*," and the above instance would be distinguished as a sectorial chimaera, owing its origin to a lateral coalescence of the tissues of scion and stock, without any actual fusion of the cells. Others are called periclinal chimaeras, where the superficial cells of the apex arise from one source, the inner cells from the other, but again without cell-fusion. It appears from detailed examination of its tissues that *Cytisus adami* is a chimaera of the latter type. Chimaeras are not hybrids in the true sense of the word. There is no nuclear fusion, but the buds arise from a mechanical coalescence of tissues from the two parents at the junction of stock and graft. Each retains its own individual qualities, however closely the two may appear to be physiologically related together.

But occasionally a true graft-hybrid may occur, produced by fusion of cells and of their nuclei. An example is seen in *Solanum darwinianum* raised by Winkler, which is found to be intermediate between Nightshade and Tomato even in the number of its chromosomes. The nuclei of the former show on division 72 chromosomes, but those of the latter have only 24. The germ-cells of *S. darwinianum* are found to have 48, that is $\frac{24+72}{2}$. It may therefore be concluded that a fusion of a nucleus of Nightshade (72) has actually occurred with one of Tomato (24), giving 96, which on reduction to form the germ-cells appears as 48. If this be so, then *S. darwinianum* is a true graft-hybrid. (For an explanation of the behaviour of chromosomes in Reduction see Chapter XXXV.)

The horticulturalist also induces the formation of adventitious buds, and some plants respond freely. If a lamina of *Begonia* or of *Gloxinia* be cut transversely across the main ribs, and be cultivated in heat on damp soil, buds may be formed in relation to any cut vein. These buds root themselves in the soil as new plants. It is stated that each bud arises from a single cell of the parent leaf. (Fig. 176.) Certain Fern-rhizomes, and even the bases of their leaves behave in a similar way ; but it is in the Mosses that there is the most remarkable profusion of this adventitious development from single cells of the injured part. If moss plants be chopped up into small pieces, any piece in which an uninjured cell remains may start a new vegetative growth, and lead ultimately to a new moss plant.

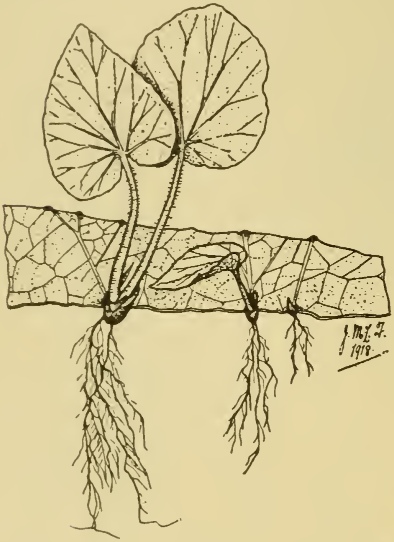

Fig. 176.

Part of leaf of *Begonia*, bearing adventitious buds after cultivation, in heat, on moist soil.

There are certain weeds of farm land which depend upon a somewhat similar vegetative multiplication for their survival, when the land is worked by plough and harrow. The Couch Grass (*Triticum repens*), and the Common Horsetail (*Equisetum arvense*) are cases in point. Any node serves to provide new buds ; and as the long underground rhizomes are broken up in preparing the soil, this does not eliminate, but tends to spread the weed.

It thus appears that vegetative extension and propagation of the individual is a very wide-spread feature, both in Flowering Plants and in those lower in the scale. It is effective in wild life, as well as under the hand of the gardener. A very considerable proportion of the perennial plants which we see have been so produced. This applies especially to the Grasses and Sedges, whose perennial rhizomes are constantly growing forward, and as constantly rotting progressively from the base. But probably the most prominent, and at the same time familiar example of all is the Bracken Fern, which covers immense areas, and is widely spread all over the world. Its underground rhizomes branch freely; if a single specimen be dug up, and followed backwards, the brown region of decay is soon reached. Young seedling Brackens are rarely met with in the open. Here then is a case where the apical growth and branching of the individual are practically unlimited, and where its vegetative increase in number of physiologically independent units appears to be unlimited too. It may be held as a type of that vegetative spread and multiplication which, though it involves no special development for the purpose, is frequent among perennial plants.

CHAPTER XIV.

THE INFLORESCENCE, AND THE FLOWER.[1]

In Flowering Plants *Sexual Reproduction* is carried out in the Flower. It results in the *production of Seed.* Contained in each ripe seed is the *Germ of a new individual.* The Flower which serves this uniform purpose of producing new germs may take an infinite variety of forms in plants. But however various the appearance of the Flower may be in outline, or in the number or complexity of its parts, comparison shows that the organs which are directly connected with the sexual process, and the details of that process, are in all cases essentially the same. This suggests that *the differences are accessory, and that the propagative process itself is the real end.*

THE FLOWER.

The Flower is found to consist of parts which fall into certain definite groups, or kinds of organs. But they may vary greatly in number, while all the kinds of organs need not be represented in the same flower. Some like the Water-Lily, or the Rose or Quince, consist of numerous parts representing all the kinds of organs (Fig. 177). In other cases the flower in the strict sense may comprise only a few parts, or in extreme cases only a single one of them, as in the Spurge (Fig. 178). There is usually a prolongation of the stalk to bear the floral parts; but it terminates abruptly and is apt to be more or less widened out laterally, so that the appendages can be closely crowded upon it. This widened tip of the stem is called the *floral receptacle* and since its apical growth stops, the result is that the flower is always distal,

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[1] This chapter will be best understood after a number of the types of Floral Construction described in Appendix A have been dissected and examined.

that is, it is borne at the end of its stalk. The parts which the receptacle bears may be grouped as :—

(1) *Sepals*, which are the lowest and outermost parts. They are usually leaf-like, being firm and green in texture. They constitute the *Calyx*, the office of which is protective to the inner parts of the young bud (Fig. 177, *Sep.*).

(2) *Petals*, which lie internally to them, and are usually delicate in texture and in tint. They constitute the *Corolla*, and serve chiefly for attracting attention by colour and scent (Fig. 177, *Pet.*).

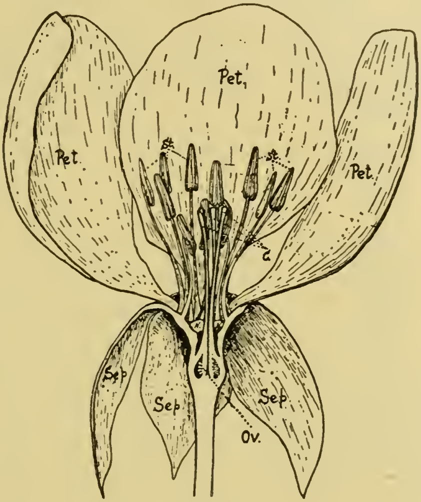

Fig. 177.

Vertical section through a flower of the Quince, *Cydonia* (*Rosaceae*). *sep*=sepals. *pet*=petals. *st*=stamens. *c*=apices of the carpels, elongated into styles. *ov*=ovules. *n*=nectaries. The receptacle is here hollowed out, so that the carpels appear sunk down into a cavity. (After Church.)

(3) *Stamens*, which are inserted internally to the petals, and are usually club-shaped, and yellow in colour. Each bears *Pollen-Sacs*, commonly four in number. The stamens are styled collectively the *Androecium*,[1] and their function is to produce *Pollen* (Fig. 177, *St.*).

(4) *Carpels*, one or more of which occupy the centre, and are usually of pod-like form, and either green or colourless (Fig. 177, *c*). They are styled collectively the *Pistil*, or *Gynoecium*,[1] and their

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[1] The correct spellings of these words, as based on derivation, are *androecium* and *gynaeceum*. But as it is inconvenient to maintain this difference in spelling in view of the cognate meanings of the terms, it is best to sacrifice strict accuracy, and to assimilate the spellings. The words will therefore stand in the text as *androecium* and *gynoecium*.

functions are to receive the pollen, and to enclose and protect the *Ovules.* (Fig. 177, *ov.*) Under favourable conditions each ovule is able to produce a single new *germ*, and to develop into a mature *Seed.*

The relations of these floral parts to the receptacle are similar to those of the foliage leaves to the stem; for they arise laterally upon it, and their succession is such that the oldest are the lowest, or outermost, and the youngest the innermost, or nearest to the tip. *No buds are produced in their axils.* As in the foliage shoot the appendages may be arranged *spirally, or in whorls*, but in the flower the latter is the more common. The members of the successive whorls usually alternate with one another. This is convenient for their close packing in the bud. The parts of the flower are as a rule closely aggregated together, while those of the vegetative shoot may be separated by long internodes. But all normal leafy shoots terminate in a bud, and so, at least in the young state, the two are alike in this also. *There are thus marked analogies between the foliage shoot and the flower. Both are constructed on the same plan. There is, however, one absolutely distinctive character which separates them. It is the presence in the Flower of the Organs of Propagation, called Sporangia.* These have no correlative in the vegetative region. They are organs of a separate category altogether. *Accordingly the Flower may be defined as a simple Shoot which bears Sporangia.*

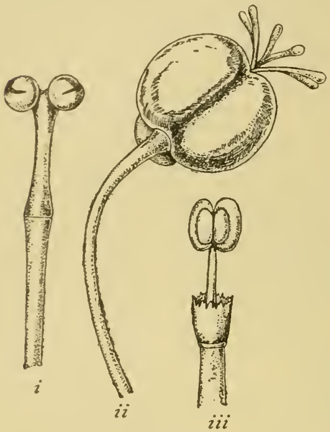

FIG. 178.

(i) Single male flower of Spurge (*Euphorbia*), consisting of one stamen, with abortive perianth. (ii) Single female flower, consisting of three carpels, and an abortive perianth. (iii) Single male flower of *Anthostema* (Euphorbiaceae).

In the Flowering Plants the *Sporangia are of two sorts*, viz. *Pollen-Sacs* and *Ovules.* In very many cases these are both present in the same flower, which is then called *Hermaphrodite.* But in others only one or the other is present. When the flower contains stamens bearing pollen-sacs, but no carpels, it is described as *Staminate*; when it has carpels bearing ovules, but no stamens, it is called *Pistillate.* The biological importance of these differences of distribution is great, as they are closely related to the mechanism of intercrossing.

The two types of sporangia, viz. pollen-sacs and ovules, and the parts that bear them, viz. the stamens and carpels, are often described as organs of sex, and flowers in which only one or the other occur are called " male " or " female." It is better to call them staminate and pistillate. All the old terminology of the flower has been based upon a misconception. It should be clearly understood that there has been an error of description. It is almost impossible to eradicate that error without discarding much of the current terminology, which it is hardly necessary to do provided that the difficulty is clearly realised. The early writers suffered from an imperfect knowledge of fact, and a want of proper comparisons. For our present purpose those comparisons cannot be made intelligible till certain plants lower in the scale have been examined. At the moment the conclusion must be stated without the detailed grounds for it. It must suffice to say here that *the sporangia of the Higher Plants produce SPORES (pollen-grains, and embryo-sacs), and it is from these that the actual sexual organs originate. But neither stamens nor carpels, nor pollen-sacs nor ovules, are themselves organs of sex. They are all parts of the neutral plant, specialised in relation to the sexual organs which it is their ultimate function to produce.* (See Chapters XV. and XVI., also XXXIV., XXXV.)

THE INFLORESCENCE.

The *Flower* defined as above is usually marked off from the vegetative system that bears it as a definite unit. When borne singly, as in the Tulip or Buttercup, no one has any doubt what is meant by the term. But such units are often borne in large numbers together upon a *common branch-system, or Inflorescence*, as in the trusses of a Horse-Chestnut, or a Lilac ; and sometimes the flowers of an inflorescence are so closely packed together that the whole may be mistaken for a single flower, as in the Daisy. It is thus necessary to analyse the branch-systems that bear the individual flowers.

The *Inflorescence* often presents marked features, and as these recur in related forms they have their value in classification. The methods of branching in an inflorescence, which are often very complicated, are the same as those found in the vegetative region. Here as there *axillary branching prevails.* The leaf, in the axil of which a flower-bud arises, is usually small and simple by reduction ; sometimes it is abortive. These reduced leaves are termed *Bracts.* Where they are borne upon axes of relatively higher order they are commonly smaller, and may be styled *Bracteoles.* But there is no real difference, except in their relation in the branch-system. The bracts serve to protect the buds while young. The production of many flowers together, so as to form a conspicuous group, even though the flowers may be individually small, brings advantages in mutual protection ; but still more in relation to the transfer of the pollen. In particular, a complicated branching not only gives the opportunity for a larger output of seeds, but it may also provide a succession of flowers which bloom during a prolonged period, instead of simultaneously; thus the physiological drain of flowering is distributed in time. These are among the biological advantages gained by complicated inflorescences.

The characteristic features which inflorescences show depend upon four main factors: (i) the arrangement of the leaves (bracts) in the axils of which the branches arise; (ii) the proportion of intercalary growth of the several axes; (iii) the number of flower-buds produced; and (iv) the succession in which the buds mature. Of these the most important is the last, and inflorescences may be classed according to its consequences as *Definite* or *Indefinite.* If a distal flower blooms first, that will stop the apical growth of the main axis, and all further flowers must be borne on lateral axes. Such inflorescences are termed *Definite*, or *Cymose* (Fig. 179, *A*, *B*). They commonly develop *sympodially*, that is, the lateral axes grow so as to overtop the main axis. But if the buds on lateral branches bloom first, the apex may still continue to grow, and to form additional bracts and flowering buds. Such inflorescences are called *Indefinite*, or *Racemose* (Fig. 179, *C*, *D*, *E*). They usually work out along *monopodial* lines: that is, the main axis remains dominant, and the lateral axes are accessory.

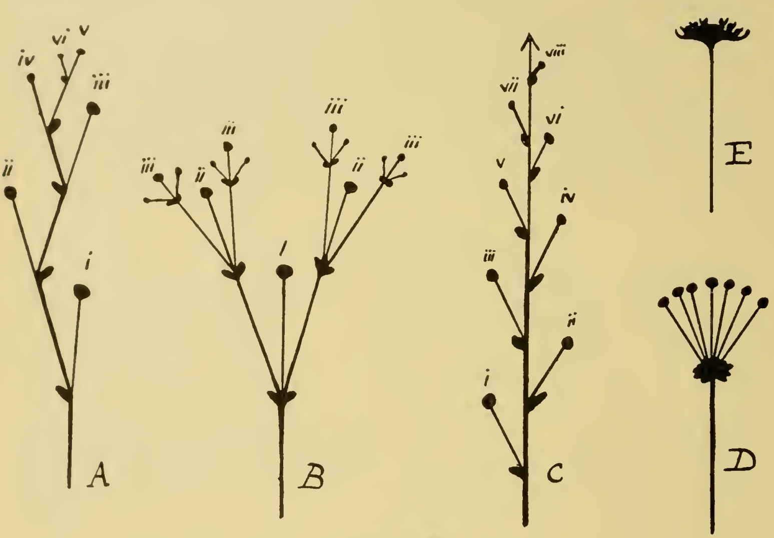

FIG. 179.
Diagrams of common types of Inflorescence. *A*, *B*, definite; *C*, *D*, *E*, indefinite. The numbers indicate the succession of the flowers. See text.

The simplest *Cymose* or *Definite* inflorescence is illustrated by the Tulip, with its solitary flower terminal on the *peduncle*, or main flower-stalk. But in the bulb below, an axillary bud matures during the season, which will repeat the flowering axis in the next year, and so on. The tulip is then a definite inflorescence, with an interval of a year between its flowers. Its branch-system is sympodial, each succeeding axis overtopping its predecessor. The Buttercup shows a similar condition, but its sympodial character appears in the flowering shoots of the single season. (Fig. 179, *A*.) In these cases the leaves are alternate, so that each lateral branch is solitary. But if the leaves which serve as bracts in a cymose inflorescence are opposite, as they commonly are in the Pink Family, and in many Gentians, the main axis will bear two lateral branches at the same level. (Fig. 179, *B*.) The result is what is called a *Dichasium* (Fig. 180). The difference depends here upon the leaf-arrangement, but the method is the same as before; and a number of sympodia are the result, instead of only one. Various other Cymose inflorescences are built up on fundamentally the same principle, but differing in the orientation and succession of the bracts, and consequently of their

FIG. 180.
Inflorescence of Centaury: a dichasium. (After Figuier.)

FIG. 181.
Inflorescence of Verbena: a spike. (After Figuier.)

individual flowering branches, or *pedicels*. Examples are seen in the common Rock Rose, and in *Echeveria*.

The simplest *Racemose*, or *Indefinite* inflorescence is the *Spike*, where flowers in an acropetal sequence are seated directly in the axils of the bracts borne by the main axis or *peduncle*, as in *Verbena* (Fig. 181). Or the lateral flower-stalks (*pedicels*) may be elongated, giving the condition of the typical *Raceme*, as in the Currant (Fig. 182). Or again the pedicels may be themselves branched, as in the Vine, giving the *panicle* (Fig. 183). Such differences depend partly upon differences of intercalary growth, partly upon branching of a higher order. In all of them the distal buds develop latest. It happens, however, not uncommonly that the characters may be mixed. For instance, a cymose tendency may appear in the higher branchings of a panicle ; as is well seen in the inflorescences of Figwort, where the terminal flower of the lateral branches blooms before those seated below.

Fig. 182.
Inflorescence of Currant : a raceme. (After Figuier.)

The racemose type is particularly subject to extreme differences of growth in length. The result is seen in certain inflorescences which characterise large families. The most important are the *Umbel* and the *Capitulum*. Both result from suppression of growth in length. If the axis be abbreviated in the part that bears the pedicels these will all appear to originate from the same level, giving a candelabrum-like branching, called a *simple Umbel* (Fig. 179, *D*). The subtending bracts are also grouped into a close investment just below the group of branches It is called collectively an *involucre* and serves for protection in the young state (Fig. 184). The branching may be repeated in each of the pedicels, each being provided with a *partial involucre* of bracts. The result is the *Compound Umbel* (Fig. 185). But as in other complicated inflorescences, the bracts of the partial, and even the general involucre, are liable to be reduced, or entirely absent. The closely grouped buds protect one another while young, so that the bracts become superfluous, and are liable to be suppressed. Such inflorescences are characteristic of the Umbelliferae; but various degrees of abbreviation of the axes are found in other families, giving rise to modifications of the raceme or panicle sometimes described as corymbose.

Fig. 183.
Inflorescence of the Vine: a panicle. (After Figuier.)

If, however, intercalary growth be reduced both in the peduncle and the pedicels, all the flowers will appear aggregated in a dense head. The axis of the whole inflorescence is then usually enlarged into a *general receptacle*, upon which numerous flowers are seated. Such an inflorescence is called a *Capitulum* (Fig. 179, *E*). It is characteristic of the Compositae. Here again the bracts form a general involucre protecting the whole head, while a bracteole normally subtends each flower borne on the receptacle (Fig. 186). But as these are closely packed, they must mutually protect one another. The bracteoles are then superfluous, and are often absent, as they are in the Oxeye Daisy and the Dandelion (Fig. 480, App. A). Similar capitula are found in the Sheep's Bit (*Jasione*) among the Campanulaceae, and in the Teasel and Scabious among the Dipsaceae. It is in fact a character recurrent in several distinct families, though it finds its headquarters in the Compositae. Its biological effect is that an inflorescence acts functionally in the same way as a single flower.

FIG. 184.
Inflorescence of *Astrantia*: a simple umbel. (After Figuier.)

FIG. 185.
Inflorescence of Chervil: a compound umbel. (After Figuier.)

Inflorescences usually develop on a *radial* plan, especially those of indefinite type. But many definite inflorescences appear distinctly *dorsiventral*. These are so arranged that each flower as it blooms is directed upwards, thus securing prominence at the time of pollination. This is seen in the Forget-me-nots

FIG. 186.
Inflorescence of Daisy: a capitulum. (After Figuier.)

and Rock-Roses. In the Grasses, which are racemose, even upright inflorescences may be dorsiventral. This is seen in the Cock's-foot (*Dactylis*), and the Mat-weed (*Nardus*).

METHODS OF COMPARISON OF FLOWERS.

No attempt will be made here to describe fully the wide range of difference in construction of Flowers, nor to treat those differences systematically, as a basis for a natural grouping into Families. Such details will be left over to Appendix A. It must suffice to illustrate the *methods* by which such comparisons are most easily presented, and to state the *leading factors* upon which these differences depend. Certain essential facts of floral construction may be obtained from a median vertical section (Fig. 177, p. 255). This will give the form and proportion of the receptacle, and the relative levels of the successive organs which it bears. But it cannot indicate their number, or fully disclose their position relative one to another. Such facts may be obtained by observation from above, and be plotted into a *floral diagram* (Fig. 187). This allows of the representation of each constituent part. It also gives the orientation of the flower relative to the axis and subtending bract. The side next the axis is described as *posterior*, that towards the bract *anterior*. The plane including the axis and the midrib of the bract is called the *median plane*; that at right angles to it the *transverse plane*. It is thus possible to plot the constituent parts in ground plan, and to describe them in their relation to these planes. But the floral diagram gives no record of the elevation. Accordingly it must be used in conjunction with vertical sections in order to complete the study. A compact mode of registering both is found in the *floral formula*. If S represent the Sepals, P the Petals, A the Androecium, and G the Gynoecium, the number of parts of each may be added as a numeral (∞ indicates an indefinite number). Where the Calyx and Corolla are not differentiated, P may stand for Perianth. Where the parts of one category form more than one whorl, this may be shown by giving a separate figure for each. The mutual relations of the parts can be indicated by brackets, thus showing where parts are united. The position of the outer parts relative to the gynoecium

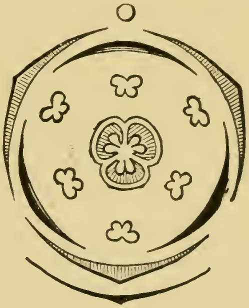

FIG. 187.

Floral diagram of Liliaceous Flower. (After Eichler.) The small circle above represents the axis; the bract is shown below, black.

is suggested by a line above or below the latter. Other details are sometimes introduced into floral formulae, but it is best not to overload them. As examples the following formulae for common flowers may be given :

Lily, P_{3+3}, A_{3+3}, G $\underline{(3)}$. (Compare Fig. 187.)
Buttercup, S_5, P_5, A ∞, G $\underline{\infty}$. (Fig. 452, App. A.)
Myrrhis, S_5, P_5, A_5, G $\overline{(2)}$. (Fig. 468, App. A.)
Primrose, (S_5), $\underbrace{(P_5), A_{0+5},}$ G $\underline{(5)}$. (Fig. 470, App. A.)

[For details which will explain these formulae see Appendix A.]

FACTORS LEADING TO DIFFERENCES OF FLORAL CONSTRUCTION.

The leading factors upon which the differences of floral construction chiefly depend will now be stated and discussed. They are these:

(i) Differences in the arrangement of parts on the receptacle.
(ii) Meristic differences.
(iii) Fusion of parts.
(iv) Pleiomery.
(v) Meiomery.
(vi) Various development of the floral receptacle.
(vii) Differences of symmetry.

Each of these will be discussed and illustrated.

(i) *The arrangement of the parts upon the receptacle* may be either *spiral*, as in *Adonis* (Fig. 188) ; or *cyclic*, as in *Ornithogalum* (Fig. 187) ;

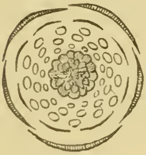

Fig. 188.
Floral diagram of *Adonis*. (From Strasburger.)

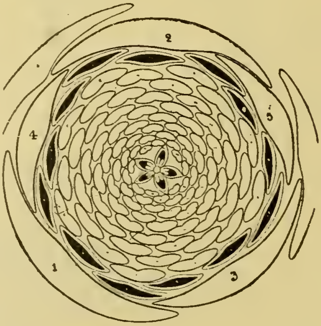

Fig. 189.
Floral diagram of *Helleborus*. (After Church.)

or an intermediate condition (*hemicyclic*) may be found between them, as in some of the Buttercup Family (Fig. 189). The cyclic type is however prevalent, especially in highly organised flowers. Since the spiral is characteristic of many primitive flowers and these graduate into cyclic types, the facts suggest that the cyclic state may often have been derived in Descent from condensation of a spiral scheme. Whether arranged in whorls or in spirals, *the parts of successive series alternate as a rule.* This allows of their being closely packed in the bud. *They are formed in acropetal succession.* Occasionally it is otherwise, but the most prominent exceptions occur where an organ has been reduced, as in the calyx of the Compositae.

(ii) *Meristic differences.* The number of parts in each successive category may differ in different flowers, and these are called meristic differences. In spiral types the numbers are relatively large and indefinite (Figs. 188, 189); in cyclic types they are smaller, and usually definite (Fig. 187). Where the whorls are well defined the actual numbers of parts in each may be compared, and are found to vary in different flowers. Some *fundamental number*, commonly three, four, or five, then rules in the construction of each flower. Such flowers may be described as trimerous, tetramerous, or pentamerous respectively. But the fundamental number rarely holds through all the whorls, though the Flax is an example of this (S_5, P_5, A_5, G_5). Usually the androecium shows larger, and the gynoecium smaller numbers than the sepals or petals.

Not only are meristic differences common between different families, genera, or species, but even between different flowers of the same inflorescence. As regards families, the Crassulaceae show meristic variation in high degree, the fundamental figure rising in the House-leek to as many as twenty, whereas in *Sedum* it is commonly five. Within the family of the Liliaceae *Maianthemum* has 2-merous flowers, most Liliaceae have 3-merous, but *Paris* has 4-merous, or even 5-merous flowers. Within the Primulaceae *Glaux* sometimes has 4-merous, *Primula* 5-merous, and *Lysimachia* 6-merous flowers, and others have still higher numbers. Within the genus, *Gentiana campestris* has 4-merous, and *G. amarella* 5-merous flowers, while species of *Saxifraga* may show flowers 5-, 6-, or 7-merous. In the same inflorescence *Adoxa* and *Ruta* both show meristic variation. In *Ruta* the terminal flower is 5-merous, and the lateral flowers 4-merous. In *Adoxa*, as a rule, the terminal flower is 4-merous, and the lateral flowers 5-merous. Such facts are a warning against any undue faith in numbers of parts as themselves indicative of affinity.

(iii) *Fusion of parts.* In some simple flowers like the Buttercup all the floral parts are *separate, or free* from one another. This state is probably primitive, and corresponds to the condition seen in most vegetative buds. But in many flowers certain parts are found to be *fused together* in the mature state. There is a real continuity of tissue between them. A familiar instance is the Primrose, where the corolla can be pulled away in one piece, though its margin clearly shows five petaline lobes. Further, if the corolla of the Primrose be opened out, five stamens will be seen attached to the inner surface of its tube. So not only is there a *cohesion* of the five petals to form a tubular corolla, but also an *adhesion* of the stamens to it. *COHESION of parts of the same category* (*such as petals with petals*), *and ADHESION of parts of different category* (*such as stamens to petals*), *are common in flowers, and may be held as secondary modifications of their free condition, as seen in the primitive state.*

This view is borne out by the study of development. For where the parts are fused in the mature state, they still originate as separate papillae of tissue from the growing point of the flower, just as the foliage leaves usually do. It is later that the growth extends from the individual bases of these papillae into the region between them. Consequently when mature they appear as though borne up on a common base. This is well shown in the flower of the Compositae, in which there is cohesion of the petals to form the tube of the corolla, and adhesion of the stamens to the inner surface of that tube. Fig. 198, p. 273, (v) and (vi) show how that adhesion arises. In (v) the stamens and petals are independently inserted on the hollowed receptacle ; but the line where basal growth will take place is indicated. In (vi) the result is seen ; for they are there borne up on a common base, which has been the result of that growth.

(iv) *Pleiomery.* By this is meant that the number of parts of one category is greater than the fundamental number for the whole flower. It is most frequently seen in the androecium, so that the stamens are in excess of the other parts. It may be a question exactly how this comes about in each individual example. *Branching or fission* of originally single parts may account for some cases ; *interpolation* of additional parts, where there is room for them on the receptacle, may explain others. The distinction between these is not always clear ; it turns upon comparison, and the observation of details of development. The essential feature is, however, that *more parts of one category are produced than the other whorls of the flower would give reason to expect.*

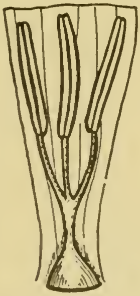

FIG. 190.
Group of three stamens of *Vellozia*, taking the place of one stamen in the normal Liliaceous flower. (After Eichler.)

Fission is most easily recognised where two or more stamens stand side by side in the place normally occupied by one ; it then sometimes happens that they arise from a common stalk. The case of *Vellozia* (Fig. 190) gives a good example. *Interpolation* of extra parts may give very similar results. Sometimes it is *individual* *parts*, sometimes *additional whorls* that are added. All these methods appear exemplified in the Rosaceae. The following diagrams may be quoted as illustrating the pleiomeric variations within that family, though without suggesting any actual line of Descent (Fig. 191). In *Sibbaldia*, the pentamerous flower has five stamens. *Quillaija* has two whorls of five (diplostemonous), and this probably represents the fundamental type for the Rosaceae, as it corresponds to that of related families with the formula (S_5, P_5, A_{5+5}, G_5). But in the Rosaceae the matter does not stop there. Further steps are taken till an indefinite number of stamens is arrived at. For instance, in *Agrimonia odorata* there is an outer whorl of five and an inner of ten (II.). In *Potentilla* there may be two whorls of ten stamens each (III.); in *Mespilus* there may be four whorls of ten each; while in *Rubus* (IV.), taking account only of the two outermost whorls, that next to the pentamerous corolla consists of ten stamens, but it is followed by numerous stamens disposed in irregular groups varying from one to four; those groups alternate with the stamens of the outer whorl. This points to an irregular interpolation of extra stamens. Such comparisons suggest that in the Rosaceae three sources of pleiomery of stamens have occurred, (i) fission, (ii) interpolation of individual stamens, and (iii) interpolation of extra whorls of stamens.

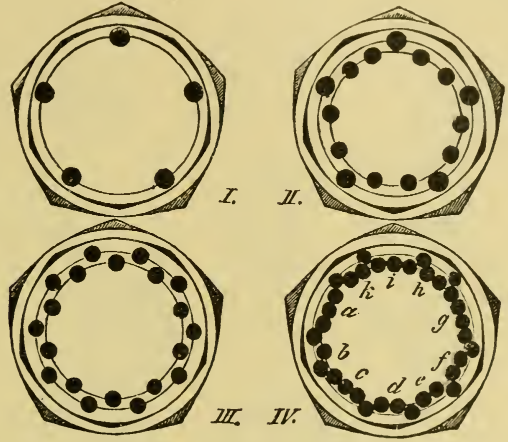

FIG. 191.

Floral diagrams of various Rosaceae (carpels omitted). I. *Sibbaldia cuneata*, and some species of *Agrimonia*. II. *Agrimonia odorata*: the first whorl of five stamens is followed by one of ten. III. *Potentilla*: the pentamerous corolla is succeeded by a whorl of ten stamens, alternating with ten stamens of the second whorl. IV. *Rubus idaeus* (special case). The pentamerous corolla is followed by a whorl of ten stamens, and from one to four stamens according to the growth of the zone of the floral axis are interpolated in the intervals between each pair of the first stamens, not only one as in III. There are three at *a*: one at *b*: three at *c*: two at *d*: two at *e*: two at *f*: four at *g*: two at *h*: three at *i*: two at *k*. (After Goebel.)

The *diplostemonous state*, where the stamens are twice as many as the petals, is common in those Dicotyledons and Monocotyledons which have cyclic flowers. Many polypetalous Dicotyledons show it, but with slight modification of position of the stamens, which suggests that it may have originated in different ways. It is represented also in the Gamopetalous Dicotyledons: these are divided into Tetracyclicae which have only one whorl of stamens, and Pentacyclicae which have two; making in all five cycles of floral parts. The Pentacyclic type is prevalent also in the Monocotyledons, as shown by the Liliaceous type of flower, with its many derivatives. The biological meaning of such facts is to be found in the larger supply of pollen thus provided to meet the risks of failure in pollination.

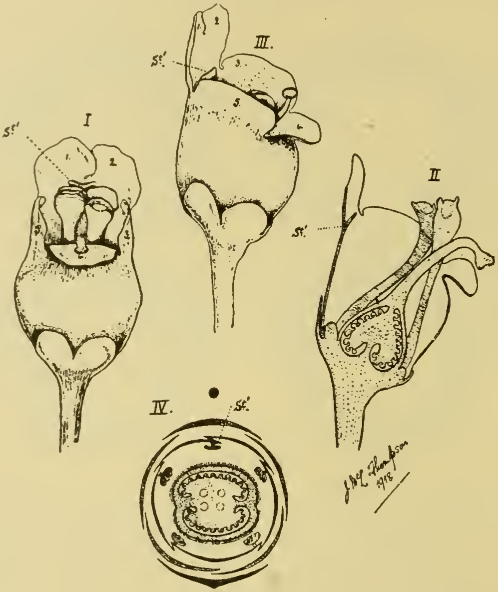

Fig. 192.

Flower of *Scrophularia nodosa*, which is pentamerous. The five stamens are represented, but the posterior stamen (*st'*) has no anther: it is merely a vestigial staminode which marks the place of a normal stamen.

In "*doubled*" *flowers* similar features of pleiomery are seen. "Doubling" often consists merely in a petaloid development of stamens; and it most commonly occurs in flowers with an indefinite number of stamens. But it often involves also an actual increase in number of the petaloid parts, effected by methods of fission, as well as of interpolation of extra whorls, or of extra individual parts.

(v) By *Meiomery* is meant that the number of parts of one category stands below the fundamental number for the whole flower. It is most often seen in the gynoecium; but it appears also in the androecium, especially in flowers where the mechanism is highly specialised. It occurs less frequently in the outer floral parts. In the gynoecium it may be referred to a fading out of the activity of the floral shoot, or even a deficiency of room for the full number of parts. The result is that the carpels are frequently fewer than the other parts. For instance, in the Compositae, the Umbelliferae, and most Gamopetals there are only two carpels in the pentamerous flower. But in many cases it is clear that the smaller number is the result of *abortion* of parts which comparison with allied plants would show as actually present. Sometimes those parts are represented by *vestigial remains*, marking the position which those parts should hold, though they do not come to functional maturity. A good case of a vestigial stamen (*st.*) is seen in *Scrophularia* (Fig. 192).

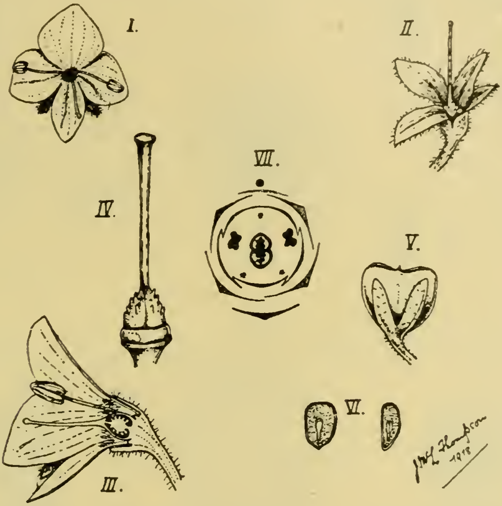

FIG. 193.

Flower of *Veronica Chamaedrys*, typically pentamerous, but the posterior sepal is abortive: the two obliquely posterior petals are fully fused to form apparently one: only the two obliquely posterior stamens are developed.

Meiomery may appear in any of the floral parts ; often it is seen in several of them in the same flower. A complete whorl may be absent : for instance the *corolla* in the Pearl-Wort (*Sagina apetala*) in the Pink Family, and *Glaux* among the Primroses : or one of the whorls of stamens may be absent, as in the Primrose. The most marked examples in the *androecium* are related to increasing precision of the floral mechanism. For instance in the Orchidaceae, derived from an Amaryllidaceous type with six stamens, *Anastasia* has three, *Cypripedium* two, and *Orchis* only one—the anterior stamen. Ginger has also only one, but it is the posterior. All of these are highly specialised types : their meiomery by abortion has followed parallel, but quite distinct lines. The Valerianaceae show various degrees of abortion of the stamens ; but they also have a reduced gynoecium. Here three loculi are present in the ovary, but only one bears a fertile ovule. The same is the case in the Oak; also in the Coco-Nut. Here the three depressed scars on the shell indicate the three carpels, but only the one that can be pierced by a pin matures its seed, and forms a germ.

A beautiful case of meiomery, involving several steps, is seen in the Scrophulariaceae. The flower is typically pentamerous, but it becomes reduced to apparent tetramery. In the Mullein (*Verbascum*) the formula is S_5, P_5, A_5, G_2. But in *Scrophularia* the posterior stamen is represented by a non-functional staminode (Fig. 192), while in others of the family it may be absent. In *Veronica* the two anterior stamens are also abortive. The two posterior petals fuse so that the corolla appears to be four-lobed; the posterior sepal, which is present in the Mullein, is represented in some species of *Veronica* by a sepal smaller than the rest; in other species it is absent, as in *Veronica Chamaedrys* and the most of the Rhinantheae. Thus the flower, though typically pentamerous, has by stages of meiomery become apparently tetramerous. (Fig. 193.) Similar changes occur in the Plantains and Teasels.

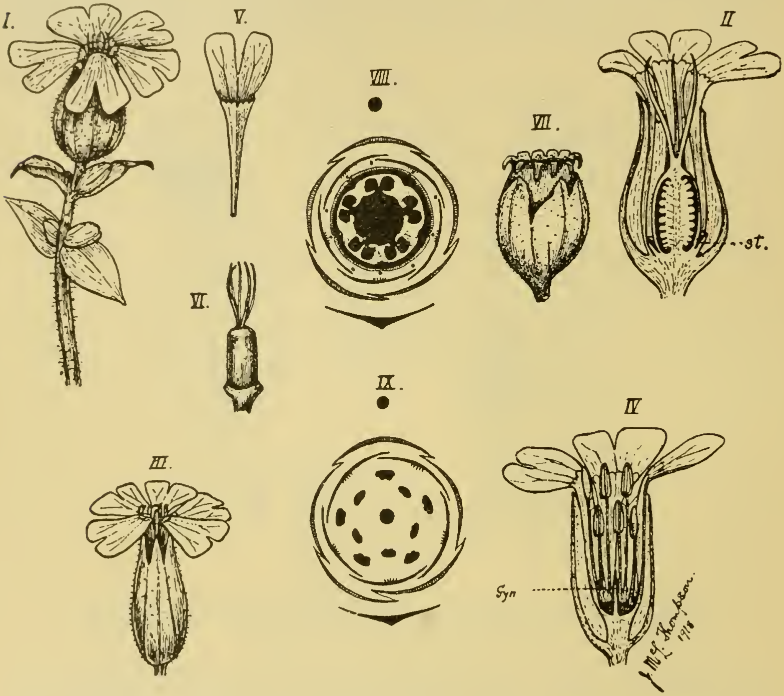

FIG. 194.

Dissections of flowers of *Lychnis dioica*. I., II., VIII., the pistillate flower in which the stamens are represented only by staminodes (*st*). III., IV., IX., the staminate flowers in which the gynoecium is represented only by a vestigium (*gyn*).

Such examples serve to show that meiomery by abortion may affect any of the series of parts, and not unfrequently more than one of them in the same flower. It is probably the cause of greater divergence of detail in flowers than any other factor.

The most important cases of meiomery are those where one or other of the essential organs may be wholly abortive. It frequently occurs that flowers typically hermaphrodite may be *staminate or pistillate, by abortion* of one or other of the essential parts. A good example is seen in *Lychnis dioica* (Fig. 194). The Pink family to which it belongs have usually hermaphrodite flowers ; but here the species is dioecious, which means that some plants have only staminate others only pistillate flowers. An examination of each of them shows that in the staminate flowers an abortive gynoecium occupies the centre (iv.) ; in the pistillate flowers ten staminoides, or abortive stamens, surround the base of the ovary (ii.). Since these parts correspond in position to the parts normally present in allied plants, they indicate that *L. dioica* is dioecious by abortion. There is evidence that this form of reduction has been of frequent occurrence in the evolution of Flowering Plants.

Such results are sometimes seen in extreme form, and nowhere better than in the Spurge. Comparison indicates that the Euphorbiaceae are related to the Geranium Family, members of which are typically hermaphrodite. Some of the Spurge Family (*e.g. Andrachne*, *Phyllanthus*) have calyx and corolla represented, but only stamens or carpels, never both. Others show steps of further reduction of floral structure, till in *Euphorbia* itself the staminate and pistillate flowers reach a very simple condition. The former appear as a single stamen, with a ring half way up its stalk. This represents the abortive perianth. The pistillate flower consists of three coherent carpels, with a rim below, which represents again the abortive perianth (Fig. 178, p. 256). The facts justify the conclusion that there is here a very advanced state of meiomery. Such extreme reduction is usually connected with a close crowding of numerous flowers into an aggregated inflorescence.

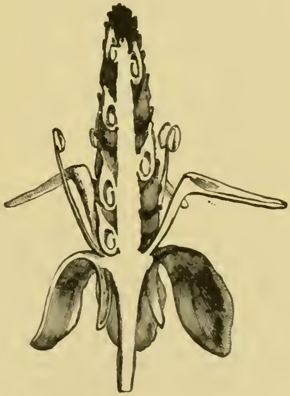

FIG. 195.

Vertical section of flower of *Myosurus* as an example of an hypogynous flower. (After Figuier.)

(vi) *Various development of the floral axis or receptacle* accounts for very considerable differences of floral construction. As a rule the parts of the flower are closely packed upon the shortened and distended axis. In primitive types, such as the Buttercup, or Mousetail (Fig. 195), the receptacle is conical, and the sepals, petals, stamens and carpels succeed one another upon it without any interval. Where the stamens are thus seated below the carpels the condition is described as *hypogynous*, and the *ovary superior*. Occasionally in such types the axis may be elongated, so that there is an interval between the series of parts. In the Passion Flower the stamens and carpels are thus carried up a considerable distance above the sepals and petals. In the Caper Family the carpels alone are raised thus on an elongated axis. More frequently there may be a local widening out of the receptacle, in the form of a ring or cup, by growth of tissue beneath the insertion of the lower parts. The sepals, petals, and stamens may together be carried outwards upon its margin, while the gynoecium occupies the centre of the cup. This occurs frequently in certain families, and is well seen in the Rosaceae (Fig. 196, Peach). Occasionally an isolated genus shows it, as in *Subularia*, among the hypogynous Cruciferae. It may be regarded as a local modification of the hypogynous state, and is described as *perigynous*.

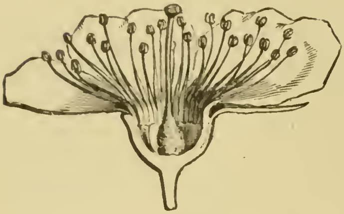

Fig. 196.

Vertical section of flower of the Peach, as an example of a perigynous flower. (After Figuier.)

A more important modification is that which leads to the sinking of the gynoecium downwards into the tissue of the abbreviated axis. This gives the *epigynous* condition, with so-called *inferior ovary* (Fig. 197, Fuchsia). The way in which this comes about is best illustrated by observing the development of a flower of an epigynous type, as may be easily done in the Sunflower or others of the Compositae (Fig. 198).

Fig. 197.

Vertical section of flower of the Fuchsia, as an example of an epigynous flower. (After Figuier.)

If median sections be cut of a young head of Sunflower, the general receptacle will be seen to bear flowers of different ages, the oldest at the outside and the youngest nearest the centre. Each arises in the axil of a bract, and the youngest may have the form of a simple convex papilla (i.). But as the growth at the centre is slower than at the periphery, the flower becomes first flattened and then hollowed. Five rounded bosses appear on the margin of cup, which are the five *petals* (ii.). The hollow surrounded by them deepens, and five other bosses appear internally to, and alternating with them. These are the stamens

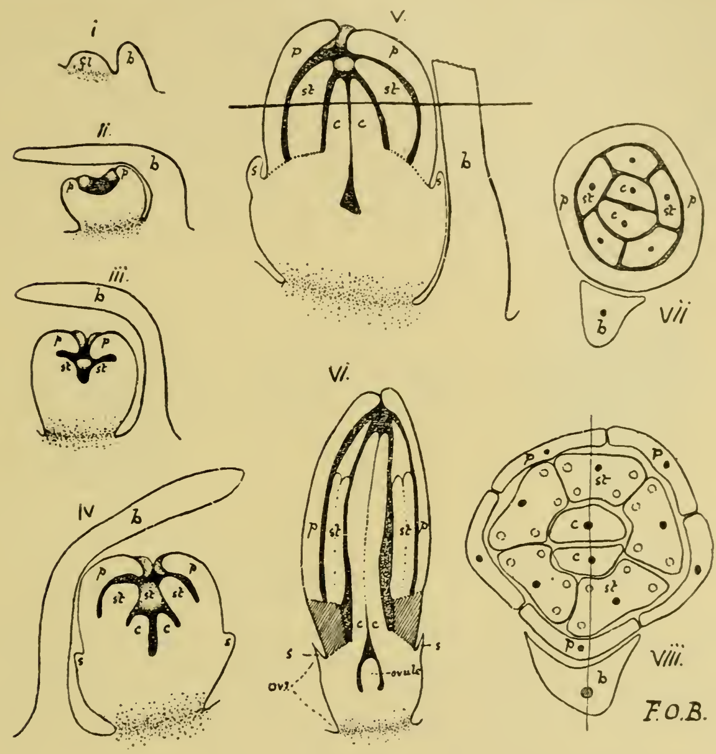

FIG. 198.

i.-viii. Successive stages in the development of the individual flower of the Sunflower; i.-vi. in vertical, vii., viii., in transverse section. *fl*=flower. *b*=bracteole. *p*=petal. *st*=stamen. *c*=carpel. *s*=sepal. (i.-v., vii. and viii. × 60. vi. × 16.) The shaded zone in vi. is the result of intercalary growth originating at the dotted line in v.

(iii.). By their formation the hollow is narrowed, and presently from its shoulders two other upgrowths are formed. These are the *carpels* (iv.). Meanwhile two small outgrowths may be seen at the outside, which previously was smooth. These are two teeth representing the *reduced calyx*, which thus appears delayed out of the normal succession. The carpels are in contact above, and enclose a cavity, which is the ovarian cavity, and the organic apex of the flower lies at the bottom of it (v.). It is here that the single *ovule* arises (vi.), and thus the ovary containing it lies apparently below the other parts. It is described as *inferior*, and the flower as *epigynous*. But it is clear that the succession of parts, excepting the reduced calyx, is acropetal, and the carpels are actually nearest to the apex. *Thus the epigynous state results from the relatively slow growth of the apex, which is overtopped by the stronger growth around it.*

(vii) *Differences of Symmetry.* In many flowers, such as the Buttercup, Rose, or Tulip, the parts may develop equally on all sides of the axis, giving a *radial or actinomorphic symmetry.* This is believed to be a primitive condition, and it is found in flowers which are not highly specialised. It prevails in spiral or hemicyclic types. In others the development may be unequal on different radii, so as to give the flower a lop-sided form ; but almost always so that it can be divided by at least one plane of symmetry into two equivalent halves. Such flowers are called *dorsiventral, or zygomorphic*, and the Aconite, Laburnum, and Toadflax are examples (Fig. 199). The plane of symmetry is usually the median plane ; but sometimes it is oblique, as in the Horse Chestnut ; or transverse, as in *Corydalis*. Zygomorphy is very common, it occurs in most families, and it is characteristic of some throughout, as in the Orchidaceae, or Labiatae. Its importance lies in relation to the transfer of pollen by animal agency. The most perfect mechanisms for this end are found in zygomorphic flowers. It is a derivative or specialised state, and comparison shows that it has been acquired by modification from the radial state, along many distinct lines of descent.

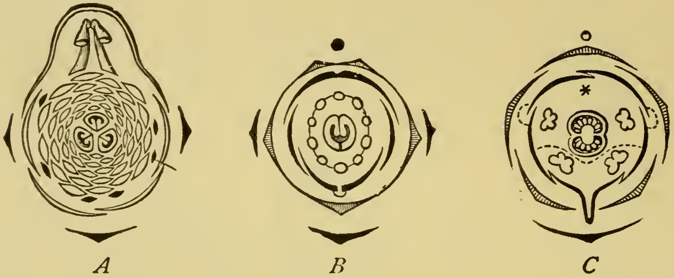

Fig. 199.
Diagrams of zygomorphic flowers. *A*, of Aconite (Ranunculaceae). *B*, of the Laburnum (Leguminosae). *C*, of Toadflax (Scrophulariaceae). (After Eichler.)

The Biological Specialisation of the Flower.

Diversity of floral structure is very fully illustrated in the Angiosperms. But however varied, or sometimes even extravagant the structure of flowers may appear to be, each flower should, in point of final analysis, be regarded as a simple shoot bearing sporangia, modified in the course of its evolution along lines of specialisation such as those specified above. Structurally its shoot-nature is evident in the less specialised examples, though in the more highly specialised it may be so hidden by peculiarities of form as to be recognisable only after careful analysis and comparison. Moreover, those several factors of specialisation, which have been discussed and illustrated in the preceding pages, may take effect in the most varied combination, so that the analysis which is required to reduce a complicated flower to terms of construction comparable to that of an ordinary leafy shoot may demand both skill and insight. But this is greatly aided if the student can realise, in the first place, the probable evolutionary steps by which the peculiar structure was produced : and secondly, the biological advantage which follows from it. The most obvious end served by the mechanism of the flower is the transfer of pollen from the stamen to the carpel. This is a necessary step, though by no means the only important one, in normal reproduction. For carrying this out Seed-Plants are dependent upon external agencies, such as wind, water, or animal activity. Since Plants are fixed in the soil and immobile, such agencies must be resorted to if the advantage of intercrossing is to be secured. It is such considerations as these which make the variety and intricacy of the forms which flowers show biologically intelligible, and give a special interest to the study of their evolutionary origin.

It is possible by comparison to follow the general trend of evolutionary advance from floral types which may be held to be relatively primitive to those which are advanced and specialised. The former are more like the normal vegetative shoots in the arrangement and mutual relations of their parts : the latter diverge in more or less marked degree from that simple state. It is generally accepted that a primitive type of Angiospermic flower was hermaphrodite, and that its numerous parts were inserted separately, and in acropetal order upon an elongated receptacle ; and that they were arranged after a spiral plan. This type of construction is seen in the Magnoliaceae, and other related types, such as the Buttercups and Water-lilies. On the other hand it seems probable that very simple unisexual flowers also existed in early times, such as are seen in the Willows. It is significant that both the Magnoliaceae and the Salicaceae occur early as fossils, and are in fact recorded from low horizons of the Cretaceous Period. It is, however, in the hermaphrodite types that the lines of floral specialisation can be most readily traced.

An early line of specialisation led towards a cyclic arrangement of the parts, their number becoming at the same time more definite. The outer whorls were differentiated as the protective calyx and the attractive corolla. These steps are illustrated among the Ranunculaceae, which include both hemicyclic and cyclic flowers (Figs. 188, 189). The best examples of the cyclic state are, however, found among the more advanced types, where that feature is constant (Figs. 187, 192). Once the cyclic flower was established, other biologically effective modifications followed. The sepals became united into the mechanically stronger gamosepalous calyx. The petals also became coherent, thus acquiring mutual strength, and at the same time fencing round the honey-secretion at its base. Moreover the gamopetalous corolla has often assumed forms that suit the convenience of the insect-visitors: colours and odours that attract; and it even shows distinctive lines that guide the eye to where the honey lies. The stamens become adherent to the corolla-tube. Such features go habitually with that lop-sided or zygomorphic development which secures a convenient alighting platform, and ensures a definite position for the visitor. The result of this precise mechanism is that there is economy in the amount of pollen necessary to make pollination a reasonable certainty.

So long as the flower is not highly specialised a large production of pollen, and a large number of carpels and ovules will be advantageous or even necessary, for this will multiply the chances of successful propagation. It is then natural to find that pleiomery of stamens and carpels is common in non-specialised types. For instance, the Ranunculaceae (Figs. 188, 189), and Rosaceae (Fig. 191), the Lime, and the Mallow are all polypetalous flowers of radial construction, and they have as a rule numerous stamens and carpels. But their haphazard methods of pollination and of seed-distribution entail waste. Economy comes with specialisation, such as is seen in the Gamopetals, and in the more highly adapted Monocotyledons. In them meiomery appears both of stamens and carpels. The former may be reduced from the fundamental number of the flower to two [*Veronica* (Fig. 193), *Salvia*, *Cypripedium*], or to only one (*Centranthus*, *Orchis*, Ginger). The carpels of highly adapted flowers often number only two, and they may be reduced to one, as in the Papilionaceae. The ovules themselves are frequently solitary where the seed is large, and its chances of distribution and germination are good, as they are in the Coconut and Cherry, and in the Grasses. Thus there is a biological *rationale* underlying pleiomery and meiomery, both of which may be held as advances from a relatively primitive state, where the fundamental number ruled through all the floral whorls.

The behaviour of the floral receptacle is biologically the most important of all. Primitive flowers are hypogynous, exposing their carpels on an elongated receptacle (Fig. 195). By shortening its growth the epigynous state is produced (Figs. 177, 197), and the carpels are immersed in the tissue of the axis. Thus they secure at once the nursing advantages of additional protection, and of a near relation of the ovules to the sources of supply. All the factors upon which diversity of floral structure depends are biologically intelligible. All lead to a higher probability of successful propagation. It is, however, worthy of remark that the flower does not really differ in respect of them from the foliage shoot: for all of the modifications can be matched by special instances of development in the vegetative region. But features that are exceptional in the vegetative shoot are common in the floral region, and it is that which makes the structure of the flower seem peculiar. The real distinction between the vegetative and the propagative shoot lies not in form, or texture, or colour, or number or relation of the parts, but in the fact that sporangia are present in the flower, while they are absent from the foliage shoot.

The fact that the flower is constructed fundamentally on the same plan as the foliage shoot did not escape the attention of the early botanists. Moreover, they noted that it is universally preceded by some form of vegetative shoot in the individual life of the higher plants. In annual plants this is obvious enough: it is only after the establishment of the leafy plant that the flower-buds make their appearance. But in the case of many of the plants that expand their flowers in the early spring the matter is not so simple, and one is apt to forget the swollen underground parts from whose stores the flowers draw their material. It is needless to elaborate by examples the simple fact that in all cases nutrition must precede propagation. It was this fact that formed the foundation of *Goethe's Theory of Metamorphosis*. He recognised under this name the process by which one and the same organ, for instance the leaf, presents itself to us in various modifications, such as the foliage leaf, sepal, petal, or stamen. He distinguished as "progressive metamorphosis" those changes of type of the appendages which proceed from the cotyledons or seed-leaves, through the foliage region and bracts to the flower, and finally to the perfected fruit. On the other hand he designated as "retrogressive metamorphosis" that process by which the succession appears reversed; as for instance in abnormal or doubled flowers, when a stamen or a carpel develops as a petal, or even as a foliage leaf. These general ideas of the relation of the vegetative and floral regions were amplified and made more definite by later writers, and were for a long time widely held. *Thus it* *became a general belief that the flower had resulted from changes wrought in some pre-existent vegetative shoot.*

So long as we direct our attention solely to the Flowering Plants this opinion might stand. But as the nineteenth century drew on, knowledge of the lower forms greatly increased, especially in the case of such plants as the Ferns and Club-Mosses. This has supplied the material necessary for a revised theory of the origin of the flower. Checked by these comparisons we may now figure, on a basis of fact, rather than of semi-poetical surmise, how the flower as distinct from the vegetative region originated in the higher plants. The main point to bear in mind is that the propagative function must have recurred in each fully completed life-cycle throughout descent. Hence the production of sporangia was never an innovation, and they cannot at any time in the course of descent have been imposed upon a pre-existent vegetative system, as Goethe's theory would assume. The facts suggest that *the whole shoot of relatively primitive Vascular Plants was non-specialised. It served general purposes, both for vegetation and propagation. But in the course of evolution of higher types differentiation took place, so that a certain region became exclusively vegetative, while another produced sporangia. Thus a theory of* SEGREGATION *takes the place of a theory of* METAMORPHOSIS. The vegetative phase naturally comes first in the individual life, so as to supply the necessary materials for propagation. Once these two pristine functions were allocated to distinct regions of the plant, each was open to its own distinct specialisation. And so it comes about that while in simple cases there may be some similarity between the flower and the foliage shoot, the two may diverge widely in more advanced types. But, however greatly they may differ, the flower and the foliage shoot are to be held as the results of segregation of parts of an originally general-purposes shoot. This gives a natural meaning to those structural resemblances, which are sometimes so striking, between the foliage shoot and the flower which it ultimately bears.

In such discussions as this the antithesis between the flower and the foliage shoot is apt to be drawn more strongly than the facts warrant. The flower is not always clearly defined from the vegetative region. Comparison of the flowers of Cactaceae and Magnoliaceae, and of some Grasses such as *Streptochaete*, show that bracts may merge gradually into floral organs. A further comparison with Conifers, Cycads, and Club-Mosses will confirm the view that the two regions have not always been as distinct as they now appear to be in the Higher Flowering Plants.

In the earlier part of this Chapter the more important lines have been sketched along which the analysis of floral construction may be undertaken. Such analysis is a necessary basis for comparison, and ultimately for classification. But this will not be pursued further at present. It is also necessary as a step towards realising how the mechanism of the flower works. An engineer cannot properly understand his engine till he has taken it down. But the engine will not work till the parts are again assembled. Similarly the student must not be content with the mere analysis of the flower. After analysis he must assemble the mechanism again, either mentally, or by reference to another specimen, and study it as a whole. He will then be in a position to understand how the various features which the flower shows may each contribute to the biological end which the flower has to serve. This aspect of floral construction has been lightly sketched in the latter part of the Chapter. It is important to realise that *each flower functionates as a whole*, just as much as any machine. Each part has its own share leading towards the common end. That end is the production of the *germ contained in the seed. The transfer of the pollen is only one step towards that end, and a comparatively early one.* It is carried out in relation to the showy parts unfolded at the time of blooming, and thus gains an undue prominence. But the interest does not stop when the flower fades. *Fertilisation, which follows after blooming, is actually the central feature, for it initiates the germ.* It is a necessary prelude to the nursing of the germ within the ovule. The protection of the ovule meanwhile within the carpel, itself either free or sunk into the tissue of the axis, is also important as contributing to the final result. Not only then should the flower itself be studied as a whole, but the propagative process also ; and Pollination, with its accessories of form, colour and scent, should be put into its proper place as one incident only, though an essential one, in the complete propagative story.

Note.—Special attention is drawn to the detailed description of various types of floral structure given in Appendix A. The facts there described will illustrate the preceding chapter. They are placed in the Appendix not because they are unimportant, but so that the description of the reproductive process should not be broken by a mass of detailed facts, however apposite those facts may be to the process itself.

CHAPTER XV.

THE STAMEN AND POLLEN-SAC.

All the facts brought forward in the preceding chapter may be observed under a hand lens, or under low powers of the microscope. But observation under higher powers is necessary for obtaining an intelligible grasp of the details of propagation in Seed-Plants. The minute structure of the outer envelopes can be dismissed briefly. The *sepals*, which are usually green and relatively firm in texture, repeat in their structure, though on a reduced scale, the features of foliage leaves. Their epidermis bears stomata, and the mesophyll below, though small in quantity, contains chlorophyll, and is traversed by vascular strands after the manner of other leaves. The *petals* also, though wider in expanse and more delicate in structure, are constructed on a similar plan. But the green of chlorophyll is replaced in them by other colours. The blues, reds and intermediate shades of flowers are due to pigments (*Anthocyanins*) dissolved in the cell-sap. Yellow colours are given by pigments confined to bodies called *Chromoplasts*, which are frequently of irregular crystalline form (Fig. 200). Usually these yellow pigments are the same as occur in the leaf, namely *Carotin* and *Xanthophyll* (see p. 117). Sometimes both sources of colour may be present in the same petal, and even in the same cell. The streaky colouring of Parrot Tulips arises from the irregular distribution of the chromoplasts in addition to the soluble colouring. The outer floral envelopes take no direct part in propagation. Indirectly they serve that purpose: the sepals

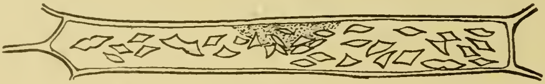

Fig. 200.
Single cell of a petal of *Senecio*, showing numerous chromoplasts of semi-crystalline form. (× 800.) (After Schimper.)

by the protection which they give to the inner parts of the young bud; the petals by giving scent, and a wide expanse of coloured surface, by which means the flower is made attractive. Both parts are subject in special cases to modification of form and character in relation to pollination; but these details must be left aside for the present. After the flower is full blown, the petals wither and fall away. The sepals frequently fall away also, as in Crucifers and in the Buttercup. Sometimes they drop even before the flower is full blown, as in the Poppy. In other cases they persist, as in the Rose, Violet, or Pea, though their further use is not obvious.

The *stamens* which lie within are essential for propagation. Their function is to produce *pollen-grains* which, after further development, give rise each of them to two *male fertilising cells*, or *gametes*. The form and structure of the stamens may vary in detail in special cases. But in the great majority of flowers they conform to one simple type, consisting of a cylindrical stalk or *filament*, which is continued upwards into the distal *anther* (Fig. 201). This is two-lobed, the lobes being attached laterally along the filament. While young the outer surface of the anther is turgid, and unbroken. When ripe it opens, sometimes by pores, as in *Solanum*, but usually by longitudinal slits, right and left, which gape widely, as in *Iris* or *Caltha*. Thus the *pollen* is shed as *grains*, usually separate and of yellow colour. The ripening of the stamens coincides with the blooming of the flower; but in cases where the stamens are numerous they may open in succession, so that the shedding of the pollen may be spread over a lengthened period. After the pollen is shed the stamens usually fall away, or sometimes they persist in a withered state; but they serve no further function.

FIG. 201.

Stamens of Iris: that on the right shows dehiscence. (After Figuier.)

FIG. 202.

Sections of the anther of *Caltha*. *A*, before dehiscence, showing the four pollen sacs still closed. *B*, after dehiscence, showing the sacs open, and the slits gaping widely. Centrally lies the vascular strand, shaded. (Enlarged.) F. O. B.

If the anther of any ordinary stamen be cut transversely it is found to contain four *sporangia*, or *pollen-sacs*, two being placed on either side of a central connective, which is simply a continuation upwards of the filament. A single vascular strand which traverses the filament is continued upwards into the anther, where it fades out usually without any branching (Fig. 202, *A*). Stamens arise as exogenous growths from the axis, and in acropetal succession. In "doubled" flowers they not infrequently appear as transformed into petals, or even into green leaves. This suggests a foliar nature. But for a full understanding of their relation to foliage leaves comparison will be needed with corresponding parts in early fossils. For close comparison the material is gradually becoming available: but at the moment that relation appears as an evolutionary problem rather than a demonstration.

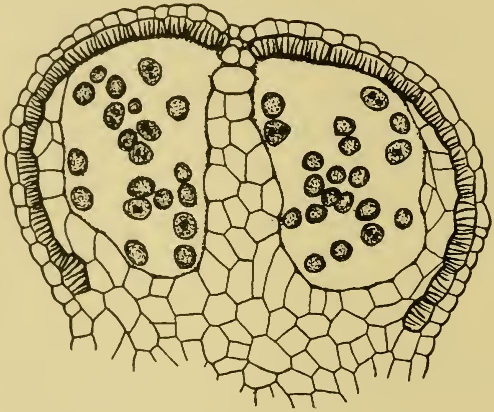

FIG. 203.
Lobe of anther of *Caltha* cut transversely, showing two pollen-sacs at maturity, with the fibrous layer immediately below the epidermis. For details see text. (× 100.) F. O. B.

It may, however, be accepted that *stamens are parts specialised for bearing pollen-sacs or micro-sporangia.* Each pollen-sac is enclosed till it is ripe by a wall consisting of several layers of cells. In most stamens the slit of dehiscence runs longitudinally, following the line where the walls of the two sacs of one anther-lobe join with the septum that separates them (Fig. 201). There the cell-walls are thin and the cells themselves are rounded off by intercellular spaces, so that they easily come apart. The slit thus formed gapes widely, owing to the action of the walls of the pollen-sacs. Below their superficial epidermis lies a *layer of fibrous cells*, the inner cell-walls of which are thicker than the outer, while fibrous bars running outwards along their lateral walls prevent radial collapse. The effect on these cells of drying as the anther ripens is that their outer walls shrink, while the thick inner wall retains its form. The result of the shrinkage of the outer side of the fibrous layer will naturally be to reduce the curvature of the convex sporangial wall, and the slit gapes widely (Fig. 202, *B*). The dusty pollen-grains are then readily removed. There are various differences in detail of the dehiscence of anthers, particularly in highly specialised flowers. But in all ordinary flowers where the pollen is dry and powdery, the way in which it is set free is essentially like that described.

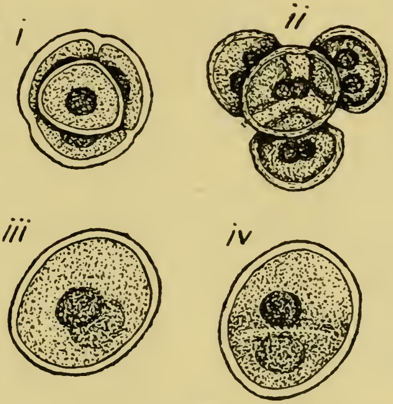

FIG. 204.

Pollen-tetrads and pollen-grains of *Caltha*. (i) a tetrad, with each cell uninucleate. (ii) an older tetrad, with the grains almost separated, each containing two nuclei. (iii, iv) mature pollen-grains, showing the larger vegetative cell, and the smaller antheridial mother-cell. (× 550.) F. O. B.

The pollen itself varies greatly in different plants, in the form and size of the grain, in the sculpturing of its walls, in colour, and in the dryness or stickiness of its surface. But these differences are only external. *There is a remarkable uniformity of the internal structure of the pollen-grains of Flowering Plants* (Fig. 204, iii, iv). They are *two-celled.* One cell is usually the larger, and it is called the *vegetative cell*, because it is from it that the pollen-tube is formed, and it does not take any direct part in the reproductive process. It consists of cytoplasm and a nucleus. The smaller cell is the *antheridial mother-cell* ; it also has cytoplasm and a nucleus, and is marked off from the other by a plasmic film, not by a cell-wall. The two-celled state of the pollen-grain may be attained while it is still in the unopened pollen-sac.

The early stages of segmentation of the stamen may be followed by study of the flowers of *Chrysanthemum* (Fig. 205, i.-iv.). The stamen first appears as a rounded papilla of tissue. It is covered by a layer of cells which divide only by walls perpendicular to the surface, so that the layer maintains its identity. It develops into the *epidermis* (i.). The young stamen soon shows four angular projections, which represent the four pollen-sacs. They project owing to the active growth and division of the hypodermal cells (ii. iii.). In the earliest state the hypoderma also appears as a single layer all round (ii.); but as it grows older certain of its cells enlarge at the angles of the section, and divide by walls parallel to the surface. Outer *parietal* cells are thus cut off from inner cells which are *sporogenous*, and give rise ultimately to the pollen (ii. iii.). The outer cells undergo further division by walls parallel to the first, forming usually three cells each (iv.). Of these the outermost cells provide, after further growth and division, the *fibrous layer*; while the innermost, which adjoin the sporogenous cells, form part of the nutritive tissue known as the *tapetum*. The sporogenous cells themselves, which are shaded in Fig. 205, ii.-iv., are easily distinguished not only by their origin, but also by their dense protoplasmic contents. The steps thus described are found to be very constant in the anthers of Flowering Plants. They provide material for comparison with other sporangia. There is some latitude, however, in the number of the divisions, and the figures show this even in the single case of *Chrysanthemum*. Where the stamen is large and its walls thick, as in the Lily, more numerous divisions of the hypodermal cells may provide a sporangial wall thickened by extra layers.

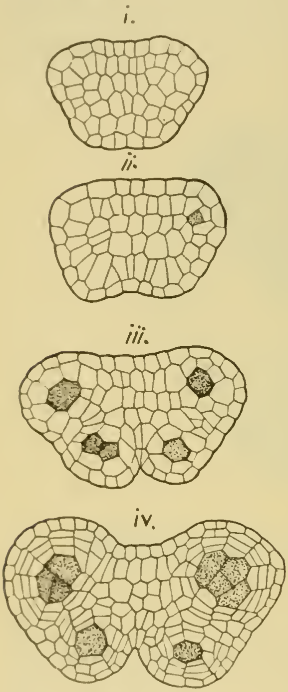

FIG. 205.
Successive stages in the early development of the anther in *Chrysanthemum*. (After Warming.) (× 300.) The sporogenous cells are shaded. For details, see text.

As the pollen-sac develops, the layer next below the epidermis first acquires a store of starch (Fig. 207) which is converted later into the thickening of the walls characteristic of the *fibrous layer* (Fig. 203). Within this lie the featureless cells of the intermediate layer. The group of sporogenous cells increases in size, and often also in number of cells by division. Each of these cells is called a *pollen-mother-cell*. The group of them occupies the centre of the projecting sporangium, and is invested by the *continuous sheath of the tapetum* (shaded in Figs. 206, 207). This appears as a single layer of large cells with very thin walls and granular contents. It is the result of development of the cells on all sides adjoining the sporogenous group. Fragmentation of the nucleus frequently happens as its cells grow old. Its function is to nourish the developing pollen. As the grains mature the cells of the tapetum gradually collapse, their substance being absorbed by the pollen. In the mature pollen-sac only vestiges of them remain lining the sac internally (Fig. 203).

The *pollen-mother cells* are all derived by division from the inner product of the hypodermal cells. They vary in number in different anthers. *Caltha* gives an average example, in which from 14 to 16 appear in each transverse section of a pollen-sac (Fig. 206). They are characterised by very thin walls, a dense, non-vacuolated cytoplasm, and a proportionately very large nucleus. At first they are closely fitted together, without intercellular spaces (*a*). But presently the pollen-sac distends, and the pollen-mother cells round themselves off, and become suspended individually in a liquid medium which fills the spaces between them (*b*). Meanwhile the tapetal cells, from which the liquid probably arises, retain their form, though their nuclei often multiply by fragmentation.

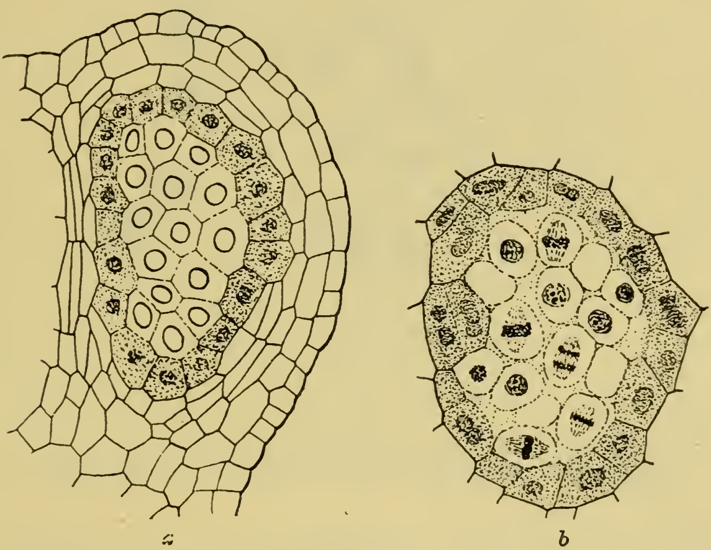

FIG. 206.

a*, *b, successive stages of development of the contents of the pollen-sac of *Caltha*. See text. (× 100.) F. O. B.

As the pollen-mother-cells separate they enter on the *tetrad-division*. Each nucleus divides first into two, and then into four. These rapidly repeated divisions are characteristic of all spore-formations, and have an important relation to the constitution of the nuclei themselves (see p. 563). The four resulting nuclei are first enclosed in the single protoplast. But soon each is separated by a partition-wall, and is surrounded by a quarter share of the cytoplasm. The *pollen-tetrad* is thus constituted. The four cells are still enclosed by the common wall; but later each cell deposits a special wall round itself. The common wall, which was of a mucilaginous character, is then dissolved, with the result that the four cells become dissociated as independent pollen-grains (Fig. 204, i, ii). Meanwhile the single nucleus of each has divided, giving the two nuclei present in the mature grain (Fig. 204, iii, iv).

This description of the development seen in *Caltha* applies for the development of the pollen in all ordinary Dicotyledons. In Monocotyledons the process is essentially the same. But the pollen-mother-cell, after the first nuclear division, is itself partitioned by a wall into two cells, in each of which the second nuclear division follows. The final result is thus the same, except that the arrangement of the tetrad is not tetrahedral, as it usually is in Dicotyledons. But the grains lie in pairs, the longer axis of one pair being at right angles to that of the other. These are minor points; in all essentials the tetrad-division which produces the pollen is the same throughout Flowering Plants. Figs. 204, 206, 207.

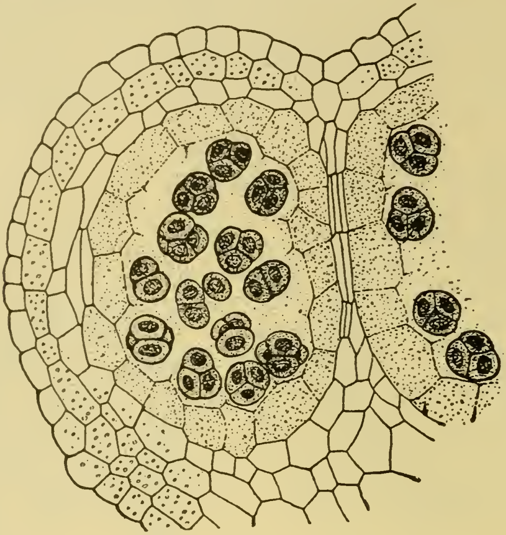

Fig. 207.

A later stage of development of a pollen-sac, showing the young fibrous layer, containing starch. The tapetum (shaded) surrounds the sac in which the tetrads float freely. (× 100.) F. O. B.

For the present this brief description must suffice. But later (Chapter XXXV.) the details of behaviour of the nuclei in this important process of tetrad-division, and chromosome-reduction will be described and discussed at greater length (p. 563). The pollen-grains, as their development shows, are produced from internal tissues of the plant, and are set free by rupture of the superficial tissues. Such bodies are called *spores*, and the pollen-grains being of relatively small size are called *micro-spores*. A step in their production is the *tetrad-division*. The tetrad breaks up later into its *four constituent spores*. *Tetrad-division is a constant feature in the production of spores in all spore-bearing Plants*, such as Mosses, Ferns, and Seed-Plants. When a marked feature such as this recurs with constancy in a large group of organisms, even though they may differ in many respects, it may be assumed that it has some special significance. In this case the importance of the tetrad-division lies partly in the provision of numerous easily transferred bodies, which carry out an essential function in the propagative process. But a more important point is that *in the course of the tetrad-division the nuclei undergo the change called REDUCTION.* Certain formed bodies, *chromosomes*, present in constant number in each nucleus on division, are reduced, in the course of the process, to half their original number in each nucleus. All the products of further division of nuclei so reduced have the same smaller number. The ordinary nuclei of the plant have a number of chromosomes which may be represented as "$2x$," and they are called *diploid.* The nuclei that result from reduction are found to have only "x" chromosomes, and are described as *haploid.* The constitution of the nucleus and its behaviour in reduction will be discussed again in detail in Chapter XXXV. Meanwhile we note that *an essential change has occurred during the tetrad-division, and that the nuclei produced within the pollen-grain are themselves haploid.* It is then not simply a separation of vegetative cells that occurs in the production of pollen. The grain as it leaves the anther conveys with it nuclei that differ in an essential feature from those of the ordinary vegetative cells of the Plant. The process of *reduction* in the tetrad initiates a *sexual phase*, or *Gametophyte.* The result of its further development will be certain cells, which are capable of taking a direct part in sexual reproduction: they are in fact the *male gametes*, or *male sexual cells.*

CHAPTER XVI.

THE CARPEL AND OVULE.

The *Gynoecium*, or *Pistil*, occupies the centre of the Flower. Its office is to produce ovules, and after their fertilisation to nourish and protect them, together with the new germ that each may contain. This nursing function is continued till the time of ripeness, when the Seeds are shed. The Gynoecium is thus the most persistent part of the Flower. While the sepals, petals, and stamens are liable to fall away after the period of blooming, the gynoecium remains attached until the seed is ripe, continuing to draw from the receptacle the nourishment required for the germ. The term *Fruit* is applied to the whole Pistil when fully matured.

The Gynoecium is composed of *Carpels*, which may vary in number in different cases from many downwards to one. Associated with them are the *Ovules*, or *Mega-Sporangia*, which also vary from large numbers in some cases down to one in others. Two parts of the gynoecium may be distinguished by their structure and function. A distal region, which offers at the time of blooming a receptive surface for the pollen-grains: this is called the *stigma*; and a basal part, distended as the *ovary*, which encloses the ovule or ovules. Frequently, and especially in syncarpous pistils, an elongated region intervenes which is called the *style* (Fig. 209).

The Carpels are leaves. Often that can easily be recognised, as in the Pea, where the pod represents a single carpel; or in *Caltha*, where there are many (Fig. 208). In this case they are all separate from one another (*apocarpous*), and their foliar nature is undisguised. Each leaf is folded so as to envelop the ovules borne on its margins, while the midrib is turned outwards from the centre of the flower (Fig. 210). The foliar nature of the carpels is less easily recognised where they are united (*syncarpous*), as they are in the Lily. But even there a transverse section shows by its outline, by the arrangement of the vascular strands, and by the position of the ovules that the compound structure is referable in origin to three fused leaves (Fig. 211). Moreover cases of partial fusion are found, for instance in *Colchicum*, where the three carpels are fused below, but extend upwards as separate styles. Their relative positions are, however, the same as of those in the completely syncarpous Lily. Biologically the advantage of a

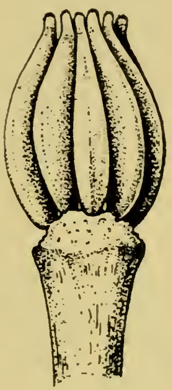

FIG. 208.
Whole gynoecium of *Caltha*, consisting of many carpels, all separate.

FIG. 209.
Pistil, or gynoecium of Lily, showing the relative positions of ovary, style, and stigma. F. O. B.

FIG. 210.
Transverse section through the separate carpels, composing the gynoecium of *Caltha*. F. O. B.

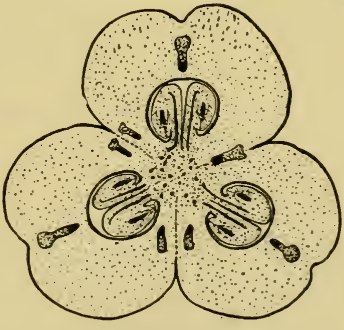

FIG. 211.
Transverse section of the syncarpous ovary of Lily, showing the three folded and fused carpellary leaves, bearing ovules on their margins. F. O. B.

coherent gynoecium over that with separate carpels lies in the more effective protection and nutrition of the ovules. But it presents fresh difficulties in the liberation of the seeds when ripe.

The structure of the gynoecium is further complicated by the fact that the carpels are frequently sunk into the tissues of the enlarged receptacle, a condition which serves still more completely the purposes of protection and nutrition of the ovules; for it brings them closer to the nutritive supply that comes from below, and it makes a thicker protective wall possible (Fig. 212). Naturally this goes along with fusion of the carpels. The result is a massive body formed partly from the floral receptacle, partly from the carpels. It is *syncarpous*, and being apparently below the other floral parts it is styled *inferior*. The development of such a gynoecium has been traced in the structurally simple, though highly specialised case of *Chrysanthemum*, where there is only one cavity of the ovary, and one ovule (Fig. 198, p. 273). But in relatively primitive cases there are several loculi, corresponding to the number of the carpels, and there may be many ovules in each, as in the *Quince* (Fig. 212, *A*), or *Iris* (Fig. 213).

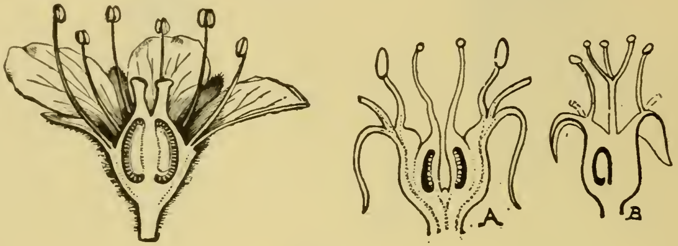

FIG. 212.

To the left, median section of the flower of Saxifrage, showing the carpels half sunk in the receptacle, and coherent for the greater part of their length. (After Figuier.) *A*, similar section of the Quince, showing an apparently inferior ovary, but the styles and stigmas are separate. *B*, same for Apple, showing styles united, but stigmas still separate. (After Warming.)

Various intermediate states serve to explain how the inferior syncarpous ovary may have come into existence. For instance, in *Saxifraga* the two carpels are united through about half their length, and are partially sunk below the other parts in the tissue of the axis (Fig. 212). Other intermediate states are seen in the Pomeae. For instance, in *Cotoneaster* the flower is little removed from the perigynous state. In *Cydonia* the ovary is more distinctly inferior, but the carpels are not fully united, each having a separate style, while the apex of the abbreviated axis lies in a deep depression between them (Fig. 212, *A*). In the closely related Apple their fusion is more advanced, so that there is a common style, but a distinct stigma for each carpel (Fig. 212, *B*). The last step of fusion would be their coalescence to a single stigma, as is seen in the Lily (Fig. 209). Such fusion of carpels, with or without their sinking into the receptacle, has developed progressively, and has appeared repeatedly in distinct evolutionary lines. The result is a solid and massive gynoecium, whether with superior or inferior ovary. A transverse section of the inferior ovary may still show evidence of its carpellary origin almost as clearly as in the superior ovary. This is seen in *Iris*, where notwithstanding that the carpels are sunk in the receptacle, their structure, and even the arrangement of the chief vascular strands resembles in some degree that seen in the superior ovary of the Lily (Fig. 211). The conclusion follows that in such cases the gynoecium is still to be referred in origin to foliar structures, more or less completely fused with or sunk into the tissue of the receptacle.

FIG. 213.
Transverse section of the inferior ovary of *Iris*. Compare the superior ovary of Lily, Fig. 211. F. O. B.

The *structure of the carpel*, where it is distinctly leaf-like, as it is in the pod of the Pea, corresponds in essentials to that of a foliage leaf, but simplified. A vascular strand usually traverses each margin, as in *Caltha* (Fig. 210). This is related to the fact that the ovules are seated there; or, as it is described, the *placentation is marginal*. It is probable that this was the regular primitive position for ovules. But sometimes they appear scattered over the inner surface of the carpellary wall, as in the Flowering Rush (*Butomus*), the Poppy, or the Water-Lily. This is described as *superficial placentation*, and it probably originated by the spread of the ovules to the surface. Sometimes they appear as though seated on a prolongation of the axis into the ovarian cavity, as in the Pinks and Primroses (Appendix A, Fig. 471, of *Lychnis*). This is called *free-central placentation*, and it also is probably derived from the marginal type, by breaking away the partitions, or septa, of the syncarpous ovary, leaving the margins with their ovules at the centre. Thus the marginal was probably the primitive, as it is certainly the prevalent position for the ovules on the carpellary leaf; and this holds equally for syncarpous ovaries (Figs. 211, 213).

The *Stigma*, or *receptive surface for the pollen-grains*, is at the distal end of the carpel. Where the carpels are separate each has its own stigma, a condition which is probably the primitive state. It is seen in *Caltha* and the Buttercup, the stigmatic area being recognised by its roughened surface. Even where the carpels are united below into a syncarpous ovary, each may separate upwards to form a distinct stigma, as in the Apple or Quince (Fig. 212, *A*, *B*). But in cases which are regarded as more advanced the fusion of the carpels may extend to their tips, and a single stigma is the result, as in the Lily (Fig. 209) or *Datura* (Fig. 214). Even here the receptive surface is lobed, and the number and position of the constituent carpels is indicated by that of the stigmatic lobes. From external observation this is often the readiest guide to the composition of the gynoecium. For instance, the two-lobed stigma of the Compositae accords with the facts of development of their flowers, in which two carpels make their appearance (Fig. 198). In *Datura* the two lobes clearly indicate the two carpels of the Solanaceae.

FIG. 214.
Stigma of Datura with pollen-grains adhering to its surface. (After Figuier.)

The roughness of the stigmatic surface is due to the outgrowth of the superficial cells as papillae (Fig. 214), the size of which is found to bear a relation to the size of the pollen-grains. The cells are thin-walled, with active protoplasts; frequently they are moist, or secrete a sticky juice, which helps to detain the pollen-grains in contact with the surface. The grains themselves have sometimes a sticky exterior, which serves the same end. A still more important feature is that the *style, by its elongation carries the stigma upwards to a level suitable for* *the deposit of the pollen* (Fig. 209). In some cases the style is absent, as in the Buttercup or Nettle. It is a feature of variable occurrence, resulting from intercalary growth which is adjustable according to the proportions of the other parts. Extreme cases are seen in the *Crocus* or in *Colchicum*, where the ovary is underground, while the style, which is six inches or more in length, carries the stigma several inches above ground, to a level a little in advance of the stamens. In the Gamopetalous Dicotyledons, and in many Monocotyledons the cylindrical style is proportional in length to the tube of the corolla, as is seen in Tobacco and *Gloxinia*, or in *Lilium auratum* and *Narcissus*.

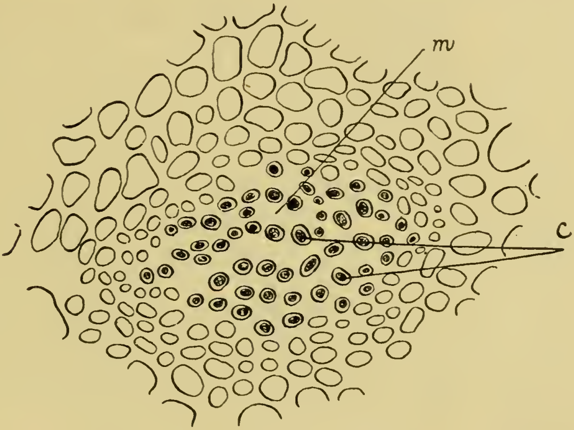

FIG. 215.
Transverse section of the style of *Salvia*, showing the cells of the conducting tissue (*c*) with swollen mucilaginous walls (*m*). (After Capus.)

The style is sometimes traversed by an open channel, so that direct access can be gained to the ovarian cavity from the stigma ; this is the case in the Violet and Mignonette. But where the channel is narrow it is commonly filled with a mass of mucilage derived from epithelial cells which clothe its surface. This is seen in the Lily and Rhododendron (Fig. 225, p. 305), in both of which a separate groove from each of the stigmatic lobes leads downwards to the common conducting canal filled with mucilage. In other cases there is no actual canal, but a column of lax tissue with mucilaginous walls traverses the style, and serves as a conducting tissue. This is found in *Salvia* (Fig. 215) ; also in the Corn Cockle (*Agrostemma*), and in the Mallow. In such cases the conducting tract is connected upwards with the separate stigmas, while downwards the channel branches so as to lead to the several loculi of the ovary.

The *ovule* at the period when it is ready for fertilisation is more or less oval in form, and it is seated upon a stalk, the *funiculus*, which is usually short (Fig. 216). It consists of a central body of conical form, which is called the *nucellus*. This is the actual *mega-sporangium*. It is invested by one, and frequently by two *integuments*, which are attached to its base, and cover it closely, leaving only a very narrow channel open at the apex, which is called the *micropyle*. The opposite end, where it is attached to the funiculus, is called the *chalaza*. A vascular strand, springing from the vascular system of the carpel, traverses the funiculus, but stops at the chalazal end of the nucellus. This leads up the supplies to the base of the sporangium. The form of the ovule varies. Sometimes it is *straight*, as in the Rhubarb, or Dock (Fig. 221, p.303); sometimes the body of the ovule is itself *curved*, as in the Kidney bean or Shepherd's Purse. In the great majority of cases the body of the ovule is straight, but it is *inverted* or *anatropous*, so that the micropyle lies close to the attachment of the funiculus on the carpel. This is seen in Fig. 216, which shows an ovule of *Caltha* cut in median section, at the time when it is ready for fertilisation. The nucellus is the essential part of the ovule, the integuments and the funiculus being accessory. They provide respectively for external protection, and for the conduction of supplies. Moreover, the nucellus is the part first formed. In a young state it may be found already well advanced, though the integuments are incomplete, and the funiculus is only beginning to assume that curvature which results in the inversion of the mature ovule (Fig. 217, p. 296).

At the period of blooming the nucellus consists of a peripheral covering of thin-walled cells, of varying bulk in different groups of plants: it encloses one large cavity, which, though its contents are complex, is developed from a single cell. This is the *Embryo-Sac*, or *Megaspore*. It attains its large size by encroaching on the adjoining cells as it develops, by a process of digestion; this leads to their collapse, and the final absorption of their substance. The sac is limited by a very thin cell-wall, and is lined by dense granular protoplasm. Within it seven nuclei are seen, of which one of large size is near to the centre (Fig. 216, *f*, *n*). As these contents of the embryo-sac are almost constant in Flowering Plants, and are all accessory to the production of the new germ, they demand special attention. There are two groups of three cells each, one fixed at the micropylar end, the other at the chalazal end of the embryo-sac. The latter are often large, with well-marked nuclei, each of which is surrounded by an area of granular cytoplasm marked off by a plasmic film, not by a cell-wall. It is called the *antipodal group* (*ant.*), and it occupies the base of the embryo-sac, just above the chalazal ending of the vascular strand. At the micropylar end is another group of three cells, called the *egg-apparatus* (*e.a.*). One of the cells projects further into the cavity than the other two : it is the *Ovum*, or egg-cell which after fertilisation initiates the new germ. The other two, called the *Synergidae*, are of equal size, but smaller than the ovum. The egg-apparatus is attached just below the micropyle. In *Caltha* two layers of cells are seen to intervene (Fig. 216, *nuc*), but in other plants the number may be larger ; on the other hand in many ovules the embryo-sac is found to abut directly on the micropyle. The large cavity of the embryo-sac is filled by vacuolated cytoplasm, while in the centre the large *fusion-nucleus* (*f.n.*) with a prominent nucleolus is suspended by cytoplasmic threads. Though ovules of Flowering Plants may vary in form, in the complexity of their

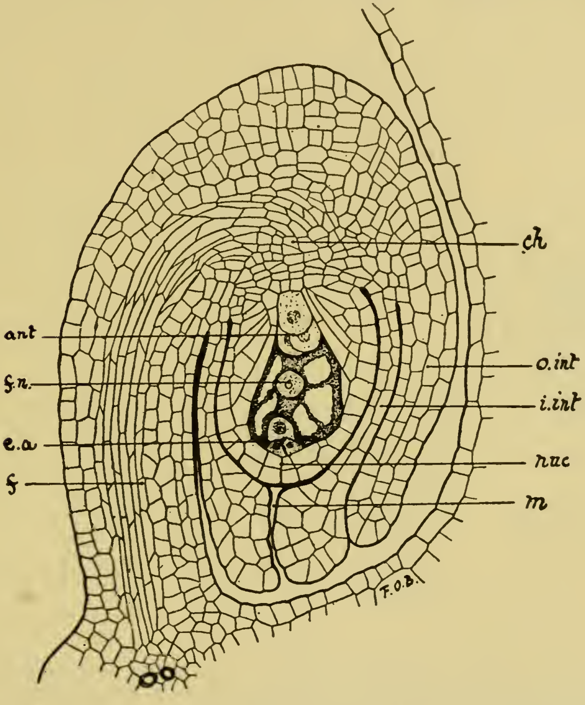

Fig. 216.

Median longitudinal section of an ovule of *Caltha*, at the period of fertilisation. *f*=funiculus. *ch*=chalaza. *o. int*=outer integument. *i. int*=inner integument. *nuc*=nucellus. *m*=micropyle. *e. a*=egg-apparatus. *ant*=antipodals. *f.n.*=fusion nucleus. (× 110.)

construction, in the number of the integuments, and even in the number of their embryo-sacs, there is a marked constancy in the number and position of the bodies contained in the embryo-sac at the time of fertilisation.

The following description of the development of the ovule relates primarily to the type seen in the relatively primitive family of the Ranunculaceae. It appears at first as a rounded papilla of tissue, which develops directly into the *nucellus* or *megasporangium*. By active growth and cell-division it is carried up upon the elongating funiculus. Meanwhile by outgrowth of a ring of tissue at the base of the nucellus the inner integument first appears. The outer integument follows as a growth on the side which will be turned outwards as the ovule becomes inverted; later it coalesces with the stalk so as to invest the nucellus on all sides except that of the stalk (Fig. 217). As the ovule grows older the curvature increases till it is completely inverted. Meanwhile the integuments extend over the nucellus, covering it in, except for the narrow channel of the micropyle (Fig. 216).

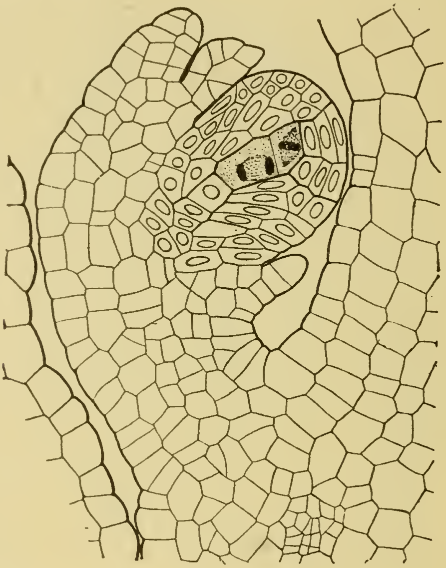

FIG. 217.

Median section of a young ovule of *Caltha*, anatropous curvature still incomplete, and the nucellus only partially covered by the integuments. The spore-mother-cell has divided once, and the second division to form the tetrad is already indicated by the nuclear spindles. (× 200.) F. O. B.

The chief interest lies in the *origin and development of the embryo-sac*. It has been stated that the nucellus is a megasporangium, and the embryo-sac a megaspore. It is because of the manner of their development that these parts are so recognised. The young nucellus first appears as a hemispherical upgrowth: it consists internally of a number of radial rows of cells, covered by a superficial layer. The latter divides in *Caltha* into two or more layers at the tip of the nucellus, forming a cap of tissue covering the radial rows within. It is from the central row of the internal cells that the embryo-sac arises. The condition in *Caltha* is relatively simple. The terminal cell of the central row undergoes division into two, and then into four (Fig. 217). This is in fact a *tetrad-division*, and the mother-cell which divides is of hypodermal origin. It has been shown that this division is accompanied by *reduction of chromosomes* of the nuclei to the half number, as in the pollen-tetrad. The resulting four cells are arranged in a row; pollen-tetrads are sometimes found to have the same arrangement. The conclusion follows that *the tetrad thus produced in the ovule is the correlative of a single pollen-tetrad, and each of the four cells might become a spore.* This actually happens in the pollen-sac; but in the ovule as a rule only one of the four potential spores develops further. *The lowest cell of the four enlarges at the expense of the others*, which collapse, and are crushed out of shape. The embryo-sac encroaches also on the surrounding cells of the nucellus, which give way to allow of its increase in size. Thus, as shown by its development, the *embryo-sac is the single spore of a tetrad*: as it develops to a large size it is styled a *mega-spore*.

In other cases the structure may be *more complex than in Caltha.* A considerable number of Flowering Plants show rapid growth and division of the superficial cells at the tip of the nucellus, so as to form a considerable pad of tissue covering the hypoderma. This is seen in *Rosa livida* (Fig. 218), which also shows numerous hypodermal cells with dense contents, each divided into a cell-row. The basal cell of each row is an embryo-sac mother-cell; the distal cells are parietal cells, comparable with the parietal cells of the pollen-sac (compare Fig. 205). There is thus in *Rosa* a plurality of mother-cells, as is usual in pollen-sacs; while the parietal cells, which are absent in *Caltha*, are here present, and strengthen the comparison with the pollen-sac. Such conditions, which are not infrequent among the more primitive Dicotyledons, indicate that the pollen-sac and the ovule, though differing in form, have essential features in common. Both are sporangia, though they have diverged in details of development.

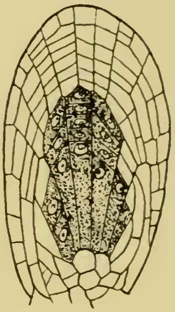
FIG. 218.
Young nucellus of ovule of *Rosa livida*. See text. (After Strasburger.)

Other ovules again are *simpler than Caltha.* For instance, in *Monotropa* the nucellus is represented only by a single layer of cells, surrounding one central row, which consists of the embryo-sac itself and two sister cells (Fig. 219, i.). Here there are no parietal cells, and the tetrad itself is represented only by three cells, the uppermost cell of the tetrad not having undergone the second division. The two sister cells are later disorganised, and make way for the embryo-sac; and finally the single layer of the nucellus is also absorbed (Fig. 219, viii.); so that *at fertilisation the embryo-sac is all that represents the nucellus.* A still simpler condition as regards the origin of the embryo-sac though not of the whole structure, is seen in *Lilium.* Here, as in most Monocotyledons, the parietal cells are absent. Further, the hypodermal cell of the central row itself becomes directly the megaspore-mother-cell, and reduction takes place not in the preparation of the mother-cell, but during the first divisions within it. The whole development is here condensed, and stages seen elsewhere are entirely omitted.

There is thus considerable latitude in the details of the nucellus, associated with marked differences in its bulk. Speaking generally, the nucellus is more bulky in relatively primitive types, such as the Rosaceae and Ranunculaceae, and especially in the Fagales. It is less bulky in advanced types, such as the Gamopetalous Dicotyledons, or the Orchids. But the former often make up for this by the elaborate structure of their single integument.

In sharp contrast to this variability of the nucellus, or megasporangium in Flowering Plants, is the dead level of uniformity shown by the embryo-sac or megaspore, and its contents. So great is this that, putting aside the few exceptions that exist, one description will serve for all Angiospermic Plants. It is based upon the observations of Strasburger on the transparent ovules of *Monotropa* (Fig. 219). The lowest of the three cells resulting from division of the megaspore-mother-cell is the future embryo-sac (i). It enlarges at the expense of the other two, which collapse, and their disorganised remains appear as a cap covering the micropylar end of the sac (ii-vi). The nucleus divides into two parts, which pass to opposite ends of the sac, while a vacuole appears between them (ii). These again divide (iii), with the result that two nuclei are formed at either end (iv). These four divide once more (v), and the resulting nuclei arrange themselves in the characteristic way common to embryo-sacs (vi). Three are grouped at either end, each surrounded by its own area of cytoplasm, limited by a plasma-film. Those at the chalazal end form the *antipodal*

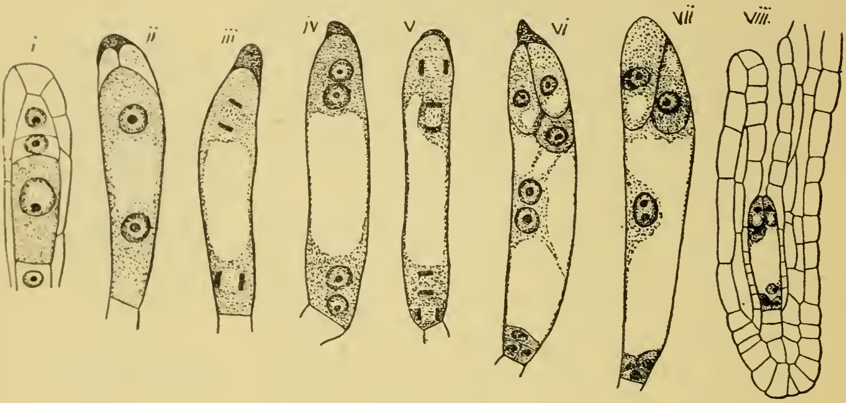

FIG. 219.
Stages in the development of the embryo-sac of *Monotropa*, after Strasburger. See Text below. (i.-vii. × 400. viii. is less highly magnified.)

group ; those at the micropylar end form the *egg-apparatus*. The latter consists of the *two synergidae* which occupy the extreme apex, and the *ovum* attached rather lower. The odd nuclei from each end approach one another, and finally coalesce (vi, vii) to form the *central fusion-nucleus*. The embryo-sac is then ready for fertilisation.

All the nuclei resulting from this development of the contents of the embryo-sac are *haploid*. Reduction has already taken place in the divisions of the mother-cell. The embryo-sac, or megaspore, being one of the products of that operation, its nucleus is already reduced. The whole group of nuclei, together with the cytoplasm that surrounds them, may be recognised as the *sexual phase* or *gametophyte*. It is characterised by differing in the constitution of its nuclei from the ordinary vegetative cells of the plant: all its cells are primordial cells, that is, they are not surrounded by cell-walls, but are delimited by plasmatic films. The *Ovum* is that cell of the gametophyte which will be fertilised. It is the *female gamete*, or *sexual cell, which is to take part in sexual reproduction.*

CHAPTER XVII.

POLLINATION AND FERTILISATION.

"POLLINATION" and "Fertilisation" are often used as synonymous terms. This may have been natural when in 1793 Sprengel published his novel observations under the title "The Secret of Nature discovered in the Structure and Fertilisation of Flowers." But at the present day there is little excuse for such laxity. It is well to be clear in the correct meaning of these words when applied to the Higher Flowering Plants. By "pollination" is meant merely the transfer of the pollen from the anther to the receptive surface of the stigma, and it was this that was discussed by Sprengel, and later by Darwin and others. By "fertilisation" is meant the actual coalescence of two cells: the one is the male gamete derived from the development of the pollen-grain; the other is the ovum contained within the ovule. Obviously some interval must elapse between the events of pollination and fertilisation; it is usually short, but may in extreme cases be as long as a year, or more. *Pollination precedes fertilisation in the Flowering Plant, and is a means to that end; but fertilisation is the end itself.*

The mechanical problem of propagation in Flowering Plants is complicated by the fact that the Plants themselves are immobile. Being rooted in the ground they cannot like the Higher Animals move to seek their mate. The cells that are to carry out fertilisation, viz. the male and female *gametes*, are produced more or less widely apart from one another. They are themselves incapable of movement, while one of them (the ovum) is deeply embedded in the tissues of the ovule, and covered in by the carpel also. This brings the advantage of protection and nutrition of the germ, but it also greatly complicates the problem of sexual propagation. The steps that are necessary to carry it out are first the transfer of the movable, though non-motile pollen-grain from the anther to the surface of the stigma of the same, or a corresponding flower. That transfer is called *Pollination.* The second step is the *germination of the pollen-grain*, with the formation of a *pollen-tube*, which makes its way from the stigma to the micropyle of the ovule, and conveys the contents of the pollen-grain or microspore to the embryo-sac, or megaspore. The final step is the fusion of the *male gamete*, which the tube conveys, with the *female gamete or ovum.* This fusion is called *Fertilisation.* These several events must be considered separately and in their natural succession.

The distance through which the pollen-grain must travel from the pollen-sac to the stigma varies greatly. In flowers such as the Buttercup, containing both stamens and carpels (*hermaphrodite*), the distance may be small. But in many cases only stamens or carpels are produced in the individual flower, and the grains must then be transferred from one to the other. If the staminate and pistillate flowers are borne on the same plant, the condition is described as *diclinous*, as in the Hazel, Beech, or Oak. They may, however, be borne on distinct plants, which are then styled *dioecious*, as in the Rose-Campion, or Willow. These are examples of the separation of the pollen-sacs and ovules *in space.* But there may also be separation of them *in point of time.* For even where they are seated side by side the pollen-sacs may not shed their pollen at the time when the stigma is ready to receive it. Two possible cases exist. The stamens may shed their pollen before the stigma of the same flower is fully matured, as in the Willow-herb, or in the Compositae. This is the more common state, and it is described as *protandrous.* Or the stigma may mature first, and be no longer receptive when the stamens of the same flower shed their pollen. This is the less common state, and it is seen in the Figwort and Plantain. It is described as *protogynous.* Obviously the practical effect is the same as the separation in space, for in either event the pollen must be brought from elsewhere, if fertilisation is to succeed. In such cases the distance to be traversed may be considerable, and the plant has no means of its own for making the transfer.

Use is then made of outside agencies, such as the movements of wind or water: or advantage is taken of the mobility of animals. The mechanism of flowers has been specialised in the most remarkable manner in accordance with these methods of transfer. Where use is made of *wind* the flowers produce abundance of dry dusty pollen, easily shaken out in clouds from anthers often balanced on very flexible filaments. The stigmas meanwhile are much branched and feathery, so as to expose a large surface for catching the grains. These features go with close grouping of the flowers, which are individually small and inconspicuous. Where *animal agency* is used, the flowers are attractive and conspicuous by their scent, by honey-secretion, and by widely expanded floral envelopes of bright colour. The latter attract the eye, the former the other senses of the animal, for instance a bee, and lead her to visit the flower for her own purposes of gathering honey or pollen. Incidentally the floral mechanism is so arranged, in size and form of the parts, that pollen, often of a sticky nature, is deposited on her body as she visits the flower. The flower may be so formed as to lead her, for sake of convenience, to take a definite position: consequently the pollen is deposited on a definite part of her body (Fig. 220). The result of repeated visits to a succession of flowers of like construction will then be that, if the stigmas correspond in position to the spots on which she bears the pollen, they may probably receive some part of it. Thus unwittingly she will have been the agent of transfer of the pollen from the pollen-sac to the receptive stigma.

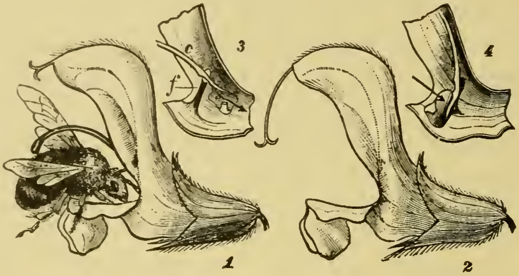

FIG. 220.

Pollination of *Salvia pratensis.* 1, Flower visited by Humble Bee, showing the projection of the curved connective from the helmet-shaped upper lip, and the deposit of the pollen on the back of the Bee. 2, Older flower, with connective withdrawn and elongated style. 4, the staminal apparatus at rest, with connective enclosed within the upper lip. 3, the same when disturbed by the entrance of the proboscis of the Bee in the direction of the arrow. *f*=filament. *c*=connective. *s*=the obstructing half of the anther, which produces no pollen. (After Strasburger.)

Such mechanisms have been elaborated in the course of Descent in an infinite variety of detail. This is the biological meaning of the attractive features which flowers have assumed. It may even be seen how certain floral types have been adjusted in relation to the visits of certain animals, and show development parallel with them. A good instance is that of the Aconite and the Humble Bee, to whose visits the Aconite flower offers convenient access. A study of their distribution across Europe and Asia shows that the northern limit of occurrence of the two organisms almost exactly coincides. This suggests the importance of the Humble Bee in the transfer of the pollen of the Aconite, while the food which the flower offers may in some measure react in determining the distribution of the bee. The methods of transfer of the pollen may thus be varied. But the essential feature of them all is the same, viz. the conveyance of an immobile body essential for propagation from the pollen-sac, where it is produced, to the surface of the stigma where it can germinate. (For numerous instances of the methods of pollination, as illustrated by various examples described in detail, see Appendix A.)

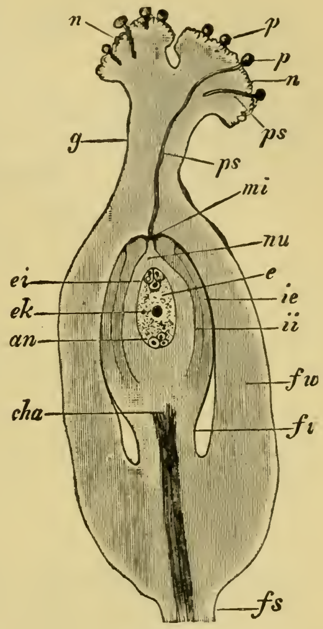

Fig. 221.

Ovary of *Polygonum Convolvulus* at time of fertilisation. *fs*=base of ovary. *fw*=wall of ovary. *fi*=funiculus. *cha*=chalaza. *nu*=nucellus. *mi*=micropyle. *ii*=inner integument. *ie*=outer integument. *e*=embryo-sac. *ek*=central fusion nucleus. *ei*=egg-apparatus. *an*=antipodal cells. *g*=style. *n*=stigma. *p*=pollen-grains. *ps*=pollen tubes. (× 48.) (After Strasburger.)

The *germination of the pollen-grain* takes place normally on the stigma. (Figs. 221, 222.) But it can be induced in a nutritive medium, apart from the stigma, such as a solution of cane sugar of suitable strength. This makes it possible to observe the origin and behaviour of the pollen-tube. The germination may be very rapid. From fresh pollen of the Wild Hyacinth, placed in a 7-10 p.c. solution, pollen-tubes will be produced at a normal summer temperature in about 15 minutes, and in an hour will have grown to a length several times the diameter of the grain. In some cases the structure of the wall of the grain does not indicate where the tube will be formed. But in others its origin is determined structurally. In the Willow-herbs and Geraniums three points of origin are present on each grain. Frequently their number is greater, as in the Corn Cockle (Fig. 222, *A*) ; but of the 40 or 50 points of exit there seen, only one gives rise to a tube. A curious exception is seen in the Mallow, where numerous tubes emerge, which firmly anchor the grain. (Fig. 222, *B*).

The effect of external influences upon the growth of the tube can be studied in culture-experiments. If grains be germinated in a suitable solution under a cover-glass, the tubes, as they first issue, point indiscriminately in all directions. But soon those near the margin turn inwards from the source of free Oxygen: they are *negatively aerotropic* (Fig. 223). If a similar culture be prepared, and a piece of the style and stigma of the same species be introduced with the pollen-grains, the tubes curve towards it, and especially towards the cut surface (Fig. 224). They are *positively chemotropic.* Their behaviour on the stigma, where they take a course in close contact with the moist cell-walls, shows that they are also *positively hydro-*

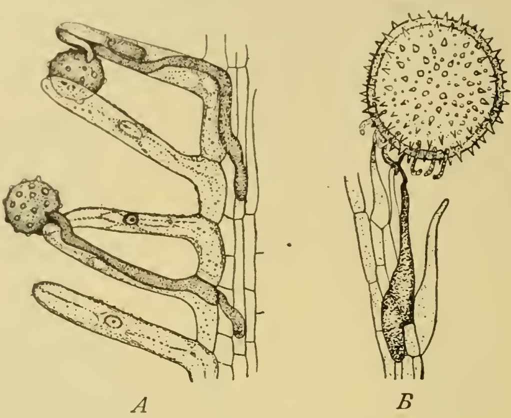

FIG. 222.
A = Pollen-grains of Corn Cockle (*Agrostemma*) showing numerous possible points of origin for pollen-tubes, but only one tube, which penetrates at once a papillar cell of the stigma. *B* = a similar condition in Mallow (*Malva*), but here numerous small tubes are formed for attachment. (After Strasburger.) (× 120.)

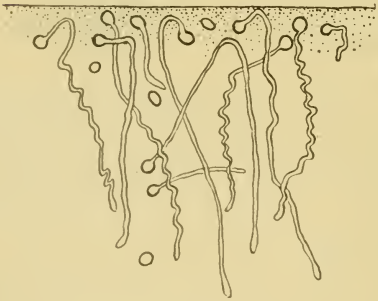

FIG. 223.
Pollen grains germinated in a nutritive medium, under a cover glass, of which the margin is shown. The tubes curve away from the margin, that is, away from the supply of oxygen. (After Molisch.)

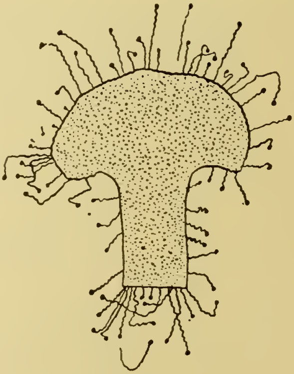

FIG. 224.
Result of culture of pollen-tubes of *Narcissus Tazetta* in neighbourhood of the style and stigma, in 7 per cent. sugar after 16 hours. Diagrammatic. (After Molisch.) (× 10.)

tropic (p. 160). These three factors are effective in deciding the course of the tube when it germinates normally upon the stigma. They lead it to apply itself closely to the surface cells.

On germination the contents of the pollen-grain pass over into the growing tube. The nucleus of the vegetative cell with its cytoplasm usually passes out first, while the *antheridial-mother-cell* is embedded in the rearward part of the vegetative cytoplasm. It soon *divides to form two gametes*, the nuclei of which follow the vegetative nucleus (Fig. 226). As the tube lengthens, the grain as well as the older part of the tube is thus emptied of its contents. Successive lengths are then shut off from the distal part of the tube that is still full, by plugs of cellulose, so that as the tube advances it is still possible to preserve its turgor. Thus provided, the tube can advance through long distances to reach the ovule. (Compare Fig. 221.)

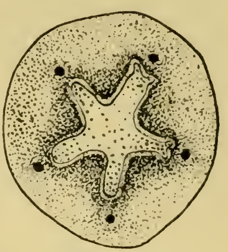

FIG. 225.
Transverse section of the style of *Rhododendron*, showing the five-rayed channel lined with epithelium, and filled with mucilage: it is traversed by the pollen-tubes, which appear as compressed dots in the section. (F. O. B.)

From the surface of the stigma, the pollen-tube, under the combined influence of its negative aerotropism, positive hydrotropism, and positive chemotropism, is brought into close relation with the moist stigmatic tissues. Where there is an open channel the pollen-tube does not need to penetrate the tissue. Even where, as in Lily or Rhododendron, the channel is filled with mucilage the tubes penetrate the secretion, but not the cells which produce it (Fig. 225). There is little apparent difference in those cases where, as in *Salvia*, there is conducting tissue with mucilaginous walls (Fig. 215); for there the pollen-tubes penetrate the mucilaginous middle lamella, passing between the cells themselves. This is in fact the commonest way for the tube to enter the tissue of the stigma,

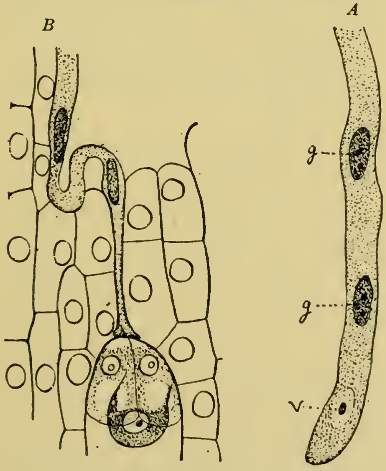

FIG. 226.
A, Pollen-tube of *Orchis latifolia* teased out from the ovary. *v*=vegetative nucleus. *g*, *g*=gametes. (× 500.) *B*, pollen-tube of the same penetrating the micropyle: its gametes still in the tube. The two synergids and the ovum (shaded) are clearly shown. (× 300.) (After Strasburger.)

and it is well illustrated in the Grasses. Here the tubes force their way between the stigmatic cells, penetrating the middle lamella of their walls. But occasionally the cells of the stigma are themselves perforated. This is seen in the Corn Cockle (*Agrostemma*), where the pollen-tube traverses the delicate cell-wall of the stigmatic papilla (Fig. 222, *A*). The protoplast of the perforated cell is not killed, and it may even continue its movements for a time, and retain its turgescence. The tube passes out between the walls of the subjacent conducting cells, and continues its course in that way. The Mallow behaves similarly, with the further feature that a number of tubes are formed from each of the large grains, serving to fix the grain on the surface of the stigma. One tube, however, grows larger than the rest, and conveys the essential contents of the grain (Fig. 222, *B*). It thus appears that pollen-tubes behave upon the surface of the stigma like the filaments of parasitic Fungi, which similarly either follow the surface of the invaded tissue or grow between its cells; but sometimes they penetrate the cells themselves. There is no doubt that in its course the pollen-tube also draws nourishment from the tissue it traverses.

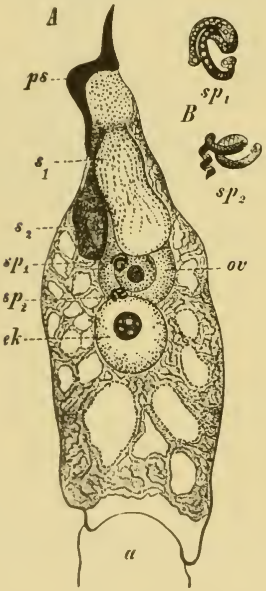

FIG. 227.

A, embryo-sac of *Helianthus annuus* (after Nawaschin). *B*, the male nuclei more highly magnified. *ps*=pollen-tube. $s_1 s_2$=synergidae. sp_1, sp_2=male nuclei. *ov*=egg-cell. *ek*=central fusion-nucleus of embryo-sac. *a*=antipodal cells. sp_1 fertilises the egg; sp_2 fuses with the fusion-nucleus of the embryo-sac. (From Strasburger.)

Passing thus down the style and into the cavity of the ovary, the tube is often conducted mechanically by directing hairs towards the ovule, which in the common inverted type has its micropyle close to the wall of the ovary. The last part of the course is believed to be influenced by the synergids; in some cases a drop of fluid, derived perhaps from them, is exuded from the micropyle. Whatever the influences may be, the tube enters the micropyle and impinges closely on the apex of the nucellus; where that tissue has already been absorbed, it may advance directly upon the embryo-sac, close to the egg-apparatus (Fig. 226, *B*).

The passage of the pollen-tube direct to the micropyle is the usual, and probably the primitive course. Fertilisation in that way is called porogamy. But in a considerable number of plants it takes a course through the superficial tissues of the ovule. Sometimes it passes through the funiculus to the chalazal end of the embryo-sac, as in the Walnut and *Casuarina*: this is called chalazogamy. Sometimes an irregular course may be pursued, by traversing the integuments, as in the Elm. But here the course appears to be very inconstant. It is doubtful whether these irregularities have any special significance, but it is worthy of remark that they occur in relatively primitive Families of Flowering Plants.

The pollen-tube on entering the micropyle conveys with it the two male gametes enclosed in the cytoplasm of the tube (Fig. 226, *A*). Probably the turgor of the contents has its effect in rupturing the soft tip of the tube, and extruding its contents. The nuclei of the two gametes can shortly afterwards be recognised in the embryo-sac. The one passes into the ovum and fuses with its nucleus. The result of fusion of the male and female gametes is the *zygote*. The other passes on to the central fusion-nucleus and coalesces with it (Fig. 228). The mechanism of the movements within the embryo-sac is uncertain. It has been suggested that protoplasmic streaming may assist it. On the other hand, the peculiar form which the male nuclei sometimes take suggests independent movements, like those of the sperms of lower plants to which they correspond functionally (Fig. 227, *B*). Meantime the synergids shrivel, and begin to disorganise. Clearly their function is completed on fertilisation.

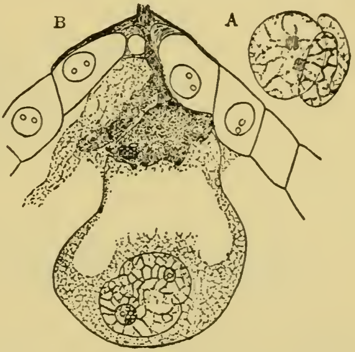

Fig. 228.

Behaviour of the male and female nuclei of Lily in fertilisation. (Mottier.) *A*, vermiform male nucleus applied to the egg-nucleus (*Lilium Martagon*). *B*, egg-cell of *Lilium candidum* showing sexual nuclei in act of fusing. The nuclear membranes have disappeared at the place of contact.

In the case of *Lilium* the more or less spiral form of the male nucleus, when it penetrates the ovum, has been seen to be retained till it is applied to the nucleus of the ovum. But the nuclei gradually become alike in shape, size, and structure. Both are in the resting condition, and have a nucleolus (Fig. 228). The nuclear membrane then disappears at the place of contact, their cavities become one, the chromatin-reticulum of the one unites with that of the other, and the resulting fusion-nucleus can scarcely be distinguished from the nucleus of an unfertilised egg. Finally the nucleoli fuse also. The details of the fusion of the second male nucleus with the central fusion-nucleus of the embryo-sac in *Lilium* resemble those in the egg, but the process is complicated by the fact that it may synchronise with the fusion of the two polar nuclei, so that a triple fusion may be seen actually in progress (Fig. 229). But in most plants the polar nuclei fuse before the access of the second male gamete.

The act of Fertilisation in the Higher Flowering Plants is thus a double one, involving the ovum and the central fusion-nucleus on the one hand, and the two male gametes on the other. The nuclei of the male gamete and ovum are both haploid, being cells of the gametophyte generation, derived from spore-mother-cells which have undergone reduction. The fusion of the gametes restores the original number of chromosomes. *The nucleus of the zygote is diploid, and that diploid cell originates the new germ.* The central fusion-nucleus had already resulted from the fusion of the two polar nuclei. On its fertilisation by the second male gamete a third nucleus coalesces with it. This triple fusion is unique, so far as present observation extends. It may have its physiological importance in relation to the developments that follow, for the triple fusion initiates the endosperm.

FIG. 229.

Fusion of the second male nucleus with the polar nuclei in *Lilium Martagon*. *A*, an S-shaped male nucleus applied to the upper polar nucleus. *B*, the second male nucleus (shown only in part) and the two polar nuclei close together. *C*, all three nuclei fusing. (After Mottier.)

An important feature characterising the intricate changes in the embryo-sac of Flowering plants is the extraordinary constancy in the number and behaviour of the cells involved. Plants which differ widely in form, internal structure and biological character, as well as in the number and relation of their floral organs, show a remarkable uniformity in these details. Exceptions do exist, but they are few relatively to the majority which conform. This indicates that probably each step is significant in the success of the sexual propagation, though it is not possible to assign with certainty its exact function to each. One general conclusion follows from comparison with forms lower in the scale, though the foundations for it can only be given on a later page; it is that the parts directly involved in the sexual propagation of Flowering Plants represent, in a vestigial form, parts which are more fully represented in more primitive organisms. . They all belong to the Gametophyte, or Haploid Generation. Here they appear as only a few cells contained on the one hand in the microspore, or pollen-grain, and its tube ; on the other in the megaspore, or embryo-sac. But these represent in their position in the life-cycle that haploid generation which will be seen later in larger proportions and greater independence in such plants as the Ferns and Mosses. In either case, however, it is *Syngamy*, that is the fusion of primordial gametes to form a zygote, which *closes the haploid phase.* This event forms the starting point for the new diploid individual, which is the *Germ* or *Embryo.*

CHAPTER XVIII.

THE EMBRYO AND THE SEED.

In normal cases if no pollen-tube arrives at the micropyle of the ovule, and the ovum is consequently not fertilised, the ovule develops no further. But if fertilisation by a pollen-tube has been carried out, changes follow not only in the ovum itself and the other contents of the embryo-sac, but also in other parts of the ovule. The term *Seed* is applied to the body which results from this further development of the ovule, while the germ which originates from the fertilised ovum is called the *Embryo*.

After fertilisation the earliest changes appear in the embryo-sac itself. The synergidae shrivel, and a cell-wall is deposited round the *fertilised ovum*, or *Zygote*, which remains attached at the micropylar end of the embryo-sac. It soon elongates, its free end extending into the cavity of the sac. Meanwhile its nucleus, which has resulted from the fusion of the male and female nuclei, divides, showing the double number of chromosomes characteristic of the *diploid* generation. The zygote then divides into two cells by a transverse wall, and this may be followed by further divisions in planes parallel to the first; so that a simple filament, or *Pro-embryo*, is formed (Fig. 230, i). The very first division of the zygote stamps the polarity of this pro-embryo, and from that point on defines its apex and base. The basal end of the pro-embryo remains attached to the micropylar end of the sac, the apical end projects into the cavity, and produces the embryo. It is a significant fact that in the great majority of Flowering Plants, though not in all, this filamentous stage, showing polarity and consisting of a varying number of cells, appears first. It has the practical result of carrying the embryo deep down into the sac, but it may also have a phyletic meaning, as indicating an ancestral filamentous construction. The pro-embryo then differentiates into two regions: a free apical part which develops into the massive *Embryo*, and an attached basal part which remains filamentous. This is called the *Suspensor*, since it holds the embryo in a definite position during its early development, surrounded and nourished by the semi-fluid contents of the enlarging sac.

The Embryo.

Among Dicotyledons the embryo of *Capsella*, the Shepherd's Purse, in which the development was first followed out in detail, serves as a very general type. The filamentous pro-embryo (Fig. 230, i.) has the cell at its basal or micropylar end greatly enlarged. The cell at the apical end is relatively small at first, but it gives rise to the greater part of the embryo, a smaller part originating from the next lower cell. The apical cell enlarges into a spherical form, and divides into octants, by walls at right angles to one another and to the outer

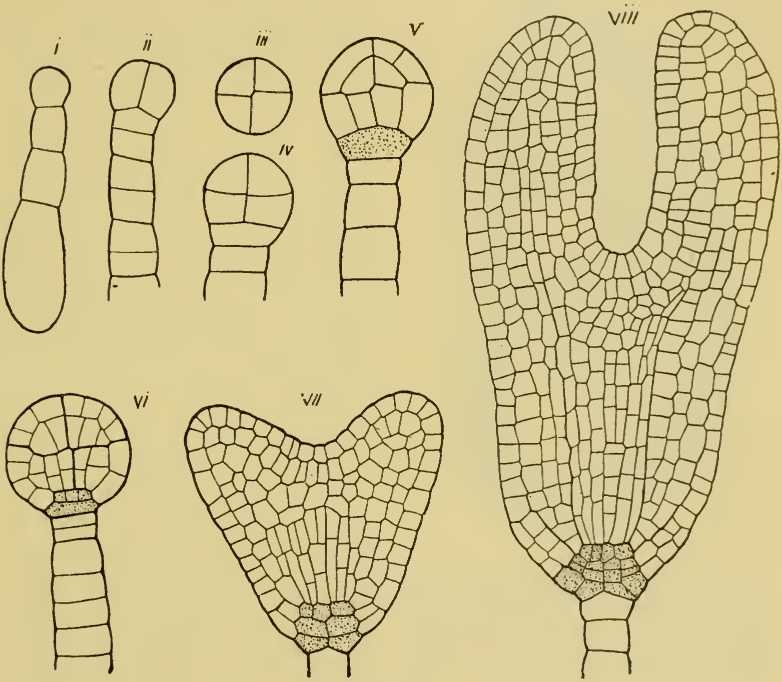

Fig. 230.

Embryos of *Capsella* in various stages of development. (i-v after Famintzin; vi-viii after Hanstein.) The hypophysis and its products are shaded. All these embryos have the apex upwards, and the root downwards. But it is to be remembered that the root always points to the micropyle of the ovule, as seen in Fig. 231.

surface (anticlinal). Their position is uniform, and the first is usually longitudinal (ii.), but their succession may vary. This suggests that no great morphological value can be set on their order of appearance (iii. iv.). Later each octant divides into an outer and inner cell, by a wall parallel to the surface (periclinal); the superficial cells thereafter divide only by anticlinal walls, and the layer thus produced is called *dermatogen*, because it forms the epidermis (v.-viii.). The inner cells divide again periclinally to form an inner and an outer series; this is more regular in the lower tier of octants, which will form the hypocotyl and root. The inner series constitutes the *plerome*, which forms the stele; the outer is the *periblem*, which forms the cortex (vi.-viii.). Meanwhile the cell of the pro-embryo adjoining the lower tier of octants (the *hypophysis*, here shaded) has enlarged, and divided (vi. vii.), so as to form a group of cells which encroach into the spherical embryo. It provides the apex of the root, which is thus attached to the suspensor, and it is always directed towards the micropyle. The upper tier of octants soon gives rise to two projecting lobes (cotyledons), which bear no constant orientation relative to the first segmentations. Between them is a smooth groove, where the plumule will arise later. It is now possible to recognise the position of all the parts of the germ, viz. the radicle, the two cotyledons, and the plumule between them. In the Shepherd's Purse the seed is exalbuminous (p. 317), and the embryo develops fast in bulk, and in length (Fig. 231). But the ovule is of the type with a curved embryo-sac. The embryo, as it grows, adapts itself by curving also, and soon fills the greater part of the sac. Meanwhile the plumule at last appears at the base of the groove between the cotyledons. Its position coincides with the intersection of the octant walls.

FIG. 231.

Shepherd's Purse. Photomicrograph of young seed, showing embryo, endosperm centrally, and developing testa on the outside. (× 125.) The micropyle is directed upwards and to the left, and the root-tip is directed towards it. (After Coulter and Chamberlain.)

Accordingly its position was defined by the first segmentations of the zygote. Thus the embryo of a typical Dicotyledon springs from the two distal cells of the filamentous pro-embryo. The larger part, including the cotyledons, plumule, hypocotyl, and most of the root, arises from the distal cell; the tip of the root originates from the cell next below it; the rest of the pro-embryo acts as an organ of attachment.

While the *Capsella*-type shows the embryogeny usual in Dicotyledons, aberrant forms are not uncommon. But as they are mostly sporadic in their distribution they do not suggest any consistent basis for morphological argument. It is rarely that a family includes many aberrant types : an exception is seen in the Leguminosae, where the peculiarities are most marked in the suspensor. Of the rest, the most interesting variants are the pseudo-monocotyledonous embryos. In certain plants that are clearly Dicotyledons in their general characters, only one cotyledon appears. This is seen in *Carum bulbocastanum, Eranthis hyemalis* and *Cyclamen persicum* ; and it is probably due to abortion of one of the cotyledons. But in some cases it is believed to result from a lateral fusion of the two cotyledons to form one, as in *Ranunculus Ficaria*. Much other evidence suggests that the Monocotyledonous state is derivative from that of the Dicotyledons. This conclusion is further countenanced by the fact that occasionally Monocotyledons are found with two cotyledons (*Agapanthus*), or even four growing points may appear on a peripheral zone (*Cyrtanthus*). In such cases the apex of the axis would be central and terminal, as in the *Capsella*-type. But in most Monocotyledons it is lateral, as it is in *Alisma*.

The development from the zygote in *Alisma* or *Sagittaria* is held as typical for a large number of Monocotyledons. The first divisions give rise to a three-celled pro-embryo, of which the basal cell (*q*) is enlarged, and does not divide further (Fig. 232, i.). The middle cell divides into several cells (*m*, *n*, *o*, *p*, Fig. 232, ii.). The distal cell divides into quarters, and subsequently by anticlinal and periclinal walls so as to form the single terminal cotyledon (Fig. 232, ii.-v., *l*). Meanwhile in the tier of cells below this (Fig. 232, ii. to v., *m*) a lateral depression begins to appear, which develops into the apex of the axis. This is then lateral in origin, while the cotyledon is terminal. The hypocotyl and root-tip spring from the next two tiers (*n-o*, Fig. 232, ii.-v.). It thus appears that the reference of the several parts to cells of the pro-embryo differs in the *Alisma*-type from that in the *Capsella*-type. The most remarkable difference lies in the lateral origin of the apex of the axis in *Alisma*, while in the *Capsella*-type the cotyledons are lateral, and the apex distal.

In a number of Monocotyledons the embryo differs from the *Alisma*-type. The most interesting are those in which the apex of the axis originates from the terminal cell of the pro-embryo. This occurs in the Dioscoreaceae and Commelinaceae (Fig. 233), also in *Zanichellia* and others. There is reason to believe that the stem-tip in the embryo of the Monocotyledon was originally terminal, as in the Dicotyledons, but that in most types it has been forced to one side by the strong growth of the single cotyledon. If this were so the *Alisma*-type would be a derivative, and secondary condition, and an apparent anomaly would thus be explained. For among Vascular Plants the embryos of the *Alisma*-type are the only exceptions to an otherwise general rule; which is, that the apex of the shoot bears a constant and close relation to the centre of the distal tier of cells composing the embryo.

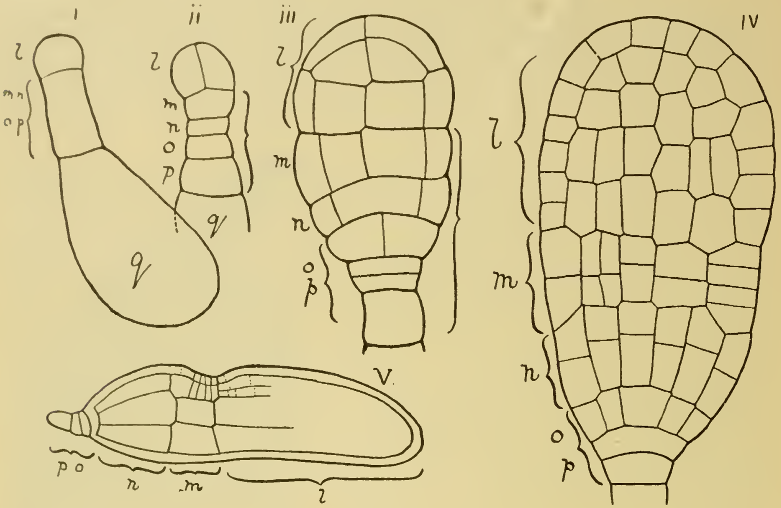

FIG. 232.

Successive stages of development of the embryo of *Alisma*, after Famintzin. *l*, *m*, *n*, *o*, *p*, *q* represent successive cells of the pro-embryo, and the tissues derived from them by division.

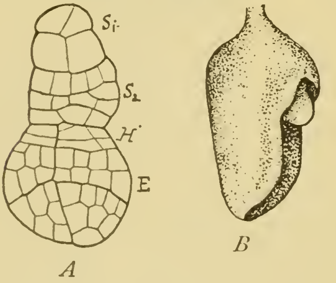

FIG. 233.

Embryos of *Tamus*. (After Solms-Laubach.) *A*, younger; *B*, older. $s_1 s_2$=suspensor. *H*=hypophysis. *E*, body of the embryo. Here the embryology is more nearly of the type of *Capsella*.

The very peculiar structure of the embryo in Grasses has caused much discussion (App. A, Fig. 503, p. 658). The question has arisen whether the "scutellum," which faces the endosperm, and acts as a sucker from it, is or is not the cotyledon. The view now held as probable is that the cotyledon is highly specialised. A basal part of it appears as the scutellum, the distal part of it as the "cotylar sheath." The origin of the plumule appears here also to be from the apex of the embryo.

The three primary *antipodal cells* (*ant.* Fig. 216, p. 295) have no wall up to the time of fertilisation. Their subsequent behaviour is variable. Sometimes they are at once disorganised; but in most other cases they remain functional. They may grow to large size, as in many Ranunculaceae; or they may undergo fragmentation of nuclei, and even cell-division, so as to form a considerable tissue, as in the Compositae and other Gamopetals. Their use appears to be to act as intermediaries between the vascular supply and the enlarging embryo-sac, before the endosperm is organised as a tissue. To that end they sometimes develop as suckers penetrating the chalaza. But in any case they only help towards the final end, which is the full development of the germ.

The Endosperm.

The triple fusion, of the two polar nuclei with the second male gamete, has already been noted (Figs. 227, 229). The first division of the resulting triple-fusion-nucleus usually precedes that of the zygote (Fig. 234, i. ii.): it is repeated synchronously, in rapid succession, so that the numerous nuclei formed are found to be in corresponding stages of division, and their number at any moment is some power of

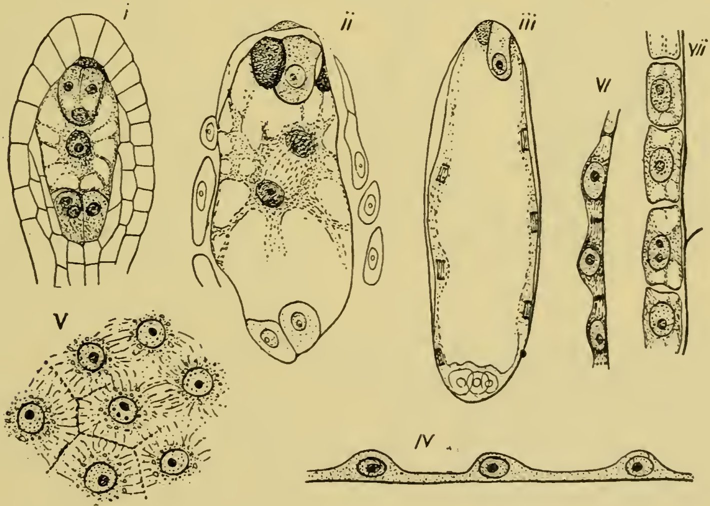

Fig. 234.

Successive stages of development of the endosperm in *Myosurus*. (After Strasburger.) (i.-ii. and iv.-vii. × 400; iii. × 170.) i. shows state at fertilisation. ii., embryo-sac much enlarged, and first division of the fusion-nucleus. iii. shows embryo-sac still more enlarged; it is on a lower scale of magnification. iv.-vii., stages of cell-formation round the numerous nuclei, derived by division from the fusion-nucleus.

two. Their chromosome-number is at first diploid, but the number is not strictly maintained. Meanwhile the embryo-sac grows rapidly, and the large central vacuole is surrounded by a thin peripheral film of cytoplasm, in which the free nuclei are embedded (Fig. 234, ii.-vi.). Partition-walls are formed later, isolating each nucleus in its own cytoplasmic area. Sometimes several may be present in a single cell, but when this is so they commonly fuse together. The embryo-sac is thus lined internally by a flattened layer of uni-nucleate cells, surrounding a large central vacuole (vii.). These cells then grow inwards, and divide, encroaching on the central cavity: this they ultimately fill with the compact tissue of the endosperm, which embeds the embryo. Sometimes, however, a central cavity may still remain. This is the case in the Coconut, where the cavity is filled with the "milk," which is actually vacuole-fluid, while the white flesh is the tissue of the endosperm, which has not filled the very large embryo-sac.

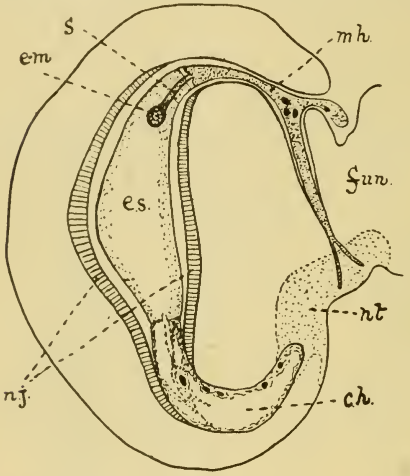

Fig. 235.

Median section of an ovule of *Rhinanthus minor*, showing haustoria. (After Balicka-Iwanowska.) *s*=suspensor. *em*=embryo. *e.s.*=embryo-sac. *fun.*=funiculus. *n.j.*=nutritive jacket. *nt.*=nutritive tissue. *c.h.*=chalazal haustorium. *m.h.*=micropylar haustorium.

The above description applies to ordinary types of ovule. But there is a considerable variety of detail in the behaviour of the embryo-sac and its contents after fertilisation. Frequently the first division of the fusion-nucleus is followed by a cell-wall dividing the sac into two chambers; this is seen in some Monocotyledons, and in many Dicotyledons, especially among the Gamopetals. Sometimes the development proceeds no further; but usually divisions may be continued in one or the other, or in both of the chambers.

More marked modifications are connected with the nourishment of the embryo-sac. In relatively primitive types like *Myosurus* the sac merely increases greatly in size, encroaching upon the surrounding tissues, which make way for it. Their cells collapse and their substances are absorbed into the growing sac, which acts thus parasitically upon them (Fig. 234, ii.). But in more specialised types, such as the Gamopetals, the nursing of the embryo-sac is more exact. Their ovules have only a single integument, while the embryo-sac soon crushes the small nucellus out of existence. The innermost layer of the integument then abuts on the growing sac, and forms an epithelial jacket of prismatic cells (Fig. 235, *n.j.*). This serves as a permanent nourishing tissue, which acts till the embryo-sac is well advanced.

In addition to this the embryo-sac itself may frequently put out local *haustoria*, which penetrate to favourable sources of nourishment. A good example of this is seen in *Rhinanthus* (Fig. 235), where, in addition to the epithelial jacket (*n.j.*), haustoria are formed at both ends of the sac. The chalazal end (*c.h.*) extends so as to reach a mass of nutritive tissue (*nt.*) close to the end of the vascular strand. From the micropylar end a similar haustorium (*m.h.*) passes through the micropyle, and traverses the funicle towards the same source of supply. The haustorial connections may be still more elaborate in other plants (*Plantago*). Such arrangements indicate the importance of the nourishment of the sac, especially in its earlier stages. They also provide interesting analogies with the behaviour of parasites, whether among the Fungi or in Flowering Plants.

The *function of the endosperm* is to provide temporary nourishment for the embryo which it surrounds. But the amount of the supply, and the time when it is yielded to the embryo may vary. Two main types of seed arise accordingly. In the first the embryo grows slowly, and keeps in close touch with the endosperm, which remains relatively large till the seed is ripe; it embeds the embryo and is stored with food. The result of this is the "albuminous" seed (Fig. 239). It is probably a relatively primitive state, and it is found in such families as the Ranunculaceae and Magnoliaceae, and in most Monocotyledons. Moreover, all Gymnosperms have seeds of this type. In the second the embryo develops more quickly. It absorbs the available nourishment early, so that at ripeness little or nothing remains of the endosperm. Its function has been temporary. Such seeds are called "ex-albuminous" (Fig. 239). Intermediate states are found, as in the Leguminosae, which, though usually held to be exalbuminous, have in many cases a band of mucilaginous endosperm covering the embryo (Fig. 237). While the substances stored in the endosperm provide for the further growth of the germ, they also supply the staple food of man in the various cereal grains.

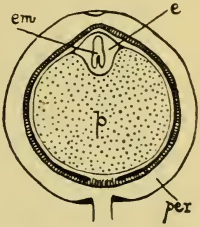

Fig. 236.

Vertical section through a Peppercorn. *em*=embryo. *e*=endosperm. *p*=perisperm. The testa is shaded. *per*=pericarp. (After Baillon.)

In some cases the store of food for the embryo may in part be outside the embryo-sac, in the chalazal region of the nucellus. Such tissue is called *perisperm*, and it is found in the Peppercorn (Fig. 236), or the seed of the Water-Lily. The difference from an ordinary albuminous seed is morphological rather than physiological. But in the great majority of cases the nucellus is obliterated early, owing to the precocious growth of the megaspore which it envelops while young. Accordingly, it is not represented as a rule in the ripe seed, except by the remains of its tissue, which are crushed between the firm seed-coat and the endosperm or embryo within.

On the other hand, the integument or integuments persist, developing into the *testa, or seed-coat.* Their tissues become indurated, of stony or leathery texture; but there is a good deal of variety in the detail. Usually the outermost layer, but not infrequently some layer more deeply seated, develops its cells in prismatic form and thick-walled. Others may also harden: but the inner, softer layers are often compressed. The tissues lose their cell-contents, serving only the purpose of protection to the germ and the stores within. (Fig. 237.) When this condition is reached in many-seeded ovaries the tissue of the funicle dries, and being brittle, the connection between the seed and the parent plant is severed. It is now independent, and the new individual has to fend for itself.

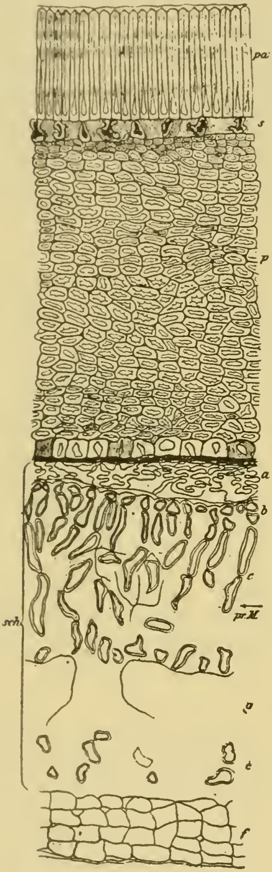

FIG. 237.
Section through testa, and mucilage-endosperm of seed of *Gymnocladus canadensis.* *pa*=palisade layer. *s*=supporting layer. *p*=thick-walled tissue. These form the testa. *sch*=mucilaginous endosperm of this Leguminous seed. (After Nadelmann.)

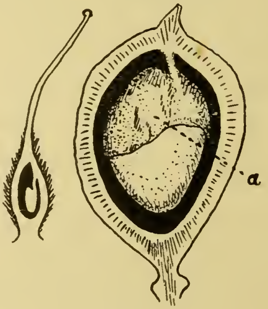

FIG. 238.
Young carpel, and fruit of *Copaifera.* *a* indicates the arillus which spreads from the micropylar end of the pendent seed. (After Baillon.)

Other developments, having special biological value, are sometimes formed during the ripening of the seed. Superficial cells may grow into long *hairs,* as in the Cotton, Willow, or Poplar. These are effective in the transfer of the seed by the wind. Succulent bodies may sometimes be formed by local hypertrophy; such as the massive enlargement of the micropylar region to form the "caruncle" of the Spurges. A growth may proceed from the base of the ovule, appearing as an extra integument, or *arillus* (Fig. 238). The Mace sold by grocers is an example of this. It appears after fertilisation as a partial covering, highly coloured and strongly flavoured, round the true seed, which is sold as the Nutmeg. The bright orange sheath round the ripe seeds of the Spindle Tree is of the same nature. In both cases the aril is exposed as the fruit ripens, and its presence is believed to promote distribution of the seeds by Birds. But such developments are infrequent.

Each seed contains normally a single germ, together with a store of nutriment either in the germ itself or in the accessory tissues. (Fig. 239.) As it ripens it dries out. In this state, after separation from the parent, it may undergo a period of rest. But sooner or later its function is to establish a new individual. In order that this may be most effectively done it is important that each seed should have the chance of independent germination, a condition which is secured by dispersal of the seeds.

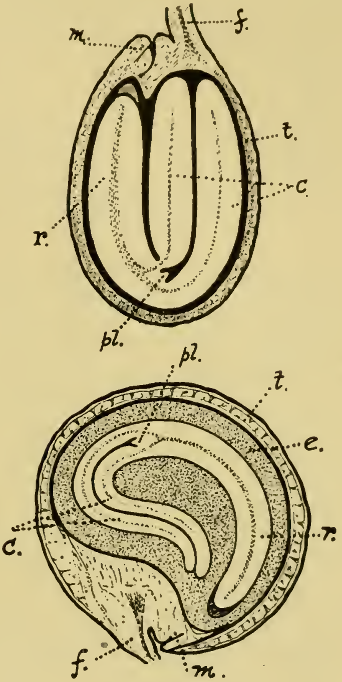

Fig. 239.

Seeds in median section: the upper (*Capsella*) exalbuminous, the lower (*Datura*) albuminous. *f*=funiculus. *m*=micropyle. *t*=testa. *e*=endosperm. *c*=cotyledons. *pl*=plumule. *r*=radicle. (Enlarged.) (Dr. J. M. Thompson.)

Each seed thus represents a single matured megasporangium, or ovule. It is a composite body comprising parts derived from three generations. The seed-coat, and the perisperm when present, consist of tissues of the parent diploid plant. The endosperm is usually held as representing, in a specialised and altered state, the haploid female prothallus, or gametophyte generation. The germ, which results directly from fertilisation, represents the new diploid generation. That these are all closely related in the seed of Flowering Plants is a late and derivative state, which cannot be properly understood till certain lower types have been described, and compared with it.

CHAPTER XIX.

THE FRUIT AND SEED-DISPERSAL.

THE effects of Fertilisation extend in Flowering Plants beyond the ovule or megasporangium to the carpels, and often also to the floral receptacle. The mature Pistil or Gynoecium is called the *Fruit*. Sometimes this term is applied in a strict sense to the ripened pistil only. But it may be used in a more extended sense to include the receptacle, or even other parts when they also undergo changes consequent on fertilisation. This wider use of the term accords with the definition of the Flower as a simple shoot bearing sporangia. The Fruit would then be the whole of that simple shoot developed in the interest of the ovules which it bears.

According to the structure of the flower that produces it, the fruit may comprise one carpel or more. The carpels may be separate or united. They may in more specialised types be sunk down in the tissues of the receptacle. Such differences of the gynoecium existed already in the flower, and they remain as the fruit ripens, giving variety to the construction of its different types. It would be possible to analyse and describe the several kinds of fruits on the basis of their *morphological* structure, and it is necessary to do this when the chief purpose is systematic classification (see Appendix A). But another method is to examine them from the *biological* point of view. The function of the fruit is then taken as the basis of their study, and the attempt is made to see how each type is fitted for its performance. That is the aspect which will now be developed.

The functions of the maturing fruit are the *protection* and *nourishment* of the ripening ovules, and the *dispersal* of the seeds. It will not be necessary to dwell upon the first, for it is so obvious. In superior fruits the ovule, or ovules, are covered in by carpels, and attached to them by their funicles. In this way effective protection and nourishment are afforded during development. But they are still better secured in inferior ovaries; for in these the ovules are surrounded also by the massive tissue of the receptacle, while they are brought nearer to the source of vascular supply by their deeply sunken position. The protection becomes more effective as the maturing of the gynoecium proceeds, for its tissues frequently become more bulky and succulent. But still more is this so in others which harden with age. Extreme cases are seen in nuts or stone-fruits, where the woody tissues of the carpel reinforce, or sometimes mechanically replace the seed-coats. Since the seed with its nutritive store offers attractions to animals as food, the biological importance of such strong mechanical protection should be duly recognised.

But the biological fact which has dominated the evolution of the fruit, as regards its development after fertilisation, more than any other is the need for the dispersal of the seeds. The greater their number the greater is the need for it. Sooner or later each seed should have the opportunity of germination. This is carried out with the best prospect of success where each is isolated from its neighbours. Moreover, a wide dispersal leads to the spread of the species, and thus helps it in that competition for room in an overcrowded world which has been called the Struggle for Existence. The size of the individual seed is an important factor in the problem of dispersal. Clearly, the larger the seed the better is the chance of successful establishment of the young plant on germination; for the larger the store it carries with it the larger the vegetative system it will be able to form before it has to depend on its own resources. But the larger the seed the less easily will it be transferred from point to point. There are thus two conflicting factors of success. In the course of evolution plants have severally struck their own balance between these opposing factors, and the variety of fruit-construction shows in what different ways the problem may be solved. The success of each may be measured by the survival, numbers, and spread of those plants which have adopted them. These are the underlying conditions which should be kept in mind in studying the structure of the fruit, and its relation to seed-dispersal.

It is probable that a primitive type of gynoecium was apocarpous, containing a number of ovules. Such a carpel is seen in the pod of a Pea, or in the follicle of *Caltha* or *Aquilegia*. Along several lines of Descent comparison suggests that there has been a reduction in the number of ovules to a single one. This is illustrated in the Ranunculaceae. The Helleboreae have follicles and are probably a central type (*e.g. Helleborus, Aconitum, Caltha*, Fig. 240). In the carpel of *Anemone* only a single ovule matures, though several are initiated but remain vestigial (Fig. 241, *a*). In Rue and Buttercup only a single ovule is present (Fig. 241, *b*). On the other hand, the number of carpels in the Helleboreae is about five: but a much larger number is seen in *Anemone* or Buttercup; the more numerous carpels make up for the reduction of the ovules to one in each. Similarly in the Leguminosae a primitive type is seen, with many ovules in each carpel in the Pea or Bean. But *Copaifera* contains but two ovules, of which one only ripens into an unusually large seed (Fig. 238, p. 318). Again, in the Rosaceae, in *Spiraea* or *Cydonia* each carpel is many-ovuled; but in the Potentilleae, Rubeae and Roseae each has only one. The loss of number is, however, made up by the greater number of carpels. In the Pruneae, on the other hand, the single carpel contains two ovules, of which usually only one matures; but it grows into a large kernel. The gynoecium of the Oak is trilocular, with two ovules in each; but only one of the six ovules matures into the seed in the large acorn. The Coconut again shows three loculi, but only one matures its single very large seed. A similar condition on a smaller scale is seen in Valerianaceae, while the gynoecium, with a single loculus and a single ovule in each flower, becomes the rule in the Teasels and Composites: these may be held to be examples of an extreme state.

FIG. 240.

FIG. 241.

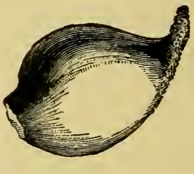

FIG. 242.

FIG. 240. Follicles of Aconite. (After Figuier.)
FIG. 241. *a*, Carpel of Anemone, with abortive ovules. *b*, Carpel of *Thalictrum*. (After Prantl.)
FIG. 242. Achene or nut of Buttercup. (After Figuier.)

Such evidence clearly indicates a progressive reduction in number of ovules produced and matured in the cases quoted. It often goes with increase in size of the individual seed, as in the Plum, Oak, and Coconut, which gives greater certainty of successful germination. But some families show the converse, viz. that there has been a progressive increase in number of the seeds, though the individual size of the seeds is diminished. The most marked examples are seen where some irregular form of nutrition makes germination hazardous: for instance, in the mycorhizic Orchidaceae, where over a million seeds have been estimated as the product of a single capsule. In many of the mycorhizic Ericaceae the seeds are numerous; and the same is seen in the parasitic Rafflesiaceae or Balanophoreae. In such cases the large number of seeds covers the risk of germination.

Such differences in number and size of the seeds must profoundly affect the mechanical problem of seed-distribution. The minute seeds of an Orchid can be scattered by a breath, but this would have no appreciable effect upon a Coconut in its natural husk.

Dissemination of Seeds

Seeds being immobile require some agent outside themselves for their dispersal. Various means are effective. Sometimes the dispersal may be dependent upon the structure of the pistil, as in explosive fruits. But usually it is carried out by means of transfer outside the plant, such as currents of air, or water, or the movements of animals. There is an obvious analogy in this between seed-dispersal and the transfer of pollen. In both cases the immobile plant depends upon external agencies for transfer of essential parts. But the two present quite distinct problems. In pollination the end is to deposit the pollen-grains upon the stigma, and the more accurately this is done the better. In seed-dispersal the end is simply the wide separation of the individual seeds. Accuracy is of less importance.

In primitive types of fruit, as the carpellary wall matures, its tissues commonly become hardened. Where the seeds are numerous they require to be set free for germination. The natural course is by *splitting or dehiscence of the carpel*; and this is carried out in various ways. A split most naturally follows along the line of the coalescent margins of the folded leaf. This is the case in the follicle of Aconite (Fig. 240). A similar split may also sever the carpel at its midrib, as in the pods of Peas and Laburnums. The case of syncarpous fruits is not so simple. Their capsules open sometimes by longitudinal slits, as in *Cardamine* (Fig. 101) or *Hura* (Fig. 102), sometimes by transverse slits, sometimes by valves or pores: and this may occur either in superior or in inferior fruits. The seeds can thus escape, leaving the carpellary structure behind as an empty husk. On the other hand, in cases where the carpels are separate, and the number of the seeds in each is reduced to one, dehiscence is unnecessary, while the firm tissue of the carpel may form an additional protective wall. The resulting *achene*, or *nut*, is then shed bodily, as if it were a single seed, though it is strictly speaking a fruit. This is seen in the Buttercup (Fig. 242), or *Potentilla*. It may happen also in syncarpous pistils where only one seed matures, as in the Hazel, Acorn, or Coconut. A peculiar case is that of the Umbelliferae, where the inferior ovary splits into two halves, each corresponding to one of its two carpels, and each containing a seed. Each half is practically equivalent to an achene (Fig. 490, vi., Appendix A, p. 638).

To *release* the seeds as separate bodies is one thing, to *disseminate* them is a different proposition. By various modifications of the ripening pistil this second end may also be secured, sometimes by the activity of the pistil itself, but oftener through the medium of external agencies. The plant itself may disperse its seeds by means of various mechanical arrangements, which often result from the sudden release of strains set up in the carpellary walls as they dry in the process of ripening. An instance is seen in the common Hairy Cress (*Cardamine hirsuta*). Its fruit is the usual siliqua of the Crucifers; but the lateral valves, on splitting from their base, curl so sharply upwards that the seeds are forcibly thrown out (Fig. 101). The method of the Geranium is similar, though differing in detail. Here only one seed is ripened in each of the five carpels. By splitting from the base, and sudden curling of the carpel upwards, the relatively large seed is slung out at a distance (Fig. 243). One of the largest and most effective of these explosive fruits is that of the Sand-box Tree (*Hura*, Fig. 102). It is composed of 12 to 18 woody carpels, each containing one seed about ½ inch across. As the fruit hangs ripe upon the tree, the carpels suddenly split apart, and their woody shells take a twisted form, thus relieving the previous strains. By the sudden change the seeds may be thrown to a distance of some thirty yards from the tree. Another method is seen in the tricarpellary capsule of the Violet. When ripe the three carpels separate, and each boat-like carpel then presses its margins laterally together as it dries, and pinches the smooth seeds, which are thus shot out to a distance. Such examples illustrate the mechanical methods of dispersal seen in dry fruits.

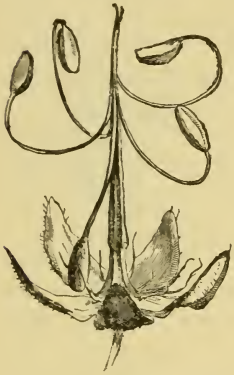

Fig. 243.
Sling-Fruit of Geranium.
(After Figuier.)

In some pulpy fruits the principle of the squirt is used. The fruit of the squirting Cucumber (*Ecballium*) hangs pendent as it ripens, and its outer pericarp is kept tense by the semifluid contents. When ripe it breaks away at the stem, opening a basal pore. As it drops the contents are sprayed out of it, seeds and all, to a considerable distance, scattering as they fall.

Dissemination by Wind and Water.

More frequently the motor impulse is from without, the chief agents being *wind*, *water* or some *moving animal.* Wind acts directly upon small seeds, such as those of Orchids, scattering them as it would so much dust. It may act less directly where the seeds are larger, and the dehiscent fruit is borne on a stiff stalk, as in the gaping follicles of the Aconite, which, shaken by the wind, scatter their seeds all round the parent (Fig. 240): or in the Poppy (Fig. 244) or Canterbury Bell, which do the same; but here the dehiscence is by pores, the principle being that of the Pepper-box.

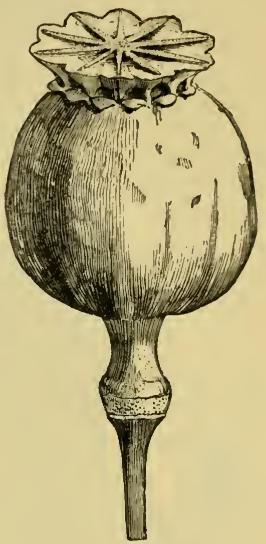

Fig. 244.
Capsule of Poppy opening by pores below the star-shaped stigma. (After Figuier.)

The wind would no doubt influence the fall of any seeds; but the development upon them of tufts of hair, or of broad thin wing-like surfaces, enhances its effect upon their transfer, even where the seeds are relatively large. Such developments are sometimes upon the seed itself, as in the case of dehiscent fruits: or they may be formed by the carpellary walls where the fruit is one-seeded, or where it breaks into one-seeded parts. The development of hairs on the seeds themselves is seen in the Willow and Poplar, in Cotton (Fig. 245), and in the Willow-herb. When in any of these the fruit splits, the seeds are set free, each with its hairy parachute, which supports it in the breeze,

Fig. 245.
Seed of Cotton with superficial hairs. (After Figuier.)

Fig. 246.
Fruit of Valerian. (After Figuier.)

so that it may be conveyed to a distance before reaching the ground. In many Valerianaceae (Fig. 246) and Compositae (Fig. 247), where the fruit is one-seeded and does not split, the calyx is persistent, and developing as the feathery pappus buoys up the inferior achene when set free, so that it may be conveyed to a distance before reaching the ground. The development of flattened wings upon seeds or fruits is closely analogous. Examples in the case of winged seeds are seen in the Bignoniaceae (Fig. 248), and of winged fruits in the Elm, Ash or Sycamore (Fig. 249). It is noteworthy that winged seeds and fruits are most common where the plants that bear them are of some stature, or are climbers ; so that they have to fall a considerable distance. The wind has thus a chance of scattering them far and wide.

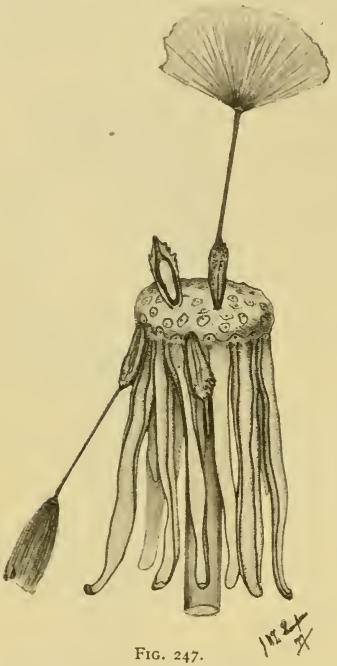

Fig. 247.

Fruit of Dandelion, with pappus as parachute. Note the absence of bracteoles on the general receptacle.

For large seeds a more effective means of transit is by water, which in commerce is a very efficient method for goods generally. Given a movement of water and a floating seed or fruit, dispersal is easy. The Water Lily is an example. The large berry ripens under water. It there splits, and the coherent mass of seeds, each with bubbles held in its aril, floats to the surface. There the seeds separate, drifting about till the bubbles are liberated by the decay of the aril. The seeds thus dispersed then sink. More striking examples are seen in littoral or estuarine plants, of which the seeds or fruits are often very large : for provided they float the size is immaterial. In *Barringtonia* (Myrtaceae), *Scaevola* (Goodeniaceae), and *Heritiera* (Sterculiaceae), which are all estuarine plants, the relatively large fruits have a fibrous

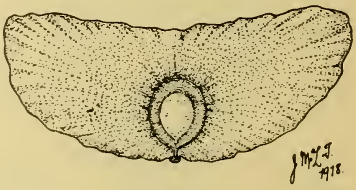

Fig. 248.

Winged seed of one of the Bignoniaceae. (Reduced.)

fruit-coat (pericarp), with air-spaces. Their large fruits can thus be easily floated away as they drop, by a stream or by tides. But extreme cases are seen in *Nipa*, *Cocos*, and *Lodoicea*, all of them littoral and estuarine Palms. Their fruits have fibrous husks with air-chambers, and this serves to float them. Each contains a single seed. Those of *Lodoicea*, the Double Coconut of the Seychelles, are the largest known. They may be carried long distances by ocean currents.

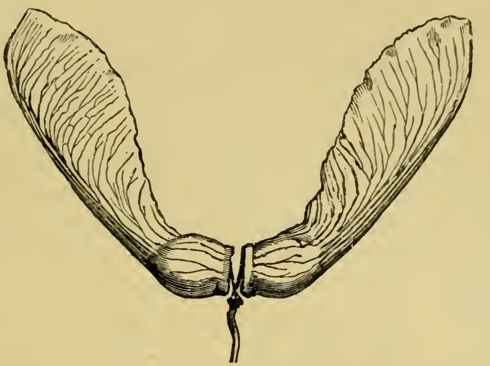

FIG. 249.
Samara, or winged fruit of Sycamore, dividing into two. (After Figuier.)

FIG. 250.
Fruiting annual plants of *Salsola*, caught at a wire fence, as they were rolled by wind over level sand, on the coast near Adelaide, Australia.

Some plants show curvatures of the fruit-stalk, or of the shoot generally, which aid in the dissemination, or even in the exact deposit of the seeds. The fruit-stalk of the Ivy-leaved Toad-flax may be seen to direct its fruit to the crannies of the rock or wall in which it grows, so that its seeds are shed directly on the spot suitable for their germination. Some denizens of arid soil curl up their branches as they dry into a sphere, which when detached may be rolled great distances by the wind over flat ground, scattering their seeds as they go. This is seen in the "Rose of Jericho" and in the Grass, *Spinifex*. It is shown graphically in a species of *Salsola* which grows on the coast near Adelaide (Fig. 250).

Dissemination by Animals.

In various ways Plants may make use of the free movements of *animals*, which while serving their own ends become the involuntary agents of dispersal. The living seeds may be conveyed by them *externally*, attached to their coats or other parts of their bodies: or *internally*, as ingested food: or they may be actually carried by them intentionally. For the first no special development is actually necessary in the seed or fruit. They may stick to the feet of animals clogged with mud, especially birds. Darwin removed the soil from the foot of an injured partridge, and obtained from it no less than 82 seedlings. But many fruits and seeds are provided with means of attachment; where the seeds are small, a sticky glandular secretion may serve, as in some Salvias. But many fruits develop as "burrs," being provided with hooks of various origin, which attach them to fur or feathers. In the Burdock the tips of the bracts are hooked: in *Bidens* spines representing the calyx bear reflexed teeth (Fig. 251, *E*): in Cleavers (*B*), or the Carrot there are hooked emergences on the wall of the inferior ovary: in the "*Echinella*" section of the

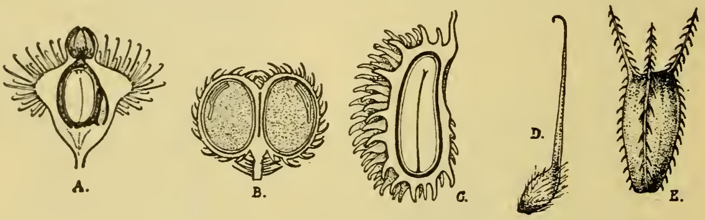

Fig. 251.
Fruits with hooked outgrowths, effective in transfer by animals. *A*=*Agrimonia* (Le Maout.) *B*=*Galium* (Le Maout). *C*=*Cynoglossum*. *D*=*Geum*. *E*=*Bidens*.

Buttercups, or in the Hounds-tongue (*Cynoglossum*) (*C*) they are on the superior achene: in the Water Avens (*Geum rivale*) (*D*) a single hook is formed half way up the style of each carpel. Such instances taken from different families, and involving quite different parts, show that these effective developments have originated repeatedly, and independently of one another.

A second and more prevalent means of dispersal is *internally*, as ingested food. It is secured by development of succulent tissues in close relation to the seeds. Here it is found that most diverse parts are involved, even in nearly related plants. Pulpy fruits occur in almost every family; even among the Grasses, which have characteristic dry grains, certain Bamboos bear a succulent fruit. The pulpy tissue often involves the whole carpellary wall, and the seeds are embedded in it: this is the case in the berries of the Grape, or Currant, the one being a superior the other an inferior ovary (Fig. 252). Or it may be only the outer part of the wall that is pulpy, while the inner is stony, as in the drupe of Cherries or Plums (Fig. 253). Sometimes parts other than the pistil itself may be involved, for instance the receptacle may be convex, and succulent, and bear the dry achenes (which are the true fruits in the restricted sense) upon its surface, as in the Strawberry (Fig. 254). Or it may be concave, and the achenes be borne within its hollow cavity, as in the "hip" of the Rose. In the Fig it is the massive axis of the condensed inflorescence that

FIG. 252.

Berries of the Currant. (After Figuier.)

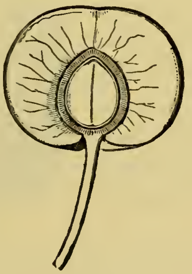

FIG. 253.

Drupe of Cherry. (After Figuier.)

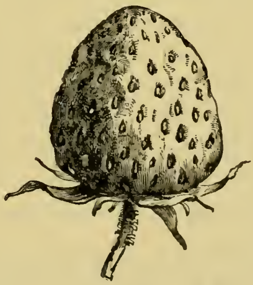

FIG. 254.

Succulent receptacle of Strawberry. (After Figuier.)

becomes concave and pulpy, while the achenes produced by the numerous flowers are contained within it (Fig. 255). Lastly, the perianth may be persistent, as it is in each of the aggregated flowers of the Mulberry, and becoming pulpy they embed the true fruits, which are achenes (Fig. 256). It is needless to multiply instances. Those quoted suffice to show how various are the parts that offer attractions by their succulent development to fruit-eating animals. Colour, scent, flavour and organic content, all attract them to these fruits as food. In the haste of feeding they do not exclude, but bolt the seeds, which may thus be carried by them internally to a distance before being voided with their *excreta.*

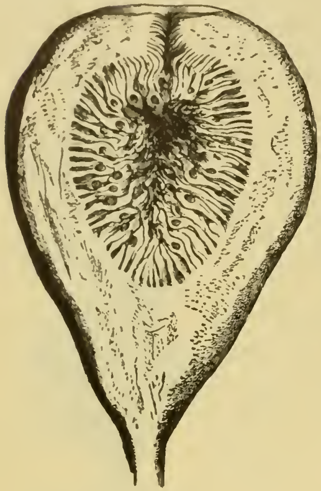

FIG. 255.
Succulent hollowed axis of the inflorescence of the Fig, bearing achenes within. (After Figuier.)

In these cases the animal is an unwitting agent. Another method, less effective but still to be reckoned with, is by means of intentional transfer of fruits or seeds for the animal's own purposes. Squirrels, some birds, and ants hoard stores of food in the form of nuts, etc.; sometimes the store is not fully exhausted, so that the live seeds germinate apart from the parent plant. But more exact results come where masses of esculent tissue, often containing oil, occur on the surface of the seed, in the form of caruncles, as in the Violaceae, Euphorbiaceae (Fig. 479, vii.-viii., Appendix A), and Leguminosae. Observations have been made on the actual transfer of the seeds of Gorse by ants, and the spread of that plant on certain moor-lands can be definitely ascribed to this agency.

FIG. 256.
A "Mulberry" composed of many flowers, whose succulent perianths enclose each a dry achene. (After Figuier.)

Lastly, man himself is the most potent agent in the distribution of plants, though his influence is as often destructive as constructive. He consciously introduces plants of economic value to new areas, and clears off the native flora to make way for their cultivation. But he also unconsciously carries with him the seeds of certain plants, which appear as " weeds " wherever he goes. The

Nettle, the Shepherd's Purse, and the greater Plantain are the commonest of these.

All such means for the dissemination of seeds as those described are to be held as offsets to the limitation imposed upon plants by their fixity of position. They are themselves immobile, as are also their seeds; but a spread of their seeds is essential for the survival of a species, or its spread to new stations. The measure of its success may be illustrated by a few examples. Darwin remarks that no cultivated plant has run wild on so enormous a scale as the Cardoon Thistle (*Cynara carduncculus*), introduced from Spain to La Plata. It has spread so as to cover large areas to the exclusion of other plants. Its "pappus" carries its fruits down the wind, after the manner of other Composites, and its spread shows the effectiveness of the method. A more recent example is that of *Lantana aculeata*, a native of Mexico, which was introduced into Ceylon as a garden plant in 1828, and has since spread all over the island, taking up waste land to the exclusion of other plants. It is spread by birds, which eat its pulpy fruits. Where forest fires occur in Canada the "Fireweed" (*Epilobium angustifolium*) at once occupies the cleared ground. It reaches the sterilised surface by its light seeds being supported in the wind by superficial hairs. A census was made some years ago of plants found growing in humus borne on the stumps of pollard Willows near Cambridge. The seeds or fruits from which they sprang would have had to be raised about eight feet above the ground. Of the total of nearly 4000 records, 44.62 p.c. were plants with fleshy fruits, 25.18 p.c. had winged or feathered fruits or seeds, 16.47 p.c. had burred fruits, 10.75 p.c. had seeds so light or small as to be easily wind-borne. Thus the presence of all the plants observed upon the stumps, excepting about 3 p.c., is accounted for by recognised methods of seed-dispersal. Such examples show the practical results of transport of seeds by the methods described, and give some idea also of the rapidity of their effects.

An experiment on the grand scale was made in the formation of a completely new Flora of the Island of Krakatau, and fortunately its results were followed by competent observers, who kept careful records. These form the best authenticated story of the natural formation of a plant-population in an area where none was living before. Up to 1883 the islands forming the small group in the Sunda Strait between Java and Sumatra, of which Krakatau is the largest, were covered by dense vegetation. From May to August of that year successive volcanic eruptions resulted in the complete sterilisation of the surface, which was covered with hot stones and ashes. Thus, on cooling an uninhabited desert was exposed, lying at a distance of fully twelve miles from the nearest vegetation. Since then a new Flora has sprung up upon the islands. This has been studied at intervals. The late Dr. Treub, who visited Krakatau in 1886, concluded that the first colonists were blue-green Algae associated with Diatoms and Bacteria. These formed a suitable *nidus* for the spores of Mosses and Ferns, and for the seeds of Flowering Plants adapted for dispersal by winds. On the beach were found the fruits and seeds of Flowering Plants carried by water, some of which had germinated ; many of them belonged to the characteristic strand-flora of the Malay region. But the plants introduced by animals or by man were not found by him on this visit, which took place only three years after the eruption. In 1897 Penzig visited the island, and estimated that of the Flowering Plants noted 60.39 p.c. had reached it by ocean currents, 32.07 p.c. by wind agency, and only 7.54 p.c. had been transported by fruit-eating animals and man. On a subsequent visit by a party of botanists in 1906, the results as stated by Ernst show that though these proportions for Flowering Plants were not exactly maintained, still the largest number were borne by water-transit, and the smallest by animal agency. Thus for an oceanic island the most effective agency of transit is water ; wind-carriage takes a middle place, and transit by animal agency is the least effective of the three. These are the results which would naturally have been anticipated.

PLANT-POPULATION.

A very important factor in the maintenance and spread of a species is the actual number of germs produced. The third Chapter of Darwin's *Origin of Species* deals with the geometrical ratio of increase of living things. Following Malthus he there points out that there is no exception to the rule that every organic being increases at so high a rate that, if not destroyed, the earth would soon be covered by the progeny of a single pair. Linnaeus had already calculated that if an annual plant produced only two seeds, and their seedlings next year produced two, and so on, then in twenty years there would be a million plants. This is, however, a very slow rate of breeding. The following table gives the results of careful computation by Kerner of the number of seeds produced in a single season by an average specimen of each :

Henbane (*Hyoscyamus niger*) - - -	10,000
Radish (*Raphanus Raphanistrum*) - -	12,000
Plantain (*Plantago major*) - - - -	14,000
Shepherd's Purse (*Capsella Bursa-pastoris*) -	64,000
Fleabane (*Erigeron canadense*) - - -	120,000
Tobacco (*Nicotiana Tabacum*) - - -	360,000
Flixweed (*Sisymbrium Sophia*) - - -	730,000

The Orchidaceae are extreme cases of productivity: the estimates of seed-production in them are as follows:

	Per Capsule.	Per Plant.
Cephalanthera	6020	24,080
Orchis maculata	6200	186,300
Acropera	371,250	74,000,000
Maxillaria	1,756,440	

Such figures convey little more than a general impression of vastness: but evidently the number of germs produced is far in excess of the actual requirement to make up directly for losses by death. There is in fact an immense margin, which may be regarded as a very efficient reserve to meet all the contingencies involved in the establishment of the germ till it reaches propagative maturity. Such a reserve is necessary, for the risks of youth are great. Many seeds fall victims to the predatory attacks of animals, which naturally divert to their own uses the food-stores laid by for the germ. Many never reach a situation fit for their germination. Many young plants are killed off almost at once by unfavourable conditions, such as unsuitable temperature, or drought, or unseasonable changes while in the defenceless condition of the seedling. Competition with the same or other races of plants destroys others. Fungal attack also takes its toll, and especially in the seedling state. But notwithstanding the number, and insistence of these risks, an overplus remains in any surviving species. This not only keeps the race in being, but in most cases provides for its spread into fresh areas, where, however, it is liable to be checked by various limiting factors. Moreover, the large numbers, and the competition which necessarily follows, provide material for Natural Selection to work upon: and it is the fittest that will be the most likely to survive.

On the other hand, carefully recorded cases under the favoured conditions of cultivation illustrate how prolific plants may be, even where the productivity in number of seeds is not specially high. A good example is seen in the "Marquis" Wheat, which was derived from a single head in 1903, as a result of hybridisation. It has since been spread through Canada and the United States. In 1918 it was sown on 20,000,000 acres of land, and yielded some 300,000,000 bushels of grain. So wonderful a result in a cultivated plant under control, in a limited number of years, illustrates the effect of a geometrical ratio of increase, such as might often be possible in Nature, if the circumstances were equally favourable.

LATENT PERIOD.

After seeds are shed and distributed they usually undergo a *period of rest.* During the autumn and winter of temperate climates they become buried in the soil. They naturally fall into chinks and crannies, and are often covered by rotting leaves; they are also washed into the soil by rain, or drawn below by the restless activity of earthworms, or covered by their castings. But some work their own way into the soil by hygroscopic movements, as in *Avena*, or *Stipa*, or *Erodium.* A few even bury their fruits as they mature by geotropic curvature of the fruiting stalk, as in the Earth-nut (*Arachis*), or the subterranean Clover. In one way or another they become covered, and in the dormant season there is plenty of time for the process.

A latent or resting period is commonly determined by climatic conditions of drought in the tropics, or of cold in temperate climates. But a latent period may be self-induced, in which case the seeds will not germinate till after a period of rest. In this respect seeds vary. Some will germinate immediately they are matured if the conditions are favourable. It is this that makes the difficulty with cereal crops in a warm, wet autumn: for those conditions stimulate immediate germination, and the grain is liable to sprout in the stook before it can be harvested. But as a rule a period of rest follows on ripening. The seed dries out, and in that state it remains stationary, but retains its vitality, being specially resistant to extremes of drought and heat. Examples of an obligatory resting period have been quoted in Chapter IX., p. 140. If such seeds are collected in autumn, and exposed to conditions favourable for germination, they remain passive till the spring, when they will germinate almost simultaneously. Other plants again have, in addition to seeds that germinate in the first year, other seeds which require a longer rest: Laburnum, wild Mignonette, and field Clover are stated to be among these, while the Cockleburr (*Xanthium*), with its two fused fruits, is also said to germinate one in the first, the other in a later season.

Akin to such questions is that of the length of time during which seeds can retain their vitality. This varies in the individuals of any sample of seeds saved under apparently uniform circumstances. As the period is lengthened the proportion of seeds that germinate diminishes. Oily seeds retain their vitality a shorter time than starchy seeds; and those kept dry retain it longer than those kept damp. But to extend this possibility of survival to the so-called "mummy-wheat" is too long a step to seem probable. A. de Candolle, after examining the evidence up to 1882, concluded that no grain taken from an ancient Egyptian sarcophagus and sown by horticulturalists has ever been known to germinate : nor is there any trustworthy evidence up to the present date. The condition of grains known to have been taken from mummies is as though they were charred, and the germ perished. On the other hand, seeds of *Nelumbium* from Sir Hans Sloane's collection were germinated by Robert Brown after being dry for at least 120 years.

Low temperature arrests physiological activity : but Brown and Escombe showed that the vitality of seeds is not destroyed by exposure even to extremes of cold. They submitted seeds of twelve plants of different affinities to a temperature varying from 183 to 193 degrees below zero centigrade, for over 100 hours. As a result their powers of germination showed no appreciable difference and they produced healthy plants.

CYCLE OF LIFE.

The germination of the seed, and the re-establishment of the sporophyte as its result, completes the normal cycle of life of the Flowering Plant. The leading incidents of that cycle may be represented by a diagram, which will serve later as a means of ready comparison with types of vegetation lower in the scale (Fig. 257). It will be found in them all that the leading events succeed one another in a sequence that is uniform, however different the details may appear. Two critical points in the cycle are marked by the fact that the individual life is there presented in each case by a single cell. They are the *Spore* and the *Zygote* : the former follows on reduction, and

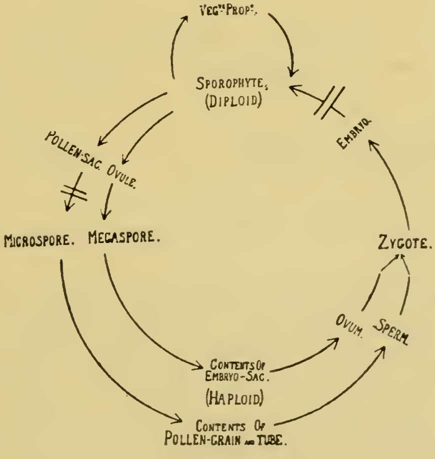

FIG. 257.

is haploid; the latter results from fertilisation, and is diploid. Between these, and derived respectively from them, are two phases of cellular amplification, each forming a soma, or plant-body. The one is the *Sporophyte*, or rooted plant, which springs from the Zygote, and is diploid; the other is rudimentary in the Flowering Plants, though it is more fully represented in lower forms. It is initiated by the haploid spore, and is itself haploid. It consists here of only a few cells contained on the one hand in the embryo-sac, on the other in the pollen-grain and tube. It is called the *Gametophyte*. These two phases together constitute the alternating Cycle of Life of the Flowering Plant, which thus shows vestigial relics of an *Alternation of Generations*.

This succession of events may often be obscured by vegetative propagation, by means of buds originated in various ways. But, as shown in Chapter XIII., this is a mere process of extension, or repetition of the individual sporophyte. It appears as though it extended the cycle, but it does not really introduce any new feature. It may be fitly represented as a supplementary cycle outside the main diagram (Fig. 257).

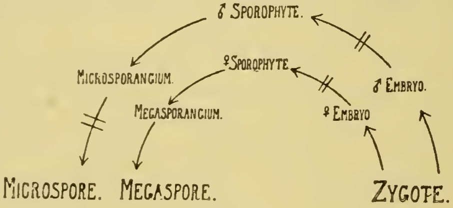

Fig. 258.

The doubling of part of the main cycle indicates sex-differentiation, the male and female developments running parallel. This is a feature which is very prominent in Flowering Plants, and for them the cycle is thus doubled for about three-quarters of its extent It will be found on applying a similar method successively to plants lower in the scale that in them the sexual differentiation becomes progressively a less marked feature. But meanwhile it is important to note that the extent of this differentiation is not itself constant in Flowering Plants. In certain plants the flowers are hermaphrodite, as in the Buttercup. The diagram as in Fig. 257 applies to such cases. The sex-differentiation appears in them only on formation of the pollen-sacs and ovules, which are in the same flower. But in others the plant is itself either male or female, and the species dioecious, as in the Willow. This condition may be represented by an amended diagram (Fig. 258). For us here the point of importance is this. That the stage at which difference of sex is first recognisable in the individual life is not fixed for all Flowering Plants. In hermaphrodite plants it appears only in the several organs of the individual flower. In dioecious plants the difference extends to the whole sporophyte plant. These observations will be of value for comparison with forms lower in the scale of vegetation. But such questions cannot be fully treated till these organisms have been described. Nor can the origin and real nature of that complex body, the seed, be properly understood till it can be examined comparatively. A knowledge of the propagative methods of more primitive plants must first be acquired; and the comparisons which follow from it will be taken later (Chapter XXXIV., p. 543).

CHAPTER XX.

EVOLUTION, HOMOPLASY, ANALOGY, AND HOMOLOGY.

In the preceding pages the Higher Plants have been described with only occasional allusion to organisms which, being simpler in their structure and mode of life, are placed lower in the scale of the Vegetable Kingdom. In taking the Highest Plants first, a similar sequence has been followed to that which has ruled in the development of the Science itself, as its history plainly shows. It was natural that the earlier observers should direct their attention to those plants which were most obvious, and seemed to them to be the most useful and common. Consequently the structure of the science was founded at first upon observation of Flowering Plants. Later, when botanists began to examine smaller and simpler organisms, the tendency was to interpret them in terms of the Higher Plants. But this procedure is a practical inversion of the course which the real history of the Vegetable Kingdom is now believed to have taken. Comparison of the simpler organisms with the more complex has led with ever increasing certainty to the conclusion that the latter were derived by Descent from the former. The simpler organisms are now held to represent types such as appeared earlier upon the Earth. The more complex types, on the other hand, are held to have been derived from ancestors simpler than themselves, and to have been later in their origin. This being the view generally entertained, it will be well for us to break off for the moment from the discussion of the higher forms, and to set back to those lowest in the scale. By doing so, and then by proceeding gradually to those which are more complex, it will be possible to trace in general those lines along which Evolution appears to have progressed in producing the Higher Forms of Vegetation.

While we thus consciously adopt the general conclusion that the origin of the various forms of Plant-Life was by gradual Evolution through long ages of Descent, it must be clearly understood that this is nothing more than a theory. Evolutionary History as a whole is not, and cannot be, a result of actual demonstration. It has not been possible to produce detailed proof of the evolutionary history of any wild species, or genus, whatever the probability may seem to be as to the source from which it sprang. But so many facts can be explained by the *theory of Evolution* that it is now generally accepted as giving the most intelligible account of the probable origin of the Organic World as we see it.

The evidence upon which its probability rests, is derived (i.) from *Comparisons* based on external form and internal structure : (ii.) from a study of the Ontogeny, which means the history of development of the individual from the egg to the adult : (iii.) from *Palaeontology*, which means the study of fossils in their stratigraphical sequence : this demonstrates their Distribution in Time : and (iv.) from the evidence given by the *Geographical Distribution* of organisms upon the Earth's surface at the present day. If the theory be true, the results derived from these several methods of enquiry should coincide, and that coincidence should apply not only for Plants, but for the Animal Kingdom as well. It is the high degree of coincidence seen in the evidence derived from all of these sources, for the two Kingdoms of Living Beings, which has led to the general acceptance of a Theory of Evolution.

The facts of *Variation* and of *Heredity* constitute the basis upon which Evolution is believed to have worked. In Plants, as in Animals, the offspring shows a general resemblance to the parents. But that resemblance, however close, is not exact. The *individual variations from type* may be greater or less : often they are very slight indeed. They differ also in respect of their hereditary transmission to a succeeding generation. Some are not transmitted, so far as present evidence goes, and consequently they are not available in Evolution. These are called *Fluctuating Variations* or *Modifications*. Others are evidently heritable and are transmitted to the offspring ; these are called *Mutations*. The problem of variation is dealt with more fully in Chapter XXXV. In the meantime it may be noted that any process in Nature that would bring about a summing together or accumulation of the heritable differences which exist would tend to establish in the race such differences as characterise species, genera, and successively larger groups. Such a process is found to be actually at work in *Natural Selection*. It produces its effect by *rejection of the less fit, and survival of the fittest.* Its recognition as a feature affecting all wild life was a novel factor introduced into Biological Science by Darwin.

The efficiency of Natural Selection as a means of accumulating new characters depends upon the fact that the production of germs is carried on at a higher rate than would suffice simply to restore losses by death. This has already been shown for Flowering Plants in Chapter XIX., p. 332, where extreme cases of prolific propagation have been quoted. The lower organisms as a rule reproduce prolifically also, and often with extreme rapidity. An overplus of young individuals is indeed a general feature of plant-life. Since each of the offspring is normally capable of reproducing as prolifically as the parent, if all came to maturity the numerical increase would be in a geometrical *ratio.* But all of the individuals produced do not and cannot come to maturity, so as again to propagate their species. There could never be room or opportunity for nutrition of them all upon the earth's surface. Their number leads to a competitive *struggle for existence.* In ordinary vegetation the number of established plants remains approximately constant in any given area as the result of that struggle. If this be so, the average mortality of the offspring of an annual would involve all of the germs of each season but one : and in the case of perennials only a fraction of that number of survivors would come to functional maturity. It is upon the enormous overplus of individuals produced that Natural Selection works. The most likely to survive are the strongest, or those which present some favourable variation from type. Those that are weaker or less suited to their environment are the more likely to succumb. The result of Natural Selection will therefore be the *Survival of the Fittest* together with *the perpetuation of favourable variations from type.*

A special *Mechanism of Heredity* is shown to exist by the facts of sexual reproduction, as seen in the higher types both of Plants and of Animals. Such reproduction is referable to the sexual cells alone. In Flowering Plants it has already been seen that the new individual, with all its characteristics of structure and function, is derived from the ovum fertilised by the male gamete. These cells must then be the bearers of all those characteristics which are transmitted from the parent to the offspring. For the maturing of the sexual cells, and the part which their nuclei are believed to take in the segregation, transmission, and distribution of hereditary features, reference must be made to Chapter XXXV., where the details of the chromosome-cycle are given for the Higher Plants, together with a brief account of Mendelian segregation and its implications. Though the corresponding facts have not yet been recorded for the lower organisms with the same detail as for the higher, there is reason to believe that they are of general application wherever sexuality exists: for the details so far observed in the lower resemble closely those for the higher forms. The conclusion may then be applied generally *that the sexual cells are the bearers and the distributors of hereditary characters.*

But there are many simple organisms, often unicellular, in which no specialised phenomena of sex are known. They may show a multiplicity of forms ranked as genera and species, notwithstanding that they are sexless. This suggests that the absence of a specialised mechanism of heredity does not entail an absence of variation, nor even of the hereditary transmission of characters. Probably such simple organisms as these are really primitive. Sexual reproduction developed as a later condition and brought with it various advantages: among the most important is the orderly distribution of the hereditary characters (Chapter XXXV.). It thus appears that a Theory of Evolution is of general application to organisms higher or lower in the scale, and that it finds its true basis in the facts of variation. An essential feature is that certain structural variations are heritable. By Natural Selection these are sifted out, perpetuated, and even accumulated. Other factors may also be at work: but these are commonly held to be the most important. *The central problem of Evolution will therefore lie in the origin of those variations that are heritable: while the mechanism of their transmission to, or distribution among, the offspring naturally takes its place as accessory.*

Using some such evolutionary theory as a working basis, a succession of organisms may be passed in review, starting with those that are relatively simple and proceeding to those that are more complex. But in doing this it is necessary to remember that Evolution has not been a simple matter. Organic life has progressed along a great number of distinct Lines of Descent, which may have been divergent, parallel, or convergent as regards their characters. Moreover, while the progressions which may be traced will in the main be from simpler to more complicated states of organisation, the converse may sometimes be the case. It has been seen in Chapter XII. how parasitism in Flowering Plants, which in part or in whole relieves them of the function of self-nutrition, often leads to a reduction of the vegetative system. It has been noted that *Cuscuta* has dispensed with its foliage leaves as a consequence of its parasitism. An extreme case is seen in *Rafflesia* with its huge flower, while its absorbent vegetative system has been reduced almost to the level of that of parasitic Fungi (p. 227). Thus *a simpler structure may sometimes appear as a consequence of evolutionary changes, though in the great majority of cases evolution leads to greater complexity.* Such considerations as these must be borne in mind while examining and comparing organisms from an evolutionary point of view. Many other precautions are also necessary before Lines of Descent can be traced with any degree of probability. If we figure to ourselves the whole plan of Descent of Plants as a highly ramified tree, or group of trees, the great majority of living species would correspond only to the distal twigs, while their connections downwards to earlier branches, which represent their ancestry, are mostly wanting. At best they are suggested perhaps by a few isolated, archaic forms, or vaguely sketched in by occasional fossil remains of earlier time. It may even be a question whether there is really any connection downwards to a single trunk: for it is quite reasonable to suppose that the Evolution of the Vegetable Kingdom may have been not monophyletic, that is, along a single main line or *phylum*, but polyphyletic, that is, along a plurality of lines. Notwithstanding the uncertainty on points even so important as this, a belief in Evolution appears to be fully justified by the facts. Origin by Descent should therefore form the constant background to any intelligent comparison of living Plants when taken in progressive sequence, leading as it habitually would from those which are relatively simple to those which are more advanced.

Homoplasy.

In Chapter XI. (p. 193) special modifications of form which lead to successful life under special conditions have been designated *adaptations*. There is reason to believe that they have arisen in the course of Descent in relation to those conditions: in fact, that the plants which show them have been *adapted to their environment*. If two or more races of plants quite distinct from one another in Descent have developed independently under similar conditions, and been adapted thus to those conditions, a similarity of contour or of structure may be expected to result. A parallelism of development, or as it is called *Homoplasy*, would then be seen. Such similarities in distinct races would be described as *homoplastic*. Having been distinct in origin throughout, such similarities are clearly no real evidence of relationship of the plants which show them. A good example of this is seen in *Cactus* and *Euphorbia*, two genera widely apart in the System of Flowering Plants. Both of these genera show turgid succulence of the stem and reduction of their leaf-area as an adaptation to conditions of drought (Fig. 141). However similar to one another in vegetative structure such plants may appear to be, the difference of their floral characters shows that they are not really akin. Moreover, the succulent Cacti are characteristic of the American Continent and the Euphorbias of Africa. Thus both their floral structure and their distribution suggest that their vegetative resemblance indicates homoplasy. Similar arguments will apply to the climbing habit by means of twining stems or tendril-like leaves: to the spinous development of stems and leaves: to parasitism: to zygomorphy in vegetative shoots and in flowers: to gamopetaly and epigyny: and to many other familiar features that have been already noted in Flowering Plants. Such characteristics cannot safely be held as evidence in themselves of affinity of the plants which show them, since they may appear independently in plants otherwise quite distinct. They are often merely examples of Homoplasy. Such homoplasy, or parallel development, is thus a familiar fact in Flowering Plants. In the study of the lower organisms the observer should be prepared to meet with similar consequences of adaptation, resulting from a like accommodation to the same conditions of life in organisms not closely related by Descent. He should be willing to agree that in them also apparent similarity of characters may not be a sign of affinity, but only of homoplastic adaptation. Especially will this be so for the vegetative system, which is not so reliable a guide as the more stable organs of propagation. All parts are, in point of fact, subject to adaptation under the varied circumstances of life. Consequently it is not upon single characters, which may be only homoplastic adaptations, but upon *the sum of all the characters, external and internal*, that the affinity of plants, whether high or low in the scale, is to be judged. *This is the broad base upon which a Natural System of Classification should rest.*

Homology and Analogy.

The fact of widespread homoplastic adaptation makes it necessary to have some more reliable basis for the classification of the parts of the Plant than mere comparison of their external form or even of their internal structure. Such classification of parts must be based upon their origin, and upon the place which they take relatively to other parts at the time when they first appear. Following this method, *those parts of the individual, or of different individuals, species or genera, are distinguished as* homologous *which have the same relation to the whole plant-body, whatever their function or external conditions may be.* On the other hand, *parts may resemble one another in form or in function, though they may differ in their relation to the whole plant-body. Such parts are described as* analogous *one with another.*

FIG. 259.

Shoot of Butcher's Broom (*Ruscus aculeatus*) after Figuier. Note the small scale-leaves in the axils of which the flattened axes (phylloclades) arise; also the flowers arising from the surface of the phylloclades in the axils of other scale-leaves.

Examples of analogy of parts have already been noted : for instance, in those woody climbers which support themselves by reflexed hooks (Fig. 143). These hooks may actually be axillary buds (*Sageretia*, *Carissa*), or reflexed pinnae (*Desmoncus*), or recurved stipules (*Zizyphus*), or merely superficial prickles (*Lantana*, *Calamus*). Functional similarity in parts of diverse origin is seen also in tendrils, which may actually be axes (*Vitis*, *Bauhinia*), or leaf-blades (*Lathyrus aphaca*, Fig. 148), or distal parts of the leaf (*Cobaea*, *Vicia cracca*), or lateral appendages at the base of the leaf (*Smilax*). Again, spinous development may appear in stems (*Crataegus*), or leaves (*Berberis*), or stipules (*Acacia*), or in roots (*Acanthorhiza*). On the other hand, axillary buds may develop flattened and leaf-like, as in the "phylloclades" of *Ruscus* (Fig. 259). But their position, and the fact that they bear flowers proclaim their shoot-character, notwithstanding their leaf-like appearance. Such examples might be indefinitely multiplied, showing how common is homoplasy in parts that are only *analogous*, and not really comparable one with another in point of origin and position.

There may be various degrees of that closer correspondence of parts which would justify their being held as *homologous*. The strictest conception of homology is that designated *Homogeny*. Lankester defined as homogenous those structures which are genetically related in so far as they have a single representative in a common ancestor. This definition implies repetition of an individual part bearing a definite relation to the whole organism, just as the hand of a child repeats in position and in its qualities the hand of the mother. Clearly, in Plants with their continued embryology, the recognition of such individual correspondence is rarely possible. The indefiniteness in number of the appendages produced by any growing shoot precludes it. And yet the leaves of a shoot are comparable in other respects. Thus it is only in a less stringent sense than homogeny that the homology of the foliar appendages can be admitted in organisms which produce an acropetal succession of them as flowering plants do.

It may be suggested that the successive production of appendages on the growing axis of a plant finds its correlative in the "serial homology," or, as it has been called, the "homodynamy" seen in animals. But the "segments" of the animal body have not their counterpart in the plant-body. Attempts have been made, it is true, to reduce the shoot to an articulate series of constituent parts, each consisting of a portion of the axis bearing one or more appendages. But though it is possible to analyse some few shoots in this way, the method is not generally applicable, and the analysis itself bears evidence of its artificiality. It should be realised that the evolution of the Higher Animals and of the Higher Plants has pursued distinct lines. The two Kingdoms cannot be assumed to have adopted like methods of advance.

In Plants lower in the scale the categories of parts are less clearly defined than in the Higher Flowering Plants, and in the simplest types the several parts cannot be distinguished at all. This suggests that such categories of parts do not represent any essential plan of construction applicable to plants generally, but that they are consequences of progressive evolution in organisms that meet in a similar way the requirements of a life common to them all. It raises also the question whether on the one hand all the parts classed together, such as leaves, had really a common origin by Descent. There is reason to think that leaf-like bodies have originated separately in numerous distinct phyletic lines: for instance, among the Higher Algae, in the Bryophytes, and in Vascular Plants. In fact, while we group those parts that are held as homologous into certain morphological categories, such as leaf or axis, these are not to be held as definite or of universal application. They are rather to be regarded as being based upon such uniformity of result as has been achieved in Descent by various types of organisms. This view gives a true or evolutionary basis to the distinction between homology and analogy. Those parts are held to be "*homologous*" which had fallen *relatively early in Descent* into such relationships as characterise that category of parts to which they are referred: those are held to be only "*analogous*" which have undergone their specific modification *relatively late in Descent*, after the characters defining their morphological category had already been acquired.

MORPHOLOGICAL CATEGORIES OF PARTS.

Classifying the parts of the Higher Plants by the relations which they bear to the whole plant-body, and not merely according to function, they are found to fall into certain categories, and the parts so grouped together are held to be "homologous" one with another, whether they be borne on the same or on different individuals. The seedling plant consists of *Root* and *Shoot* (Figs. 2, 4). The primary shoot is the whole product of the plumule on germination, and the primary root is the product of the radicle of the seedling. Each of these parts is distinct from the other in origin and character, and each is capable of indefinite amplification and of the production of parts similar to itself. Since these regions of the plant are distinct in origin, and in their relation to the whole plant-body, no homology can be recognised between them or their parts. The distinction between these regions seen in the Phanerogamic seedling is of wide application. *Root and Shoot constitute the fundamental categories of parts seen in Vascular Plants, and to one or other of them all the parts of the vegetative system may be referred.*

The *Root* presents few morphological difficulties, its cylindrical shape being remarkably uniform. It has been shown in Chapter VI. how lateral roots originate endogenously and in acropetal succession on the main root. They repeat its characters, and these may be repeated again in roots successively of higher order. However complex the root-system may become, it is easily analysed, and all its branches are held as equally of root-nature and homologous.

The *Shoot* being both complex and variable in the relation of its parts, presents many morphological problems. The fundamental relations of its constituent parts, the *axis* and *leaf*, have been defined in Chapter V., p. 69. The relations of the vegetative and floral regions have been discussed in Chapter XIV., p. 277. Both are referred in origin to the "general-purposes-shoot," from which they are held to have been derived by a process of segregation. It may also be held that scale and foliage leaves, bracts and bracteoles, and the successive series of sepals, petals, stamens, and carpels are all types of foliar appendage borne upon the axis. They are all so far homologous that their relations to the axis which bears them are those already defined: for they arise as lateral outgrowths from the apical cone, springing from superficial and underlying tissues. They appear in acropetal succession, and do not as a rule repeat the characters of the axis which bears them. Their apparent differences depend upon the fact that they are specialised in their development to serve particular purposes in the plant.

The shoot, thus composed of a simple axis and leaves, is the unit from which even the most complex plant-bodies are built up. In carrying this out, the shoot-unit may be multiplied in three ways: (i) by axillary branching, (ii) by distal branching, and (iii) by adventitious buds.

The first (i), that is *axillary branching*, is the common type for Flowering Plants, a new apex being constituted in the angle between leaf and stem, and the new shoot repeating the characters of the original one (Figs. 5, 6).

The second (ii), viz. *distal branching*, arises from the apical cone above the youngest leaves and independently of them. It is not typical of the Higher Flowering Plants, but it is a marked feature in the Pteridophyta, and it is well seen in Lycopods and Ferns, and also in the Algae (Fig. 289). It commonly results in the formation of two equal shoots in place of one, by dichotomy. But various stages of inequality of the forking are found which lead from equal dichotomy to definite dominance of one shank over the other; so that a monopodial branching may result, where one shank takes a definite lead over the other, and actually precedes it in time. It is regarded as probable that an association of the weaker shank of a distal branching with the base of the next lower leaf may have been the actual source of axillary branching. In this case the two types of branching are not essentially different from one another, and both may be held as repetitions of the original shoot.

The third (iii), viz. *adventitious budding*, has already been described in Chapter XIII., p. 246. Whether produced naturally or artificially induced, the buds appear in abnormal position and number, and are not to be held as parts of the shoot-unit but as accessory, resulting from a new growth-stimulus. *Adventitious roots* may also be formed at various points on the shoot-system, but neither are they to be held as parts of it. Adventitious buds and roots may both be regarded merely as repetitions of parts by establishment of a new growth-stimulus at points which do not follow the usual sequence. The parts produced may be held as generally homologous with those which appear in the regular succession.

The leaf of Dicotyledons varies greatly in size and form. It is commonly described as consisting of *Lamina* and *Petiole*, with or without *stipules* (Chapter V.). While this treatment may be convenient in relation to its functional activity, it does not give any satisfactory morphological insight into the construction of the typical leaf of a Dicotyledon. It is in reality a simple *Rachis*, or a modified branch-system based on it. That this is so may often be clearly seen from the cutting of the margins of the blade, or in its venation (Figs. 260-3). The fact is, however, disguised by (1) the dorsiventral structure, which leads to the branches, or pinnae, being ranged in two lateral rows: (2) by the frequent condensation of the branches borne by the rachis into a coherent blade: and (3) by the intercalation in the course of its development of a petiole of greater or less length. In order to place the morphological treatment of a Dicotyledon leaf upon a rational basis the *rachis* should be distinguished from the *pinnae* and *stipules*, and these from the *pinnules*, or branches of higher order. It will then be seen that the axis bears to the rachis a like relation to that which the rachis bears to the pinnae, and, in doubly pinnate leaves, the pinnae to the pinnules (Figs. 260, 261). The construction of the whole

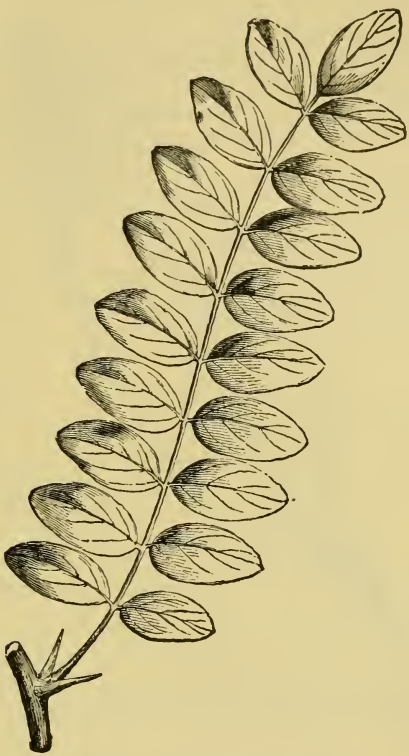

Fig. 260.
Pinnate leaf of *Robinia*, after Figuier.

Fig. 261.
Doubly pinnate leaf of *Gleditschia*, after Figuier.

shoot thus becomes intelligible, and comparison is facilitated with the stem and fronds of the Pteridosperms, Cycads, and Ferns, in which the leaf is obviously a branched system (Chapter XXXI.). Rachis, pinnae, and pinnules are in fact categories of parts of the shoot which rank naturally with the category of the axis itself. They all represent correlative grades in the branching of the shoot as a whole. But the distal branch-system of a leaf thus composed is so often greatly

Fig. 262.

Leaf of Sweet Chestnut (*Castanea vesca*), after Figuier. Here the fundamental pinnate branching is shown by the veins, but the whole is condensed into a coherent blade.

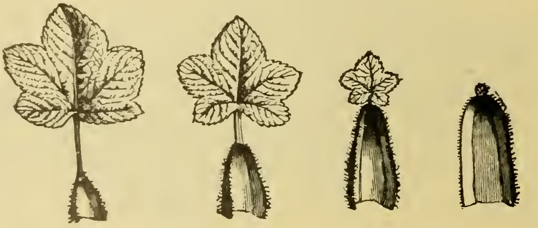

Fig. 263.

Stages of transition between scale and foliage leaf, in *Ribes*, after Figuier.

condensed, by marginal fusion of lobes and veins, that it appears collectively as a unit, and so it seems to justify its designation collectively as the " *lamina* " (Figs. 262-3).

Explanatory terms for the three regions, into which the leaf appears to be divided in many Dicotyledons, help in upholding this view of it as a branch-system. The rachis springs laterally from the stem : and three parts of it may be commonly distinguished by their form and function, as :

(1) The *hypo-rachis* or *leaf-base*, to which the stipules are attached, if present; though frequently there are none.

(2) The *meso-rachis* or *petiole*, which results from an extension of a middle region *intercalated* between the leaf-base and the blade. If the intercalation of the petiole begins above the extreme base the position of the stipules suggests that a first pair of pinnae had been left behind in the process.

(3) The *epi-rachis*, which embodies the whole of the distal branch-system. It is composed of lateral rows of potential pinnae, or of these either separate or fused in various degrees laterally, to form the flanges of a *coherent blade* or *lamina* (Figs. 260-3).

The value of such terms is that they fix the attention on the *branch-system as a whole*, though its branching may be obscured, or even absent in many flowering plants, especially where the leaves are small, and in the Monocotyledons (Fig. 264). A diverse development of the individual leaves of many Dicotyledons may accentuate the character of these three regions, even in the leaves of the same individual plant. For instance those of *Ribes* (Fig. 263) : for they are differentiated in form according to their function. To the left in the figure is the normal foliage leaf, with its sheathing base, its petiole, and its lamina, all present. In the leaf to the right the protective hypo-rachis is largely developed, and the other parts are vestigial : while the two middle figures show the petiole, or meso-rachis, in various degrees of *interpolation* between the other parts. Thus each region of the leaf may be specialised to perform its several functions : (1) bud protection, (2) adjustment of leaf-mosaic to avoid overshadowing, and (3) exposure of receptive surface for sunlight. But all three involve parts of one rachis.

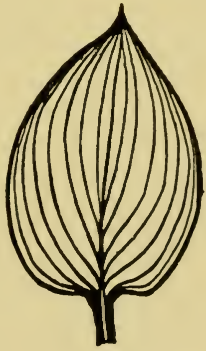

FIG. 264.

Funkia grandiflora, upper part of petiole and " iamnia". (Reduced after Mrs. Arber.)

The leaf of a typical Monocotyledon, such as *Funkia* (Fig. 264), presents a distinction of sheathing base and blade similar to that in many Dicotyledons. But the broad expanse of the latter originates not by fusion of pinnae, but by lateral expansion of mesophyll between the parallel veins of the distal part of the rachis, which is here unbranched. Thus we see that the blade of *Funkia* is not the developmental homologue of that of an ordinary Dicotyledon, but rather its analogue.

Doubts may thus arise as to the strict correspondence between leaves of Dicotyledons and Monocotyledons. But when we come to the leaves of Mosses and Liverworts any doubts of strict homology with those of Flowering Plants approach to a certainty. For they are parts of the gametophyte or haploid phase, not of the diploid sporophyte, and there is reason to believe that those two somatic phases have been distinct throughout Descent (Chapter XXX.). Further, any strict homology between the leaves of Vascular Plants and the leaf-like parts seen in highly organised Algae must be held as still more doubtful (Chapters XXI.-XXIII.). Before any such comparisons can be accepted as having strict morphological value, the argument must be based not on general preconceptions or surmises, but on the demonstration of similar evolutionary sequences, among organisms nearly related to one another. Hitherto this has not been done.

The truth seems to be (1) that in plants at large, whether in the sporophyte phase or in the gametophyte, advantage has been taken of the evolutionary development of lateral flattened surfaces, and their expansion as organs of photosynthesis; (2) that such development may have arisen either in the diploid or in the haploid soma: and (3) that it may have arisen independently along a plurality of evolutionary lines. In other words, *that the development of the category of leaves has been widely polyphyletic.*

Minor appendages, in the form of *Hairs* and *Emergences* are produced irregularly, and often in large numbers, scattered over the surfaces of the shoot. They may appear at any point on axis or leaf, and also on the surface of roots, as root-hairs (Figs. 56, 57, 60, 61, 68). The *Hair* is usually defined as a product of the epidermis only: but the *Emergence* as involving also the subjacent tissue. This is, however, an arbitrary distinction, though it separates roughly the more delicate from the coarser. As a morphological category hairs and emergences take a quite subsidiary place, and do not rank equally in position or constancy with the leading categories of axis, rachis, pinna, or pinnule.

The *sporangia* have been described for the Higher Flowering Plants in Chapters XV. and XVI.: those of Pteridophyta and Bryophyta in Chapters XXX. to XXXII. Our question will be, what relation do sporangia bear to the categories of the vegetative parts on which they may be seated. As regards the Higher Plants their origin has been from time to time referred to Metamorphosis of various parts of their vegetative system. But Von Goebel, in 1881, laid it down, on the basis of wide comparison with those plants lower in the Scale of Descent, that *Sporangia are organs* SUI GENERIS, *as much as are shoots and roots: and that they are not referable, through metamorphosis, to any other category of parts, whatever their position relatively to these.* That view may be generally adopted, and recent palaeontological discoveries have tended to confirm it. For instance the Bryophyta with their leafless sporogonia, have been traced back to the Carboniferous Period, while the Psilophytales, including the leafless *Hornea*

(Fig. 372A), belong to the Devonian Age. Both of these suggest that there is no need to call in "metamorphosis" to account for the early establishment of spore-bearing parts. These fossils show that *in them tetrad-division has been an earlier and more stable feature of the Hofmeisterian cycle than the evolution of leaves themselves.* (See Chapter XXXIV., p. 545.)

The sporangia of the Higher Plants vary in size, disposition and number. But however inconstant in these points, there is essential uniformity in the development of their contents, which when mature are represented by the pollen-grains (microspores) and the embryo-sac (or megaspore) (Chapters XV., XVI.). In either case a fundamental feature in their production is the *tetrad-division* of the spore-mother-cell. (See pp. 282-3, and 296-7.) This event involves *Meiosis*, and is inherent in spore-formation, not only in the Higher Flowering Plant but also in such of those lower in the scale as possess sexuality. In fact *syngamy* and *meiosis* may be regarded as correlated phenomena, which recur constantly, not only in the Higher Plants but also in those lower in the scale—as will be seen in Chapters XXI. to XXXIII. *This is in itself further evidence of the homology of sporangia at large.*

In the lower forms of vegetation, more clearly than in the specialised Flowering Plants, another category of parts is seen, viz. the *gametangia*, or sexual organs, which produce respectively the male and female sexual cells or *gametes*. In all but the most primitive plants the gametangia may be readily distinguished as male and female. The former are called *antheridia* and they produce *spermatozoids*, which are usually numerous from each; the latter are called *oogonia* or *archegonia*, and they produce one or more *eggs* respectively. The gametangia are described for the leading types of Pteridophyta and Thallophyta in Chapters XXI. to XXXIII. In the more primitive types, and particularly among the Algae, the gametangia are all alike: but in the more advanced they differ according as they are male or female. Hence it may be concluded that they are all homologous, though differentiated in relation to sex, and to the act of syngamy. The events of *syngamy* or fertilisation, and of *meiosis* or reduction appear as complementary features, alternating in the Hofmeisterian Cycle (Fig. 427). This is seen most obviously in the Archegoniatae (Chapters XXX. to XXXII.). In the Algae and Fungi it is less obvious, owing to their smaller size, and their more rudimentary sexual differentiation. On the other hand, in the Phanerogams the process of syngamy is obscured, partly by simplification of the parts directly involved in their subaerial fertilisation. Notwithstanding these differences, as seen in the whole evolutionary sequence, there can be little doubt of the *Homology of the sexual process in them all, and in the gametangia which produce the gametes themselves.*

The determination of all questions of homogeny, homology, and analogy must ultimately be based upon a knowledge of Descent. Until the phyletic lines for any series of plants are demonstrated the recognition of such relations of their parts cannot rest on more than carefully balanced opinion. A comparative examination of organisms *lower in the scale*, and ultimately a grouping of them into phyletic sequences, will therefore be necessary before a final basis can be found for the classification of their parts. The point of view from which their study is at present to be approached is that they will supply a basis, however imperfect, for such a classification. This will not only help to explain their own mutual relations, but also to illuminate the morphology and classification of plants higher in the scale of Vegetation. It is only by such comparative study that the details of the structure and propagation seen in the Higher Flowering Plants can be reasonably interpreted. In particular, the *Seed*, which is the most distinctive feature of the Higher Plants, cannot be properly understood unless it be shown by comparison with more primitive plants how that very complex body came into existence.

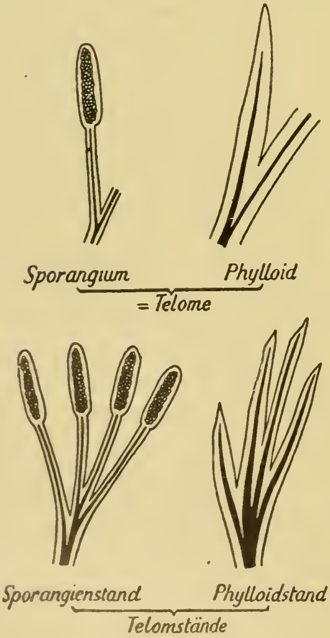

Fig. 264A.

Diagrams of "Telome und Telomstände," after Zimmermann; fertile to the left, sterile to the right.

TELOME.

The term "*Telome*" has been recently introduced by Zimmermann to connote a category additional to the parts of the sporophyte already recognised in this chapter as taking part in the organisation of cormophytic plants (see Zimmermann "Phylogenie der Pflanzen." Jena, 1930, pp. 58-70). The telome is associated specially with spore-production, and is in fact a primitive spore-producing organ, whether the individual be sterile or fertile. Its recognition tends to clarify the morphological analysis of plants of complex construction. But it is most readily recognised in certain ancient fossils of relatively simple form, such as the Psilophytales (Fig. 372A): while each sporogonium of a Bryophyte might also be held as an isolated telome (Fig. 352).

The fertile telome consists of a distal tract containing spores, seated on a stalk usually traversed by a vascular strand that conveys nutrition from below. Here as elsewhere the function of nutrition precedes spore-formation, hence the distal position of the fertile cyst, or sporangium. This biological succession of events underlies the scheme of development of all self-nourishing vegetation. It has been further suggested that the whole wealth of form that characterises living cormophytes may have been built up from such telome-units, by branching and general elaboration that has resulted in the vegetative system that bears the fertile region distally.

The detailed realisation of cumulative growth in producing from individual telomes complex bodies, such as are seen in the Higher Plants, has been imagined as yet, rather than demonstrated by actual developmental observation, or by comparison of successive stages of branching. And a vast amount of comparative study, of early fossils as well as of living plants, will be required before such an origin could be accepted as other than frankly speculative, rather than demonstrational.

DIVISION II.

THALLOPHYTA.

CHAPTER XXI.

THALLOPHYTA.

INTRODUCTORY.

THE Angiosperms have been described in some detail in the preceding Chapters. They form the chief constituent of the Flora of the Land, and are recognised as the highest types of Plant-Life. But the Gymnosperms, Pteridophyta, and Bryophyta are also prominent features in Land-Vegetation. For instance large areas are covered by Pine Forests: Ferns, Club-Mosses, and Horsetails are world-wide in their spread: and Mosses and Liverworts are present in quantity wherever there is sufficient moisture for them to flourish. These large Divisions of the Vegetable Kingdom are held to occupy a middle position between the highest and the lowest Plants. The consideration of them will, however, be held over for the present, until that residuum has been considered which remains after all of these have been excluded. The residuum comprises the *lowest and simplest of plant-organisms.* These are very numerous both in individuals, and in species and genera. Individually they are often small and inconspicuous, and many of them are dwellers in water. Nevertheless, on the basis of their nutrition and of the encystment of their cells they are properly ranked as Plants. They are collectively designated THALLOPHYTA, or thalloid Plants, since a general feature in them is the absence of that differentiation of the shoot into axis and leaf which is characteristic of the higher forms. They include the *Algae*, *Fungi*, and *Lichens.*

It must not be assumed that all the organisms thus grouped under the common head of Thallophyta are necessarily akin to one another. They are found to be naturally separable into distinct groups or *phyla*. The plants belonging to the several phyla may be so arranged as to show progress from simpler to more complex forms. Such sequences probably represent with some degree of accuracy *Lines of Descent*. Commonly the simpler terms of these distinct phyla are more alike than those which are more advanced. Thus the *Lines of Descent are divergent*, and the Thallophytes would therefore appear to represent a brush of phyletic lines radiating outwards from some simpler source. Though there is at present no trustworthy evidence that any of the Thallophyta now seen living have themselves achieved that highest development seen in the Land-Vegetation, many have advanced far in their evolution. In mere size the Brown Seaweeds include the gigantic Tangles, which are among the largest of living organisms. In complexity of propagative method no group of Plants shows more intricacy than the Red Seaweeds. In physiological resource the Fungi are the most diverse. But each of these includes simple types, which link up more easily with other classes of organisms than do the extremes. Each phylum appears to have worked out its own divergent line of advance independently of the rest. Some degree of parallelism in the progressions may then be anticipated, and is actually found to exist.

The readiest basis of distinction of these natural groups of Thallophyta is by colour. The most important cleavage is according to the presence or absence of chlorophyll, or of some of its derivatives. This separates the FUNGI, which have no chlorophyll or kindred colouring matters, from the ALGAE, which have. The Algae again fall into distinct groups on the basis of colour-difference. Those which have full green chlorophyll, such as is seen in Land-Vegetation, are designated the *Chlorophyceae*. Others are characterised by their olive green or brown colour, which is due to a mixture of pigments of which chlorophyll is one. It is characteristic of the Brown Tangles, or *Phaeophyceae*. A third series have a prevalent red colour also due to a mixture of pigments, which again includes chlorophyll, and they are called the *Rhodophyceae*, or Red Seaweeds. These colour-distinctions are not absolutely constant but, together with other characteristics, such as the nature of the flagella, or organs of propulsion of the motile stages, and the forms in which storage materials occur in the cells, they afford a true indication of the several distinct groups.

It may be objected that, while the Thallophytes are classified by colour, in Flowering Plants such differences were not taken into account in their classification. But in dealing with Organic Nature, which has progressed along individual lines, consistency of method in classification is not possible, if the grouping is to follow the course which evolution has apparently taken. The reason why the method adopted for Flowering Plants will not apply for the Thallophytes is that in the former the change to irregular nutrition happened late. The seed-bearing parasites are plainly Flowering Plants that have changed their mode of nutrition. But in the case of the Fungi we are dealing with a very ancient change. Fungi existed in the Palaeozoic Period. Thus their irregular nutrition will have influenced their development from very early times.

The colourings have a physiological meaning. The absence of chlorophyll indicates dependent nutrition, as in the Fungi. The colours distinctive of the three groups of Algae are related to photosynthesis. A brown or red tint makes self-nutrition possible deep down in sea-water. Speaking generally, the Red Seaweeds are prevalent at the lower levels while the Browns extend from the highest levels downwards, but stop short of the greater depths. The Greens are more widely diffused, but they occur mostly at the higher levels, and they are the prevalent Algae of fresh water.

If we accept this general view of the Thallophytes, it becomes a question whether there is any living group of organisms which represents approximately a source from which they may have originated. It is a very general opinion that such a source is to be found among the Flagellatae, a family which it is difficult to refer definitely either to the Kingdom of Animals or of Plants. It includes many of those organisms which cause certain diseases in man and other animals, and these are more definitely animal in their characters. But others, such as *Euglena*, possess features characteristic rather of Plants. *Euglena* is found commonly in summer, colouring the foul water that drains from manure heaps a bright green. The organism is then seen in the motile state, as a free-swimming, naked protoplast of elongated form, propelled by a single flagellum (Fig. 265). There is a central nucleus (*n*), several green-coloured chromatophores which vary according to the conditions (*ch*), a contractile vacuole (*v*), communicating by a canal or funnel with the exterior, and a red eye-spot or stigma lying at the junction of canal and vacuole. The flagellum passes downwards through the canal, and is attached by a branched base to the inner surface of the vacuole. In this state *Euglena* can feed itself by photosynthesis, but it probably obtains simultaneously some degree of saprophytic supply from the foul water in which it lives. When well nourished it may contain large paramylon bodies, but not starch. It multiplies by fission, the nucleus dividing first

(Fig. 266). When starved for a lengthened period an encysted form is assumed. The chromatophores diminish in size and colour, and storage materials appear in the contracted protoplasm, which is then surrounded by a thick wall (Fig. 265, *D*). In this state it can resist conditions that are adverse. But when these are favourable again the cyst germinates; its wall becomes mucilaginous; the

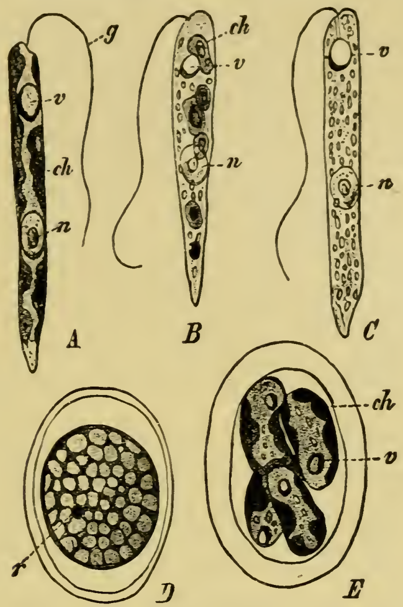

FIG. 265.

Euglena gracilis. *A*, Form with green chromatophores (*ch*); n=nucleus; v=vacuole and red eye-spot; g=flagellum. B=hemi-saprophytic form with small green chromatophores. C=colourless saprophytic form occurring in nutrient solutions, in absence of light. D=resting cyst of the form C: r=red eye-spot. E=germination of the resting cyst of the form A, by division into four daughter cells, which later escape. (After Zumstein.) (A, C × 630; B × 650; D, E × 1000.) (From Strasburger.)

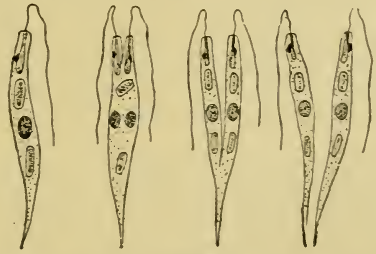

FIG. 266.

Successive stages of fission of *Euglena*: semi-diagrammatic.

contents usually divide into two or four (*E. gracilis*), or even more parts (*E. viridis*), which, after showing movement within the wall, are finally set free as naked protoplasts (*E.*). Some Flagellates show sexuality; this has been noted also for *Euglena*, but needs confirmation.

The common *Euglena viridis* does not grow well in spring water, but it flourishes in water containing organic impuruties. Probably photosynthesis is its chief mode of nutrition, but it can also act as a partial saprophyte. This is more clearly seen in *E. gracilis*, which has been shown to be either autotrophic or purely saprophytic according to circumstances. Fig. 265, *C*, shows the colourless form grown in the dark in a nutritive medium. The chromatophores are reduced to small pale plastids, but still the organism appears well nourished. This saprophytic type can then be restored to the autotrophic condition by exposure to light. It thus appears that certain Flagellates may temporarily or permanently make use of a saprophytic mode of nutrition.

Organisms which show characters so versatile suggest several distinct lines along which evolution is possible; and those lines if realised would give rise to features characteristic of the largest groups of living beings. The motile green form with the capacity for photosynthesis, if it becomes encysted, loses its motility while it achieves protection. The encysted form of *Euglena* after division of its protoplast is so like certain *Algae* allied to *Palmella* that it has been called the "*Palmella-state*." The resulting cells remain grouped for a time. If that state became permanent, and the divisions numerous, a cell-colony would be formed of a type characteristic for certain simple types of Plants. But the protoplasts of *Euglena* may after division escape and become motile again as primordial, that is naked cells, a condition which is seen repeated commonly in the propagative cells of Plants up to the Gymnosperms. *Thus the encysted state of Euglena suggests a possible mode of initiation of the encysted construction characteristic of Plant-Forms* (compare Chapter X.). *But most of them still retain the primitive primordial cell in reproduction.*

The saprophytic mode of life in *Euglena*—or parasitic, as it is in many other Flagellates, which are then independent of light and chlorophyll—suggests a distinctively animal existence. Here motility is retained, and encystment appears only as an occasional incident. This behaviour of *Euglena*, an organism in which sexuality has not hitherto been verified fully, indicates that the segregation of Animals and Plants may have antedated sexuality. But such ideas must not be taken for more than they are worth, since they raise questions which cannot be definitely answered. Nevertheless they are worthy of consideration as giving a point of view which will have its value in directing the study of the lower organisms, whether of the Animal or of the Vegetable Kingdoms.

The instability of nutritional method in *Euglena*—and especially its mixed nutrition, partly photosynthetic and partly saprophytic, as it grows strongly in foul water—finds its parallel in the mixed nutrition of many land-living Plants. It seems probable that irregular nutrition has been widespread, from very low forms such as *Euglena* to the highest Flowering Plants (Chapter XII.). At various points in the series the dependence upon physiological supply other than by photosynthesis may have been accentuated. The parasitic Seed-Plants, such as *Viscum* or *Cuscuta*, and the saprophytes, such as *Neottia* or *Monotropa*, are cases where it was adopted relatively late, in forms with their character already stamped as Seed-Plants. The various groups of Fungi are cases where the physiological dependence was established early, but after the encysted state had been definitely adopted. A similar segregation, but earlier still, with absence of encystment, would account for the establishment of the Animal Kingdom.

Such suggestions as these are based upon the actual facts observed in simple organisms referable to the Flagellatae. It may be uncertain whether or no these forms were or were not like the original sources from which Vegetable and Animal Life sprang. They serve, however, to give some idea of the possible origin and early relations of the larger groups of living organisms, and of their differentiation on the basis of nutrition, and of certain fundamental features of their structure. In point of habitat the significance of these comparisons cannot be mistaken ; for all these organisms are either aquatic, or at least they live where water is readily available. It has been concluded from this general fact that Life, whether of Animals or of Plants, originated in the water, and probably in the first instance in the water of the ocean itself. This is the position here adopted as a Working Hypothesis, to be accepted until it is disproved. In studying those few selected examples of the Thallophyta which it is possible to describe in this book, they will be held as illustrations of primitive Plant-Life. But the members of any definite natural affinity may be seriated, so as to illustrate progress from simpler to more complex conditions, and so it may be found possible, upon a basis of comparison —but always open to correction as new knowledge is acquired—

to trace the probable origin of many of those features which characterise organisms higher in the scale. For instance, by comparison of members of more than one natural sequence of living organisms, the suggestion is clearly given how differentiation of sex arose. This is only one instance of those illuminating consequences which follow from the comparative study of organisms lower in the scale with those which are more advanced. It is in fact upon the cumulative effect of such comparisons that it has been found possible to base a rational theory of Descent, applicable to Organic Life as a whole.

Towards the end of the last century Klebs called attention to the affinity between the *Flagellata* and the *Algae* : the view now generally held is that the old distinction between the two cannot be maintained. Indeed, from the botanical standpoint, it has been suggested that the term *Flagellata* should be discarded. The most primitive group of plants, the *Protophyta*, would then include both the flagellate and algal types of organisation, such characteristics as motility, the possession of a cell wall and sexual reproduction, having appeared at different stages in the evolution of the different Classes of this large and varied group.

CHAPTER XXII.

GREEN ALGAE (*CHLOROPHYCEAE*).

GREEN Algae are a heterogeneous assemblage of forms. Some are marine: others live in fresh water. Some are unicellular, some colonial (Chlorococcales, Volvocales): others, which are multicellular, consist of a simple filament, with various degrees of its branching (Ulotrichales); or they may form widened flat expansions (Ulvaceae): others again are coenocytic, not being partitioned into cells or only partially septate as in the Siphonales. A frequent feature is the enlargement of the chloroplast into a body often of complicated shape. One or more of these *chromatophores* may be present in the cell, and each may contain one or more highly refractive *pyrenoids*, spherical bodies which act as centres for the formation of starch. The variety of the form and structure of the plants is matched by the diversity of their propagation. Some multiply by simple fission (*Pleurococcus Naegelii*): others undergo conjugation of equal, non-motile cells (Conjugatae); but most of them produce motile zoospores produced in cells which may be called *sporangia*, and gametes produced in cells which may be called *gametangia*. The latter show in more than one natural series evidence of a progressive sexual differentiation (Ulotricales, Siphonales, Fig. 275). The effect of a general study of these Algae is to suggest that they may all represent steps in advance from the Protophyta; and that they contribute many distinct lines in which an increasing complexity of development of their encysted phase, and a differentiation of sex have been independently achieved. A few examples will be described which illustrate the great variety of structure and propagation that these plants show.

VOLVOCALES AND CHLOROCOCCALES.

The Volvocales include unicellular and colonial organisms which are typically motile throughout the vegetative phase or readily resort to the motile condition. In the simpler forms the individual consists of a single ciliated cell: in the more complex forms many such cells are aggregated together. The fact that the Volvocales are sometimes claimed by zoologists shows how closely the two Kingdoms are related by these primitive creatures. A simple example of them is seen in *Sphaerella* (*Haematococcus*) *pluvialis*, a unicellular organism frequent in water-butts and puddles (Fig. 267). Its motile stage is an oval cell (*A*) with a protoplast containing a large chromatophore, and several pyrenoids. It is surrounded by a mucilaginous cell-wall, through which two cilia project. It readily becomes encysted forming "Red-snow" in high latitudes, which is its "Palmella" stage. From this, after division (*B*), the contents escape as motile *zoospores*, which may grow and again divide. *Gametes* are formed by division of a mother-cell into 8, 16, or 32, which escape as motile *isogametes* all alike (*D*), and conjugate in pairs (*E*) to form encysted zygotes (*F*, *G*).

Chlamydomonas has a similar life-history. In some species sexual reproduction takes place by the fusion of isogametes whereas in others the gametes are of different size (*heterogametes*). In the latter a fertilisation of the larger female gamete (*egg*) by the smaller male gamete (*spermatozoid*) occurs. The zygote undergoes a reduction division on germination.

The sex-difference thus indicated in *Chlamydomonas* is much more marked in *Volvox globator*. This organism appears in ponds or pools of fresh water, in the form of hollow free-swimming spherical colonies (Fig. 268, *A*). Each is composed of a film of cells embedded in mucilaginous cell-walls, through which pairs of cilia protrude on the outer surface. The whole colony shows a slow rolling movement due to their activity. It propagates vegetatively by subdivision of certain larger cells, each forming a daughter-colony within the parent, which are set free by its disorganisation. A greater interest attaches to the sexual propagation. Large non-motile female cells (*eggs*) project into the cavity (*D*) and are there fertilised by minute motile *spermatazoids* produced by subdivision of antheridial cells (*B*). A thick-walled resting zygote is the result, which may germinate to form a new colony.

This series of members of the Volvocales illustrates steps in the origin of sex. In *Sphaerella* the gametes are all alike. In *Chlamydomonas* they are alike in some species, but unequal in others in point of size. In *Volvox* that inequality is more marked, and the behaviour of the large inactive egg is contrasted with that of the minute and

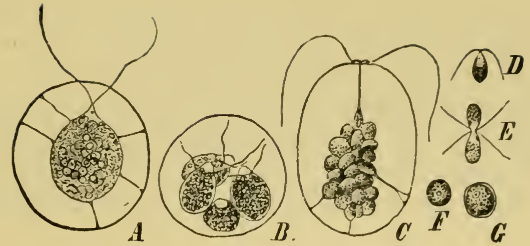

FIG. 267.

A, *B*, *Sphaerella* (*Haematoccus*) *pluvialis* (× 360); *A*, swarming cell ; *B*, formation of swarm-spores *C-G*, *Haematococcus Bütschlii* ; *C*, formation of gametes (× 400) ; *D*, gamete ; *E*, conjugation of two gametes ; *F*, *G*, zygotes (× 800). (*C-G*, after Blochmann, from Strasburger.)

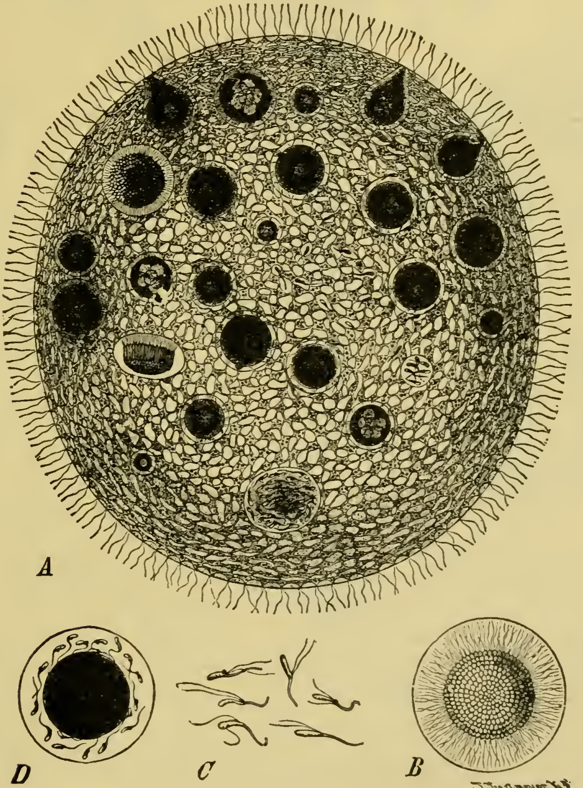

FIG. 268.

Volvox globator. *A*, colony showing various stages of development of ova and spermatozoids (× 165) ; *B*, bundle of spermatozoids formed by division of a single cell (× 530). *C*, spermatozoids (× 530). *D*, egg-cell surrounded by spermatozoids in the mucilaginous membrane (× 265). (After Cohn, from Strasburger.)

numerous motile spermatozoids. The series will be found to run parallel in these respects to those in other groups of Algae.

In organisms such as *Chlamydomonas* and *Sphaerella* there may be a brief, non-motile phase at the time of vegetative reproduction. In the Chlorococcales this non-motile phase tends to be prolonged, the zoosporic phase being of comparatively brief duration. The common soil alga, *Chlorococcum humicolum*, Fig. 269, consists of small spherical cells each with a cell wall, a parietal chloroplast and internal structure not unlike that of *Chlamydomonas*, except that the stigma and contractile vacuole are absent. This type of cell is typical of many of the Chlorococcales. On attaining a certain size, the protoplast undergoes a succession of divisions into 2, 4, 8, etc. parts; each part becomes ovoid in shape and develops two flagella. The retaining membrane is then ruptured and these naked zoospores are set free. After a period of movement, the flagella are withdrawn, a cell wall is formed, and a new *non-motile* vegetative phase is begun. The close assemblage of many zoospores may lead to the production of a green stratum consisting of closely addressed cells of irregular shape and unequal size. In some instances the swarmers behave as gametes, sometimes of unequal size, and these fuse together in pairs to form a spherical zygote which becomes a new individual. No cases of oogamy are known in this Order. Like the Volvocales, which are probably closely related, the Chlorococcales include both unicellular and

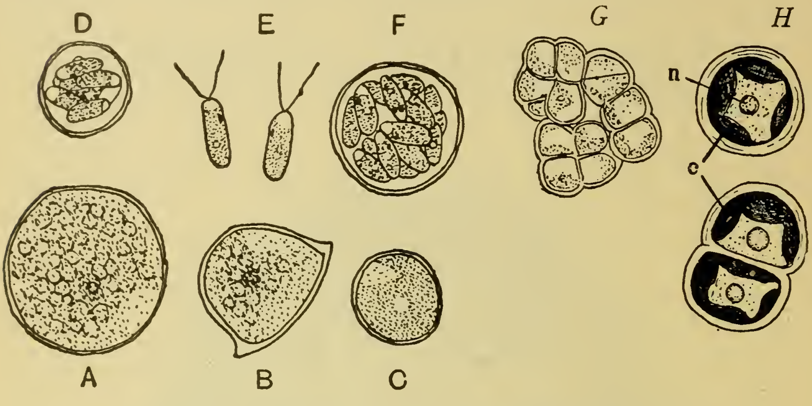

Fig. 269.

Left: *Chlorococcum humicolum*. *A-F*, various stages in the life-history. *A*, *B*, *C*, non-motile cells; *D*, *E*, *F*, motile stages (× 800). (From Chapman's, "An Introduction to the Study of Algae." Cambr. Univ. Press.)

Right: *Pleurococcus Naegelii* Chod. *H*, cell structure and division; *n*, nucleus: *c*, chloroplast. (After Fritsch and Salisbury.) *G*, packet of cells resulting from division. (After Chodat.)

colonial forms, the remarkable organism, the Water-net, *Hydrodictyon reticulatum*, representing the highest state of organisation in the Order.

The very common unicellular green alga, *Pleurococcus Naegelii*, Chod. (*Protococcus viridis*), Fig. 269, found as a green incrustation on the windward side of tree-trunks, walls, etc., was formerly placed in this group. It is now considered to be a very reduced member of a considerably more advanced group, the Chaetophoraceae. Multiplication is by cell-division, Fig. 269, no motile stage and no resting stage being known to occur.

ULOTRICHALES AND OEDOGONIALES.

These Algae show some advance in development of their plant-body, owing to repeated cell-division, the products of which remain associated together to form simple filaments, as in *Ulothrix* or *Oedogonium*; or the filaments may be branched, as in *Bulbochaete*; or flattened expansions may be formed, as in *Ulva* or *Enteromorpha*. The plants inhabit salt or fresh water, or may even grow in moist air, as *Hormidium* does. *Ulothrix*, which may be taken as a first example, is commonly found attached to stones washed by a quickly running stream: but some of its species are marine. The unbranched filament consists of a series of discoid cells, each with a zonal chloroplast, and it is attached by a basal rhizoid (Fig. 270, *A*). Its propagation though varied is rudimentary like its vegetative structure. Motile *zoospores* may be produced either singly from a cell, or by division of its contents; they escape through an opening of the cell-wall into

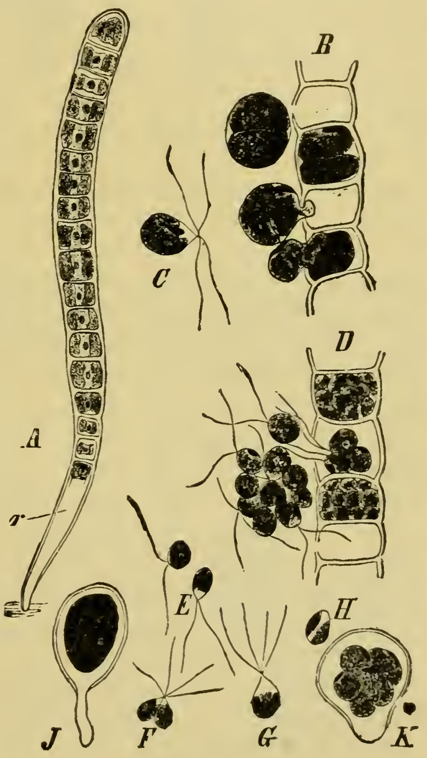

FIG. 270.

Ulothrix zonata. *A*, young filament with rhizoid *r* (× 300). *B*, portion of filament with zoospores escaping from a zoosporangium. *C*, single zoospores. *D*, formation and escape of gametes from a gametangium. *E* = gametes. *F* = conjugation. *G* = zygote. *H* = zygote. *J* = zygote after period of rest. *K* = zygote after division into zoospores. (After Dodel Port.) (*B*-*K* × 482.) (From Strasburger.)

the water (*B*). The cell which produces them may be called a *zoosporangium*. According to the number of the divisions the zoospores may differ in size. The large *macrozoospores* have each *four cilia* attached to the narrower end of its pear-shaped body (*C*); the smaller *microzoospores* have *four* or *two cilia*. After a period of movement, they settle, form a cell-wall, and affix themselves to some solid substratum: growing out transversely to their former axis and dividing, each may form a new filament. The *gametes* are also produced in a similar way, from a cell which may be called a *gametangium*: but their divisions are more numerous, their size smaller, and they bear only *two cilia* (*E*). The gametes, which are all alike in size and form, escape from the cells: if those from different filaments meet they coalesce in pairs, the result being a four-ciliate *zygote*, which soon loses its cilia, settles and forms a cell-wall. After a period of rest it germinates, the contents dividing, and escaping as zoospores, which grow into new filaments (*J*, *K*); the first division is a reduction-division.

Ulothrix takes a low place both as regards structure and propagative method. The differentiation of its sexual cells is imperfect. Not only is there no distinction of sex in the form of gametes, but occasionally the gametes may themselves germinate without fusion. They are strikingly similar in form and origin to the zoospores. The facts are in accord with the theory that fusion of gametes (*syngamy*) is a means of strengthening otherwise weak cells, which were originally organs of vegetative propagation.

Oedogonium and Bulbochaete are also filamentous Algae, but with more elaborate structure of their cells. Various species are very commonly found attached to stones or submerged parts of plants in quiet fresh water. Their cells are uninucleate, and contain a single reticulate chromatophore. They may be propagated by motile cells, or zoospores, which are formed from the whole content of a cell. Each escapes through a transverse slit in the wall into water, having an oval form, with a fringe of cilia round the colourless anterior end (Fig. 271, *A*, *B*). After a period of movement the zoospore settles, forms a cell-wall, and grows directly into a new individual. The plants are readily distributed by this means. The sexual organs of *Oedogonium* are antheridia and oogonia, which differ in size. The *oogonium* is a large barrel-shaped cell, containing a single egg. It opens at maturity by a transverse slit, as in the liberation of the zoospores; but the *ovum* remains *in situ*, and is motionless (Fig. 271, *C*, *D*). At the same time cells, of the same of of a separate filament, undergo repeated divisions to form short discoid cells, which are the *antheridia*. Each, on opening in the same way, sets free two *spermatozoids*, the result of division of its protoplast. They resemble the zoospores in form, but are smaller.

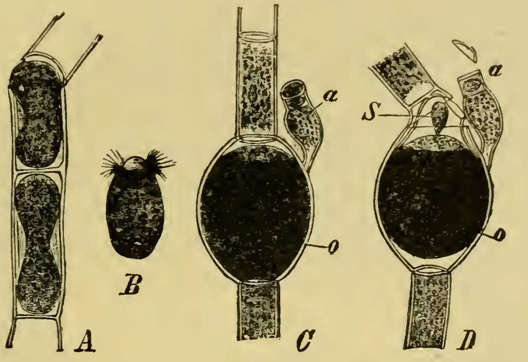

FIG. 271.

Oedogonium. *A* = escaping zoospores. *B* = free zoospore. *C* = sexual organs before fertilisation. *D* = in process of fertilisation. *O* = oogonia ; *a* = dwarf-males. *S* = spermatozoid. (After Pringsheim, from Strasburger.) (× 350.)

In some species special small plants (dwarf males) are produced from a special type of swarmer known as an *androspore*, these being produced singly within flat, discoid cells (*androsporangia*) which result from repeated transverse division of the filament. The androspores attach themselves in the neighbourhood of the oogonium, and dividing into a few cells, liberate their spermatozoids close to the opening (Fig. 271, *C*, *D*).

Fertilisation follows by fusion of the spermatozoid at the receptive spot of the ovum, and the coalescence of the nuclei has been observed. The zygote forms a firm protective wall : it is stored with nutriment, takes a brown or red colour, and may enter a period of rest. Its germination presents a point of special interest. The outer wall bursts and the contents escape, contained within a delicate membrane. The protoplast then divides usually into four cells, which ultimately escape as motile zoospores (Fig. 272). It has been ascertained in *Oedogonium capillare* that the zygote nucleus undergoes a *reduction division* : hence the Oedogonium plant is typically *haploid*. Unfertilised oogonia may occasionally germinate directly. In some instances the zygote gives rise to a single large

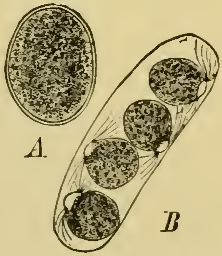

FIG. 272.

Bulbochaete intermedia. *A* = oospore. *B* = formation of four zoospores in the germinating oospore. (After Pringsheim, from Strasburger.) (× 250.)

and presumably diploid swarmer. Hence, in addition to the regular features of the life-cycle, certain irregularities may occur, as in other classes of plants. All species with dwarf males are *dioecious*, *i.e.* the male and female gametes are produced on different plants.

A point of interest in these, as it is also in other Confervoid Algae, is that they illustrate degrees of sexual differentiation. *Ulothrix* has isogametes : *Oedogonium* heterogametes. It is not suggested, however, that these particular genera are closely related to one another by descent. Another feature is the similarity of the gametes to the zoospores, of which they appear as smaller examples. This suggests that gametes may actually be in origin of the nature of zoospores specialised in relation to sexual fusion.

SIPHONALES.

The Siphonales have already been discussed in Chapter X., in respect of their peculiar structure (p. 171, Fig. 105). They are *coenocytes* that is, they are not partitioned into separate cells, but the plant-body consists of a large non-septate sac, limited by a cell-wall, and kept firm enough by internal turgor to preserve its form in the quiet water in which as a rule these plants live. This condition is shown in a less complete form in some members of the Order, where septa occur at intervals, but the protoplasts lying between these are multi-nucleate, and hardly warrant their designation as cells. This is also seen in *Cladophora*, a very common genus of fresh- and salt-water Algae. Clearly the non-septate state is mechanically ineffective. It has been pointed out (p. 172) how, as a set off against it, the more complicated forms of the Siphonales have acquired additional mechanical strength, either by internal cellulose ties, as in *Caulerpa* (Fig. 273), or by matting

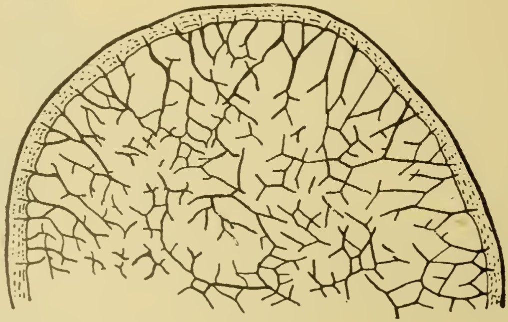

FIG. 273.

Part of a transverse section of *Caulerpa*, showing the thick outer wall, and the reticulate rods of cellulose, which act as ties, and give added rigidity. F. O. B. (× 50.)

of their branches together, as in *Codium*, or by cementing those branches together, as in *Halimeda*. But these are concessions to an essentially weak construction. It is only possible to carry it to any considerable size when living in water, and all the larger forms are marine. *Vaucheria* is an exception: for though many of its species float in water, some live on moist soil, exposed to the air. But the members of the genus consist only of simple or branched filaments, and when living aerially they lie procumbent.

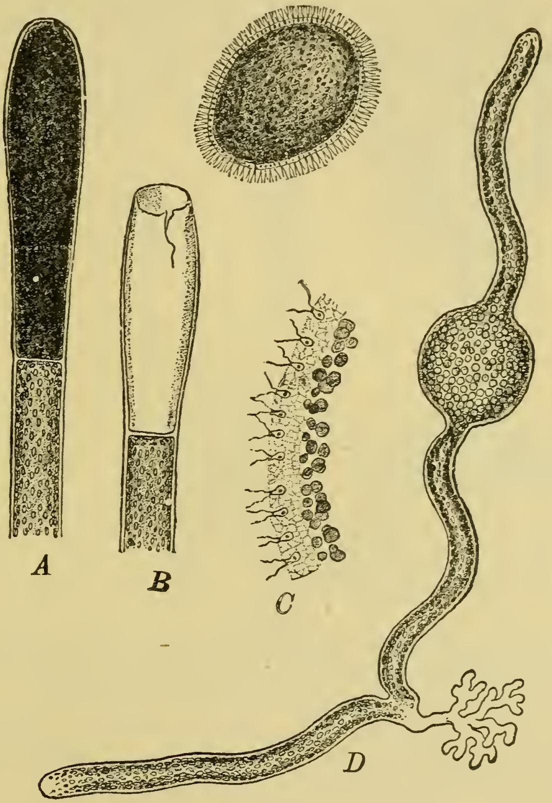

FIG. 274.

Vaucheria sessilis. *A* = young sporangium. *B* = zoospore, with the sporangium from which it has escaped. *C* = a portion of the peripheral zone of a zoospore. *D* = a young plant, with rhizoids, developed from a zoospore. (*A*, *B*, after Götz; *D* after Sachs; *C* after Strasburger.) (From Strasburger.)

The cytoplasm of these plants contains many small chloroplasts, and numerous nuclei usually lying internally to them. Centrally is a large vacuole. In *Vaucheria* the product of photosynthesis appears as oil, but others of the Siphonales may contain starch, which is commonly present in Green Algae. The general physiology of a coenocytic, or, as it has been called, a non-cellular plant, is probably like that of any ordinary green plant. The difference lies in the mechanical construction.

Vegetative propagation is carried out in various Siphonaceous Algae by non-motile, or by motile cells, produced in large numbers in special branches, and liberated into the water. *Vaucheria* is an exception, in that the whole contents of such a branch-ending, which are previously shut off by a septum, are discharged as a single ciliated zoospore, large enough to be seen with the naked eye. The escape is effected in the early morning; after a period of movement the zoospore comes to rest, and germinates directly into a new plant (Fig. 274). In structure the zoospore shows the cilia in pairs, each pair related to a nucleus which is superficial, while the chloroplasts lie within. The origin and structure of the zoospore suggests that it represents the undivided contents of a whole zoosporangium, such as may be seen in other Siphonales.

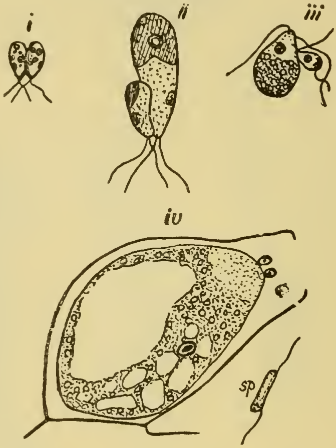

FIG. 275.

Gametes of various Siphonales, illustrating differentiation of male and female. i = *Acetabularia*, isogametes; ii = *Bryopsis*; iii = *Codium*; iv = *Vaucheria*. In ii and iii the gametes are unequal, but still motile; iv in the large egg is stationary, while the smaller spermatozoid is motile. (Taken from Oltmann's *Algae*.)

The Siphonales reproduce sexually: but degrees of difference in size of the gametes are seen. The differentiation thus indicated must be held as distinct from, though parallel with that already described in the Volvocales and in the Ulotrichales and Oedogoniales. In *Acetabularia* the gametes are of equal size, and those produced from different gametangia, or from different plants fuse in pairs (Fig. 275, i.).

In *Bryopsis* the size is unequal (ii.); while *Codium* shows still greater inequality (iii.).

In *Vaucheria*, Fig. 275 (iv.), which is the most advanced of all in sexual differentiation, the large non-motile egg, retained in the oogonium, is fertilised by a small spermatozoid. The facts suggest again a progression from isogametes to a distinction of egg and spermatozoid, but in a series of Algae quite distinct from those previously described.

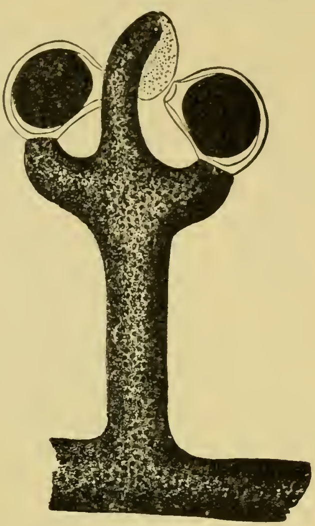

Fig. 276.

Sexual branch of *Vaucheria terrestris*, bearing distally a curved male gametangium or antheridium as it is called: and right and left oval oogonia.

The sex-organs of *Vaucheria* arise close together as short lateral branches (*V. sessilis*), or borne together on the same branch (*V. terrestris*, Fig. 276). The male, or *antheridia*, are horn-like curved bodies; the female, or *oogonia*, are oval. In the antheridium a septum cuts off the multi-nucleate protoplast from the parent tube: each nucleus becomes the centre of a spindle-shaped spermatozoid; and these escape, with their paired cilia pointing fore and aft, through an opening at the distal end. The *oogonium* also at first contains numerous nuclei embedded in protoplasm stored with many globules of oil. But, as the ovum matures, all the nuclei but one wander back into the parent filament, which is then shut off from the oogonium by a wall. Meanwhile a beak has formed at the distal end of the oogonium, which then opens by swelling of the wall, a portion of the colourless contents being emitted. The uninucleate egg then lies open for fertilisation by the small motile spermatozoids (Fig. 275, iv.). It appears that self-fertilisation from an adjoining antheridium is the rule. The fusion of the two nuclei has been observed to form the nucleus of the zygote. Then follows storage of further oil, a change of colour of the contents, and the formation of a thick wall. In this state, as an *oospore*, a period of rest follows. Germination takes place by rupture of the thick wall, and the direct formation of a new filament from the contents.

In such organisms as these it has been found that there is no obligatory succession of events in the life-history. It lies in the hand of the experimenter to determine by altering the conditions what form of propagative organ shall be produced. This has been shown with particular clearness in the case of *Vaucheria*. If the plant be kept first in a flowing stream of water, as it may be in a glass tube, it simply grows vegetatively. If it be then transferred to still water, zoospores are produced. This also follows on flooding, in the case of terrestrial forms. If it be desired to produce sexual organs, the plant should be well nourished, for instance by exposure to good light, or cultivation in a weak sugar solution. A rise of temperature also encourages their production. Speaking generally, light produces sexual organs, shade zoospores. A third type of propagative organ is formed in some species (*V. geminata*). Under dry conditions the filament, dividing up into short lengths, forms *aplanospores* with thick walls. These can stand drying up. All of these propagative organs are biologically suitable to the spread and survival of the plant in its native habitat. When flooded in cool weather it forms zoospores. When there is risk of drying up in summer after exposure to light and heat it forms zygotes or aplanospores, which can tide over the period of drought ; but on germination, whether of the zoospores, zygotes, or aplanospores, either zoospores or sexual organs may be formed first on the young plant, according to the conditions.

In *Vaucheria* it is probable that reduction takes place at the first nuclear division in the germinating oospore ; and hence the vegetative plant is typically haploid. But in *Acetabularia* and related genera the plant is diploid, with reduction occurring at the formation of the gametes.

CONJUGALES.

A considerable series of common Green Algae belong to the Conjugales, a group which stands aloof from the Chlorophyceae in the more restricted sense. One large family of these is the Zygnemaceae, filamentous Algae native in still water : the most familiar example being *Spirogyra*. Another family, the Desmidiaceae, are mostly unicellular, and very beautiful. They are found in quantities in peaty pools. The two families are grouped together because of the structure of their uninucleate cells, which contain complicated chromatophores ; and because both show *conjugation of non-motile gametes*.

The well-known genus *Spirogyra* includes numerous species, of which the filaments float commonly unattached in still fresh water, and with no distinction of apex and base. They are slimy to the touch, owing to their outer wall being mucilaginous. Each filament is partitioned by transverse septa into cells, each of which may be detached from its neighbours by shock, when its convex ends demonstrate its internal turgor. Growing on and dividing, each may form a new filament. Each cell is practically an individual (Fig. 277, cell *h*). It is cylindrical, the proportion of length to breadth varying in different species. Within the external wall is a layer of colourless cytoplasm surrounding a central vacuole, in the middle of which the single nucleus is suspended by colourless threads. The most marked feature is the green spiral chromatophore, which gives the genus its name. One or more of these, according to the species, may lie embedded in the peripheral cytoplasm, coiled corkscrew-fashion. As in the Conjugales generally, pyrenoids occur in the chromatophores: they are highly refractive, and form centres for the formation of starch, while the threads that suspend the nucleus usually run out to them.

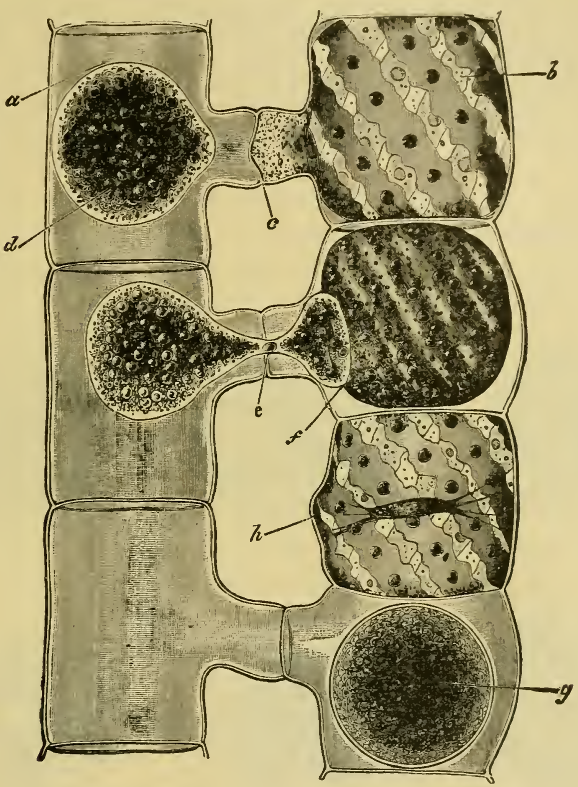

Fig. 277.

Two filaments of *Spirogyra*, which illustrate various stages of conjugation. *a*, *b*, have formed outgrowths which have met at *c*; the protoplast *d* is contracted to a dense sphere. The next lower pair of cells show conjugation, the protoplasts fusing at *f*. In *g*, conjugation is complete, a zygote having been formed by the fusion of two protoplasts, *h* shows a cell not in conjugation. (After Kny.)

Vegetative propagation is simply by division of the cells, which occurs during the night, and may be continued indefinitely. As the season progresses the filaments conjugate. Adjacent filaments put out processes from cells opposite one another, which meet, flatten, and fuse at their tips, the intervening wall being absorbed. Their protoplasms contract: one of them contracts earlier than the other; it then passes bodily through the now open tube, and its cytoplasm coalesces with that of the other cell, while its chloroplast becomes disorganised (Fig. 277). The nuclei remain for a time distinct. The zygote changes to a reddish colour, fats are stored in it, and a thickened wall is formed. Freed from the parent filaments it remains dormant. On germinating the outer wall ruptures, while the inner covers the enlarging protoplast. The nuclei fuse, and later undergo tetrad-division, with reduction. But only one of the four survives as the nucleus of the cell from which, by division, the new haploid filament arises.

In *Mesocarpus* the conjugation is similar, except that the zygote is formed actually in the tube connecting the conjugating cells.

Conjugation in the *Desmids* is essentially similar. The behaviour of the zygote on germination has been followed (Fig. 278), and there also, after

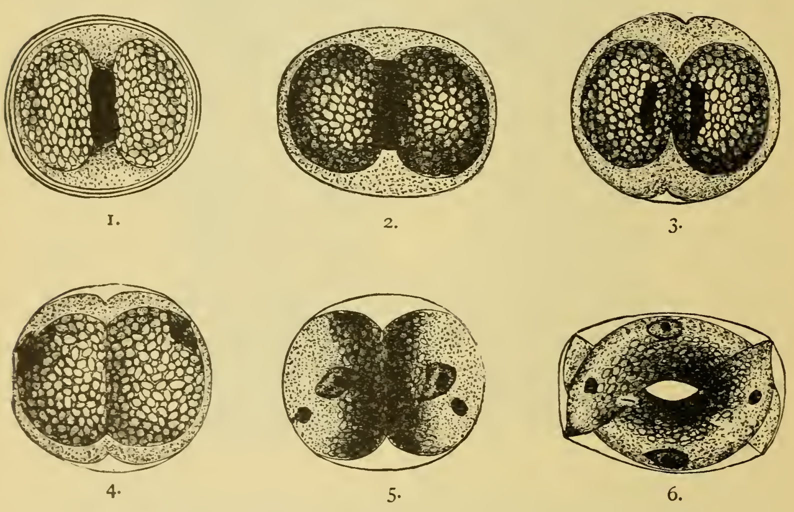

Fig. 278.

Syngamy and germination of a Desmid, *Closterium*, after Klebahn. 1, zygote before nuclear fusion; 2, first nuclear division; 3, binuclear stage; 4, second nuclear division; 5, two cells, each with a small and a large nucleus; 6, formation of two new *Closterium* cells each with one large nucleus; the other is disorganised. (From Oltmanns.)

delayed fusion, the fusion-nucleus divides first into two and then into four; but two are atrophied, while the others remain as the nuclei of the two new cells formed on germination. Thus in the Conjugales there is a tetrad-division, and a presumable reduction which follows on conjugation, just as tetrad-division follows on sexual fusion elsewhere.

It is different in the *Diatoms*, a distinct class of unicellular Algae with very many forms, marine and fresh-water, great numbers of which are found in the floating "Plankton." Their chloroplasts are brown, and the uninucleate protoplast is enclosed between two silicified shells with delicate sculpturing, which fit over one another like the two parts of a pill-box. Vegetative division results in regular decrease in size of the cells, till a limit is reached, from which recovery is usually by conjugation, resulting in *Auxospores*. The nuclei of the conjugating cells of certain types, such as *Rhopalodia*, first divide into four: each cell then divides into two gametes with two nuclei in each of them, one large and one small: the gametes then fuse in pairs, the larger nuclei also fusing, while the smaller disintegrate. Here also there is a tetrad-division, but it *precedes* conjugation, while in the Conjugales it *follows*. It may then be concluded that the vegetative phase of the Conjugales is haploid, while that of certain Diatoms is diploid. These facts have their importance in questions to be discussed in Chapter XXXIII.

Examples such as these from the Green Algae show how diverse those plants are in structure and in propagative method. It may be held that they sprang from some common source, including motile and non-motile forms, such as the Protophyta: and this would seem probable from their characters, both vegetative and propagative. But the differences which they show suggest a plurality of lines of parallel development. More especially does this emerge from their comparison in respect of sexual differentiation. The steps of distinction of male and female gametes correspond in several large Orders, e.g. Volvocales and Ulotrichales, though these series are sharply distinct in vegetative structure. The only possible conclusion from such facts is that the distinction of the sexes has been achieved not only once, but in a number of distinct evolutionary series. There has, in fact, been *parallel development*, or as it is styled, *homoplasy*. The spermatozoids and ova of *Volvox*, *Oedogonium*, and *Vaucheria* are not then to be held as homogenous, that is, produced from a common ancestry that bore spermatozoids and eggs; but *homoplastic*, that is, each has arrived as a result of independent sexual evolution from some ancestry which had not male spermatozoids or female eggs, but undifferentiated gametes as the propagative organs.

While a majority of Green Algae are typically haploid organisms, and undergo reduction at the first nuclear division in the zygote, there are others, e.g. among the Siphonales, which are typically diploid organisms. Thus the Green Algae give some indication of the very considerable diversity of life-cycle which is characteristic of the Algae as a whole. This aspect is discussed in greater detail at the end of Chapter XXIII.

Myxophyceae (Cyanophyceae).

The Blue-green Algae are unicellular, or filamentous. They are found living either in water, or on surfaces which are habitually moist. A common type is seen in *Gloeocapsa*, where the oval or spherical cells have a swollen cell-wall. This holds the cells together after fission, in rounded colonies which break up by disorganisation of the wall. It is commonly found on the inner surfaces of the glass of damp greenhouses (Fig. 279). *Oscillatoria* is a filamentous type, which is common on damp walls and rocks. Its pale green filaments show slow swinging movements, hence the name (Fig. 279A). They consist of disc-shaped cells, which multiply by division. In some of the larger forms granules of irregular form are found in the so-called *central body*, which react to stains like chromatin and divide before cell-division takes place.

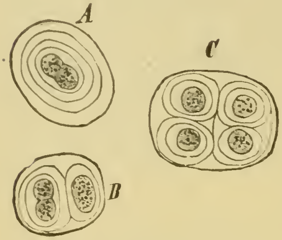

Fig. 279.

Gloeocapsa polydermatica. *A*, in process of division; *B*, to the left, shortly after division; *C*, a later stage. (× 540.) (From Strasburger.)

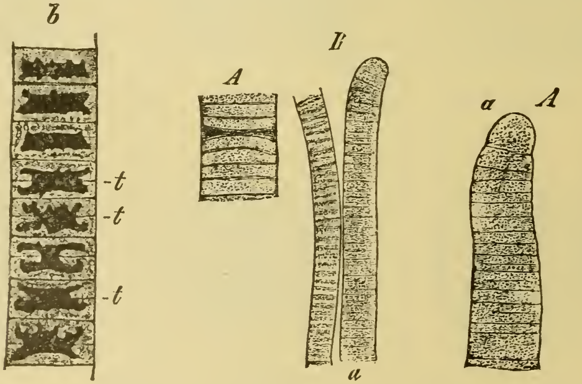

Fig. 279A.

A, *Oscillatoria princeps*: a terminal portion of a filament; *b*, portions from the middle of a filament, properly fixed and stained; *t*, cells in division. (× 1080.) *B*, *Oscillatoria Froelichii.* (× 540.) (From Strasburger.)

The filaments, which are unattached, may break up at any point into several shorter lengths; but in other cases special cells (heterocysts) occur at intervals in the filaments, which appear to determine their breaking up into shorter lengths, as in *Nostoc* or *Rivularia*. Some of these fission-Algae take part in the formation of Lichens: thus *Collema* has *Nostoc* as its Algal constituent. Others, such as

Anabaena, lead an endophytic life, contributing probably to an irregular nutrition, as in the roots of Cycads. In the establishment of the new Flora of the volcanic Island of Krakatoa (p. 331), Blue-green Algae were among the first colonists, taking their part in the preparation of an organic soil for larger developments to follow. Certain of these Algae allied to *Anabaena* often appear suddenly in large quantities on the surface of fresh water, causing the phenomenon known as " water bloom," or the " breaking of the meres." One of these, with a deep red colour (*Trichodesmium erythraeum*), floats in ocean-waters, and becomes prominent when massed together by wind and tidal streams. It has thus attracted attention in various oceans, and has given its name to the " Red Sea."

CHAPTER XXIII.

BROWN ALGAE (*PHAEOPHYCEAE*).

THE Brown Algae, or *Phaeophyceae*, include a large proportion of the Seaweeds commonly found between the tide-marks, and extending downwards to greater depths. Some of them are delicate filamentous growths, branched or unbranched (Ectocarpales). Others are larger and more complicated in structure, with ribbon-shaped thallus (*Dictyota*). Some, of leathery texture, attain gigantic dimensions, the Tangles of the colder oceans being among the largest of living beings (*Laminaria*, *Nereocystis*, *Macrocystis*). The most familiar are the species of *Fucus* found on all British coasts, of which *F. vesiculosus* is the Common Bladder Wrack. The smaller forms show gradual steps of increasing complexity, from the simple septate unbranched filament, through various modes of branching and cortication, to the massive tissue-formation seen in the larger Tangles. Even the largest of them may thus be referred ultimately in origin to the simple filament

The thallus of the larger forms is usually flattened, and bilaterally symmetrical (p. 205). It shows forked branching, often very perfectly dichotomous, and in a single plane. The result is that the whole frond is fan-shaped, as is seen particularly well in the native species *Fucus serratus* (Fig. 280). The thallus is attached by a holdfast to some firm body such as a rock; but the gulfweed (*Sargassum bacciferum*) is exceptional in floating freely, in which state, however, it probably propagates vegetatively: organs of sexual reproduction only occur on attached plants. The holdfast of Tangles applies itself so closely to the irregularities of the surface that the stalk will often break before it would come away. In *Fucus* it is discoid; in *Laminaria* and others it may be branched and root-like. But its function is only mechanical, not absorbent. The thickness of the stalk which arises from it is proportional to the size of the thallus it has to moor. A plant so constructed is well fitted to resist the swirl of the waves, keeping its hold, and though pliant, retaining the form of its leathery frond. Its form gives a large proportion of surface to bulk for exposure to its liquid environment. Plants are normally buoyed up by the water, but when exposed between tide-marks they subside to form a dense stratum whereby the plants mutually protect one another from drying.

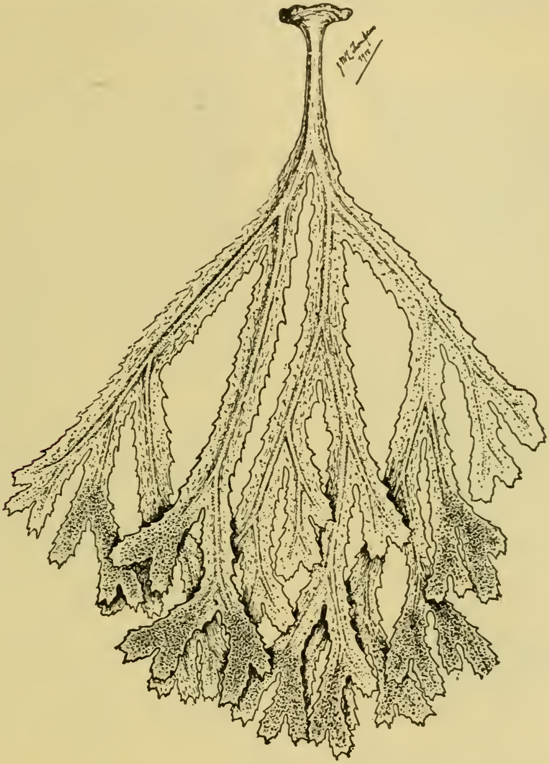

Fig. 280.

Drawing of a plant of *Fucus serratus*, showing the fertile distal ends of the longer branches. (¼ Nat. size.)

There is in many of these seaweeds a localised apical growth with distal branching. In *Fucus* the growing point lies in a depression at the extreme tip. In others (*Dictyota*, *Sphacelaria*) the apex projects. The segmentation of the apical cell is often very regular, the form and succession of the segments varying in accordance with the form of the tip itself. In other cases intercalary growth is dominant. This is seen in the simple filaments of the Ectocarpales, and in the more complex thallus of *Cutleria*. But it is shown on the large scale in

Laminaria, where a new frond is formed each season between the old one, which is thrown off, and the persistent stalk (Fig. 281).

In simple forms the cells are all alike. Soft cell-walls surround a uni-nucleate protoplast, which includes simple brown chromatophores. The plastid pigments are chlorophyll, xanthophyll and carotin, together with *fucoxanthin* which masks the others and is peculiar to the group. The products of photosynthesis are soluble carbohydrates like *laminarin* or *mannitol*. In larger forms the tissues are differentiated. For instance, in *Fucus* the cells of the superficial layer are thin-walled, and divide actively; they are covered externally by a layer corresponding to cuticle. They are the chief seat of photosynthesis, and of tissue-formation. Passing inwards from this layer the mucilaginous cell-walls become more and more swollen, so that the deeper-seated tissues of an old thallus consist of a bulky mucous matrix, in which the cells themselves appear as a complicated network (Fig. 282). Centrally there is a firmer conducting cord, which is well defined in old stalks of the larger Tangles. It contains many tubes with sieve-structure and callus, closely comparable to the sieve-tubes of Vascular Plants, and serving like them for transport. In large stalks an ill-defined cambial activity provides for thickening and increased mechanical strength. This is still further secured by "intrusive hyphae," which burrow through the softer tissues, and brace them together. In this way they acquire their tough and resistant but yet pliant character. We thus see that both in external form and internal structure the Brown Seaweeds cover a wide range, from the simple to the complex.

FIG. 281.

Laminaria, thallus showing a new frond, intercalated between the stalk and the old frond, which is being thrown off. (Reduced.) (After Strasburger.)

In their sexual propagation they also show an advance, which runs in some degree parallel with their structural progress. The propagative cells are produced in *sporangia* and *gametangia*. The former which produce zoospores are borne both by the simpler and more advanced types but they are absent in *Fucus*. Successive steps in differentiation of the sexes may be found within the Brown Algae. The simplest forms produce *isogametes* which are *motile*. More complex forms show differentiation of sexes, the small *spermatozoids* being *motile*, but the larger *ova* are *non-motile* primordial cells.

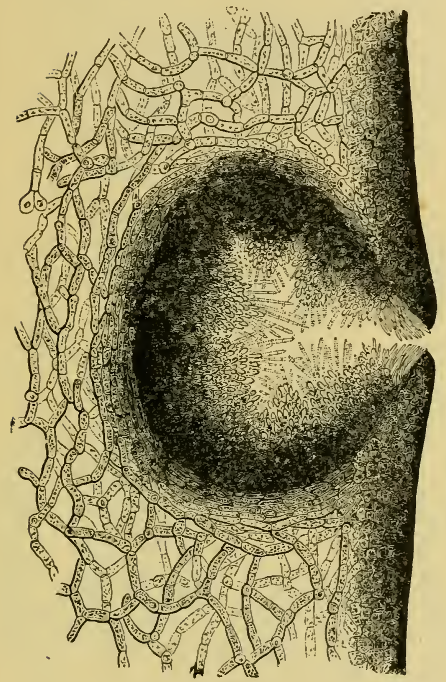

Fig. 282.

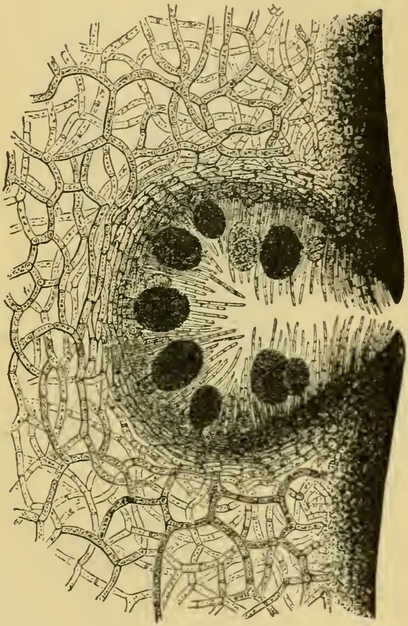

Fig. 283.

Fig. 282.—Mature male conceptacle of *Fucus serratus*, filled with branched antheridia hairs. (After Thuret.) Fig. 283.—Mature female conceptacle of *Fucus serratus*, ontaining unbranched hairs, and oogonia. (After Thuret.) Incidentally these drawings show the structure of the mature thallus (p. 358).

The Phaeophyceae, which comprise eleven Orders, collectively illustrate: (i) an advance in vegetative organisation from simple filamentous plants to plants of large size and elaborate organisation; (ii) alternation of generations from simpler types in which the gametophytic and sporophytic generations are alike in their vegetative development to those in which the sporophyte shows a marked preponderance over the gametophyte; and (iii) an advance from isogamy to oogamy.

The propagative cell of the Brown Seaweeds is very constant in its primitive form. It is actively motile in water when set free.

It is a pear-shaped, nucleated protoplast, with two cilia attached laterally so that one is directed forwards the other backwards. They are inserted close to a red eye-spot, which as a rule is closely related to a yellow chromatophore (Figs. 284, *B*; 287, 3). The constancy of this type shows the probable phyletic unity of the Brown Algae.

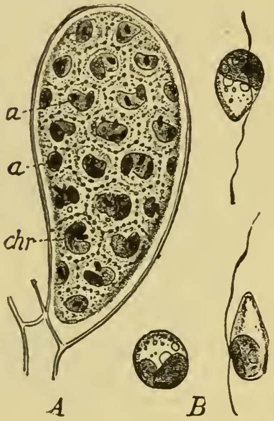

Fig. 284.

A, *Pleurocladia lacustris*. Unilocular sporangium with its contents divided up into zoospores. *a* = eye-spot. *chr* = chromatophore. (After Klebahn.) *B* = *Chorda filum*, zoospores. (After Reinke.) (From Oltmanns' *Algae*.)

Fig. 285.

Ectocarpus siliculosus. 1, female gamete surrounded by a number of male gametes. 2-5, stages in the fusion of gametes. 6, zygote after 24 hours. 7-9, fusion of the nuclei as seen in fixed and stained material. (1-5 after Berthold; 6-9 after Oltmanns.) (From Strasburger.)

In the simplest of the Phaeophyceae, the *Ectocarpales*, the complete life-cycle, as in *Ectocarpus* or *Pylaiella*, involves an alternation between (i) a diploid plant bearing asexual, *unilocular sporangia*, Fig. 284, in which reduction division takes place during the formation of the zoospores, and (ii) a haploid plant, bearing *plurilocular sporangia* (=*gametangia*) from which haploid isogametes are liberated and fuse in pairs, Fig. 285. Thus, a zoospore from a unilocular sporangium gives rise, on settling and germinating, to a haploid gametophytic plant; a zygote on germination gives rise to a diploid sporophytic plant. The haploid and diploid plants are so similar in size and structure as to be described as identical; hence they may be considered to exemplify *homologous* or *isomorphic alternation.* Both phases of the life-cycle have accessory means of vegetative propagation: diploid plants may be propagated over several generations by diploid zoospores released from *plurilocular sporangia*; haploid plants may be similarly propagated by swarmers (apogamous gametes) from the plurilocular sporangia or gametangia. The sporophytic plant is always recognisable as that which bears unilocular sporangia as well as plurilocular sporangia. Environmental conditions influence the preponderance of one or other of the two alternating phases : thus plants of *Ectocarpus* in Northern Europe are mainly sporophytic whereas those on the Mediterranean coast are mainly gametophytic.

The *Ectocarpales* show various stages in sexual differentiation. Although in *Ectocarpus* the male and female gametes are morphologically identical, physiological differences may be observed. Those gametes which are functionally female tend to move more slowly and for a shorter time and to become centres of attraction for the still motile males. In some species the gametes are of unequal size (*heterogamous*) and in related genera within the Order there may even be an advance to incipient oogamy. In *Cutleria* (Cutleriales) the two gametes differ obviously in size (Fig. 286).

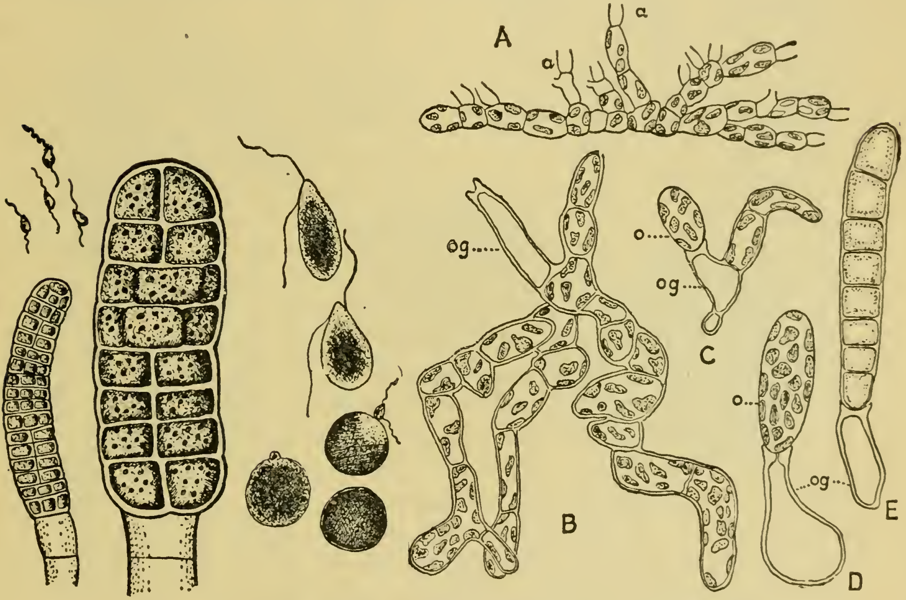

Fig. 286.

On left, *Cutleria multifida*, showing the smaller, male gametangia (or plurilocular sporangia) and the larger female. Top-left are spermatozoids, top-right are ova. Below are three stages of fertilisation. (× 500.) (After Reinke.)

On right, *Laminaria digitata*. *A*, Male gametophyte ; *a*, empty antheridia. *B*, *C*, *D*, Female gametophytes (*B* is large, *C* small, while *D* is reduced to a single oogonium) ; *og*, oogonium ; *o*, ovum. *E*, young sporophyte, still seated on the empty oogonium. (*A* × 600 ; *B* × 292 ; *C* × 322 ; *D* × 625 ; *E* × 322. After H. Kylin.)

In *Dictyota dichotoma* (*Dictyotales*) there is also isomorphic alternation of generations, the sporophytic plant bearing *tetraspores*. Separate plants in *Dictyota dichotoma* bear respectively tetraspores, oogonia, and antheridia. The nuclei in the first of these plants are diploid, with 32 chromosomes. The nuclei of the male and female plants are haploid, with only 16 chromosomes. Reduction takes place when the tetraspores are formed, and these on germination give the sexual plants. The analogy of the tetraspores with the spore-tetrad in Land Plants is obvious. But here the haploid gametophyte and the diploid sporophyte are alike in form.

In contrast to the *isomorphic alternation* seen in the *Ectocarpales, Dictyotales,* etc. the *Laminariales* afford remarkable examples of *heteromorphic* alternation. In this Order the large plant itself—for example *Laminaria* as already described, Fig. 281—is the diploid sporophyte : the gametophyte, by contrast, is a minute, filamentous plant. In club-shaped, unilocular sporangia, borne on rough patches on the frond of *Laminaria,* reduction takes place and haploid zoospores are liberated. These give rise to minute, filamentous male and female gametophytes (Fig. 286) ; the former are branched and bear antheridia while the latter consist of a few cells, and in extreme cases may be reduced to a single cell, and bear oogonia. The naked egg-cell which emerges from the oogonium and remains attached thereto, grows into the diploid sporophyte on fertilisation.

The Fucales are conspicuously oogamous. The sexual organs are in *conceptacles*, cavities hollowed out of the thallus (Fig. 280). *Fucus serratus* (Common Wrack) bears the male and female organs on distinct plants, but in many species they may appear in the same conceptacles. A median section through a male conceptacle shows how the flask-shaped cavity opens to the outside by a narrow pore, and is at maturity filled by richly branched hairs, which arise from the tissues bounding the conceptacle, and bear the numerous minute *antheridia*, or *male gametangia* (Fig. 282). The female conceptacle is of like structure, but bears unbranched hairs, and associated with them are the large *oogonia*, or *female gametangia*, which are large enough when mature to be seen with the naked eye (Fig. 283).

The antheridium itself is an oval unicellular body, surrounded by a cell-wall. When young it contains a single nucleus, which divides to form 64 nuclei, each of which becomes the centre of a spermatozoid. The cytoplasm divides into as many portions, and each is found to contain a red eye-spot beside the nucleus (Fig. 287, 2). The contents slip out when ripe from the ruptured outer wall, as a mass still surrounded by the inner wall : this soon deliquesces, and sets them free as 64 *motile spermatozoids*, each with the characters usual for the Brown Seaweeds (3, 4). The oogonia though larger are of the same pattern. Each has at first one nucleus ; but here it divides to form only eight, and the cytoplasm undergoes cleavage into *eight large ova*. They are also shed in the same way, and round themselves off as 8 *non-motile eggs* (5). [See also Fig. 288, *D.E.*]

A comparison of the antheridium with the oogonium in the Fucaceae shows that they are probably results of differentiation from a common source. When an oogonium is to be formed, a cell of the wall of the conceptacle projects without branching into the cavity, and divides to form a stalk-cell and an oogonium (Fig. 288, *A*, *B*, *st*.). In *Sarcophycus*, however, the stalk is branched, and a succession of oogonia may be produced, as is seen in the antheridia of *Fucus*. On the other hand, the antheridial hair of *Fucus* may start precisely in the same way as the oogonium, the terminal cell forming the first antheridium. But the growth does not stop there: the stalk-cell shoots out laterally and produces another antheridium, and the process may be continued with irregular sympodial repetition (Fig 287, I). This finds its biological explanation in the need for a continued supply of numerous spermatozoids, so as to secure fertilisation over a prolonged period. The large number is further ensured by the divisions in each cell being continued to 64.

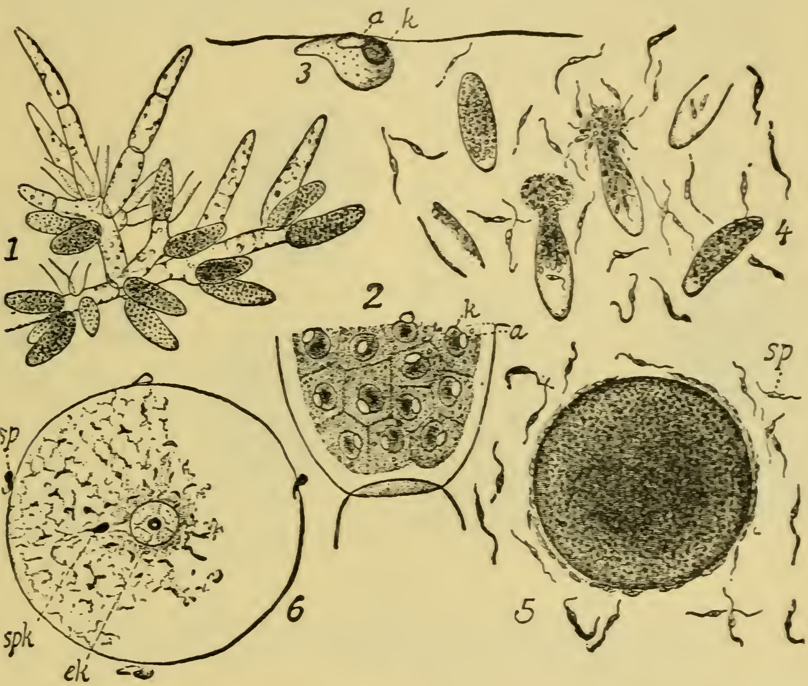

FIG. 287.

Fucus. 1, group of antheridia. 2, part of an antheridium showing developed spermatozoids. 3, spermatozoid; *a* = eye-spot; *k* = nucleus. 4, isolated antheridia liberating spermatozoids. 5, ovum surrounded by spermatozoids. 6, section through a fertilised egg; *ek* = nucleus of egg; *spk* = nucleus of sperm; *sp* = spermatozoids. (1, 4, 5 after Thuret; 2, 3 after Guignard; 6 after Farmer.) (From Strasburger.)

The solitary oogonia, with their few ova, find their biological elucidation in the facts that the ova are large and have a strong chemotactic influence on the motile spermatozoids. Their size gives a high degree of certainty of successful germination if once fertilised. Their attractive influence secures a high probability of fertilisation, notwithstanding their immobility, which has followed on increase in size. But *Fucus* is not the last term of the series of reduction of the oogonium. In *Ascophyllum* only four ova are matured in each, in *Pelvetia* two, and in *Himanthalia* and others only one. Vestigia of the atrophied eggs are found, which clearly indicate that their number has been reduced. Thus the Brown Algae form a coherent series of sexual differentiation. Their sexual cells probably originated from motile cells all alike. The first functional though not formal distinction of sex is seen in *Ectocarpus siliculosus* (Fig 285). Steps in loss of motility are seen in other species, and in *Cutleria* (Fig. 286). while in *Fucus* the large ovum is entirely non-motile (Fig. 287). Finally, in *Himanthalia* a single ovum occupies the whole oogonium: its large size giving such security of germination as to justify the reduction in number to one. The whole series thus illustrates steps in sexual differentiation, which are biologically intelligible.

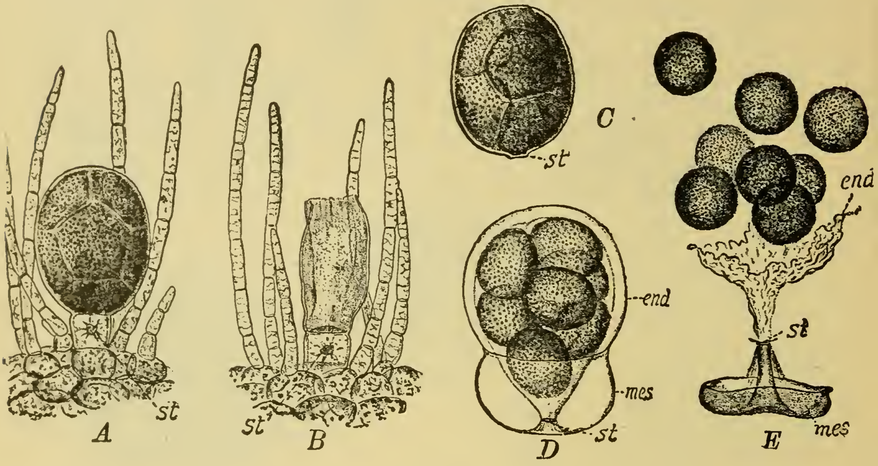

FIG. 288.

Fucus *A*, oogonium, the contents of which have divided into eight eggs. *B* = oogonium, from which the contents (*C*) have been extruded. *D*, *E*, liberation of the eight eggs; *st* = stalk; *mes* = middle—*end* = inner layers of the oogonial wall. (After Thuret.) (From Strasburger.)

In Fucoids which live submerged the gametes may be set free at any time. But when exposed between tide-marks it will be chiefly on the rising tide that they are liberated. Exposed to the air the mucous thallus shrinks on drying, and the pressure of the contracting tissue may be seen to squeeze out the ripe antheridia and oogonia, which may be recognised by their yellow or olive colour, through the open pores of the conceptacles. If these be collected fresh in separate watch-glasses in sea water, the final liberation of the minute motile spermatozoids (Fig. 287, 4) and of the much larger non-motile eggs (Fig. 288, *E*) can be easily followed. If then a drop of water containing the former be added to a drop containing ova on a slide, many spermatozoids will be seen to collect round each ovum, which thus shows its attractive influence on their movements (Fig. 287, 5). But only one penetrates each egg, and its nucleus has been followed on its course through the cytoplasm till it fuses with the nucleus of the ovum (Fig. 287, 6). The rest at once move away, as though a repellent influence from the egg had replaced the previous attraction.

The immediate consequence of fertilisation is the deposit of a cell-wall covering the zygote. It settles on some solid substratum, and germinates directly into a new *Fucus* plant. Stones on a rocky shore where Fucoids grow may be found in summer covered by a dense growth of myriads of these young plants (Fig. 289).

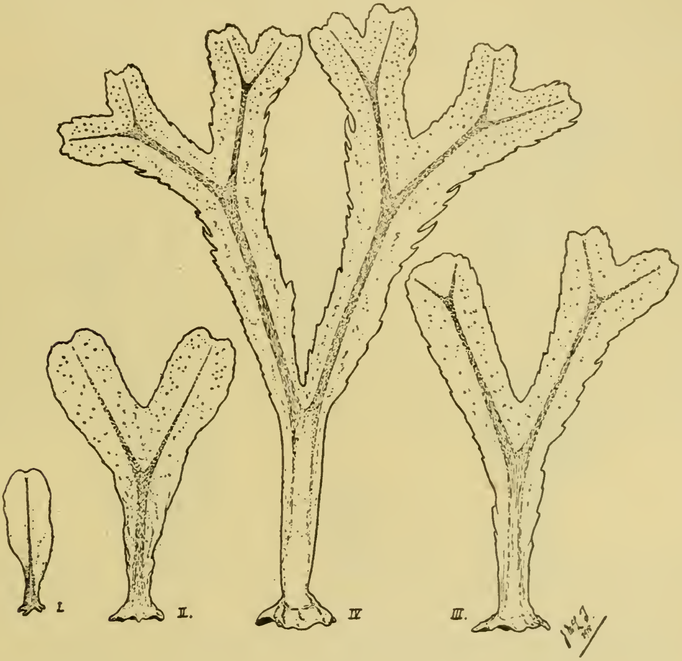

Fig. 289.

I.-IV. Drawings direct from successively older plants of *Fucus serratus*, showing the regular dichotomy.

In the life-history of *Fucus* the increase in numbers is exclusively through the sexual process. There is no production of zoospores, nor any non-sexual propagation, as there is in the simpler Brown Seaweeds. The *Fucus* plant is diploid and reduction takes place in the first divisions respectively of the antheridial and oogonial cells. The haploid phase is extremely brief and there is, strictly speaking, no alternation of generations as in *Laminaria*. By comparison with the very reduced gametophyte of *Laminaria*, it has been suggested that in the Brown Algae there has been a progressive retrogression of the haploid phase culminating in the condition found in *Fucus*. In this view, the first two nuclear divisions in the antheridium and oogonium are regarded as a tetrad division within a sporangium ; the subsequent developments are held to represent all that remains of the greatly reduced gametophyte generation. Such conceptions, should, however, be viewed with caution. An alternative hypothesis, for which there is evidence among several of the less specialised groups, is that the reproductive mechanism in the *Fucales* had its origin in a tendency for the asexual zoospores (produced in unilocular sporangia) to behave as gametes. As the Fucales are undoubtedly advanced forms with a long history behind them, the matter under discussion is clearly one which calls for a suspension of judgment until further data are available.

It seems clear from the peculiarity and the constancy of form of their motile propagative cells that the Brown Seaweeds are a naturally related group of organisms. They illustrate steps of advance in respect of form, structure, and propagative method ; and these follow for the most part along parallel lines. Accordingly they may be held to represent a progressive series. That they are ranked as Thallophytes is no sufficient reason for holding them all as primitive. Their higher terms show high structural adaptation to their requirements, and they are in their own habitat eminently successful plants. These may therefore be held as the ultimate exponents of an evolution limited by its surroundings, and distinct from other lines of Descent.

RED ALGAE (*RHODOPHYCEAE*).

The Red Algae (*Rhodophyceae*) are a separate group, distinguished by their method of propagation from all others. They are mostly marine, spreading from the zone between tide-marks to deeper levels, and finding their limit at about 150 feet below low-water mark. Their colour varies from pink to purple, or reddish brown. This is due to chromatophores containing red pigment which masks the chlorophyll. The colouring has its relation to light. The greatest activity of photosynthesis is in light complementary to the colour of the plant. Ordinary green plants make special use of the rays at the red end of the spectrum ; but for Red Algae rays further along the spectrum are effective, and it is the rays towards the blue end of the spectrum which penetrate into the depths of sea water. But all of the *Rhodophyceae* are not red. It is significant that *Lemanea*, which is exposed to ordinary sunlight in shallow fresh-water streams, is olive-green.

In form the Red Algae are various, but never large. They include plants which in form and colour are among the most beautiful, and therefore are prized by collectors. They may consist merely of branched septate filaments : or fronds, variously thickened and flattened, may be formed by matting and webbing of many filaments together. Often they are fan-shaped and sometimes lime-encrusted. In the warmer waters some of these contribute to the formation of Coral reefs, and have been active in this way from early geological times. The chief feature they have in common is their method of sexuality, which may be illustrated in the simple case of *Nemalion*. The male organs are unicellular, the whole content of each cell escaping as a naked, *non-motile spermatium* (Fig. 290, 1). The female organ is a *carpogonium*, consisting of a cell with an enlarged base, and elongated upwards into a filamentous *trichogyne*. This receives the non-motile spermatium, and then shrivels. Carpospores then arise directly or indirectly from the enlarged base. *Fertilisation is indirect*, in the sense that the nucleus of the spermatium received by the trichogyne is passed down to the base of the carpogonium, where fusion and bud-formation follow (Fig. 290, 4, 5). This is the leading character of the Red Algae, and it is worked out in some of them with extreme complication of detail in the method of transfer of the nucleus. An example of a not infrequent type of fruit-body of Red Seaweeds is shown in *Harveyella* (Fig. 291), where the carpogonium produces branches (black in the figure), from the ends of which the carpospores are given off.

FIG. 290.

Nemalion multifidum. 1, Branch bearing antheridia to the left and a carpogonium to the right, with spermatia, some of which adhere to the trichogyne. 2-5 are successive stages of development of the very simple fruit bearing the carpogonial buds. (After Kny.)

In some Red Algae such as *Nemalion*, which is one of the simplest of them all, no other propagative organs are known. But in most of them *tetraspores* are found, in the production of which reduction of chromosomes has been demonstrated. The nuclear cycle has been fully worked out in the genus

Polysiphonia, where tetraspores and sexual organs are borne on separate plants. The carpospore is diploid and on germination gives rise to a tetrasporic plant (sporophyte) which bears tetraspores, reduction taking place in their formation. The haploid tetraspore grows into the sexual plant. The fusion of a spermatium and a carpogonium produces the diploid carpospore: and so on. There is thus a regular alternation of tetrasporic and sexual plants But in form these are closely alike. The case is comparable with that of *Dictyota*; and questions of the origin of alternation in the Red Algae are raised similar to those for the Brown.

Alternation of Generations in the Algae.

The very considerable *diversity of life-cycle* shown by the Green, Brown and Red Algae has been made evident in the preceding pages. At least four main types can be distinguished. Thus most of the Chlorophyceae and Red Algae such as *Nemalion* are *haploid organisms*, with reduction taking place at the first division in the zygote. In these organisms the diploid condition is confined to the zygote itself. In a second type of life-cycle, typical of some of the *Siphonales* probably of all the *Bacillariophyceae* (Diatoms), and of the *Fucales* among the Brown Algae, the plant is *diploid*; reduction division takes place at the formation of the gametes, and the haploid condition is limited to the brief phase prior to the fusion of the gametes. A third type consists of the alternation of two *morphologically similar individuals*, one haploid and gametophytic, the other diploid and sporophytic. Such *isomorphic* or *homologous alternation* is found in the *Cladophorales* and *Ulvaceae* among Green Algae, in *Ectocarpales* and *Dictyotales* among Brown Algae, and is typical of all the more advanced Orders of Red Algae; in the Brown and Red Algae reduction division takes place in the unilocular sporangia and tetrasporangia respectively. Lastly, *heteromorphic alternation* is met with in such Brown Algae as the *Cutleriales* and *Laminariales*, and it may be, if we accept one interpretation given above, also in the *Fucales*. In these instances the very large and conspicuous sporophytic plant stands in marked contrast to the minute gametophyte, but both are equally required to complete the cycle. Such Algae not only remind us strongly of the life-cycle in the Pteridophyta, but might be regarded as another instance of the rise and predominance of the diploid generation. But from a knowledge of the other types of life-cycle given above it will be seen that while the Hofmeisterian doctrine of alternation—founded originally for higher plants—applies in detail to some Algae, it cannot be extended to the group as a whole. (See Chapter XXXIV.)

Comparison with the Bryophyta, Pteridophyta, and Seed-Plants suggests that it is in the tetraspores of the Algae that the nearest correlatives are found to the spores produced in them by tetrad-division. In so far as their place in the chromosome-cycle is concerned these spores may be held as comparable with those of Archegoniate Plants. In Chapter XXXIV. the general relation of the somatic to the chromosome-cycle is considered at some length. The view is there advanced that the latter is the more stable in plants at large, and is therefore to be held as the more important in comparison, with its normally alternating events of syngamy and reduction.

CHAPTER XXIV.

FUNGI. INTRODUCTORY.

The character which all Fungi have in common is a negative one: the *absence of chlorophyll*, or of any kindred colouring matter by means of which they can carry on photosynthesis. They are therefore sometimes called colourless; but many of them, and especially the large Toadstools, are brightly coloured, though with pigments quite distinct from chlorophyll. The absence of chlorophyll is associated with the fact that they are able to acquire their supplies indirectly: that is, either by a *parasitic* or a *saprophytic habit*. These methods of nutrition have already been discussed in Chapter XII., as they are seen in Seed-bearing Plants. A mere negative character, such as the absence of chlorophyll, is not in itself a sound basis for classification. At once the doubt is aroused whether all the Fungi are really "blood-relations." Such Phanerogamic parasites and saprophytes as were described in Chapter XII. are without chlorophyll. But they are for the most part referable to well-known Natural Families, a fact which signifies that their ancestors were green, and that the parasitic or saprophytic habit was adopted relatively late in the Evolutionary History, after the seed-habit was already established. No one would suggest that these plants should be ranked as Fungi, nor assume that they are all "blood-relations."

It is probable that a like story accounts for the origin of the Fungi, and that they also sprang from self-supporting ancestors. But there is reason to believe that at least the majority of them adopted irregular nutrition early. The opportunity for parasitism and saprophytism was open from the earliest times, wherever organisms grew closely crowded, or their decaying bodies were massed together. The study of fossil plants has shown that organisms characteristically fungal existed from the earliest geological horizons from which there is any reliable record. In the Devonian Period, long before there were any Flowering Plants, there is abundant evidence of Fungal structure existing under conditions favourable to that habit. It does not, however, follow that all organisms which adopted a "fungal" habit early were allied to one another, nor that all Fungi originated at the same time. The existence of parasitic and saprophytic Seed-Plants is a warning against such an assumption. We should rather be prepared to recognise that "*Fungi*" *have originated along more than one line of Descent, and probably at different times, from very early periods onwards.* It is natural to seek for some Algal origin for them, for in many features they resemble Algae. At least two general sources can be suggested, though the actual points of connection by descent may have been numerous. One is from non-septate Algae, such as the Siphonales. This might have given rise to those non-septate Fungi which are called Phycomycetes, from their Alga-like features. The other is from septate Algae; and the view

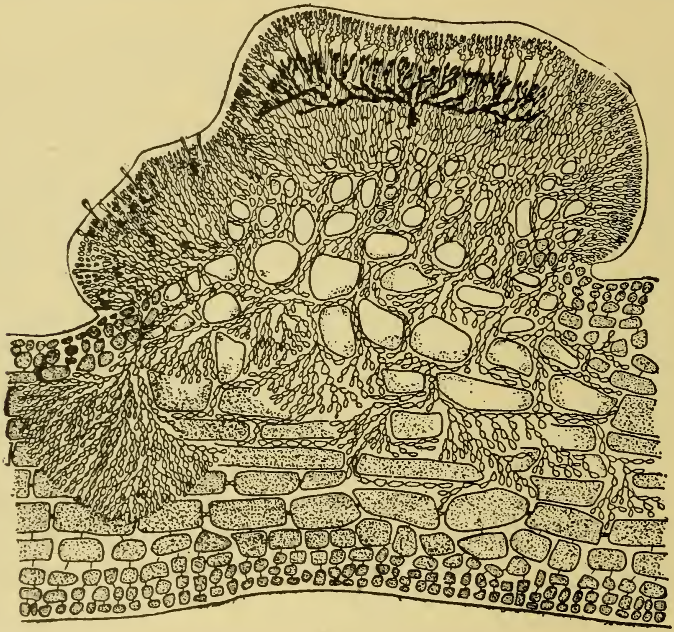

Fig. 291.

Harveyella mirabilis, growing as a colourless parasite on the thallus of *Rhodomela*, one of the Red Algae. Longitudinal section of *Rhodomela* bearing the parasite, with a mature cystocarp, the fertile filaments of which are black. The cells of the host with food-material are dotted; those which are exhausted are left blank. (After Sturch.)

has often been put forward that the septate filamentous Red Algae gave rise to some of the septate Fungi ; but these may have arisen independently from a more primitive source, the Protista, i.e., primitive organisms not definitely distinguished as plants or animals.

The lower organisms, and especially those of aquatic life, live habitually in close juxtaposition. As a rule any large Seaweed or submerged fresh-water plant bears innumerable smaller organisms attached to its surface. Sometimes they penetrate into its tissues. Some by preference frequent certain hosts. Thus *Polysiphonia fastigiata* is regularly borne on the Brown Tangle *Ascophyllum nodosum*, and its filaments extend deeply into its tissues. The proof of actual parasitism is here incomplete, though the regularity of occurrence arouses suspicion. But there can be no doubt of the physiological dependence in *Harveyella mirabilis*, which grows as a colourless parasite penetrating the tissue of *Rhodomela*, one of the Red Algae (Fig. 291). By structure and propagative organs the parasite is clearly another Red Alga, which acts like a true Fungus. Among the Green Algae, *Coleochaete*, one of the Chaetophorales, grows habitually on the surface of submerged plants. The allied *Cephaleuros virescens*, though still green, penetrates the tissues of the leaves of *Camellia*. Other similar cases might be quoted from allied septate Algae. Again, the green Siphonaceous *Phyllosiphon* lives habitually in the intercellular spaces of the leaf of *Arisarum*, causing discoloured patches. Such examples, which might be greatly extended, show how juxtaposition may give opportunity for parasitic encroachment. They are seen in modern living forms referable to recognised groups of Algae. They suggest how in the past fungal parasitism may have arisen. They also prove that the " Fungal " condition may be arising now, as in the past, and along a plurality of evolutionary lines.

The Fungi are very various in habit, and in form. The most familiar types are the large Mushrooms and Toadstools,—or " seats of death," so called in allusion to the poisonous character of some species. Many of these grow on decaying humus, and like the Common Mushroom are saprophytes. Others are parasites, like the large shelf-fungi (*Polyporus*), which grow out from the trunks of trees, and are the cause of the perishing of the heart-wood in hollow timber ; or like the Honey-Agaric (*Armillaria mellea*), which kills forest trees by attacking their soft and nutritious cambium (Fig. 292). But apart from these there are multitudinous smaller Fungi, such as the parasitic Mildews and saprophytic Moulds, while the unicellular Yeasts show the simplest structure of them all. However complicated and various their structure may be, it is based upon the *simple or branched filament, or hypha*. The whole system of such hyphae is called a *mycelium*. Such filaments may grow singly, as in the Moulds and Mildews, or they may be massed together so as to form the complex bodies of the larger Fungi. When closely appressed the septate filaments may seem to form a definite tissue ; but it is in origin always a *false tissue*, or *pseudo-parenchyma*, made up from independent filaments, not a true parenchyma produced by segmentation of cells with a common origin. Many Fungi form large solid masses of such pseudo-parenchyma, which are called *sclerotia*, and serve for storage during a resting period (Fig. 293). The hyphae are limited by a cell-wall, composed of substance differing in its reactions from ordinary cellulose: they may be septate or non-septate, and in the former case there may be considerable variety in the number of the minute nuclei in their colourless protoplasts. Chromatophores are absent, and there is no starch, its place being taken by *glycogen*, or by globules of oil. Thus structurally the cells of Fungi resemble those of Algae, but without the chloroplasts or chlorophyll.

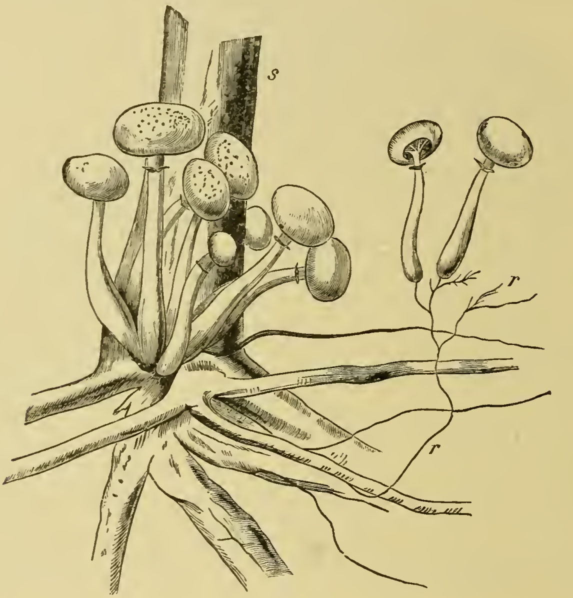

Fig. 292.

Base of a young tree (*s*) killed by *Armillaria mellea*, which has attacked the roots, and developed rhizomorphs (*r*) and fructifications. To the right the fructifications have been traced by dissection to the rhizomorphs that produced them. (After Marshall Ward.)

The success of the Fungal nutrition, whether parasitic or saprophytic, depends greatly upon their *power of penetration* of the nutritive medium. It has been shown in various cases that this is due to a digestive secretion, and the same probably applies generally. A highly refractive drop may sometimes be seen on the end of the hypha, which is believed to contain a *digestive ferment* (Fig. 294, i. ii.).

A ferment has been extracted from large cultures of a certain *Botrytis*, and found to act upon cell-walls, causing them to swell. Such swelling is a feature of the perforation by the invading hypha, which first softens the cell-wall, and then penetrates the softened mass, finally emerging on the other side (Fig. 294, iii.-viii.). This power of perforation has been found in certain cases to depend upon the nutrition of the Fungus: for instance, *Sclerotinia sclerotiorum* can only penetrate living tissue after a period of saprophytic nutrition. There is, however, another side to such questions in the case of parasitic attack: viz. the power of resistance of the victim, which depends partly upon the thickness of the protective walls, but probably also on the presence or absence of inhibiting substances. Thus fungal attack may be regarded as a balance of physiological powers between the invader and the host. In fact, it stands on a footing similar to that of mycorhiza in Phanerogamic Plants, or of conditions of symbiosis generally (see Chapter XII.).

FIG. 293.
Sclerotium of Ergot of Rye (*Claviceps*), a mass of pseudo-parenchyma formed in the ovary of Rye: above is the style still covered by remains of "Honey-Dew" (see p. 425, Fig. 325, *a*).

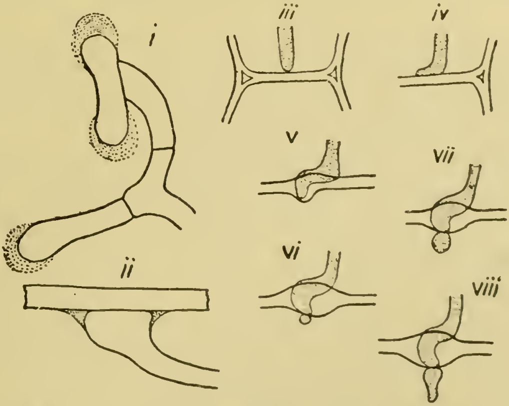

FIG. 294.
Successive stages of the penetration of cell-wall of Lily by the hypha of the Fungus causing the Lily disease. (After Marshall Ward.)

It is along such lines that the explanation must be sought for the condition known as "*epidemic*," where by a sudden outburst a disease becomes prevalent. Examples have been seen in the Irish Potato Famine, the Coffee Disease of Ceylon, or the Lily Disease which in 1888 made the cultivation of Lilies in the Thames Valley a failure. In such cases the disease is not necessarily a new one. The novelty lies in the success of the invader. It appears to be due to a change of balance between attack and resistance. That balance may be affected either by physiological strengthening of the parasite, or by weakening of the host. Sometimes the same circumstances may affect both. In the Lily Disease and the Potato Disease a cold wet season, while it favours the fungus, produces a thin-walled, watery host, readily susceptible to attack. A similar epidemic of "damping off" by *Pythium* may at any time be induced by cultivation of Cress overcrowded, in moisture and heat (see p. 400).

FIG. 295.

Portion of the root of a Crucifer malformed owing to the presence of *Plasmodiophora*. (After Woronin; from Marshall Ward.)

The effect of the parasitic invasion may be the death of the host, where vital parts are destroyed, as in attacks by *Pythium*, or *Armillaria mellea* (Fig. 292). But in many cases the attack is tolerated by the host, with only partial injury. It is often the leaf, or only certain tissues of the leaf, which are attacked, the result being a loss of efficiency by the host while the parasite gains access to the sources of supply. The host may even be stimulated to greater action, with the effect of swelling and extra divisions of its cells. The result may be various *malformations*, such as are seen in the familiar leaf-curl of Peaches or the swollen patches of Cluster-Cups (Fig. 337, p. 437).

The attack may, however, be upon the stem or root, or even the ovary. The effect is to produce swellings and malformations such as those of the roots of Crucifers, called "Club-root" (Fig. 295), or of the grain of "Ergot of Rye" (Fig. 293).

Some Fungi lead a constantly parasitic life, as the Rusts (Uredineae) do. Others are as constantly saprophytic, like the Saprolegniae. Others again may be sometimes the one, sometimes the other: and this may be so in the individual life. Thus *Pythium*, the "Damping off Fungus," attacks the seedling-host and kills it, but continues to live on the corpse (p. 400). It is first parasitic, then saprophytic. But the converse has been shown in *Sclerotinia sclerotiorum*, where a period of saprophytic nourishment is a necessary condition for its success in perforating the living host. It has been regarded as a fungus which is in course of "education" for passage from the saprophytic to the parasitic life. It is thus impossible to lay down any general rule of priority for parasitism or saprophytism: and it is only in certain cases that the one habit or the other can be assigned to any definite systematic group.

The life of Fungi is very varied. No organisms show greater resource in the acquisition of food. But their propagative methods are no less effective. Originally sprung from aquatic organisms, some show this clearly in their reproductive organs, which often involve *motility of zoospores in external water*, as in many Phycomycetes. But the more advanced types are commonly propagated by means which are clearly related to *life in the air*. In most Eumycetes minute bud-like bodies called *conidia* are borne in prodigious numbers, and they are small enough to be carried as dry dusty bodies through the air. The conidia of common Moulds are present everywhere about the dwellings of man: so that any suitable medium is apt to be invaded by them, provided the conditions of temperature and moisture are favourable. This explains the apparently spontaneous appearance of moulds on bread, leather, jam, etc., when kept in a confined space. The spread of fungal diseases is usually by similar means. One of the most surprising facts in this relation is the very constant recurrence of certain Fungi on isolated and restricted media. The horns of sheep cast away on a Scottish hill-side are commonly invaded by a horn-destroying Fungus, *Onygena*. But any one such horn may be isolated far from any visible source of infection. This shows the ubiquity of fungal germs. It suggests also the other side of the question, the vast number of germs that never find the suitable *nidus*.

Like other Thallophyta, Fungi may bear *organs of sex*, which lead up to the production of accessory spores with attendant reduction division. They thus show a life-cycle with successive phases comparable with that of autophytic plants. But in many of these which are regarded as the most advanced, and especially in the larger Agarics, sexual propagation is not normally carried out and the organs of sex may be actually absent. Various stages of functional perversion, and of atrophy of the sexual organs, are illustrated by less advanced Fungi. Most Fungi have thus two forms of propagative organs in their life-history: *conidia*, which are minute bud-like bodies easily detached from the parent, which they produce vegetatively; and *spores* (p. 401), which are formed as a consequence of a sexual process, or take the same place in the life-cycle in those cases where sexuality is absent. Some Fungi have more than two modes of propagation. The propagative bodies may differ in appearance, though they are really mere stages in one life-history: for instance, conidiophores and spore-fruits. Sometimes in parasitic Fungi these stages may appear on different hosts, as in the Rust of Wheat, where the one stage is on the Wheat, another on the Barberry (p. 432). Naturally, before the facts were fully known, such stages were liable to be regarded as different Fungi, and described by distinct names. For instance, the Rust on Wheat was called *Puccinia*, while the stage on the Barberry was described as *Aecidium*. Later these were proved to be merely parts of the same life-history, and they were given a single designation. But in many Fungi the life-history

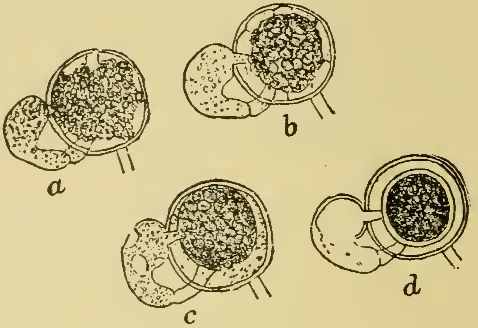

FIG. 296.

Development and fertilisation of the ovum of *Pythium*. The granular protoplasm of the oogonium (*c*) collects into a ball, and the antheridium sends in a fertilising tube. In (*b*) and (*c*) transmission of contents into the ovum is shown. (*d*) The ovum has formed a cell-wall, and lies loosely in the oogonium. Highly magnified. (After Marshall Ward.)

is not yet fully known, often because one stage is commoner, or more obvious than another. Those Fungi in which the knowledge of the life-cycle is incomplete are called "*Fungi Imperfecti*", and they constitute a large proportion of the described species.

It will be gathered from the preceding pages that the Fungi provide characters, vegetative, propagative, and also functional, which will serve for their classification, though the data may often be insufficient for a final decision. Those Fungi which have *non-septate hyphae* are called Phycomycetes. Their structure is relatively coarse, and corresponds in this, as well as in the absence of septa, to what is seen in the Siphonales. They are divided into two sub-classes, according to the sexual organs. Where these can be distinguished as male (*antheridia*) and female (*oogonia*) they are called *Oomycetes* (Fig. 296). To these belong such parasites as the *Peronosporeae*, for instance, the Potato Fungus (*Phytophthora*); also the saprophytic family of the *Saprolegniae*, which includes the "Damping-off Fungus" of seedlings (*Pythium*). The latter live on vegetable or animal matter decaying in water. In the second sub-class there is *conjugation* of similar bodies to form a *zygospore*, as in the common Mould, *Mucor* (Fig. 297). These are designated the *Zygomycetes* and have been referred in origin to Algae of the type of the living Siphonales. The Phycomycetes are dealt with in Chapter XXV.

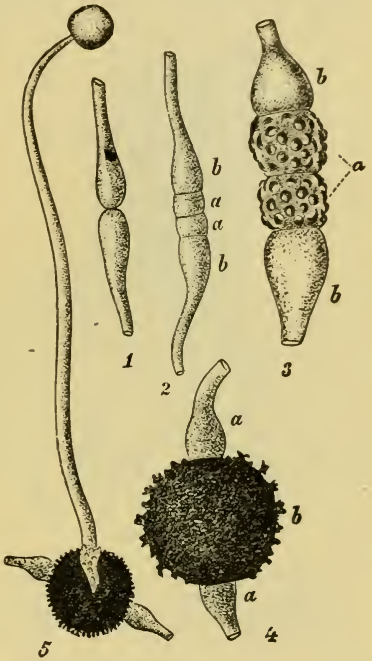

Fig. 297.

Mucor Mucedo. Different stages in the formation and germination of the zygospore. 1 = two conjugating branches in contact. 2 = septation of the two conjugating cells. 3 = more advanced stage: the conjugating cells are still distinct from one another. 4 = ripe zygospore (*b*) between the suspensors (*a*). 5 = germinating zygospore with germ-tube bearing a sporangium. (After Brefeld.) (1-4 × 225, 5 × *circa* 60.) (From Strasburger.)

The great bulk of the Fungi are probably distinct in Descent from these. The structural distinction lies in their *septate hyphae.* The constituent "cells" between the septa vary in length and in nuclear condition. In some cases the nuclei are small and numerous: in others there is a pair of nuclei, or only one. These septate Fungi are sometimes called Eumycetes. The sexual organs of many of them show a resemblance to those of Red Algae, especially when there is a *female oogonium* with *trichogyne*. But in many of them such organs of sex have not been found, and there is reason to believe that they are no longer sexually produced. They are divided into two sub-classes, according to the method of production of their spores. In the first the spores are commonly eight in number, and are produced internally within a closed body, the *ascus*. These are called *ascospores*, and the sub-class the Ascomycetes (Fig. 298). To them belong many Moulds, Ergot of Rye, the edible Truffle, etc. Examples will be described in Chapter XXVI.

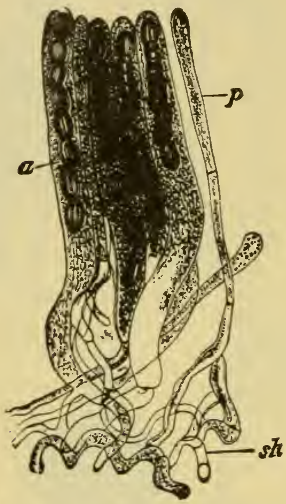

Fig. 298.

Portion of the hymenium of the Morel (*Morchella esculenta*). *a* = asci, each containing eight ascospores. *p* = paraphyses. *sh* = subhymenial tissue. (× 240.) (After Strasburger.)

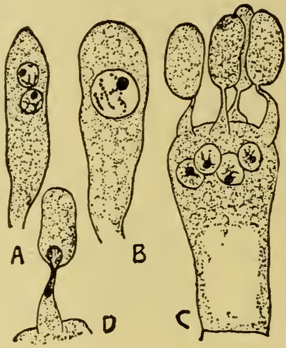

Fig. 299.

Honey Agaric (*Armillaria mellea*). *A*, young basidium with two primary nuclei. *B*, after fusion of the two nuclei. *C* = a basidium of *Hypholoma appendiculatum* before the four nuclei derived from the secondary nucleus of the basidium have passed into the four basidiospores *D* = passage of a nucleus into the basidiospore. (After Ruhland.) (From Strasburger.)

In the second sub-class the spores are produced externally, commonly to the number of four, upon a body called a *basidium*. They are called *basidiospores*, and the sub-class the Basidiomycetes (Fig. 299). To them belong the Mushrooms and Puff-balls ; also the large series of parasitic Rusts, which being more primitive in their characters than the rest, give probable clues to the origin of the Basidiomycetes. They will be described in Chapter XXVII. Both the ascospores and the basidiospores are to be held as equivalent to *tetraspores*, being related either actually to a process of nuclear reduction, or at least holding a position in the cycle following closely upon the period when reduction would occur in a normal cycle where sexual organs are present.

The Fungi may then be grouped thus :

Class.	Sub-Class.	Examples.
Phycomycetes (non-septate)	*Oomycetes*	*Pythium*, *Phytophthora*.
	Zygomycetes	*Mucor*, *Empusa*.
Ascomycetes (septate ; with asci)		*Sphaerotheca*, *Eurotium*, *Peziza*.
Basidiomycetes (septate ; with basidia)		*Puccinia*, *Ustilago* *Agaricus*, *Boletus*, *Scleroderma*.

A Note on Terminology.

Propagative cells of Fungi which are produced asexually and externally are usually described as *conidia* : those produced within a spore-case or *sporangium* are usually described as *spores*. The stalks or filaments bearing sporangia or conidia are described as sporangiophores and conidiophores respectively. Some spores may be no more than vegetative organs of reproduction, but others, such as *ascospores* and *basidiospores*, follow on a process, or substitute process, of sexual reproduction and occur at a definite point in the nuclear cycle.

CHAPTER XXV.

PHYCOMYCETES.—(*a*) OOMYCETES.

Two of the commonest and most destructive of fungal parasites will serve to illustrate the Oomycetes. They both belong to those non-septate Fungi which habitually produce distinct male and female organs, comparable to those seen in the higher Siphonaceous Algae, such as *Vaucheria*. Like them also they include in their life-history a stage where zoospores are motile in water. This, together with their close dependence upon moisture during vegetation, justifies for them the name *Phycomycetes*, or Alga-like Fungi.

THE "DAMPING-OFF FUNGUS" (*Pythium debaryanum*).

When Mustard and Cress are sown thickly, and kept too warm and damp, the seedlings are liable to the disease of "damping-off", the plants quickly rotting with an unpleasant smell. Many other seedlings, and especially Cucumbers and Melons, are subject to it; in fact, the disease is one of the commonest difficulties of the gardener, and ruins the efforts of many amateurs. It makes its appearance at definite spots in the seed-beds, and if not checked it spreads thence in ever-increasing circles. The first sign is the collapse of a seedling, owing to the shrinking of its cortex, usually at some point above the soil-level, the stem being no longer able to support the weight above (Fig. 300). If the diseased plant be examined microscopically its tissues will be found to be riddled through and through by rather coarse colourless threads, enclosed by a cell-wall and filled with

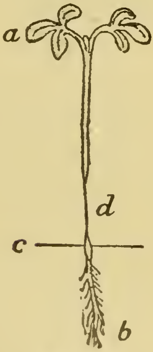

FIG 300.
A young Cress-seedling attacked by *Pythium* at *d*, just above the ground-line *c*. *b* = root. *a* = cotyledons and plumule. (Nat. size.) (After Marshall Ward.)

granular protoplasm which contains numerous nuclei. The threads traverse the cell-walls of the host with the greatest ease (Fig. 301), while collapse of the cells and loss of mechanical firmness lead to the falling over of the diseased plant. Left to itself in moist air the disease may spread from plant to plant, the hyphae passing out from the tissues and forming cottony growths through the damp air: they are coarse enough to be seen with the naked eye. The affected seedlings soon become a putrid mass of decay. The fungus that causes the trouble is *Pythium debaryanum*, which belongs to the large family of the Peronosporales. Most of these plants live actually in water, and cause decay in submerged plant- and animal-matter. One of them, *Achlya*, appears with a high degree of certainty on dead flies, if left floating in foul water.

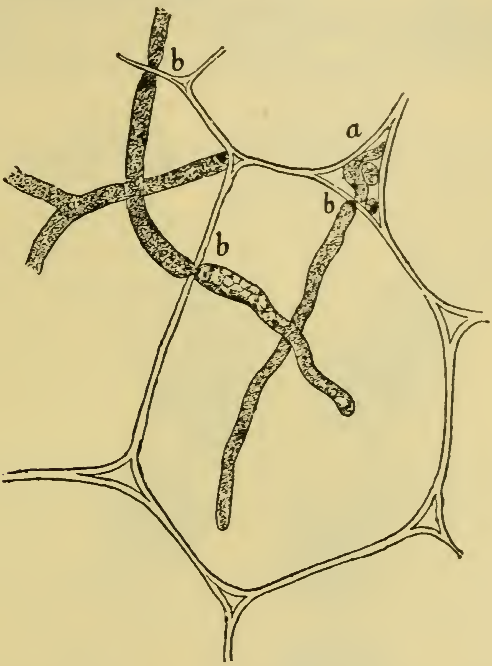

FIG. 301.

Small portion of cellular tissue of a *Potato*, showing the passage of the hyphae of *Pythium* through the cell-walls at *b*. At *a*, hyphae are seen in an inter-cellular space, one of which has then entered the large cell. Highly magnified. (After Marshall Ward.)

Pythium propagates both vegetatively and sexually. The vegetative propagation is by sporangia (Fig. 302, *c*), formed usually from the ends of the hyphae, by their swelling to an oval form. They contain fine-grained protoplasm and are shut off by a septum. The sporangium is readily detached and germinates directly if the circumstances are favourable. It then grows out into a fresh hypha which may directly infect a new victim. In other circumstances the germinating filament may expand into a spherical body, and the contents passing into it undergo division into a number of *zoospores* capable of movement (Fig. 303). These escape by rupture of the vesicle as minute colourless, kidney-shaped bodies with two active cilia. Provided water is present, they can swim to and even climb up the stem of other seedlings, and, coming to rest, perforate the superficial

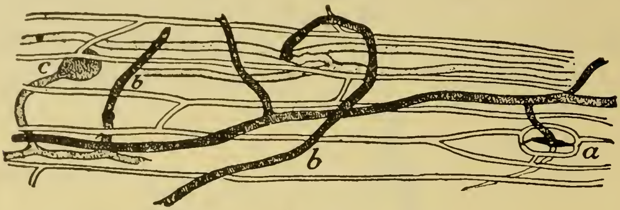

FIG. 302.

Portion of tissue near *d* in Fig. 300, highly magnified. The hyphae are seen running in all directions; at *a*, one passes through a stoma; at *c*, a sporangium is about to form. (After Marshall Ward.)

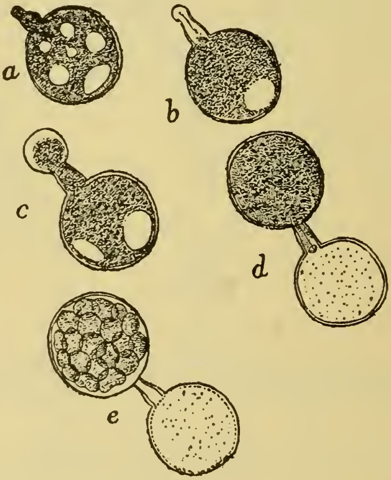

FIG. 303.

Germination of a sporangium of *Pythium debaryanum* in water. The tube put forth at *a* begins to swell at the end (*b*, *c*), and dilates (*d*), receiving all the protoplasm, which rapidly breaks up into zoospores (*e*). The whole process occupies about a quarter of an hour. Highly magnified. (After Marshall Ward.)

cell-walls, causing a new infection. It is in this way that the attack commonly appears some way up the stem. This method of propagation may be continued throughout the season.

It is found that the disease is liable to reappear in the following year in seedlings grown on soil that has been badly affected before. This has been explained by the discovery of an alternate mode of *sexual propagation*, which produces *oospores*: these retain their vitality through the winter. If an infected plant be kept moist, or even immersed in water for a few days, the hyphae begin to form swellings at their ends, like the sporangia but larger (*oogonia*). Presently in these the protoplasm begins to draw away from the wall, and rounds off as a central sphere (the *ovum*). Meanwhile another branch, or the end of another hypha, grows up with a smaller swelling, which is also cut off by a septum (the *antheridium*). It comes into contact with the first, and puts out a slender tube which penetrates the cell-wall and extends to the ovum (Fig. 304, *b*). This is the *fertilising tube*, which transmits its contents into the ovum. After fertilisation the zygote surrounds itself with a cell-wall, which soon thickens, but retains a smooth surface. This is the *oospore*, which can retain its vitality through the winter (Fig. 304, *d*). The oospores will not germinate at once, but require a period of rest. In the spring under favourable conditions the thick wall bursts and a hypha is produced, which soon develops sporangia and zoospores as usual. The initial infection of cultures of seedlings in each year is from this source, the resting spores being present in the soil. But besides this the fungus can continue its life as a saprophyte . for its activity does

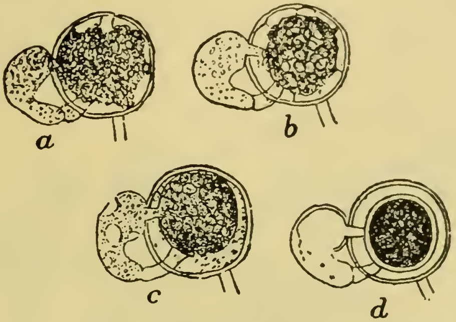

FIG. 304.

Development and fertilization of the ovum of *Pythium*. The granular protoplasm of the oogonium (*c*) collects into a ball and the antheridium sends in a fertilising tube. In (*b*) and (*c*) transmission of contents into the ovum is shown. (*d*) The ovum has formed a cell-wall, and lies loosely in the oogonium. Highly magnified. (After Marshall Ward.)

not end with the death of its host. There is in fact no absolute line between the parasitic and the saprophytic habit.

The risk of attack on the seedlings may be reduced by avoiding too close sowing and too moist culture; also by avoiding the use of soil in which infected seedlings have been raised. The risk may be further reduced by raising the soil before sowing to a temperature that will kill all the germs that it contains.

The Potato Fungus (*Phytophthora infestans*).

The Potato Fungus is the cause of what is commonly known as the "Potato Disease," which is always a risk to the crop in damp, warm seasons. In the years 1845-1850 the disease already known in America assumed epidemic virulence in Ireland, causing the great famine. Since that time the potato crop has never been entirely free from it. The disease makes its appearance upon the leaves and stems as spots at first small and pale-coloured, but as they enlarge the centre of each becomes brown, and extends, though still with a pale margin, till the spots run together, and the whole leaf or even the whole shoot may be affected (Fig. 305). If leaves with young infected patches be examined on a damp still day, or better, if they be kept in moist still air under a bell-glass, white glistening filaments will be found on the lower surface. They are large enough to be seen with the naked eye, and are the *sporangiophores* of the fungus. They bear

Fig. 305.

A Potato-leaf, showing the spots and patches of "Potato-disease", due to *Phytophthora infestans*. In the darker patches the tissues are quite dead. The margins of the spots would show the hyphae of the fungus projecting from the surface. (After Sorauer; from Marshall Ward.)

numerous small white powdery bodies, which are really comparable with the sporangia of *Pythium*; these are very readily detached. These sporangiophores spring from the mycelium, which permeates the mesophyll of the leaf in the diseased patch (Fig. 307). The mycelium consists of coarse non-septate, branched hyphae, which traverse the intercellular spaces, coming into close contact with the moist walls of the cells. They are also able to penetrate the softer middle-lamella of the cell-walls, where two cells adjoin, and this brings them into still closer relation to the cells, and the nourishment which these can supply (Fig. 306). Though the cells of the potato are not as a rule perforated, they lose their vitality and collapse, probably owing to a toxic influence. The brown discolouration at the centre of the infected spots is due to their decay.

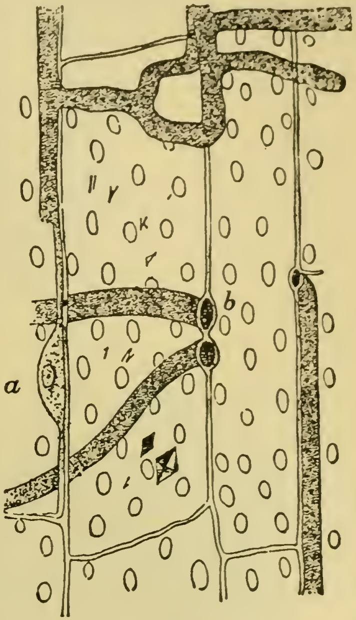

Fig. 306.

Piece of the tissue of the stem of a Potato-plant, showing the hyphae of *Phytophthora* penetrating the middle lamella of the cell-walls. *a* = nucleus of a cell. Highly magnified. (After Marshall Ward.)

The rapidity of the spread of the disease is one of its most surprising features. The fact that it habitually spreads down the prevailing wind indicates that it is due to wind-borne sporangia. The *sporangiophores* project through the stomata on the lower surface of the leaf and branch repeatedly (Fig. 307). The end of each branch may swell into an inverted pear-shaped *sporangium*, which is constricted off from its very thin stalk. If growing in still air the first sporangium may be turned aside, the stalk growing on sympodially, and proceeding to form a second sporangium, and so on (compare Fig. 179, p. 258). Thus a succession of sporangia may be produced for a considerable time, each readily detachable and easily borne by the wind.

Germination takes place only in presence of moisture. The protoplasm of the sporangium divides into about ten parts, which by rupture of its apex escape into the water in the form of *zoospores*, very like those of *Pythium*; they are motile for a time by means of two cilia

(Fig. 308). Coming then to rest, the cilia are dropped: each zoospore rounds itself off, and, investing itself with a wall, puts out a hyphal tube. If this takes place on the surface of a potato leaf, as it well might do under conditions of rain or heavy dew, all is ready for the infection. This may be either by entry through the pore of a stoma or by direct perforation through the epidermal wall (Fig. 309). By either route the germ-tube of the parasite may reach the intercellular spaces and establish a new infection.

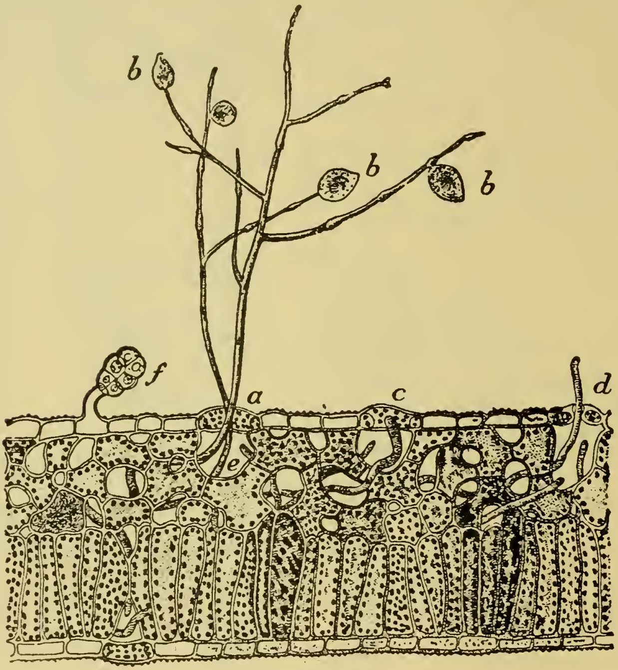

FIG. 307.

Section of Potato-leaf, in the tissues of which is the mycelum of *Phytophthora*. The hyphae run between the cells and send out through the stomata, *a*, *c*, *d*, the aerial branches which bear the sporangia, *b*. The dark parts of the tissue of the leaf show where the cells are dying from the effects of the parasite. Highly magnified. The normally upper surface of the leaf is here turned downwards. *f* is a glandular hair of the Potato. (After Marshall Ward.)

It is not only the leaves but also the stems and tubers of the Potato-plant that may be traversed. The mycelium spreads through the tissues down the haulms to the tubers. Young tubers may be infected by way of the "eyes", the lenticels or through wounds. Tubers thus infected may decay at once under moist conditions and when other saprophytic organisms are present, otherwise a dry-rot results. Tubers in the latter condition may be among those harvested. But such tubers often decay during the winter. If however, they are not heavily infected and are used as "seed" potatoes for a new crop, the mycelium perennating in the tubers provides a source of infection in that sporangiophores develop on short aerial

FIG. 308.

Stages of germination of one of the sporangia of *Phytophthora*. *a*, the ripe sporangium in water. *b*, protoplasmic contents breaking up into blocks, which separate and escape (*c*, *d*) as minute kidney-shaped zoospores (*e*), each with two cilia. *f*, *g*, the zoospores coming to rest, and losing its cilia. *h*, *i*, *j*, *k*, stages of germination of the zoospore. Highly magnified. (After Marshall Ward.)

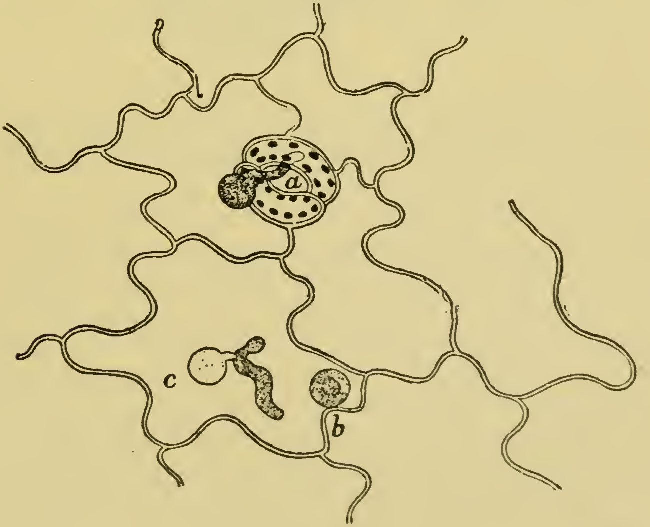

FIG. 309.

Germination of zoospores of *Phytophthora* on the epidermis of Potato. At (*a*) the germ-tube is entering a stoma. At (*c*) it bores directly through the cell-wall. Highly magnified. (After Marshall Ward.)

shoots which grow out from the tubers. There may be also other sources of reinfection. The control measures to be taken are to destroy by fire all infected haulms and leaves, to avoid carefully the use of tainted " seed " tubers ; and, as a preventive, to spray the young growing crop with suitable disinfectants, especially if the season is wet in the middle summer. But a more hopeful line of prevention is by the use of " immune varieties," which are able to resist the attack of the parasite.

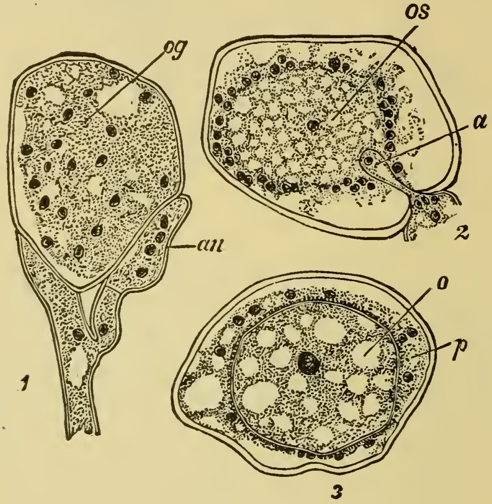

Fig. 310.

Fertilisation of the Peronosporales. 1. *Peronospora parasitica*, young multinucleate oogonium (*og*), and antheridium (*an*). 2. *Cystopus candida*. Oogonium with the central, uninucleate egg (*os*), and the fertilising tube (*a*) of the antheridium which introduces the male nucleus. 3. The same. The fertilised egg (*o*) surrounded by periplasm (*p*). (After Wager. × 666.) (From Strasburger.)

No mention has been made of sexual reproduction in the Potato Fungus. As a matter of fact sexual organs have not been proved to exist in *Phytophthora infestans* under normal conditions of life. Like some other plants it seems to be able to propagate itself indefinitely without the recurrence of sexual reproduction. But under special conditions of saprophytic culture the sexual organs have been produced, though it is still doubtful whether they are ever formed when the Potato Fungus is growing on the living host. In other members of the Peronosporales the details which have been frequently observed show a striking parallelism with those of *Vaucheria*. The sexual organs have been found in *Peronospora* and *Cystopus* to be formed within the host-plant (Fig. 310). The *oogonium* appears as a spherical swelling on the end of a hypha, while a thinner branch, arising as a rule below it on the same hypha, forms the *antheridium.* Each is shut off by a septum, and contains dense protoplasm with numerous nuclei. A single egg, or ovum, is differentiated in the middle of the oogonium, by passage of all the nuclei but one to a peripheral position. The *uninucleate ovum* is then delimited from the *multinucleate periplasm.* The antheridium penetrates the oogonium by means of a *fertilising tube*, the apex of which opens into the ovum, and transmits a single male nucleus (Fig. 310, *a*). The resulting zygote soon surrounds itself with a membrane, while the periplasm contributes to the thickening of its wall. A period of rest may ensue. On germination the contents of the zygote divide, giving rise to a number of *zoospores*, which may cause a fresh infection in the same way as those produced from the sporangia.

The parallel between this structure and that of *Vaucheria* is close as regards the origin of the uninucleate ovum. The method of fertilisation by a fertilising tube in place of the liberated spermatozoids moving freely in water, offers an interesting parallel with the pollen-tube in Seed-Plants. In both cases the male gamete is conveyed to the female by a method suitable for land-living plants. Comparison shows that both are modifications of organs originally developed to secure fertilisation through the medium of external water. The question will naturally arise whether any fungal type still shows a motile male gamete. This is found in *Monoblepharis*, a fungus that lives saprophytically in water (Fig. 311). Here a terminal oogonium contains a single ovum, which is fertilised by spermatozoids, each motile by a single cilium. This case is unique among Fungi. It holds a place comparable with the motile spermatozoids of the Cycads and Ginkgo, in that it gives evidence of the transition from an aquatic to a terrestrial type of fertilisation. (Compare Chapter XXXIV.)

The origin of such Phycomycetous Fungi as those described may have been from some Siphonaceous source. In the case of parasites the first step would be the adoption of an endophytic life, as in *Phyllosiphon.* This would be naturally followed by parasitic nutrition and loss of chlorophyll and chloroplasts. As regards the propagative organs, the sporangium of *Pythium* or of *Phytophthora* are such as to make for easy detachment and transport through the air. But it shows its real nature on germination by producing zoospores which are liberated in water. In this connection it may be noted that in the Peronosporales as a whole there is a marked tendency for the sporangium to become, or to behave as, an air-borne conidium, as in *Peronospora* in which zoospores are unknown. Sexual reproduction in the

Peronosporales is not unlike that seen in *Vaucheria*: the former do not liberate free spermatozoids but transfer a single gamete by a tube, as in the higher land-living Plants. The oogonium retains its character, as in *Vaucheria*. Such considerations may be held to justify the recognition of Fungi included among the Oomycetes as possibly of Siphonaceous origin, from types already advanced in their sexuality. On the other hand it has been suggested that the origin of the Phycomycetes is to be sought among the colourless Protophyta and that they have developed along lines parallel to, but independent of, those leading to the Green Algae.

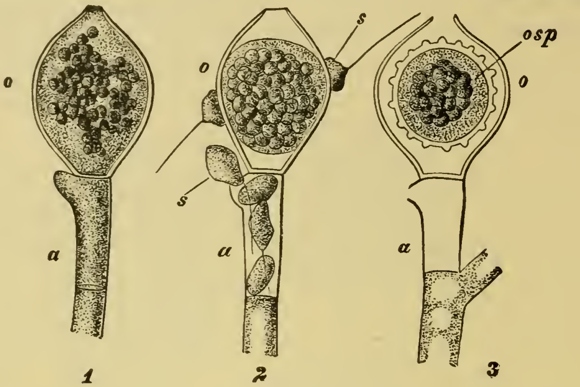

FIG. 311.

Monoblepharis sphaerica. End of a filament with terminal oogonium (*o*) and an antheridium (*a*). 1, before formation of the gametes. 2, spermatozoids (*s*) escaping and approaching the opening of the oogonium. 3, *osp*, ripe zygote and an empty antheridium. (After Cornu. × 800.) (From Strasburger.)

PHYCOMYCETES.—(*b*) ZYGOMYCETES.

THE MUCORS.

The Zygomycetes include many common Moulds. They are mostly saprophytes, though some of them are parasites not only on other plants and animals, but even on one another. They are characterised first by their coarse non-septate hyphae, but more particularly by the manner of their sexual reproduction, which results from the fusion of two similar, multinucleate branch-endings, to form a single large resting-spore, or *zygospore*. The chief representatives are the Mucors (Mucorales) found on decaying organic matter in moist circumstances. If moist bread, horse-dung, brewer's grains, or other organic substances be kept warm for a day or two under a bell-glass, Mucorineous Moulds will almost certainly appear. They are often of considerable stature. *Phycomyces nitens*, which comes commonly on brewer's grains, may be several inches in height, the coarse *sporangiophores* ending in *sporangia* easily seen with the naked eye.

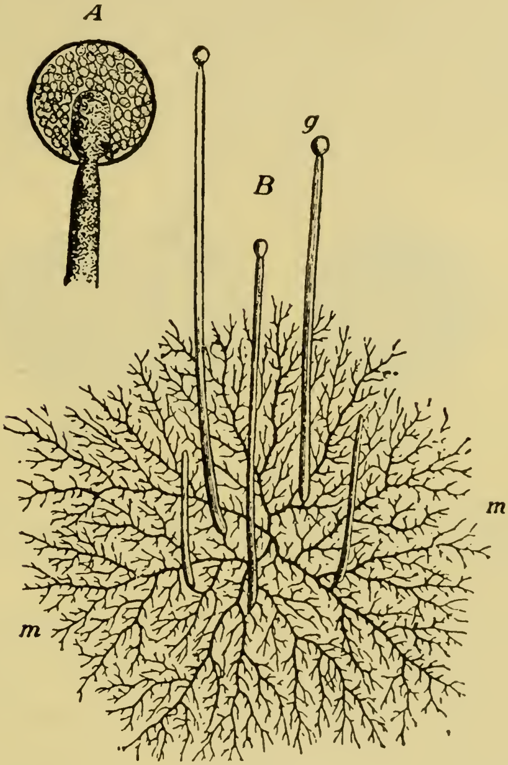

FIG. 312.

A plant of *Mucor*, showing the mycelium of branched hyphae (*m*) and sporangiophores (*g*). *A* is a single sporangium more highly magnified, containing spores. (After Brefeld.)

Another common type is *Empusa muscae* (Entomophthorales), which lives parasitically on the House Fly. In autumn the infected flies become sluggish, and finally resting on a window pane, or elsewhere, they appear as though surrounded by a white halo. This is formed by the conidia thrown off to a distance by the stalks that bear them, which radiate outwards from the body of the fly killed by the fungus in its vegetative stage. Thus, while most of the fungi of this group are saprophytes, some may be parasitic, even on animals.

If the stalks, or sporangiophores, of *Mucor*, or *Phycomyces* be followed to their base, they are found to arise from finer filaments forming a profusely branched *mycelium*, which traverses the substratum. A good idea of its nature is obtained by culture from the spore on a glass surface (Fig. 312). It is then seen how, starting from the spore as a centre, the mycelium may radiate outwards, with successively finer branches of its non-septate tubes. Each of the thick upright *sporangiophores* bears one sporangium on its end, which when ripe consists of a brittle external wall surrounding many spores embedded in a mucilaginous matrix, while centrally is a large columella (Fig. 313, 1). It is difficult to see this structure satisfactorily in ripe sporangia mounted in water, owing to the swelling of the mucilaginous matrix, which bursts the wall and scatters the spores (Fig. 313, 2). Their dissemination may thus normally take place by the agency of water, though *Mucor* can also disperse its spores in dry air.

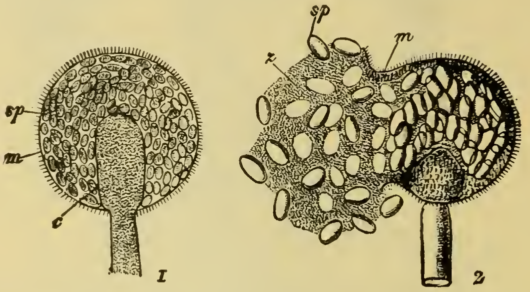

FIG. 313.

1, *Mucor Mucedo*, a sporangium in optical longitudinal section. *c* = columella. *m* = wall of sporangium. *sp* = spores. 2. *Mucor mucilagineus*, a sporangium shedding its spores; the wall (*m*) is ruptured, and the mucilaginous matrix (*z*) is greatly swollen. (After Brefeld, 1 × 225; 2 × 300, after v. Tavel.) (From Strasburger.)

Though this is the case for the typical Mucors, there are many Mucorineous Fungi in which the dissemination of spores is through the air. They are found among those smaller forms which live parasitically on the larger Mucors, and frequently appear upon old cultures of these as flocculent growths attached by suckers to their sporangiophores (*Chaetocladium*, *Piptocephalis*). In these parasites the sporangiophores are profusely branched, and they bear many unicellular, conidium-like bodies, easily detached, and carried by the wind. That they are really sporangia of very reduced form is indicated by intermediate types, with minute sporangia, which contain a few spores. Even *Mucor* itself, when starved, may produce such small sporangia, which show how the still simpler condition may arise. The family thus illustrates a transition from water-dispersal, by spores produced internally in few large sporangia, to dispersal through the air of sporangia reduced to a single cell.

and produced in larger numbers. The latter may be held as a derivative condition.

A very peculiar mode of dispersal is by forcible projection of the whole sporangial head. This is seen in *Pilobolus*, whence its name. This fungus appears with a high degree of certainty on dung kept under a bell-glass. The sporangium is constructed like that of *Mucor* ; but at ripeness it breaks away from the stalk, which has become turgid with sap under osmotic pressure. By the principle of the squirt this fluid is thrown out to a distance of some inches, carrying with it the sporangial head. A somewhat similar projection happens in *Empusa*, but here it is a sporangium reduced to the state of a single " conidium " that is discharged ; these conidia by adhering to any solid body, cause the halo previously mentioned. There is thus a considerable variety in the methods of dissemination in the Zygomycetes.

The spores of many of the Mucorales contain more than one nucleus. There are said to be two in *Pilobolus*, and many in *Sporodinia*. In the latter, which grows parasitically on large saprophytic species of *Boletus*, the sporangial head is first shut off by a septum : this becomes convex, and forms the central columella. The large polynucleate mass of protoplasm filling the head then undergoes cleavage into a number of parts, each containing several nuclei. These round themselves off and form the spores. Such cleavage of the contents of the sporangium is the typical method of formation of spores in the Mucorales. The final result is the same in all : viz. germination under favourable circumstances to form a new non-septate, and polynucleate mycelium.

The mycelium of *Mucor* may vary in its mode of growth according to the medium. If it be submerged in fluid it shows the *Oidium*-condition, where, dividing into short lengths, each of these may increase by a process of budding not unlike a yeast. Or again, if the conditions are unfavourable, the starved mycelium may divide transversely, and the portions become thick-walled, as so-called *Chlamydospores*, a state reminiscent of the behaviour of *Vaucheria geminata* under like conditions (p. 372). When the circumstances are again favourable, either of these states may pass over into the normal mycelium again.

The chief alternative mode of propagation is, however, by the production of *Zygospores*. In many Mucorales this is normally a rare event, in others common. One dominating circumstance, the fact of a difference of the nature of sex, has been observed, which may explain the rarity of its occurrence. The essential feature is the coalescence of the ends of two equal club-shaped hyphae to form a single fusion-body, which is the zygospore. Two hyphal branches (*progametangia*), either of the same mycelium (*Sporodinia*), or of distinct mycelia (*Mucor stolonifer*, and other Mucors), growing towards one another, meet at their apices (Fig. 314). From the end of each a conjugating cell or *gametangium* containing protoplasm with many nuclei is cut off by a transverse septum from the basal *suspensor.* Their apices flatten, and the gametangia fuse, the wall separating them being absorbed. Many nuclei are involved; these fuse in pairs and the result on maturation is a *zygospore* (Fig. 314, 4). The large protoplast is stored with nutritive material, while the outer wall thickens, often forming characteristic bosses externally (Fig. 314, 3, 4). In this condition the zygospore may undergo a period of rest, and is resistant to unfavourable conditions. But suitable conditions induce germination, and they determine what follows. Sometimes there is a formation of a vegetative mycelium, sometimes, as in Fig. 314, 5, an immediate formation of a sporangium: the spores produced in the latter are the first stage of the new gametophyte.

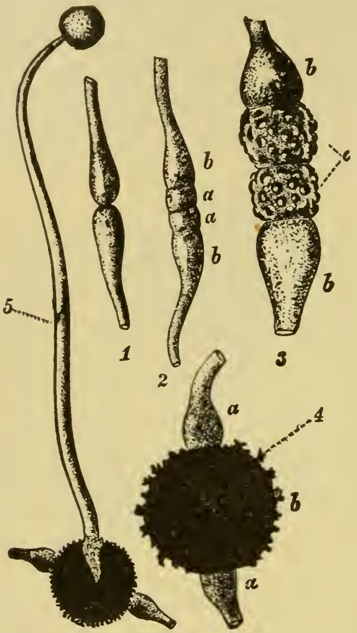

FIG. 314.

Mucor Mucedo. Different stages in the formation and germination of the zygospore. 1 = two progametangia in contact. 2 = septation of the two gametangia. 3 = more advanced stage; the conjugating cells are still distinct from one another. 4 = ripe zygospore (*b*) between the suspensors (*a*). 5 = germinating zygospore with germ-tube bearing a sporangium. (After Brefeld.) (1-4 × 225; 5 × *circa* 60.) (From v. Tavel.) (From Strasburger.)

A remarkable fact is the occurrence in some Mucors of "*Azygospores*," that is, bodies that resemble zygospores in their structure and covering, but are produced without any fusion.

According to their power and readiness for conjugation the Mucorales have been divided into two groups. The *Homothallic*, which form zygospores on two branches of the same mycelium, so that by sowing a single spore zygospores may be obtained. This is seen in *Sporodinia*, in which the zygospores may often be obtained in the open in autumn. Others are called *Heterothallic*, where the presence of two individuals of two different types is necessary for the production of zygospores (*Rhizopus*, *Mucor*, *Phycomyces*) These types are distinguished as + and −, rather than as male and female, because in many species there is no recognisable difference of form or structure, but only of function. If either be cultivated pure, and apart, the mycelium bears no zygospores. But if cultures of the + and − types be started apart and meet, a profuse formation of zygospores appears along the line of junction (Fig. 315). The facts thus disclosed give a ready explanation of the rarity of zygospores in certain cases, and their frequency in others.

The facts of the life-history in the Zygomycetes show a less direct dependence of these plants on external liquid water than in the Oomycetes, for there are no zoospores motile by cilia. Still the dissemination of the spores in the Mucors is through swelling of mucilage in water, or ejection where liquid pressure gives the propulsive power. The series with branched sporangiophores, and wind-borne conidium-like bodies is a step still further away from dependence upon the water-medium. Comparison suggests for the more primitive sporangia such as *Mucor* an origin from a sporangium like that of a Siphonaceous Alga. The loss of motility of the spores which is involved is readily understood in organisms living in moist air in place of water.

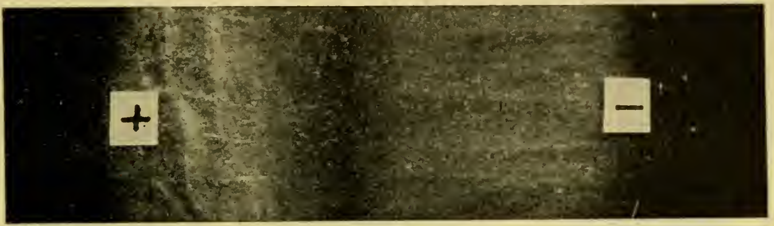

FIG. 315.

Result of a plate-culture of the heterothallic *Mucor hiemalis*, made by Prof. Drummond. + and − strains were started on opposite sides of the plate. The dark line transversely between these shows where the cultures meet, and the zygospores were formed. (½ natural size.)

The formation of zygospores presents the unusual condition of the fusion not of single cells as in the Conjugatae, but of coenogametes to form a coenozygote. There is reason to believe that numerous nuclear fusions take place : in fact that the formation of the zygospore is a fusion of gametangia, rather than of single gametes. If two gametangia, like those of *Codium* or *Bryopsis*, were to fuse as a whole, in place of opening and shedding their gametes to fuse singly, the result would be very like what is seen in the Mucorales.

If we consider the sexual reproduction of the Phycomycetes as a whole, the Zygomycetes and the Oomycetes would appear to represent two distinct lines of evolution, the Oomycetes showing the more advanced condition, in which sexual differentiation extends to the gametangia themselves.

CHAPTER XXVI.

ASCOMYCETES.

The Fungi belonging to the Ascomycetes, the first sub-class of the septate section, are very various in habit. Many are parasites, often on leaves and stems of Flowering Plants: for instance the Mildews, such as *Sphaerotheca*. Others are saprophytes, such as the small and prevalent Moulds, *Aspergillus* and *Penicillium*. Others again form large fruiting bodies, such as those of *Peziza*, or the edible Truffle (*Tuber*), or the Morel (*Morchella*). Some are parasitic on animals, as in the case of *Cordyceps*, which invades caterpillars and the larvae of Cockroaches. The Ascomycetes are thus not only a large but very varied group of Fungi.

FIG. 316.

Portion of the hymenium of the Morel (*Morchella esculenta*). *a*=asci. *p* = paraphyses. *sh* = sub-hymenial tissue. (× 240.) (After Strasburger.)

Their characteristic feature is a club-shaped or oval body, the *Ascus*, within which *Ascospores* usually to the number of eight are contained (Fig. 316). Such asci may occasionally be produced singly in very simple forms, such as *Sphaerotheca*; but they are commonly associated together in large numbers, in fruit-bodies of various form. In many cases the development of the asci has been found to follow on the formation of *sexual organs*, of which the female is an *oogonium*, sometimes with a receptive *trichogyne*, as in the Red Seaweeds. The ascospores may therefore be held to be of the nature of post-sexual tetraspores formed after reduction carried out in the nuclear divisions within the ascus. In other cases the sexual organs have not been found, and there is reason to believe that normal sexuality has passed into abeyance in many of these parasitic and saprophytic plants, though the asci still remain as morphologically representing the products of the oogonium. In most of these Fungi there is also propagation by means of minute *conidia*, which are buds not sexually produced. They are borne on *conidiophores*, which are various and characteristic in form.

The young unicellular ascus has originally two nuclei, which later fuse. The resulting nucleus then typically undergoes three successive divisions involving a process of reduction. Each of the eight nuclei then becomes a centre of free cell-formation; an area of cytoplasm around each is delimited by a cell-wall, leaving a residuum of cytoplasm which embeds the spores till ripeness. Ultimately, the spores are liberated, in the majority of cases by forcible ejection, more rarely by disintegration of the ascus-wall. Sometimes the spores are shot out for a distance of a foot.

THE MILDEWS (*Erysiphales*).

The Mildews are Ascomycetous Fungi, parasitic on the leaves of various plants. They take their name from the fact that the patches

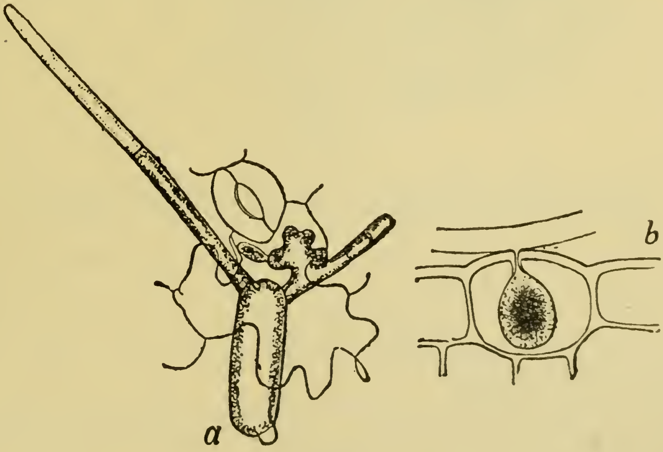

FIG. 317.

a = a germinating conidium of an *Erysiphe*, showing how the young germ-tube at once attaches itself by a haustorium to the epidermis. *b* = a haustorium in section. (After De Bary, highly magnified.) (From Marshall Ward.)

of the disease appear white and floury, owing to the formation of their *conidia*, produced from a cobweb-like mycelium, which grows on the outside of the infected leaf. Its hyphae are attached to the leaf by *haustoria*, which penetrate the outer walls of the epidermal cells, the connection being established immediately on the germination of the infecting conidium (Fig. 317). As the season progresses small dark specks make their appearance, large enough to be seen with the naked eye. These are the fruits, or *perithecia*, each containing one or more *asci*. In damp weather these parasites develop quickly, a fact that has drawn almost superstitious attention to them. A very common example is seen in *Podosphaera clandestina*, which infests the leaves of the Hawthorn in any warm and wet autumn.

Fig. 318.

Piece of epidermis of Hop, showing mycelium (*b*) and perithecia (*a*) of the Hop-mildew on its surface. *h* is a large hair. At (*b*) the first beginnings of a perithecium. Magnified. (After Marshall Ward.)

A still simpler one, *Sphaerotheca Humuli*, causes a disease on the cultivated Hop, though it may occur also on many other plants. The effect of Mildews on the infected plant is that the diseased areas take a pale colour, nourishment being withdrawn from them. But there is no malformation.

After the Hop Mildew has established itself, and formed a branched, septate mycelium, certain hyphae grow vertically upwards from the leaf-surface without branching: they segment transversely into short lengths, which become detached in basipetal series as *conidia*, easily removed when ripe by a breath of air. They will germinate on a moist leaf, and cause new infections during the summer (Fig. 317). But later the fruit-bodies (*perithecia*) appear, which provide for the winter's rest (Fig. 318). They arise where the branched hyphae cross or touch one another. Two short branches grow erect, and a uni-nucleate cell is shut off from the end of each. One which is larger is recognised as the *oogonium*, the other which is smaller is the *antheridium*. They fuse, and the nucleus of the latter passes into the former, which then becomes surrounded by an investment of up-growing filaments, forming an outer shell to the fruit. Meanwhile the oogonium divides into a row of cells, and the penultimate cell forms the *single ascus*, with eight *ascospores* (Fig. 319, *C. s.*). Protected by the outer shell, and attached by long filaments which grow out from their surface, the fruits remain fixed to the leaves, which fall and rot. In the following spring they rupture, and the ascospores are shed. In favourable conditions germination ensues.

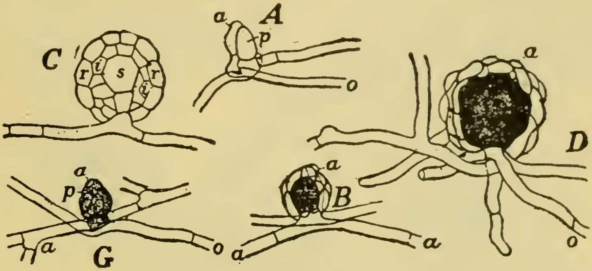

FIG. 319.
Various stages in the development of the perithecium of the Hop-mildew, showing the contact of the two short branches (*A*), one of which (*p*) gradually becomes invested by enveloping branches (*B*). The envelope forms the wall of the perithecium, and the single ascus is formed from the enclosed branch. (*C. D.*) Highly magnified. (After De Bary.) (From Marshall Ward.)

This is one of the simplest of Ascomycetous fruits. In *Erysiphe* and others hyphae are produced from the female organ, and these bear numerous asci. The fruit-bodies of the larger Ascomycetes are in general more complex.

Moulds (*Plectascales*).

If bread, or any organic body such as leather or jam, be kept in a closed damp space, for instance under a bell-glass, or in a damp cupboard, it will become mouldy. This is due to the germination upon it of air-borne germs of Moulds that are always present about the dwellings of man. These Moulds at first form isolated patches on the bread, which then run together, covering the whole surface, and also penetrating inwards. There are many different Moulds that may thus appear, and they grow mixed together, or they may be segregated into distinct, purer patches. Where this occurs the two commonest are readily distinguished by their stature and colour. Low-growing, velvety, blue-green patches are *Penicillium crustaceum*; coarser, olive-green patches, with mop-like heads, of size visible to the naked eye, are *Eurotium* (*Aspergillus*) *herbariorum*. As the patches of the latter grow older, minute yellow specks may appear upon them: these are the *Eurotium*-fruits, a stage originally described as a distinct fungus. A breath will carry away the numerous *conidia* from such a culture in a dense cloud. They form part of the ordinary dust of dwellings, and this accounts for the constant appearance of the Moulds on organic substrata where the conditions are favourable to heir growth, as in the moist air in a close cupboard, or under a bell-jar.

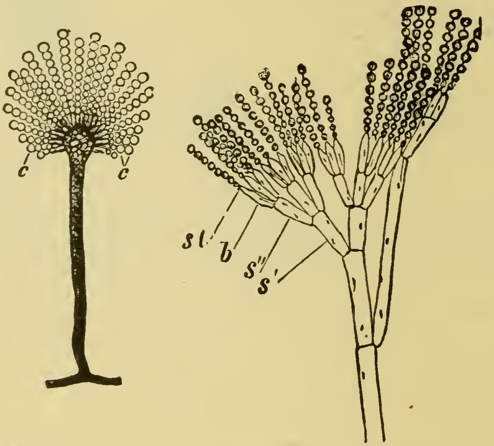

FIG. 320.

Conidiophores of *Eurotium herbariorum* (to the left) and of *Penicillium crustaceum* (to the right). (From Strasburger.) Highly magnified.

If a sample of *Eurotium* be taken, the branched and septate mycelium is seen to ramify over and penetrate into the organic substratum, deriving nourishment till able to propagate. Stout branches then rise upright as *conidiophores*, which swell upwards into a spherical head (Fig. 320). On this numerous conical *sterigmata* bud forth, each giving rise to a chain of *conidia*, formed in basipetal succession. The oldest is distal, and successively others are abstricted off: an arrangement which provides for the due nourishment of each, and the ready removal of those that are mature by any breath of air; for these minute polynucleate conidia are very lightly attached. They germinate readily in water or damp air, and the mycelium permeates any nutritive medium; thus they serve for the quick spread of the

Mould. The corresponding conidiophores of *Penicillium* are constructed on a similar plan, but are much smaller. Instead of bearing a mop-like head, they are repeatedly branched, giving them a brush-like appearance, while from the end of each branch a basipetal chain of conidia is abstricted, as before (Fig. 320).

The alternative method of propagation follows in *Eurotium* on a rise of temperature, and results in the production of small yellow fruits. When ripe each contains numerous asci, and spores. Similar fruits are formed also in *Penicillium*, but more rarely. The development originates in either case from a twisted oogonial branch, which is associated with an *antheridium*. As in *Sphaerotheca* these sexual organs become enveloped in a pseudo-parenchymatous covering, derived from the mycelium that bears them. The oogonium divides into a number of cells, from which strong hyphae arise. These are nourished by the surrounding tissue, and produce the numerous oval *asci*, each with eight *ascospores*. In *Penicillium* the structure of the fruit-body is more complicated than in *Eurotium* (Fig. 321). In either case the result at ripeness is that the fruit appears as a dry spherical sac, filled with ascospores set free by the disappearance of

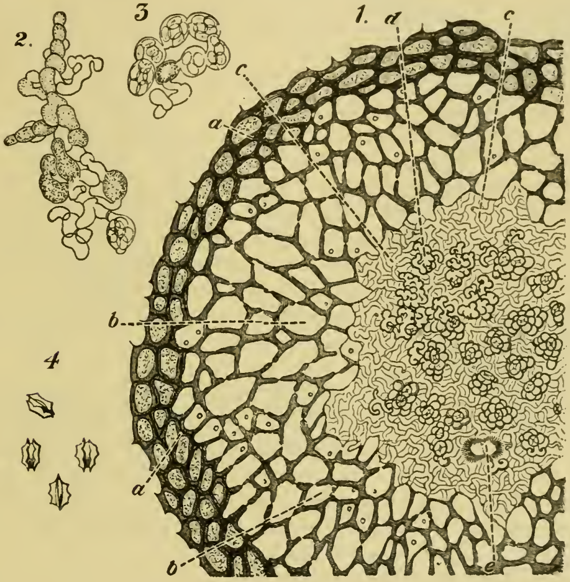

FIG. 321.

1, Section through part of a fruit of *Penicillium*; *a*, *b*, pseudo-parenchymatous covering; *d* = ascogenous hyphae. 2, 3, ascogenous hyphae with asci, more highly magnified. 4, ascospores. (After Brefeld.)

the ascus-walls, and of the nutritive tissues that embedded them (Fig. 321, 2, 3, 4). On germination the ascospores form a new mycelium like the original one.

In *Eurotium* both the antheridial and oogonial cells are multinucleate, and it appears that sometimes a normal sexual fusion takes place. But in others the antheridium degenerates, and sexual fusion is replaced by a fusion of oogonial nuclei in pairs. Thus *Eurotium* illustrates that degradation of sexuality, evidence of which is common among the Fungi.

The type of life-history seen in these simple Mildews and Moulds is common for other Ascomycetes, though it may be worked out with greater complication. But in many of them the sexual organs are so degraded that they, or their equivalents, if present, have hitherto escaped observation. There is normally an alternation of generations, the critical points of which are the sexual fusion in the oogonium and the reduction which precedes the formation of the ascospores. The stage of the ascogenous hyphae, which intervenes between these events may be regarded as a *diploid sporophyte.* The rest is held to be the *haploid gametophyte,* which is liable to indefinite repetition by means of conidia. The fruit-body is then a composite structure, consisting essentially of the ascogenous hyphae, constituting the sporophyte, which is enveloped in a covering derived from the mycelial gametophyte. The nearest analogies are with the fruiting bodies of the Red Seaweeds.

On the fertilisation of the oogonium in some Ascomycetes the male and female nuclei fuse in pairs and diploid nuclei result. These pass out into the *ascogenous hyphae* which grow out from the oogonium. The *young ascus* typically develops from the penultimate cell of an ascogenous hypha. *This cell always contains two nuclei.* These fuse together and therefore produce a nucleus which is tetraploid. Subsequently, as the ascus develops, three successive nuclear divisions take place, thereby producing the eight nuclei for the eight ascospores. The first division is a meiotic division, the second is a mitotic division, and the third a second meiotic division. This remarkable phenomenon of a second reduction division, on which a considerable amount of investigation has been carried out and which is still a matter for controversy, is known as *brachymeiosis.* Where no genuine sexual, or substitute sexual, fusion has taken place in the oogonium, only a single reduction division takes place in the young ascus.

OTHER TYPES OF ASCOMYCETOUS FUNGI.

Both the mycelial and the fruiting stages of Ascomycetous Fungi are subject to modifications according to habit and circumstance, and either may attain large size in some of the representatives of the family. The mycelium may, by repeated branching and knotting together of its hyphae, form dense masses stored with nutritive material, hard and dark coloured, called *sclerotia.* When the rest of the mycelium is killed off by dry or cold weather these remain uninjured, and may germinate after a period of rest, forming at first fresh superficial mycelium and conidia ; but, later on, outgrowths may spring directly from them, as in some species of *Peziza*, which bear broad disc-like fruits. Those Ascomycetes which have such flat open fruits as are seen in *Peziza* are ranked as *Discomycetes* (Fig. 322). The most notorious sclerotia are those of *Claviceps* *purpurea*, the Ergot of Rye, a fungus which causes a disease on Rye-crops. The fungus attacks the ovaries of the Rye and other Grasses at the flowering period, spreading over them and causing the condition known as " Honey-Dew." This is the conidial stage, and it is spread from plant to plant by insects, which are attracted by a sugary secretion in which the conidia float (Fig. 323, *a*, *b* ; also Fig. 293, p. 395). But the effect becomes more apparent as the Rye-crop ripens, for in place of the normal grains long curved bodies project from the ear (Fig. 323, *c*). These are the *sclerotia* of the fungus, which fall off at the time of ripening of the grain. They are the commercial source of supply of a useful drug. In this resting stage the winter is passed. In spring the sclerotia germinate, forming numerous pinhead-like growths, which bear the flask-shaped perithecia characteristic of the large group of the *Pyrenomycetes* (Fig. 323, *d*, *e*). Finally in these the asci and thread-like ascospores are matured at about the time when the Grasses flower. It has been proved experimentally that hyphae from the germinating ascospores

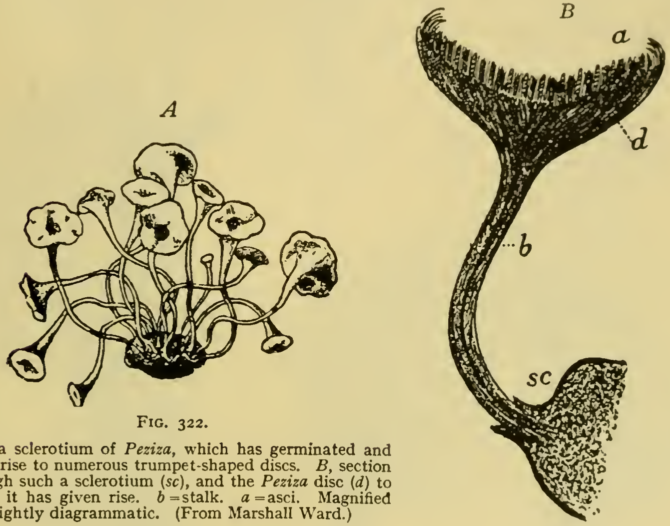

FIG. 322.

A, a sclerotium of *Peziza*, which has germinated and given rise to numerous trumpet-shaped discs. *B*, section through such a sclerotium (*sc*), and the *Peziza* disc (*d*) to which it has given rise. *b* = stalk. *a* = asci. Magnified and slightly diagrammatic. (From Marshall Ward.)

invade the Grass-flowers, causing the development of the conidial stage again. The life-history is here essentially the same as before, but with the addition of the resting sclerotium.

Fig. 323.

a, *b* = conidial stage of *Claviceps*, developed in the flower of Rye. *c* = sclerotia replacing the grains of the ear of Rye. *d*, *e* = germination of the sclerotia in spring. See Text. (After Tulasne.) (From Marshall Ward.)

The fruit-bodies are very complex in some of the larger saprophytic Ascomycetes. An extreme case is seen in the edible Morel (*Morchella esculenta*), in which the external hymenial surface is convoluted and thereby accommodates a vast number of asci (Fig. 324). It is possible to refer this to an elaboration of the Discomycetous type, as it is seen in *Peziza* (Fig. 322). But in the Truffle (*Tuber*) the equally numerous asci are borne internally, in the large underground tuberous fruit (Fig. 325).

ASCO-LICHENES.

There is a series of Ascomycetous Fungi which live in symbiotic relation with Algae, and thus constitute compound bodies which are called *Lichens.* The physiological relation of the two distinct organisms is not unlike that of the Fungus and Host-plant in mycorrhiza, but there is here no intra-cellular digestion (Chapter XII.). The Lichens are very various in form. In simple cases they may be filamentous, as in *Ephebe*, which is like a filamentous Alga with a fungus growing in its mucilaginous walls. Some appear as flat gelatinous thalli, readily swelling with water, as in *Collema*, which is based upon the gelatinous Alga, *Nostoc.* Others are more firm in texture, and form variously flattened thalli, more or less closely attached to the substratum of rocks, roofs, or tree-trunks, etc. Others again are erect or pendulous, and often branched, rising freely from their base of attachment. In texture they are brittle when dry, but more or less leathery when moist, and they vary greatly in colour from grey to more vivid yellow, or even red. They are curiously

FIG. 324.

Morchella esculenta, the fruiting body of the Morel. The convoluted folds of surface are covered by the hymenial layer, bearing asci. ($\frac{4}{5}$ nat. size.) (After Strasburger.

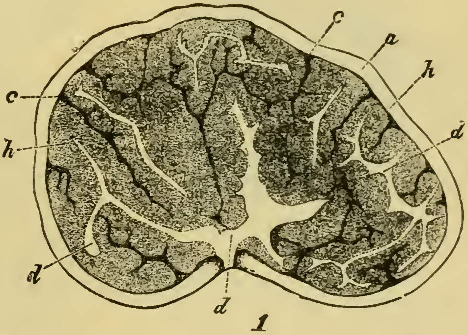

FIG. 325.

Tuber rufum : a Truffle. The fructification in vertical section (× 5). *a* = cortex. *c* = dark veins of compact hyphae. *d* = air-containing tissue. *h* = ascogenous hyphae, with numerous asci. (After Tulasne ; from Strasburger.)

susceptible to impurities in the air, and are therefore absent from urban areas (Fig. 326).

Their structure shows two distinct constituents. Certain cells have algal characters, and often closely resemble Algae known in the free state; they contain chlorophyll or some related colouring matter, and are photosynthetic. They are distributed variously in the thallus, often in a definite *gonidial layer*. These cells are closely invested by the fungal constituent, which is composed of septate and branched hyphae, twigs of which enwrap the algal cells, establishing intimate physiological relations (Fig. 327). Not only does this dual organism flourish, but it may also propagate as such. In wet weather many Lichens are covered by a mealy powder, extruded from within. Examination shows that it is composed of *soredia*, which are bodies containing both constituents of the thallus; one or more algal cells are enveloped in a weft of fungal hyphae. Each soredium is thus able to grow directly into a new Lichen.

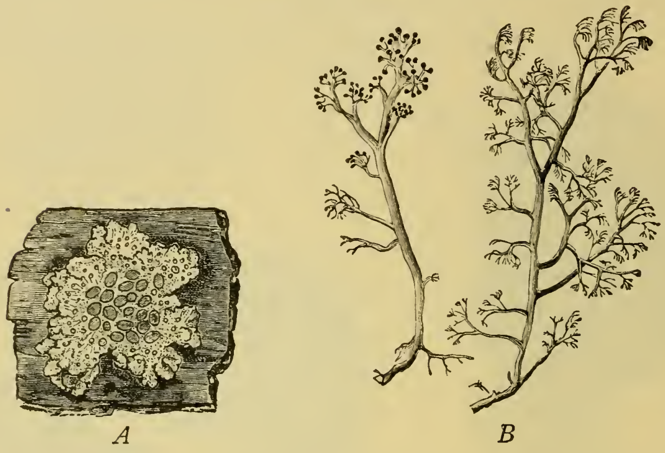

FIG. 326.

A = *Xanthoria* (*Parmelia*) *parietina*, the common foliaceous yellow Lichen. *B* = *Cladonia rangiferina*, a fruticose Lichen. Both bear ascus-fruits, and are shown natural size. (After Strasburger.)

The fruiting bodies of the Lichens are, however, produced from the fungal constituent only, and most of them closely resemble those of Discomycetous and Pyrenomycetous Fungi in form and construction (Fig. 326, *A*). In the Iceland Moss (*Cetraria Islandica*), which is officinal, the fruits appear as marginal discs. When cut vertically they show a superficial *hymenium*, with numerous asci arranged as in *Peziza* (compare Fig. 322, *B*, p. 425). Male sexual organs are sometimes borne, as minute, non-motile bodies (*spermatia*), which are produced in flask-shaped *spermogonia*, contained in the marginal teeth of the thallus. Female organs have been seen in some of the Lichens (*Collema*, etc.) to have the form of a coiled *oogonium*, with a receptive *trichogyne* that projects to receive the non-motile spermatium, as in the Red Seaweeds. But it seems probable that in many of the Lichens, as in many advanced Fungi, the sexual organs even if morphologically present are not functional.

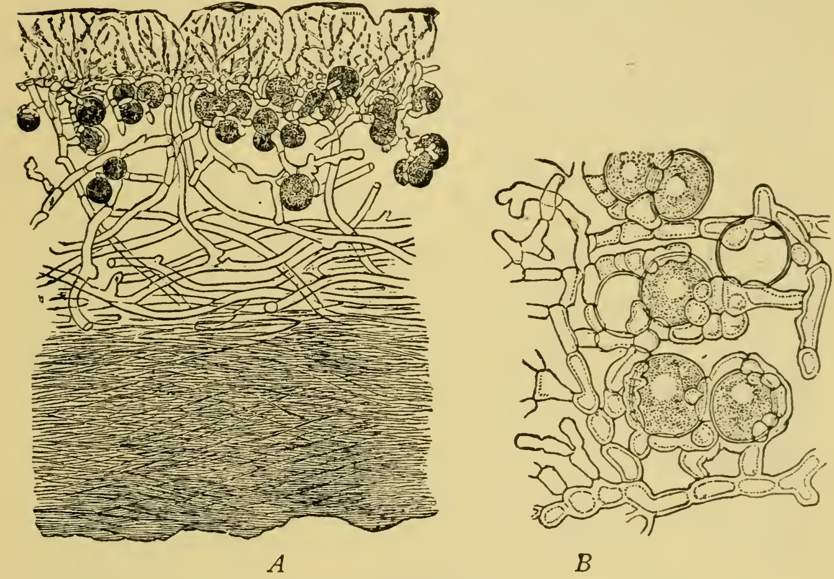

FIG. 327.
Cladonia furcata. *A* = vertical section of the thallus showing the inverted gonidial layer below the cortical sheath (× 330). *B* = part of the same highly magnified, to show the mode of attachment of the hyphae to the gonidia (× 950). (After Bornet.)

The establishment of a new Lichen from the germination of the ascospore depends upon the presence of the algal partner. This is not left to chance, but is provided for, in some cases at least, by "*hymenial gonidia*": these are small algal cells which develop in close relation to the asci. When the fungal spores are ejected some of these adhere to their sticky walls, and thus the two partners germinate together from the first.

The close similarity in structure, nutritional behaviour, and propagative method with the Ascomycetes makes it probable that the Asco-Lichens have arisen from Ascomycetous Fungi which have adopted a symbiotic relation with Algae, and become dependent upon them. Now, some of the Lichen-Fungi have been cultivated in nutrient media when they produce a small thallus *without gonidia.* And again, the algal cells have been isolated and have been found to continue their normal life as free-growing Algae. Indeed they have been found to agree in detail with certain species of the lower Algae. Finally, synthetic experiments have been successfully carried out in building up a Lichen from its two constituents when grown together. The proof that the Lichen consists of a coalition of two organisms living in symbiotic relation seems thus complete. That the symbiosis is a mutual advantage is clear from the healthy growth. It may be held that the alga contributes fresh organic substance by photosynthesis, while the fungus supplies water and soluble salts, which it is specially able to extract and convey.

CHAPTER XXVII.

BASIDIOMYCETES.

THE Basidiomycetes form the second sub-class of the septate Eumycetes. They include most of the large Fungi, such as the Mushrooms, Toad-stools, Shelf-Fungi, and Puff-Balls. These are almost all saprophytes. But the Basidiomycetes also include the Rusts and Smuts, which are parasitic forms causing disease. Some of these are the most injurious pests to cereal crops, such as the Rust of Wheat or the Smut of Oats. Some Basidiomycetes also take part in the formation of certain types of Lichens. They are thus very varied in their habit, and include many familiar objects. The characteristic feature is the *Basidium*, which takes a place in the life-cycle corresponding to the ascus in the Ascomycetes; for in both of them there is nuclear reduction, and both produce post-sexual spores equivalent to *Tetraspores*. But while in the ascus they are formed internally (Fig. 316, p. 417), in the basidium they are borne externally, as *Basidiospores* (Fig. 328).

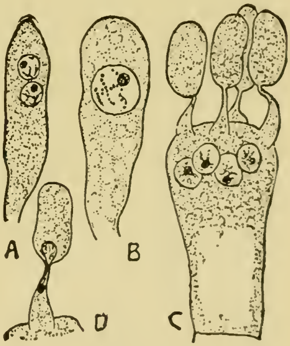

Fig. 328.

Honey Agaric (*Armillaria mellea*). *A*, young basidium with two primary nuclei. *B*, after fusion of the two nuclei. *C* = a basidium of *Hypholoma appendiculatum* before the four nuclei derived from the secondary nucleus of the basidium have passed into the four basidiospores. *D* = passage of a nucleus into the basidiospore. (After Ruhland.) (From Strasburger.)

In the Basidiomycetes normal sexuality has not been shown to exist, while it is only in the Uredinales or Rusts that organs are found which, though not always functional as such, are held to be of the nature of sexual organs. This would indicate that the Uredinales are relatively primitive types of the Basidiomycetes. It may be held as probable that all these Fungi were derived from a sexually reproducing ancestry; but that the sexuality is in abeyance in the more advanced parasites and saprophytes, while evidence of it remains in the more primitive Rusts.

The *basidium* resembles the ascus in containing *two nuclei* when young. As in the ascus these first fuse with one another, and then follows division, first into two then into four, which is accompanied by *nuclear reduction*. In the more primitive types (Uredinales, Tremellales), the basidium divides after the fusion: in the Rusts it appears as a short mycelium (promycelium), from which four cells are partitioned off; each of these puts out a short beak, or *sterigma*, and bears a *basidiospore* (Fig. 335, p. 436). In the more advanced types, such as the Toad-stools and Puff-balls, the basidium does not divide into distinct cells; but sterigmata are formed, and each produces a basidiospore, which behaves in the same way as in the Uredinales. The difference is that the basidium remains undivided (Fig. 328).

UREDINALES.—RUST-FUNGI.

The Rust-Fungi are very prevalent parasites on the shoots of many plants, and as their mycelium lives in the intercellular spaces of the infected tissues, and draws nourishment from the cells, the host-plant suffers, though it is not immediately killed. If the host be perennial, the fall of the leaf or dying down of the aerial shoot rids it temporarily of its enemy, and the parasite has to make a new infection in the succeeding season. It is only occasionally, as in *Gymnosporangium* on the Juniper, that the fungus perennates in the host. A very large number of Rust-Fungi are known, and they show a high degree of specialisation in their parasitism, being mostly restricted to certain genera, or even species of host; while in not a few cases their elaborate life-cycle is completed by stages of growth upon two distinct and successive hosts. This is described as *Heteroecism*. The name Rust is derived from the fact that the *Uredospores* produced by the fungus in summer—and some-

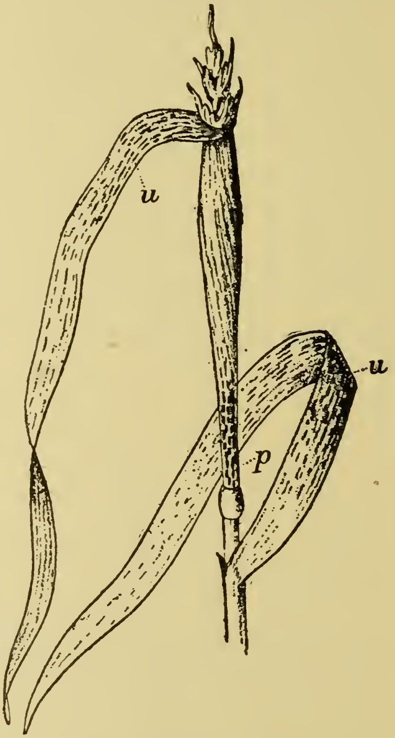

FIG. 329.
Upper portion of a stalk of Wheat, with groups of uredospores (u) on the leaves, and dense masses of teleutospores (p) on the fast-ripening leaf-sheath and straw. (After Marshall Ward.)

times called summer-buds—are of the colour of rust of iron. They are found in such quantity as to attract public attention, and this provided the name.

The most familiar example, as it is also economically the most important, is the Rust of Wheat, *Puccinia graminis*. In June and July the green leaves of the Wheat are often seen to lose their colour (Fig. 329). Yellow patches appear between the veins, and run together into lines that follow the softer mesophyll. The epidermis bursts, and innumerable orange bodies are set free, which are easily carried as dust by the wind. These are the *Uredospores* of the Rust. A part of a field thus diseased is a centre of infection, and the fungus may often be seen to spread from it down the prevailing wind. This production of spores, which represents so much material robbed from the developing crop, may continue till autumn; then gradually the patches of disease change in colour to a dark purple-brown. This is due to the formation in them of a new kind of propagative body, the *Winter-bud* or *Teleutospore*, which is firmly attached to the straw, and dies down with it, or is removed with the crop. These spores retain their vitality till the next spring, when they germinate (Fig. 335, p. 436).

The result of their germination has been shown experimentally to be the infection of the leaves of the Barberry plant, and the production of a second stage, which appears as red or yellow blotches, thicker than the healthy parts of the leaves that bear them: small dark spots open on the upper surface (*spermogonia*), and numerous widely gaping cups (*aecidia*) are clustered together on the lower surface. This stage was first described as "Cluster-Cups," and regarded as a distinct fungal disease under the name of *Aecidium berberidis* (Fig. 330). But it is now known that the spores produced by the cups are able on germination to cause a new infection of the leaves of the Wheat plant, which results again in the growth of a mycelium bearing the uredospores. There are thus two stages of the disease, the one on the Wheat or other Grasses, the other on the Barberry. Long before it was proved that these two different-looking diseases were only stages in one life-history, a connection between the two had been suspected. It was thought that the Barberry was in some way injurious to Wheat. But it was not till late in the Nineteenth Century that the cycle was completely demonstrated. A similar heteroecismal life is now known for numerous species of Rusts. One of the commonest is *Puccinia caricis*, of which the uredospores and teleutospores are on leaves of species of *Carex*, and the aecidium-stage on the common Nettle, causing contorted swellings upon its stem and leaves. Thus the Rust of Wheat is an example of a life-history that is not uncommon.

FIG. 330.
Part of shoot of Barberry with leaves attacked by *Puccinia graminis* which forms yellow cushions, or cluster-cups, on the leaf-blades and stalks. (After Marshall Ward.)

Sections through a diseased leaf of wheat in summer reveal the branched and septate hyphae closely packed in the intercellular spaces, and investing the green cells. They accumulate below the epidermis, forming a dense mass or sorus, the end of individual hyphae swelling into the uredospores, which, increasing in bulk and number, burst the epidermis, and are shed (Fig. 331). Each spore is covered by a thick wall, containing dense protoplasm with oily globules, and *two nuclei*. Their walls are marked by thin spots round the equator. It is from these spots that the germ-tubes emerge when grown in water (Fig. 332). If this germination takes place on a wet leaf of wheat, the tube growing over the surface finds entry by a stoma (Fig. 333), and

FIG. 331.
Longitudinal section of a leaf of Wheat, showing a tuft of uredospore bursting through the epidermis. Highly magnified. (After Marshall Ward.)
(It will be realised from this illustration that *uredospores* are really *conidia*: for historic reasons, however, it is convenient to retain the term *uredospore*.)

at once gains access to the nutritive cells. In about a fortnight the infected spot will be producing fresh uredospores.

The teleutospores may arise from the same spot as the uredospores, but later in the season. They differ from them in being closely packed and firmly attached, as well as in structure. Each spore is spindle-shaped, and is partitioned into two cells, each with a dark brown coat (Fig. 334). Like other cells of the mycelium and the uredospores themselves, each cell contains two nuclei. They do not germinate till the following spring. In March or April, after a few hours in water, each cell puts out a delicate tube (Fig. 335). This, after segmenting to form four distal cells, constitutes what has been called the *promycelium*,

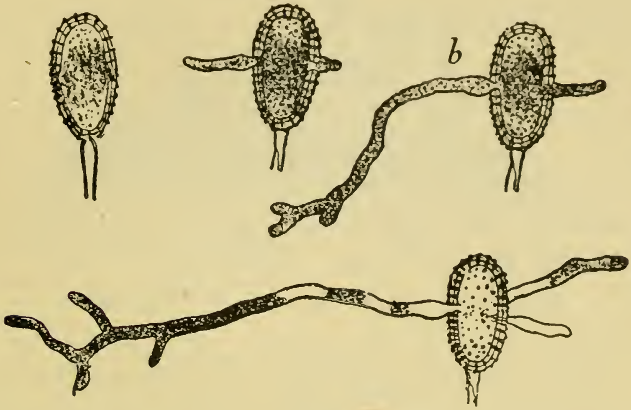

FIG. 332.
Germinating uredospores, showing various stages of development of the germ-tubes, *a*, *b*, *c*. Very highly magnified. (After Marshall Ward.)

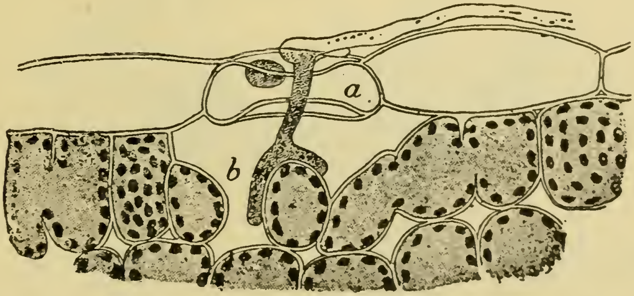

FIG. 333.
Longitudinal section of a leaf of Wheat, showing a germ-tube from a uredospore passing through a stoma (*a*) into the intercellular space (*b*). Very highly magnified. (After Marshall Ward.)

which is really a *septate basidium.* The first step is the fusion of the two nuclei to form one. Then follows its division into two and into four—in fact a *tetrad-division*, followed by partitioning of the four cells. Each cell then forms a process, or sterigma, on the end of which a

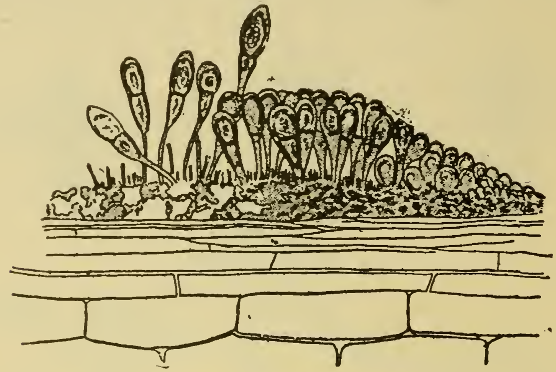

Fig. 334.
Longitudinal section through sorus of the teleutospores of *Puccinia*, on a stalk of Wheat-straw. Highly magnified. (After Marshall Ward.)

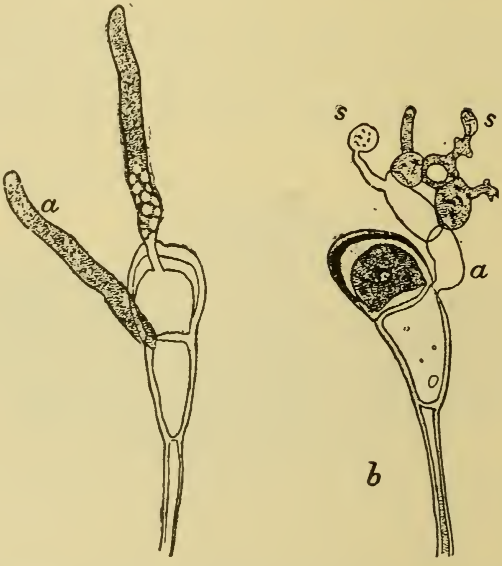

Fig. 335.
Two teleutospores of *Puccinia* germinating. In the one to the left each cell has given off a promycelium, or basidium (*a*, *a*); to the right only the lower cell has done so, and the promycelium has given rise to four sterigmata, bearing sporidia (*s*, *s*) or basidiospores as they are better called. Very highly magnified. (After Marshall Ward.)

swelling appears, and into it the protoplasm and nucleus pass. These are sometimes called sporidia: each is the product of a reduction-process and is recognised as a *basidiospore* (Fig. 335, *s*, *s*). Their peculiarity is that they do not cause infection of the Wheat, but can penetrate the epidermis of the Barberry. Acting on suspicions already aroused, De Bary succeeded in carrying out an experimental infection in 1864. He found that the basidiospores, easily shed from the sterigmata, germinate to form a germ-tube, which can directly penetrate the epidermal wall of the Barberry (Fig. 336). This initiates the second phase: and as the basidiospore itself is haploid, so is the stage produced from it on the Barberry. *Each cell has only a single nucleus*, which may be held to indicate a haploid condition, as in the gametophyte.

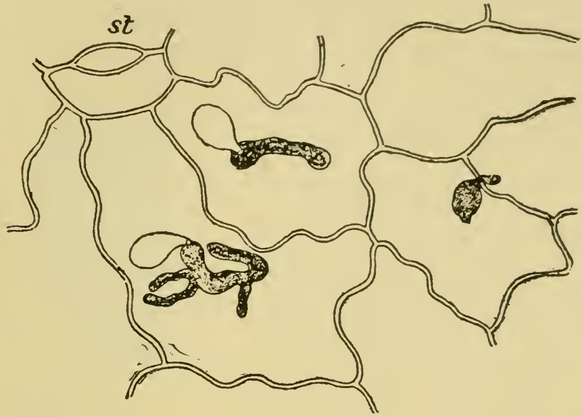

FIG. 336.
Sporidia, or basidiospores, of *Puccinia*, germinating on the epidermis of a Barberry leaf, and putting out germ-tubes, which penetrate the cell-walls. Very highly magnified. (After Marshall Ward.)

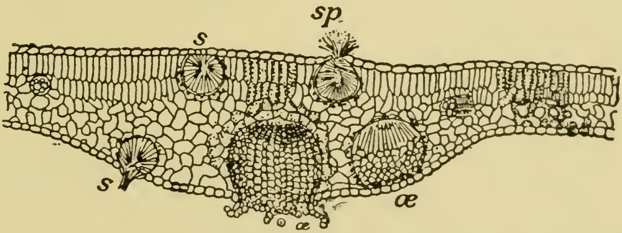

FIG. 337.
Vertical section through a patch of aecidia (*æ*) and spermogonia (*s*) on the Barberry leaf, showing the swelling of the diseased part. The small aecidium to the right has not yet burst. Highly magnified. (After Marshall Ward.)

A section through an infected spot on the Barberry leaf shows the effect of the attack in the greatly increased thickness as compared with the normal leaf (Fig. 337). The enlarged cells of the mesophyll appear enveloped by fungal hyphae which choke the intercellular spaces. They are massed chiefly at points towards the upper and lower surfaces, to form bodies of considerable size. The first are the flask-shaped *spermogonia* composed of hyphae pointing radially inwards, while from the end of each a minute non-motile *spermatium* is abstricted. These have not themselves been found capable of causing infection; but they may stimulate development and are possibly male organs (*sp*). The spermogonia secrete a fluid, sometimes described as "nectar" in which large numbers of spermatia may be present. Projecting beyond the spermogonial opening or *ostiole* are long *flexuous hyphae*. The bodies on the lower surface are larger and develop into the cup-like *aecidium-fruits*. Each is composed of an outer sheath or peridium, while the cup is filled with filaments rising from the base, from each of which a chain of *aecidiospores* is produced. The oldest are distal, and they are shed in succession from the downward-turned cups (Fig. 337, *æ*). When ripe they are *bi-nucleate*. De Bary in 1865 showed that if sown on young grass-leaves they infect them, and produce the Rust again. Thus there are two stages in the life-cycle, which differ in host and in propagative organs: the one has paired nuclei, and may be held as a *diploid sporophyte: it grows on the Grass.* The other has a single nucleus in each cell, and may be held to be a *haploid gametophyte: it grows on the Barberry.*

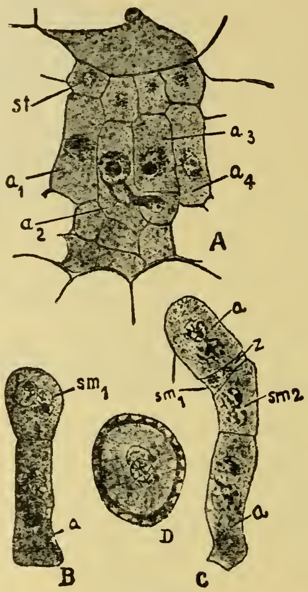

Fig. 338.
Phragmidium violaceum. *A*, portion of a young aecidium; *st*, sterile cell; *a*, fertile cells: at a_2 the passage of a nucleus from a neighbouring cell is seen. *B*, formation of the first mother-cell, *sm*, from the basal cell (*a*). *C*, a further stage, in which from sm_1 the first aecidiospore (*a*) and the intercalary cell (*z*) have arisen; sm_2 the second mother-cell. *D*, ripe aecidiospore; note the paired nuclei. (After Blackman.) (From Strasburger.)

The problem of sexuality in the Rusts is still not entirely solved. In some species, cluster-cups develop after infection by a single sporidium; in others mycelia from two sporidia must meet, or a mycelium must be stimulated by spermatia of a different strain. In other words it is now recognised that whereas some Rusts are *homothallic*, others like *Puccinia graminis* are *heterothallic* (see p. 416) ; the latter require the association of hyphae from two complementary strains before cluster-cups and aecidiospores are developed. This association may be brought about by the overlapping of pustules. Insects visiting the spermogonia for " nectar " bring about a transference of spermatia and these may become intimately associated with flexuous hyphae of the opposite sex. Spermatial nuclei then enter the hyphae and the subsequent nuclear divisions and migrations bring about the cytological condition necessary for the development of aecidiospores. In all cases, *nuclear pairing* is believed to occur at the base of young aecidia. It has been traced in *Phragmidium violaceum*, as consisting in the passage of the nucleus of one cell into a neighbouring cell (Fig. 338, *A*), very much as has been seen in certain apogamous Ferns (Fig. 403, p. 508). But here the nuclei do not fuse at once ; the receptive cell remains bi-nucleate, and divides as such into a chain of bi-nucleate spores (*a*) and sterile intercalary cells (*z*) (Fig. 338). Each chain of spores appears to be initiated in this way. A similar process has been seen in *P. speciosum*, and other Uredinales. This discovery made it possible to relate the life-history of the Uredinales to that of other plants. The state with paired nuclei is held as the correlative of the diploid sporophyte, and that with a single nucleus in each cell as the haploid gametophyte. The events may then be summarised as follows :—

A. *Sporophyte on Grass*
(paired nuclei).
- i. *Mycelium*.
- ii. *Uredospore* (repeating the mycelium).
- iii. *Teleutospore* (winter's rest).
- iv. *Nuclear fusion* in germinating teleutospore.
- v. *Basidium* (= promycelium), equivalent of a spore-tetrad, with *reduction*.
- vi. *Basidiospore* (= sporidium).
- vii. *Infection* of Barberry plant.

B. *Gametophyte on Barberry*
(uni-nucleate).
- viii. *Mycelium*.
- ix. *Spermatium*.
- x. *Nuclear association*.
- xi. *Aecidiospore* (bi-nucleate) (Fig. 338, *D*).
- xii. *Infection of Grass-leaf*.

There are many of the Uredinales that do not show so elaborate a series of stages in the life-cycle as the Rust of Wheat. The uredospores may be omitted, or the aecidia ; or some may have neither aecidia nor uredospores. The spermogonia may also be omitted : so that in these last the life consists of a repetition of teleutospores with subsequent germination.

The Rust disease is difficult to check, and its distribution is worldwide. One obvious measure would appear to be to remove the alternative host, the wild Barberry. This has been done in wheat-growing districts in England, but definite consequences from it are uncertain. It is significant that Wheat-Rusts abound in South Africa, Australia, and parts of India, where no species of *Berberis* are indigenous. The most effective remedy is to plant only the seeds of varieties of wheat that are known to be *immune* to the disease, by resisting the infection. Progress has already been made in the production and circulation of such immune varieties. But owing to the minute specialisation characteristic of many Rusts a variety may be immune in one country and susceptible to the same Rust in a different climate: so delicate is the balance which exists between the attacking and resistant powers of two organisms. (Compare Chapter XII., on Irregular Nutrition.)

USTILAGINALES (SMUTS).

The Smut-Fungi (Ustilaginales) are also parasites on Grasses, certain of them causing diseases on Oats, Barley, Wheat, and Maize, which culminate in the fruiting Ear. The diseased grain is replaced by a mass of dusky spores, corresponding in their behaviour to the teleutospores of the Uredinales (Fig. 339). For like them they germinate after the winter's rest, forming a *basidium* (promycelium) with effective *basidiospores* (sporidia). The germs may have remained in the soil of the field from the previous season; or the crop may have been harvested and the straw used for bedding, passed to the manure-heap, and then carted out on to the land again. Either way the soil in which the grain germinates will have been infected.

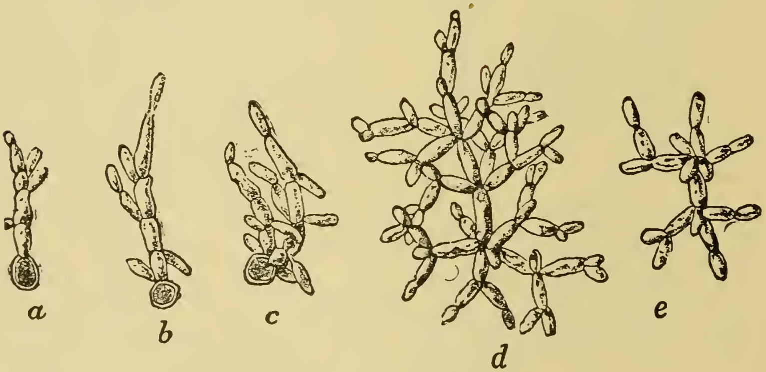

FIG. 339.

Teleutospores or brand spores of *Ustilago* germinating, and giving off basidiospores or sporidia. (*a*) germinated in water only. *b*, *c*, *d*, *e* in nutritive solutions, where they continue to sprout. Very highly magnified. (After Brefeld, from Marshall Ward.)

A further point of importance is that in a nutritive liquid, like the foul water of the manure-heap, the spores formed on germination continue to multiply by *budding*, thus increasing the chances of infection (Fig. 339, *d*, *e*). The detached spores then conjugate and begin a bi-nucleate stage, which is able to penetrate the tissue of the seedling corn but not of the adult. The plant, once infected, grows on as though quite healthy till the flowering period. Then the parasite, the mycelium of which has followed its growth internally, fastens on the ovary where nutritive material is concentrated, and diverts the food from the formation of the grain to the nutrition of a mass of its own spores. For prevention of the disease "dressing" of the seed-grain with disinfecting mixtures is practised. But equally important is to prevent the manure being contaminated by the spores from the smutted crop of a previous year.

HYMENOMYCETALES.

The life-history of the Rust of Wheat has been described in some detail as giving an example of a Basidiomycete which still shows evidence of sexuality, both morphologically and physiologically; though it is altered from what was probably its normal and original course. In the rest of the Basidiomycetes such evidence is wanting. They may provisionally be held to be saprophytes and parasites which were descended from an ancestry with normal sexuality, but have advanced further in the elimination of their sexual process. In some species variation is ensured by the association of mycelia of different origin. The basidia (Fig. 328) are borne on fruit-bodies, which are often large and brightly coloured. They arise from a *mycelium* which acquires the necessary nourishment sometimes parasitically but more often from saprophytic sources. The basidia are borne in various ways, and this gives distinctive characters to the main groups

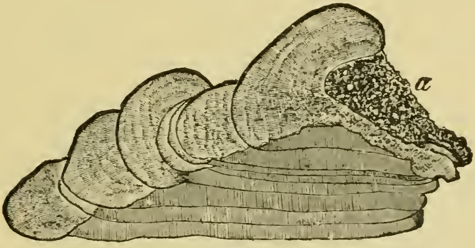

FIG. 340.

Fomes igniarius. Section through an old fructification, showing annual zones of growth. *a* = point of attachment upon the tree which is its host. The porous hymenium is directed downwards. (½ nat. size.) (From Strasburger.)

of these Fungi. Thus in the *Gasteromycetes* the fructification is closed, the basidia being produced internally, and the spores set free by rupture, as in the Puff-Balls. In the *Hymenomycetes* the basidia are borne collectively in a definite layer called a *hymenium*, exposed to the air, from which the spores are shed, as in the Mushrooms, Toadstools, and Shelf-Fungi (Figs. 340, 341).

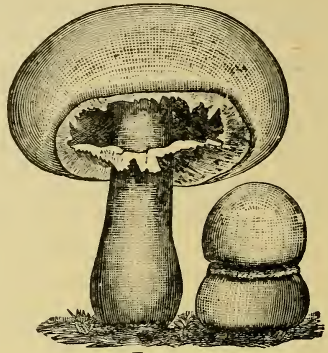

FIG. 341.
Psalliota (*Agaricus*) *campestris*. Mushroom. The hymenium covers the surface of the radiating, downward-directed gills. To the right a young fructification or "button" Mushroom. (Reduced.) (From Strasburger.)

The *mycelium* may obtain nourishment in various ways. It is sometimes parasitic as in the Honey Agaric (*Armillaria mellea*), which penetrates the trunks of forest trees, ravaging the cambium, and killing them (see Fig. 292). Many of the Shelf-Fungi (*Polyporus*) grow parasitically at the expense of the heart-wood of trees, making them hollow. The infection comes through injury by wind, which exposes the internal tissues to the invading spores. The mycelium may live for years, digesting the lignified walls, till it is sufficiently nourished to form a fruit-body (Fig. 342). On the other hand the Dry Rot Fungus (*Merulius lacrymans*) lives saprophytically, its mycelium digesting the substance from dead wood-work in houses

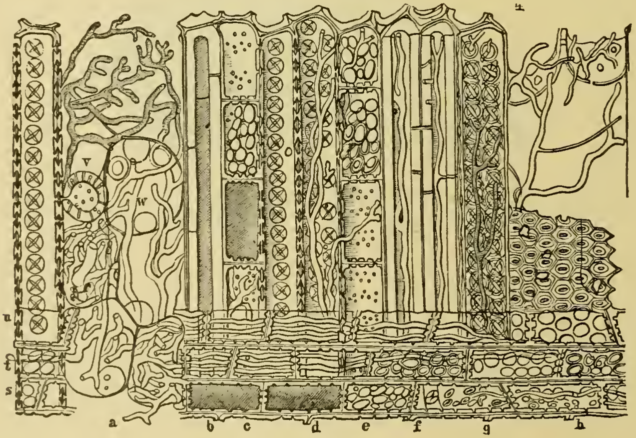

FIG. 342.
Radial longitudinal section through wood infested with ***Fomes igniarius***.
Highly magnified. (After Hartig.)

and ships, where confined in a close damp space. Later it forms the cake-like fruit bodies. The Common Mushroom is an example of a very common habitat of saprophytic mycelium, viz. in the sod of grass-land. It is found especially where horses have been grazing (Fig. 343). But the mycelium can be bought in bricks of "mushroom-spawn," made up of a compost of dung, clay, and loam, in which it can be seen as fine white threads, either spreading as single hyphae, or as numerous hyphae running parallel so as to form thicker strands. If the brick be broken into pieces and spread through a similar compost, and kept warm and moist in the dark, the mycelium grows; in a few weeks it forms mushrooms of various size. The last stages of development of mushrooms appear to be rapid. This is due to the fact that the tightly packed threads that compose a "button" mushroom undergo rapid extension, with absorption of water. (Figs.

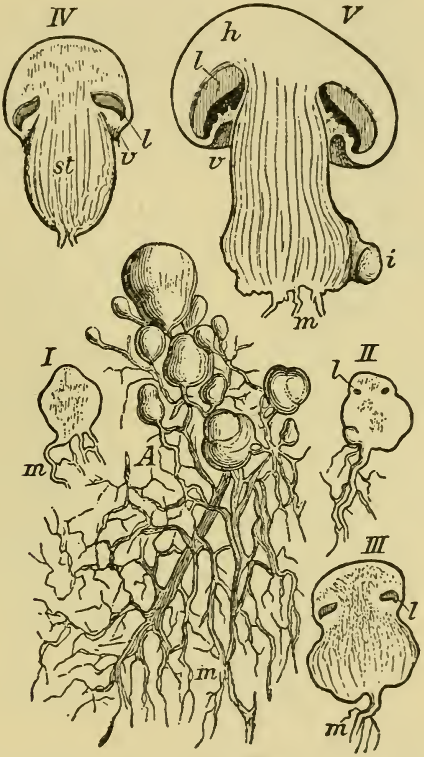

FIG. 343.
A, mycelium of the Mushroom, with young fruiting bodies attached. I.-V., successive stages of development of "Mushrooms." (Natural size.) (After Sachs.)

341, 343.) The apparently fresh formation of mushrooms from day to day in the fields is thus accounted for. The button-mushrooms are hidden in the grass till the extension takes place.

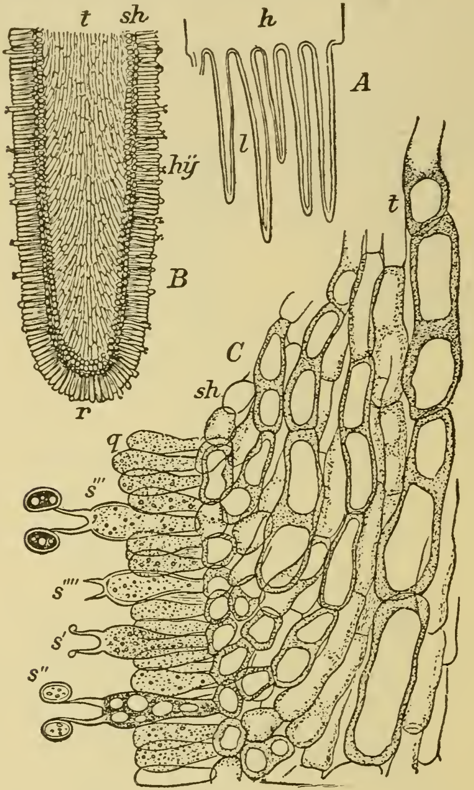

FIG. 344.

Structure of the hymenium of the Mushroom *Psalliota* (*Agaricus*) *campestris*. *A* is a vertical section through the pileus traversing several gills (*l*). *B* shows the structure of one gill more highly magnified : *hy* = the hymenium. *C* shows a small area of the hymenium in section (× 350). The basidia project, each bearing two basidiospores, that number being exceptional but regularly present in the Mushroom. (After Sachs.)

The Mushroom as commonly known is the fruiting-body, borne on the nutritive mycelium. It has the usual toad-stool form, with a stalk or *stipe* bearing the hemispherical *pileus* (Fig. 341). As in all large fungal bodies, it consists of false tissue. The hyphae composing it take first a parallel course so as to form the stipe, they then diverge upwards so as to form the wide-spread pileus. In the button stage the margin of the pileus is connected with the stipe by a thin covering of the *velum* ; but this is ruptured as the mushroom expands, leaving a ring round the stipe (Fig. 341). The radiating *gills*, which hang vertically from the lower surface, are thus freely exposed. It is upon the gills that the *hymenial layer*, bearing the *basidia*, is borne. The colour of the gills is at first pink, but it gradually grows dark brown with age. This is due to the colour of the spores (*basidiospores*) produced in large numbers all over its surface. If a young expanded pileus be laid face downwards upon a sheet of paper, after a few hours a print of the gills will have been traced by the deposit of their spores.

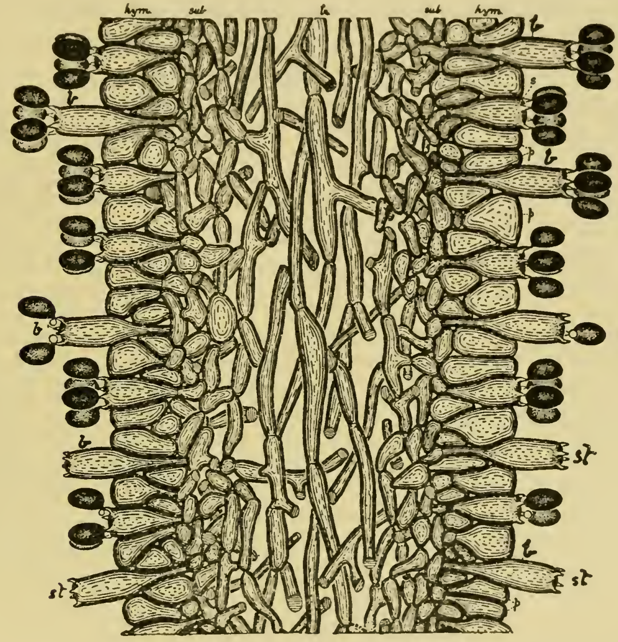

Fig. 345.

Coprinus sterquilinus. Section through a gill, showing hymenium (*hym*), subhymenial layer (*sub*), and trama (*tr*) ; the basidia (*b*), each bearing four basidiospores, or only the sterigmata (*st*), from which the spores have been already thrown off. (After Buller.)

A vertical section through the *gills* shows that they consist of a rather lax central region, which supports the more compact *hymenium* that completely covers their surface (Figs. 344, 345). It is composed of narrow *paraphyses* which surround the more bulky *basidia*, the ends of which project, and in the Mushroom bear each two sterigmata, with a basidiospore on the end of each. The number two is, however, exceptional among Basidiomycetes. The basidia of the Honey-Agaric, or of *Coprinus*, are typical (see Fig. 345). There the fusion-nucleus divides into four, four sterigmata are formed, and one of the nuclei squeezes through the narrow channel into the basidiospore which each sterigma bears.

In the Mushroom the germination of the spores presents a difficult problem. It seems probable that one incident, and perhaps a necessary one, is that they should pass through the alimentary tract of some herbivorous animal: for the spores would naturally be taken in with the grass they eat, while the Mushroom grows on old pastures manured by their dung. Related fungi do not always present such difficulties, and are readily raised from spores. In the case of the Mushroom no other propagative bodies exist, nor have any sexual organs been recognised. The fruit-bodies arise from a mycelium with paired nuclei. The young basidium contains two nuclei which later fuse. The fusion-nucleus undergoes two divisions—involving reduction—and each of the four nuclei formed becomes the nucleus of a basidiospore. The fact that in the Hymenomycetes there is a fusion of paired nuclei followed by reduction shows that the basidiospores are of the nature of tetraspores.

On the germination of the basidiospore a considerable mycelium of uninucleate cells may be formed. Between different hyphae fusions or anastomoses are common, the attendant nuclear migrations restoring the binucleate condition. Such binucleate hyphae, on further growth, may give rise to the fructifications described above. Some of the Hymenomycetales are self-compatible so that fusions may take place between hyphae of the same mycelium and thus the fructifications may eventually be obtained from the germination of a single spore. But, as pure culture experiments have shown, many others are self-incompatible and hyphal fusions and nuclear transferences between compatible strains are necessary for the development of fructifications.

BASIDIO-LICHENS.

Certain Basidiomycetous Fungi take part in the composition of Lichens, but this is much less frequent than in the Ascomycetes. The most familiar example is the genus *Cora*, found not uncommonly in the tropics, growing on the ground or on trees. Its form is not unlike a *Stereum*, or *Thelephora*; and, like them, its hymenium is on the lower surface. The fact that the fungal constituent of some Lichens can be referred to Basidiomycetous Fungi may be held as a final proof of their being compound organisms (see pp. 427-428).

FUNGI AS SUBAERIAL PLANTS.

The Fungi, sprung perhaps from various Algal sources, show some degree of adjustment to subaerial life parallel to that already seen in Green Plants. But as the hypha is the basis of their construction, their vegetative system gives less opportunity for adaptive change than their propagative organs.

The most striking modifications are seen in the Phycomycetes, which bear similarity to non-septate Algae in having motile zoospores and gametes. Among the Oomycetes the aquatic origin is clearly reflected in the germination of the sporangia, where each bursts and gives rise to zoospores motile in water (Figs. 303, 308, pp. 404, 409). The sporangium in fact appears to be like the sporangium seen in many Algae, but reduced in size and detachable, thus permitting of its distribution by air currents, though its germination is still carried out in water. Similarly in the Zygomycetes the large sporangium of *Mucor* is also effective for water-distribution of its spores, though they are not themselves motile (Fig. 313, p. 414). But within the family of the Mucorales the sporangium is liable to be reduced in size, with increase in its numbers, till in *Chaetocladium* and *Piptocephalis* it matures as a single detachable cell : in fact it is an air-borne conidium, the large numbers of these conidia compensating for the reduction from the sporangial condition. The Oomycetes and Zygomycetes thus suggest a parallel progression from sporangia producing numerous spores to small wind-borne bodies, ranking as conidia. The profuse propagation of the Eumycetes by various types of detachable unicellular buds, also called conidia, acts biologically in the same way, as a means of subaerial propagation and distribution. But the phyletic origin of such conidia was probably from a source distinct from that of the Phycomycetes.

On the other hand, the sexual organs of *Pythium* and *Cystopus* correspond in form and general characters to those of the Siphonales, such as *Vaucheria*. But in place of a dehiscent antheridium, shedding spermatozoids motile in water, a fertilising tube is found, which, like a pollen-tube, transfers its contents directly to the ovum (Fig. 310, p. 410). It is in fact an antheridium, which being subaerial in its development does not dehisce to set free motile gametes. In the Mucorales the zygospores may very probably be regarded in the same way, but referable to a more primitive state of sexuality. Two distal gametangia, instead of dehiscing and their separate gametes fusing, conjugate as a whole, producing the coenocytic zygospore (Fig. 314, p. 416). Such examples accord with the general reference of Land-living Plants in their origin to an aquatic ancestry ; and they illustrate how the modifications in Thallophytes may run parallel with those of organisms higher in the scale. They go far to support the general thesis that Plant-Life originated in the water and spread later to land-surfaces.

CHAPTER XXVIII.

THE BACTERIA.

THE Bacteria include a vast number of minute saprophytic and parasitic organisms which have multiplication by fission and the absence of the photosynthetic pigments as common features. They are among the simplest of organised plants and include the most minute of living beings. They stand rather isolated from the other Thallophytes. Most of them have more or less conspicuous gelatinous walls, surrounding a protoplast in which, though granules of chromatin may be detected, there is no fully organised nucleus. Sexuality is absent. In contrast to this simplicity of structure and life history they show the greatest possible variety of physiological activity: in fact, therein lies their special interest and importance. Indeed some which appear identical in form may have different physiological powers, and are accordingly distinguished as "physiological species."

Their cells may be spherical (*Coccus*), or rod-shaped (*Bacillus*), or slightly spiral (*Vibrio*), or strongly spiral (*Spirillum*), or straight and slender (*Cladothrix*), or grouped in cubical packets (*Sarcina*). They have a superficial membrane, and protoplasmic body, sometimes with chromatin-granules, but no definitely formed nucleus. Many of them are motile, and bear cilia varying in number and position in different types. Their multiplication is by fission. Their mode of life is best illustrated by an example.

The Hay-Bacillus (*B. subtilis*) can be obtained in any decoction of hay, in hot or even in boiling water. If the fluid is filtered and set aside for 48 hours it will be found to be swarming with ciliated Bacilli, while at the surface a scum is formed, which is the "zoogloea" condition of the same plant. In old hay the *Bacillus* is in the resting condition, as spores, the protoplasm having contracted away from the wall, and being surrounded by a thick membrane (Fig. 346, *c*).

The spores can resist even the temperature of boiling water, and pass still living into the decoction. There they germinate into active Bacilli, motile in the liquid by cilia (Fig. 346, *a*, *d*). But those which rise to the surface lose their motility (*b*), though continuing to divide; they form thick gelatinous walls, and so they remain associated together as the scum of the zoogloea (*e*). If the supply of organic material is exhausted they pass again into the resistant spore-stage. It thus appears that a single boiling of the medium containing spores of *B. subtilis* is not enough to sterilise it, for the spores can resist 100° C., at least for a time. For complete sterilisation it is necessary after boiling to incubate the culture at a favourable temperature of 37° C. for 48 hours, during which time the spores will all pass into the active but vulnerable state. Then a second boiling will completely sterilise the liquid. This method is commonly used in the preparation of media for the culture of Bacteria.

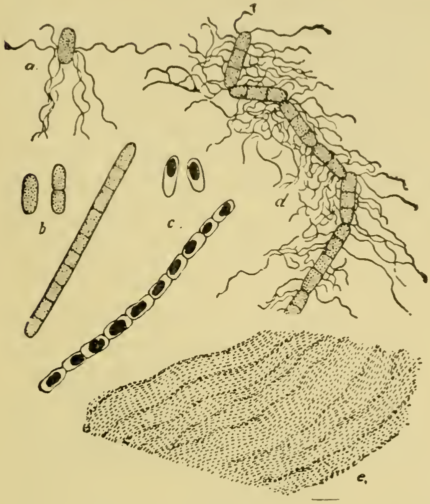

FIG. 346.

Bacillus subtilis. *a*, *d*, motile cells and chains of cells; *b*, non-motile cells and chains of cells; *c*, spores from the zoogloea; *e*, the zoogloea. (After A. Fischer. *a*-*d* × 1500; *e* × 500.) (After Strasburger.)

It is important to realise the great rapidity of multiplication of Bacteria. Under favourable conditions *B. subtilis* is found to divide once in about 20 minutes. If this pace be continued by all the progeny for 8 hours the result from a single Bacillus would be over 16 millions. It is not, however, the rapid multiplication and easy transfer of these minute bodies alone which gives the Bacteria their importance. A still more interesting feature is the variety of their physiological powers. Being as a rule parasitic or saprophytic plants, they depend for their supply of food and energy upon breaking down more complex organic compounds into simpler ones: and they do this in the most various ways. The end products of such changes are chiefly carbon-dioxide and water. In fact, Bacteria are the great scavengers of the world, restoring organic material to the sources from which it came. But in the course of the process many steps may intervene: and by-products may be produced which are sometimes useful, though often harmful to other organisms, and to Man.

Where suitable food-material is available Bacteria may multiply indefinitely. But there are important external checks which control them. Many Bacteria are susceptible to injury by light. This has been shown for the Anthrax-Bacillus, by growing it on culture-plates, partly exposed to light and partly shaded; and the results have been verified in various others. The destructive effect lies in the blue-violet end of the spectrum. After incubation in the dark for three or four days, the area of a plate exposed for a time to such rays at the beginning of the experiment will remain clear, while the shaded portion will be covered by bacterial colonies: this shows that the bacteria exposed to light had been killed. Such facts are of prime importance in relation to general health: for sunlight thus offers a natural and wide-reaching check upon the spread of many harmful germs.

The relation of Bacteria to the free oxygen of the air is also a matter of importance. Like other organisms they may be distinguished as aerobic and anaerobic, according to their dependence upon the presence of free oxygen or their independence of it (p. 136). But no sharp line can be drawn between these two modes of life. Many Bacteria carry on their life with absorption of oxygen, like other plants. If they have a power of movement they are attracted by oxygen, crowding around air-bubbles. But some of the most deleterious, such as the Bacillus of Tetanus, flourish only in the absence of free oxygen, obtaining their supply of energy at the expense of the organic material which they destroy. Some Bacteria that cause butyric fermentation behave in this way. Such activity may be compared with that of the bottom-yeast of beer-vats; in both cases the activity is anaerobic. It is this mode of life, together with the toxines which result from it, that makes the Tetanus-Bacillus specially dangerous in wounds.

Such questions as these are, however, the material for more special treatises than this. It must suffice here to have pointed out that the partial decompositions due to bacterial action are of most varied importance, economically and socially. Physiologically they may be referred for the most part to that degradation of organic material which supports parasitic and saprophytic Life.

On the basis of nutrition Bacteria have been classified into three groups: (i) *Prototrophic* or *autotrophic*, those which require no organic compounds at all for their nutrition. These are represented by the nitrifying Bacteria which live in open nature, in the soil, and are never parasitic. (ii) *Metatrophic*, those which cannot live unless they have organic substances at their disposal, both nitrogenous and carbonaceous. They occur in the open, and are saprogenic and sometimes parasitic (facultative parasites). (iii) *Paratrophic*, those which develop normally only within the living tissues of other organisms, and are true and obligatory parasites, such as the germs of Tubercle or Diphtheria.

This classification may be extended, however, to all other organisms. All green autophytes are prototrophic in the same sense as the first group of Bacteria. All fungi and animals are metatrophic, except the parasitic forms, which are paratrophic. Thus in point of fact the Bacteria exemplify types of nutrition which run parallel with those seen in larger organisms.

Bacterial germs are widely diffused in air, water, and soil, as well as on or within living organisms, whether animals or plants. Their activities are so various that it will be best to illustrate them by a few examples rather than to mention many.

Among the Bacteria that live in water *Crenothrix polyspora* is notorious for choking pipes of water-supply, and making the water undrinkable, though apparently not poisonous. Lille, Rotterdam, Berlin, and Cheltenham have suffered from it. It is probably world-wide in distribution: but being an Iron-Bacterium, it finds a special opportunity for development in the water-conduits of towns. It shares with other Iron-Bacteria, such as *Leptothrix ochracea*, the power of oxidising oxide of iron to the hydrated oxide, which is deposited in the walls of its cells, and when these are massed together, it appears as those ochre-coloured deposits of bog iron ore not uncommon in the beds of ferruginous streams. These are filamentous Bacteria, and they grow attached at their base to solid objects (Fig. 347). Somewhat similar are the Sulphur-Bacteria, such as *Beggiatoa*, which grow in sulphurous springs. They separate sulphur from sulphuretted hydrogen, which is then deposited in their cells. The green and purple sulphur bacteria are remarkable for the fact that they depend for their carbon supply on carbon dioxide and sunlight. They are, in fact, photosynthetic, though the process differs in certain respects from that in green plants.

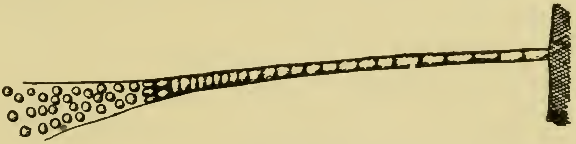

FIG. 347.
Crenothrix polyspora. (After Ellis.) (Mature specimen. × 250.)

Both the Iron- and the Sulphur-Bacteria are prototrophic, that is independent of organic compounds for their nutrition. It is otherwise with *Bacillus radicicola* already described in relation to the nodules of the Leguminosae (pp. 127, 235). These bacteria exist freely in the soil, and when the opportunity offers they penetrate the root-hairs. The *Bacillus* within the nodule is paratrophic but with a special power of fixing free nitrogen. This it shares with another soil-bacterium, *Clostridium pasteurianum,* which however is metatrophic: when grown in a nutritive solution with sugar it is found to take up nitrogen from the air. In either case free nitrogen of the air is brought into combination.

Other Bacteria are engaged in bringing about changes in nitrogenous bodies already present. Various putrefactive organisms, chiefly bacteria, break down more complex organic bodies into simpler. In the case of nitrogenous compounds the organic nitrogen is ultimately liberated as ammonia. This ammonia is probably "mineralised" before it can be used again by green plants. It is oxidised in the soil, and combined with a base to form nitrate. This is known as "nitrification." It is carried out by certain prototrophic bacteria everywhere present in the soil. The change is effected in two steps: the nitrite bacterium (*Nitrosomonas*) oxidises the ammonia into nitrous acid, and the nitrate bacterium (*Nitrobacter*) converts it into nitric acid (Fig. 348).

FIG. 348.

Nitrifying bacteria. (After Winogradsky.) *a, Nitrosomonas europaea,* from Zurich: *b, Nitrosomonas javanensis,* from Java: *c, Nitrobacter,* from Queto. (From Fischer, *Vorl. ü. Bacterien.* × 1000.)

Both organisms are aerobic, and they are always present together in Nature, so that the compounds formed by one are immediately taken up by the other, and the end-product is nitric acid in the form of nitrate, which is then available as plant-food.

These examples of organisms in water and in soil will serve to suggest the activity of Bacteria in Nature. They have also wide-reaching effect in manufactures. For instance, acetic-acid bacteria convert alcohol into vinegar: butyric bacteria cause the "retting" of Flax and Hemp: bacteria take part in the preparation of Indigo; while the flavours of cheese, butter, and tobacco depend for their market-value upon the exact type and conduct of the partial decomposition of their constituents by bacterial action.

We are most directly interested in those bacteria that affect Man, and other animals. Many metatrophic forms flourish on the mucous membranes of the mouth, nose, and alimentary canal, etc., and accompany the individual through life without doing harm. But many other paratrophic bacteria, entering the tissues, are the active causes of disease. Thus, suppuration is caused by various *Cocci*: acute lobar pneumonia by a *Diplococcus*: anthrax, or malignant pustule, by *Bacillus anthracis*: lock-jaw by *Bacillus tetani*: tubercle by *Bacillus tuberculosis*: cholera by the "comma-bacillus," *Vibrio cholerae,* etc. (Fig. 349.) The actual intrusion of the organism is the first essential of disease, but the serious consequences are due to the action of poisons, or *toxines,* produced by the micro-organisms, and liberated into the system of the host. The host defends itself by the action of the white blood-corpuscles, and other cells, which take up and digest the invading bacteria: these cells have accordingly been called "*phagocytes.*" The process is physiologically similar to that carried out by the cells of the digestive tract in the mycorrhizic Orchidaceae, described in Chapter XII. p. 231. But there is also another line of defence which forms the foundation of the serum-treatment now so widely applied. It is based on the fact that in certain instances, when a bacterial toxine is introduced into the circulation of an animal in suitable amounts, there is developed in the blood-serum of the animal a substance which has the property of neutralising the toxine, and is called an *antitoxine.* Various specific antitoxic sera are thus prepared, and are used either as *preventive* or as *curative* agents. This is not the place to discuss the phenomena of immunity, but it may be stated that immunity is of two main types :—it is directed either against the growth of the bacteria, on the one hand ; or against the action of their toxines, on the other.

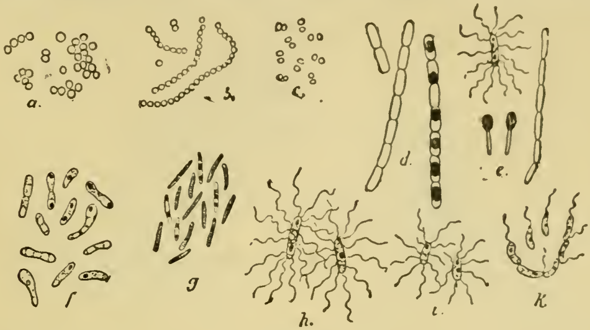

FIG. 349.

Pathogenic Bacteria. *a*, Pus cocci ; *b*, erysipelas cocci ; *c*, gonorrhoea cocci ; *d*, splenic fever bacilli ; *f*, diphtheria bacilli ; *g*, tubercle bacilli ; *h*, typhoid bacilli ; *ι*, colon bacilli ; *k*, cholera bacilli. (From A. Fischer, *Vorl. ü Bacterien.* × about 1500.)

During recent years a number of important anti-bacterial drugs have been synthesised and given wide clinical application. The discovery of the non-toxic, anti-bacterial substance Penicillin, produced during the growth of the green mould *Penicillium notatum* and related species on suitable media, marks the beginning of a new era in the treatment of wounds and diseases, Staphylococci, Streptococci and Pneumococci being among the organisms most readily affected.

The invasion of plant-tissues by Bacteria does not appear to be so common as of animal tissues. The reason probably is that the cell-walls prove an obstacle to ready infection : but a good example is seen in the *Crown Gall*, which occurs on various cultivated plants, and especially on fruit trees. It is prominently seen on the Paris Daisy (*Chrysanthemum frutescens*), on which it is very destructive to nursery stock, being highly contagious. The galls are formed just under the ground on the collar or root, and grow rapidly to a large size, decaying at the end of the season, but forming new galls in the following season round the edge of the old wound, and so on. The causal organism is *Bacterium tumefaciens*, which has been isolated, and gives like characters both in America and in Britain. All infected stock should be burned, and quicklime worked into the tainted soil.

It will be gathered from the examples mentioned above that the various modes of life of Bacteria, however peculiar, are such as to rank with the activities of the Fungi, and that they may be compared with those seen in other representatives of the Vegetable Kingdom.

CHAPTER XXIX.

INTRODUCTORY TO LAND-VEGETATION.

THE Thallophyta are essentially aquatic in their characters. Most of the Algae are actually water-living organisms: and though some of them exist on land-surfaces, they are restricted as a rule to moist situations, and none of those now living have achieved a dominant position in subaerial vegetation. In the last paragraphs of Chapter XXVII. (p. 444) it has been shown how Fungi, though referable in origin to Algal sources, and showing evidence of it particularly in the Phycomycetes, have in many of their characters become specialised so as to accommodate them to subaerial life. Even extreme examples of this mode of life are still traceable by comparison to an Algal origin. The conclusion may then be held as justified for the Thallophyta generally that they originated in water.

We pass now to Plants which have acquired a firmer hold on exposed Land-Surfaces, though still retaining features which show that they were ultimately of aquatic origin. They may be held as the *Amphibians of the Vegetable Kingdom*, being specialised in their vegetative structure to subaerial life, but still retaining certain features which indicate their dependence on external liquid water. The most striking of these is that their fertilisation is carried out by spermatozoids motile in water (*zoidiogamic*). The life-cycle cannot be completed without this stage, which is clearly reminiscent of their flagellate origin. The Plants in question are sometimes styled the ARCHEGONIATAE, a term which comprises the relatively simpler Mosses (BRYOPHYTA) and the more complex Ferns (PTERIDOPHYTA). The feature which they have in common justifying that inclusive name is the female organ, or *Archegonium* (Fig. 350). This is a more or less flask-shaped body enclosing and protecting a single ovum or egg, which is thus enveloped in the tissue of the parent.

The ovum of Land Plants cannot, as in *Fucus* and other aquatic plants, be safely extruded from the parent to fend for itself. An unprotected primordial cell would have a poor chance of survival if exposed to the drying influence of the air. *The ova of the Archegoniatae are accordingly retained within the tissue of the parent,* and are produced singly. The archegonium is in fact a nursing organ, and the constancy of its occurrence, with only minor differences of detail in the Bryophyta and Pteridophyta, may be taken as evidence how essential to survival of subaerial plants is the protection and nursing of the germ. It may be said generally for subaerial Animals and Plants that an *internal embryology in one form or another is an essential factor of life upon exposed land-surfaces.* It is this which follows on fertilisation of the ovum of the Archegoniatae so safely hidden within the archegonium.

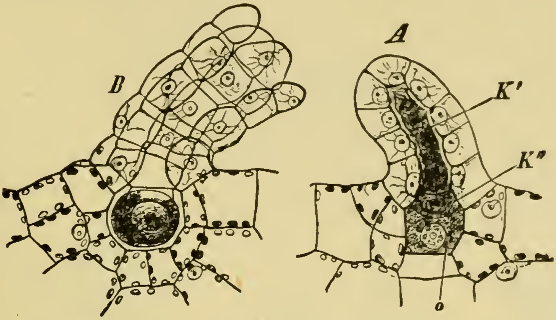

Fig. 350.
Archegonia of *Polypodium vulgare*. *A*, still closed. *o* = ovum. *K'* = canal-cell. *K"* = ventral canal-cell. *B* = an archegonium ruptured. (× 240.) (After Strasburger.)

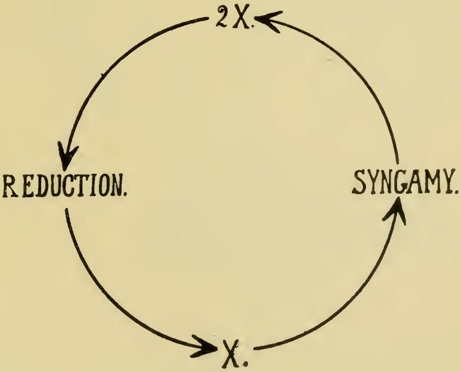

Fig. 351.

The origin of a somatic development, or formation of a plant-body, may be at either of two points in the life cycle: often at both points. This has already been foreshadowed in such Thallophytes as *Dictyota* (p. 384), and *Polysiphonia* (p. 387), both of which show two alternating "generations." The limits between these are on the one hand the zygote, in which by syngamy the chromosomes are doubled in number: on the other the tetrad-division, in which

FIG. 352.

Catharinea (*Atrichum*) *undulata*. The leafy gametophyte, or Moss Plant, bearing capsules, or sporogonia, which are the dependent sporophyte generation. (After Schimper.)

by reduction the original number of the chromosomes is restored. The cycle may be represented diagrammatically by Fig. 351, and the *two phases, the haploid* ("X") *and the diploid* ("2X") *constitute the alternating "generations." They appear as the gametophyte and the sporophyte respectively.* These "generations" may bear varying proportions one to the other, that which is the more prominent and obvious being referred to in popular phraseology as "the plant." But it is, in fact, only one phase of the complete life history. For instance, *in the Bryophytes it is the X-generation or gametophyte which is the more conspicuous*, and in a Moss the leafy body which is called the "Moss-Plant" turns out to be the gametophyte and bears the sexual organs, while the sporophyte is the capsule dependent upon it (see Fig. 352). This is so for all of the Bryophytes. *In the Pteridophytes, however, it is the 2X-generation or sporophyte which is predominant*, and the leafy structure known as the "Fern-Plant" is the sporophyte generation, while the gametophyte is the relatively small prothallus which produces it (Figs. 353, 354). This is so for all of the Pteridophytes. When it is remembered that in *Dictyota* and *Polysiphonia* the two generations are very much alike, this difference of balance will seem less strange than it might otherwise appear to be. For the progression to a leafy shoot may in fact have been carried out in either of them.

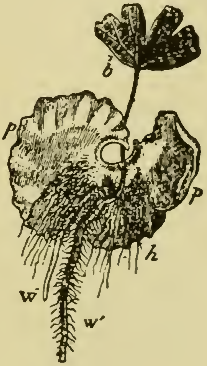

FIG. 353.

Adiantum Capillus Veneris. The prothallus, *pp*, seen from below has a young Fern-plant attached to it. *b* = first leaf. *w*, *w'* = first and second roots. *h* = root hairs of the prothallus. (× about 30.) (After Sachs.)

Most of the Archegoniatae possess a *shoot composed of axis and leaves*, a type of development of the plant-body which is continued in Seed-Plants, and is evidently suited, by its relatively large proportion of surface to bulk, to the conditions of subaerial life. Exposure to the air of organs charged as they are with water leads to transpiration. Their ventilation-system of intercellular spaces opening at the numerous stomata facilitates this. The loss is made good from an absorptive system in the soil, which is itself nourished by the activity of photosynthesis in the shoot. This implies both water-conduction and transit of plastic materials by means of a *vascular system*, such as is found in all of the larger forms of land-living plants, in which the "plant" is in all cases the sporophyte generation (Fig. 257, p. 335).

The climax of the sporophyte-generation is the formation of *spores*. It is better to call those spores which follow immediately on the tetrad-division specifically *tetraspores*. The Archegoniatae probably sprang from some Algal source which had its chromosome-cycle already defined, and produced spores which were all alike (*homosporous*). The earliest land-plants were similarly homosporous. In the first instance a high output of spores was the end to be gained, and the whole development of the sporophyte in the primitive Archegoniatae serves this object, though with different degrees of efficiency. In the dependent capsule of the Bryophytes life is short. Spore-production happens once for all in each individual. All the spores of one capsule mature at once, and the capsule itself dies. It is the gametophyte of a Moss that perennates. But in the Pteridophytes the gametophyte is short-lived. It is the neutral generation which is predominant, rooted in the soil, and usually perennial. The plant may in that case produce not one crop of spores only, but many in successive years. Moreover, in the more advanced types a succession of separate

FIG. 354.
Adult plant of *Dryopteris* (*Nephrodium*) *Filix-mas*, grown in the open. Much reduced. An example of the Sporophyte, or diploid generation of a Fern, established independently in the soil.

sporangia may be borne in each season, and the spore-production may thus be spread over a long period. This with many accessory features marks the Pteridophytes as higher in the scale of Land-Vegetation than the Bryophytes, foreshadowing that climax of Land-Vegetation which is seen in the Flowering Plants. Nevertheless, apart from the differences of balance and of special development of the two generations, the life-cycle of the Bryophytes and Pteridophytes is essentially alike. The Archegoniatae may then be held as the primitive vegetation of the Land, sharing with the Seed-Plants the advantages of subaerial life, but still tied down by their primitive method of fertilisation to habitats where external liquid water is at least occasionally accessible.

DIVISION III.

BRYOPHYTA.

CHAPTER XXX.

MUSCI AND HEPATICAE: MOSSES AND LIVERWORTS.

The Bryophytes include two Classes, represented by very numerous species, widespread in all lands except in those of persistent drought. They are the *Musci* or *Mosses*, and the *Hepaticae* or *Liverworts*. These form a very natural alliance, and indeed are distinguished from one another only by minor characters. Everyone knows the general appearance of Mosses, as low-growing leafy plants, chiefly found in moist surroundings. The Liverworts, with a similar habitat, have commonly a flattened form described as a *thallus*; but some of them bear small leaves. Thus the Bryophytes may be either *leafy* or *thalloid*. All the Bryophytes show a cycle of life of the same general plan, having two alternating generations. That green and often leafy structure which is recognised as the "*Moss or Liverwort-Plant*" turns out on examination to be the *gametophyte*. It bears the sexual organs, while the *sporophyte*, which is produced from them and bears the spores, is the well-known *Capsule*, or *Sporogonium* (Fig. 355). In all the Bryophytes the spore-bearing generation is dependent upon the gametophyte throughout its existence. It never fixes itself directly in the soil. Thus the leading morphological feature is *the relatively high vegetative development of the sexual generation*, which is able to carry on active nutrition and propagation, and commonly persists as a perennial. There is no elaborated root-system. It is true Mosses and Liverworts have rhizoids; but both depend for their water-supply not only upon localised absorption by these, but also upon general absorption by their whole surface, as opportunity offers for it. In either case they are dependent for their normal development on sufficient water-supply: and this directly determines

FIG. 355.

Catharinea (*Atrichum*) *undulata*. The leafy gametophyte, or Moss Plant, bearing capsules, or sporogonia, which are the dependent sporophyte generation. (After Schimper.)

their distribution. A rough estimate of the dampness of climate in a locality may even be founded on the proportion of the Bryophyta in its Flora.

Musci, or Mosses.

Mosses are usually gregarious. The leafy plants are often massed together in tussocks or cushions with their small stems upright, and occasionally branched. Sometimes they may be isolated and straggling, with more frequent branchings. They are fixed in the soil or some other substratum by numerous rhizoids springing from their base (Fig. 356), or from a creeping rhizomatous shoot from which the upright stems arise (Fig. 355). Their stature is never great, and often they are very minute. Though they are commonest where moisture is plentiful, and sometimes grow actually in water (*Fontinalis*), or along its edge (*Porotrichum alopecurum*), they often flourish in stations apparently the most unpromising, such as exposed rocks or roofs, tree-trunks, and wall-tops. Here they may be dried to crispness in summer. But they recover at once after a shower of rain. This capacity of resisting drought, and of instant recovery by surface-absorption of water, is one of the causes of their biological success; for by entering thus a state of physiological inhibition, they can tide over extreme conditions.

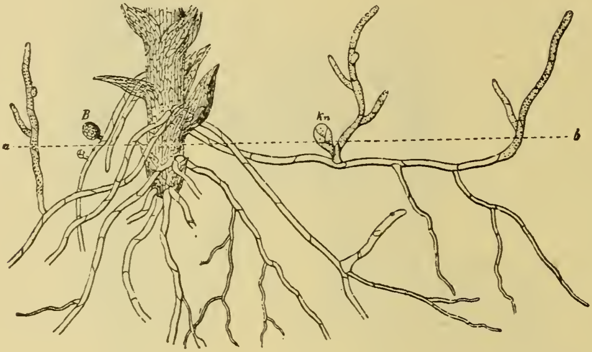

Fig. 356.

Lower part of stem of a Moss (*Barbula muralis*) with protonema. *a-b* shows the soil-level. *B* is a young gemma. *kn*=a bud that would grow into a new plant. (After H. Müller.)

The best way of presenting the life-history of a Moss is by starting from the *spore* (*tetraspore*) shed from the ripe capsule. The spores are so minute that they are readily carried as dust by the breeze. A striking instance of their ubiquity is seen where ashes are left after a fire in woods, or even on cinder paths. A certain Moss, *Funaria hygrometrica*, commonly makes its appearance there, though none of the species may be seen in the near neighbourhood. But occasionally the method of spread is more precise. Thus the spores of some Mosses are sticky, and readily carried by insects. This is so with the dung-infecting *Splachnum*, the agent of its spread being the dung-fly. Scattered in one way or another, the spore germinates in presence of moisture, giving rise to filaments, which as they grow are partitioned into cells, and soon branch. Some of the branches are exposed at the surface of the soil, and develop chlorophyll. Others penetrating the soil are colourless, or have brownish walls ; they serve as rhizoids (Figs. 356, 357). The filamentous system thus produced is called *protonema*, and the formation of Moss-Plants is regularly preluded by this filamentous stage. If grown in dim light the protonema may increase indefinitely, but with full exposure it sooner or later forms Moss-plants. These arise as buds, each taking the place of a branch of the protonema, and may be held to be a condensed form of it. The segmentation of the bud is from an initial cell, by walls with rather more than 120 degrees of divergence, as shown in ground plan (Fig. 357, *d*, *e*). Each segment gives rise to a leaf of the Moss-Plant, borne on the upward-growing stem. Bud-formation does not check the growth of the protonema, which may still extend indefinitely. Branches from the rhizoids may anywhere rise above ground, sooner or later

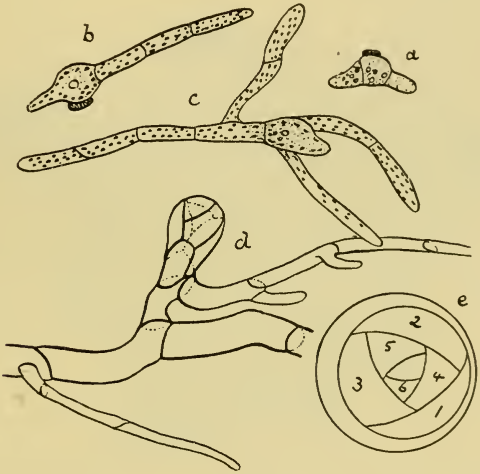

FIG. 357.

a, *b*, *c*, germination of Moss-spores to form protonema. *d*=formation of a bud laterally upon the protonema. *e*=diagrammatic plan of the segmentations of *d*, as seen from above. (After H. Müller.)

forming new buds (Fig. 356). In this way the usual gregarious habit of Mosses is established.

In the smaller Mosses the structure of the leafy Plant is very simple. The leaves may consist only of a single layer of green cells (Fig. 76, p. 115), with a strand of elongated cells forming a central vein, which stops at their bases: the stem is here traversed by an independent conducting cord (*Mnium*). But in *Polytrichum*, and other large Mosses, there is a conducting system consisting of a central column of water-conducting tissue, upon which strands from the leaves are applied. Each of these consists of hydrom (xylem) and leptom (phloem) (Fig. 358). Thus in the gametophyte of the larger Mosses a structure is seen which offers an analogy with that of the sporophyte of Vascular Plants.

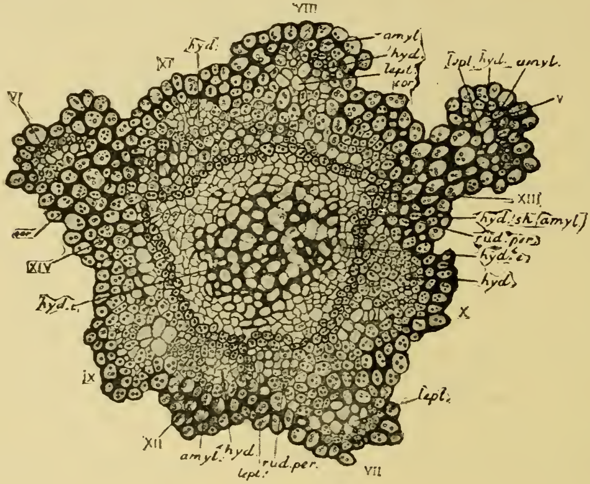

Fig. 358.

Transverse section of the central tissues of an aerial leafy stem of *Polytrichum commune*, showing entry of leaf-traces into the mantles of the central cylinder. The leaf-traces are numbered from without inwards. *amyl*=starchy parenchyma. *hydr*=hydrom. *lept*=leptom. *hyd. sh.*=hydrom-sheath. *rud. per.*=rudimentary pericycle. × 200. (After Tansley and Chick.)

A curious structure is seen in the leaves of *Polytrichum*, and some other large Mosses, which is probably effective in collecting and retaining water during rain. The flat blade bears on its upper face numerous longitudinal plates of chlorophyll-parenchyma, sometimes overlapped by the membranous margins of the leaf. In *P. commune* (Fig. 359) the distal cells of each plate are enlarged, so that its chlorophyll-cells abut upon an almost closed space. As the leaf flattens when moist and curls its margins upwards when dry, the access of atmospheric air to the parenchyma is controlled as it is by the automatic stomata in Vascular Plants. But this is only an analogy, for the surfaces of the lamellae are actually the outer surface of the leaf thrown into deep folds, and the leaf itself is part of the gametophyte, not of the sporophyte.

An example in the Moss-Plant of extreme simplicity is seen in *Buxbaumia*, which habitually grows on humus soil, or rotting tree-stems. Its male plant consists of only a single hollowed leaf, surrounding an antheridium. The female consists of a few leaves, and neither are green. There is an extensive green protonema, but the rhizoids show a hypha-like habit, and establish very close relations with the humous substratum. The sporogonium itself is relatively large in *Buxbaumia*. The evidence of *saprophytism* is strong, and it seems probable that many Mosses share that mode of irregular nutrition in varying degree.

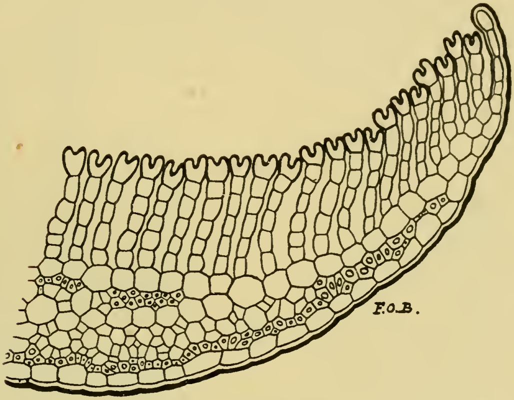

Fig. 359.

Half of a transverse section of a leaf of *Polytrichum commune*, showing the longitudinal plates cut in section.

Among the many special adaptations seen in the gametophyte of Mosses one of the most peculiar is that of the Bog-Mosses (*Sphagnum*) : it is shared in some degree by the quite distinct genus, *Leucobryum*. The tissues of stem and leaf include not only living cells with active protoplasts, but also dead cells of larger size, with their walls propped out by annular or spiral fibrous thickenings, and opening by round pores to the outside. They form a capillary system by which water is retained as in a sponge. It is this structure which gives *Sphagnum* its value for surgical dressings. These Mosses occupy large areas under cold wet climates, and their dead bodies are the chief constituent of *peat*.

The permanent establishment of new Moss-Colonies is largely due to the profusion of their methods of vegetative propagation. *Protonema* is a regular preliminary to the formation of Moss-Plants. A filament may arise from any undamaged cell, either of the plant itself or of the protonema. If a sod on which Mosses are growing is inverted and kept moist, protonema and ultimately a new crop of Moss-Plants will arise from the rhizoids already there. If leaves or stems be chopped up, any undamaged cell may grow out under favourable circumstances into protonema, giving rise to a new crop. But besides this, in many Mosses certain parts are so developed during normal life that they are readily detached as *gemmae*, which may start new colonies in fresh stations. The protonema itself may break into short lengths (*Funaria*), or bulbils may be formed upon it (*Barbula*) (Fig. 356, *B*), or gemmae may be formed on the surface of the leaves (*Grimmia*), or in terminal cups (*Tetraphis*). Whole leaves, slightly modified for the purpose, may sometimes be detached, as in *Aulacomnion palustre* (Fig. 360). In any case protonema is formed first, and subsequently Moss-Plants as buds upon it.

FIG. 360.
Leaf-gemmae of *Aulacomnion palustre*. The drawing shows the gemmae, and scars where some have been shed. (F. O. B.)

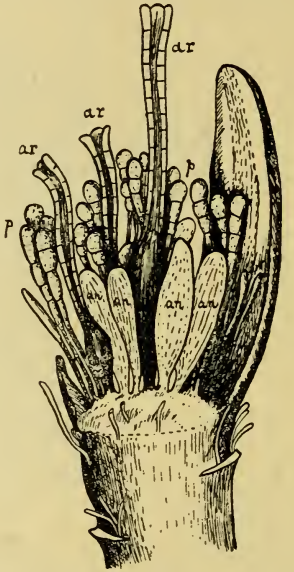

FIG. 361.
Meesia uliginosa, Hedw. (After Hedwig, 1787.) Showing antheridia (*an*), and archegonia (*ar*), with paraphyses (*p*), on same axis.

Frequently it is by such means that Mosses are spread. But a more certain transfer to longer distances is by the minute spores produced in the capsule, or *sporogonium*, which thus reveals itself as the *sporophyte generation* (Fig. 355). This like other sporophytes results from propagation by sexual organs borne by the gametophyte. The antheridia and archegonia of Mosses are sometimes borne on the ends of the main stem (acrocarpic), sometimes on short lateral branches (pleurocarpic), and this character is useful in the classification of Mosses. They are often protected by specially developed "perichaetial" leaves, which give an almost flower-like appearance (*Polytrichum*). In some Mosses the antheridia and archegonia are grouped together, as in *Meesia* (Fig. 361); but commonly they are separate, either on distant branches of the same plant (*Funaria hygrometrica*), or on different plants (*Polytrichum*, *Buxbaumia*). Their presence upon the Moss-Plant makes it evident that it is the sexual generation, or *Gametophyte*.

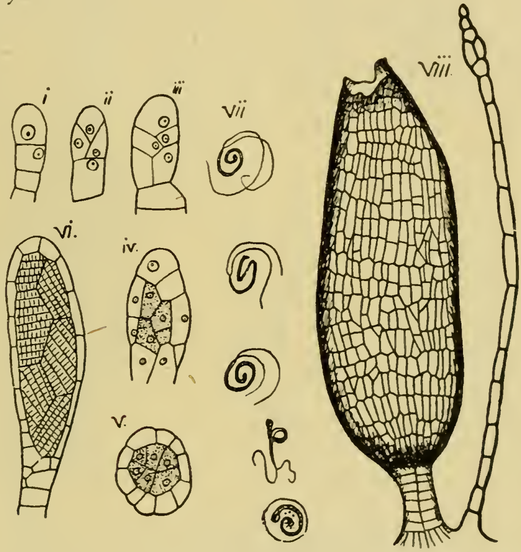

Fig. 362.

i.-vi. Stages in development of the antheridium of *Funaria hygrometrica*, after Campbell (× 400). vii. Spermatozoids of *Funaria*, after Campbell, and Sachs. (× 800.) viii. Empty antheridium of *Andreaea*, with paraphysis, after Kühn. (× 135.)

The analogy between the arrangement and distribution of the stamens and carpels in the flowers of Angiosperms and the sexual organs in the perichaetia of Mosses is obvious. But it must always be remembered that the two sides of this comparison are essentially different. The antheridia and archegonia of Mosses are the real sexual organs borne by the gametophyte, and they contain the gametes; the ovules and pollen-sacs of Angiosperms are parts of the sporophyte, specialised so as to produce the highly modified gametophytes, which in their turn produce the gametes.

Both types of sexual organs project freely from the surface of the plant. Each originates from a single cell, by a segmentation which shows a continued apical sequence, and is quite distinct from that seen in the sexual organs of Pteridophytes. The *antheridium* (Fig. 362, i.-viii.) is a club-shaped body, seated on a short massive stalk, and it is frequently large enough to be seen by the naked eye. It consists of a peripheral wall of tabular cells, covering a mass of cubical spermatocytes (vi.). It bursts when ripe at the distal end (viii.). There is often a special cap of mucilaginous cells, which produce and control the pore of exit. The spermatozoids can then escape in a thin stream, embedded in mucilage from which they soon escape. In cases where the perichaetial leaves face upwards, a shower of rain would bring the rupture about, and the mucilaginous contents may be seen and collected on a slide in a drop of water. The biciliate *spermatozoids* may then be observed in active movement (Fig. 362, vii.).

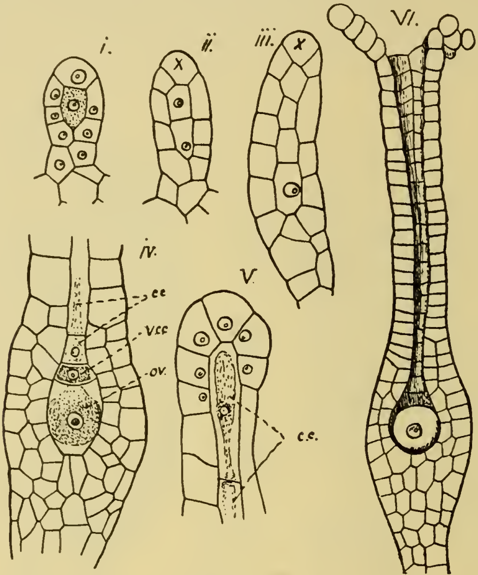

Fig. 363.

i.-v. Stages in development of the archegonium of *Funaria*, after Campbell (× 400). vi. Mature archegonium of *Andreaea*, after Kühn (× 250). i. shows cover-cell separated from central-cell (shaded). ii. iii. cover-cell (x) undergoing segmentation as an initial cell, giving rise to three rows of lateral and one of basal segments: the former constitute the "neck," the latter are the canal-cells. iv. shows the ovum (*ov*), ventral canal-cell (*v.c.c.*), and canal-cells (*c.c.*). *V.* shows the apex of the neck before rupture, with canal-cells (*c.c.*) within.

The *archegonium* is a flask-shaped body with a long neck (Fig. 363). It is seated on a massive stalk, and it also arises from a single superficial cell. When mature it consists of a peripheral wall, which in the lower ventral portion is double, but the neck consists of a single layer built up of six rows of cells, as against four in the Pteridophyta. The wall encloses a central series, consisting of canal-cells (*c.c.*) which may sometimes be very numerous, a ventral-canal-cell (*v.c.c.*), and the ovum (*ov.*). At maturity the end of the neck opens in presence of water, owing to pressure of mucilaginous swelling within ; a funnel-like channel then leads down to the ovum (Fig. 363, vi.). Spermatozoids, motile in the water, may be seen to enter it, and there is reason to believe that their movements are directed by diffusion from it of some soluble substance, such as cane sugar. It will be noted how perfect is the protection of the ovum within the archegonium, and that the protection continues after fertilisation. This retention of the ovum within the parent plant is a general feature of subaerial vegetation, and may be held to have been a leading feature in its success.

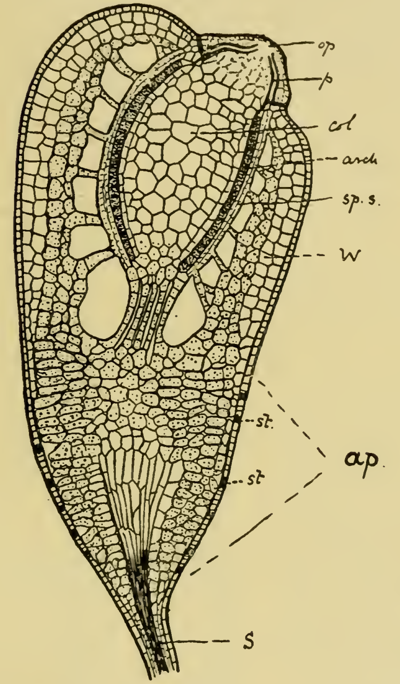

FIG. 364.

Median section of an immature sporogonium of *Funaria*. *s*=seta. *ap.*=apophysis. *w*=water-storage-tissue. *st.*=stomata. *sp.s.*=spore-sac. *arch.*=archesporium. *col*=columella. *p*=peristome. *op*=operculum. Based on a drawing by Haberlandt. (× 20.)

The result of fertilisation is the *Sporogonium* (Fig. 355, p. 461). It usually appears as a radially constructed body, seated in the tissue of the Moss Plant, and bearing at the end of a long stalk (*seta*) a more or less oval head (the *capsule*), which at ripeness contains very numerous spores. It is covered at first by a hood or cap (*calyptra*), which falls off at maturity, disclosing a lid, or *operculum*. This finally separates by a transverse split, and falling away opens the capsule, just as the lid might be taken off a covered jar. In most Mosses a fringe of ragged filaments, the *peristome*, is thus disclosed, which by their hygroscopic movements serve to distribute the dry and dusty *spores* (Figs. 364, 367). The sporogonium is usually green while young, but yellowish or brown when ripe. This is due to photo-synthetic tissue, which is specially developed at the enlarged base of the capsule (*apophysis*), where also stomata may be found, providing for ventilation (Fig. 364, *st.*). But such tissues dry up at maturity, so that the capsule is then full of the yellowish dusty spores.

The sporophyte thus constructed is *dependent* throughout its existence upon the gametophyte: it bears *no appendages*, and normally it never branches. The spores all originate from *one continuous spore-sac* contained in the capsule. These features are common for the Bryophyta, and mark a simpler grade of evolution of the diploid generation than is seen in the Pteridophyta and Seed-Plants. Whether this is a primitive simplicity, or a consequence of reduction, is a question which can only be discussed on grounds of broad comparison.

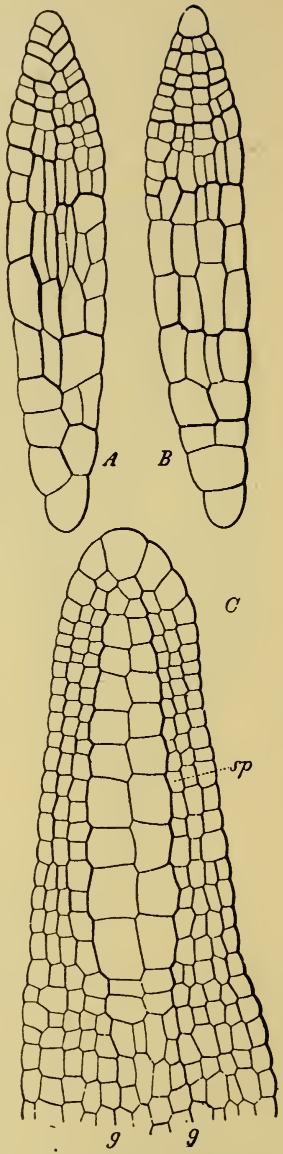

FIG. 365.

Ceratodon purpureus (after Kienitz-Gerloff). *A*, *B*, young embryo seen from points of view at right angles to one another. *C*=an older embryo. *gg*=outer limit of the endothecium. *sp*=outer spore-sac.

The Moss Sporogonium is without any of those lateral appendages which are so conspicuous a feature in Vascular Plants. Its external form contrasts with theirs in being simple. It is essentially a spindle, with polarity defined as apex and base. Transverse expansion accounts for the origin of the oval capsule on the end of the seta. But this capsule is a complicated body in the higher Mosses. Its complexity arises from an advance in internal structure, which thus contrasts with its simplicity of external form. To understand it the best approach is through development.

The zygote first divides by a basal wall, which is transverse or slightly oblique to the axis of the archegonium. This at once defines the polarity. It is succeeded by a brief apical growth in the epibasal half, with a two-sided apical cell. The hypobasal half also segments, but less regularly, boring its way downwards into the tissue of the parent (Fig. 366). A spindle-shaped body is thus produced (Fig. 365, *A*, *B*). Subdivision of the segments gives a central tract (endothecium), and a peripheral tissue (amphithecium) (Fig. 365, *C*). The former is the exclusive source of spore-formation; the latter produces the external tissues of the wall, parts of which are photosynthetic while young. Thus far the sporogonium is enclosed in the growing venter of the archegonium (Fig. 366). As it develops further the lower part remains thin, forming the seta, which may be traversed by a conducting strand (Fig. 364). But the distal part enlarges to form the capsule. A layer of cells is there cut off from the periphery of the endothecium, and acquires dense contents. This is the *archesporium*, which is shaped like a barrel without ends (*arch*. Fig. 364). Within it is the large-celled water-storage tissue of the columella. The amphithecium, limited now by a superficial epidermis with stomata, forms a lacunar photo-synthetic tissue, with a large and continuous air-space outside the archesporium. This tissue is specially active in that region called the apophysis, where the stomata are most frequent (*st*., Fig. 364). In some Mosses it is enlarged as a very effective organ of nutrition.

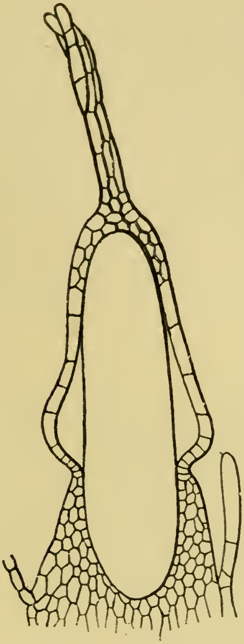
FIG. 366.
Young sporogonium of *Physcomitrella patens*, shown in outline, shortly before the rupture of the archegonial wall. (After Hy.)

As the development proceeds the cells of the archesporium divide repeatedly, forming a thick cylinder of *sporogenous cells* surrounding the columella, and limited externally by a double layer of cells of the amphithecium. This constitutes the *spore-sac*. Its cells then separate, and rounding off in a liquid that fills the sac, each undergoes *tetrad-division*, and finally produces four spores. *Reduction* takes place as usual, common numbers of chromosomes for Mosses being 12-6. The numbers are low for Bryophytes generally. The mature spore is very minute, and almost spherical, and it contains globules of oil.

Meanwhile above the fertile region certain inner cells of the amphithecium undergo changes of induration of the cell-walls to form the *peristome*, which is closely related to the liberation of the spores (*p*., Fig. 364). As its structure differs in detail in various Mosses, it provides facts valuable in their classification. The case of *Fontinalis* serves as a good example of a complicated peristome, as it is seen after the operculum falls away. It is double (Fig. 367). The inner peristome forms a sort of connected lattice-work which will allow the spores to pass singly through its pores, but prevents them all falling out at once. The outer consists of 16 teeth, which are really strips of thickened cell-wall, separated from one another by the breaking down of the thinner lateral connections. They show movements with changes of moisture in the air, and catching one on another by their rough edges, they give flicking jerks on release, which throw the spores to a

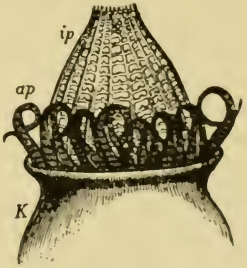

FIG. 367.
Fontinalis, apex of capsule (*K*) after shedding the operculum. *ap*=outer peristome. *ip*=inner peristome. (After Schimper.) (×50.)

distance. The spores thus shed germinate to form protonema, as seen above (Fig. 357, p. 463).

The Mosses show by their ubiquitous spread that they are a successful type of Land Vegetation, though restricted by dependence on water not only for their fertilisation, but also for their physiological activity. Their capacity for retaining their vitality under drought, and their subsequent recovery often saves them. But the feature which leads most directly to their success is their profuse vegetative propagation by protonema and by gemmae. Not only do the latter secure their spread, but the former provide also for their persistence in the soil whenever conditions at the surface are unfavourable. The prevalence of Mosses in all relatively humid climates is thus easily explained.

HEPATICAE OR LIVERWORTS.

The Life-Cycle of Liverworts is on the same plan as that of the Mosses, the gametophyte being the predominant generation. In the simpler types it is thalloid, and may be forked. *Pellia*, which is common on moist clay banks, is constructed like a large flat thallus, of form similar to that of a Fern-prothallus, with rhizoids on the lower surface, but no other appendages. Most Liverworts, however, bear appendages. Thus the thalloid *Riccia* has scales upon the ventral (lower) surface of its fleshy thallus. Moreover, its upper surface is deeply penetrated by narrow air-canals, each bounded by four rows of chlorophyll-containing cells, of which the outermost may be enlarged. The result is a ventilated photosynthetic structure. In the series of the Marchantiales this ventilated construction is further developed, so as to render the thallus very efficient for photosynthesis on land. For instance, in *Targionia* (Fig. 368), the flattened thallus, bearing ventral scales below, and fixed by rhizoids in the soil, is differentiated into a massive lower region chiefly for storage

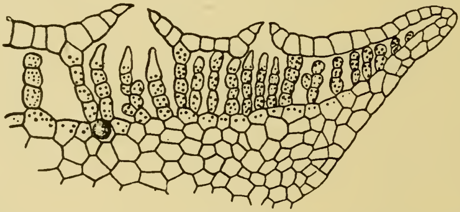

FIG. 368.
Vertical section through part of the thallus of *Targionia*, showing the cavities opening by pores on the upper surface, and containing filaments of chlorophyll-cells. (× 75.)

(though it is also penetrated by a mycorrhizic fungus through the root-hairs), and an upper photosynthetic region marked by large, overarched air-chambers. Each of these communicates with the outer air by a large pore, which is more or less under control. From the floor of the chamber arise active green cells, grouped in simple, or branching filaments. Such developments, with varying detail, are characteristic of the Marchantiales. The analogy with Angiospermic leaves is obvious, but the origin of the structure is here quite different, being chiefly due to surface-involution.

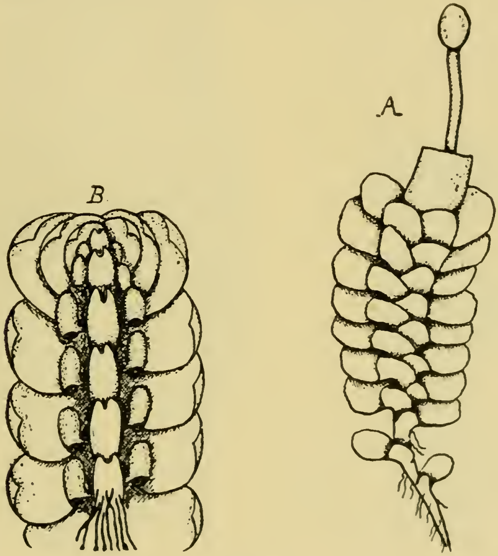

Fig. 369.

A, *Scapania nemorosa*, dorsal view of the leafy shoot, which bears a sporogonium at its tip. *B*, *Frullania tamarisci*, view of leafy shoot from below, to show the ventral row of leaves, and the two lateral rows, of which the lower lobes form pitchers. *A* has the "succubous," *B* the "incubous" disposition of the leaves. (After Cavers.)

A distinct line of vegetative advance is shown by the Jungermanniales, in which successive steps may be found from the thalloid state, through various forms of marginal lobes, to a full leafy development. In the truly leafy Liverworts there is a ventral row of leaves, and a row of lateral leaves on either side. These leaves are more or less clearly two-lobed, and the lobes are often unequal (Fig. 369, *A*). Sometimes a lobe may become highly specialised, as in *Frullania* (Fig. 369, *B*), where that which is downward-directed develops as a water-sac, or pitcher, effective in collecting and holding water in this epiphytic or rock-dwelling genus. On the other hand, in *Trichocolea* the leaves may be divided into narrow laciniae, which collectively hold water as in a sponge. Thus it appears there is a wide scale of adaptation of the gametophyte in Liverworts. Its results offer analogies with the special adaptations seen in the sporophyte of Flowering Plants.

The sexual organs are essentially similar to those of the Mosses; but there are differences in their segmentation. This suggests that their origin may have been distinct. In the thalloid Liverworts they are always borne on the morphologically upper surface; but by various means they are carefully protected, being sometimes sunk deeply in the thallus (Fig. 370). In the Jungermanniae they are covered in by envelopes, the number and variety of which give useful features in classification. A particular interest attaches to those which develop a "marsupium," that is a nursing-sac surrounding the archegonia, and penetrating deeply into the soil. Such arrangements, both in the vegetative structure of the gametophyte and in the

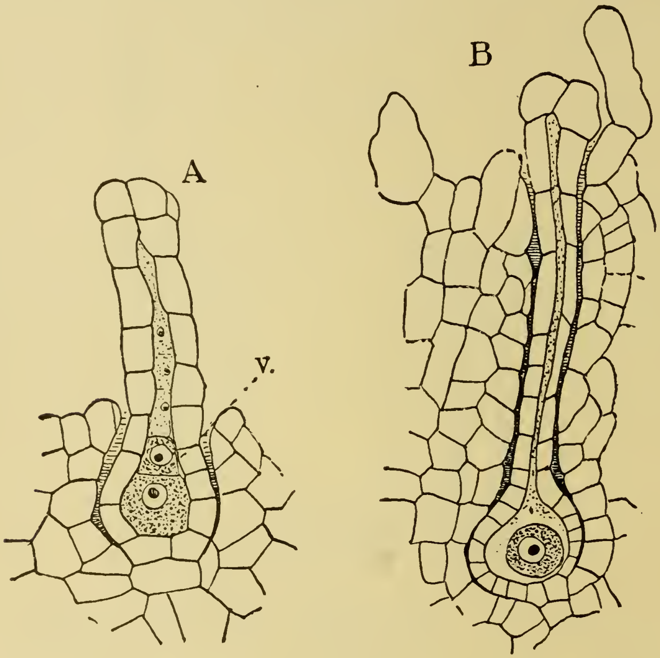

Fig. 370.
A = archegonium of *Riccia trichocarpa*, showing ventral canal-cell (v) and ovum. (× 525.)
B = ripe archegonium of *Riccia glauca*. (× 260.) (After Campbell.)

disposal and protection of the sexual organs, suggest that the Liverworts are making the best of subaerial life, to which their simple structure is not in itself well suited. Their fertilisation is by means of spermatozoids motile through water.

The sporogonium itself is on a simpler scale than that of the Mosses. Excepting the peculiar group of the Anthoceroteae, it is not structurally specialised for carrying on photosynthesis, nor is there any complete columella. Moreover the ripe sporogonium is longer enclosed in the archegonial wall; but it bursts it at maturity, when the seta elongates, bearing outwards the spherical head. There is no operculum, but the relatively thin wall bursts, usually into four valves, and the spores, interspersed among fibrous elaters that help to distribute them, are exposed as a flocculent mass to the breeze, and are scattered in the dry state. Though the details are different from those of the Mosses, the end is the same (Fig. 371).

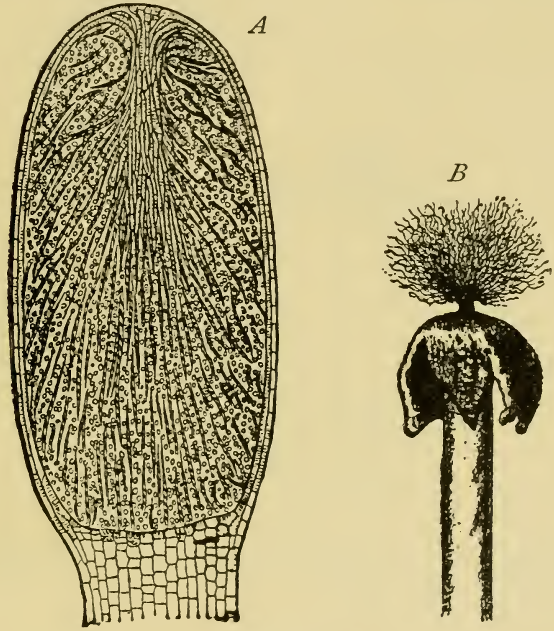

FIG. 371.

A, Ripe capsule of *Aneura pinguis* in longitudinal section. From the summit an elaterophore hangs into the spore-cavity, in which are many spores and detached elaters. Magnified. (After Goebel.)

B, Capsule of *Pellia calycina*, burst, and emptied, showing the valves of the wall recurved, and an elaterophore rising from the base, bearing many threads. (After Goebel.)

On the other hand, certain Liverworts have very simple sporogonia. This is conspicuously the case in the *Ricciaceae* (Fig. 372), where it is spherical, with no distinction of apex and base, and no elaters. The sporogonial wall is one layer thick, and is disorganised at ripeness.

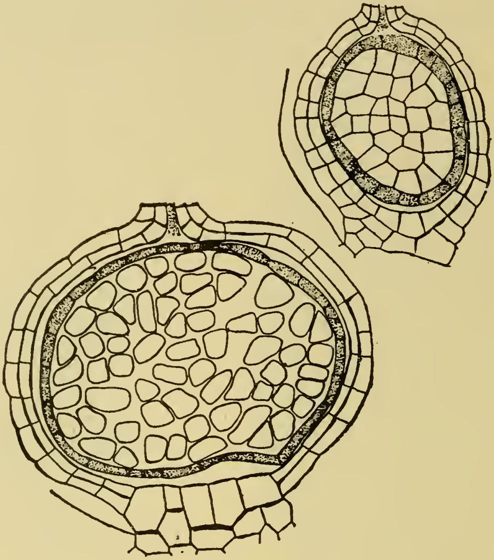

FIG. 372.

Ricciocarpus natans. Young sporogonia still surrounded by the archegonial wall. The younger (× 666) shows the wall of the sporogonium shaded, surrounding the sporogenous cells. In the older (× 560), these are separated as the free spore-mother-cells. (After Garber.)

The spores are scattered on decay of the thallus. This is the simplest condition of the sporophyte known in Archegoniate Plants. It is a familiar subject of comparative discussion whether the simplicity that *Riccia* shows is really primitive or the result of reduction from some more complex type.

Comparing the facts from the Mosses and Liverworts it is apparent that both are " amphibians " in the sense that they live on exposed land-surfaces, but cannot complete their life-cycle without the presence of external liquid water. This tends to restrict them to moist situations. In any organism with a life-cycle punctuated by the two stages of the spore and the zygote, there are two possibilities of somatic expansion, viz. in the diploid sporophyte and in the haploid gametophyte. In the Bryophytes the second alternative has been fully exploited. Their characters depend upon the development of the gametophyte to the highest condition in which it is seen in Land Vegetation. The details of this development run parallel with those of the sporophyte in Vascular Plants, so that the two present a series of analogies. The most striking are seen in the organs of photosynthesis, in the conducting tracts, and in the grouping of the organs of sex. In the sporophyte of Vascular Plants the typical photosynthetic organ is the leaf-blade, with its ventilated mesophyll and stomatal control. In the gametophyte of Mosses and Liverworts a similarly ventilated structure is seen in the leaves of some of the larger Mosses (Fig. 359), and in the thallus-structure of the Marchantiales (Fig. 368). These are, however, parts of the gametophyte, and the ventilated structure is here produced mainly by involution of the outer surface, while in Vascular Plants it arises from intercellular splitting of the cell-walls. The physiological end is the same in both cases, but the place and the means are different. Plainly these are the results of parallel evolution, or homoplasy.

So also the conducting tissues seen in the stem of large Mosses, such as *Polytrichum*, show in their connections with the leaves, as well as in their construction of hydrom and leptom, similarities with the conducting system of Vascular Plants (Fig. 358). But again the comparison is between the gametophyte on the one hand and the sporophyte on the other ; while the isolation of such phenomena in the larger Mosses indicates that the conducting tissues are an adaptive feature specially developed in them, and not general for all Mosses. Again the similarity of structure to that seen in Vascular Plants must be held as homoplastic.

There is also a very peculiar analogy between the flowers of Angiosperms and the so-called " flowers " of Mosses, where the perichaetial leaves surround the sexual organs, as the perianth surrounds the androecium and gynoecium in Flowering Plants. There is even parallelism in the distribution of the sexes, for such " flowers " in Mosses may be hermaphrodite or unisexual. Notwithstanding this likeness it is necessary to keep clearly in mind that such comparisons deal with essentially different things, though both involve the sex-distinction (p. 256). The interest of them lies in the fact that the similarity exists at all.

Such comparisons show how nearly the evolution of the gametophyte in the Bryophyta may follow along the same lines of adaptation as the sporophyte of Vascular Plants. The end is the same for both, viz. to develop on land as large a vegetable system as possible, so as to provide material for the largest possible number of germs. The one phylum has solved it by enlargement of the sporophyte, which thus becomes the substantive "Plant" of vascular types. The other has solved it by elaboration of the gametophyte, which has similarly become the substantive "Plant" of the Bryophytes.

For a less condensed treatment of the Bryophyta see *Primitive Land Plants*, Chapters I. to VI.

THE PSILOPHYTALES.

Till recently it had been thought that among Plants of the Land the widest gap of organisation lay between the Bryophyta and the Pteridophyta, notwithstanding that the life-cycle of both is essentially the same. Even now the distinction seems wide when only living examples of them are compared. But in late years there have been discovered from rocks of Devonian Age, and widely spread geographically, fossils grouped as a new Class of the Psilophytales. Their sporophytes only are known, but these are clearly vascular land-plants of rudimentary organisation. They are rootless, and the simplest of them leafless. The general character of two of the best known types is shown in Fig. 372 A, which represents reconstructions of them after Kidston and Lang. *Hornea*, the smaller, has a tuberous base attached within the soil by rhizoids. From this a bifurcating cylindrical shaft rises erect and leafless. Some of its finer branches bear terminal sporangia. The larger plant, *Asteroxylon*, has dichotomously branched leafless rhizomes without absorbent hairs: their finer branchlets ramify in the peat in which the plants grew. From these sprang large branching and erect trunks. They had localised growing points, and bore simple microphyllous leaves; but these were absent from the smaller distal branchlets which dichotomised freely, and bore terminal sporangia. The structure of these plants is very completely known. They are quoted here as examples of early vegetation of the land, which offer illuminating comparison on the one hand with the sporogonia of the Bryophytes, and on the other with the sporophytes of the simpler types of Pteridophytes previously known.

There are obvious restrictive defects in the organisation of the Mosses and Liverworts, which account for their dwarfed habit. In the sporophyte we note its physiological dependence on the gametophyte, and the absence of continued apical growth and branching. But the diploid phase of vascular plants is habitually fixed in the soil and diffuse in form: these features appear in rudimentary outline in the very ancient Psilophytales. Hence we may rightly see in them types which suggest that varied advance which characterises the Pteridophytes, and vascular plants generally. Without suggesting close affinities by descent with any of these, the early existence of the Psilophytales suggests an intermediate state of that elaboration of the sporophyte which has resulted in the characteristic Flora of the Land. By the discovery of these and other archaic forms the gap in organisation between the Bryophyta and the Pteridophyta has been narrowed, not only in theory but by observed fact. Nevertheless in the absence of the gametophyte of these fossils, the method of establishing the independence of the sporophyte remains still an open problem.

Fig. 372 A.

Reconstruction by Kidston and Lang of the Rhynie fossils named above.

Reduced in scale.

But light is shed upon it by the Psilotales, which of living plants appear to be the nearest allies of the Psilophytales. Their prothallus and embryology have now been observed. In them we see that the freedom of the sporophyte follows simply and directly on decay of the prothallus. With such facts in view, the relation of the Bryophyta to the Pteridophyta becomes more intelligible now than it was before the discovery of the Psilophytales, or the completion of the life-history of the Psilotales. For a more complete treatment of the Psilophytales, see *Primitive Land Plants*, Chapters VII., VIII.

DIVISION IV.

PTERIDOPHYTA.

CHAPTER XXXI.

FILICALES.

The Pteridophyta include the Club-Mosses (*Lycopodiales*), the Horse-tails (*Equisetales*), and the Ferns (*Filicales*), together with certain other less familiar types of Plants, some of which are only known as Fossils. All of these Classes were represented in the Palaeozoic Period : there is thus no doubt of their extreme antiquity, which is shown by their characters as well as by their history. They differ from the Bryophyta in that *the leafy* " *Plant* " *is the diploid generation or Sporophyte*, and it bears spores : whereas in Mosses and Liverworts the " Plant " is the haploid or sexual generation, and it has been seen that it bears antheridia and archegonia.

A difference in proportion of the leaves of the sporophyte plant is very marked among the Pteridophyta. In the Lycopodiales and Equisetales the leaves are small (*microphyllous*), and the axis relatively large (Figs. 404A-406, 413A). But in the Filicales the leaves are relatively large (*megaphyllous*), and often highly branched, giving the well-known character of the foliage of Ferns (Figs. 354, 373). In both the shoot is traversed by a conducting system of vascular tissue, often highly elaborated, and accordingly the whole Division has sometimes been styled the *Vascular Cryptogams*. In all of them the *gametophyte* is relatively inconspicuous, and is described as the *Prothallus*. The life-cycle is essentially uniform for them all, and their natural relationship may be accepted, notwithstanding the differences which distinguish the several Classes of them. For the present purpose it will suffice to select a few examples, of which the most important will be some common Fern from the large series of the Filicales, and *Selaginella* from among the Lycopodiales.

FILICALES.

The living Ferns include more than 7000 species, widely spread over the earth's surface from the Equator to the Arctic Regions. Some 39 of these are British. Though a few live actually in water, others are distinctly xerophytic, and able to resist extremes of drought.

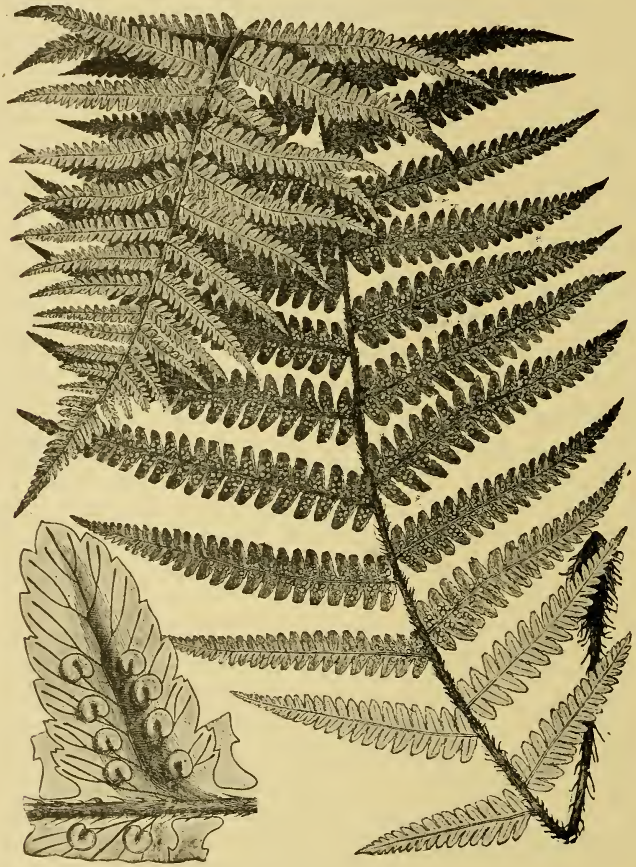

FIG. 373.

Dryopteris Filix-mas, Rich. Fertile leaf about one-sixth natural size, the lower part with the under surface exposed. To the left a single fertile segment, bearing kidney-shaped sori, enlarged about seven times. (After Luerssen.)

But the vast majority live in moist and often in shaded positions, and, as will be seen later, external liquid water is necessary for the completion of the normal cycle of their life. The Fern Plant is with very few exceptions perennial. It consists of a shoot which may or may not be branched, and is attached to the soil by numerous fibrous roots. The shoot consists of axis and leaves, as in the Flowering Plants, but usually without axillary buds. The leaves are large in proportion to the stem that bears them. Often they are highly branched, with two rows of lateral pinnae that are branched again repeatedly. This, together with their delicate texture, gives the feathery appearance to the leaves of most Ferns (Fig. 373). It is specially conspicuous in the large Tree-Ferns, where each leaf may be many feet in length. This habit (megaphyllous) contrasts strongly with that of the Lycopods with their small unbranched leaves (microphyllous).

The Coal Period has been sometimes described as "The Age of Ferns." It is true that large-leaved Fern-like Plants were frequent then. But many of these have been lately shown to have been Seed-bearing Plants (Pteridosperms), whereas Ferns have no seeds. The question has then been raised whether true Ferns existed at all at that early time. There are at least three types which can only have been Ferns that did live then, and *Botryopteris*, of which the stele is shown in Fig. 375, is an example. Some Ferns resembling these early fossils survive to the present day. But many of the Ferns we know are relatively modern. It is doubtful whether at any time a more varied Fern-Flora has existed on the earth than at the present day. If that be so, the present is as much the age of Ferns as any that has gone before.

The Ferns show a comparatively primitive cycle of life. It consists of two alternating and physiologically independent phases, or generations, the one diploid (non-sexual), which is the *sporophyte*, the other haploid (sexual), which is the *gametophyte*. The former is what is known commonly as the *Fern-Plant*; the latter is a small green scale-like body, which is called the *Prothallus*. As the former is the better-known phase, it will be described first.

Male Shield Fern and Bracken.

The large-leaved shoot of the Fern Plant may grow upright, and usually unbranched, as in Tree-Ferns, and the Royal Fern (*Osmunda*); or obliquely, as in the common Shield Fern (*Dryopteris*) (Fig. 374, *A*); or horizontally with a creeping habit, as in the Bracken (*Pteridium*) or the Common Polypody. When upright, the internodes are short, and the numerous leaves take that basket-like grouping so well seen in the Shield Fern. When creeping the internodes are longer, so that the leaves are isolated, as on the underground rhizome of the Bracken, the leaves being here the only part above ground. The stems of Ferns have unlimited apical growth, and sometimes fork at their ends. But buds may also appear at the leaf-bases, a condition seen in the old leaves of the Shield Fern (Fig. 374, *B*). A general peculiarity of Ferns is the crozier-like curvature of their young leaves, the adaxial face growing at first more slowly. But later it catches up the abaxial face, so that the leaf flattens out as it matures. This habit is effective

Fig. 374.

Dryopteris Filix-mas, Rich. *A*, stock in longitudinal section. *v* = the apex. *st* = the stem. *b* = the leaf-stalks. *b'* = one of the still folded leaves. *g* = vascular strands. *B* = a leaf-stalk, bearing at *k* a bud with root at *w*, and several leaves. *C* is a similar leaf-stalk cut longitudinally. *D* = a stock, from which the leaves have been cut away to their bases, leaving only those of the terminal bud. The spaces between the leaves are filled with numerous roots, *w*, *w'*. *E*, stock from which the rind has been removed to show the vascular network, *g*. *F* = a mesh of the network enlarged, showing the strands which pass out into the leaves. (After Sachs.)

in protecting the curled tip of the leaf, since in Ferns apical growth is long continued, and the apical tissues are delicate. The stem and leaves, especially while young, are often densely covered either with hairs (*Osmunda*) or chaffy scales (*Dryopteris*), which protect the young parts against drought, but are liable to fall away later.

In their general construction Ferns resemble Flowering Plants. They have a superficial *epidermis*, and a conducting system of *vascular tissue*, embedded in *ground-tissue* which is parenchymatous: but often it also encloses strands or islands of hard brown *sclerenchyma*, while hard stony or horny sheaths frequently form the surface of stem and leaf-stalk. The epidermis and ground tissue call for no detailed description. The chief interest lies in the vascular system. In ancient fossil Ferns, such as *Botryopteris*, in many primitive living Ferns, and generally in young sporelings there is a simple *stele* of a type called a "protostele," having a solid xylem-core, and phloem surrounding it. This is believed to have been the primitive structure for them all. It is well shown in *Botryopteris* (Fig. 375). Occasionally this state may be retained through life (*Hymenophyllum*, *Lygodium*).

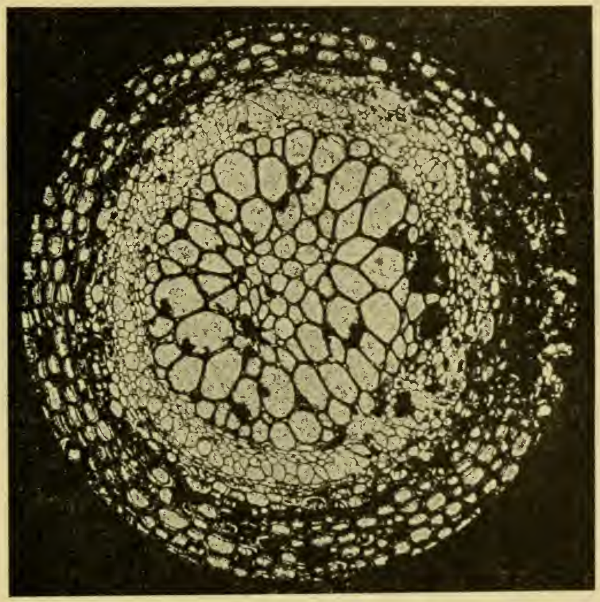

Fig. 375.

Transverse section of a fossil-Fern, *Botryopteris cylindrica*, showing a protostele with solid central core of xylem, and peripheral phloem. This is a fossil from the Palaeozoic Period, and it illustrates how perfect the preservation of structure may sometimes be in fossils of very early times.

But in the vast majority of Ferns the stele expands as the plant grows stronger, and the leaves larger. In various ways it becomes segregated into a number of vascular strands (*meristeles*), arranged in a cylindrical network (Fig. 374, *E. F*). Each mesh in *Dryopteris* corresponds to the insertion of a leaf-base, and is called a *foliar mesh, or gap*. The vascular strands that run out into the leaf, called collectively the *leaf-trace*, arise from the margin of it, and the cortex and

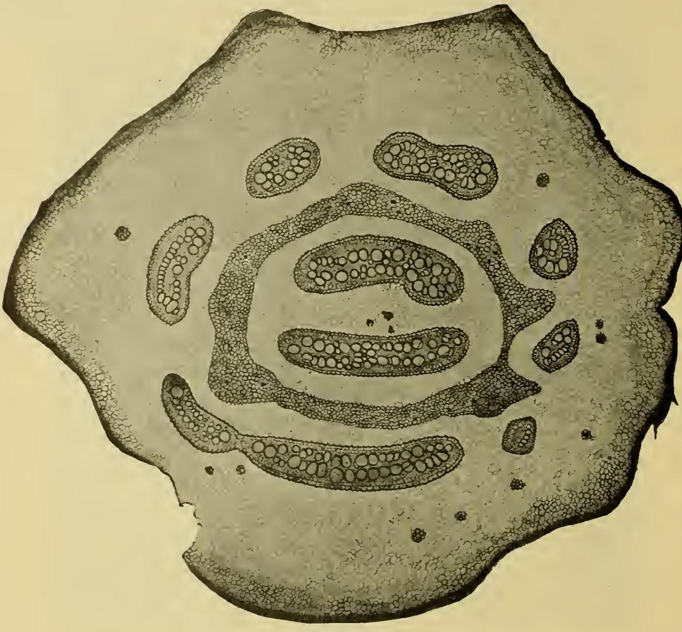

FIG. 376.

Transverse section of rhizome of Bracken, showing the outer and inner series of meristeles, and the irregular bands of sclerenchyma between them. These are embedded in soft ground-parenchyma, with a hard sclerotic rind. (× 10.)

pith are in direct communication through the foliar gaps. This is readily understood if the vascular skeleton be dissected out, as it is seen in Fig. 376 A. In transverse sections the meristeles would appear as a ring of isolated tracts, and this gave rise to the misleading term " polystelic " as applied to such stems. But the dissection shows that they are all parts of one cylindrical network, which arises through dilatation of the protostele of the sporeling (compare Figs. 374, 375). A similar disintegration of the leaf-trace may be followed in *Dryopteris*, and many of the larger Ferns. A simple strand appears to have been the primitive type of trace, and it is seen generally in the leaves of their sporelings. But a plurality of strands appears in the adult leaf-stalk of most modern Ferns (Fig. 374, *D*). The several strands of *Dryopteris* can be traced into the pinnae and pinnules where they fork freely and end blindly (Fig. 373). But in broad-leaved Ferns such as the Adder's Tongue, and particularly in those of more advanced type, such as *Onoclea* and *Woodwardia*, a network of veins may arise by their lateral fusion, after the manner of Dicotyledons (Fig. 46). Both types serve the same purpose, that of supply within the flattened blade ; but the netted venation is functionally the more efficient. Moreover, comparison shows that it is a derivative state, based on an originally forked venation.

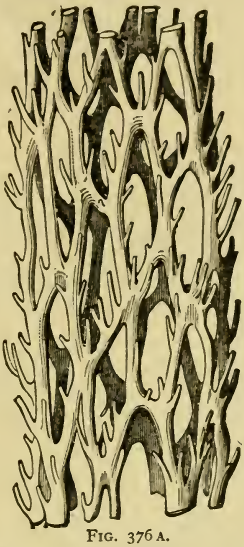

FIG. 376 A.
Dictyostele of the Male Shield Fern dissected out, showing the overlapping leaf-gaps which allow communication between cortex and pith. (After Reinke.)

It thus appears that the vascular system in the leaves of Ferns resembles that of Flowering Plants more nearly than does that of their adult stems. The diversity in vascular structure between the stems of Ferns and those of Seed Plants arises from an essential difference in their way of solving a fundamental problem of support and of supply (see Chapter XXXVI). In the Bracken and Shield Fern the conducting tracts are all of *primary* origin. They may be traced continuously to their source immediately below the growing point itself, and their outline there corresponds to that which they show when mature. As will be seen in Figs. 376-378, there is no cambium in their make-up. Ferns by their stelar elaborations make the best of this primitive scheme of vascular construction. On the other hand, cambial activity, as described for Dicotyledons and Gymnosperms in Chapter IV, is an automatic means of meeting the growing demands of increasing size. But it is a morphological afterthought : the tissues it produces being of *secondary* origin.

For the study of the tissues composing a vascular strand a rhizome with long internodes, such as the Bracken, gives the best results. In a transverse section taken between the leaf-insertions an outer and inner series of vascular strands is found, separated by an incomplete ring of sclerenchyma. The outer series corresponds to the mesh-work of *Dryopteris*, the inner are accessory or medullary meristeles (Fig. 376). Each one is circumscribed by a complete endodermis. This is usual in Ferns. Each consists of a central core of xylem, surrounded by phloem; in fact they repeat the main structure of the protostele itself. A transverse section of one of them, examined under a high power, gives the following succession of tissues (Fig. 377). Passing inwards from the starchy ground-tissue, with intercellular spaces (*g*), the layer of brownish cells of the *endodermis* (*e*) forms a continuous barrier, delimiting the strand sharply. Within it follows the *pericycle*, with its cells not very regularly disposed, but corresponding roughly to the cells of the endodermis, both having been derived by division from a single layer. Within this comes the *phloem* (*ph*), with large *sieve-tubes*

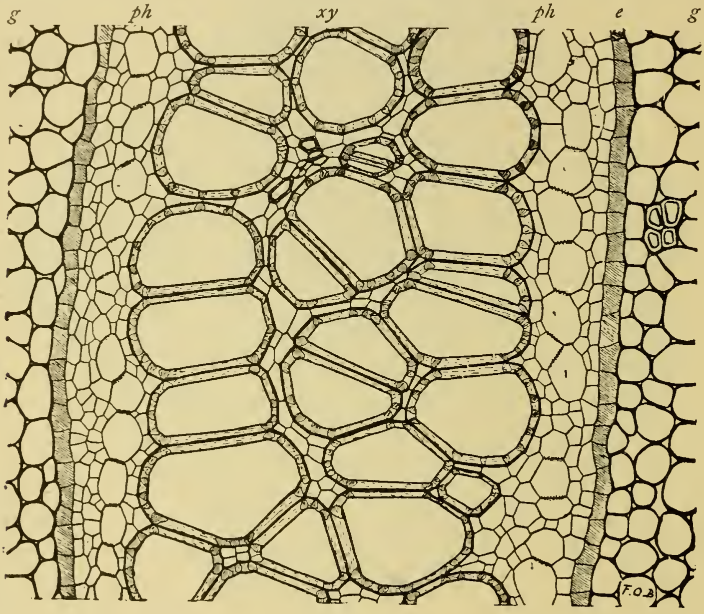

Fig. 377.

Part of a transverse section of a meristele of Bracken. *g*=ground parenchyma. *e*=endodermis. *ph*=phloem with sieve-tubes. *xy*=xylem, with large scalariform tracheides. Some smaller tracheides lying centrally are the proto-xylem. Note that no intercellular spaces are seen within the endodermis. (× 75.)

as the characteristic elements. They are thin-walled, with watery contents. The lateral walls where two adjoin bear the sieve-plates, which are recognised by glistening globules that adhere to them. They are embedded in parenchyma, which extends inwards into the xylem, and may be called collectively *conjunctive parenchyma*. The chief features of the *xylem* (*xy*) are the *tracheides*, which are relatively large, with a very characteristic polygonal outline. They have woody walls, and no protoplasmic contents. Where two adjoin the walls are flattened, and of double thickness, showing that each has its own share of the thickening, which overarches the pit-membrane as in the pits of Conifers. The structure is in fact essentially the same, only in Ferns the pits are liable to be extended transversely. But where the tracheide abuts on parenchyma-cells the pits are narrower. Internally, and usually about the foci of the elliptical meristele, smaller tracheides are found. These are the first-formed tracheides, or *protoxylem*. The meristele of a Fern is thus concentric in construction; it is strictly delimited, and has no provision for increase in size.

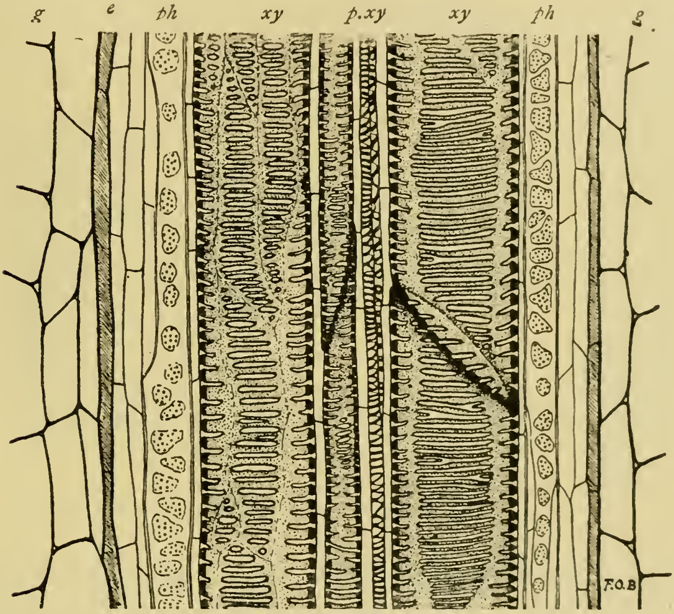

Fig. 378.
Longitudinal section of meristele of Bracken. Lettering and magnification as in Fig. 377.

A transverse section gives only one aspect in which such complicated tissues should be studied. Its interpretation is aided by longitudinal sections (Fig. 378). It is then seen that the sieve-tubes, which are elongated and pointed, bear their numerous sieve-areas upon the lateral walls: and that the spindle-shaped tracheides bear also upon their lateral walls those transversely elongated pits which give them the so-called scalariform appearance.

The *tracheide* of the Fern resembles that of the Pine in being of spindle-form, with its thickened lignified walls marked by bordered pits. (See p. 530.)

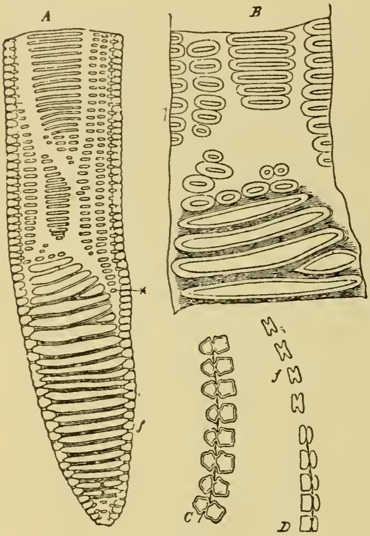

Fig. 379.

Tracheides of *Pteridium*. *A* = the end and about one third of the length of a tracheide with part of the lateral wall in surface view, showing scalariform marking (× 100). *B* = part of *A* magnified 200. *C* = thin longitudinal section through a lateral wall where two tracheides adjoined (× 375). *D* = similar section through oblique wall at *f* (× 200). there the pit membranes are not visible. (After De Bary.)

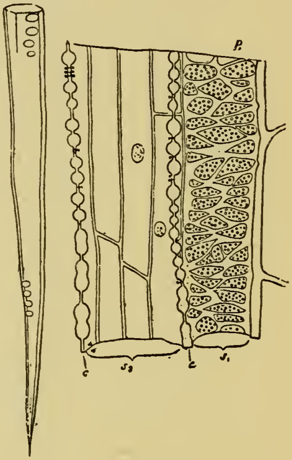

Fig. 380.

Sieve-tubes of *Pteridium*. *A* = end of a tube separated by maceration (× 100). *B* = longitudinal section through phloem showing one sieve-tube with the sieve-plates (s_1) in surface view. *c*, *c* are walls shown in section, bearing sieve-pits (× 200).

But whereas the pits in the Pine are circular, those in the Fern are liable to be transversely elongated, as is natural in tracheids so wide as these are. Their features are well seen in longitudinal sections, but better if they are isolated by maceration (Fig. 379, *A*). The elongated pits lie parallel to one another, and this is specially well seen where two wide tracheids have faced one another. From the ladder-like appearance that results they have been called *scalariform tracheids*. Examined under a high power the double outline of the pits is seen, and when the pits are small and circular the similarity to those of the Pine is plain (Fig. 379, *B*). In most Ferns the pit-membranes persist, but in *Pteridium* they appear to be liable to be broken down, and the cavities thrown together, technically as in vessels. The tracheides of the protoxylem are seen in longitudinal section to be spiral or reticulate, as in other Vascular Plants (Fig. 378, *p.xy*).

The *sieve-tubes* are also spindle-shaped, and are without companion-cells. Their cellulose walls are swollen. Where two sieve-tubes adjoin, numerous thinner sieve-areas of irregular outline are borne. They are found to be perforated by very fine protoplasmic threads extending between highly refractive globules that adhere to the walls (Fig. 380). Such tracheides and sieve-tubes are characteristic of Ferns, and with differences of detail, they are present in other Pteridophytes as well.

The anatomy of the *leaf* in Ferns resembles that of Seed-Plants down even to the collateral structure of the vascular strands. Being chiefly shade-loving plants chlorophyll is usually present in the cells of their epidermis, and the differentiation of the mesophyll into palisade and spongy parenchyma is not marked (Fig. 381). In these respects they resemble the leaves of Angiosperms of similar habit. In the *roots* of Ferns, as in those of Seed-Plants, there is a superficial piliferous layer, a broad cortex, and a contracted stele. But usually the inner cortex is very strongly lignified, up to the endodermis, which is thin-walled (Fig. 382). The pericycle which follows is variable, sometimes being greatly enlarged as a water-storage-tissue. The protoxylems are peripheral, and two or sometimes more in number, the phloem-groups alternating with them. In fact the root of a Fern is constructed essentially on the plan of that in Seed-Plants. As there is no secondary thickening the roots of Ferns are all fibrous. The lateral roots arise opposite to the protoxylems, and there they originate from definite cells of the endodermis, which may often be recognised beforehand by their size and contents.

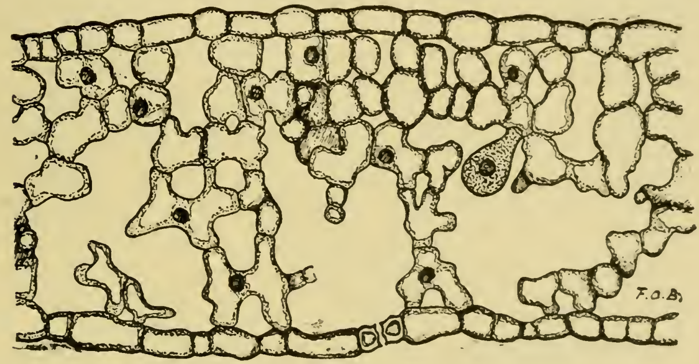

Fig. 381.

Transverse section of part of pinnule of *Dryopteris* (× 150), showing epidermis, and the spongy mesophyll, with an internal glandular cell.

While we recognise the substantial similarity of Ferns and Seed-Plants in respect of form and structure of stem, leaf, and root, these plants differ in the construction of their *apical meristems*. In Seed-Plants these are small-celled tissues, and more or less definitely stratified (pp. 17, 89). In Ferns such as *Osmunda*, *Dryopteris* or *Polypodium*, a single large cell, the *apical* or *initial cell*, occupies the tip of each growing part. It has a definite shape; it shows continued though slow growth, and segments are cut off from its sides in definite succession. As the whole tissue of the stem, leaf, or root is derived from such segments, the whole of each part is referable in origin to its apical cell, which maintains its identity throughout. The form of the cell in roots, in most stems, and in some leaves (*Osmunda*) is that of a three-sided pyramid; but where the organ is flattened, as in some stems (*Pteridium*), and almost all leaves, it has two convex sides, and is shaped like half of a biconvex lens. In the former case the segments are cut off in regular succession from the three sides (Figs. 383, 385), in the latter alternately from the two sides (Fig. 384). The further subdivision of the segments to form the tissues is represented in surface view for the case of *Osmunda* in Fig. 383: and Fig. 384 shows, in the surface view of a young leaf of *Ceratopteris* how the whole member may be built up from such segments. In roots the segmentation is complicated by the origin of the root-cap. This is provided by a segment cut off from the frontal face of the pyramid, after each cycle of three has been cut off from its sides (Fig. 385). Thus every fourth segment goes to form the protective cap, and renews it from within. Not only does the leaf also show continued growth and apical segmentation from its two-sided apical cell, but the lateral wings or flaps originate by the activity of rows of marginal cells. There is also a definite segmentation seen in the origin of the sporangia. Thus Ferns have not stratified meristems like

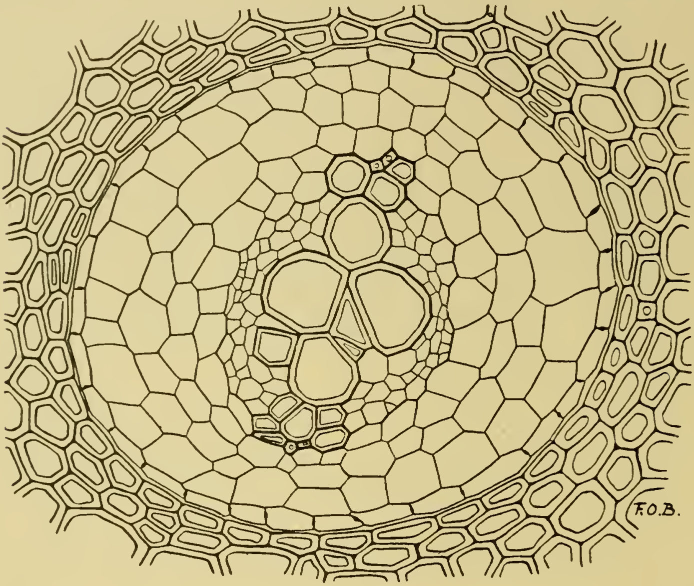

FIG. 382.

Transverse section of a root of a Fern (*Pellæa*) (× 150). Outside lies the sclerotic cortex, limited internally by a definite endodermis. There are two groups of protoxylem; a very broad pericycle, of 3 or 4 layers, surrounds the vascular tissues.

Seed-Plants. The tissues of all their parts originate from segmentation of superficial cells. This is a general character of the Pteridophyta, though the details of their segmentation and the number of the initial cells are open to variation.

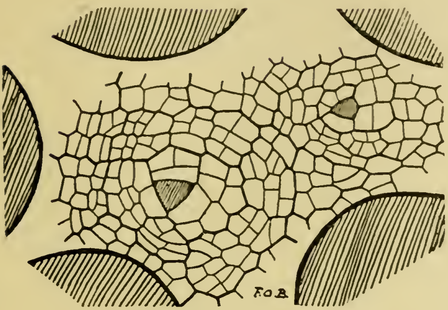

Fig. 383.

Apex of stem of *Osmunda regalis*, seen from above, showing the three-sided apical cells of stem, and of leaf; and the bases of the older leaves shaded. The successive segments of the apical cell form the whole of the apical cone. (× 83).

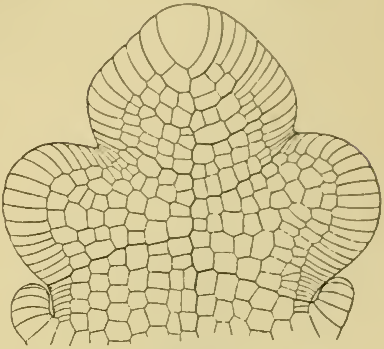

Fig. 384.

Young leaf of *Ceratopteris*, in surface view, after Kny; showing two-sided apical cell; and the marginal series, continuous round the young pinnae. The latter do not correspond in number to the segments from the apical cell.

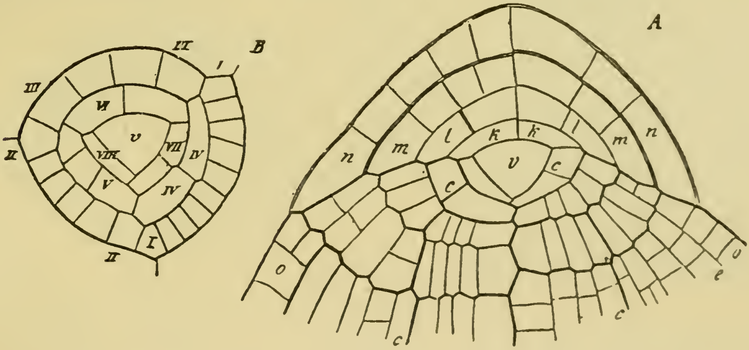

Fig. 385.

(× 250.) *A* = longitudinal section through apex of the root of *Pteris*. *B* = transverse section through the apical cell of the root and neighbouring segments of *Athyrium*. (After Naegeli and Leitgeb.) *v* = apical cell. *k*, *l*, *m*, *n* = successive layers of root-cap. *o* = dermatogen. *c* = limit of stele. (From Sachs.)

Thus constituted the Fern-Plant carries out its Life on Land in essentially the same way as Seed-Plants. The structural differences are those of detail, the most important being the absence of secondary thickening in the stem. These plants have no automatic provision for increasing mechanical strength with size. In Tree-Ferns this deficiency is made up for partly by masses of hard brown sclerenchyma, which accompany and enclose the flattened meristeles; and their margins are usually curved outwards, thus securing increased mechanical resistance on the same principle as in corrugated columns. Their strength is further increased according to size and age by the development of masses of sclerotic, adventitious roots, matted together to form a thick investment to the original trunk, and adding to its stability by a method comparable mechanically to a cambial thickening, though quite different in origin. But such mechanical provision for increase in size is only partially effective. There is no evidence that Ferns ever ranked among the largest of living Plants.

FIG. 386.

A pinna of a Fern (*Woodwardia*) showing many sporophytic buds on the upper surface. They correspond in position to sori on the lower surface, which are abortive, and they may be held to be substitutionary growths.

Many Ferns increase in number by *vegetative propagation.* This may follow simply on continued growth and branching, as in *Pteridium*, where the rhizome forks frequently. Whenever progressive rotting extends from the base beyond a branching, the two apices grow on as independent plants. In this way the Bracken multiplies habitually. In *Dryopteris* buds are formed near the bases of the leaves in old plants. Again, as rotting proceeds from the base, these buds become isolated, and root themselves as new individuals (Fig. 374, *B*, *C*). In other Ferns, as in the various species of *Asplenium* so commonly grown in dwelling rooms, buds or bulbils arise on the lamina. Being very lightly attached to the leaf they are readily shed, and root themselves independently in the soil. In some cases vegetative buds may replace the sori (Fig. 386). Such vegetative propagation of the Fern-Plant is a mere repetition of the sporophyte generation. But sooner or later the Fern-Plant bears the *spores*, which start the alternate generation.

The *spores* are produced on certain leaves of the mature plant which are therefore called *sporophylls*, to distinguish them from those which are only nutritive. In *Dryopteris* nutritive leaves and sporophylls are alike in outline. The young plant only produces the former. But the leaves of older plants bear on their lower surface, and chiefly in the apical region, numerous groups of organs which are green or brown according to age. These are called *sori*, and consist of *sporangia* with certain protective structures. The sori vary greatly in size and form in different Ferns, which are classified according to their characters. In *Dryopteris*, as the name implies, they are kidney-shaped, as is seen in Fig. 373. Each sorus is seated on a vein, which provides its necessary nourishment. It is protected by a covering called the indusium, of kidney-like outline, beneath which are numerous sporangia. If a leaf bearing mature sori be laid on a sheet of paper to dry, with its lower surface downwards, the indusia shrivel, and the bursting sporangia shed the spores in such numbers that they give a clear print of the outline of the sporophyll upon the paper. The spores are dark-coloured, very minute, and are produced in millions.

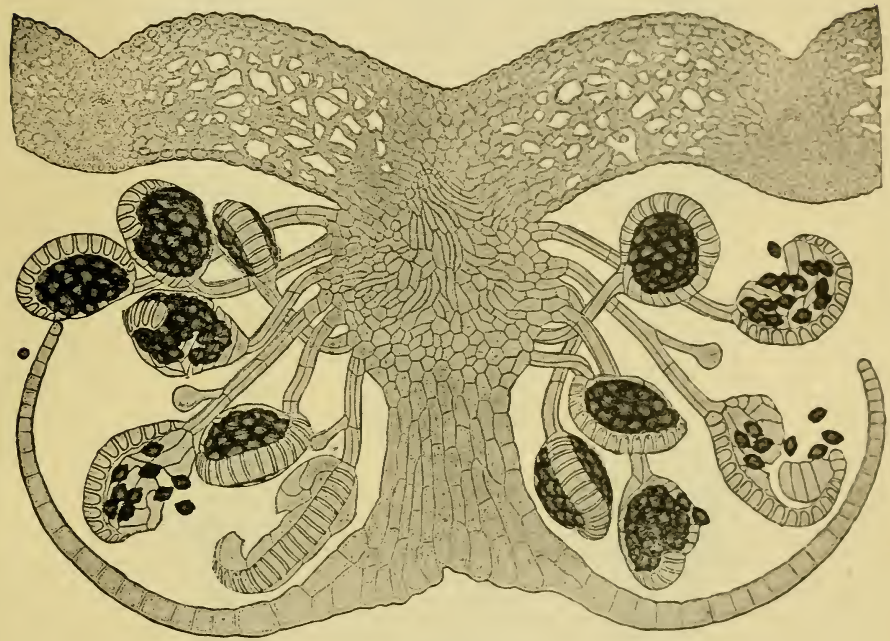

Fig. 387.
Vertical section through the sorus of *Dryopteris Filix-mas*. (After Kny.)
The adaxial surface is uppermost.

A vertical section through the sorus of *Dryopteris* shows an enlarged receptacle, traversed by the vascular strand. The indusium rising from it overarches the numerous sporangia which are attached basally by long thin stalks (Fig. 387). The head of each sporangium is shaped like a biconvex lens; its margin is almost completely surrounded by a series of indurated cells, which form the mechanically effective *annulus*. This stops short on one side, where several thin-walled cells define the *stomium*, or point where dehiscence will take place (Figs. 387, 389, 4*a*). Within are the dark-coloured *spores*, which on opening a ripe sporangium carefully in a drop of glycerine may be counted to the number of 48. Normally the sporangia open in dry air, and the dry and dusty spores are forcibly thrown out.

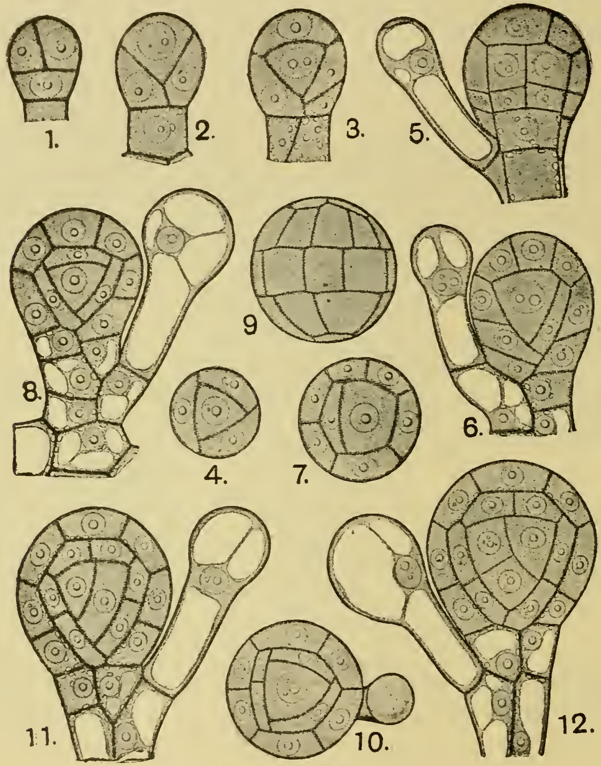

Fig. 388.
Successive young stages in the segmentation of the sporangium of *Dryopteris Filix-mas*. (After Kny.)

The origin of a sporangium is by outgrowth of a single superficial cell of the receptacle, which undergoes successive segmentations as illustrated in Fig. 388, 1-3. A tetrahedral internal cell is thus completely segmented off from a single layer of superficial cells constituting the wall. The former undergoes further segmentation to form a second layer of transitory nutritive cells called the *tapetum* (Fig. 388, 6-12), subsequently doubled by tangential fission (Fig. 389, 1).

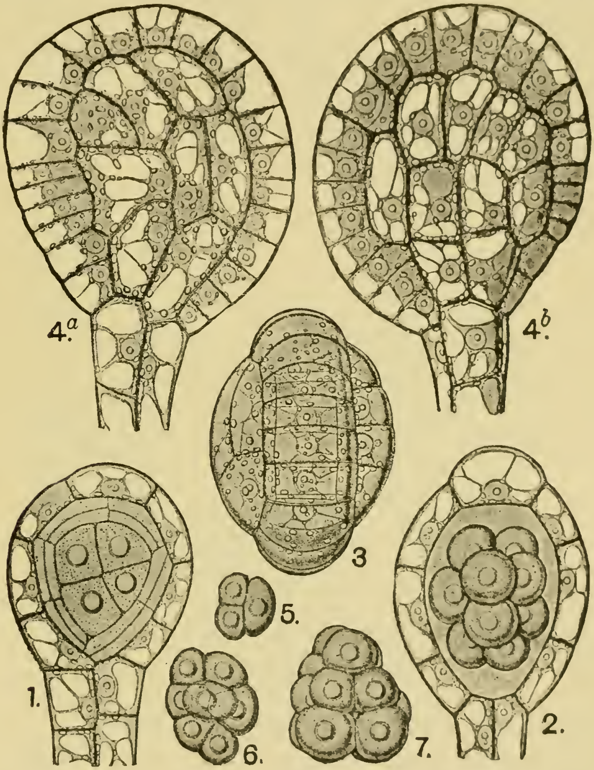

Fig. 389.
Later stages of development of the sporangium of *Dryopteris Filix-mas*.
(After Kny.)

The tetrahedral cell which still remains in the centre, having grown meanwhile, undergoes successive divisions till twelve *spore-mother-cells* are formed (Fig. 389, 2-7). These become spherical, and are suspended in a liquid which, together with the now disorganised tapetum, fills the enlarged cavity of the sporangium. Each spore-mother-cell then divides twice to form a *spore-tetrad*: in this process, just as in the formation of pollen-grains and other spores, the number of chromosomes is reduced to a half. Finally the resulting cells separate on ripening as individual *spores*, each covered by a protecting wall, rugged and dark brown at maturity. Owing to the absorption of the liquid contents of the sporangium the separate spores are dry and dusty, and are readily scattered. Since each of the 12 spore-mother-cells forms four spores, their number is 48 in each sporangium. Each mature spore consists of a nucleated protoplast, bounded by a colourless inner wall, and a brown epispore bearing irregular projecting folds.

Meanwhile the wall of the sporangium has differentiated into the thinner lateral walls of the lens-shaped head, and the annulus, which is a chain of about 16 indurated cells surrounding its margin (Fig. 389, 4*a*, 4*b*). These form a mechanical spring, which on rupture of the thin-walled stomium becomes slowly everted as its cells dry in the air, and then recovering with a sudden jerk throws out the spores to a considerable distance (Fig. 390). Dry conditions are necessary for this last phase of spore-production, viz. the dissemination of the numerous living germs. Each spore is a living cell, and may serve as the starting point for a new individual.

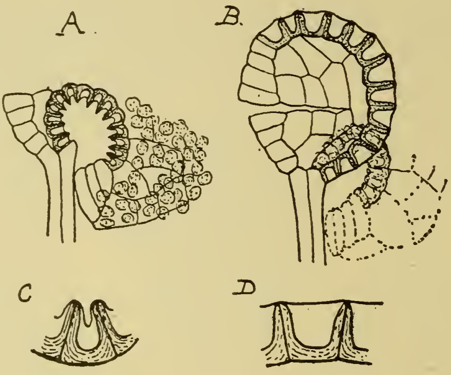

FIG. 390.
A = sporangium with annulus everted. *B*, a similar sporangium after recovery by a sudden jerk. *C*, condition of cells of the everted annulus. *D* = cells of annulus before eversion (see p. 167).

The dry conditions which are necessary for the dissemination of the spores do not suffice for their further development. Moisture and a suitable temperature are required for their germination. The outer coat then bursts, and the inner protrudes, cell-division appearing as the growth proceeds (Fig. 391). The body that is thus produced is called the *prothallus*, and it may vary in its form according to the circumstances. It usually grows first into a short filament attached by one or more rhizoids to the soil (4). It then widens out at the tip to a spatula-like and finally to a cordate form (Fig. 392). But when closely crowded the filamentous form may be retained longer (Fig. 393, 1). The body of the prothallus, exclusive of the downward-growing rhizoids, consists of cells which are essentially alike, arranged at first in a single-layered sheet. The peripheral parts retain this, but in the central region, below the emarginate apex, the cells divide by walls parallel to the flattened surfaces, and thus a massive central cushion is formed. The mature cells are thin-walled, with a peripheral film of protoplasm surrounding a central vacuole, and embedding the nucleus and numerous chloroplasts: intercellular spaces are absent (Fig. 19, p. 37). The whole body is thus capable of an independent physiological existence, nourishing itself by absorption from the soil, and by photo-synthesis (Fig. 392). But there is a large proportion of surface to bulk, and no serious resistance is offered to the evaporation of water from it in dry air. Comparing the prothallus with the Fern-Plant as regards the water-relation, it is plainly less adapted for life on land, and more immediately dependent on moisture.

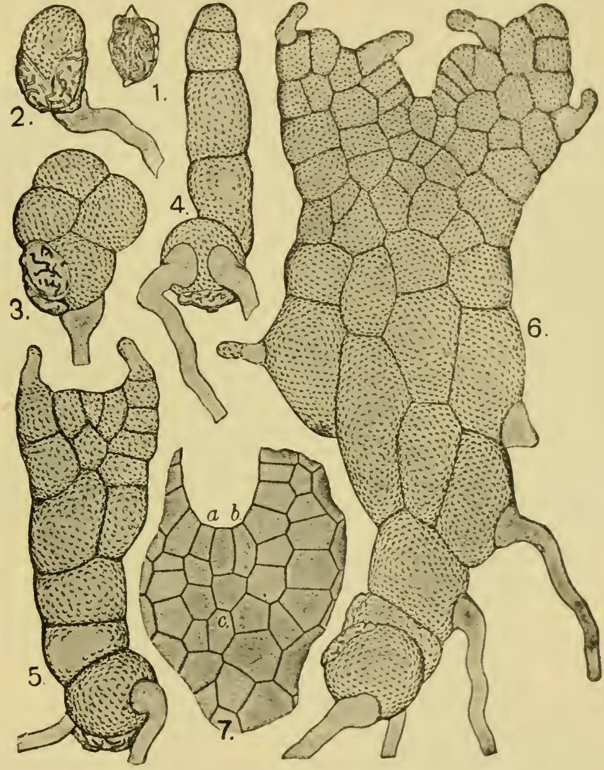

Fig. 391.
Successive stages in germination of the spores of *Dryopteris Filix-mas*, to form the prothallus. (After Kny.)

The prothallus thus constituted is capable in some cases of vegetative propagation by "gemmae." But this *gametophytic budding* is less common here than in the Bryophytes.

The dependence on moisture is still more obvious in the behaviour of the *sexual organs* which the prothallus bears. These are male and female, and they may be found on the same prothallus (Fig. 392), or on different prothalli (Fig. 393, 1). In the former case the *antheridia, or male organs*, commonly appear first, and the *archegonia, or female organs*, later. There may thus be a separation of the sexes either in time or in space. The flattened prothallus of the ordinary cordate type usually bears both sex-organs. When growing under normal circumstances on a horizontal substratum it produces them on its lower surface, the antheridia in the basal or lateral regions, the archegonia upon the massive cushion. The latter develop in acropetal order, the youngest being nearest to the incurved apex of the prothallus. The position of the sexual organs is evidently favourable

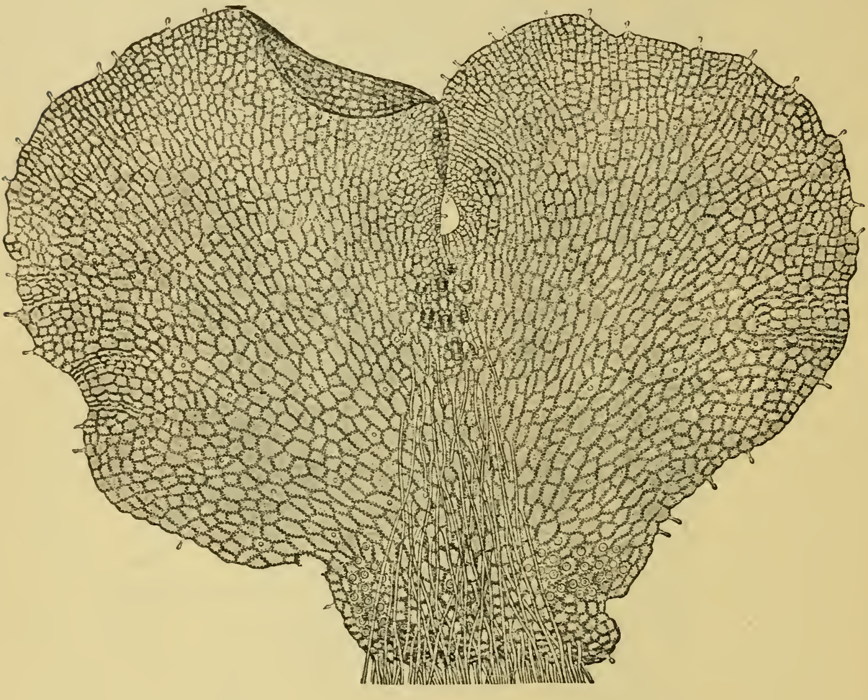

FIG. 392.
Mature prothallus of *Dryopteris Filix-mas*, as seen from below, bearing antheridia among its rhizoids, and archegonia near to the apical indentation. (After Kny.)

to their continued exposure to moist air, or to liquid water which is necessary for carrying out their function.

The antheridium, which arises by outgrowth and segmentation of a single superficial cell (Fig. 393, 2, 3), consists when mature of a peripheral wall of tabular cells, surrounding a central group of *spermatocytes* (Fig. 393, 4, 5). The antheridium readily matures in moist air, but it does not open except in presence of external water. This causes swelling of the mucilaginous walls of the spermatocytes, and increased turgor of the cells of the wall. The tension is relieved by rupture of the wall at the distal end, and the spermatocytes are extruded into the water; in this the remaining cells of the wall assist by their swelling inwards, and consequent shortening (Fig. 393, 6). The spermatocytes thus extruded into the water which caused the rupture,

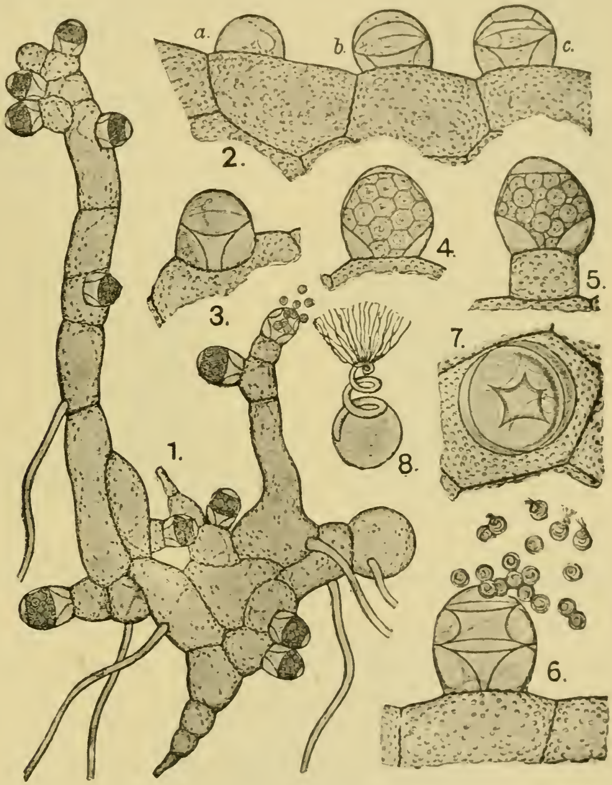

FIG. 393.
1, an attenuated male prothallus of *Dryopteris Filix-mas*. 2-5, stages of development of the antheridium. 6, 7, ruptured antheridia. 8, a spermatozoid highly magnified. (After Kny.)

soon show active movement, and the spermatozoid which had already been formed within each of them escapes from its mucilaginous sheath, and moves freely in the water by means of active cilia attached near one end of its spirally coiled body (Fig. 393, 8).

The archegonium also originates from a single superficial cell, and grows out so as to project from the downward surface of the thallus. It consists when mature of a peripheral wall of cells constituting the projecting neck, and a central group arranged serially. The deepest-seated of these is the large *ovum*, which is sunk in the tissue of the cushion ; above this is a small *ventral-canal-cell*, and a longer *canal-cell* (Fig. 394, *A*). If prothalli be grown in moist air, and only watered by absorption from below, the archegonia having no direct access to liquid water will remain closed. Fertilisation is then impossible. But if they are watered from above, as they would be by rain in the ordinary course of nature, the external water will bathe them, and rupture will result. This may be observed in living archegonia which have been kept relatively dry, and then mounted in water. The neck bursts at the distal end, owing to internal mucilaginous swelling, and its cells diverge widely. The canal-cell and ventral-canal-cell are extruded, and the ovum remains as a deeply seated spherical protoplast, while access to it is gained through the open channel of the neck (Fig. 394, *B*). Thus the same condition leads to the rupture both of the male and female organs. In nature a shower of rain would supply the necessary water, which would serve also as the medium of transit of the spermatozoids to the ovum. But the movements of the spermatozoids are not subject to blind chance. It has been shown that diffusion of a very dilute soluble substance, such

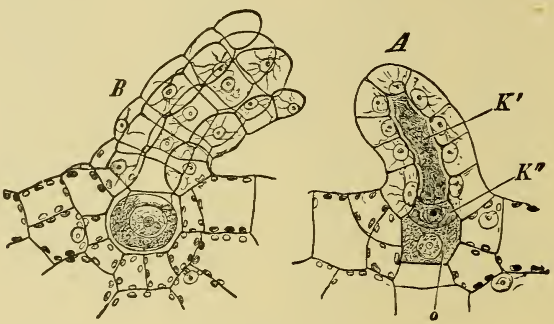

Fig. 394.
Archegonia of *Polypodium vulgare*. *A*, still closed. *o*=ovum. *K'*=canal-cell. *K"*=ventral canal-cell. *B*=an archegonium ruptured. (×240.) (After Strasburger.)

as malic acid, into water serves as a guide, the spermatozoids moving towards the centre of diffusion. Probably it is in this way that they are attracted to the neck of the archegonium, which they may be seen to enter, and finally one spermatozoid coalesces with the ovum (Fig. 395). Fertilisation is effected by entry of the male nucleus into the female nucleus, and their complete fusion (Fig. 396). Thus the

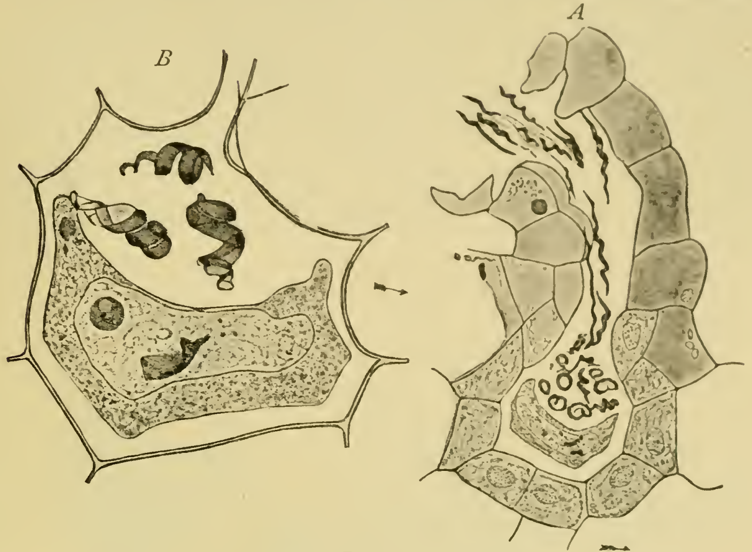

FIG. 395.
Fertilisation in *Onoclea sensibilis*: the arrows indicate direction to the growing point. A = a vertical section through an archegonium probably within ten minutes after entrance of the first spermatozoid. (× 500.) B = vertical section of the venter of an archegonium, containing spermatozoids, and the collapsed egg with a spermatozoid within the nucleus. Thirty minutes. (× 1200.) (After Shaw.)

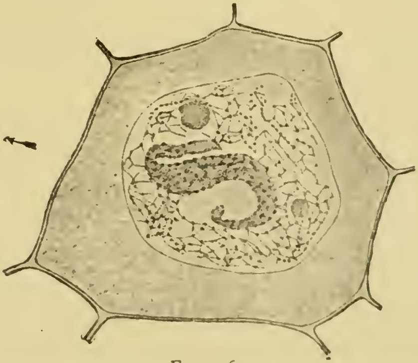

FIG. 396.
Horizontal section of an egg, showing coiled male nucleus within the female. Twelve hours. (× 1200.) (After Shaw.)

presence of external water is essential for fertilisation in Ferns. Their normal life-cycle cannot be completed without it.

The immediate consequence of fertilisation is growth and segmentation of the *zygote*, which first secretes a cell-wall. It divides into octants, four of which constitute an *epibasal hemisphere*, directed towards the apex of the parent thallus, giving rise to *axis* and *leaf* of the sporeling; four form a *hypobasal tier*, which gives rise to the first *root* and a suctorial organ called the *foot*. These parts are soon distinguishable by their form and structure, and are seen in their relative positions, but still enclosed in the enlarged venter of the archegonium, in Fig. 397. Soon the cotyledon and first root burst their way out: the former expands as the first nutritive leaf, the latter buries itself in the soil (Fig. 399). At first the young Fern-Plant is dependent upon the prothallus that encloses it, but by means of its cotyledon and its root it soon becomes self-dependent, and the prothallus rots away. It is then only a matter of time and opportunity for it to attain characters similar to those of the parent Fern-Plant.

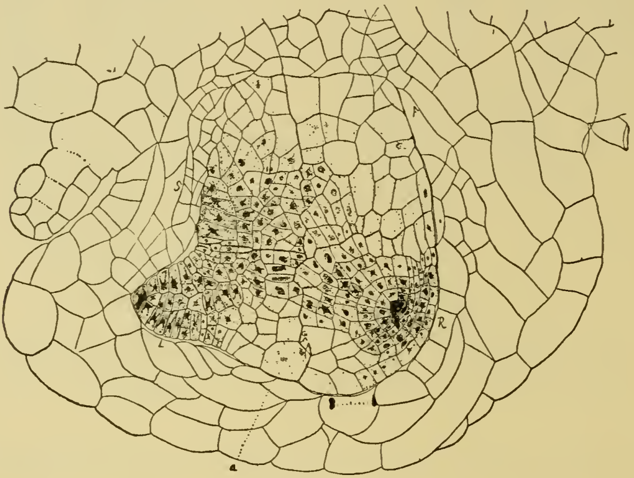

FIG. 397.

Embryo of *Adiantum concinnum* in the enlarged venter of the archegonium, so far advanced as to show the parts of the embryo. The epibasal hemisphere is to the left, the hypobasal to the right. *L* = leaf or cotyledon. *R* = root. *S* = stem. *F* = foot. (After Atkinson.)

These are the salient features in the life-cycle of a Fern as it is seen in its simplest form. They may be represented graphically to the eye in a diagram (Fig. 400, p. 506). The two most notable points are those where the individual is represented only by a single cell, viz. the *spore*, and the *zygote*. These are two landmarks between which intervene two more extensive developments, on the one hand the sexual generation or prothallus, on the other the spore-bearing generation, or Fern-Plant. If the events above detailed recur in regular succession the two phases of life will alternate. Of these the one bears sexual organs, containing sexual cells or gametes, and it may accordingly be called the *gametophyte*; the other is non-sexual, but bears sporangia containing the spores, and is accordingly called the *sporophyte*. The study of Ferns, and of Pteridophytes at large, leads to the conclusion that this regular alternation is typical for them all. These two alternating generations differ not only in form but also in their relation to external circumstances, and especially in the water-relation. The sporophyte is structurally a land growing plant, with nutritive, mechanical, and conducting tissues, and a ventilating system. Not only is it capable of undergoing free exposure to the ordinary atmospheric conditions, but dryness of the air is essential for the final end of its existence, viz. the distribution of its spores. On the other hand, the gametophyte is structurally a plant ill-fitted for exposure, with undifferentiated and ill-protected tissues and no ventilating system, while the object of its existence, viz. fertilisation, can only be secured in the presence of external liquid water. As regards the water-relation

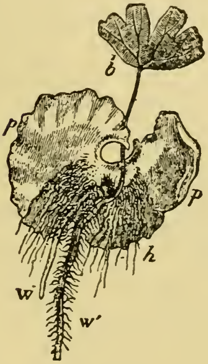

FIG. 398.

Adiantum Capillus Veneris. The prothallus, *pp*, seen from below has a young Fern-plant attached to it. *b*=first leaf. *w*, *w′*=first and second roots. *h*=root hairs of the prothallus. (× about 30.) (After Sachs.)

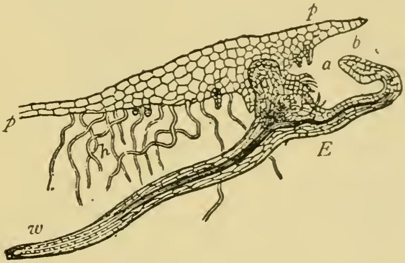

FIG. 399.

Adiantum Capillus Veneris. Longitudinal section through the prothallus, *pp*, and young Fern-plant *E*. *h*=root hairs of prothallus. *a*=archegonia. *b*=the first leaf. *w*=the first root of the embryo. (× 10.) (After Sachs.)

the whole life-cycle of a Fern, or of Pteridophytes generally, might not inaptly be designated as *amphibious*, since the one phase is dependent on external fluid water for achieving its object of propagation, while the other is independent of it.

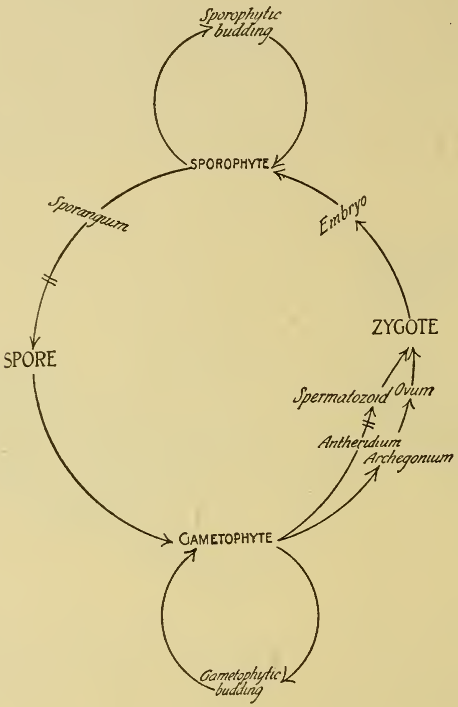

FIG 400.
Diagram illustrating the cycle of life of a Fern.

The normal cycle thus presented to the eye involves differences of nuclear condition of the alternating phases, those differences being established respectively by fertilisation and by the tetrad-division. The *sporophyte* or Fern-Plant is *diploid*, and the number of chromosomes is usually very large (about 90 for *Athyrium*, 144 for *Dryopteris pseudo-mas*, but 32 for *Marsilia*). This number is reduced to one-half in the tetrad-division of the spore-mother-cells, and the spores on germination produce the *gametophyte* which is *haploid*. But in fertilisation, when the gametes fuse, the diploid number is restored. This normal cycle corresponds to that seen in higher forms, the substantive Plant being in all cases the diploid sporophyte.

The cycle as thus defined is liable to certain modifications. Some involve the introduction of new incidents, others the excision of certain phases. For instance, buds may be produced either on the Fern-Plant or on the prothallus, which repeat respectively the one or the other (Fig. 386, p. 494). These are merely amplifications of the *soma*, without any change of constitution of the tissues, or of the nuclei. But others are of the nature of short-cuts. For instance, a prothallus may arise from the Fern-Plant without the intervention of spores (*apospory*), as in certain forms of *Athyrium* or *Polystichum* (Fig. 401, *A, B*). Or a Fern-Plant may spring directly from a prothallus without the sexual process (*apogamy*), as in *Pteris cretica* (Fig. 402, *C*). Such examples show that the events of the life-cycle are not immutable. But they raise difficulties of interpretation in terms of chromosomes.

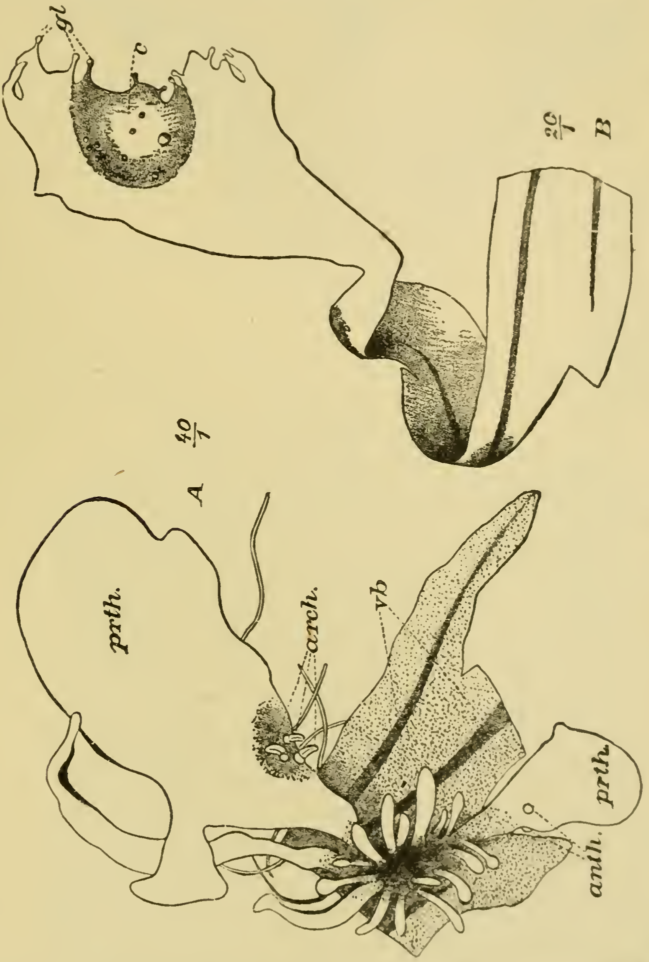

Fig. 401.

A, part of a pinnule of *Athyrium Filix-foemina*, v. *clarissima*, showing vascular bundles (*vb*); from the position of a sorus numerous prothalli have grown out, not derived from spores (apospory), bearing antheridia, and archegonia. *B*, tip of a pinnule of *Polystichum angulare*, v. *pulcherrimum* (× 40), which has grown out directly into a prothallus. *c*=cushion. *gl*=glands. (× 20.)

In the relatively simple case of *Dryopteris pseudo-mas*, var. *polydactylum*, a young sporophyte is produced as a direct outgrowth from the prothallus. By a careful examination of the bud-forming tissue it has been found that the bud

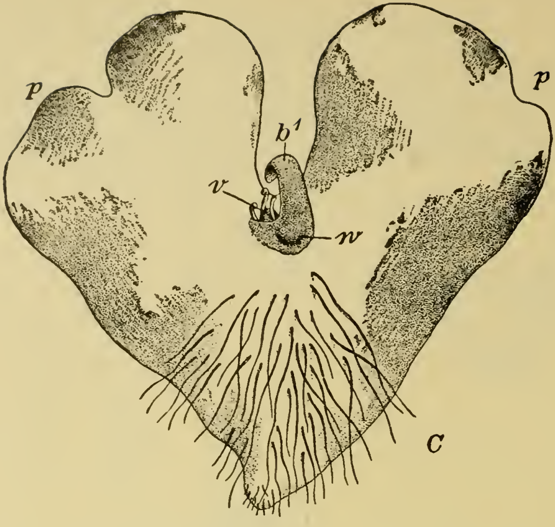

FIG. 402.

Pteris cretica; prothallus seen from below, bearing an apogamous bud derived not by fertilisation but by direct growth from the cushion. (After De Bary.)

FIG. 403.

Dryopteris pseudo-mas, var. *polydactylum*. Tissue of prothallus where an apogamous growth is to be found, showing on the left a cell with two nuclei, while an adjoining cell has none. At the centre a nucleus is seen passing through a perforation of the wall, and fusing immediately with that of the cell it enters. (After Farmer, Moore, and Miss Digby.)

is preceded by a sort of irregular fertilisation. The nucleus passes from one cell through a pore in the cell-wall into the next cell. There it fuses with the nucleus of the invaded cell (Fig. 403). Doubtless there is here a doubling of the chromosomes, as in normal fertilisation; and such a cell, like a false zygote, may serve to initiate the sporophytic bud. The process has been styled *pseudomixis* to suggest a comparison with sexuality, while marking its distinctness from it.

In other cases careful investigation has shown that a gametophyte may be diploid. Transition from one generation to the other may then be repeated, while uniformity of chromosome-number is maintained throughout. This is seen in *Athyrium filix-foemina*, var. *clarissima*, where the number is 90, approximately that for the normal sporophyte of that species. The same is the case for certain plants of *Marsilia Drummondii*, which are diploid throughout, with 32 as the number. It is probable that the converse is the case for *Dryopteris pseudo-mas*, var. *cristata* (Fig. 404), for the chromosome-number throughout was found to be variable, from 60 to 78, while in that species the normal number for the sporophyte is 144. Not only do such cases show that the usual chromosome-cycle may be departed from, but also that the external characters are not directly dependent upon the chromosome-number.

The cycle of life of a Fern shows more clearly than that of any of the Vascular Plants hitherto described the antithesis of the two generations which constitute it. Each can grow, nourish itself, and even multiply independently of the other. It is true that the young sporophyte is nursed temporarily in the parent prothallus. But this is only a transient event and is soon over. A similar nursing period, with much greater adaptive detail that lends added efficiency, is seen in the Seed-Plants. The main difference between the Seed-Plant and the Fern lies in their spores. The former are *heterosporous*, the latter are, with few exceptions, *homosporous*. The advantage of the large female spore is that it contains already a supply of nourishment for the young germ after fertilisation, so that a vegetative prothallus is not necessary. Especially is this so in Seed-Plants where the spore is retained in the tissue of the parent, and can draw nourishment continuously from it. On the other hand, in the primitive homosporous state, as it is seen in the Bryophytes and Pteridophytes, the

FIG. 404.
Dryopteris pseudo-mas, v. *cristata* (Cropper). Drawing by Dr. Lang showing apogamous transition from prothallus to sporophyte, and subsequent aposporous transition from sporophyte to prothallus at the apex and margins of the leaf.

individual spores are small and they are cast out in large numbers to fend for themselves. It is then incumbent on each spore, when it germinates, at once to increase its slender store, otherwise it cannot produce gametes, or nourish the resulting germ. Hence the independent vegetative existence of the gametophyte, and its immediate formation of photosynthetic tissue when it germinates.

Further, the difference in biological relation of the two generations to water is very marked. The prothallus, which is semi-aquatic, is the less prominent, and its growth is normally limited in size and duration. The Fern-plant, which is definitely terrestrial in structure and function, is in the ascendent, and its growth is unlimited in size and in duration. A Fern is like a man with one foot in the water and one on land. But the foot that is on land is more firmly set than the other. In the Bryophytes, however, the balance is the other way : it is the gametophyte-foot that is more securely placed, and the sporophyte is dependent on it, not temporarily, but up to the time of maturity of its spores. There is no doubt that the Pteridophytes are a real advance on the Bryophytes, as regards success in growth on land. The essential features of superiority of the Pteridophytes over the Bryophytes consist, first, in the establishment of the sporophyte as an independent Plant, rooted in the soil : secondly, in the production of spores, not matured simultaneously and once for all in a single capsule, but in numerous capsules matured independently, and spread over a long period of time, even over many seasons where the plant is perennial. This feature is universal for all the higher types of the Vegetable Kingdom. Its effect is to increase the possible output of spores : and it tends to make fertilisation a more rare event, instead of a recurrent necessity for the survival of the race. This is an obvious advantage for land-living plants which retain their primitive method of fertilisation, as the Ferns do. In point of fact, it is in the larger Pteridophytes, such as the Tree-Ferns, that the climax of numerical production of homosporous spores has been attained.

For a more explicit description of the Ferns see *Primitive Land Plants*, Chapters XVI. to XXIII.

CHAPTER XXXII.

LYCOPODIALES.

The Lycopodiales, or Club Mosses, to which *Lycopodium* and *Selaginella* belong, are Vascular Plants of varied land habit. They have relatively small leaves (*microphyllous*), borne upon a preponderating axis which is usually branched, and is rooted in the soil. The branching of both root and stem is typically *dichotomous*, but frequently transitions may be seen to *monopodial branching*: that is, where a new branch arises laterally below the apex of the originating part. Many early fossils belonging to this Class, for instance *Lepidodendron* and *Sigillaria*, were tree-like: others were relatively small, as are all the living Lycopods. More or less definite fertile *cones* or *strobili* are borne on the ends of their branches. Somewhat compressed in the axil of each leaf is a single *sporangium* that opens when ripe like an oyster, by a marginal slit. These characters are common for the Lycopodiales, modern and ancient.

This Class is represented in the British Flora by some five species of *Lycopodium* (Fig. 404 A): they are native on heaths and moors, chiefly in hilly districts. Nearly 100 other species are widely spread through the temperate zones and the tropics. They are mostly low-growing plants, but some are epiphytes. There is in Britain only one native species of *Selaginella* (*S. spinulosa*), a minute plant of mossy hill-sides (Fig. 404 B). But over 300 species of the genus are spread through the tropics. Many species are in cultivation. They are mostly low-growing and shade-loving plants of straggling habit. Another British representative of the Lycopodiales is that curious inhabitant of fresh-water lochs, *Isoetes lacustris*, with its long leaves crowded upon a short succulent stock, which is fixed in the mud at the bottom, by dichotomising roots. These relatively inconspicuous plants are the meagre present-day representatives of the Lycopodiales, a type of which grew to tree-like size in the Coal Period, and contributed largely to the organic remains preserved as Coal. *Isoetes* appears as the nearest living ally of these fossil plants.

The Lycopodiales are divided into two series, the ELIGULATAE, in which a single sporangium is borne in or near to the axil of each leaf of the fertile cone, but without any ligule. Here the sporangia and spores are all alike, the plants being *homosporous*. The Eligulatae include the genera *Lycopodium* and *Phylloglossum*. But *Selaginella* and *Isoetes* are included in the LIGULATAE, in which the sporangium is accompanied by a minute scale or *ligule* borne on the upper surface of each leaf: it is inserted on the distal side of the sporangium (Figs. 407-409). Here the sporangia are of two types, producing respectively *male microspores* and *female megaspores* (*heterosporous*). Most of the fossil Lycopods belong to the Ligulatae.

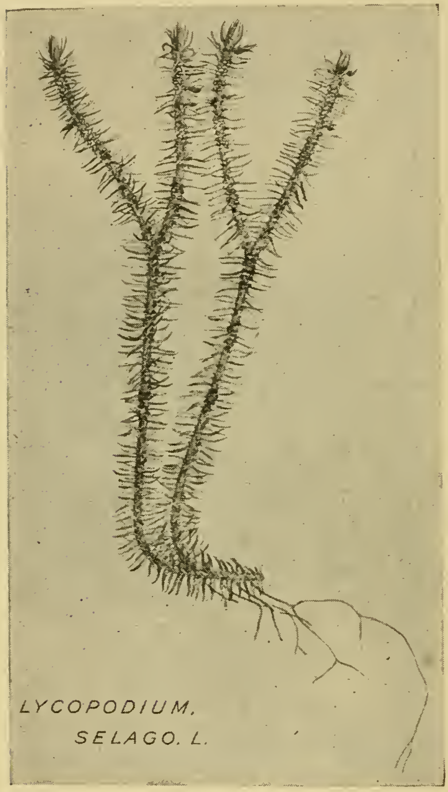

FIG. 404 A.
Whole plant of *Lycopodium Selago*, showing ascending and upright habit, as developed when growing protected by Heather. The equal dichotomy and the alternating sterile and fertile zones are seen, and the forking of the roots. Distally bulbils are borne. Reduced.

Having chosen *Dryopteris* and *Pteridium* as the chief examples of homosporous Ferns,—a condition which is shared by *Lycopodium* among the Club Mosses,—*Selaginella* will be taken for special treatment as a type of these, while it also illustrates the heterosporous state.

SELAGINELLA.

A primitive type of *Selaginella* had an upright radial axis, with leaves of equal size all round it; and this is the case in *S. spinulosa*.

But most living species have a much-branched, dorsiventral shoot of an "espalier" type, sometimes simulating highly compound leaves (Fig. 405). On these shoots the actual leaves are disposed in four longitudinal rows, those on the lower flanks being larger, those on the upper smaller. Such shoots are commonly propped up by root-like organs (*rhizophores*) borne at the forkings of the shoot, and themselves showing very regular dichotomy. They are not actually roots, but on reaching the ground they give rise to roots endogenously: hence their name. Structurally *Selaginella* is relatively simple. The vascular system is essentially of the same type as in simple Ferns. It consists of sharply circumscribed stelar tracts, with tracheides but no vessels, and peripheral phloem. Each is surrounded by an endodermis, which in many species shows the cells laterally separated as radiating "trabeculae." In the smaller species the stele remains simple, but in some of the larger it may be disintegrated, somewhat

FIG. 404 B.

Plant of *Selaginella spinulosa*, with root-system springing from swollen knot at base of the upright hypocotyl. Here there are no rhizophores. Natural size.

after the manner of Ferns. In the larger fossils, however, cambial increase was introduced, providing a massive tract of secondary wood, to serve the upright and tree-like trunks of *Lepidodendron* and *Sigillaria*. A vestige of such structure still persists in the abbreviated and succulent stock of *Isoetes*.

The greatest interest lies not in the structure of the Ligulatae, but in their *sporangia*, and the germination of the spores: for these give lines of comparison with the Seed-Plants on the one hand, and with homosporous types on the other. The strobilus or cone that bears them is distal on a vegetative branch, and even in the flattened species of *Selaginella* it has the radial form, all the sporophylls being of equal size (Fig. 406, *A*). A longitudinal section shows that a short-stalked sporangium is borne in the axil of each. These sporangia are of two sorts, which are associated in the same strobilus but disposed in various ways in different species. In *S. inaequalifolia* those on the right side of the section shown in Fig. 406, *B*, are all *megasporangia*, with four large spores in each; those on the left-hand side

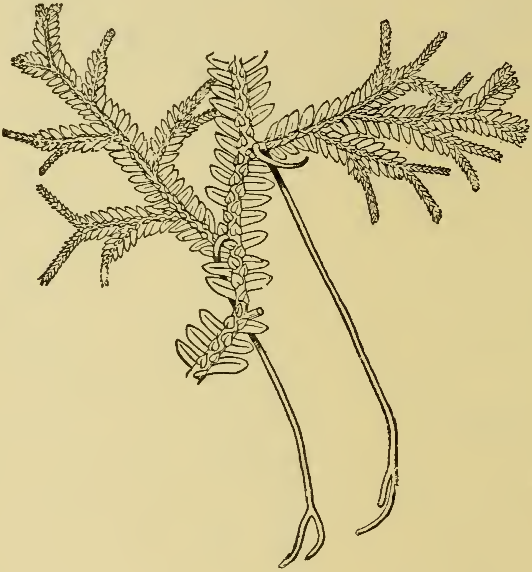

FIG. 405.

Part of the shoot of *Selaginella Martensii*, showing its "espalier" form and minute unequal leaves. It is seen from above, and the forking rhizophores are directed downwards. (Nat. size.) (After Goebel· from Strasburger.)

are *microsporangia*, containing many small microspores. In form the sporangia are alike; they differ in the number and size of their contents. A mature microsporangium, with its subtending sporophyll and ligule, is shown in median section in Fig. 407. The line of dehiscence is distal, where the cells of the wall are smallest, and the structure of the cells of the wall is such as to lead to its valves being everted as they dry on ripening, so that the spores are shed. The mature megasporangium behaves in a similar way, but the spores are ejected forcibly by pressure of the everted valves upon them (Fig. 408). The spores fall upon the soil and germinate together. *Thus both the megaspores and microspores are shed from the parent plant.*

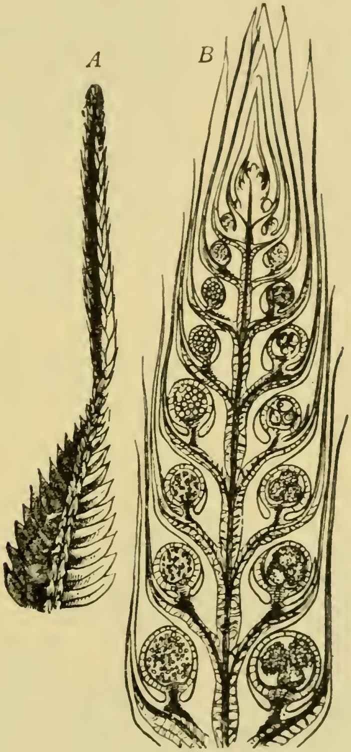

FIG. 406.

Selaginella inaequalifolia. *A*, fertile branch, half natural size. *B*, its tip in longitudinal section, and enlarged, with microsporangia to the left, and megasporangia to the right. (After Sachs.)

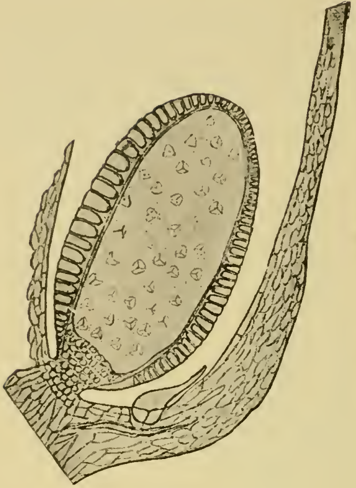

Fig. 407.

Microsporangium of *Selaginella apus*, in median vertical section, containing numerous microspores. The ligule is seen in Figs. 407, 408, as a small tongue-like body, rising from the base of the leaf. (× 55.) (After Miss Lyon.)

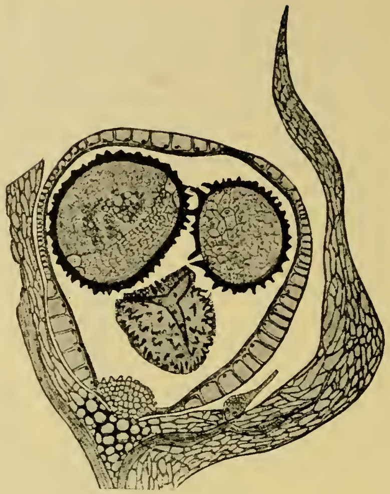

Fig. 408.

Megasporangium of *Selaginella apus*, in median vertical section, showing three of the four megaspores. (× 21.) (After Miss Lyon.)

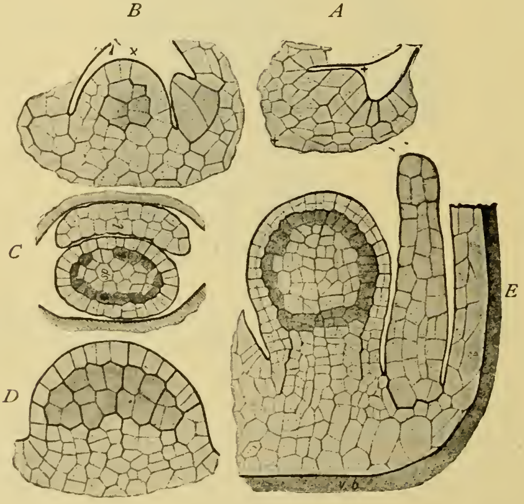

Fig. 409.

A, *B* = radial sections through young sporangia. *C* = transverse section of one more advanced. *D* = tangential section. *E* = radial section of an older sporangium, with ligule: the tapetum is shaded, and the sporogenous cells lie within. (*A*, *B*, *C*, *D* = 350; *E* = 200.) F. O. B.

The sporangium arises in the axil of the sporophyll, just within the ligule. After the first segmentations are past it is found to consist of a short thick stalk, bearing the slightly flattened sporangial head. This contains a group of sporogenous cells, from which later a surrounding tapetal layer is cut off. Outside this is a wall composed of two layers of cells (Fig. 409, *E*). Later the spore-mother-cells round themselves off, becoming isolated in a liquid that fills the enlarging cavity. *Up to this point it is impossible to tell which type of spore the sporangium will produce. This fact indicates that the megasporangium and microsporangium are differentiated from one original type.* In the case of a microsporangium all the spore-mother-cells undergo the tetrad division, and a large number of microspores is the result. But if it is to be a megasporangium, only one (in some species two) of the spore-mother-cells develops further (Fig. 410), the rest becoming disorganised. The four megaspores, with rugged walls, occupy the whole sporangium at maturity (Fig. 408).

FIG. 410.
Selaginella spinulosa. Section of megasporangium, showing the single fertile tetrad still very small, and the rest of the sporogenous cells arrested. (× 100.) F. O. B.

The germination of both types of spores may begin before they are shed, but it is continued on the moist soil. The *microspore* first partitions off a lenticular cell, which, as it appears to perform no function, and does not develop further, may be held as vestigial, representing the vegetative region of a *male prothallus*. The rest of the contents segment to form a wall of eight sterile cells surrounding a numerous group of *spermatocytes* (Fig. 411, *A*). This is in fact the correlative of an *antheridium*: the whole male prothallus thus consists of a

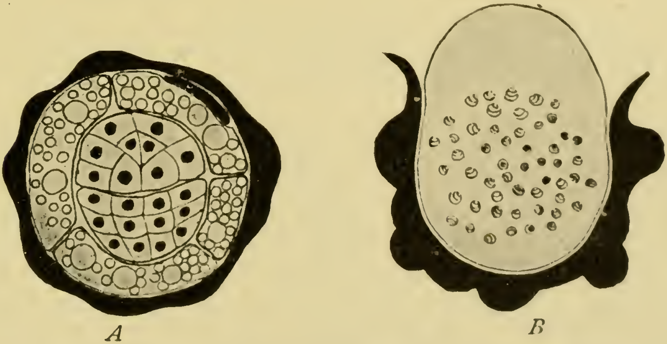

FIG. 411.
A, microspore of *S. apus* after germination. *B*. the same just before extrusion of spermatozoids. (After Miss Lyon.)

vestigial vegetative region, and a single antheridium. In certain cases starved Fern prothalli may be found of almost equal simplicity. A mucilaginous change appears in the walls of the central mass of cells. Meanwhile their protoplasts form each a single curved *spermatozoid*, motile in water by two cilia. Swelling of the mucilage by water bursts the wall of the spore, and the spermatozoids escape (Fig. 411, *B*).

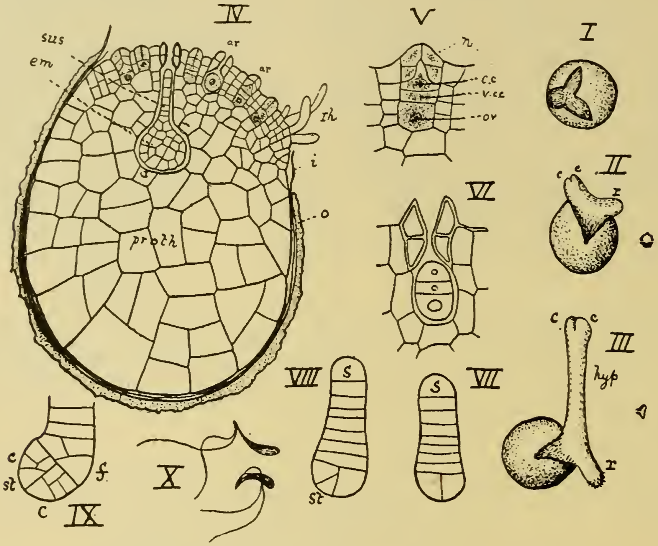

FIG. 412.

Embryology of *Selaginella denticulata*, after Bruchmann. I.-III. (× 12½) show germination of megaspore. IV. vertical section of megaspore showing prothallus, archegonia, and embryo (*em*) with suspensor (*sus*) (× 50). *V.*=a mature archegonium. VI.-IX.=stages of developing embryo. X.=spermatozoids of *S. cuspidata*, after Belajeff. (× 250.)

The germination of the *megaspores* produces an internal tissue of greater extent, which may be styled the *female prothallus.* Its development begins below the meeting of the three converging ridges of the tetrahedral spore, and it extends into the spore-cavity, which is stored with nutritive material (Fig. 408). The increase in bulk of the contents ruptures the wall of the spore along the three converging ridges, so that the surface of the tissue is exposed (Fig. 412, I.). Near the central point the first archegonium appears, while laterally others may be formed later, but not in regular succession. A vertical section through a megaspore of *S. denticulata* shows it completely filled with tissue of the prothallus, while its exposed surface bears rhizoids (*rh*) and archegonia in various stages of development (*ar*) (IV.). The archegonium consists of a neck (*n*) composed of two tiers of four cells each : a canal-cell (*c.c*), ventral-canal-cell (*v.c.c.*), and the ovum (*ov.*) ; all of which were derived by segmentation from a single superficial cell of the prothallus (V.). When mature the neck is open, the canal-cell and ventral-canal-cell have disappeared, and the *ovum*, which is now a rounded primordial cell, is open to access of the spermatozoids. As both types of spore germinate together, *fertilisation* is readily carried out. If the germination of the two types of spore is compared with that seen in Ferns, it appears that while in both the vegetative region of the prothallus is reduced, and does not take part in active nutrition, the antheridium and the archegonium are in essential correspondence with the like parts in Ferns.

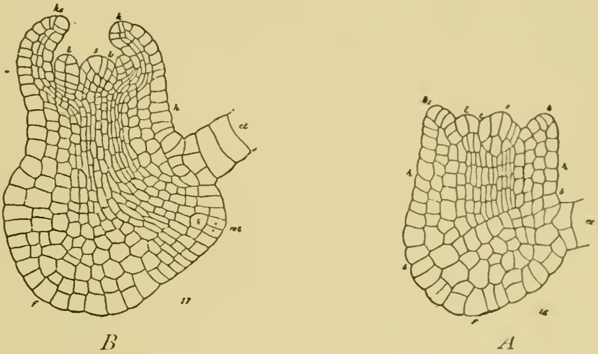

FIG. 413.

Embryos of *Selaginella denticulata*, after Bruchmann. *et* = suspensor. *wt* = root. *f* = foot. *bb* = basal wall. *h* = hypocotyl. *s* = apex. *k*, k_1 = cotyledons. *l* = ligule. (After Bruchmann.)

After fertilisation the *zygote* secretes a protective wall, and elongating in the axis of the archegonium, segments repeatedly (Fig. 412, VI.-VIII.) to form a filamentous suspensor (*s*) which thrusts the embryo down deep into the prothallus (IV.). The distal cell soon enlarges, and divides. It gives rise centrally to the apex of the stem (*st*), with cotyledons right and left (*c*, *c*). Meanwhile unequal growth turns it to one side, and the convex side enlarges into the suctorial " foot " (IX. *f*). Lastly, the first root (*wt*, Fig. 413, *A*, *B*) is initiated by periclinal divisions close to the attachment of the suspensor, and on the same side of the embryo. All the parts of the young embryo have thus been produced, while the apex of the axis occupies the distal position from the very first in the curved embryo. As the axis and root grow they protrude from the ruptured spore, the root turning downwards, and the elongating hypocotyl turning upwards (Fig. 412,

II. III.). The cotyledons already bear ligules (*l*, Fig. 413). The further development is merely a matter of continued growth and branching, which result in the establishment of a young *Selaginella*-plant similar to the parent.

If the embryology of *Selaginella* is compared with that of a Fern, the most marked difference is seen to lie in the presence of the filamentous suspensor. There are, however, certain primitive Ferns in which a suspensor is present, as it generally is in Lycopods and Seed-Plants. It seems probable that it is really a primitive organ, but that it has been eliminated in the more modern Ferns, and some other Pteridophytes, though retained by Seed-bearing Plants.

The leading events in the life-cycle of *Selaginella* correspond clearly to those of a homosporous Fern (see Diagram, Fig. 400). The microphyllous sporophyte is the correlative of the megaphyllous Fern. Sporangia are borne by both, and chromosome-reduction in the formation of the spores establishes in both their haploid state. The germinating spores produce the prothalli, and ultimately antheridia and archegonia. After fertilisation a new sporophyte arises in both cases from the zygote. All these events follow in the same succession in *Selaginella* and in *Dryopteris*, and the several stages may be held as homologous. The chief difference lies in the two distinct types of spore in *Selaginella*. *The distinction of these appears late in the individual development.* At first all the sporangia are alike, with numerous spore-mother-cells in each. The microsporangia behave like those of homosporous types, such as *Lycopodium* or *Dryopteris*, all the spore-mother-cells undergoing tetrad-division and forming microspores. But in the megasporangium of *Selaginella* only one of them as a rule shows tetrad-division, the rest giving up their substance to that one (Fig. 410). The result is that each individual spore of the megasporangium is hypertrophied as a *megaspore*, and stored with nutritive material. The conclusion to be drawn from these facts is that the difference between these spores, which are then described as *heterosporous*, has been secondarily acquired from the primitive homosporous state, and that it is founded on nutrition. Comparison supports this inference: for there is evidence of like progressions from the homosporous to the heterosporous state in the Equisetales and in the Filicales. In the latter, the Hydropterideæ also show identity of early development of the sporangia, whether they are to be megasporangia or microsporangia. It is concluded, therefore, that *heterospory has been homoplastic* in distinct phyla: that is, that *it has been initiated more than once in Descent.*

The biological advantage which follows on the adoption of heterospory lies in the fact that a large and well-nourished megaspore forms a better starting point for the new embryo than an independent prothallus which has to elaborate its own supply. The megaspore draws upon the ample resources of the parent sporophyte, and when shed it already contains sufficient food to start the embryo well on its way. This is seen in the germinating megaspores of *Selaginella*, where the sporeling may attain considerable size before the store is exhausted (Fig. 412, III.). Its root and shoot are then able to take up nourishment independently of the prothallus. This heterosporous condition had already been adopted by Palaeozoic Lycopods, so that it is not a modern device.

ADOPTION OF THE SEED-HABIT.

Certain of the Palaeozoic Lycopods had, however, gone a step further than the state seen in *Selaginella*. *They retained the megaspore within the tissue of the parent*, so that its nutrition could be continued without the interruption caused by shedding of the spore. In *Lepidocarpon* and *Miadesmia* a seed-like structure actually existed, though not exactly of the same type as that which has become a constant and permanent feature in Seed-Plants. A similar condition, but carried out in greater perfection, is seen in certain Fern-like Plants of the Palaeozoic Period. They are called Pteridosperms from the fact that they produced seeds containing a megaspore. This retention of the megaspore finds its biological justification in the fact that thereby the nutrition of the germ is still more effectively secured than it is by simple heterospory. *It thus appears that certain Pteridophyta illustrate steps essential in the institution of the Seed-Habit. These are, first, the adoption of heterospory, and, secondly, the retention of the megaspore upon the parent plant.*

The establishment of the Seed-Habit was undoubtedly the greatest evolutionary advance towards a specific Flora of the Land. Its effect is shown by the prevalence of Seed-Plants upon exposed Land-Surfaces. In any ordinary landscape it is the Seed-Plants, whether Angiosperms or Gymnosperms, which strike the eye, and appear to make up the majority of the Vegetation. Though the Angiosperms date back only to the Cretaceous period, the more primitive Gymnosperms are of much earlier origin, while the archaic Pteridosperms, Fern-like Plants which bore seeds sometimes of considerable size, carry the Seed-Habit far back into the Palaeozoic Age. Thus, though the Angiospermic development is relatively recent, the Seed-Habit was initiated in the very remote past.

It has been pointed out that the Pteridophyta retain their primitive zoidiogamic fertilisation, a fact that has tended to restrict their spread on exposed land-surfaces. Also it has been noted that certain of them have taken the forward steps to heterospory, and to the retention of the megaspore upon the parent plant. Both of these essential steps towards the Seed-Habit can be adopted while still retaining zoidiogamic fertilisation. It will be seen later that some Seed-Plants still carry out their fertilisation by means of freely moving spermatozoids, thus giving strong evidence of their Descent from a Pteridophytic source. But the vast majority of Seed-Plants have adopted the *siphonogamic* mode of fertilisation, by means of a pollen tube, as already described for the Angiosperms in Chapter XVII. This finally emancipated them from the embarrassing tie which zoidiogamy imposed. Combining the Seed-Habit with siphonogamic fertilisation the Seed-Plants became in actual fact Plants of the Land, independent of water except such as can be extracted from the soil by their roots. This was probably the chief factor leading to their present dominant position.

The Equisetales.

The Equisetales, or Horse-tails, can only be briefly described here, though they should not be omitted : for they figured largely as the Calamarians in the primary rocks from the Devonian Period onwards, while the Class survives in the cosmopolitan genus *Equisetum*. Whereas the Calamarian fossils often attained tree-like proportions, the living types are relatively small. Nevertheless the general organisation of the Class is very uniform, the stem being dominant and the relatively small leaves disposed upon it in successive whorls with intervening internodes. This type of construction is sometimes described as " articulate." It is shared by another Class of fossils, the Sphenophyllales : but these are all extinct.

As in the Ferns, the sporophyte of the Equisetales is the substantive plant, while the gametophyte is relatively small. The habit of an *Equisetum* is seen in Fig. 413 A, with its webbed leaf-sheaths present alike on the rhizomes and on the aerial shoots : both of these may be branched. Buds and related roots arise at the nodes. The result is a certain uniformity of the microphyllous habit, its differences depending mainly upon the degree of development of the branching. A solitary distal fertile cone or strobilus may be seen on each fertile branch. It consists of a central axis bearing lateral *sporangiophores*, disposed less regularly than the leaves. Each sporangiophore supports a number of large *sporangia* pendent from its peltate end.

Anatomically the internode presents in transverse section a well-marked epidermis with stomata leading to a broad, well-ventilated and photosynthetic

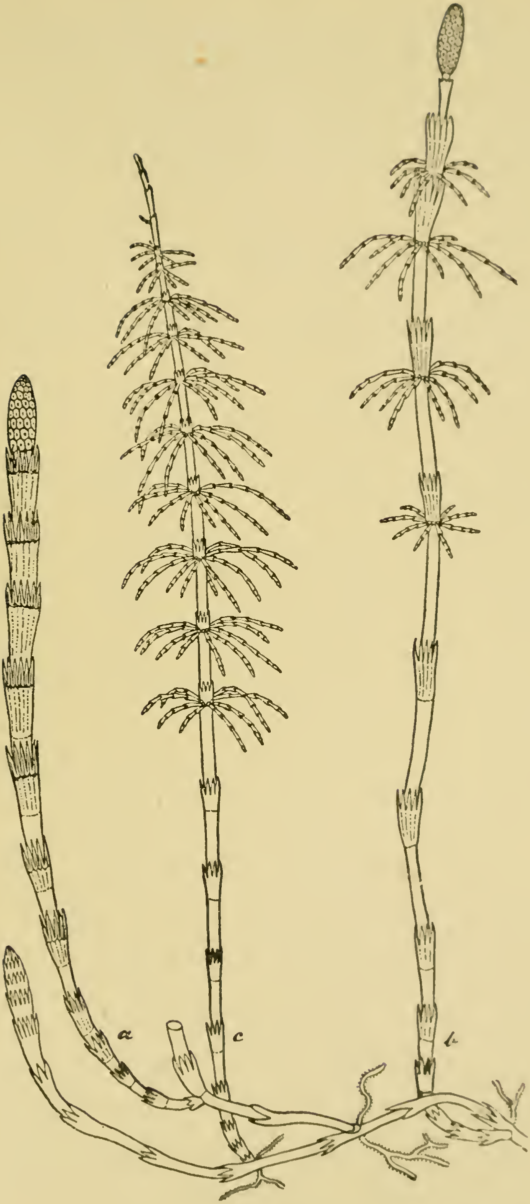

FIG. 413 A.

Equisetum pratense, Ehrh. Rhizome with unbranched fertile shoots (*a*), a fertile shoot which has begun to form branches (*b*), and a young sterile shoot (*c*). Natural size. (After Duval-Jouve; from Rabenhorst's *Krypt. Flora.*)

cortex. Centrally there is a large pith-cavity. Round this vascular strands are disposed in a regular cylinder, their number corresponding to that of the leaves in each whorl, and with details related to the moist habitat of these plants. There is a near analogy with the structure of certain seed-plants, but there is no persistent cambium in the living species of *Equisetum* : though in the Calamarian fossils, while the primary scheme is the same, an active ring of cambium led to the development of a massive woody trunk.

The sporangia are large, and each contains numerous homosporous spores. These germinate and produce autotrophic, dorsiventral prothalli, bearing numerous erect lobes. The gametangia are essentially of the Fern type : but the embryo appears as a spindle-shaped body, the initial cell at its apex being defined by the first segmentations. It is difficult to bring these features into any near relation either with those of Ferns or of Lycopods. Perhaps the nearest comparison among living plants would be with *Tmesipteris*. But the facts of segmentation of the zygote bear a special value, since *Equisetum* is the only genus of the ancient Articulate Plants in which the embryology is known. The Horse-tails appear as an isolated type in modern vegetation, and present a phyletic problem of their own.

A more full description of the Equisetales will be found in *Primitive Land Plants*, Chapter X.

DIVISION V.

SEED-PLANTS.—GYMNOSPERMS.

CHAPTER XXXIII.

CONIFERAE: THE SCOTS PINE.

The description already given in Chapters I. to XIX. has presented the structure and development of the Higher Flowering Plants, or Angiosperms, in which the ovules are protected by a carpellary wall, and the pollen-grain is received upon a stigmatic surface. These Plants appeared relatively late in Geological Time. Their records date back only to the Cretaceous Period. Comparative evidence supports the conclusion that they are the culminating types of Vegetation, and rightly occupy the highest position. Their ready adaptability to their surroundings has contributed to their success in the struggle for existence, as shown by the profusion of their forms now living. In fact, they are the dominant types of the Present Day.

But Seed-Plants long ante-dated the Angiosperms. Seeds existed in the Devonian Period. They belonged to forms corresponding more nearly to those living Plants which are collectively named *Gymnosperms*, than to the Angiosperms. This gives a special interest to the study of the living representatives of the Gymnosperms, a class which have as their leading characteristic the *free exposure of their seeds*, a carpellary protection being absent. Being simpler in their propagative methods, as they are also in certain structural features, and having existed in earlier geological periods than the Angiosperms, they are naturally held as the more primitive Seed-Plants, and as such they may be expected to offer features valuable for comparison with the Pteridophyta. This is found to be the case, and it is this which makes the study of them of special value.

The living Gymnosperms may be regarded as the survivors of a large class of Plants of earlier periods, and accordingly their representatives appear rather isolated and distinct from one another. They comprise the Cycadales, Ginkgoales, Gnetales, and Coniferales. The last is the leading Class of living Gymnosperms, and it includes the greatest number of species. They are called the Coniferales from the fruiting body usual for them, which is composed of closely packed hard woody scales, as is well exemplified by the ordinary Fir Cone (Fig. 414, *A*.) In some, however, a definite woody cone is not formed.

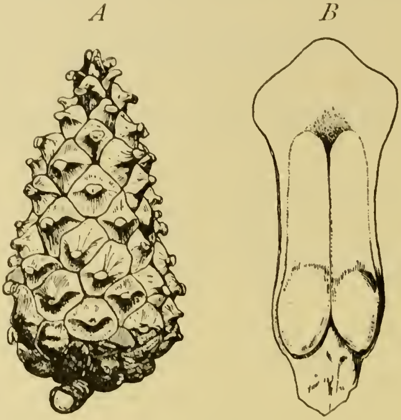

FIG. 414.

A = mature cone of the Scots Pine, natural size. *B*, a single scale of the cone, seen from above, showing the two ovules, together with the outline of the film of tissue which separates with the ripe seed. Enlarged. (After Le Maout.)

CYCADALES.

The Cycadales are represented at the present day by nine genera, and about 100 species of Fern-like Plants, widely distributed in Tropical and Sub-Tropical regions. These are the relics of a Flora which appears to have reached a climax in numbers and importance in the Oolitic and Cretaceous Periods. In habit they are megaphyllous, often with upright stems, and pinnate or sometimes doubly pinnate leaves. The texture of their leaves is stiff, leathery, and even spinous, and they are constructed on a plan like that of the Marattiaceous Ferns, but specialised for withstanding drought. Their stems are thick and fleshy, and comparison of their internal structure points again to the Marattiaceous Ferns, to which some of the related fossils correspond in marked degree.

The Cycads are reproduced by seeds. The ovules (megasporangia) from which they are matured are borne freely exposed upon the margins of the carpels, or megasporophylls: these are often associated in closely packed cones. On other plants staminal cones are borne. The stamens, or microsporophylls, bear numerous pollen-sacs (microsporangia) on their lower surface. The pollen-grains (microspores) from these gain direct access to the micropyle of the exposed ovule, and form short pollen-tubes, which have been found in *Cycas* and *Zamia* to discharge motile spermatozoids as the fertilising bodies into a liquid secreted by the nucellus (Fig. 415). In many respects the living Cycadales show points for comparison on the one hand with the primitive Ferns, on the other with the remaining Gymnosperms. But the feature which possesses the greatest comparative interest is that the *motile spermatozoid* is retained by them as the means of fertilisation. *Ginkgo biloba*, the only living representative of the Ginkgoales, a family well represented in the Jurassic Period, is also fertilised by motile spermatozoids. The existence of zoidiogamic fertilisation in two families of ancient Seed-Plants still living, and so distinct as these, is held as strong evidence of the origin of Seed-Plants from a Pteridophytic ancestry.

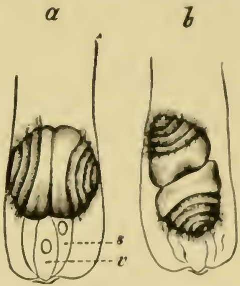

FIG. 415.

End of pollen-tube of *Zamia*, a Cycad, showing the prothallial cell (*v*), the sterile sister-cell (*s*), and the two spermatozoids. *a*, before movement of the spermatozoids has commenced. *b*, after beginning of ciliary motion. (× about 75.) (After Webber, from Strasburger.)

CONIFERALES.

The Scots Pine.

The leading class of living Gymnosperms is the *Coniferales*, so named from the fruiting body with its hard woody scales, as seen in the ordinary *Fir-cone*. The vast forests of such Conifers, existing in temperate and sub-arctic zones, are the sources of the supply of softwood, wood-pulp, turpentine and pitch. In the native British Flora the Gymnosperms are represented only by Conifers, such as Scots Pine (*Pinus sylvestris*), the Yew (*Taxus baccata*), and the Juniper (*Juniperus communis*); but many more are familiar in cultivation in shrubberies and woods. Over the world at large they include a number of other forms, somewhat loosely related, but with common features that indicate their primitive character. Among them are some of the largest and oldest of living organisms, such as the Big Trees of California (*Sequoia*, see Frontispiece). Another well-known and peculiar form is the Monkey Puzzle (*Araucaria imbricata*).

The seed of the Scots Pine, and of other Conifers, produces on germination a seedling with a dominating main axis, which grows upright, and keeps as a rule its radial construction. Radiating groups of branches are borne at intervals upon it, which take a more or less flattened form; and as they do not grow so strongly as the main stem the result is the pyramidal habit so well seen in the Christmas

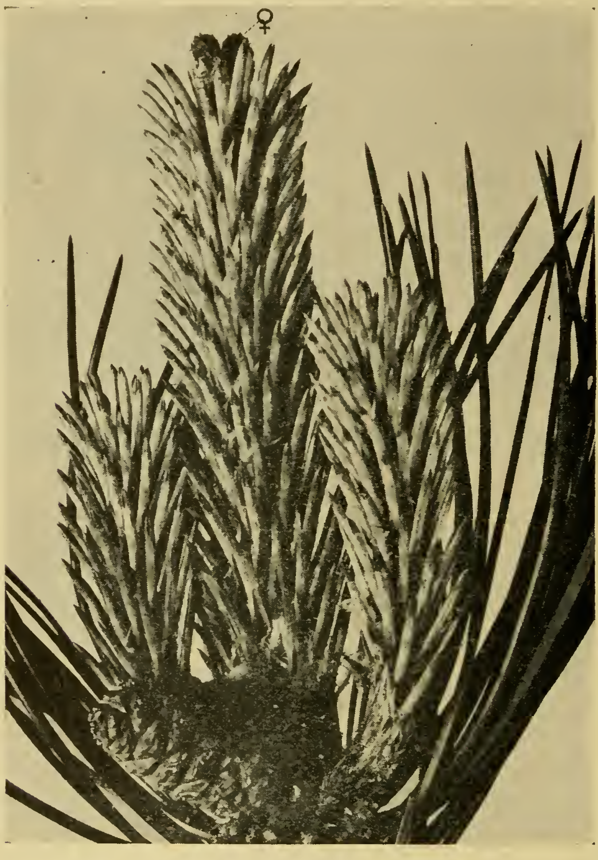

FIG. 416.

Branch-end of *Pinus nigra* (Arnold) bearing laterally two shoots of unlimited growth, and a cone replacing a third one. Each is covered by numerous "foliage-spurs" bearing two "needles." At the base of the figure these are fully developed; above they are half-grown, the shoot having been cut in spring. Two young female cones (♀), at the distal end, are at the period of pollination. (After Groom.)

Tree (*Picea*), and in the young Scots Pine. Sometimes this habit is maintained throughout life; but often, as in the Scots Pine, the form becomes irregular as the tree grows older. The Coniferae are as a rule closely gregarious, and they then form very exclusive forests. The lower branches die off in the crowded woods, giving the clean trunks without knots that are specially valued as timber, and supply naturally-formed masts, spars, and telegraph-poles.

The Scots Pine, like most of the family, is characterised by leaves of relatively small size, simple form and stiff texture. These are xerophytic features, and are well illustrated by the " needles " of the Pine. Their structure, with sunken stomata, a well-developed cuticle, and a large proportion of bulk to surface bears this out. Hairs are absent from their smooth surfaces.

In some of the Coniferae the vegetative leaves are all of essentially the same type, as in the Juniper. But in the Scots Pine some of them are developed as protective scales, others as green foliage leaves, and the mutual arrangement of these two types is very characteristic. It is closely connected with the fact that all the axillary buds do not develop alike. Those at the end of the annual increment of growth are unlimited, and form the radiating group of branches of each successive year already noted. Those lower down develop only as limited *foliage spurs*, which remain short, bearing only a few membranous scales, and distally a few long green " needles " (Fig. 416). In the seedling plant green foliage leaves may follow the cotyledons on the main axis. But in the later stages the main axis and the woody branches bear only scale-leaves, while the green needles are always borne on the foliage-spurs. In the different species of *Pinus* the number of needles on each spur varies : in *P. monophylla* it may be only one. The Coniferae are mostly evergreens like the Scots Pine, Yew, and Juniper. But some, like the Larch, shed their leaves in autumn, or even their short leafy shoots, as in *Taxodium*.

The root-system starts in all cases with a tap-root ; but it seldom maintains its lead. Lateral roots arise from it, and they form the chief attachment of the mature tree, which is often shallow-rooted. Some of them, as in the Scots Pine, are mycorrhizic, the roots being invested by a fungal felt, which acts as an intermediary between the root and the soil (p. 228). But as seedlings can be raised in pure cultures without the fungus, its presence, however advantageous, is not necessary.

The external characters of the Coniferae thus briefly sketched stamp the appearance of most of them. The general plan of their Plant-body or sporophyte is the same as that seen in Angiosperms. It is the working out of the details that gives the special characters of the Coniferae. Their habit is easily distinguished from that of the broad-leaved Dicotyledons, and still more easily from the Palms and other large Monocotyledons. A feature which has its bearing upon the habit and spread of the family is the rarity of vegetative propagation. In Nature it hardly ever occurs, and the forester finds it impracticable. Virtually all individuals are raised from seed. This is in marked contrast to the Angiosperms.

There is no need to describe the minute structure of the vegetative organs, since it corresponds in essentials to what has been seen in Angiosperms. It must suffice to note certain features of comparative importance. The stem is constructed on the same plan as that of the woody Dicotyledons, with indefinite secondary thickening of the vascular ring originating from a cambium (compare Fig. 35, p. 57). It results in the Scots Pine in a woody trunk marked by annual rings and medullary rays, while externally are phloem and a scaly fissured bark (see Fig. 42, p. 64). *Resin-passages* permeate all the tissues irregularly. They are specialised intercellular spaces, lined by an epithelium, which deposits the sticky resin in the passages. It exudes from them under pressure of the surrounding tissues whenever the plant is broken or cut. The most notable structural feature is that the *wood is composed entirely of tracheides*, each developed after tangential division from a single cambial cell (Fig. 417). They are uniform in shape, as the cambium is, and are not deformed as the wood of the Dicotyledons is, by sliding growth, or by unequal development of the individual cells. The wood is consequently of that even texture seen in "deal." The tracheides are lignified, and their radial walls are marked by *circular bordered pits.*

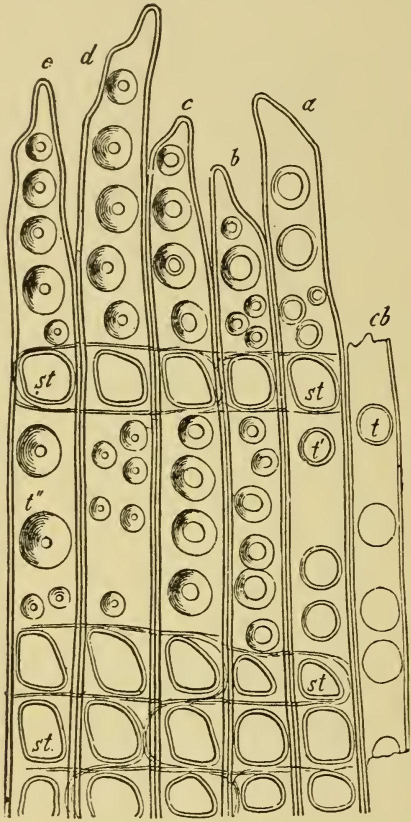

FIG. 417.

Tracheides of Pine, seen in radial section. *a-e*, are successive tracheides of one radial row. *cb*=cambium. *t*=young pit of cambium. *t′*, *t″*=older pits. *st*=pits of larger area facing the oblong cells of the medullary ray. (×550.) (After Sachs.)

The bordered pit which is found widespread in the tracheae of vascular plants, is seen in perfection in the wood of Conifers. The pit originates as a circular area of wall which remains thin, while the rest of the wall thickens.

But the thickening encroaches upon the area of the pit, and overarches it (Fig. 418, *C*, *D*, *E*). As seen in surface view a double outline then appears. The outer circle corresponds to the area of the pit-membrane, the inner to the limit of the overarching; and the greater the thickening the further these outlines will be apart. Meanwhile the centre of the pit-membrane itself thickens, forming the "torus" (*A*, *C*), which serves mechanically to meet the risk of rupture following on any unequal pressure on the two sides. For the torus would, as the membrane yields, press against the overarching lip (*B*). The prevalence of bordered pits indicates that they are functionally important. They may be recognised as a compromise between the conflicting requirements of ready transit of liquid between thick-walled cells and the maintenance of mechanical strength. For the former a large pit-membrane is an advantage, but it would weaken the wall. This difficulty is met by the overarching as seen in the bordered pit, by which the strength of the woody wall is maintained.

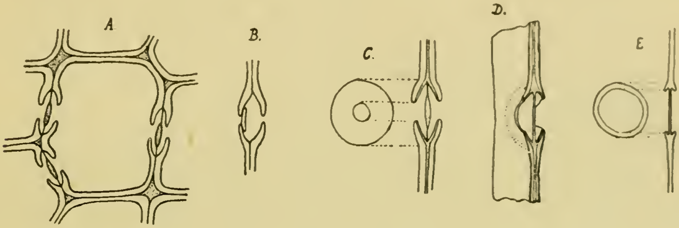

Fig. 418.

Bordered pits of tracheides of Pine. *A* = a whole tracheide in transverse section with pits in its radial walls. *B* shows the torus pressed to one side. *C*, *D*, *E* illustrate the development, and the relation of the structure as seen in section to the double outline as seen in surface view. *E* shows this in the young state. *D* rather more advanced. *C*, mature.

The phloem consists chiefly of *sieve-tubes* (*v*, Fig. 419), which are also arranged in regular radial rows, but without companion-cells. They have cellulose walls and sparing contents. Cells of phloem-parenchyma are also present. The sieve-pits (*vt*) are mostly on the radial walls, and thus correspond in position to the bordered pits in the tracheides. The secondary tissues are traversed by medullary rays, as in Dicotyledons (*em*, *sm*, *tm*). They include cells that retain their protoplasm, while minute intercellular spaces pass radially inwards between their cells. They serve accordingly for radial ventilation, as well as for storage within easy reach of the conducting phloem. Though the plan of construction of the vascular tissues of Gymnosperms is the same as in Dicotyledons, the details of their development are not so elaborate.

The chief comparative interest of such a plant as the Scots Pine lies not so much in the form and structure of the sporophyte-plant, as in the details of its propagation. This is carried out, as in the Angiosperms, by organs grouped as *Flowers*, which are "*male*" or "*female.*" In the Scots Pine these may be borne on the same tree, though often on distinct branches. The female flower, pink and succulent at pollination, matures into the hard woody cone, from which the name Coniferae is derived (see Figs. 414, 416). When ripe it consists of a central axis bearing in a complex spiral numerous woody *ovuliferous scales.* As the cone ripens the scales turn back, and two seeds may be seen freely exposed on the upper surface of each. When fully ripe each seed separates from the scale, together with a thin film of superficial tissue, which on detachment helps to float it away on the breeze (Fig. 414, *B*). The seed is protected by a seed-coat, covering a bulky endosperm, with a large embryo enclosed in it, which has many cotyledons, a plumule and radicle. The seed is thus "albuminous," and in essential points it corresponds to that of Angiosperms. But in the Scots Pine it takes two years to produce, and the details of its production give important features for comparison.

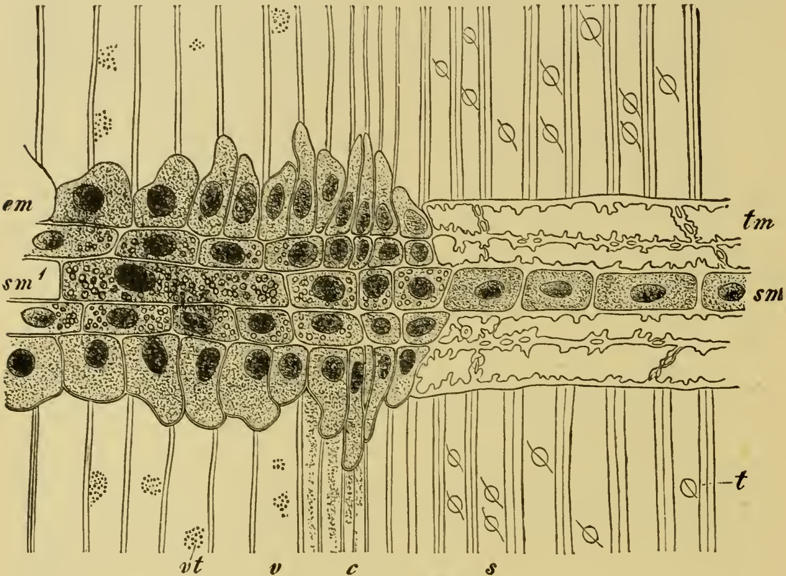

FIG. 419.

Radial section of Pine stem, at the junction of wood and bast. Phlœm to the left, xylem to the right. *s*=autumn tracheides. *t*=bordered pits. *c*=cambium. *v*=sieve tubes. *vt*=sieve pits. *tm*=tracheidal medullary ray cells. *sm*=medullary ray cells in the wood containing starch. *sm'*=the same in the bast. *em*=medullary ray cells with protoplasmic content. (×240.) (After Strasburger.)

Both the types of flower are axillary in their origin. The male flowers are produced in large numbers, replacing the weak foliage spurs (Fig. 420). The female take the place of the stronger branches of unlimited growth, and are produced in smaller numbers (Fig. 416).

As these project at the time of pollination above the end of the extending shoot, they are in the best possible position for receiving the wind-borne pollen. The *male flower* is enveloped below by membranous scales, and bears distally numerous *sporophylls* or *stamens*, each with two pollen-sacs on its under side (Fig. 421, *B*, *C*). The pollen-grains are peculiar in bearing right and left of the grain itself air-containing sacs (wings) which give a low specific gravity to the whole grain, and so aid its transfer by the breeze (Fig. 421, *D*). At the time when it is shed, the grain of *Pinus* contains, in addition to the vestigial remains of two obliterated cells of the male prothallus, one nucleated cell

Fig. 420.

Pinus nigra, Arnold. Shoot bearing male flowers in place of foliage-spurs. (After Groom.)

attached laterally (the *generative cell*), and a free nucleus (the tube nucleus) enclosed in cytoplasm which fills the rest of the grain.

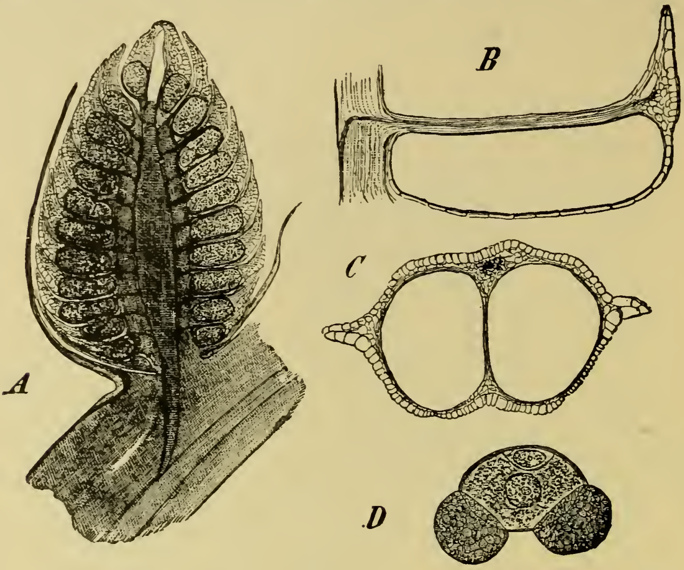

Fig. 421.
Pinus montana. A longitudinal section of a ripe male flower (× 10). *B*, longitudinal section of a single stamen (× 20). *C*, Transverse section of a stamen (× 27). *D*, a ripe pollen grain of *Pinus sylvestris*. The obliterated prothallial cells are not shown. (× 400.) (After Strasburger.)

The male flower is thus a simple shoot bearing sporangia. The *female flower* may also be regarded as a simple shoot. It consists of an axis bearing numerous scales that are at first succulent, but finally woody. They are arranged on a complex spiral plan. One of these scales removed from the young pink cone at the stage of pollination shows a double structure. A smaller lobe, sometimes called the

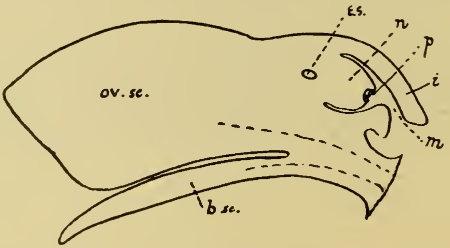

Fig. 422.
Median section of ovule and scales in Pine at time of pollination (after Coulter). *b. sc*=bract scale. *ov. sc*=ovuliferous scale. *n*=nucellus. *i*=integument. *m*=micropyle. *e.s.*=embryo-sac. As the two ovules lie side by side, only one of them is seen in the radial section. *p*=pollen-grain on nucellus.

bract-scale, bears on its upper surface a larger and thickened lobe, sometimes called the *ovuliferous scale* (Fig. 422). It seems probable that this is a local upgrowth of tissue from the surface of the former, though as the cone grows older it becomes woody, and is by far the more prominent feature of the two. Other interpretations of the cone have been given; but if this view be accepted, then the whole cone is a simple flower bearing many complex sporophylls. Attached to the upper face of the ovuliferous scale are *two ovules*, which are not enveloped by a carpel as in the Angiosperms, but are fully exposed, with their wide micropyles directed downwards. Each ovule consists of a nucellus corresponding to that of the Angiosperms, surrounded by a single integument, and with a wide micropyle (*m*, Fig. 422). The pollen-grains being produced in enormous numbers, and floating away on the dry air of a June day, are scattered over the female cones, of which the scales then stand apart to receive them. A drop of fluid extruded from the micropyle

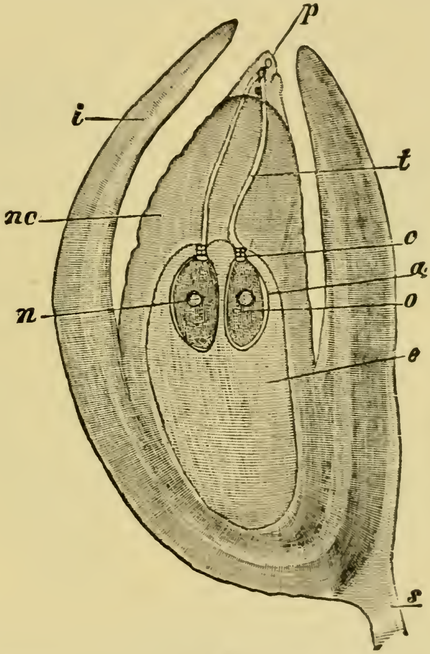

FIG. 423.
Median longitudinal section of an ovule of *Picea excelsa* at time of fertilisation. *e*=embryo-sac filled with tissue of the female prothallus. *a*=archegonium, showing venter (*a*) and neck (*c*). *n*=nucleus of ovum. *nc*=nucellus. *p*=pollen-grains. *t*=pollen-tube. *i*=integument. (× 9.) (After Strasburger.)

catches them and is then absorbed. Thus *the pollen-grains are landed directly on the apex of the nucellus*, where they are constantly to be found in sections cut through the ovule (*p*, Fig. 423). Excepting that there is no receptive stigma the process is not unlike that in wind-pollinated Angiosperms.

Differences of great comparative interest lie in the details within the ovule itself. The ovule originates as in Angiosperms, and as in them the embryo-sac is one cell of a tetrad produced in the young nucellus; its nucleus is therefore haploid. (See p. 297.) But an essential difference is that in *Pinus*, and all other Gymnosperms, nuclear division proceeds to a high number in the young embryo-sac. Cell formation follows, and *the sac is thus filled before fertilisation by a bulky tissue of the endosperm, or female prothallus* (Fig. 423, *e*). At the time of fertilisation, which in *Pinus* and *Picea* happens about the middle of June of the year after pollination, the female prothallus bears at its micropylar end three to six large *archegonia*, of which two commonly appear in a median longitudinal section of it (Fig. 423, *a*). Each of these originates from a single superficial cell of the prothallus, and

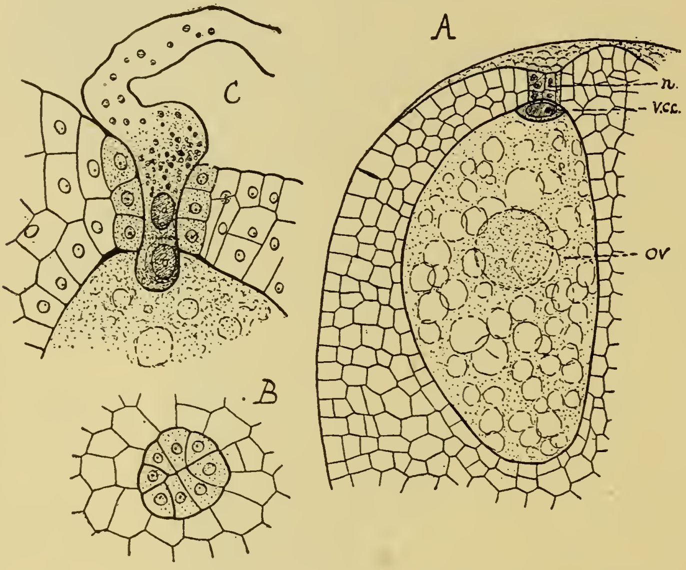

FIG. 424.

Picea vulgaris. *A* = longitudinal section through apex of female prothallus, and one archegonium. *n* = neck. *v.cc* = ventral canal cell. *ov* = ovum. *B* = neck seen from above. *C* = entry of pollen-tube with gametes into the canal of the archegonium. (*A* × 100; *B*, *C* × 250.) (After Strasburger.)

consists of a large nucleated *ovum*, with a small lenticular *ventral-canal-cell* lying above it, which is cut off from the ovum shortly before fertilisation. Covering this is a group of cells two or more tiers in depth, forming the channel of the neck (Fig. 424, *A*). The ovum of *Pinus*, as is not uncommonly the case in Gymnosperms, is large enough to be seen with the naked eye. The archegonia lie in a slight depression of the surface of the prothallus. The last step before fertilisation is the collapse of the ventral-canal-cell, which takes no direct part in propagation.

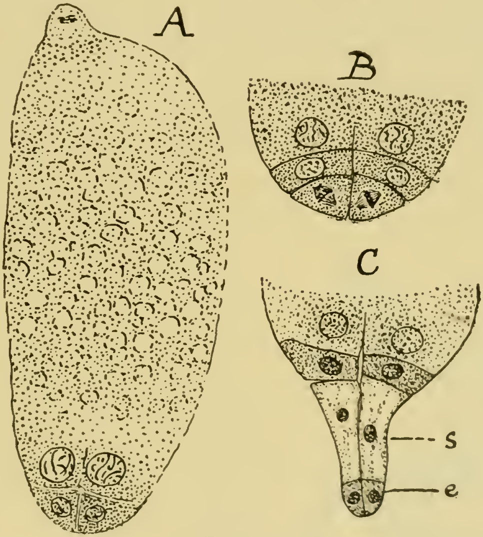

FIG. 425.

Pinus Laricio, stages of embryology. *A* shows two tiers of four cells at base of the archegonium. *B* shows three tiers, and the last division proceeding in the lowest tier. *C* shows the tier of suspensors (*s*) elongating, and carrying forward the lowest embryonic tier. (After Coulter and Chamberlain.)

In the Scots Pine a whole year elapses between the pollination of the young pink cone and the act of fertilisation. But in Conifers generally the times are different. With or without a lengthened interval each pollen-grain, germinating on the apex of the nucellus, forms a pollen-tube, which penetrates the nucellus, passing towards the apex of the prothallus. Meanwhile its generative cell has divided to form a stalk-cell and a body-cell. The former breaks away from its attachment, and the contents of the grain enter the tube. The body-cell divides during transit to form the *two male gametes*. Thus provided, the tube enters the neck of an archegonium, and the gametes are transferred into the ovum (Fig. 424, *C*). The nucleus of one of the gametes fuses with the nucleus of the ovum. The result of the fusion is the *zygote*. Both the ovum and the male gamete were haploid, and the consequence of their fusion is to initiate the new diploid phase, which forms the *embryo*. The detail of embryology is variable in different genera of Conifers, and rather complicated.

In *Pinus* and its allies the nucleus of the zygote divides at once, first into two and then into four. The resulting nuclei sink to the base of the egg, lying in a single plane. Divisions follow to form four tiers consisting of four cells each (Fig. 425). Of these the lowest but one elongate as the suspensors (*s*); the lowest form the embryonic tier (*e*). In the Pines these may either form together a single embryo, or they may separate, each borne on its own suspensor, and so four embryos may result from one fertilisation. As there are several archegonia, and each may be fertilised, a high degree of *polyembryony* is possible. As a rule one embryo in each ovule secures the ascendency over the others, and the rest are absorbed. It has been calculated that in the Scots Pine only about one per cent. of the potential embryos are matured.

The maturing embryo, borne on the end of its elongating suspensor, is thrust downwards into the substance of the endosperm. With less regular segmentation than that in Angiosperms it matures into the germ, which in the ripe Pine-Seed is cylindrical in form. It is terminated by an apical cone, round which cotyledons, varying to the number of fifteen, are arranged in a ring. The radicle is massive, with the large root-cap characteristic of Gymnosperms. The female prothallus persists as the nutritive endosperm ; the nucellus is crushed between the enlarging endosperm and the hardening seed-coat. The seed is thus albuminous, which is the case for all Gymnosperms, a fact which suggests that this is the primitive state for the seed generally. Its parts when mature correspond in nature and position to those of the seed in Angiosperms (Fig. 426, I.).

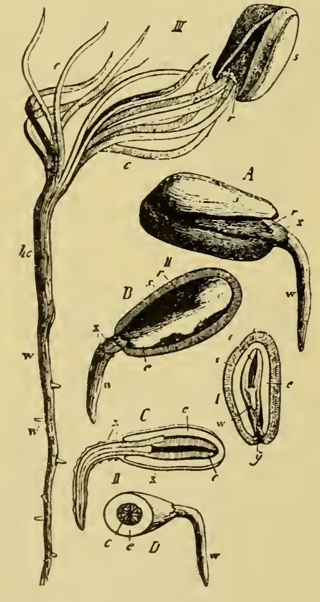

Fig. 426.

Pine seed and germination. I. Median section of seed; *y*=micropolar end. II. germination. III. Ditto later; *s*=seed-coat; *e*=endosperm; *c*=cotyledons. *w*=primary root; *hc*=hypocotyl. (After Sachs.)

A period of rest is followed by germination of the seed. The embryo, drawing upon the nutritive endosperm, enlarges, and the radicle projects and grows down (Fig. 426, II.) The hypocotyl elongates, and the seed is carried above ground. The tips of the cotyledons remain within it till the store is exhausted, when it is cast off, and the cotyledons expand round the central plumule (Fig. 426, III.). Thus the seedling is established.

Comparison between Pteridophytes and Seed-Plants.

The Gymnosperms offer natural lines of comparison on the one hand with the heterosporous Pteridophyta, and on the other with the Angiosperms. The general features of the life-cycle are the same in them all. Hence it may be concluded that the comparisons are legitimate, as between cognate organisms. In all of them the sporophyte is the dominant "plant," while the gametophyte shows progressive degrees of elimination as an independent vegetative structure. Comparing *Pinus* as an average Gymnosperm with *Selaginella*, which may be taken as a fair example of a heterosporous Pteridophyte, the "plant" bears in either case two kinds of sporangia. The microsporangium of *Selaginella* corresponds to the pollen-sac of the Pine, since both produce spore-mother-cells, and these after tetrad-division form microspores, which are shed on rupture of the sporangial wall. The megasporangium of *Selaginella* corresponds to the nucellus of the ovule of *Pinus*, which is, however, protected by the extra covering of the integument. In the ovule, as in the megasporangium of *Selaginella*, a tetrad-division leads up to the formation of the megaspore. In *Pinus* only one megaspore or embryo-sac is matured. In *Selaginella* commonly four, and occasionally more: but sometimes two, or even one only. Thus in point of origin, in the manner of production, and sometimes also in number, the megaspore of *Selaginella* corresponds to the embryo-sac of *Pinus*. An essential difference may appear to lie in the fact that in *Selaginella* the megaspore with its thick protective wall is shed on rupture of the megasporangium: while in *Pinus* the megaspore or embryo-sac is retained within the nucellus, and is thin-walled. But this retention of the megaspore within the sporangium gives the biological advantage of continued nutrition, to which a thick and rugged wall would be an unnecessary obstacle. The facts thus point to the conclusion that the thin-walled embryo-sac of *Pinus* is a retained megaspore, and that we see in it a derivative state which has been universally adopted by Seed-Plants. (Compare Fig. 412, IV., with Fig. 423). It has already been noted that certain fossil Lycopods had done the like.

Turning next to the products of germination of the spores, that is, to the gametophyte generation, a comparison must be made of the reduced and modified prothalli resulting respectively from the microspores and megaspores.

The microspore of *Selaginella* produces a single vegetative cell, and an antheridium with a wall and many spermatocytes, each of which gives rise to a freely motile spermatozoid. In the pollen of *Pinus* two vegetative cells are formed, and obliterated in the developing grain, and three further divisions follow. But there is no cellulose antheridial wall, and only two spermatocytes appear, which remain non-motile. Clearly this is a state further reduced and specialised as compared with *Selaginella*. But it has been noted in *Cycas* and *Ginkgo* that the gametes are motile spermatozoids, and in *Microcycas* they are numerous. Such instances show that the products of germination of the microspores of Gymnosperms are sometimes motile like those of *Selaginella* and other Pteridophytes: but they suggest that in other cases the motility of the gametes has been lost in the course of evolution. This change is also seen in Seed-Plants generally. (Compare Figs. 227, 229.)

The megaspore of *Selaginella* begins to produce a prothallus while still within the sporangium, and continues its development after it is shed. It bears archegonia which are exposed by rupture of the rugged wall, and are fertilised by spermatozoids moving freely from the germinating microspores. One or several embryos are produced. Similarly in *Pinus* the female prothallus (endosperm) is formed within the megaspore (embryo-sac), and produces archegonia. But it remains embedded in the sporangium (nucellus), where fertilisation takes place by non-motile gametes conveyed by the pollen-tube to the neck of the archegonium. Several of these may be fertilised, and a plurality of embryos be initiated. It follows that the contents of the megaspore of *Selaginella* and of the embryo-sac of *Pinus* are homologous, both being female prothalli, produced by germination of the megaspore. (Compare Figs. 412, IV., and 423.) The only new structure is the integument of the ovule of *Pinus*: the rest are modifications in accordance with Life on Land, of parts already present. The biological probability of the several steps disclosed by this comparison is such as to justify their acceptance as evolutionary history. Those steps are, the retention of the megaspore upon the parent plant, and the loss of its protective wall: the development of the pollen-tube (perhaps as an extension of a single antheridium): and the loss of motility of the gametes.

Comparison on the other hand with the Angiosperms shows that while there is a general correspondence in the propagative method, the balance between the alternating generations is still more uneven in them than in such Gymnosperms as *Pinus*. The germination of the microspore of the Angiosperm shows only a single division prior to the formation of the two gametes. But a still broader difference is seen between the contents of the embryo-sac in Gymnosperms and in Angiosperms: this is especially apparent at the time of fertilisation. In the former the embryo-sac then contains a massive tissue of the endosperm (female prothallus), with fully formed archegonia hardly differing from those of some Pteridophytes (Fig. 423). But in the Angiosperms it contains only the egg-apparatus, the antipodals, and the central-fusion nucleus with its cytoplasm (Fig. 216). The difference is so wide, and the reduction of the female gametophyte so far-reaching, that it is still a problem for the comparative morphologist whether the several contents of the Angiospermic embryo-sac are really comparable to prothallial structures. All this points to the conclusion that in the Angiosperms we see a final state of reduction of the female gametophyte, the initial steps of which were taken when heterospory and retention of the embryo-sac on the parent were first adopted.

The general result which follows from such comparisons is that the Gymnosperms are confirmed in their position as primitive Seed-Plants. This harmonises with the fact that they are represented far back in Geological History. The application to them of the name Archisperms appears justified. If their origin by Descent is to be traced, it is to plants of the nature of the Pteridophytes that we should look: and by preference to some Fern-like source. The modifications which they show are all explicable as adaptations to the Land-Habit. More especially is this the case in their substitution of siphonogamy for zoidiogamy. With the loss of motility of the spermatozoid the last direct index of their aquatic ancestry was relinquished, and these primitive Seed-Plants became in the full sense Plants of the Land.

Those more recent, and still more advanced Plants of the Land, the Angiosperms, owe their dominant position to their greater adaptability. Its results have been illustrated for their vegetative system in Chapters X., XI.: and for their propagative system in Chapter XIV. Ample evidence of it is also provided by the plants described specifically in Appendix A. The chief features of their further advance in the propagative region are seen, first, in the elaboration of the floral envelopes, by which are secured the attraction and mechanical direction of the animal agents of pollination. Secondly, in the gynoecium. Here the carpels envelop the ovules, giving a much more efficient protection than the integument alone can do. In more advanced epigynous types the carpels and the ovules within them are sunk down into the massive tissue of the axis, thus giving additional security, as well as ready nutritive supply. Lastly, the evolution of a receptive stigma, and of the conducting tissue of the style, combined with the wonderful mechanisms of pollination seen in Angiosperms, stand in strong antithesis to the primitive and haphazard methods seen in Gymnosperms. Such features, together with those more specialised details of the contents of the pollen-tube and embryo-sac already mentioned, leave no doubt in assigning the highest place in the Vegetation of the Land to the Angiosperms.

If any further testimony were required to the accuracy of this comparative conclusion, it would be found in the fact that it is in general harmony with the chronological succession of plant-remains demonstrated by Geologists.

CHAPTER XXXIV.

ALTERNATION OF GENERATIONS, AND THE LAND-HABIT.

The expression "Alternation of Generations" was brought into prominence by Steenstrup, who applied it to the succession of phases in the life-history of Medusae, Trematodes, and other Animals. He defined it as "the remarkable natural phenomenon of an Animal producing an offspring which at no time resembles its parent; but itself brings forth a progeny which returns in its form and nature to the parent Animal." The publication of Steenstrup's essay preceded the demonstration by Hofmeister of the life-history of Mosses, Ferns, and Conifers. These researches disclosed phenomena of Alternation in Plants superficially so like those in Animals that it was natural to use the same terms in describing them. But later it has become clear that the resemblance is not an exact one, and that the "generations" in Plants differ more essentially from one another than those in Animals, to which the terms were originally applied.

In many Plants the distinctness of the sporophyte and gametophyte is marked by form and structure; for instance, that between the prothallus and the Fern-plant. Nevertheless some contemplated the possibility of the sporophyte having originated as a modification of a gametophyte, and described the alternation as one of "homologous" generations. Others, impressed with their distinctness not only in form but also in their probable origin as indicated by comparison, held the two generations to be "antithetic," that is, distinct in their origin and history from one another. The discussion of this question seemed likely to pass into an inconclusive dialectic, when a fresh point was given to it by the discovery that in Plants there is a prevalent nuclear difference between the two generations. In such Plants as may be held to be normal, the sporophyte was found to have diploid nuclei, and the gametophyte nuclei that are haploid.

This distinction is not matched by any corresponding known difference in Animals, in which the whole body appears to be consistently diploid. Thus while Botanists have assumed the term "Alternation of Generations" first used in relation to Animals, they now apply it to a phenomenon in Plants which proves to be peculiar to them. The descriptions already given of the life-histories of Plants have provided many facts which may now be drawn together into a comprehensive statement on Alternation, and on the changes and modifications which it shows in relation to habit.

In normal Plant-Organisms which possess sexuality the fusion of two nuclei in syngamy has been found to result in a doubling of the number of chromosomes in the zygote. This has been demonstrated in so many well-authenticated cases that it may be held as a general consequence. At some other point in their life-cycle, normally before another sexual fusion occurs, there is a tetrad-division, which results in the reduction of the chromosomes again to the original number. The second process may be held to be complementary to the first, and it appears to be necessary if the number of chromosomes is to be kept within limits after repeated syngamy. The life-cycle in sexually propagated plants is thus made up of two phases: the one intervenes between syngamy and reduction and is *diploid*, *i.e.* with $2x$ chromosomes. It is commonly styled the *sporophyte*, or non-sexual generation, because it usually terminates in the production of non-sexual spores. These *spores* are consequent on a tetrad-division, and may be styled specifically *tetraspores*. The other is *haploid*, *i.e.* with x chromosomes. It is commonly styled the *gametophyte*, or sexual generation, because it normally results in the formation

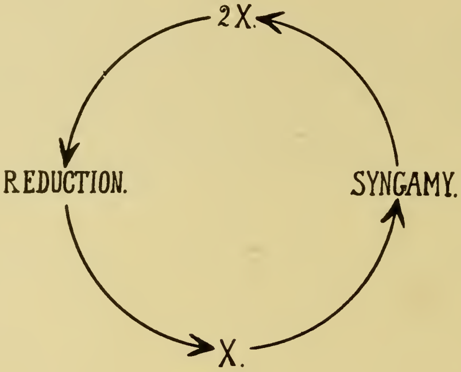

FIG. 427.

of *gametes.* The cycle thus constructed may be represented as in the diagram, Fig. 427. Since the two phases follow one another in regular succession, this phenomenon is that which is now understood as the normal *Alternation of Generations* in Plants. It is also referred to as the *Hofmeisterian Cycle.*

The deviations from the normal cycle known as *apogamy* and *apospory* have been illustrated by examples from Ferns, pp. 506-509. They connote, respectively, a direct vegetative transition from the gametophyte to the sporophyte without the act of syngamy, and a converse transition from the sporophyte to the gametophyte without the intervention of spores. Though recorded instances of such deviations from the normal are numerous, they are not standardised as the normal cycle is in archegoniate plants. This suggests that they are *ex post facto* events, illustrating the potentialities of plants at the present day rather than evolutionary features forming part of the history of the past.

It seems probable in many, though not perhaps in all phyla, that nuclear fusion and reduction remained constant features in each completed life-cycle throughout Descent. In that case two opportunities for somatic amplification were possible in Evolution from simpler forms. The one between syngamy and reduction would give rise to the body of tissue called the sporophyte : the other between reduction and syngamy would give rise to the gametophyte. If the fusion and reduction retained their identity throughout Descent, these two somata can never have been homologous : that is, homogenetic by descent. They must have been " antithetic " throughout, however nearly they may resemble one another in their characters. If they both develop in the same medium they, being in fact merely phases of the same organism, might be expected to resemble one another very closely.

That is found to be actually the case in certain Algae and Fungi. For instance, in *Dictyota* among the Brown Algae, and *Polysiphonia* among the Red, the two generations appear identical (pp. 383-390) ; they seem only to differ in their chromosome-number, and in the propagative organs which they bear. There may be a difference of potentiality between the haploid and diploid phases ; but it need not be realised where the circumstances are uniform, as when both grow in water or in moist conditions. In that case both may appear alike. But even in an aquatic environment the two generations may show marked differences as in *Laminaria.*

The Hofmeisterian Cycle.

The inconclusiveness which marked the early discussions on alternation arose partly from an assumption that what is seen normally in Ferns or Mosses, and described as the *Hofmeisterian Cycle,* is a standardised life-pattern for plants at large. There was also insufficient knowledge of the facts of nuclear structure and behaviour, particularly in the Thallophytes. But the most notable defect was the failure to take into account the diverse conditions to which archegoniate organisms are exposed. The problem before the nascent plant possessing sexuality has been to adjust its somatic development to the nuclear cycle. But these are two essentially different things. The somatic phases must undergo development in relation to external conditions, whereas the normal succession of syngamy and meiosis in the nuclear cycle is not affected by them. There is thus no ground for assuming that the two should be interlocked in any rigid scheme, such as that presented by the archegoniate cycle. All life-cycles do not, as a fact, lend themselves to interpretation in terms of the Hofmeisterian Cycle. While " antithetic alternation " is exemplified in a high degree by the vegetation of the land, it should not be forgotten that it is also characteristic of some of the Brown Algae, e.g. the Laminariaceae. On the other hand, " homologous alternation " is seen only among the Thallophyta, and particularly the Algae. Such facts uphold the conclusion of Oltmanns, that just as sexuality may be held to have arisen repeatedly and independently in various groups of the lower organisms, so may various higher families have carried out independently the establishment of two generations. Continuing this line of thought Von Goebel has affirmed that the doctrine of alternation founded originally for the Higher Plants (from the Bryophyta upwards) cannot be extended to all plants. From such views it follows that the relatively stable alternation, as described by Hofmeister for the Archegoniatae, should be discussed separately from others, and on its own merits. To secure a clear verbal contrast it will be well to drop the old terminology, which never was explicit ; and to substitute " interpolation theory " in place of antithetic, and " transformation theory " for homologous. These words are explicit in conveying the opposed theories of origin of the alternation, which differ in the fixity or otherwise of somatic development in relation to syngamy and meiosis.

Among the Algae somatic alternation may be absent. In those Algae which have been distinguished as haplobiontic, the life-cycle, as in the Red Alga *Scinaia* and a majority of Green Algae, includes only a single somatic phase ; and this is usually haploid. On the other hand the life-histories of *Dictyota* and *Polysiphonia* are *diplobiontic*, with regularly alternating haploid and diploid somata, though these are uniform in outline and evenly balanced.

With the ground thus freed from the trammels of the old assumption of uniformity in alternation, we may next enquire into the subaerial conditions under which the diplobiontic type of alternation seen in the Archegoniatae originated. It appears that the effect of Life on Land has been to stabilise the somatic and cytological relations of the Hofmeisterian Cycle. We may picture to ourselves the working out of the conditions affecting their early evolution as follows. Those simple Archegoniatae which formed the primitive Flora of the Land probably sprang from green haplobiontic Algae, inhabiting shallow fresh water or the higher levels between tide-marks. Here sexual reproduction would be effected through the medium of external liquid water. If other conditions were favourable this could be carried out by them at any time, provided water be present and the sexual organs mature. But certain types escaped competition or availed themselves of a varying water-level, by establishing themselves on land where access to liquid water was only an occasional occurrence. In these the sexual process would only be effected at times of rain or copious dews. Less dependence could then be placed upon sexuality for propagation, and some alternative method of increase would be an advantage. This was provided *by interpolation of a new somatic phase, the act of reduction being delayed by progressive sterilisation and development of the new sporophyte.* The natural result would be a multiplicity of spore-mother-cells, and a higher spore-output : moreover, such steps accord with the known facts of life among the simplest archegoniate plants. Each spore dispersed under dry conditions starts a new individual, yet all those produced by one sporophyte would be consequent on a single act of fertilisation. The organism thus leads an amphibious existence, tied down by occasional fertilisation through water, but with the resulting spores numerous, and disseminated in dry air.

The idea of this interpolation of the sporophyte as a factor in the evolution of archegoniate plants is not new. It was first brought into prominence by Naegeli as illustrating a principle of evolution in plants in his *Abstammungslehre* of 1885, though the fact of sterilisation of fertile cells to form additions to the sterile tissues in a plant possessing sexuality was well known at an earlier date (see Chapter XXXIV. : also Bower, *Primitive Land Plants*, Chapter XXIV., pp. 489-491). Such sterilisation was formulated by Naegeli thus : he states that " the phenomenon of reproduction of one stage becomes at a higher stage that of vegetation. The cells which in a simple plant are set free as germs and constitute the initials of new individuals, become in the next higher plant part of the individual organism, and lengthen the ontogeny to a corresponding extent " (*Abstammungslehre*, 1885, p. 352).

Such an interpolation of a sporophyte, hypothetically sketched here, is historically probable. Not only would an increased fertility be secured under variable circumstances but also, as Svedelius has pointed out, the multiplication of delayed acts of reduction will increase the number of nuclear combinations, and the plant thereby multiplies its chances of forming new heritable characters. Given conservatism in the mode of fertilisation, which is assumed to be inherited from an algal ancestry, *an interpolated alternation would be biologically stabilised as an outcome of migration to land.* There are no close links connecting any living green Algae with any archegoniate plants. The often-quoted genera, *Ulothrix* and *Coleochaete*, as also the isolated class of the Characeae, all stand on the haplobiontic plane, reduction being involved in the first division of the zygote. None of them has hit off the innovation of postponing reduction by the interpolation of a diploid soma fitted for subaerial life. The focal point of an interpolation theory is that certain littoral organisms did this. Once the step is taken the wide morphological gap between aquatic and subaerial vegetation explains itself : for the advancing archegoniate type would by originating a diploid soma have achieved three biological ends of supreme importance to any land-living organism : (i) a multiplication of possible combinations of heritable characters, giving the raw material for variation ; (ii) an opportunity for wide dissemination by air-borne spores ; and (iii) relief from dependence on repeated syngamy for numerical increase. The last was probably the most important for land-living plants. The superiority thus gained by the early plant-amphibians will have favoured the advance of the interpolated sporophyte, and the haplobiontic algal ancestors would be left hopelessly behind. Hence the wide gap between any green Alga and any living archegoniate plant.

The Land Habit.

No circumstance of life has more profoundly affected Organic Evolution than the progression from water to land. The further the comparative study of the simpler living beings is carried, the more the conclusion is confirmed that the birth-place of Animals and Plants was in the water. The comparative study of the Higher Animals and Plants demonstrates fully that it is in subaerial conditions that both have reached their highest development. Accordingly it becomes a question of supreme interest what are the effects impressed upon the organism by a Land Habit in place of its original aquatic surroundings. Certain factors stand out clearly. First, the mechanical requirement for support and maintenance of form. The body, whether of Animal or Plant, is nearly of the specific gravity of water. When immersed it is buoyed up, and provided the water be not itself in violent motion there is little demand on the organism for mechanical resistance. It is different, however, with subaerial organisms, which require not only to support their own weight in the lighter medium of air, but must also maintain their form under the impact of winds and other stresses incident to life on land. The larger the organisms the more insistent will be their demand. Such questions of mechanical strength have been taken up for Plants in Chapter X. and need not be discussed again here. A second factor is the need for protection of the protoplast against loss of water by evaporation. The evidence of its importance is seen in the very general presence of a cuticularised wall covering all the exposed surfaces, as well as in the simple fact that no Land-living Plant sheds its *ova* from the parent, as so many Algae do. A third factor is the need for internal aeration of the tissues wherever they assume large bulk. Another which has contributed to the moulding of Plant Organisms living on land is the requirement of a large surface of exposure to light and air for photosynthesis. Such factors as these must be considered in their effect on the Evolution of Organisms showing sexuality and alternation, as they adapted themselves to a Land Habit.

Among the various plants that show the Hofmeisterian alternation the search has naturally been for types of sporophyte which may be held as primitive. The smallest were those first selected as possible links for comparison: and in particular, *Riccia*. But in view of new detailed knowledge and of the fossil evidence, the trend of opinion is now towards Bryophytes in which both generations bore photosynthetic equipment fitted for subaerial life, as seen in the Anthocerotales (p. 475), the Sphagnales, and many Bryales (p. 476). The sporogonia of these possess stomata and internal ventilation, though frequently their stomata are imperfect and functionless. Such structure suggests for them a descending rather than an ascending scale of vegetative development. If this view be correct it will not be among the smallest and structurally simplest Bryophytes that we should seek for the key to the early history of the sporophyte in Archegoniate Plants.

A most important feature of the Land Vegetation is the *retention of the ovum* within the parent plant. It is enveloped in the archegonium. The archegonium itself is so constant in the earlier Land Vegetation that on it is based the name "Archegoniatae," so often applied collectively to the Mosses and Ferns. The explanation of the constancy of form and structure of the archegonium is to be found in the imperative need for the protection which it offers to the ovum, but without excluding access of the spermatozoid at the receptive period. The immediate consequences of this retention of the ovum are seen in the fact that Archegoniate Plants, or their Gymnospermic derivatives, form the bulk of the early Fossil Flora, and are an integral part of the Land Flora of the present day. But such organisms have not cut themselves wholly adrift from their original mode of life. They are still dependent upon external liquid water for the fertilising act itself, since it is through water that the male gamete moves to the egg. Moreover, the gametophyte with its relatively delicate structure is essentially dependent upon moist conditions for its normal growth.

Rise and Decadence of the Gametophyte.

The gametophyte has never made a real success of Life on Land, as measured by its size and structure. But this in itself makes the study of its partial success the more interesting. In Ferns and the thalloid Liverworts it is commonly a flattened thin or fleshy body of undifferentiated tissue, capable of self-nourishment and absorption from the soil. In extreme cases, growing in very moist and shaded conditions, it may even be filamentous, while the Alga-like habit may be accentuated in vegetative propagation by gemmae. The thalloid Liverworts also show this ; but in their larger forms the upper surface of the thallus may be alveolated, and the cavities occupied by photosynthetic tissue, so as to make them efficient for self-nutrition in dry air, as in the leaves of Flowering Plants (p. 472, Fig. 368). In the Mosses and leafy Liverworts, after a preliminary filamentous stage, a leafy plant is formed after the fashion of the leafy sporophyte. In the larger forms it may develop a conducting system, while sometimes, by involution of their surface, its leaves may acquire a structure efficient for photosynthesis combined with water-control (pp. 464, 465). But the size of these gametophytes is never great, and often very minute. Even in its most successful forms the sexual generation suffers from the disability of an imperfect internal ventilation. It is essentially semi aquatic, and often saves itself, as the Mosses do, by its power of dormant vitality under drought, and its readiness in surface-absorption whenever water is available. Thus constituted the gametophyte is a constant menace to the success of the Archegoniatae, as Land-living Plants. Finally, its dependence on external water for fertilisation has tended to tie the lower Archegoniatae down to limited habitats, from which they have never been fully emancipated.

Some of the most archaic plants that have survived, such as the Psilotaceae, Lycopods, and Ophioglossaceae, have underground prothalli with endotrophic mycorrhiza, and saprophytic nutrition (Chapter XII.) Incidentally it may be noted that internal ventilation is absent from these prothalli, even when their size is great. This is quite exceptional. It must suffice here to state these facts without detailed description. In view of the disabilities of the gametophyte for life on land, the underground habit and the form of saprophytic nutrition which these plants possess may well have been conditions which have determined their survival.

The difficulty presented by this dependence of the gametophyte upon external water has been met in the Higher Flowering Plants by a repetition of the method already so successful in the first conquest of the Land, viz. the *retention of the vulnerable part upon the parent.* First the ovum was retained, as in the Archegoniatae, then the whole prothallus which bears it, as in the Seed-bearing Plants. For this the way was prepared by the sexual differentiation of the spores. Within each of the phyla of Ferns, Lycopods, and Equiseta, this differentiation has taken place. In each case the original state was, as in all Bryophytes, *homosporous*, with all the spores alike, and commonly yielding on germination a bi-sexual prothallus (p. 500, Fig. 392). The first step is a separation of the sexes on distinct prothalli. A purely male prothallus has no permanent duty, but only the temporary function of producing spermatozoids. It may therefore, and it does, remain small. But the female prothallus has both to produce ova and to nourish the embryo after fertilisation. This can best be carried out by a large prothallus, which will develop better from a well-nourished spore. This is the physiological *rationale* of the origin of the megaspore as distinct from the microspore, as seen in *Selaginella*, which is heterosporous (p. 514). The same condition is also seen in certain Ferns (*Marsilia*, *Azolla*), in many fossil Lycopods, and occasionally in Equiseta also. But still the megaspore in these plants is shed from the parent before fertilisation, and is then dependent on its own resources. The longer the period of connection with the parent the better. *A further advantage was then gained by retention of the megaspore itself upon the parent plant until the embryo is far advanced.* The sporangium which thus retains its megaspore is called an *ovule*, and this matures into the *seed*, which is characteristic of all the Higher Plants of the Land (p. 521). The prevalence of the Seed-habit is the token of its success.

While a certainty of protection of the prothallus and of continued nutrition of the embryo is thus secured by retention of the megaspore, or embryo-sac, upon the parent, the steps of progress involved have reacted adversely upon the gametophyte generation. The separation of the sexes tended to relieve it of the necessity for self-nutrition. Provided the microspores are numerous, and each has a sufficiency of material to form an antheridium and spermatozoids, that would meet the requirements, and little or no vegetative tissue is needed. This condition is characteristic of heterosporous plants. It is seen in *Selaginella* (p. 517, Fig. 411), and in the pollen of Gymnosperms and Angiosperms with their vestigial male prothalli (Figs. 222, 421). On the other hand, the megaspore requires to be well nourished, in the interest of the archegonia, and of the embryo which each will bear. But it receives its supply from the parent plant, rather than by its own self-nutrition. Thus in the case of a megaspore of *Selaginella* the female prothallus is little more than a storage tissue, and a basis for archegonia (Fig. 412, iv.). Self-nutrition is reduced, or entirely absent as in the Gymnosperms ; and, finally, in the Angiosperms the female gametophyte is so transformed that it may be difficult to homologise the contents of the embryo-sac at all with a female prothallus (Fig. 216).

The spermatozoid motile in water remained, however, as the means of fertilisation even after the adoption of the Seed-habit. It is still seen in the Ginkgoaceae and the Cycads, though its unpractical nature is evident (p. 527). The last step of emancipation from the original aquatic method of propagation was the substitution of the motile spermatozoid by the non-motile gamete delivered by the pollen-tube (Figs. 226, 424). Thus the most critical point of each life-cycle, viz. fertilisation, was finally adapted to Life on Land. And so by a series of steps the gametophyte is reduced, altered, and in some cases almost obliterated. It has paid the penalty of its inability to adapt itself thoroughly to sub-aerial conditions. The climax of the gametophyte on land is attained in the homosporous Mosses and the leafy Liverworts. It appears of independent, though limited growth in the homosporous Ferns. But with heterospory it fades into insignificance, and in the Higher Seed-Plants it survives as a mere relic.

Rise of the Sporophyte.

Although Brown Algae such as the Laminariales afford evidence of the *rise of the sporophyte generation* it is *in the progressive series of Land-living plants* that this phenomenon is most strikingly disclosed. By adaptation of form and structure it has met, in its highest terms successfully, the requirements for mechanical strength, for protection under drought, for exposure of a large surface for photosynthesis, and for ventilation of extensive nutritional tissues. In all these respects it is the superior of the gametophyte, and perhaps the structural feature that has contributed most to its supremacy is the ventilation-system of intercellular spaces, controlled by stomata at their exits to the open air. This differentiates the sporophyte from the gametophyte more clearly than any other structural character, and stamps it as adapted to sub-aerial life. *The end of its vegetative existence is the formation of spores* (*tetraspores*). The more numerous these are (other things being equal) the better the chance of survival of the species, and of its spread. The vegetative development may be regarded as a means to that end, and in homosporous forms its nutritive capacity imposes a natural limit on spore-numbers. The dispersal of the spores is dependent in primitive land forms upon a dry atmosphere. This is in strong antithesis to the necessity for external liquid water for fertilisation, which is the end of their gametophyte.

The sporogonium of the Bryophyta is usually held to represent the most primitive type of sporophyte among Land-living Plants, and recent discoveries of very early fossils tend to support that opinion. Its limited plan of construction, its ephemeral character, the absence of appendages, and its dependence throughout life upon the gametophyte, are all indications pointing in the same direction. Moreover, the fact that the spore-production in each sporogonium arises from one undivided sporogenous tissue, not from a number of distinct sporangia, also points to the same conclusion. Within the Bryophyta the various forms may be seriated so as to give probable indications of progressive advance in various important characters. These suggest that in very primitive types apex and base were defined early. A sterile stalk and central columella were acquired, and later, specialised methods of spore-distribution. These rose to high efficiency in the higher Mosses (Figs. 355, 367). A well-formed epidermis with stomata is found in some of them, while beneath this lie assimilating tissues as well ventilated as in the leaves of Vascular Plants (Fig. 364). Nevertheless, the simple form, the limited apical growth, the absence of appendages, and above all the want of any direct connection with the soil, stamp even the most elaborate sporogonium as an only partially efficient structure. To achieve higher development it would be necessary to break away from so restricted a plan, which in itself is only practically possible where the gametophyte shows high elaboration, so as to supply the nourishment the sporophyte cannot wholly acquire for itself.

The Homosporous Pteridophytes are free from such restrictions. The features in which they show superiority to the Bryophyta as spore-producing plants are: (i) an unlimited capacity for apical growth; (ii) the possession of lateral appendages; (iii) a direct access to the soil by a root-system; (iv) an improved conducting system; (v) a well-ventilated photosynthetic system, with elaborate external form, and more complete differentiation of vegetative from propagative regions of the plant; (vi) the formation of numerous distinct sporangia; and (vii) the production of the sporangia not simultaneously but in succession, or even delayed, so as to spread the physiological drain over a long period. Possessed of these features the sporophyte develops as an independent, self-nourishing organism, unlimited in plan, in period of life, and in power of spore-production. It is the sphere of Special Morphology to trace the lines along which these various features may have been acquired. But the result of them is seen in varying proportion and efficiency in any ordinary Fern, or Lycopod, or Horse-tail. These are characteristic examples of the primitive Vascular Plants of the Land. They depend upon the vegetative development of a freely-rooted sporophyte for their legitimate success, while still retaining their *homosporous state.* In point of size the acme of achievement of the Homosporous Pteridophytes now living is to be found in the Filicales; though they still show for the most part a leafy shoot which serves general purposes, and is not strongly differentiated into vegetative and propagative regions.

It was the adoption of the *heterosporous state* and the retention of the megaspore and its prothallus within the megasporangium, or ovule, that paved the way for the full possession of the Land by Seed-bearing Plants. Plants thus finally broke away from dependence on external water for their fertilisation. Seed-production is carried on in a compact *Strobilus*, or *Flower*. Evidence of the steps of segregation of the "general purposes shoot" into distinct nutritive and propagative regions may still be traced in favourable cases (see p. 278). These regions once established took each its own independent line of specialisation in the evolution of Seed-bearing Plants. The vegetative region which appears first in the individual life commonly develops normal foliage; but under special conditions it may become xerophytic, scandent, parasitic, or saprophytic, the adaptive nature of the change being usually evident (Chapters XI., XII.). The propagative region or Flower also became specialised in relation to its functions. It appears later, and it is distal, since nutrition is necessary before propagation can be carried out. This distal position, while it removes the flower further from the water-supply, offers the best opportunity for transfer of pollen, whether by wind or by animal agency. The functions of the Flower are: to produce sporangia; by its structure to offer facilities for pollination, with fertilisation as its consequence; to protect and nurse the new germs up to the period of ripeness of the seed; and, finally, to secure seed-dispersal. The means by which these ends are attained are almost infinitely various. Examples are described at length in Appendix A. It is the high degree of adaptability of the Seed-bearing Plants to subaerial conditions, so as to secure these ends, that has given them their supremacy. The pollen-grains, usually dry and dusty, retain essentially the character of the microspores of the Pteridophyte. They thus allow of either self-pollination or of inter-crossing in various degrees, in organisms themselves non-motile. Commonly they are exposed at the time of flowering to dry air and full sunlight. The antheridial mother-cell within each grain is protected by the cuticularised and often coloured coat of the grain from injury by drought or intense light: its contents are not set free into water as in the Amphibious Pteridophytes, but flow into the security of the pollen-tube: there the male gametes are formed and are passed on to their destination as the tube grows (Chapter XVII.). Similarly, the ovum is never exposed. Its protection against all risks is secured by a succession of tissue-envelopes. The carpel, one or two integuments, and finally the nucellus all take their part in this duty. The ovum itself, a primordial cell not differing essentially from the exposed egg of *Fucus*, thus deeply sunk in living tissue, is immune to the risks of subaerial life. It is in a position, when fertilised, to draw its supplies during the nursing period from the embryo-sac, and the surrounding envelopes. Such conditions, combined with the effective and often elaborate means of distribution of the ripe seeds already described (Chapter XIX.), account for the Seed-Plants becoming the chief constituent of Land-Vegetation. The disabilities of the gametophyte for land-life have been evaded. In the more adaptive sporophyte the most vulnerable points in the cycle of life, viz. the period of fertilisation, and the first stages of development of the embryo are effectively protected. *Thus the sporophyte has become virtually the Plant of the Land, and the gametophyte a mere vestige.*

A strong antithesis has been drawn between the relative failure of the gametophyte and the ultimate triumph of the sporophyte in subaerial life. The two generations differ normally in chromosome-number. This seems to suggest that a higher potentiality and initiative in variation lies with the diploid state. It may not be possible to lay it down as a general proposition that a double number of chromosomes is an index of greater power of adaptability; but it is a significant fact that the highest somatic evolution both in Animals and Plants has been attained by diploid, not by haploid tissues. The gametophyte is the sexual generation, and the sexual organs are borne by it. In this it stands in strong antithesis to the sporophyte, which is a non-sexual or neutral generation, by nature and by origin. But the steps in the obliteration of the gametophyte, and in the evolution of the seed have been accompanied by a tendency for sexual differentiation to encroach more and more on the morphology of the sporophyte generation. This will be apparent on comparison of the life-cycle of a homosporous Fern (Fig. 400, p. 506) with that of a Flowering Plant (Fig. 257, p. 335). The final culmination of this is found in those Seed-Plants which are diœcious, such as the Willow, or the Yew (Fig. 258, p. 336). In these some individuals bear only staminate, others only pistillate flowers, and the plants are thus ranked as "male" or "female," though in point of fact they represent the neutral generation. The end result is thus seemingly a parallel between the Higher Plants and the Higher Animals as regards sexuality. In both the individual appears to be either "male" or "female." But this similarity is superficial rather than real, for it has been attained along quite distinct evolutionary trends in the two Kingdoms. In the Higher Animals there is a true sex-difference between individuals, the one producing male, the other female gametes. In the Flowering Plants the individual is the neutral sporophyte, which does not itself produce gametes. But in the course of Descent certain distinctive features relating to sex have become increasingly evident in the sporophyte or neutral generation. Accordingly the Flowering Plant has secured such advantages as follow from sex, through its retention of the sexual generation within it.

It thus appears that there are three forms in which somatic development may be related to the nuclear cycle characteristic of organisms possessing sexuality: (i) that in which a haploid soma intervenes between the events of reduction and syngamy: this is characteristic of haplobiontic Algae; (ii) that in which there is present not only the haploid soma as before, but also a diploid soma which intervenes between the events of syngamy and reduction: this is characteristic of the Archegoniatae, and the derivative Seed Plants; it is also seen in some Thallophytes, and is typical of the diplobiontic Algae; and (iii) that in which a diploid soma intervenes between the events of syngamy and reduction, there being no haploid soma: this is characteristic of Animals, and of certain Algae, e.g., *Fucus*, and members of the Siphonales (Green Algae). The fact that a haploid soma may exist without the diploid, while a diploid may exist without the haploid, appears to strengthen the view that the two phases seen in the Archegoniatae differ in the history of their origin: and to support for them the theory of interpolation, of which that historical difference is an essential feature. It is a recognised principle in Morphology to fix the attention upon those features that are most constant in their occurrence, and to accord to them the higher importance. Syngamy and its complementary Reduction thus take a prior place, while somatic developments appear as inconstant incidents in a more stable nuclear cycle.

SUMMARY.

The sexual act probably originated polyphyletically among primitive Algae, in some of which an early differentiation of the gametes can be traced by comparison with allied forms (Fig. 275). The two leading events of the sexual cycle are Syngamy and Reduction. In haplobiontic plants such as the Characeae they follow in direct succession. Here reduction takes place in the first division of the zygote: in *Chara* the zygote develops directly into a new haploid individual like the parent. There is thus no alternation in the full Hofmeisterian sense.

What gave rise to the Hofmeisterian Cycle appears to have been a postponing of the event of reduction and, by the interpolation of a diploid soma, the fitting of a new phase into the cycle of life. This innovation once established was seized upon in the Evolution of Plant Life on Land; for it brought important advantages, which are detailed on p. 547. The final result has been the establishment of a Land Flora such as we see living on any land surface today; and it is dominated by the diploid soma.

CHAPTER XXXV.

HEREDITY AND VARIATION

Sexual Reproduction.

In the great majority of Plant Organisms certain sexual cells called *Gametes* are produced, which fûse in pairs. The process is called *Syngamy*, or *Sexual Fusion*. The result of it is the production of a single cell, the *Zygote*, which forms the starting point for a new individual. Though such syngamy is a very wide-spread fact among living things, whether Animals or Plants, it is not universal. Some primitive organisms are without it. The whole series of the Schizophyta are examples of this, while sexuality is rare or doubtful in *Euglena* and *Pleurococcus*. In certain Plants also of advanced organisation syngamy may be absent, as in some Flowering Plants and Ferns.

A comparison of related organisms low in the scale, which show syngamy, suggests that in the first instance the fusing gametes were alike in size and behaviour, though more or less distinct in their origin. Such cells are called *isogametes*, and the process of their fusion is described as *conjugation*. It is seen in both Animals and Plants of low organisation. This condition, where the gametes show no clear distinction of sex, is believed to represent a primitive state from which distinction of sex was later derived. The isogametes themselves may be motile or non-motile. The former is seen typically in various green and brown Algae: *Ulothrix* (Fig. 270, p. 365), *Acetabularia* (Fig. 275, p. 370), and *Ectocarpus siliculosus* (Fig. 284, p. 380) are cases in point. Conjugation of non-motile isogametes occurs in the Conjugatae, such as *Spirogyra* (Fig. 277, p. 373).

If two organisms, each consisting of only a single cell, fuse to form one, the immediate result is a diminution in number to one half. This occurs in various instances, and *Spirogyra* is a case in point, for each cell of its filament is properly recognised as an individual. The same occurs in various other unicellular Animals and Plants. As these are probably primitive, they suggest that in the first instance syngamy was not a means of increase in number of individuals, though in all the Higher Plants and Animals this appears to be its natural consequence. Some believe that the chief advantage following on sexual fusion in such simple organisms lay in nutrition. If during repeated fissions cell-division was more rapid than nutritive recuperation, then fusion of two cells would be a possible form of recovery. But such fusion appears to bring with it also a stimulus to fresh activity of growth and division, which may break out at once, though in primitive organisms it follows usually after a period of rest. With this fusion there follows also the pooling of such qualities as the fusing cells themselves possess. So far as these qualities can be transmitted to the offspring, the mechanism of fusion offers the opportunity for it (see later) ; and it is significant that the fusing gametes are as a rule distinct in origin. For instance, the pairing gametes of *Ulothrix* (p. 365), or of *Ectocarpus* (p. 380), originate from different gametangia ; and the distinctness of origin is still more marked in many plants higher in the scale. It seems probable that such advantages as these, viz. nutritive recovery, stimulus to further development, and hereditary transmission, have favoured a constant recurrence of syngamy. *In the long run hereditary transmission has been the most important.*

DIFFERENTIATION OF GAMETES.

Fusion of isogametes once established led to sexual differentiation in many distinct phyletic lines, both of Animals and Plants. Comparison of closely related forms is the basis of this conclusion ; and a particularly convincing example is seen in the Brown Algae (pp. 380-382). The distinction is there found to be first a difference in behaviour rather than of form (*Ectocarpus siliculosus*). Next, a difference in size as well as in behaviour marks the female as distinct from the male, as in *E. secundus*. In *Cutleria* that difference is still more accentuated, and the larger female gamete soon loses its motility. In *Fucus* the difference in size is very great indeed, and the large female egg is never motile at all. Various other phyletic lines could be quoted showing similar examples of sexual differentiation (Fig. 275). The question naturally arises why should such progressions exist in a plurality of distinct phyletic lines? That the differentiation of gametes has occurred more than once indicates a probability that some real advantage had attended it.

The advantage appears to lie in the fact that the larger the amount of nutriment embodied in the egg, the better nourished the offspring will be in its first stages, and the better accordingly will be the chance of its passing successfully through the dangerous risks of youth. But the larger the egg the less mobile it will be. Even in the liquid medium into which the eggs of Algae are often shed, a large body is less easily moved than a small one. We naturally associate with this the fact that the larger eggs have lost their motility. This is, however, immaterial so long as the spermatozoids remain small and actively motile, provided that the egg can influence their movements, and so act as a centre of attraction to them. It has been seen that the eggs are able to do this (p. 382). Such advantages as follow from the stimulus of fusion, and the pooling of the hereditary factors of the two sexual cells can still be secured by these means. Thus the nett advantage lies with the plant which can, without sacrificing the benefits that follow from syngamy, secure also for its offspring an increased probability of successful germination. Conjugating organisms, with their small equivalent gametes, may be regarded as a plant-proletariat that produces numerous offspring with little physiological capital; so that each individual must depend chiefly upon its own efforts. The organism that shows differentiation of its gametes with an enlarged well-nourished egg is like a capitalist, whose progeny starts life well furnished with a capital of reserve food. Other things being equal, ultimate success will lie with such organisms. Both Kingdoms of Living Beings show how successful the results of differentiation have actually been: for all their higher terms have differentiated gametes.

A large naked egg, such as that of *Fucus*, may be a successful enough means of propagation in water. But it could not develop into an embryo exposed to the drying influence of the atmosphere. A necessary condition of Life on the Land is thus the protection in one way or another of the egg and the embryo. In the Evolution of Land-living Plants and Animals this necessity has played a leading part. The result is seen in the various forms of *internal embryology*: that is, the envelopment of the egg and of the embryo within the tissues of the parent. This brings also the collateral advantage of its continued nutrition. How this has worked out in detail in Mosses and Ferns, and ultimately in the Seed-Plants, has been discussed in Chapter XXXIV. Here it must suffice to remark that the subsequent changes seen in such Plants have to do with the details of transmission and of nursing of the gametes. They do not involve any further distinction of the male and female gametes, in respect of size or structure, than that already established among the Higher Thallophyta.

The Nucleus and Heredity.

To form an opinion on the function of the gametes in sexual propagation, a knowledge of their structure is necessary ; also of the relation of their structure to that of other cells of the plant-body. The nucleus, which takes a prominent part in the process of fertilisation, and itself constitutes almost the whole of many spermatozoids, will specially claim attention. Moreover, the facts already recognised in Chapter II, p. 20—that every nucleus is derived from a pre-existing nucleus, and that in ordinary cell-division the parent nucleus is partitioned into two exactly corresponding halves—suggest that the nucleus has a special relation to the facts of heredity. The detail of the process of nuclear division will then be the natural starting point for the further discussion of Heredity and Variation.

NUCLEAR DIVISION

The Resting Nucleus.

The " resting nucleus " of a vegetative cell—that is the nucleus when not in a state of division—has the appearance of a meshwork (*nuclear reticulum*) of fine threads embedded in a clear ground-substance (*nuclear sap*) and delimited from the cytoplasm by an exceedingly delicate *nuclear membrane* (Fig. 428, *a*). The stains commonly used in cytological studies do not affect the whole of the meshwork to the same extent, certain parts becoming more heavily stained than the rest. It has therefore long been customary to describe the nuclear reticulum as composed of faintly staining *linin* with localised masses of deeply-staining *chromatin*. But there may be doubt as to the morphological distinctness of these two components. Enclosed in the nucleus are one or more denser, rounded, heavily staining bodies, the *nucleoli*.

FIG. 428.

Mitosis in meristematic cells of the root-tip of the Onion (*Allium Cepa*). (× 1430.) *a*, resting nucleus; *b*, *c*, prophase; *d-e*, transition from prophase to metaphase; *f*, metaphase; *g-i*, anaphase; *j-l*, telophase. (After Belar.)

MITOSIS AND MEIOSIS.

There are two distinct normal methods of nuclear division: (*a*) *mitosis* or somatic division and (*b*) *meiosis* or reduction division. Mitosis takes place in the cells of the vegetative plant body (somatic cells) by which it increases the number of its cells during growth. Meiosis is the process, comprising two nuclear divisions of special type, which initiates the gametophyte (haploid) stage in the life-cycle of any plant that reproduces sexually.

MITOSIS.

Mitosis is a complicated process and for convenience of description may be regarded as taking place in a series of stages to which distinctive names have been given.

During *prophase* (Fig. 428, *b* and *c*) the chromosome reticulum becomes resolved into a definite number of *chromonemata*; these are long slender threads, more or less twisted, and double. The threads gradually become shorter and thicker and finally take the form of V- or L-shaped deeply staining rods, the *chromosomes*. Each chromosome, like the chromonema from which it is derived, is a double structure, being divided lengthwise into two equal halves, the *chromatids*.

In the second stage or *metaphase* (Fig. 428, *f*), the chromosomes arrange themselves in the *equatorial plane*—i.e. the plane of division of the cell—with the point of the V or L facing inwards. At the same time delicate protoplasmic threads (*spindle fibres*) appear in the dividing cell and group themselves into a spindle-shaped figure (Fig. 428, *g*) placed at right angles to the equatorial plane. The chromatids are of uniform thickness, except for certain constrictions, the number and position of which are specific for each chromosome; there is always at least one constriction, the attachment-constriction or *centromere*, which is believed to control the movements of the chromatid.

At the third stage or *anaphase* (Fig. 428, *g-i*), the halves of each chromosome (chromatids) separate and pass to the opposite poles of the spindle. It is thought that this separation is initiated by a mutual repulsion between the centromeres.

The final stage or *telophase* (Fig. 428, *j-l*) is essentially a reversal of prophase. The "daughter chromosomes," as the separated chromatids may now be called, lengthen into slender threads which become entangled together and reconstitute a "daughter nucleus" at each pole of the cell. In the resting stage the chromosomes lengthen and become threadlike, and again split lengthwise in preparation for the next division.

The nucleoli and the nuclear membrane disappear during the early stages of mitosis and reappear at telophase. The new cell-wall most commonly arises as a thin lamella ("middle lamella" or "primary cell-wall") within the *cell-plate*, a specialised layer of the cytoplasm which becomes gradually differentiated during telophase in the equatorial plane.

The outstanding features of mitosis are three.

(1) For the cells of each kind of plant (or animal) there is a definite number of chromosomes which normally remains constant for all the somatic divisions.

(2) Each chromosome separates into exactly equal halves (chromatids) which are distributed to opposite poles of the dividing cell.

Hence, (3) each daughter nucleus receives an exactly equal share of the chromosome material of the parent nucleus (Fig. 429).

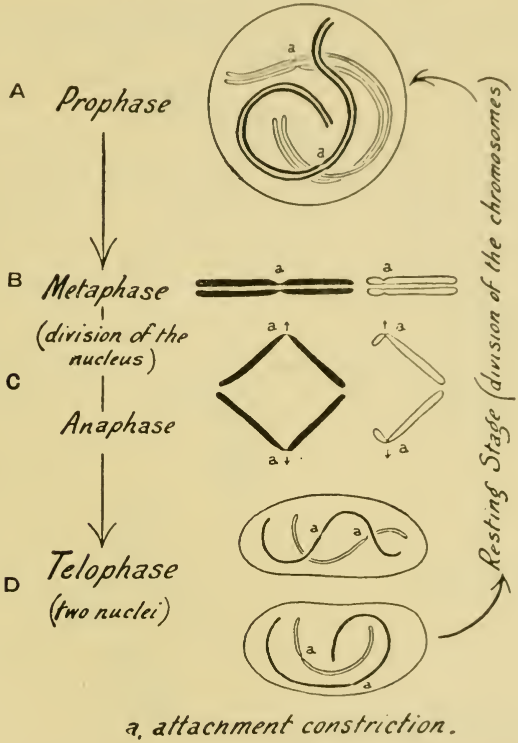

FIG. 429.

Diagram showing the changes undergone by two chromosomes in the course of mitosis. (From Crane and Lawrence after Darlington.)

If, as is generally assumed, the heritable qualities of the organism are localised in the chromosomes—as so-called *genes*—mitosis clearly provides a mechanism by means of which these qualities are transmitted unchanged at each somatic division. The fact that new individuals produced by vegetative propagation (Chapter XIII) exactly resemble the parent plant bears out this conclusion.

MEIOSIS.

The formation of tetraspores (such as pollen-grains, spores of Pteridophytes and Bryophytes, tetraspores of Rhodophyceae, ascospores and basidiospores) involves two divisions of the nucleus accompanied by one division of the chromosomes ; as a result, the chromosome number is halved. Since four tetraspores are produced from each spore mother-cell, the whole process is often described as a *tetrad-division*.

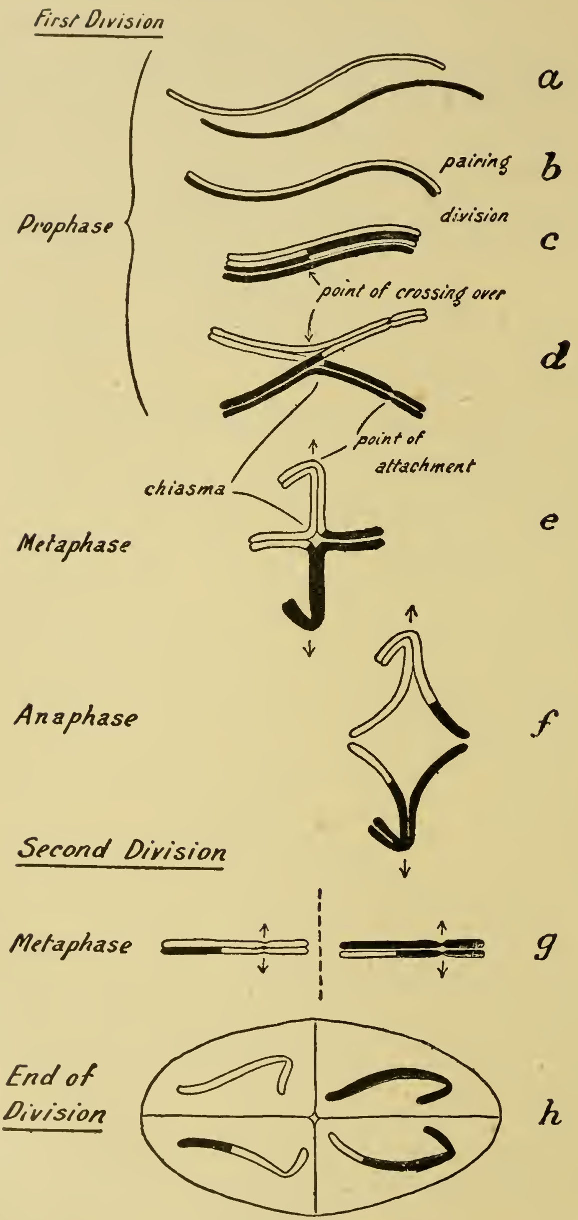

FIG. 430.
Diagram of Meiosis. For explanation, see text. (From Crane and Lawrence after Darlington.)

The essential features of meiosis are illustrated in Figs. 430 to 433. As in the case of mitosis it is convenient to distinguish a number of stages in this very complicated process.

Heterotype Division : Prophase.

In the first stage (*leptotene*) (Fig. 430, *a*, 431, 1) the chromosomes appear as long slender threads with a general resemblance to the chromonemata seen in the first stage of mitosis, except that the threads are single instead of double.

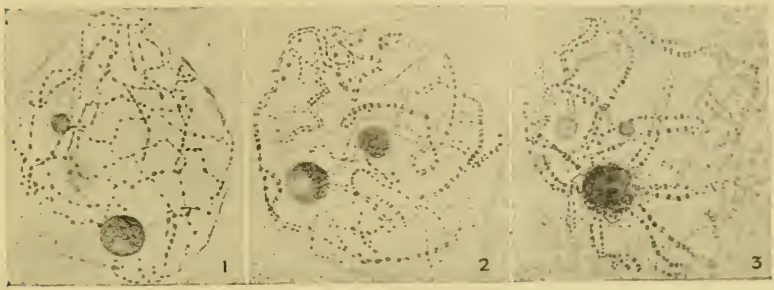

FIG. 431.

Meiosis—early stages in *Trillium erectum*. 1, leptotene ; 2, zygotene ; 3, pachytene. (From Sansome, after Huskins and Smith, by courtesy of Scientific Horticulture.)

At the second stage (*zygotene*) (Fig. 430, *b*, 431, 2) the chromosomes become associated in pairs. This association is not a random one ; the chromosomes that pair are the corresponding, similarly constituted or *homologous* ones, one of each pair being derived from the male gamete, and the other from the female gamete, which initiate this sporophyte generation.

In the third stage (*pachytene*, Fig. 431, 3) the paired chromosomes appear shorter and thicker as a result of twisting round one another.

At the fourth stage (*diplotene*, Fig. 430, *c*, *d*) the chromosomes split lengthwise into halves so that each pair now consists of four intertwined threads (chromatids), held together in pairs by the centromeres, which do not split. At this stage, or immediately prior thereto, the members of a homologous pair interchange some of their parts, a process known as *crossing-over*, only two out of the four chromatids breaking and rejoining at any one point. The homologous chromosomes then begin to separate, but not completely, being still held together at certain points—*chiasmata*—as a result of crossing-over (Fig. 433). These four stages collectively constitute *prophase*.

Metaphase.

During the fifth and sixth stage (*diakinesis* and *metaphase*) the four chromatids continue to shorten and thicken ; the nucleoli disappear ; a nuclear spindle is formed ; and the chromosome-pairs arrange themselves in the equatorial plane.

At the seventh stage (*first anaphase*, Fig. 432, 6) the paired chromosomes part company, two chromatids—held together by the unsplit centromere—passing to one pole of the cell and two to the other pole (Fig. 430, *f*).

Telophase.

At the eighth and final stage of the first division (*first telophase*, Fig. 432, 7) two daughter nuclei are formed and pass into a short resting stage (*interphase*).

Homotype Division.

A second division follows quickly in which the centromeres now split ; as a consequence the process closely resembles an ordinary mitosis, the chromosome-halves passing to opposite poles and thus into different tetraspores (Fig. 432, 8–10).

The outstanding points of meiosis are :

(1) It involves two nuclear divisions with only one division of the chromosomes. Hence,

(2) It leads to a halving of the chromosome number (reduction).

(3) Interchange of parts (crossing-over) occurs between the chromatids of each pair of homologous chromosomes.

(4) The first division of meiosis distributes the four chromatids of each pair of homologous chromosomes, so that each daughter-cell receives two.

(5) The second division distributes these two chromatids so that each granddaughter-cell (tetraspores) receives one.

(6) The four chromatids of each chromosome pair are thus distributed *at random* among the four members of a tetrad of tetraspores.

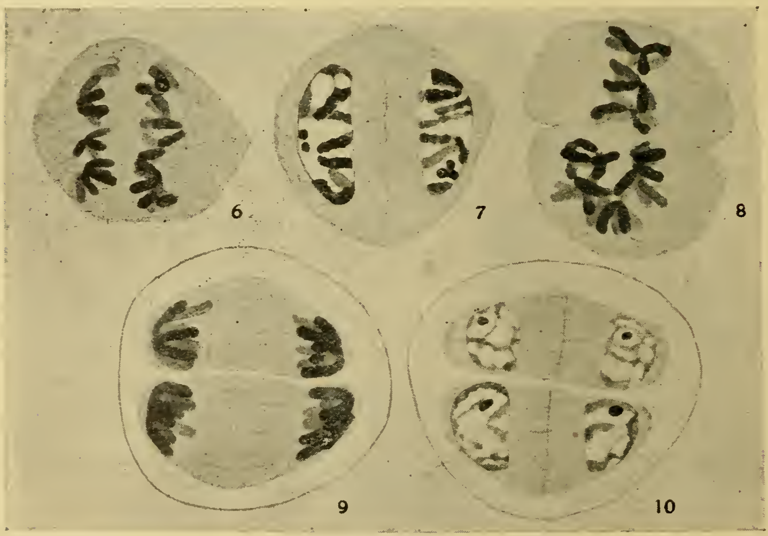

FIG. 432.

Meiosis—later stages in *Pinus Banksiana*. *1st Division* : 6, anaphase ; 7, telophase. *2nd Division* : 8, metaphase ; 9, telophase ; 10, four pollen nuclei. (From Sansome, after J. M. Beal, by courtesy of Scientific Horticulture.)

Provided that each type of tetraspore is viable, the gametophytes and ultimately the gametes formed by them will exhibit the same distribution of genes as the spores from which they are derived. The whole gametophyte generation and the gametes themselves will have the reduced or haploid number of chromosomes.

Syngamy is the fusion of gametes to produce a zygote. Notwithstanding the fact that in many Algae the gametes are of the nature of primordial cells with a considerable amount of cytoplasm, and in higher types, such as Mosses, Ferns and Seed Plants, the cytoplasm of the male gamete is reduced to negligible proportions, *fertilisation is essentially a process of nuclear fusion.* The first division of the zygote is an ordinary mitosis (apart from cases like that of *Spirogyra*, where the zygote itself undergoes meiosis on germination), with equal distribution of chromosome-halves (chromatids) ; and all subsequent vegetative divisions follow the same course. As both the male and the female gametes are haploid, syngamy restores the full number of chromosomes. The diploid sporophyte is thus initiated, and the normal nuclear cycle, diploid sporophyte—haploid gametophyte—diploid sporophyte, may be repeated indefinitely.

FIG. 433.

Camera lucida drawings of chromosomes in the prophase of meiosis. A, *Lilium pardalinum* ; B, *Fritillaria lanceolata.* Note the correspondence between the size and sequence of the particles of the pairing chromosomes. In B the four strands (chromatids) are clearly seen. There is one chiasma in each case. (From Crane and Lawrence after Belling.)

Chromosome Complement (Karyotype).

It has already been noted that the chromosome number is constant for all the somatic divisions of any normal plant. Thus the Garden

Pea has 14 chromosomes, the Gooseberry 16, Maize 20 and the Tomato 24; these, of course, are the diploid numbers, each chromosome being present in the sporophyte cells in duplicate. The actual chromosome number, though characteristic of a particular species, or race, is apparently not in itself of special significance; that is to say, there is no correlation between chromosome number (or chromosome size) on the one hand, and taxonomic position or grade of evolution on the other, at any rate in so far as the major taxonomic groups are concerned. The *constancy* of the chromosome number, however, is important as evidence that the chromosomes, though not ordinarily distinguishable as such except at nuclear division, do nevertheless retain their individuality during the resting stage. Further support for this view is provided by the many cases in which the several pairs of chromosomes are visibly—i.e. morphologically—distinct; an example is shown in Fig. 434. The type of chromosome complement characteristic of a race or individual has been termed its *karyotype.* Comparison of karyotypes within limited circles of affinity has thrown light on problems of taxonomy and evolution (see below under "polyploidy," pp. 581-584).

FIG. 434.

Somatic chromosome complements (karyotypes) of three species of *Muscari*—*M. longipes*, *M. tenuiflorum* and *M. monstrosum.* (From Sharp's *Introduction to Cytology*, by courtesy of the McGraw-Hill Book Co., Inc. After Delaunay, 1926.)

HYBRIDISATION.

If the gametes involved in producing a succession of generations were uniform throughout in their origin and hereditary constitution, the organisms produced might be expected to remain constant. But the parents that produce the gametes are not themselves as a rule exactly alike, and the gametes produced by them will therefore differ. The dissimilar can breed together within certain limits. Members of races or varieties commonly interbreed freely; sometimes species and even genera are interfertile. The artificially produced generic hybrids of certain Orchids are a well-known feature of horticultural shows; and other cases are known of fertile hybrids arising from crosses between species of distinct genera, such as the "*Raphanobrassica*" derived from a cross between Radish and Cabbage. The breeding together of members of distinct races, species, etc., is called *hybridisation*, and the offspring are known as *hybrids*. Since the experimental study of hybrids has thrown much light on the mechanism of *inheritance*, it will be treated in some detail; but before this can be done, the nature of *variation* must be briefly considered.

The characteristics of organisms have been classed under two heads: those which are heritable and those which are not. The latter category includes such features as can be related directly to the impress of external circumstances upon the parent; the former comprise those features which cannot be so related. Mutilations can be quoted as examples of characters not transmitted; likewise the immediate accommodations of the growing parts to the impact of gravity, light, etc., such as have been described in Chapter IX. However effective these may appear to be in determining the mature form of the parent, there is no reliable evidence that such *modifications* are transmitted to the offspring. But there are other larger or smaller deviations from type, appearing suddenly and individually, which have not been referred directly to known causes and are found to be heritable. Individuals showing variation of this type are called *mutants* and the process of their formation *mutation*. It may be emphasised again that modification leaves no permanent impress upon the organism so as to affect its gametes. On the other hand, it has now been established with certainty that mutation is the chief source of the variations upon which Natural Selection can work, and that it has therefore played an important part in Evolution.

MENDELIAN SEGREGATION.

It has long been known that offspring produced by the crossing of closely related forms, whether of animals or plants, do not always come true to type. But it remained for Mendel to discover, in the latter half of the nineteenth century, the laws, since verified by many observers, which operate in the distribution of the characters of the parent forms among the progeny. The following description of one sample of Mendel's experiments is based, with Professor Punnett's permission, upon passages in his book on Mendelism.

In the selection of a plant for experiment Mendel recognised that two main conditions must be fulfilled. In the first place the plant must possess evident differentiating characters; and, secondly, the experimental plants must be protected from the influence of foreign pollen during the flowering period. In *Pisum sativum* Mendel found an almost ideal plant to work with. The flowers are self-fertilising, whilst complications from insect-interference are practically non-existent. There are numerous varieties of the Garden Pea exhibiting characters to which they breed true. Mendel selected a certain number of such differentiating characters and investigated their inheritance *separately* for each character. Thus in one series of experiments he concentrated his attention on the stature of the plants. Crosses were made between tall and dwarf races, which previous experience had shown to come true to type with regard to these characters. It mattered not which was the pollen-producing and which was the seed-bearing plant; in every case the result was the same. Tall plants only resulted from the cross. For this reason Mendel applied the terms *dominant* and *recessive* to the tall and dwarf habits respectively. Seeds collected from the hybrid plants (F_1 generation) and sown the following year, gave both tall and dwarf plants among the progeny (F_2). Every individual was either tall or dwarf, and no intermediates appeared. In one series of experiments Mendel obtained 1064 F_2 plants, of which 787 were tall and 277 dwarf; that is the dominant and recessive characters occurred in the second generation of hybrids (F_2) in the approximate proportion of 3 : 1.

In the following year seeds from the F_2 generation were sown as before and produced the F_3 generation. From the seeds of the dwarfs came only dwarfs, *i.e.* the recessive character bred true. The tall plants however, of the F_2 generation now revealed themselves as being of two kinds. Some of them produced seed giving rise to tall plants only; others formed seed from which sprang both talls and dwarfs in the ratio of 3 : 1. The former, which evidently carried only the tall character, are "pure" dominants; the latter, which carried both tall and dwarf characters, are "impure" dominants. By observation of the F_3 and subsequent generations, Mendel showed that the pure dominants and the recessives always bred true, resembling in this way the original parents. The impure dominants, on the other hand, always showed *segregation*, giving dominants and recessives in the constant ratio of 3 : 1. Since the pure dominants are only half as numerous as the impure dominants, it follows that the impure dominant on being self-fertilised, produces as offspring pure dominants, impure dominants and recessives in the proportion of 1 : 2 : 1. The case of only one pair of characters has been considered here; but Mendel showed that the rule holds good for all the various pairs of differentiating characters (seven in all) studied by him; and since his time his conclusions have been verified in numerous instances both in plants and in animals.

A general scheme may be constructed to show the result of crossing individuals which each bear one of a pair of differentiating characters. If **D** represent the pure dominant; if the impure dominant, which cannot be distinguished from it by appearance, be represented by (**D**); and if **R** represent the recessive, then the following will be the scheme of inheritance (Fig. 435).

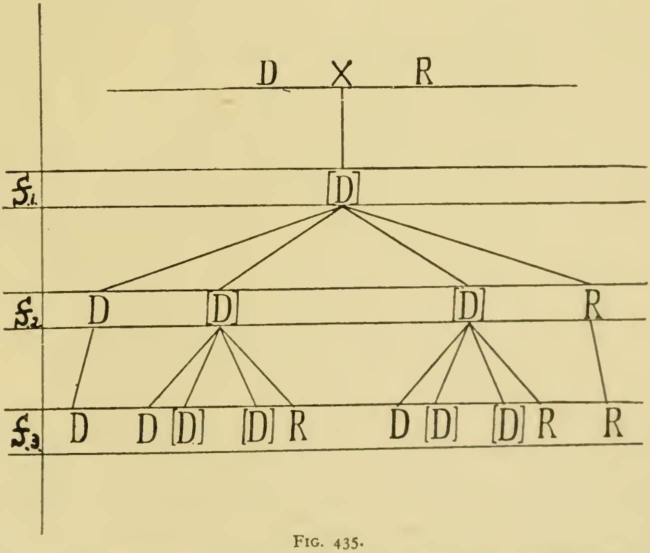

FIG. 435.

Scheme of inheritance of Dominant, D, and Recessive, R, characters resulting from the crossing of individuals which each bear one of a pair of differentiating characters, through three generations f_1, f_2, f_3. (After Punnett.)

In any sexually reproduced organism the gametes form the link between successive adult generations. The characters peculiar to the adult must therefore be represented in their heritable constitution. In a tall Pea some at least of the gametes, whether male or female, must "carry" the tall character; for from an impure tall three-quarters of the offspring are tall. If the race of tall Peas proves experimentally to be pure for that character, all the gametes must "carry" that character, and that alone. The union of two such gametes will give a zygote carrying the gene for tall character only. Such a zygote is known as a *homozygote.* But a zygote formed by the union of two dissimilar gametes—e.g. in the case of Peas where one "carries" the tall and the other the dwarf character—is termed a *heterozygote.* The plant produced from a heterozygote frequently shows the form of the pure dominant and can be distinguished from it only by the test of breeding. That, nevertheless, the recessive character is present in it is shown when such heterozygotes are bred together, one-quarter of the progeny proving recessive. It is the elements in the gametes corresponding to the differentiating characters of the zygotes that are now known as *genes* (Johannsen). Pairs of genes corresponding to pairs of contrasting characters, such as tallness and dwarfness in the Pea, are called *allelomorphs* or alleles. The heterozygote is formed by the union of two dissimilar gametes, and consequently the cells of the individual into which it grows must contain both allelomorphs. In order to reconcile these statements it must be supposed that at some cell-division previous to the formation of gametes a primitive germ-cell divides into two dissimilar portions. Instead of the two allelomorphs passing in association into both daughter-cells, the gene corresponding to the "dominant" character passes into one, and the "recessive" gene into the other. From this it follows that every gamete contains one of a pair of allelomorphs only, i.e. it is pure for that gene. In other words, *a simple heterozygote produces gametes of two kinds, and produces them in equal numbers. Each gamete is pure for one of each pair of allelomorphs.* The genes are said to segregate in the formation of the gametes.

If we now return to the details of the tetrad-division described above (pp. 563-567), it is seen that the segregation postulated as the result of Mendel's experiments is actually effected. Nuclei of two types are there segregated, each tetrad having two of each type. From the cells containing these nuclei (tetraspores) the gametes which share their genes are ultimately derived. *Two types of gametes are thus produced, as the Mendelian experiments require for their explanation.* The results arrived at first by the actual experiments in crossing, and thereafter explained on the basis of the cytological details, will be made clear by the diagram (Fig. 436).

The zygotes are represented by squares, the gametes by circles. Every zygote, being formed by fusion of two gametes, is double and contains a pair of allelomorphs corresponding to a pair of contrasting characters. These genes are represented by rectangles, the " recessive " gene being shown in black. As applied to the Peas of Mendel's experiment, the original parents (P_1) are pure tall and pure dwarf, the latter being the pollen-parent. In F_1 the heterozygote contains genes for both tallness and dwarfness, but the plants are all tall like the tall parent. On producing gametes, these plants yield equal numbers of two kinds, containing " tall " and " dwarf " genes respectively. Every ovule which contains the gene for tallness may be assumed to have an equal chance of being fertilised by a " tall " or by a " dwarf " pollen-grain, so that " tall " ovules will give rise to equal numbers of homozygous and of heterozygous talls. Similarly with " dwarf " ovules. Hence of every four zygotes in F_2, on the average one will be homozygous for tallness, another homozygous for dwarfness, and the remaining two heterozygous. These proportions, which correspond to those actually observed in breeding experiments, are represented in the middle column of the F_2 zygotes.

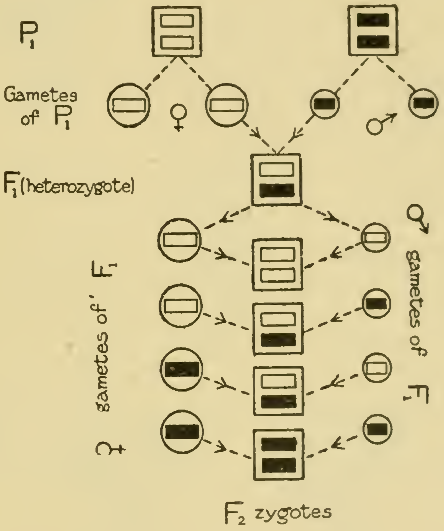

FIG. 436.

Scheme illustrating the segregation of characters of a heterozygote in tetrad-division. See Text. (After Punnett.)

The fundamental assumption made by Mendel was that of the "*purity of the gametes*"; this still holds good, except in the case of polyploids (see below, p. 581), where both allelomorphs may occur in the same gamete. The two subsidiary assumptions, which are also borne out by observation, are (1) that the different kinds of gametes are produced in equal numbers; and (2) that these gametes mate at random.

Genetics.

For various reasons the far-reaching importance of the simple principles laid down by Mendel on the basis of his own experiments was not recognised for more than thirty years. The re-discovery of his work in 1900 gave a fresh stimulus to the experimental study of inheritance, and since that date this field of investigation has developed to a remarkable extent so as to constitute a separate province of research known as *Genetics*. Much of this expansion has been due to the discovery of the chromosomes (unknown in Mendel's day) and to the increasing precision in our knowledge of the mechanism of nuclear division and in particular of the details of meiosis. At the present time genetics and cytology are indissolubly linked, and the most striking advances in the study of inheritance have been achieved by "cytogenetical" methods. Only a few of the more generally important developments in genetical knowledge will be mentioned here.

Examples of Segregation in Hybrids.

(*a*) *Involving One Pair of Characters.*

Mendel's classical experiment with tall and dwarf Peas which has been discussed in detail above, illustrates what happens in a "monohybrid" cross, i.e. one in which the parents differ in only a single Mendelian character. In the case described, the tall habit is completely dominant to the dwarf habit, so that the "hybrid tall" (heterozygous) individuals of the F_2 generation are not visibly distinct from the "pure tall" (homozygous) plants. Such complete dominance is by no means universal; in many other cases the F_1 individuals are more or less intermediate, in respect of the differentiating character, between the two parents. Thus, if a true-breeding crimson-flowered Snapdragon (*Antirrhinum majus*) is crossed with a true-breeding "ivory-flowered" (cream-coloured) individual (Fig. 437), the F_1 plants all have *pink* flowers. The F_2 generation segregates into 25 per cent. crimson, 25 per cent. ivory, and 50 per cent. pink-flowered progeny. The crimson and the ivory individuals are homozygous; the pink-flowered plants are heterozygous and on being "selfed" segregate just like the F_1 plants. Because of this *incomplete dominance* of crimson over ivory in the

Snapdragon, the F_2 generation thus comprises *three* visibly distinct forms or *phenotypes*. In the Pea, on the contrary, where tallness is completely dominant over dwarfness, the " pure talls " and the " hybrid talls " are phenotypically identical; their different behaviour after being " selfed," however, shows that they have different genetic constitutions, i.e. that they represent different *genotypes*.

Fig. 437.

" Monohybrid " Segregation. Cross between a crimson Snapdragon (shown black) and an ivory Snapdragon (shown white). The offspring (F_1) are pink (shown grey). The F_2 generation produced by self-fertilising an F_1 individual consists of crimson-, pink- and ivory-flowered plants, in the proportion indicated in the diagram. (From Shull's *Heredity* by courtesy of the McGraw-Hill Book Co., Inc.)

(*b*) *Involving Two Pairs of Characters.*

A " dihybrid " cross is one between two individuals differing in two independently segregating Mendelian characters; several such cases were examined and explained by Mendel in the Pea. As our first example we shall consider the cross between an " ivory " Snapdragon with normal flowers and a crimson Snapdragon with " peloric " flowers (Fig. 438); it should be explained that, whereas the normal form of the flower in Snapdragons is zygomorphic, races exist in which all the flowers are actinomorphic (" peloric ") and thus quite unlike the usual type in appearance. From what has been said above (p. 574), we should expect the F_1 plant from such a cross to be pink-flowered. This is actually the case, and in addition the flowers are all

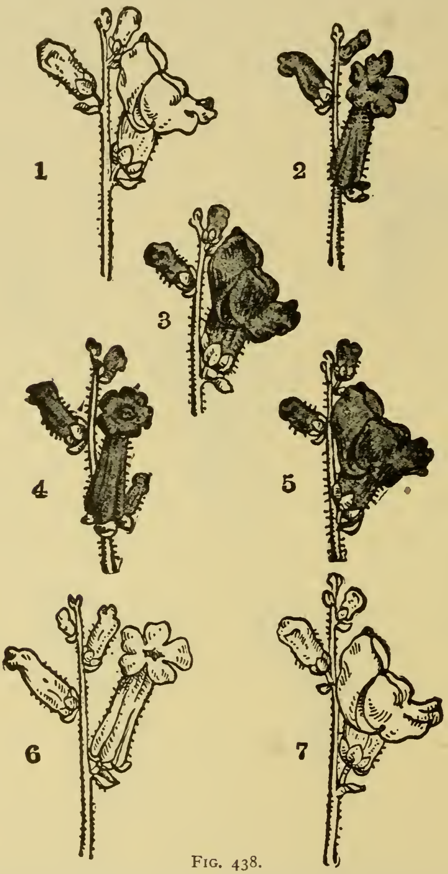

FIG. 438.

"Dihybrid" Segregation. Cross between an Ivory, Normal (1) and a Crimson, Peloric (2) Snapdragon. (3) = F_1 (Pink, Normal). 4, 5, 6, 7: four out of the six F_2 phenotypes (in the diagram no distinction is made between pink and crimson flowers—see text). (After E. Baur.)

zygomorphic, the normal flower-form being fully dominant to the peloric form. In F_2 six phenotypes appear, namely :

	In the ratios of	
Crimson, Normal - - - -	$\frac{3}{16}$ths	9 :
Pink, Normal - - - -	$\frac{6}{16}$ths	
Crimson, Peloric - - - -	$\frac{1}{16}$th	3 :
Pink, Peloric - - - -	$\frac{2}{16}$ths	
Ivory, Normal - - - -	$\frac{3}{16}$ths	3 :
Ivory, Peloric - - - -	$\frac{1}{16}$th	1

If the genes involved be represented as follows:

A = gene for Crimson flower colour } allelomorphs.
a = ,, Ivory ,, ,,
B = ,, Normal flower form } allelomorphs.
b = ,, Peloric ,, ,,

then the genotype of the Ivory Normal parent is **aaBB**, that of the Crimson Peloric parent **AAbb**. If these genes segregate independently their respective gametes will be **aB** and **Ab**, and the genotype of the F_1 **AaBb**. A plant of this constitution will produce *four* different kinds of gametes, viz. **AB**, **Ab**, **aB**, and **ab**, in equal numbers. Random mating between these can take place in sixteen different ways. The simplest method of showing the results is by means of a "chequerboard" (Fig. 439).

Pollen	AB	Ab	aB	ab
Ovules AB	(1 AABB Crimson, Normal	(2 AABb Crimson, Normal	(3 AaBB Pink, Normal	(4 AaBb Pink, Normal
Ab	(5 AABb Crimson, Normal	(6 AAbb Crimson, Peloric	(7 AaBb Pink, Normal	(8 Aabb Pink, Peloric
aB	(9 AaBB Pink, Normal	(10 AaBb Pink, Normal	(11 aaBB Ivory Normal	(12 aaBb Ivory, Normal
ab	(13 AaBb Pink, Normal	(14 Aabb Pink, Peloric	(15 aaBb Ivory, Normal	(16 aabb Ivory, Peloric

FIG. 439.
"Dihybrid" Segregation. Cross between an Ivory, Normal and a Crimson, Peloric Snapdragon. Chequerboard showing the segregation in the F_2 generation in detail.

If it is borne in mind that:

Every individual with a double "dose" of **A** will be Crimson.
,, ,, ,, ,, single dose of **A** will be Pink.
,, ,, lacking **A** will be Ivory.
,, ,, with a double or a single dose of **B** will be Normal.
,, ,, lacking **B** will be Peloric.

then it will be seen at once that the plants resulting from

	Combinations	1, 2 and 5	must be	Crimson, Normal	($\frac{3}{16}$ths)
those from	,,	3, 4, 7, 9, 10 and 13	,,	Pink, Normal	($\frac{6}{16}$ths)
,,	,,	6	,,	Crimson, Peloric	($\frac{1}{16}$th)
,,	,,	8 and 14	,,	Pink, Peloric	($\frac{2}{16}$ths)
,,	,,	11, 12 and 15	,,	Ivory, Normal	($\frac{3}{16}$ths)
,,	,,	16	,,	Ivory, Peloric	($\frac{1}{16}$th)

If all red-flowered plants, whether crimson or pink, are grouped together the ratio is :

9 Red, Normal : 3 Red, Peloric : 3 Ivory, Normal : 1 Ivory, Peloric.

This 9 : 3 : 3 : 1 ratio is the typical F_2 ratio for a " dihybrid " cross. It is the necessary consequence of random distribution of two independent pairs of allelomorphs by meiosis followed by random mating between the four resultant types of nuclei. Naturally, a close approach to the theoretical ratio, in this and in all other cases of segregation, will be realised in practice only when a sufficiently large F_2 generation is grown. In the present instance there are six F_2 phenotypes, because of the incomplete dominance of the crimson character. If both crimson flower-colour and normal flower-form had been incompletely dominant, there would have been nine phenotypes ; and if both had been fully dominant, there would have been only four. The number of distinct *genotypes* is in any case nine. Four of these, Nos. 1, 6, 11 and 16, are homozygous and when selfed will perpetuate their respective phenotypes ; the remainder are heterozygous in one or in both characters and, on being selfed, will show further segregation. The combinations of particular interest are No. 16, the homozygous Ivory Peloric and No. 1, the homozygous Crimson Normal. *In these it will be seen that the characters of the two parents have been recombined. This must necessarily arise in F_2 whenever the original parents differ in two or more independent Mendelian characters.*

The inheritance of fruit-colour in the Tomato furnishes another example of the genetical behaviour of plants differing in two pairs of genes, when crossed with one another. Tomatoes are most commonly bright red with a shiny surface ; but races are also known with matt red, golden yellow or pale yellow fruits. The fruit-colour depends upon two pairs of genes. " **R** " gives rise to red *flesh* (mesocarp) ; " **r** " to yellow flesh. " **Y** " produces a deep yellow opaque *skin* (epicarp) ; " **y** " a faintly coloured translucent skin. The genotype of the ordinary bright red tomato is **RRYY** (giving red flesh *plus* deep yellow skin). An **RRyy** tomato (red flesh *plus* pale translucent skin) is matt red ; an **rrYY** tomato is golden yellow (yellow flesh *plus* deep yellow skin) ; and an **rryy** tomato is pale yellow (yellow flesh *plus* pale translucent skin). This case is of special interest because it illustrates a very wide-spread phenomenon, namely the production of a particular phenotype through the *interaction* of the effects of different genes.

In the Tomato, the interaction is of an unusually simple and obvious nature, the outward appearance of the fruit being determined by the various combinations of two different skin-types with two different flesh-colours. In most cases, the mechanism of the interaction is far more complex and recondite. In the Snapdragon a very considerable number of genes are involved in the production of the wide range of flower-colours found among the cultivated races of this plant ; almost every one of the known shades of colour arises through the interaction of two or more of these genes.

Two further instances of gene-interaction require brief notice. In the Chinese Primula (*Primula sinensis*) the normal (palmatifid or " palm ") leaf-shape depends upon the presence of at least seven principal interacting " dominant " genes. The " recessive " genes which have been identified by corresponding characteristic leaf-shapes are " fern," " tongue," " oak," " maple," " claw " and two different " crimping " genes. All these genes, discovered in the first instance through their effects upon leaf-form, are known to influence the characters of other parts of the plant as well, in particular the shape of the corolla. A parallel case is that of the Japanese Morning Glory (*Pharbitis Nil*). Here the normal leaf-form depends upon eleven genes (ten " dominant " and one " recessive "). The gene termed " willow " not only produces the leaf-shape indicated by the name, but also causes the cotyledons and corolla-segments to be narrow and makes the flower functionally unisexual (male) ; the " maple " gene, besides affecting the form of the leaf, produces a polypetalous condition in the flower. These two cases have been mentioned for two reasons. First, the phenotypic characters involved are more clearly of taxonomic and of biological significance than the minor differences in flower-colour, which are not obviously important biologically, while they are regarded as trivial by taxonomists. Secondly, these cases illustrate the relation of certain genes to several distinct phenotypical characters which appear to have no direct morphological or physiological connection with one another ; it is probable that most if not all genes are of this *pleiotropic* nature.

Linkage.

So far, Mendelian inheritance has been considered purely in relation to genes which segregate independently of one another. In terms of the chromosome interpretation of inheritance, independently segregating genes are those which are located in different chromosomes. As a corollary, it would seem at first sight to follow that genes located in the same chromosome should always be transmitted in association with one another. If this association were absolute, then clearly all the known genes of a particular plant should be capable of classification into a number of groups corresponding to the number of chromosomes, the members of each group being always transmitted together, but segregating independently of the members of any other group.

The actual state of affairs is not so simple as this. When any plant or animal is subjected to intensive gene-analysis, the genes are found to fall into a number of *linkage-groups*, corresponding to, or at any rate not exceeding, the characteristic number of chromosomes. All the known genes of Maize, for example (over 300), can be arranged in ten linkage-groups—corresponding to the (haploid) chromosome number. The members of a linkage-group show *varying degrees of association in inheritance*—linkage, as it is called—with each other. In Mendelian experiments linkage reveals itself by the regular occurrence of marked departures from the theoretical numerical ratios of segregation, certain characters appearing in association with one another either more or less frequently than accords with normal expectation. The first case of such an aberrant ratio to be detected occurred in the early work of

Bateson and Punnett on the Sweet Pea. In this plant, purple flower colour is dominant to red, and erect standard to " hooded " (lax) standard. The experiment which led to the discovery of linkage was a so-called " back-cross " between a Purple, Erect plant heterozygous for both characters with a Red, Hooded plant homozygous for both recessive characters. The genotype of the Purple, Erect parent may be represented as **AaBb** and that of the Red, Hooded parent as **aabb**. The gametes of the former will be of four types, viz. **AB**, **Ab**, **aB** and **ab** ; those of the latter can be of one type only, viz. **ab**. The next generation would therefore be expected to consist of the four categories Purple, Erect (**AaBb**), Purple, Hooded (**Aabb**), Red, Erect (**aaBb**) and Red, Hooded (**aabb**) in equal numbers. Actually, the parental types (Purple, Erect and Red, Hooded) were found to be greatly in excess, each forming 49·5 per cent. of the whole, whereas the two re-combinations (Purple, Hooded and Red, Erect) appeared to the extent of only ·5 per cent. of each. This result was difficult to understand at the time. The view was therefore entertained by geneticists that the phenomena of linkage and crossing-over were present at gametogenesis. Meanwhile the cytologists were able to show that, in chiasma-formation (see above, p. 565), a related chromosome mechanism was, in fact, present. The explanation depends upon two additional assumptions, viz. (1) that every gene occupies a definite position (*locus*) on a chromosome and (2) that the genes are arranged along the chromosomes in a linear series like beads on a string, allelomorphic genes occupying corresponding loci on the chromosomes of a homologous pair, the " dominant " and " recessive " genes of each allelomorphic pair thus being " opposite numbers " (see Fig. 440). These assumptions are supported by adequate cytogenetical evidence which cannot, however, be discussed here.

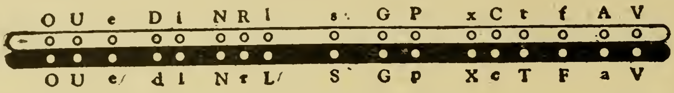

FIG. 440.

Diagram of two homologous chromosomes, maternal and paternal, indicating that similar genes are placed at the same level in the length of the chromosome. Compare with Fig. 433. (From Shull's *Heredity*, by courtesy of the McGraw-Hill Book Co., Inc.)

The cytological basis of linkage is illustrated diagrammatically in Fig. 441. Here three pairs of genes are involved **A–a**, **B–b**, **C–c**, the 'dominants" **A**, **B** and **C** having come from one parent and the " recessives " **a**, **b** and **c** from the other. **A** and **B** are situated close together, whereas the locus of **C** is far removed from both. If crossing over occurs more or less at random along the chromosomes, the chances of it occurring between **A–a** and **B–b** are small, but there is a much greater chance of its happening somewhere between **B–b** and **C–c**. **A** and **B**, and similarly **a** and **b**, will therefore tend to pass to the gametes in association with one another. Crossing over may not take between **B–b** and **C–c** either ; in that case the gametes produced will be **ABC** and **abc**. When, however, crossing over does happen in this region, the gametes will be **ABC**, **ABc**, **abC** and **abc**, the proportion of **ABc** and **abC** gametes—the " cross-over types "—depending on the frequency of crossing over between **B–b** and **C–c**. *The further apart two genes are on a chromosome, the greater will be the frequency of crossing over ; conversely, the closer the genes lie together on the chromosome, the more often will they be transmitted to the same* *gametes, i.e. the closer the linkage will be.* It is of interest to note that, if the loci of two genes are sufficiently far apart for 50 per cent. or more of crossing over to take place between them, they will segregate independently, in spite of the fact that they lie on the same chromosome. By means of intensive gene-analysis leading to the establishment of linkage groups, it is possible to construct " chromosome-maps " indicating the relative positions of the known genes in the several chromosomes.

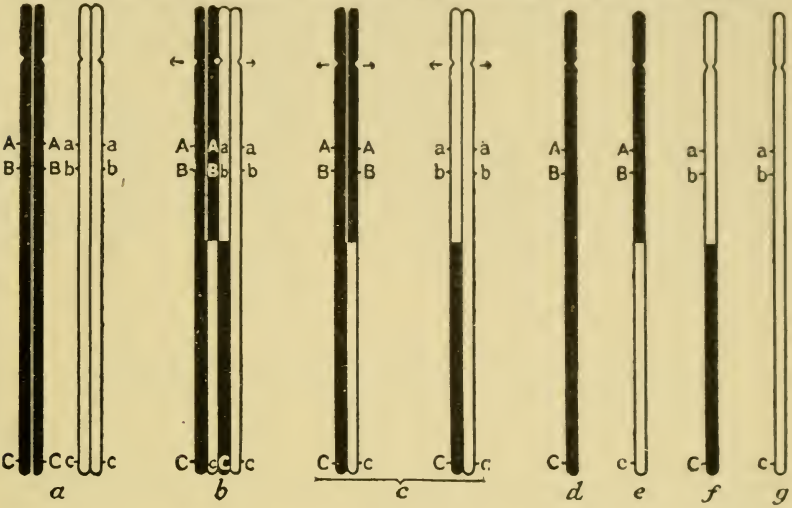

FIG. 441.

The cytological basis of linkage (diagrammatic) *a*, two somatic chromosomes carrying the genes A, B, C and a, b, c, respectively; each chromosome consists of two chromatids. *b*, During the close pairing of the chromosomes in meiosis, breaks occur in the chromatids, which join up with different partners, i.e. segments of the chromatids become interchanged. *c*, At anaphase of the first division the two chromosomes with their interchanged segments are distributed to different nuclei, and at anaphase of the second division each of the four daughter chromosomes (*d*, *e*, *f*, *g*) is distributed to a different tetraspore. *d* and *g* are non-cross-over, and *e* and *f* cross-over types. The zygotes from gametes of these four types will show independent inheritance for gene C and linkage between A and B. From Crane and Lawrence.)

POLYPLOIDY.

While gene-mutation—a change in the constitution of a gene—is the most usual source of heritable variation, there are several other ways in which the hereditary material may undergo alteration. A portion of a chromosome may break loose and (*a*) remain separate, or (*b*) rejoin in the inverted position, or (*c*) become attached to another chromosome, or (*d*) combine with other detached chromosome-segments, sometimes to form a ring. Such " chromosome-rearrangements " are shown diagrammatically in Fig. 442. The peculiar behaviour of many Evening Primroses (*Oenothera spp.*), which, although complex hybrids, breed practically true, is connected with the formation of chromosome-rings. Chromosome-rearrangements, though of frequent occurrence, will not be considered further here. An important aberration is *polyploidy*.

A polyploid organism is one which possesses more than two "sets" of chromosomes in its somatic cells. Polyploids are very common among cultivated plants. The chromosome complements of some of the cultivated forms of *Rubus* are shown in Fig. 443. The Raspberry (the variety figured is "Superlative") is a normal diploid with seven chromosome pairs (two "sets"),

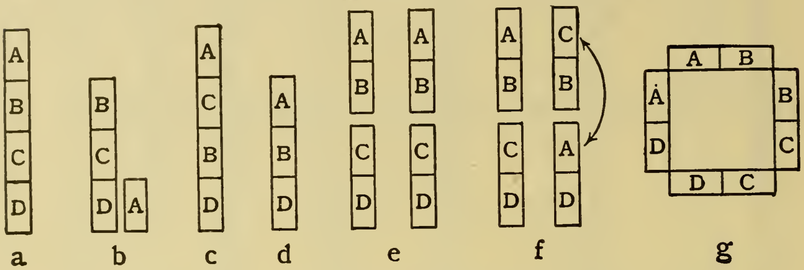

FIG. 442.

Diagram illustrating types of chromosome rearrangement. The letters indicate successive segments of the chromosomes. *a*, normal chromosome; *b*, fragmentation; *c*, inversion; *d*, deletion; *e*, a pair of normal chromosomes; *f*, reciprocal translocation of segments C and A, resulting in *g*, "ring-formation" at meiosis. (From Crane and Lawrence.)

the "Mahdi" is *triploid*, with three sets; the Veitchberry *tetraploid*, with four sets; the Loganberry *hexaploid*, with six sets; and the Laxtonberry *heptaploid*, with seven sets.

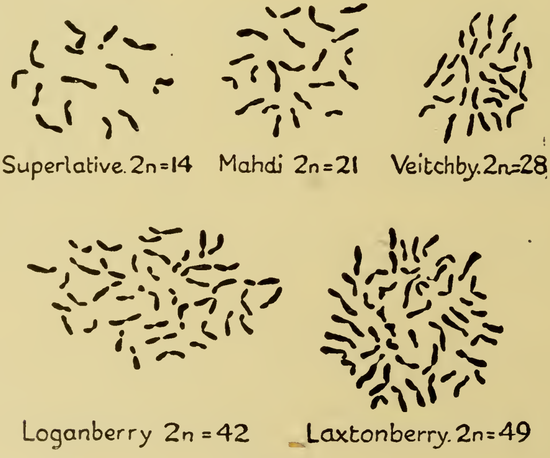

FIG. 443.

Somatic chromosome complements of some diploid and polyploid *Rubi*. For explanation, see text. (From Crane and Lawrence. After Crane and Darlington.)

Polyploids can arise in several different ways. For example (1) the chromosome number of a *somatic* cell may become doubled (Fig. 444, *a, d*). This type of polyploidy can be induced artificially in certain plants, e.g. in the Tomato by encouraging the development of adventitious buds from a wound-callus.

(2) The chromosome number may be doubled consequent upon abnormal behaviour at *meiosis*. Thus at meiosis in the F_1 generation from the cross *Raphanus* × *Brassica*, the Radish and Cabbage chromosomes cannot pair owing to the wide difference in their genic constitution. Consequently, the first metaphase follows an abnormal course, and sometimes all the chromosomes come to lie in one daughter-cell ; at the second division, two " tetraspores " result, each containing a double complement of chromosomes.

So much for the cytological origin of polyploidy. Polyploids may, however, be classified from another point of view. *Auto-polyploids* are derived from a single parent species or race ; in their cells, therefore, the chromosome complements are all similar (Fig. 444, *d*), e.g. the tetraploid Tomato. In *allo-polyploids* the chromosome sets are not all alike ; allopolyploidy is usually

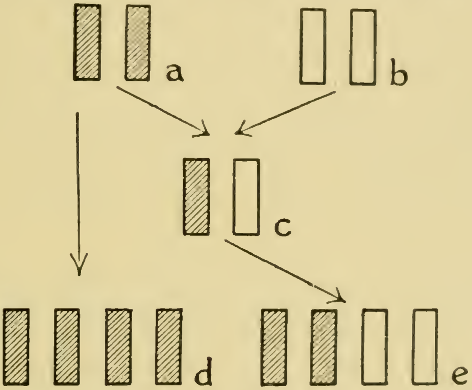

FIG. 444.

Diagram showing the origin and constitution of the chromosome complements of auto- and allo-tetraploids. *a* and *b*, diploid species ; *c*, diploid hybrid from *a* × *b* ; *d*, auto-tetraploid derived from doubling of the chromosome sets in *a* ; *e*, allo-tetraploid derived from doubling of the chromosome sets in *c*. (From Crane and Lawrence.)

a result of artificial or natural hybridisation (Fig. 444, *e*). One of the best known of allo-polyploids is *Primula Kewensis*, which arose from an artificial cross between *P. floribunda* and *P. verticillata*. Both of these species have 9 pairs of chromosomes, and the original (diploid) hybrid also had 9 pairs and was almost completely sterile. Later this gave rise spontaneously to a tetraploid race having two sets of *floribunda* and two sets of *verticillata* chromosomes, sterile with both the original parents but fertile with its own type and breeding nearly true. An allo-polyploid which has arisen in nature is the Rice-grass, *Spartina Townsendii*, which was first noted on Southampton Water in 1870, since when it has spread rapidly along the South Coast and has even crossed the Channel to France. It is believed to have originated from a natural cross between two older species, viz. *S. stricta*—known as a native of Britain for at least 300 years—and *S. alterniflora*, a more recent introduction from North America. The (somatic) chromosome numbers are : 56 in *S. stricta* ; 70 in *S. alterniflora* ; and 126 ($= 2 \times [28 + 35]$) in *S. Townsendii*. The Rice-grass breeds true and is sterile with both its presumptive parents. It is of interest that, where it has come into competition with either *S. stricta* or *S. alterniflora*, the new species has gained the upper hand.

Another example of polyploidy in Nature is provided by *Biscutella laevigata*, a Crucifer native to Central Europe and Italy, which has some races with 18 chromosomes (diploid) and others with 36 (tetraploid). The tetraploid races occur over a wide and continuous geographical area, ranging from the Alps to the Balkans. The diploid races, on the other hand, occupy several comparatively small and discontinuous areas in the valley-systems of the Rhine and of some other large rivers. The explanation suggested is that the diploid races are representatives of an ancient (inter-glacial or pre-glacial) type, while the tetraploid races are post-glacial immigrants. A similar state of affairs has been noted in the case of several North American species of *Tradescantia*.

That polyploidy has played a considerable part in producing new species is indicated by a more general line of evidence. The species of Angiosperms for which the chromosome numbers are known (several thousands) belong to about 500 genera representing a diversity of Families ; roughly 16 per cent. of these genera are made up of species forming polyploid series. Thus in various species of *Chrysanthemum* the somatic numbers are 18, 36, 54, 72 and 90, i.e. the basic number is 9, and the condition of the several species ranges from diploid to decaploid. In *Solanum* the basic number is 12, and the series ranges from 24 to 144. In *Papaver*, finally, two series can be distinguished with 7 and 11 as their respective basic numbers.

The general importance of polyploidy has been summarised as follows by Crane and Lawrence : it increases the effective range of hybridisation ; it combines the products of specific differentiation within a single (new) species ; and it increases the potential range of species variation. There may also be an increase in vegetative vigour, frost-resistance, and resistance to pathogens. In this connection, it is significant that so many valuable cultivated plants, for example Wheat and Oat, are polyploids.

GENETICS AND EVOLUTION.

In the foregoing condensed and therefore necessarily somewhat dogmatic account only a few of the more important aspects of genetics have been considered. Among the interesting topics which have been passed over as unsuitable for inclusion in an elementary discussion are : the nature and inheritance of sex ; hybrid vigour ; the definition of a " species " ; the origin and biological significance of dominance ; the causes of mutation ; the nature of genes ; and the mechanism of the action of genes upon developmental processes. The very simple cases of Mendelian inheritance and of polyploidy which have been considered in some detail may, nevertheless, provide a basis for some general reflections upon the relation of genetical data to the wider problem of evolution.

The outstanding features of Mendelian phenomena are two :

(1) Inheritance is seen to be *particulate*, the characters of the parents being transmitted individually to the offspring by genes situated at

definite loci in the chromosomes. There is no evidence of that " blending inheritance " which pre-Mendelian biologists assumed to be the rule. Although " cytoplasmic inheritance " cannot be ruled out as non-existent—indeed, there is evidence that in some instances it may be important—it is probable that the part that it plays in heredity is subordinate to the action of the nuclear genes. It should be mentioned that while, for technical reasons, Mendelian inheritance has been studied chiefly in higher organisms, it has been observed also among Mosses, Fungi and Algae (including unicellular types such as *Chlamydomonas*).

(2) Hybridisation followed by segregation has been an important source of new forms (re-combinations). Hybridisation experiments, again for technical reasons, are commonly carried out with races differing in comparatively few genes ; but what is known about " wide crosses " (between widely differing species or between distinct genera) suggests that the observed divergences from straightforward Mendelian segregation are due partly to the large number of genes involved, and partly to secondary complications such as polyploidy, chromosome re-arrangement and indirect effects of cytoplasmic differences.

Mutation is the basis of heritable variation and thus of evolution. " Heredity is essentially a conservative process. Evolution is possible only because heredity is counteracted by another force opposite in effect, namely mutation " (Dobzhansky). Strictly, the term mutation should be applied only to *gene-mutation*, i.e. to a change in the constitution of a gene ; but it is often more convenient to use the term in a wider sense so as to include such changes as chromosome-rearrangement and polyploidy, which may likewise give rise to heritable variations.

Nothing definite can be predicated as yet regarding the *rate* of origin of new species by gene-mutation alone. It is on the other hand clear that new species can arise by a sudden or " cataclysmic " method, viz., through polyploidy following upon hybridisation. So far, polyploidy has been observed only within certain groups of organisms, mainly among plants ; but within these limits there can be little doubt as to its importance as a subsidiary method of species production.

The persistence of a new form, however produced, depends essentially on the action of some mechanism of *isolation*, which prevents the new type from disappearing through free inter-crossing with pre-existing types. Geographical separation and any structural features, or physiological conditions (cross-incompatibility or hybrid-sterility) that prevent fertile union between different species, provide such mechanisms. The subject is a difficult one and has hitherto received insufficient attention.

The hypothesis of Natural Selection, which was one of the pillars of the original Darwinian theory, is quite consistent with modern genetical views, provided that it is recognised, first, that *selection operates only within genetically mixed populations and has no effect on those which are genetically uniform* ("*pure lines*") *; and, secondly, that the hereditary variations that provide the material upon which Natural Selection can operate arise by mutation, i.e. that it is mutants and not modifications* (*see above, p.* 569) *which undergo selection.*

There remains the vexed question of *adaptation.* It can hardly be disputed that a high degree of adaptation to a particular environment is one of the most striking properties of living things. On the other hand, it is impossible to believe that every individual mutation is in itself adaptive ; indeed there is abundant evidence to the contrary. In addition it is probable that some heritable characters are "neutral," in that they do not affect the chances of survival of the individual one way or the other, though caution is indicated in this connection in view of the pleiotropic action of many genes. *Adaptation may be thought of as arising by an "integration," into genotypes possessing a definite survival value, of a succession of mutational steps which are individually non-adaptive.* It should be realised that the number of possible gene-combinations within a species greatly exceeds the number of individuals of that species, so that there is ample scope for the origin of adaptations by a process of "trial and error," especially as the same mutation may occur on many separate occasions. The "opportunism" of adaptation in certain evolutionary trends (e.g. in the evolution of the pollen-tube from a rhizoid to a gamete-carrier) is suggestive. It must however be admitted that it is not possible at present to offer a satisfactory explanation of the origin of adaptation in general.

In conclusion, it may be worth while to quote a summary of Sewell Wright's views on Evolution as envisaged by a geneticist : "The most general conclusion is that evolution depends upon a certain balance among its factors. There must be gene mutation, but an excessive rate gives an array of freaks, not evolution ; there must be selection, but too severe a process destroys the field of variability, and thus the basis for further advance ; prevalence of local inbreeding within a species has extremely important evolutionary consequences, but too close inbreeding leads merely to extinction. A certain amount of cross-breeding is favourable, but not too much. In this dependence on the balance the species is like a living organism. At all levels of organization life depends on the maintenance of a certain balance among its factors." Further it may be noted that: "If the population size is small, favourable mutations may actually be lost, and evolutionary changes may proceed against the pressure and direction of selection. In large populations, however, selection will act to an amount approximately proportional to its intensity."

IRREGULAR PROPAGATION.

Some plants may eliminate normal sexual propagation, substituting for it in various ways other means of increase in numbers. Thus they forego the advantages which follow from sexuality, but not infrequently they secure greater certainty of propagation. The commonest cases are where vegetative propagation replaces partially or completely the reproduction by seed: a condition common in Nature, and seen in special degree in cultivated plants, such as the Potato, Jerusalem Artichoke, Sugar-Cane, Banana, and Pine-Apple (Chapter XIII.). In the viviparous habit of Alpine Plants the substitution of vegetative buds for flowers is probably a biological accommodation to the shortness of the Alpine summer. In other cases there may be an apparent maturing of good seeds, though the embryos within them are not sexually produced. Thus in *Funkia*, *Coelebogyne*, and others, numerous embryos arise by adventitious budding from the tissue of the nucellus, and they project like normally produced embryos into the embryo-sac. The nucellar tissue in such cases was already diploid: so that here there is neither reduction nor sexual fusion. They are peculiar examples of sporophytic budding. But as they involve a loss of sexuality, they may be described under the general term of *Apogamy*: or better, of *Apomixis*, by which is meant quite generally the absence of syngamy where it would normally occur.

Somewhat similar states, which however involve the contents of the embryo-sac, are found in *Alchemilla*, *Thalictrum*, *Taraxacum*, and *Hieracium*. In them embryos may be formed from an ovum without fertilisation. But here the egg itself has been found to be diploid, for reduction had been omitted in the development of the embryo-sac. Technically this has been described as "*somatic parthenogenesis*," which implies that the embryo springs from the ovum, but the ovum was itself diploid. A like condition has been seen in *Marsilia Drummondi*, and in *Athyrium filix-foemina*, var. *clarissima*. In such cases again no fertilisation is necessary to arrive at the diploid state. A more rare condition is that where an egg that is really haploid develops as though it had been fertilised. This is rare in Seed-Plants, but it has been observed. It has also been found to occur in *Chara crinita*.

Contrasted with these cases of apomixis, where no sexual fusion occurs, are various conditions which may be ranked as *substituted sexuality*. Here a nuclear fusion is seen, with consequences like those following on normal syngamy. But the nuclei involved are not produced in the normal way. Examples have already been described for *Nephrodium pseudo-mas*. var. *polydactylum* (p. 508, Fig. 403); and in that unusual type of nuclear association which occurs in the formation of the fruit in the Uredineae (p. 438, Fig. 338).

In the latter the association is ultimately followed by nuclear fusion, which thus, though deferred, takes its place in the cycle. The fact that similar nuclear fusions precede the formation of ascospores (p. 419) and of basidiospores (p. 432) suggests that such methods are probably wide-spread among Fungi. The nuclei involved in such cases spring not from any widely distinct sources, but from cells closely related in position and in origin. It is remarkable that these and other irregularities in the sexual cycle are found commonly among Plants represented by very numerous closely related forms. If their numerous species and varieties have resulted from mutation, then it would appear that excessive mutation may have had some influence in producing those irregularities. In organisms which mutate freely, the Mendelian sifting out, and preservation of each heritable mutation, would be a less vital matter than it is in more stable forms. This may in some degree account for such deviations from the normal sexual reproduction as have just been described.

CHAPTER XXXVI.

THE RELATION OF SIZE AND FORM IN PLANTS.

The Obconical Form.

Living Plants have now been considered in their various aspects of Form, Structure, Function, and Propagation. But there is still another point of view which emerges as the result of comparative measurement. A relation has thus been found to exist between Form and actual Size; but hitherto its study has been almost wholly omitted from the general discussion of the plant-body. Moreover, there has been a very frequent neglect of uniformity in scale of the illustrations used in comparison, which has tended to obscure the issue. But once the relation between Size and Form is brought into view on a uniform scale of measurement for each example, many observed data acquire new meanings, both functional and evolutionary.

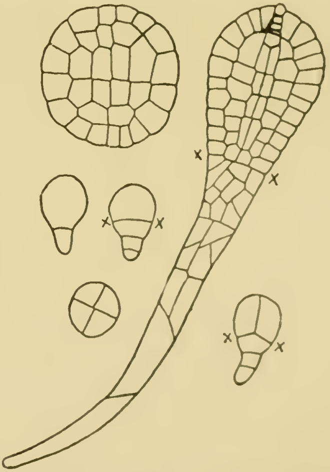

Fig. 445.
Young sporeling of *Fucus vesiculosus* in longitudinal and transverse section. (After Rostafinski.) The form is obconical, with circular transverse outline: it is only later that it becomes laterally compressed upwards. (See Fig. 289.)

The discussion of this relation starts from the fact that green plants are accumulators of material gained by photosynthesis. They are in no equivalent degree expenders. Hence they naturally work to a favourable balance of material. As the surplus of supply is used up in the growth of a plant of primary development, which has polarity in relation to some fixed stance, its outline tends to expand from the base upwards, and *the plant takes a more or less obconical form, with the vertex or cusp directed downwards.* A simple example of this type is seen in the young plant of *Fucus* (Fig. 445). It is a frequent feature in sporelings and embryos, and it also appears in many adult plants. But the result is unpractical, both mechanically in regard to stability, and physiologically in regard to the absorption and transmission of materials. Plants so constructed present an ever more insistent problem of well-being as their size increases.

Conical and Obconical Form Contrasted.

The prevalence of this type in plants of primary construction is apt to be lost sight of by the student, owing to the customary practice of presenting first to him such relatively advanced examples as Dicotyledons and Gymnosperms. His mind is thus familiarised with the idea of *conical form tapering upwards*, as seen in any forest tree: and especially in the Coniferæ, such as *Sequoia*. It is also conveyed by descriptions of cambial thickening (Chap. IV.), or by comparison of sections of woody stems taken successively from below: or again by diagrams like those of Fig. 37. But timber trees are products of relatively advanced evolution, involving *secondary*, that is, *cambial activity*. The student should therefore distinguish clearly between such conical stems, and the obconical contours that are apt to follow on *primary development*. Examples of these, which have retained that primary plan unaltered to the adult state, are shown diagrammatically for well-known plants in Fig. 446. The rubrics suggest how each has made the best of this seemingly disadvantageous scheme as its size increases. There are, in point of fact, two outstanding types of organisation of dendroid plants: the one having an obconical primary stem, which bears an enlarging distal

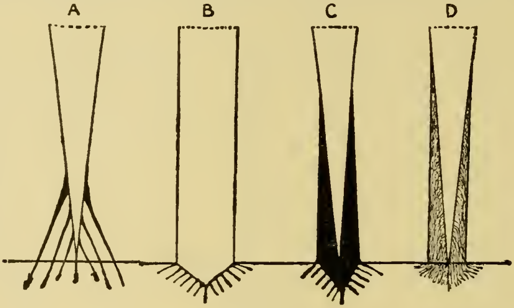

Fig. 446.

Diagrams not drawn to uniform scale, showing various methods of development of plants of primary obconical construction as their size increases. *A* = Plant of Maize or of Screw Pine, with prop-roots. *B* = Stem of *Cocos* or *Oreodoxa* showing the widely obconical base with attached roots, followed by the cylindrical trunk. *C* = *Dracaena*, with obconical primary development, supported by secondary thickening. *D* = Tree Fern, with its obconical stem supported by a massive sheath of roots.

bud and branches only occasionally, as in Ferns and Palms: the other takes a conical form as a consequence of cambial thickening (Fig. 5). Here there is profuse branching with numerous relatively small distal buds, as in forest trees. When young the two types do not seem to differ essentially from one another: but as greater dimensions are reached they tend to diverge, not only in external form but also internally.

PRINCIPLE OF SIMILARITY.

Galileo's Principle of Similarity applies to all structures, great and small, living or not living. In accordance with it, if the form of an enlarging solid body remains unaltered, its bulk increases as the cube, but its surface only as the square of the linear dimensions. In living organisms it is through limiting surfaces, whether external or internal, that physiological interchange is effected. It may be assumed that, other things being equal, the amount of substance transferred will be proportional to the area involved. Hence the importance of the principle here applied to obconical plants of primary development: for provided any surface of transit be continuous, it would increase at a lower ratio than the bulk that it encloses; and if its character remains unchanged during growth there would be a constant approach to a point of functional inefficiency. A remedy may, however, be found in *change of form* as the growth proceeds: and this is actually to be seen in most sporelings. *Any elaboration of so simple a contour as the inverted cone would tend to uphold the surface-volume ratio.*

EXAMPLES AND ILLUSTRATIONS.

The mouldings that occur in individual development of the primary plant-body, as it advances onwards from the spore or the zygote, may appear either externally or internally. A few examples will show how, by elaboration of form, certain difficulties that arise from increasing size have actually been met in Nature. Obconical sporelings present relatively simple methods. For instance in the green Alga, *Fritschiella* (Fig. 447) the germinal filament first enlarges upwards, and then branches profusely, forming a distal brush. The bulk of each thread equals approximately that of the first, though their collective bulk is great. By this elaboration of form the proportion of surface-exposure of the whole tends to be maintained. A fern prothallus (Fig. 391), or a young *Fucus* (Figs. 279, 280), widens into a thin expanse with flattened sides: this tends by a different method to uphold the surface-volume ratio. In the tissue of a young growing sporeling of *Riccia*, clefts appear in the enlarging upward growth, and these open at the surface: thus the enlarging thallus is ventilated, and the cell-surface facing the atmosphere tends to be maintained *internally* (Fig. 448). In Mosses the obconically enlarging protonemal buds become leafy upwards (Figs. 355, 356): here also the thin leaves as *external* outgrowths tend to uphold the surface-volume ratio, but by a method the converse of internal ventilation. These simple examples suggest four distinct methods for gaining that end in obconical sporelings, as their size increases. They are all taken from gametophytes. But both of the alternating phases of the life-cycle are subject to the same demand. For instance, in the sporeling of *Polypodium* (Fig. 140) the stem is obconical: it increases to about four times its original diameter before its seventh leaf is reached. But here again the surface-volume ratio tends to be upheld by foliar development, combined with internal ventilation. In point of fact these four methods may be variously combined among themselves in the organisation of vegetation generally. For instance, flattening and internal ventilation take part in the construction of any ordinary leaf-blade; and branching also in the widest sense may be

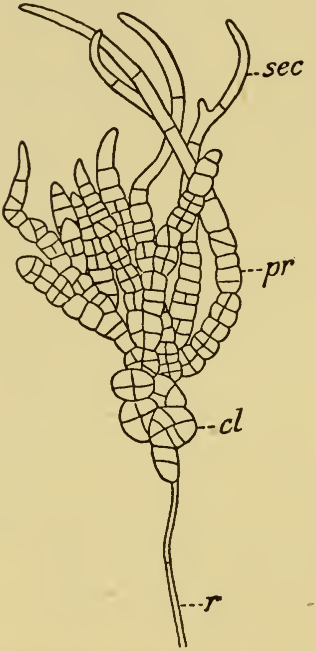

FIG. 447.

Fritschiella tuberosa. A small mature plant with a single rhizoid. *cl*=cluster; *pr*=primary; *sec*=secondary branch. (× 350.) (After Iyengar.)

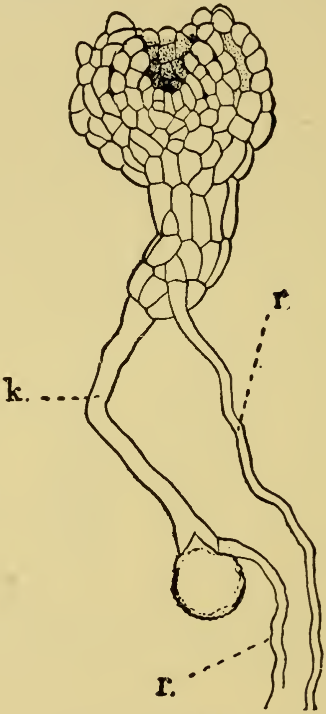

FIG. 448.

Riccia trichocarpa. Young sporeling showing spore and germ-tube, *k*; rhizoid, *r*; and the thallus enlarging upwards with sunken apex, and intercellular spaees beginning to develop. (× 85.) (After Campbell.)

involved, giving the condition seen in compound leaves and in leafy shoots at large. When they are associated also with apical growth and lobation of various orders, they lead to that due balance of surface and bulk which has made the realisation of diffuse land-vegetation possible, up to the limit of mechanical resistance (see Chapter X.).

Statement by Measurement.

To demonstrate by comparison to uniform scale that there is a real though not an exact relation between Size and Form, it will be convenient to turn to definite internal tracts, and particularly to the conducting tissues of plants of primary construction. In the fossil Fern *Botryopteris* the small protostele is cylindrical (Fig. 375), and circular in transverse section. But in those of larger size its section is stellate, with projecting flanges, the surfaces between them

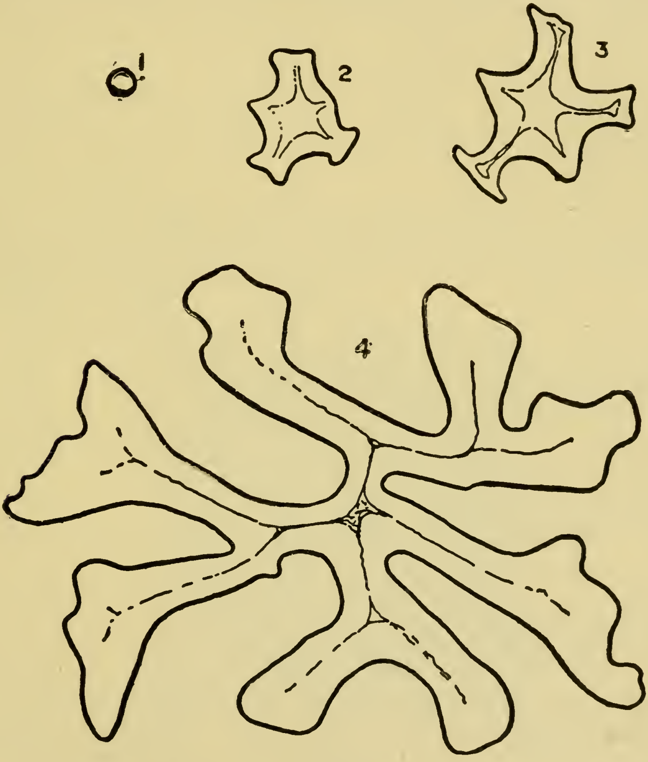

Fig. 449.

Outlines of the xylem of Coenopterid steles, all drawn to the same scale, to show their relative sizes (× 5). 1=*Botryopteris cylindrica.* 2=*Ankyropteris Grayi.* 3=ditto, larger. 4=*Asterochlaena laxa.* The elaborateness of outline increases with the size.

being hollowed. The larger the stele the deeper the involutions, and even the number of flanges increases with the size of the whole. This is shown in Fig. 449, where all are drawn to the same scale. With differences of detail similar results may be obtained from the xylem in leafy shoots of *Lycopodium*, in the leafless rhizomes of *Psilotum*, and again in roots, particularly in those of Monocotyledons where cambial thickening is absent (Fig. 58). The larger the root the more numerous are the flanges of protoxylem (p. 84). Even in the unicellular Alga, *Closterium*, where there are in each cell two flanged chloroplasts, the number of flanges varies according to the size of the cell in different species. The measurements taken from such varied objects gain in cogency by tabulation, as they are presented below for the leafless rhizomes of *Psilotum*, the leafy stems of *Lycopodium*, the roots of *Colocasia*, and for optical sections of the cells of *Closterium*.

TABLE SHOWING RELATION OF SIZE TO STRUCTURE IN LEAFLESS RHIZOMES, LEAFY SHOOTS, ROOTS, AND IN CELLS OF DESMIDS.

NAME		DIAMETER OF STELE IN MM.	NUMBER OF RAYS	APPROXIMATE RATIO
Psilotum: Sections of rhizomes from Bertrand's figures, *Arch. Bot. du Nord*, Lille, 1881	130.	20	2	10.0
	151.	32	3	10.3
	175.	40	4	10.0
	161.	60	5	12.0
	162.	70	7	10.0
Lycopodium: sections of stems, as in "Size and Form," Fig. 7, after Wardlaw	3.	19	6	3.2
	4.	26	7	3.7
	5.	38	11	3.5
	6.	66	19	3.5
	7.	88	22	4.0
Colocasia: sections of roots, as in "Size and Form," Fig. 58, after Wardlaw	1.	5	5	1.0
	2.	8	9	.9
	3.	19	14	1.4
	4.	27	21	1.3
	5.	83	38	2.2
SECTIONS OF CELLS OF SPECIES OF *CLOSTERIUM*		DIAM. OF CELL IN MM. (×810)	NUMBER OF RAYS OF CHLOROPLAST	APPROXIMATE RATIO
C. Dianæ (Fig. 37) - -		10	6	1.6
C. Juncidium (Fig. 48) - -		12	7	1.7
C. angustatum (Fig. 36) - -		20	10	2.0
C. striolatum (Fig. 42) - -		23	13	1.8
C. Lunula (Fig. 4) - -		53	15	3.5
These figures for *Closterium* are based on drawings by Miss Carter. *Ann. of Botany*, XXXIII, pl. XIV, XV.				

These varied examples show how uniformly *increase in Size is accompanied by elaboration of Form.* As they stand, the uniformity of these results points to some definite relation between Size and Form. The degree of constancy shown in the ratios is not a matter of chance, whatever may be its physiological significance. On the other hand the results have not been found referable to any external agency : they are certainly not dependent on the influence of appendages, for in three of the instances quoted there are none. The degree of constancy in the ratios in the last column is not exact: nevertheless it suggests some inner influence that controls elaboration of form in accordance with increase of size in each of the several cases.

PROBLEM OF SUPPLY TO DISTAL BUDS OF VASCULAR PLANTS.

In plants of advanced but primary organisation, obconical growth leads towards enlargement of the distal bud. This is often associated with a marked restriction, diminution, or even absence of branching, as in many Ferns and Palms (Fig. 446). In these, as development proceeds, the axis may expand to great bulk. Thus, in *Amphicosmia*, a well-grown Fern, but not of the largest size, the flattened apex, which may bear four cycles of leaf-primordia upon it, was found to be fully four centimetres in diameter (Fig. 450). Its bulk is enormous as compared with the buds of forest trees, such as the Beech (Fig. 451), where the growing

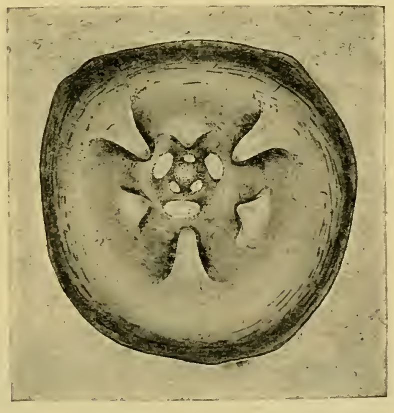

FIG. 450.

Apex of stem of a large plant of *Amphicosmia Walkerae*, shown natural size: with the arrangement of the leaves in trimerous whorls upon the flattened apical plateau.

point of a twig lies buried as a minute speck within the bud itself, which is less than three millimetres in diameter. But the Beech has the advantage of cambial thickening, which Ferns and Palms have not. Hence the problem of provision of channels of supply to stem and leaves differs in the two types: the one shows "exogenous" growth, after the old terminology: the other is "endogenous". While the former depends upon *secondary cambial increase* and accretion of *successive layers* of conducting tissue in the woody trunk, the latter shows *distal expansion of the primary stele.* The first of these modes of increase has been described at length on pp. 55 to 68: the latter is less clearly understood, and it will be reconsidered here, as it is seen in Ferns, and in Palms.

FIG. 451.
Winter-buds of the Beech (*Fagus sylvatica*), covered with protective scales (*kns*), and showing the small proportion of exposed surface in the defoliated state. Natural size. (After Strasburger.)

The general structure of an adult Palm stem, as seen in transverse and longitudinal sections, with its distended and ill-defined stele, and numerous vascular strands scattered through the pith, leads out to the successive leaf-bases, as described in most Textbooks (see p. 50, Figs. 29, 30). But few botanists who are familiar with the structure of an adult Palm or Maize plant could give a detailed account of the development of their vascular systems from the seedling upwards: few also will have themselves dissected the adult buds, or have realised that greater or less expansion of the primary stele in Monocotyledons stands in a direct relationship to formative activities in the enlarging distal bud, and its developing leaves. The stele, moreover, is responsible for distributing

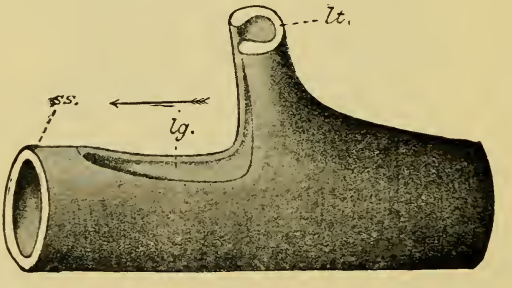

FIG. 452.
Loxsoma Cunninghami. Diagram showing the form of the medullated stele at a node of the rhizome. *ss* = solenostele; *lt* = departing leaf-trace; *lg* = leaf-gap. The arrow points towards the apex of the rhizome. (After Gwynne-Vaughan.)

the supply of nutrients required in the growing region. All this is, however, achieved in Palms in the absence of secondary accretion. As such primary development is more readily apparent in Ferns than in Monocotyledons, the former are selected here to illustrate steps of stelar expansion in relation to the enlargement of the terminal bud.

THE EXPANDING STELE IN FERNS.

The obconical enlargement habitual in the stems of sporeling Ferns is clearly seen in *Polypodium vulgare* (p. 208, Fig. 140). Not only does the axis enlarge upwards, but the stele likewise expands. Comparison shows the steps usual in them to be through *medullation* to *solenostely* (Fig. 452), and by overlapping of closely disposed leaf-gaps to *dictyostely* (Fig. 376A). This has been described briefly on pp. 485-7. It is in fact general in Leptosporangiate Ferns. For full details it must suffice to refer to *Ferns*, Camb. Press, Vol. I., Chapters VII., VIII.: *Primitive Land Plants*, Chapter XVII. and *Size and Form*, Chapter VIII.: where references are given to the extensive literature on the subject. This short précis of facts, together with the illustrations which follow, will serve as a basis for discussion of the relation of obconical growth to the expanding primary stele of the adult Fern.

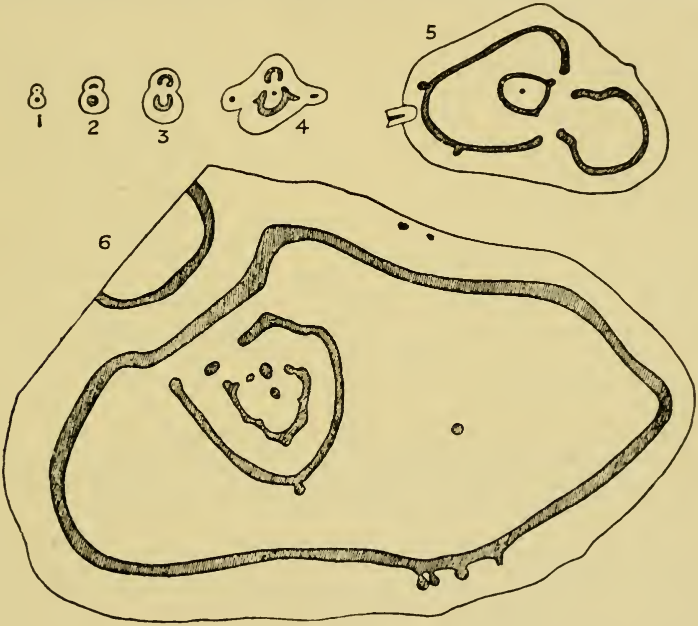

FIG. 453.

Series of transverse sections of the stem of *Pteris* (*Litobrochia*) *podophylla*, all drawn to the same scale, so as to show the great increase in size, and the progressive complexity of the conducting tracts (shaded) as the stem expands conically upwards: also the successively enlarging leaf-bases attached laterally in each. (× 4.)

In the Ferns these elaborations all start from the simple protostele, which expands upwards with the enlarging shoot. A central pith is then formed, at first small but often attaining considerable size in the adult (Figs. 140, 374). In all advanced Ferns the stelar tissue is shut off from the pith by an inner endodermis, giving the cylindrical structure known as *solenostelic* (Fig. 452). Further the tube is apt to be interrupted by foliar and other gaps, so that it appears as a network of meristeles surrounding the column of pith. This allows of ventilation inwards, a matter of some importance where the column is large, as it is in the Shield Fern (Fig. 374). In many Tree Ferns, such as *Dicksonia*, the pith may measure several inches in diameter. At first it consists of relatively inert storage parenchyma, without any conducting tissue to aid transit within its bulk. But this physiological difficulty has been met in many large Ferns by the formation of accessory conducting tracts that are present in the pith. An example of this has already been seen in the inner meristeles of the Bracken (Fig. 376). These medullary strands often take the form of concentric rings, as in *Pteris podophylla* (Fig. 453). Their number increases with the size of the stem. In the largest (6) three complete rings are seen and the inception of a fourth : and in extreme cases as many as a dozen may be found, all fitting concentrically within one another. This has been seen in the fossil genus *Psaronius*. In others, however, as in *Platycerium*, isolated strands appear dotted over the transverse section, as in the stems of Monocotyledons (Figs. 29, 30).

In the very diverse vascular types of Ferns and Monocotyledons the conducting system of each vegetative shoot forms a connected whole, and each is of primary origin only. The stelar expansion of each is correlative with the obconical enlargement towards the apical bud. The stolons of *Nephrolepis* give a clear demonstration of the relation of stelar complexity to size. Since both stolons and tubers are leafless, the modifications of form of the vascular strands are not affected by leaf-insertions, but are determined in the growing bud itself.

Where the size of the stolons in *Nephrolepis* is small the form is cylindrical, and it is traversed by a solid stelar core. But where the stolon itself swells distally into a pear-shaped tuber the stele may become variously fluted, or even disintegrated, as it is in *Nephrolepis cordifolia* (Fig. 454, *A* and *B*). At its base the solid stelar core expands first into a solenostele, and later disintegrates into a ring of meristeles (*C*). But as it passes upwards into the conical tip it gradually re-constitutes itself ; and the protostelic state is resumed (Fig. 454, *A*). The conclusion from such facts is that these converse changes, basal and apical, are related locally to the dimensions of the tuber. Such facts accord with what is seen in the leafy shoots of Ferns at large (Figs. 374, 375, 376, 376. *A*, 455). Both of these phenomena are presented by primary tissues defined at the growing point itself.

In a vertical section of the sporeling of *Polypodium vulgare* (p. 208, Fig. 140) the apical region appears broad and flattened, and the leaves arising from it are solitary. But it is a relatively small plant, its apical region being in diameter about $\frac{1}{20}$th that of the adult Tree Fern shown in surface view in Fig. 450. Here the young leaves are crowded round the growing point, each requiring its own quota of nourishment. The problem of supplying all the leaf-primordia may be held as particularly acute, at the time when a new succession of them is developing. In various degrees they will call for supplies from the expanding shoot through each leaf-base. Actually very little is known of the mode of distribution of nutrients to the growing region from below. But structurally we see in many Ferns how distribution of nutrients may be helped by accessory strands which traverse the column of the pith, either in the form of a single protostele, a solenostele, or a concentric group of them (*Psaronius*) : or again there may be a number of separate medullary strands. In point of fact, there is considerable variety in these medullary systems. *But they are all primary, differing fundamentally from the secondary growths of cambial origin, which are characteristic of "exogenous" plants.*

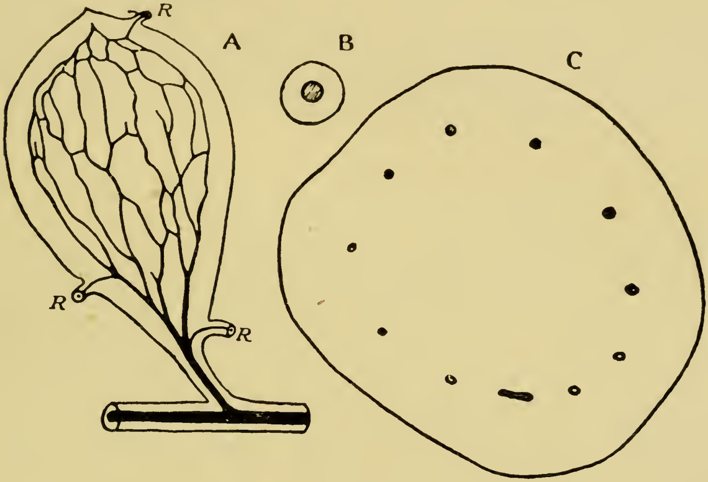

FIG. 454.

Nephrolepis cordifolia. *A* = stolon bearing a tuber, in which the protostele breaks up into a cylindrical network, contracting again at the apex. *R* = root (after Sahni). *B* = transverse section of a protostelic stolon (× 5). *C* = transverse section of tuber, showing ring of meristeles each limited by endodermis. Diameter of stolon, 1·6 mm. Diameter of tuber, 11 mm. (From *Size and Form*, p. 132.)

The functional analogy between such medullary systems as those of Ferns and the vascular strands scattered through the pith of the expanded stele of Palms, Maize, or Sugar Cane, appears obvious, though their morphological origin is not the same : nor is their physiological effectiveness identical. Nevertheless, both follow on stelar expansion. Both types might be included under the old term " endogenous " : but since the plants in which they appear have no near affinity, and arise along quite distinct evolutionary trends, their comparison cannot be held as more than one of analogy.

Whether small or great the apical bud acts as a physiological unit, and the stelar system serves it as a common unit of supply from below to the apical region. In the more advanced Ferns the conducting tissues are sheathed by *endodermis*, which by the nature of its cell-walls acts when mature as a physiological barrier (Figs. 377, 378). But its control is not complete, being subject to progressive phases of development. In its adult state it may limit gaseous interchange, and serve as an efficient boundary in guiding supplies of nutrients in solution upwards. But as the younger tissues of the growing point are approached from below the control is relaxed : in passing finally to the procambial region a point is reached where outward diffusion from the stele is no longer so restricted : the distal growing point may thus be supplied with water and solutes by upward diffusion over the whole cross-sectional area. This may roughly be compared with the spout and perforated " rose " of a watering pot. In either case the separate streams merge at last into a common supply to the region immediately below the growing point.

The apical structure of Palms and other Monocotyledons corresponds functionally with that in Ferns, though the strands differ in the former by the absence of endodermis surrounding each strand (Fig. 31). In both the existence of a medullary vascular system may find its explanation in the need for bringing adequate supplies towards the centre of a progressively expanding distal bud, *in plants of primary construction, where the apical bud and leaves are large, and are served by stems without secondary increase.*

LARGE AND SMALL BUDS COMPARED.

We may now return to the opening of this discussion on p. 589. In the words of Herbert Spencer, green plants are accumulators of material gained by photosynthesis. They are in no equivalent degree expenders. Hence they naturally work towards a favourable balance of material. One consequence of this is a prevalence of *primary expansion upwards*, and the development of large distal buds : as seen in Ferns and Palms. Here the medullary vascular tracts may serve for the transit of nutrients through the inert pith towards the centre of the apical region, with its acropetal succession of young leaves. In fact the conducting systems of Ferns and Palms, etc., on the one hand, and of woody forest trees on the other, have solved their respective problems of advancing size and internal structure in quite different ways. In the former, there has been adherence to their original scheme of *primary obconical expansion* of the shoot with dilation of the stele in relation to the single, enlarging terminal bud : in the latter, what is probably a more efficient method both for mechanical support and for supply has been evolved ; that is, for the development of a multitude of small buds that initiate a profuse branching. In these the vestigial relics of the old primary wood translocate a sufficient supply to meet the earliest demands of each small bud ; but this is supplemented without delay by continued secondary increase through cambial activity which meets both nutritional and mechanical needs. The final result of this difference in solving the fundamental problems of Size may be seen in any mixed forest, *where conical woody plants with small buds are dominant, and form the canopy beneath which the obconical and big-budded types shelter.*

The Size Problem in the Bryophytes.

Those surfaces of a plant which are in contact with a surrounding medium, such as air or water, are styled *presentation-surfaces*, whether these be external or internal. For instance, in order to uphold gaseous interchange in subaerial plants it is essential to maintain a due proportion of surface to bulk; and the like is needed also in partially or completely submerged plants. To this end Mosses and Liverworts have adjusted their form and structure up to a point, though without realising their opportunities to the full. Accordingly they afford interesting comparisons with other plants. What is commonly lacking in their organographic make-up is the combination of sufficiently elaborate external contour, with or without internal ventilation. For instance the gametophyte of the Jungermanniales is commonly leafy, though without internal ventilation (Fig. 369): on the other hand, the Marchantiales have *an internal* type of ventilation of the branched and fleshy thallus (Fig. 368): meanwhile the unbranched sporogonia of both are without ventilation. In the Mosses the plant is leafy, and often profusely branched: but even the largest of them lack the ventilated structure of Vascular Plants. Their sporogonia, however, have internal ventilation, with localised stomata (Fig. 364): but they are unbranched and leafless. *Neither phase of the life-cycle in these plants has secured full efficiency, by combining well-developed ventilation with branching of a leafy shoot, as Vascular Plants have done. In this we may see a reason for their limited stature. As a Class they are structurally doomed to be dwarfs.*

Combination of Organographic Factors.

That combination which is wanting in the Bryophytes is, however, present, together with other helpful features, in most Vascular Plants. The success of their vegetative system in developing to large size is chiefly based on such features as, (i) continued apical growth; (ii) branching of various orders; (iii) internal ventilation; (iv) a plastic primary conducting system; and (v) secondary cambial increase in many, but not in all. Collectively, and in various combination, such features as these lead to the diffuse form and elaborate structure seen in Land Vegetation. On the other hand, by comparing the striking results that have followed in Vascular Plants with the limited success of the Bryophytes, we may measure the importance of those combinations which the Mosses lack. But, as a consequence of the superiority of the Higher Plants based on such advantages as these, the Bryophytes do not offer the best field for study of the Size and Form Relation. There are in fact three grades of vegetation, differing in the degree of their adjustment to the progressive demands of increasing Size, though they are not sharply marked off from one another :

I. *Rudimentary organisms*, of submerged or semi-aquatic habit, which are for the most part built up on the cylindrical filament, such as Algae and Fungi. In these the maintenance of the surface-volume ratio does not present serious difficulty.

II. *Ordinary Land Plants*, which have met in full the demands of increasing size by the aid of structural changes recognised as secondary, such as internal ventilation and cambial increase.

III. *Primitive Land Plants known as the Archegoniatae*, which occupy a middle position, their organisation in many instances being based on primary structure only.

The study of Morphology in Plants seems to have progressed as though there were no Size Problem. One reason for this has probably been that the simplest plants of aquatic habit do not present the question in any acute form : while the higher plants of land habit have solved their problem by adaptive adjustment. But the earliest denizens of the Land, that is the Archegoniatae, have either carried out such adjustments imperfectly, or not at all. It is through them that the Problem of Size and of its consequences may be most readily grasped : and in none of them is the evidence so clear as it is in the Mosses and Ferns.

MECHANICAL LIMITATIONS.

The foregoing pages have touched upon those various devices by which plants meet more or less fully the physiological demands that follow inevitably on increase in Size. *But the direct demand for mechanical stability stands at the back of all progressive organisation.* As the size increases the strength of a structure increases as the square of the linear dimensions, but the weight or mass as the cube, provided the form and material remain the same. We have seen in Chapter X. how the simplest steps to secure stability are based on the turgidity of the encysted cell, which suffices for small organisms, chiefly aquatic. In land plants of larger size the necessary resistance may be secured by the help of cell-partitioning and of specialised sclerotic tissues, still of primary origin. A climax of such *primary* development has been reached with amazing success by Tree Ferns, Bamboos, Screw Pines, and Palms. But the most successful development of all is based on *secondary* cambial activity, as in the Gymnosperms and Dicotyledons. This provides an automatic increase, not only in the channels of supply but also in tissues of mechanical resistance. Theoretically there is no limit to growth in photosynthetic plants, based on continued embryology, combined with a geometrical ratio of branching, internal ventilation, and cambial increase. But actually there are spatial and mechanical checks on this ambitious scheme. The final check of all for subaerial plants is mechanical inability to support an indefinitely increasing load of stems, branches and leaves, and to resist the impact of winds. Even automatic cambial increase does not suffice. Overstepping the limit of resistance results in fallen trees, and stripped branches, twigs, and leaves. These mark various degrees of failure under the final test of mechanical stress.

Adaptation of Form in Submerged Parts.

Chapters V. and VIII. have shown how the internal tissues of the larger Plants of the Land are ventilated by a system of intercellular spaces, which open through the pores of the stomata and through porous lenticels. Thus they provide for that gaseous interchange with the open air that is essential for the subaerial life of Land Plants. This has been fully discussed by Haberlandt as illustrating the *Principle of Maximum Exposure* laid down in his *Physiological Plant Anatomy* (Engl. Ed., p. 276, etc.). The effect will be proportionate to the area of the internal surfaces thus exposed.

A contrast to the condition thus seen in the vast majority of subaerial plants is presented by those in which the green leaves are submerged wholly or in part. Since stomata are absent from such surfaces as face the water the ventilating system is sealed up within the investing epidermis. In them gaseous interchange can be conducted only by the slower process of diffusion through the unbroken outer surface. The sum of its activity will then depend upon the *surface-volume ratio* of the plant as a whole. This physiological problem faces all submerged green plants : it is in fact one of *size* and *form* : and the success of each individual will depend upon the measure in which that ratio is maintained. As we have seen, any elaboration of a simpler to a more complex form tends to increase it. A few familiar examples may serve to illustrate how by modification of form of the submerged parts the surface-volume ratio tends to be upheld. It is usually by disintegration of the leaf-blade, such as is seen in isolated genera and species belonging to diverse distinct families. These plants suggest that they are specially adapted to meet the physiological demands consequent on a submerged habit, and the absence of stomata.

Such examples are presented in varying degree by the many different forms of *Ranunculus aquatilis* Linn, (Ranunculacae), by *Ceratophyllum* (Callitrichineae), *Cabomba* (Cabombaceae), *Potamogeton* (Naiadaceae), *Hottonia* (Primulaceae) and *Myriophyllum* (Halorageae). In each of these examples belonging to six different families, the fully submerged leaves are disintegrated in diverse degrees, forming narrow lacineae : while those leaves of them that float on the surface of the water, together with those that are fully subaerial, have coherent or even entire blades, sometimes with stomata on the upper surface, as in *Nuphar*. Further, in *Cabomba*, or in the variety of *Ranunculus aquatilis* described as "*heterophyllus*, Fries," two distinct types of leaf are borne on the same plant :—those submerged are dissected, those floating or subaerial being lobed, or even entire. Lastly, in *Aponogeton fenestralis* (Juncaginaceae), a denizen of still waters, the broad submerged blade is perforated ; which gives as regards the surface-volume ratio, practically the same result as dissection. In all such cases, provided the thickness of the leaf be not increased, the elaboration of form will necessarily tend towards maintaining the surface-volume ratio, notwithstanding the absence of stomata from the submerged surfaces. Thus the consequent difficulty of gaseous interchange that this entails in parts that are submerged tends to be overcome.

Conclusion

In the preceding pages limiting surfaces of the plant-body, whether external or internal, have been discussed in terms of the Principle of Similarity. That progressive elaborations of form and structure take place as the size of the individual increases has been demonstrated on a wide basis. Indeed, the existence of a Size and Form correlation may now be accepted as a fact. The basic problem that awaits solution, and concerning which we have very little precise knowledge, is that of the mechanism by which the relationship is brought about. It has been seen that the adult form and structure of plants admit of interpretation in terms of function. But however plausible the biological advantage of each adjustment in form or structure, following on change in size of plants, may seem to be, the many inter-related factors, which are responsible for bringing about these adjustments, are at work primarily in the apical growing region, and must be studied there.

APPENDIX A.

TYPES OF FLORAL CONSTRUCTION IN ANGIOSPERMS.

A description of a few types of Flower, together with notes on the Natural Families to which the Plants that bear them belong, are here added, so as to illustrate more fully the methods of floral construction described in Chapter XIV. They have been selected partly because they are common Flowering Plants easily accessible to all; partly because they represent characteristic features of the Natural Families whose products are of importance to Man; partly also because of their biological interest in relation to the production and dispersal of seeds. A study of such examples will give some idea of the various forms which the flowering shoot may assume. A few added notes will help to explain in the several examples the biological advantages which follow from the form adopted.

CONSPECTUS OF THE PLANTS DESCRIBED.

MONOCOTYLEDONEAE.

ORDER.	FAMILY.	EXAMPLES.
Liliales	Liliaceae	(1) Tulip, (2) Squill.
	Amaryllidaceae	(3) Snowdrop, (4) Pheasant's Eye.
	Iridaceae	(5) Iris, (6) Crocus.
Orchidales	Orchidaceae	(7) Orchis.
Glumales	Juncaceae	(8) Wood-Rush.
	Cyperaceae	(9) Cotton-Grass, (10) Sedge.
	Gramineae	(11) Rye-Grass.

DICOTYLEDONEAE.

(Dicotyledoneae—Choripetalae).

ORDER.	FAMILY.	EXAMPLES.
Salicales	Salicaceae	(12) Goat Willow.
Curvembryeae	Caryophyllaceae	(13) Ragged Robin, (14) Campion.
Polycarpicae	Ranunculaceae	(15) Marsh Marigold, (16) Buttercup, (17) Aconite.

ORDER.	FAMILY.	EXAMPLES.
RHOEADALES	Papaveraceae	(18) Poppy.
	Cruciferae	(19) Mustard, (20) Wallflower.
GERANIALES	Geraniaceae	(21) Geranium, (22) Pelargonium.
TRICOCCAE	Euphorbiaceae	(23) Spurge.
SAXIFRAGALES	Saxifragaceae	(24) Saxifrage, (25) Currant.
ROSALES	Rosaceae	(26) Apple, (27) Strawberry, (28) Rose, (29) Cherry.
LEGUMINALES	Leguminosae	(30) Trefoil, (31) Pea.
UMBELLALES	Umbelliferae	(32) Cow-Parsnip.

(DICOTYLEDONEAE—SYMPETALAE).

(*a*) *Pentacyclicae.*

BICORNES	Ericaceae	(33) Heath, (34) Bilberry.
PRIMULALES	Primulaceae	(35) Primrose.

(*b*) *Tetracyclicae.*

PERSONATAE	Solanaceae	(36) Nightshade, (37) Potato.
	Scrophulariaceae	(38) Figwort, (39) Foxglove, (40) Speedwell.
VERBENALES	Labiatae	(41) Dead-Nettle, (42) Sage.
SYNANDRAE	Compositae	(43) Groundsel, (44) Ox-eye, (45) Cornflower, (46) Dandelion.

MONOCOTYLEDONEAE.

These Plants are characterised by the embryo bearing only one cotyledon. The leaves are as a rule alternate, with simple form, parallel venation, and a broad sheathing base. The stem and root show no secondary thickening of the type usual in Dicotyledons, their vascular strands having no cambium. The flower is constructed usually of five alternating whorls of parts, and each whorl is commonly trimerous. Most of the Monocotyledons are perennials. They include Grasses, Sedges, Orchids, and Palms. Many are rhizomatous and bulbous plants that are grown for the beauty of their flowers.

ORDER: LILIALES.

This very large Order includes plants which are naturally related together by their floral structure, though diverse in vegetative habit. The type dates back to the Cretaceous Period, and it may be accepted as underlying the floral construction of most of the Monocotyledons. Most of them are perennials, with creeping or bulbous stock (Lily, Tulip, Solomon's Seal): but some are tree-like (*Dracœna*), or shrubby

(*Ruscus*), while some are climbers (*Smilax*, *Dioscorea*). They have for the most part entire leaves, with sheathing base, and parallel venation: but the Dioscoreaceae are exceptional in having broad reticulate leaves.

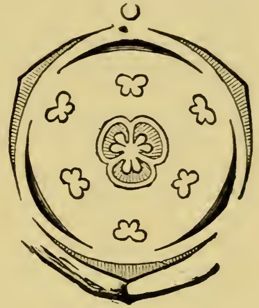

FIG. 455.
General floral diagram for trimerous Flower of the Liliales.

The flowers are constructed on a type which may be accepted as a general underlying plan for Monocotyledons, being composed of five alternating whorls of parts. The number of parts in each whorl is commonly three; but other numbers may be found, such as two (*Maianthemum*), or four, or even five (*Paris*, *Aspidistra*). The floral formula is P. $n+n$, And. $n+n$, Gyn. (n), and the floral diagram as in Fig. 455. The more primitive Liliiflorae have hypogynous flowers, but they are epigynous in the Amaryllidaceae and Iridaceae, a condition regarded as later and derivative. The ovary has one loculus for each carpel, and the anatropous ovules are seated on their incurved margins, which are fused to form an axile placenta (Fig. 457). The flowers are usually of large size, and are often conspicuous by colour and scent (Lily, Tulip). They show steps of progressive fitness for the nursing of the ovules, by various degrees of fusion of the carpels, and of sinking of the ovary from the superior position of the Liliaceae to the inferior of the Amaryllidaceae and Iridaceae. Progressive steps may also be traced in the perfection of the pollination-mechanism.

FIG. 456.
Superior gynoecium of *Lilium*, showing relative position of ovary (*ov*), style (*sty*), and stigma (*stig*). F. O. B.
B.B.

Family: LILIACEAE. *Example*: THE TULIP.

The Liliaceae may be held to represent a primitive type of the Liliiflorae. They include a large number of familiar bulbous plants, such as Garlic, Hyacinth, Tulip. The latter may be taken as an example.

(1) The Tulip plant (*Tulipa gesneriana*) at the flowering period consists of the underground bulb, bearing roots downwards from the margin of the disc-like stem, upon which the storage-scales of the bulb are seated. From its apex rises an elongated stem bearing a few foliage leaves, and a single terminal flower which is radially symmetrical. Provision for the next season is made by one or more buds in the axils of the bulb-scales, which grow into new bulbs, and each may produce a flower. Compare bulb of Hyacinth (Fig. 132, p. 198). The analysis of the flower is as follows:

Perianth segments 3 + 3, polyphyllous, inferior.
Androecium stamens 3 + 3, free, hypogynous.
Gynoecium carpels 3, syncarpous, superior. *Stigma* three-lobed, sessile. *Ovary* trilocular. *Placentation* axile. *Ovules* numerous, anatropous (Figs. 456, 457).

The floral diagram (Fig. 455) shows the regular alternation of the successive whorls of three parts. As those of each whorl are all of equal size, and excepting the carpels all separate from one another, the Tulip may be held as a relatively primitive type of Liliaceous flower. But the syncarpous state here seen is probably not the most primitive. In *Colchicum*, with its Crocus-like habit, the carpels are incompletely fused, and each has its separate style and stigma : an indication of a primitive apocarpous state. Other members of the Order show various steps in cohesion and adhesion of the outer parts. For instance, in (2) the Wild Hyacinth (*Scilla nutans*, Sm.) the stamens are adherent to the perianth-segments (epiphyllous). In the Grape-Hyacinth (*Muscari*), and the Lily of the Valley (*Convallaria*) the segments of the perianth are coherent into a bell. In some Lilies the perianth may form a long tube, while the style is proportionally elongated. But still the ovary is *superior* ; even in *Colchicum*, where it is below ground, it stands above the insertion of the long tube-like perianth. In others, as in *Hemerocallis*, the gamophyllous flower is zygomorphic. Thus the primitive state seen in the Tulip may be modified in relation to pollination by insects.

FIG. 457.

Transverse section of the superior ovary of Lily, showing the three syncarpous carpels, bearing the anatropous ovules on their infolded margins. F. O. B.

Pollination. The flower of the Tulip is conspicuous by its size and colour ; but there is no honey, though in the nearly allied *Fritillaria* a large honey-gland lies at the base of each perianth-segment. The Tulip is visited by insects for its pollen, and so crossing may be effected ; but it is not a specialised mechanism.

The *fruit* of the Liliaceae is either a capsule, splitting by longitudinal slits, and so shedding the seeds, which are flattened and readily carried by the wind ; or it may be a berry as in Lily of the Valley, or Asparagus, and thus be distributed by birds.

The Liliaceae are world-wide in distribution. Many are cultivated for the beauty of their flowers. Some yield fibres for cordage (*Phormium*), others valuable drugs (Aloe. *Colchicum*, Sarsaparilla (*Smilax*)) : others are grown as vegetables, *e.g.* Onion, *Asparagus*.

Family : AMARYLLIDACEAE. *Examples :* SNOWDROP, NARCISSUS.

Those Liliales which have the same floral plan as the Liliaceae, but with an *ovary inferior*, are grouped as Amaryllidaceae. But there is no sharp line of demarcation between the hypogynous and the epigynous types. Some genera show an intermediate state, their half-inferior ovary suggesting how the carpels may have sunk into the tissue of the receptacle, thus giving the ovules better protection, and nearer proximity to the sources of supply. The floral diagram is the same for the Amaryllidaceae as for the Liliaceae. (3) The Snowdrop (*Galanthus nivalis*, L.), or the Snow-flake (*Leucojum*, L.)

illustrate a primitive state of this epigynous type where all the parts of perianth and androecium are separate. A more advanced type, showing not only epigyny but also cohesion of the perianth, and adhesion of the stamens to it, is seen in *Narcissus*.

(4) In the Daffodil (*N. Pseudo-Narcissus*, L.), the same floral diagram (Fig. 455) and floral formula apply. But here the coherent perianth springs from the summit of the inferior ovary as a tube which separates upwards into six widely spreading segments. At the level where they diverge the tube appears to be continued into a wide trumpet-shaped *corona*. This is an accessory formation, and only appears late, after the other parts have been formed. From the inner surface of the perianth-tube, near to its base, arise the six epiphyllous stamens. They are closely grouped round the central style, whose stigma projects beyond them. Honey-secretion is provided by three deep glands in the septa of the ovary, and it flows into the base of the tube. The size of the flower allows entry to *humble-bees*, which, passing from flower to flower, make cross-pollination probable.

Narcissus poeticus, L., the Pheasant's Eye, is a species of similar construction, but with white perianth, and a corona fringed with red. Its tube is, however, narrow, and the anthers and stigma almost fill its opening. Thus it is inaccessible to bees ; but its white colour, heavy scent, and the length of the narrow tube fit it for pollination by long-tongued, night-flying *moths*. These three types of Amaryllids show how the same floral structure may be modified as a mechanism for pollination by different types of insects.

The Amaryllidaceae are less numerous in genera and species than the Liliaceae, but are widely spread, especially in the Mediterranean region, and at the Cape. They include many bulbous plants, and some that yield fibres (*Agave*).

Family : IRIDACEAE. *Example :* YELLOW FLAG.

(5) Those Liliales which have inferior ovary and only three stamens, are grouped as the Iridaceae, of which the native Yellow Flag (*Iris Pseudacorus*, L.) serves as an example. It has a branched and strongly rooted perennial stock (see Fig. 129, p. 196) and each branch ends in an annual foliage-shoot, with sword-shaped leaves, sheathing at the base. The apex of certain shoots extends upwards into the cylindrical flowering stems, which bear their first flower distally ; a second flower arises subsequently in the axil of a bract below it, and others may follow, in sympodial arrangement.

The large yellow flower is composed of the following parts (Fig. 458) :

Perianth, segments 3 + 3, gamophyllous at the base, superior ; the outer series broad and recurved, the inner narrower, and erect.

Androecium, stamens 3 + 0, free, epigynous, anthers opening outwards. It is the inner series that is absent.

Gynoecium, carpels 3, syncarpous, styles three petaloid ; ovary inferior, trilocular with axile placentation ; ovules numerous, anatropous (Fig. 213, p. 291).

The *fruit* is a dry loculicidal capsule, and the flattened albuminous seeds are scattered by the wind.

Pollination. The flower of *Iris* is more specialised in relation to insect-agency than most of the Iridaceae. Many of them, such as *Ixia*, or *Sisyrinchium*, have flowers not unlike the Snowdrop, but with only three stamens. *Gladiolus* has the same, but it is slightly zygomorphic. (6) *Crocus* has a tubular perianth greatly elongated, so that while the ovary is seated just above the underground corm, the perianth, stamens, and stigmas are above ground. But *Iris* is the most specialised of them all. Its peculiar features are that the three stamens, which open outwards, are enclosed each between one of the broad outer perianth-segments and one of the three broadly petaloid styles (Fig. 458, III, IV.). The tip of each style is two-lobed, and bears a projecting lip on its lower and outer surface. This is the *stigma*. The fact that the styles are opposite the stamens, and these opposite the outer perianth-segments, shows that it is the *inner* stamens that are wanting (V.). Honey is secreted by the inner surface of the perianth-tube, and collects round the base of the styles. Each third of the flower may be pollinated independently by humble-bees, which force their way between the perianth-segment and its opposing style. On entering, if they bring pollen, it is swept off on the projecting stigmatic lip; the stamen then deposits a fresh supply of pollen upon his body, which he carries away. Self-pollination is mechanically impossible; but cross-pollination results with high probability from a succession of visits, either to other thirds of the same flower or to different flowers. In many forms of *Iris* the parts fit so exactly as to exclude small and weak insects that would not effect pollination, but this exclusion is less perfect in others. *Iris* may be held to show a culmination of pollination-mechanism as seen in the Liliales.

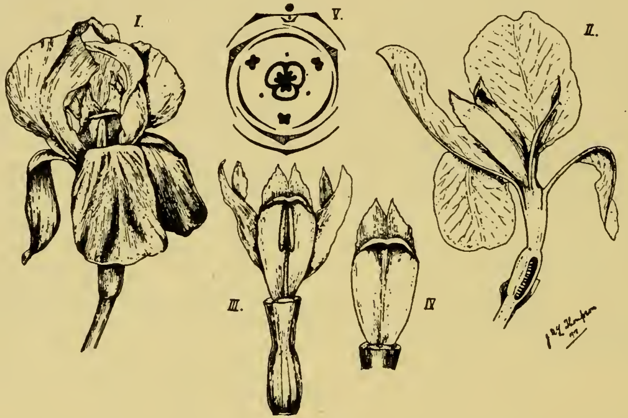

Fig. 458.

Iris Pseudacorus, L. I. Complete flower. II. Same cut in median section. III. Flower with perianth removed. IV. Single lobe of petaloid style, with stigmatic lip. V. Floral diagram.

The Iridaceae are widely spread; but are specially frequent in the Cape Flora. They include plants grown for their showy flowers (*Crocus*, *Iris*, *Gladiolus*, *Ixia*). The dried rhizomes of species of Iris give the "Orris-root," and the stigmas of *Crocus sativus* are the source of Saffron.

ORDER: ORCHIDALES.

Family: ORCHIDACEAE. *Example*: SPOTTED ORCHIS.

(7) The spotted Orchis (*Orchis maculata*, L.), which flowers early, in damp grassy ground, will serve as an example of a still higher specialisation of the flower for cross-pollination by insect-agency, which characterises the Orchidaceae. The plant is perennial, and in summer is seen to consist of an

FIG. 459.

Whole plant of *Orchis maculata*, including the swollen mycorhizic roots. (After Figuier.)

upright axis bearing sheathing leaves, and a distal spike of flowers. This springs from the apex of a palmate storage-tuber of the previous year, now shrivelled ; while a second similar tuber, young and plump, is developing as storage for the next season (Fig. 459). The new tuber bursts through from the axil of one of the lowest leaves, and bears a terminal bud seated on swollen mycorhizic roots directed obliquely downwards. Normal roots also arise from the base of the shaft. By a succession of such tubers the plants perennate from year to year.

Each flower of the spike is sessile in the axil of a large leafy bract, and is of an epigynous Liliifloral type, but specialised so as to be an accurate mechanism for pollination (Fig. 460, I.). The inferior ovary itself constitutes the stalk of attachment of the sessile flower. It shows ridges, the spiral turns of which indicate that the flower has been inverted by a half-circle-twist of the ovary (*resupinate*) (II. III.). The posterior side is thus turned to the front facing the bract. This is essential for the success of the *strongly zygomorphic flower* as a pollinating mechanism.

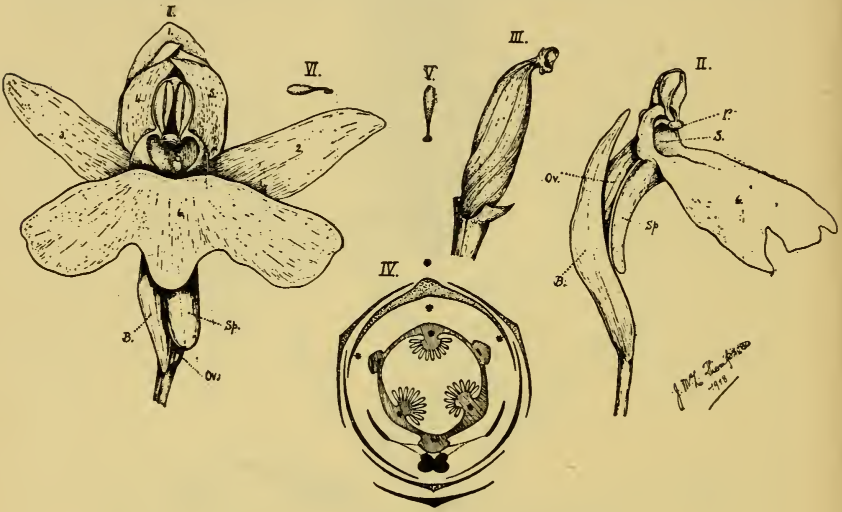

FIG. 460.

Flower of *Orchis maculata*, L. I. Whole flower in frontal view. II. Lateral aspect, perianth partly removed. III. Young fruit. IV. Floral diagram. V. VI. Pollinia in erect and curved positions. 1-6=perianth-segments ; (1) is really the anterior, but by resupination the posterior segment ; 6 is the labellum, actually posterior, but by resupination the anterior segment. *B*=bract ; *sp*=spur ; *ov*=ovary ; *s*=stigma ; *r*=rostellum.

The ground-plan of the flower is shown in Fig. 460, IV. ; it consists of :

Perianth, segments 3 + 3, polyphyllous, superior. The three outer segments are small, and of about equal size, the odd one being anterior (1). The three inner are very unequal. The posterior segment, turned by resupination to the front, forms a large platform, or *labellum* (6), and it is dilated downwards into a long *spur* (*sp*). The two smaller, together with the outer anterior segment, form a hood-like group over the *column*, which rises just behind the open entrance to the spur. It is the result of fusion of the single stamen with the short style.

The *Androecium* is represented only by a single *anterior, fertile stamen*, which, owing to the resupination, faces the observer: each of its two purple anther-lobes shows when ripe a longitudinal slit of dehiscence. The downward-directed, but really apical end of the anther is covered by the small globular *rostellum*, which obstructs the entrance to the spur (Fig. 460, I. II.).

The *Gynoecium* consists of three carpels, syncarpous and inferior. Of the three stigmas one which is not receptive is represented by the rostellum (*r*), the other two are merged into a hollow oval stigmatic surface (*s*) situated below the rostellum. A transverse section of the ovary, preferably of a flower already fertilised, shows a single cavity, with three parietal placentas, and very numerous minute ovules.

The *Fruit* matures as a dry capsule, splitting by six longitudinal slits into three larger and three smaller strips, which remain united at their ends. The minute seeds are scattered by the wind.

Pollination. The flower being resupinate, the large posterior labellum projects forward as a convenient platform for the visiting insect, while the entry to the spur is presented directly to his proboscis just below the column. But the passage is obstructed by the rostellum. On inserting his proboscis this is pushed aside. As it breaks away it lays bare two sticky discs, which adhere to his proboscis, their cement setting firmly in the few seconds during which he is engaged in probing the honey-containing tissue at the base of the spur. On his withdrawing it, the coherent contents of the two anther-lobes are themselves withdrawn, and appear as *club-shaped pollinia*, fixed by their sticky discs in an erect position. But in a few seconds this position changes, and they curve strongly forwards (Fig. 460, V. VI.). Meanwhile, if he has flown to another flower, they are in such a position that as he inserts his proboscis, they will impinge directly on its stigma, which is below the rostellum. The pollen, which is in coherent masses, is then held by the sticky stigma. Thus cross-pollination is effected with a high degree of certainty, while self-pollination is mechanically impossible. The efficiency of the mechanism is shown by the constancy with which the Spotted Orchis sets its fruit as it grows in the open. This is only one of the very various methods of pollination seen in this wonderful family. For further details reference may be made to Darwin's *Fertilisation of Orchids*.

The Orchidaceae are a very large family, chiefly tropical, and often epiphytic, though represented in the British Flora by many ground-growing species. Their interest is chiefly biological and spectacular. One of the few useful products is *Vanilla*, the dried fruit of an American climber.

ORDER: GLUMALES.

The Cyperaceae and Gramineae, which are grouped under this heading, have in common hypogynous flowers, more or less specialised in relation to *pollination by the wind*, while their flowers are often grouped in dense inflorescences. The Juncaceae may be associated with them as a Liliifloral type only slightly modified. The construction of their flowers may be referred in origin to the Liliaceous type, but the perianth is inconspicuous, and the pentacyclic, usually trimerous structure is more or less reduced in the number of the parts. The name *Glumiflorae* refers to the fact that the bracts are usually stiff and dry, and are called *Glumes* or *Paleae*, which constitute the "chaff" of Grasses. The gynoecium is superior, and though it may be trilocular with numerous ovules in the less specialised forms, in the more advanced Sedges and Grasses it is unilocular, and contains only a single ovule. The fruit then matures as a Grain, or Nut. The plants are mostly annual or perennial herbs, frequently with long internodes. The alternate leaves are sheathing below, with a simple grass-like blade, and often a ligule projecting upwards at the junction of sheath and blade.

Family : JUNCACEAE. *Example :* FIELD WOOD-RUSH.

(8) The Field Wood-rush (*Luzula campestris*, Willd.) is a perennial very common on poor grass-land. It has a Grass-like habit, but its flowers are constructed on the Lily-type. The root-stock produces leaves with sheath and blade, but no ligule. The axis elongates upwards into an inflorescence

FIG. 461.

Juncus lamprocarpus. *a*, Part of an inflorescence; single flower (*b*) and gynoecium (*c*) magnified. (Strasburger.)

FIG. 462.

Eriophorum augustifolium. 1, inflorescence. 2, a single spikelet. 3, single flower. 4, flower with bract removed. 5, fruit. (After Hoffmann; 1, about nat. size; the others × 3-5.) (Strasburger.)

bearing numerous flowers in a compact cymose group, with chaffy bracts. The flower is constructed of :

Perianth, segments 3 + 3, polyphyllous, inferior, dry and chaffy.

Androecium, stamens 3 + 3, free hypogynous.

Gynoecium, carpels 3, syncarpous, superior, with three long feathery stigmas, united below into a short style. Ovary trilocular, with one ovule in each loculus (Fig. 461, *b*, *c*).

Fruit, a capsule dehiscent loculicidally. Seed with starchy endosperm.

Pollination. The flower is strongly *protogynous* ; the feathery stigmas project, while the perianth is still closed over the unopened stamens. Later the stigmas wither, the perianth expands, and the anthers burst, setting free the dry dusty pollen, which is readily shaken out, and carried away by the breeze. There is no honey-secretion, or other attraction for insects, but cross pollination is almost certain by the agency of wind. Self-pollination is prevented by the marked protogyny. Nevertheless fruit is almost uniformly produced.

The chief genus is *Juncus*, to which the Rushes belong. They are mostly plants of moist habit, and of little feeding value for stock. Their presence in grass-land is an indication of the need for draining.

Family : CYPERACEAE. *Examples :* COTTON-GRASS, SEDGE.

(9) The Cotton-Grass (*Eriophorum vaginatum*, L.) is a tufted perennial herb of swampy moorlands, marked by its single cottony heads when in fruit. The flowering head rises about a foot from the root-stock, and is composed of a single spikelet of flowers in the axils of glume-like bracts. Each hermaphrodite flower is constructed as follows :

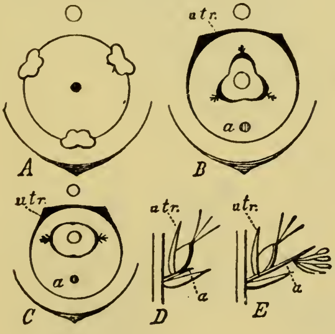

FIG. 463.

A, floral diagram of a male flower of *Carex* ; *B*, of a female flower with three stigmas ; *C*, of a female flower with two stigmas. *D*, diagram of female flower of *Carex*. *E*, diagram of the hermaphrodite spikelet of *Elyna* : *a*, secondary axis ; *utr*. utricle or bract of secondary axis. (After Eichler.) (Strasburger.)

Perianth, inferior, represented by numerous bristles, which are developed relatively late, and mature into the " cotton " of the fruit.

Androecium, stamens three, hypogynous, representing those of the inner whorl.

Gynoecium, carpels three, syncarpous, and superior, with three stigmas. The ovary is unilocular, with a solitary ovule (Fig. 462).

Pollination is effected by the wind, which also carries out the transfer of the fruit.

Fruit, a trigonous nut, with the cottony tuft of the persistent perianth attached at its base. The floral structure suggests a modification of the Liliaceous type, by cottony development of the perianth, loss of the three outer stamens, and reduction of the ovary to a single loculus with one ovule.

(10) For the structure of a Sedge, any of the following species of *Carex* will serve (*C. glauca*, Murr ; *pallescens*, L. ; *pendula*, Huds. ; *hirta*, L. ; *flava*, L. ; or *binervis*, Sm.). The Sedges are perennial herbs of swampy ground, which

put up long flowering shafts, each bearing several spikes of *unisexual flowers* (Fig. 463). In the species named, one or more of the distal spikes bears only *male flowers*: the lower lateral spikes bear *female flowers*. In the axil of each glume-like bract of the male spike is a male flower consisting only of three stamens, with no perianth or gynoecium. In a similar position on the female spikes there are found flask-shaped bodies (*perigynia*), through the open throat of which at flowering a three-branched stigma projects. The *perigynium is a bract enveloping the female flower*, which has no perianth, and no androecium, but consists of three, or sometimes two carpels, syncarpous and superior. The ovary is unilocular, the ovule solitary, and the fruit a nut. Here the flower is still more simple than in the Cotton-Grass, for there is no perianth, and as the flowers are unisexual, all that remains are the three stamens in the male, and the three carpels in the female. *Pollination* is by the wind. A large number of flowers of simple structure are aggregated in the inflorescence: cross-pollination is therefore probable.

The Sedges are of little value for fodder. Drainage of the wet ground in which they grow promotes the more valuable Grasses, from which they are distinguished by their solid stems and leaf-divergence of $\frac{1}{3}$, while in Grasses it is $\frac{1}{2}$: also by the median position of the embryo in the seed, while in Grasses it is placed laterally.

Family: GRAMINEAE. *Example:* COMMON RYE-GRASS.

(11) The Rye-Grass (*Lolium perenne*, L.) is a common grass of meadows and road-sides; its variety *italicum* is often cultivated for fodder. It has leafy stolons and ascending flowering shoots, and it is easily recognised amongst common Grasses by their long flattened form. Its flowers open in

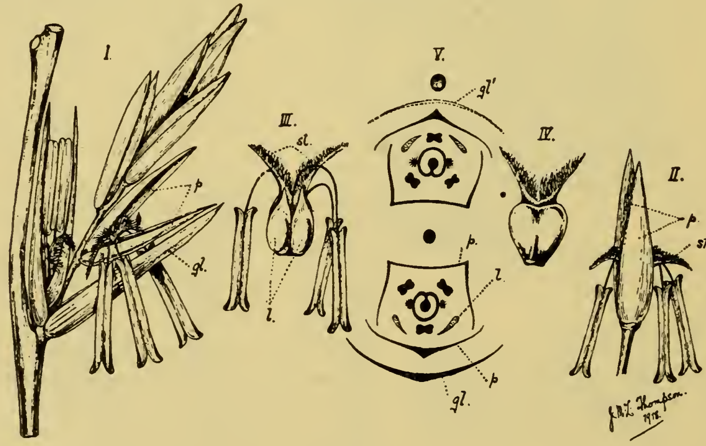

FIG. 464.

Inflorescence and flower of *Lolium perenne*. I. shows part of the main rachis, with one lateral spikelet in the axil of the single glume (*gl*). II. a single flower with its two paleae (*p*), pendent stamens, and feathery stigmas (*st*). III. flower dissected out, showing lodicules (*l*). IV. the gynoecium. V. floral diagram: *gl*=glume; *gl'*=glume which is wanting in *Lolium*; *p*=paleae; *l*=lodicules.

succession, so that it can be obtained in the flowering state throughout the summer. The flowers can be made to open at any time by keeping them warm, and in water.

The inflorescence is borne on a long stalk, above the uppermost foliage leaf, which has a split sheath, ligule, and lamina. It is a compact, compound spike, composed of *spikelets* placed edgewise, alternately on its two sides, with one terminal. Each lateral spikelet, which consists of an axis bearing flowers alternately in two rows, arises in the axil of a bract, or *outer glume* (Fig. 464, I.). In most Grasses there is a second, or *inner glume*, on the side opposite to the outer; but this, being unnecessary for protection in the dense inflorescence of the Rye-Grass, is not present, except in the terminal spikelet. Each flower is ensheathed in two further bracts or *paleae*: the *lower* and outer is *anterior*, the *upper* and inner is *posterior*, and the flower itself lies between them. At flowering they gape widely apart, so as to expose the parts of the flower (I). If a flower be found in this condition, or if the lower palea be forced back, the flower, as seen from the anterior side, will show the following parts:

(i) Two *lodicules*, which are minute, colourless, hypogynous scales, right and left of the median plane (*l*). It is by their swelling that the paleae are forced apart at the time of flowering.

(ii) Three *stamens* (*st*), hypogynous, free, with long flexible filaments, and versatile anthers, bearing powdery pollen. One stamen is median and anterior, the two others obliquely posterior.

(iii) The *gynoecium*, lying centrally, consists of a pear-shaped superior ovary, grooved on the posterior side, and bears distally, right and left, two feathery stigmas. Dissection shows a single ovule in the ovary.

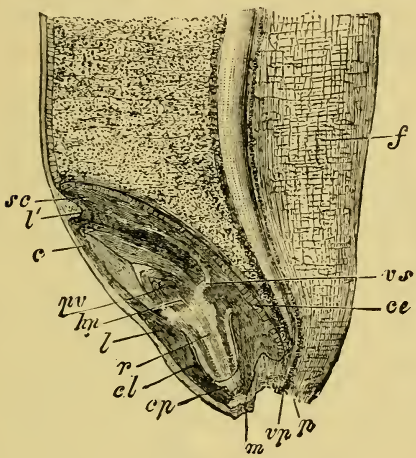

FIG. 465.

Part of a median longitudinal section of a grain of Wheat, showing embryo and scutellum (*sc*). *vs*=vasc. bundle of scutellum; *ce*=its columnar epithelium; *l'*=ligule; *c*=sheathing part of cotyledon; *pv*=vegetative cone of stem; *hp*=hypocotyl; *l*=epiblast; *r*=radicle; *cl*=root sheath; *m*=micropyle; *p*=funiculus; *vp*=vascular bundle of funiculus; *f*=lateral wall of groove; *cp*=pericarp. (× 14.) (After Strasburger.)

The number of such flowers in each spikelet varies: 8 to 10 are common numbers in the Rye-Grass, and they open at intervals in acropetal succession.

The flower may be held to be of Liliifloral type, reduced in relation to wind-pollination. The perianth is represented by the two lodicules, corresponding to the oblique anterior segments of the inner series, which being of use in separating the paleae at flowering have survived. The stamens correspond in position to the outer whorl of the Liliiflorae, while the gynoecium is held to consist of a single carpel, corresponding to the anterior carpel of the Liliiflorae.

This floral structure is very constant in the Grasses, but the flowers are variously disposed in their inflorescences. The Rye-Grass may be taken as a good example for the Family, and it is easily recognised.

The inconspicuous flowers, versatile anthers, dry dusty pollen, and expanded feathery stigmas clearly indicate *wind-pollination*, with promiscuous intercrossing. Most Grass-flowers are homogamous, that is, stamens and stigmas mature simultaneously, but some are protogynous (*Alopecurus*).

The *fruit* is a dry nut, containing one albuminous seed and a *lateral embryo.* Its structure is well illustrated by the grain of wheat or maize (Fig. 465).

The Gramineae are the most important Family in supplying the wants of man. Their fruits are the various cereal grains (Appendix B) : their foliage gives fodder for animals : sugar is yielded by the Sugar Cane ; and the Bamboo serves most various uses to the dwellers in the Tropics.

DICOTYLEDONEAE.

These Plants are characterised by the embryo bearing two cotyledons. The leaves are net-veined, usually with a narrow base, and a definite petiole. The stem and root show secondary thickening by means of a cambium. The flowers are usually pentamerous, or tetramerous, with distinct calyx and corolla. The plants are perennial or annual, many of the former developing as shrubs or trees.

The Dicotyledons are divided into two large series, according to the separateness or coherence of their petals. This distinction does not serve a like purpose in the classification of the Monocotyledons ; it has already been seen that the very natural Family of the Liliaceae is variable in this respect. But in the Dicotyledons the same variability within natural families is exceptional : therefore this distinction serves to give a natural separation of them into Polypetals, or *Choripetalae*, with the petals all separate from one another ; and the Gamopetals, or *Sympetalae*, where there is a coherence of the petals to form a united, usually tubular corolla.

The former is undoubtedly the more primitive state. It repeats the condition usual in the vegetative region, and it is characteristic of those less specialised flowers which on many other grounds are held as less advanced. The gamopetalous state is characteristic of flowers which are more specialised as pollinating machines, and they may therefore be held as more advanced. But there is no reason to hold all plants showing gamopetaly as necessarily related to one another : this would involve the assumption that the advance had happened only once in the course of Evolution. It seems probable that in a plurality of evolutionary lines the advance was made to gamopetaly, and the student should be prepared to recognise this in any sequence in which comparison makes it appear probable. In accordance with the views thus briefly sketched the Polypetals, or *Dicotyledoneae—Choripetalae*, will be taken first.

DICOTYLEDONEAE—CHORIPETALAE.

ORDER: SALICALES.

Family: SALICACEAE. *Example:* THE GOAT WILLOW.

(12) The numerous native species of Willow are trees, or shrubs, or dwarf undershrubs, which live in damp situations; almost any of them would serve to illustrate their very simple floral structure. In the large shrubby Goat-Willow (*Salix caprea*, L.) the flowers appear grouped to form the well-known Catkins or "Palms." These are of two sorts, distributed on different plants (*dioecious*) (Fig. 466). The *male catkins* appear bright yellow when in bloom, from their projecting stamens; the *female catkins* are more slender, and of olive-green colour. In each case the catkin is a spike. Its main axis bears darkly-coloured bracts, and in the axil of each of these is a single very simply-constructed flower.

FIG. 466.
Catkins of the Willow. *a*, male; *b*, female. (After Figuier.)

The *male flower* (Fig. 467, *a*) consists of two stamens, each with a long filament, which bears the anther, with sticky, not dusty pollen. There is no perianth, nor gynoecium; but on the side next the stem is a nectary, which secretes honey freely at flowering (Fig. 468, *A*, *d*). Other species may have three, four, or more stamens, but no other floral parts (Fig. 468, *C*). The *female flower* (Fig. 468, *b*) is also axillary. It consists only of a gynoecium of two carpels joined by their margins to form a unilocular, superior ovary with two-lobed stigma. The ovules are numerous, and the placentation parietal. A honey-gland is present here also between the flower and the main axis (Fig. 469, *A*, *d*).

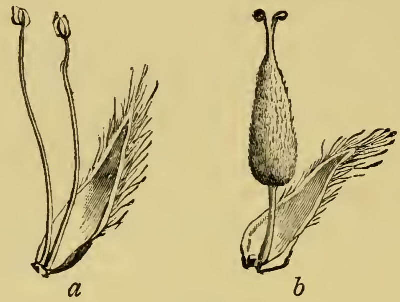

FIG. 467.

Flowers of Willow (*Salix alba*). *a*, male; *b*, female; in each case the subtending bract is also shown. (After Figuier.)

Pollination. The flowers of both catkins are visited freely by insects, both bees and moths, for honey or for pollen. Self-pollination is obviously impossible, for the plants are dioecious; but crossing follows as a natural consequence of the conveyance of the sticky pollen to the protogynous female catkins by insect-visitors.

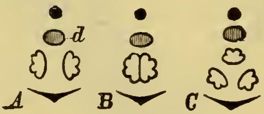

FIG. 468.

Floral diagrams of male flowers of Willow. *A*=*S. caprea*. *B*=*S. purpurea*. *C*=*S. pentandra*. (After Eichler.)

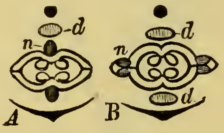

FIG. 469.

Floral diagrams of female flowers of *Salix*. *A*=*S. caprea*. *B*=*S. alba*. (After Eichler.)

The *fruit* is a tough capsule, which splits longitudinally, exposing the seeds, each with a tuft of silky hairs attached to its base, by which it is transferred by the wind.

ORDER: CURVEMBRYEAE.

Family: CARYOPHYLLACEAE. *Examples:* RAGGED ROBIN, RED CAMPION.

(13) The Ragged Robin (*Lychnis Flos-cuculi*, L.) is a herb of damp grassy ground, with perennial root-stock from which arise upright stems with simple leaves in alternate pairs. The inflorescence is a definite, regular dichasial cyme: that is, the main axis ends in the first flower; branches arising in the axils of the last leaves again terminate each in a flower, and so on (compare Fig. 179 *B*, p. 258). The flower is of a radial type, with peculiar tattered pink petals, which gives the name (Fig. 470). Its constitution is as follows:

Calyx, sepals 5, gamosepalous, inferior, dilated below, and serving as a mechanical support to the weaker parts within.

Corolla, petals 5, polypetalous, inferior, deeply notched, and again divided, bearing paired ligules at the sharp angle of the claw of each.

Androecium, stamens 10, free, hypogynous, of varying length during flowering. The 5 outer opposite the sepals, the 5 inner opposite the petals.

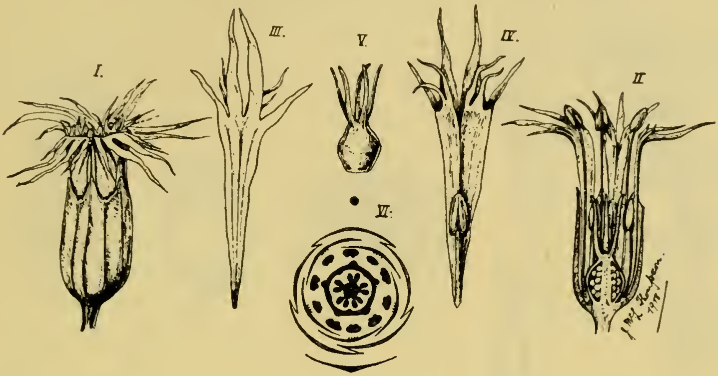

FIG. 470.
The Ragged Robin (*Lychnis Flos-cuculi*, L.) I. whole flower. II. same in section. III. petal with ligule, abaxial view. IV. petal with ligule and petaline (inner) stamen, adaxial view. V. gynoecium. VI. floral diagram.

Gynoecium, carpels 5, syncarpous, superior; ovary unilocular, ovules numerous, on free central placenta. Styles and stigmas 5, rising separately from the apex of the ovary.

Pollination. Nectar is secreted at the base of the stamens, and the flowers are visited by many insects, especially butterflies and moths. The flowers are *protandrous*; in the first stage the 5 outer stamens shed their pollen at the entrance of the tube; later the 5 inner stamens do the same; finally the 5 stigmas grow up and fill the entrance to the flower. An insect visiting the flower in either of the first stages will remove pollen on its proboscis, which it may deposit on another flower in the third stage. Intercrossing is thus probable, though self-pollination is possible.

(14) In the Red Campion (*Lychnis diurna*, L.), two types of plant are found: some with thinner stems and smaller leaves bear only staminate flowers, others with more robust habit bear pistillate flowers. These should be examined and compared (Fig. 471). In the staminate flowers the Calyx and Corolla are essentially as above described. Also the 10 stamens, but they are of unequal lengths, and they surround a minute green central process, which represents the *abortive gynoecium*. The pistillate flowers are of like structure; but here the androecium is represented by ten small conical *staminodes*, while the gynoecium is fully developed, with five carpels, a large ovary with five styles and stigmas, and numerous ovules on a free central placenta.

Pollination. Comparing the two species: in both, nectar is secreted at the base of the tube, and protected by hairs, while the weak petals and stamens are supported by the firm gamosepalous calyx. In the Ragged Robin the sexes are separated in time, the flowers being markedly *protandrous*, which gives a probability of intercrossing as a consequence of repeated insect-visits.

In the Red Campion the sexes are separated in space, being borne on distinct plants. This renders self-pollination impossible, and cross-pollination obligatory. That the latter is the derivative state is clearly shown by the presence of the abortive stamens, and pistils.

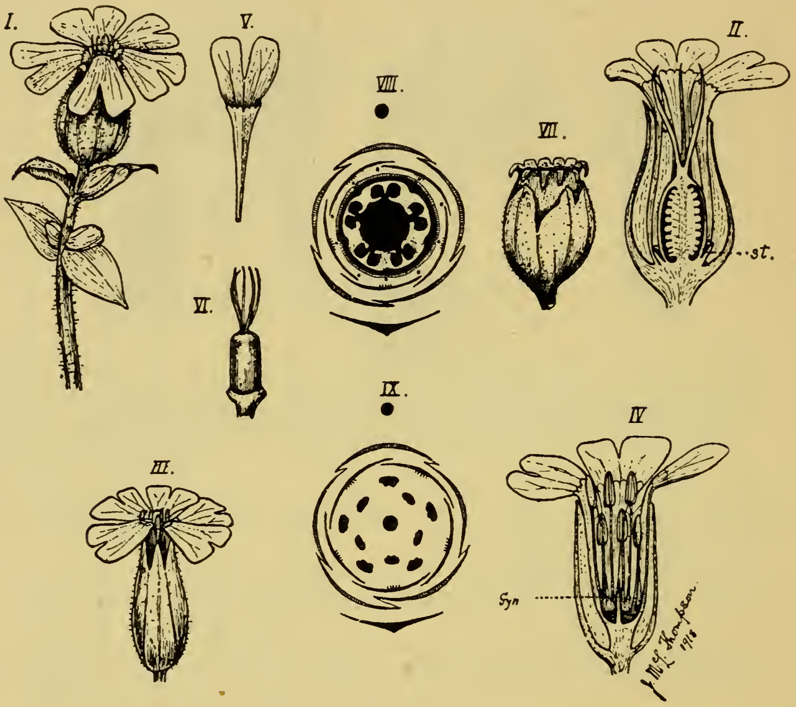

FIG. 471.

Dissections of flowers of *Lychnis diurna*. I., II., VIII., the pistillate flower in which the stamens are represented only by staminodes (*st*). III., IV., IX., the pistillate flowers in which the gynoecium is represented only by a vestigium (*gyn*).

The *fruit* is a dry capsule, which opens by teeth at the distal end (Fig. 471, VII.), and the numerous curved, albuminous seeds are scattered as it is shaken in the wind.

The products of the Order are unimportant. It is related to the Goosefoot Family (Chenopodiaceae).

ORDER: POLYCARPICAE.

Family: RANUNCULACEAE. *Examples:* MARSH-MARIGOLD, BUTTERCUP, MONKSHOOD.

The Buttercup Family is relatively primitive, as indicated by the variability of its floral construction, by the number of its parts, and the character and composition of the perianth: also by the fact that all the parts are inserted separately upon a conical receptacle. It includes herbs or shrubs of temperate and cold climates, with alternate ex-stipulate leaves, having palmate venation. They are mostly acrid, and poisonous.

(15) A simple type of their floral construction is seen in the Marsh-Marigold (*Caltha palustris*, L.), common in wet places. It is a coarse herb, with creeping rootstocks and cordate radical leaves. The flowering stems are sub-erect, with a few leafy bracts and cymose branching. The large yellow flowers consist of:

Perianth, a single series of *petaloid sepals*, 5 or more, imbricate in bud: the outermost obliquely anterior; polyphyllous, and inferior.

Androecium, stamens indefinite (80 to 150), free, hypogynous, dehiscent by lateral slits.

Gynoecium, carpels 5 to 10, apocarpous, superior. They are follicles, with margins turned centrally, to which the numerous ovules are attached in two rows (Fig. 472). Each has a terminal stigma, while near the base of each, on either side, is a group of honey-secreting hairs. Ovule anatropous.

FIG. 472.
Pistil of *Caltha*, with numerous apocarpous carpels. Enlarged.

The *pollination* is not highly specialised; the symmetry is radial; the attractions are colour, and honey on the carpels; there is slight protandry and the stamens mature in succession, so that the supply of pollen is prolonged. There is a probability of intercrossing, but self-pollination is possible.

The *fruit* is a group of follicles, which open by their ventral sutures, and gaping widely upwards allow their seeds to escape (Fig. 473, *A*).

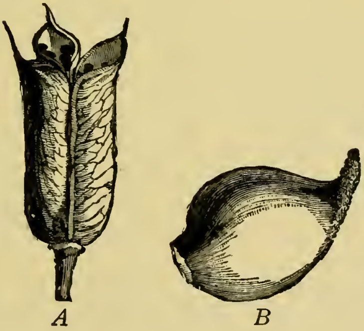

FIG. 473.
A, Follicles of Aconite. (After Figuier.)
B, Achene or nut of Buttercup. (After Figuier.)

(16) The Buttercup (*Ranunculus acris*, L., or other species) is more specialised, having both calyx and corolla; but the flower is constructed on a similar plan; as follows: (Fig. 474.)

Calyx, sepals 5, polysepalous, inferior, imbricate in bud, the outermost being obliquely anterior.

Corolla, petals 5, polypetalous, alternating with the sepals, inferior yellow, with a honey-pouch on the upper face of each, near the base (Fig. 474, 2).

Androecium, stamens indefinite, free, hypogynous; the outermost maturing earliest.

Gynoecium, carpels indefinite, apocarpous, superior: each contains only a single anatropous ovule; otherwise similar in form to the fewer and larger carpels of *Caltha*.

The general conditions of *pollination* are the same as in *Caltha*, but with honey at the base of the coloured petals.

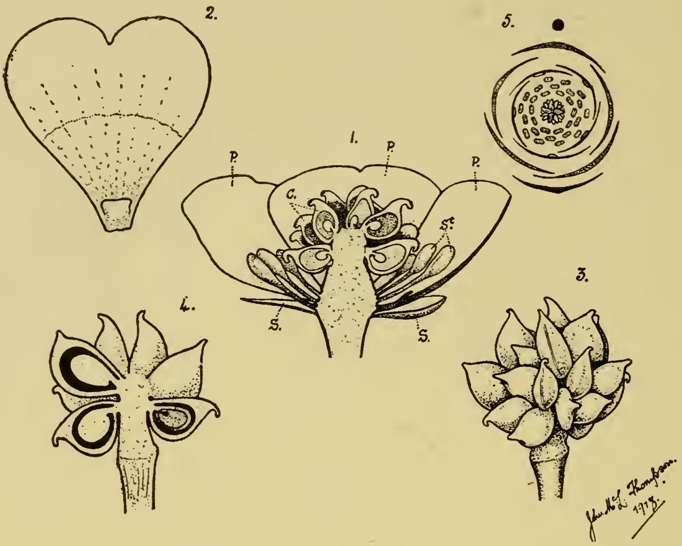

Fig. 474.
Buttercup (*Ranunculus acris*, L.). 1, Flower in median section. 2, a single petal. 3, the gynoecium. 4, the same in section. 5, floral diagram.

Each carpel matures as a dry indehiscent *nut*, falling away with its single seed within (Fig. 473, *B*). Comparing with *Caltha* the flower is more elaborate and probably derived from the type of the Helleboreae, by conversion of the outermost stamens first into honey-leaves, as in *Helleborus* or the Globe-Flower, then into large honey-bearing petals, as in the Buttercup (compare Fig. 189, p. 264). The carpels meanwhile had their ovules reduced to one each, while the propagative power was made up by increase in the number of carpels.

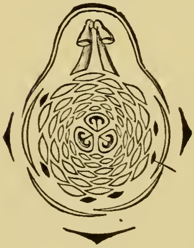

Fig. 475.
Floral diagram of *Aconitum*. (After Eichler.)

(17) The Monkshood (*Aconitum Napellus*, L.) is a perennial with swollen storage roots, commonly grown in gardens: it is an important drug. Its inflorescence is a raceme, developing as a cymose panicle below. The flower shows median zygomorphy (Fig. 475), and consists of:

Calyx, sepals 5, polysepalous, inferior, corresponding in number and position to the Buttercup, but petaloid; the posterior sepal enlarged as a hood.

Corolla, petals usually 8, of which the two obliquely posterior are elongated into stalked glandular spurs (nectaries), covered by the hooded sepal; the rest are small; polypetalous, inferior.

Androecium, stamens indefinite, spirally arranged, free, hypogynous.

Gynoecium, carpels usually 3, apocarpous, superior. Follicles and their dehiscence as in *Caltha*.

Comparing this flower with *Ranunculus* or *Helleborus*, it is clearly a zygomorphic development of the same type. The flower is protandrous. The sepals give colour-attraction, and the honey is conveniently placed for humble-bees in the posterior, spurred petals, while the whole is sheltered by the hood. The protandry makes cross-pollination highly probable from successive visits. After shedding their pollen the filaments curve back so as to expose the receptive stigmas. Self-pollination is thus improbable.

ORDER: RHOEADALES.

Family : PAPAVERACEAE. *Example :* THE RED POPPY.

(18) The Common Corn-Field Poppy (*Papaver Rhoeas*, L.) is an annual which ripens its seeds before the corn is cut, and it is thus ready to spring again in the next season. The plant, which is bristly and contains a milky juice, consists of a leafy stem branched below. The solitary flowers are terminal on their long hispid stalks, the buds hanging down, but the stalks are straight when flowering, and in fruit (Fig. 476). The flower consists of :

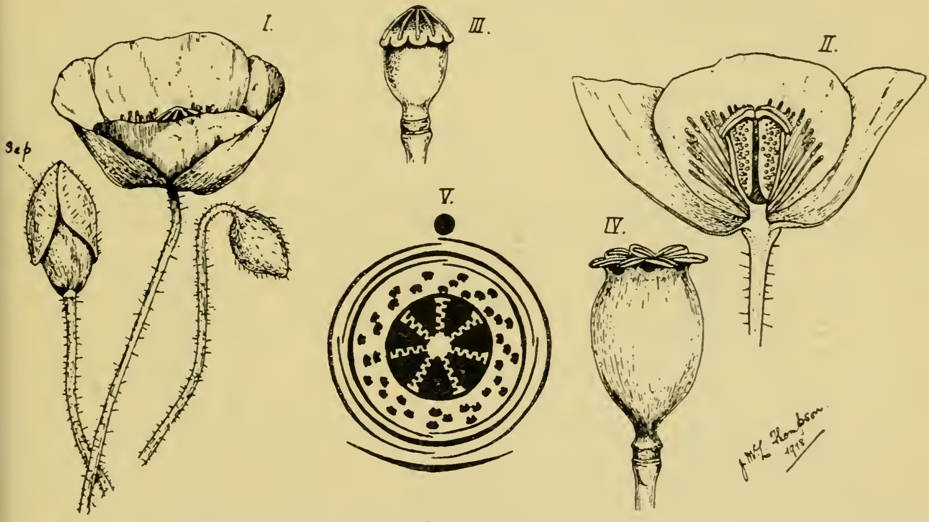

FIG. 476.

Red Poppy (*Papaver Rhoeas*, L.). I. flower and buds, with sepals falling away. II. flower in median section. III. gynoecium. IV. ripe fruit, with dehiscent pores below the star-shaped stigma. V. floral diagram.

Calyx, sepals 2, polysepalous, inferior, falling off at the opening of the bud.

Corolla, petals 4, polypetalous, inferior, wrinkled in bud, two lateral, two antero-posterior.

Androecium, stamens indefinite, free, hypogynous.

Gynoecium, carpels 8-12, syncarpous, superior; the stigma sessile, star-shaped; the rays of the star indicate the number of the carpels. The ovary is unilocular: beneath each ray of the stigma (that is, at the junction of the carpels that compose it) a flat partition extends radially towards the centre, but without reaching it. The small and numerous ovules are borne superficially on these plates. In others of the Poppy family the carpels may be fewer, and in *Chelidonium* only two, as in the Cruciferae. *Fruit,* a dry capsule opening by pores below the stigma. Seeds with oily endosperm: they are scattered out by wind shaking the pore-capsule (see Fig. 244, p. 325).

Pollination. The showy flower attracts insects which come to collect pollen. There is no honey, and the flower is radial: it is not a highly specialised type. Promiscuous cross-pollination may follow from insect visits, but self-pollination is also possible. *Papaver somniferum,* L., the Opium Poppy, belongs to the family.

Family : CRUCIFERAE. *Example :* THE CHARLOCK.

(19) The Charlock, or Field Mustard (*Brassica Sinapis,* Visiani), is the common weed that colours cornfields yellow in early summer. It is an annual, with stem and leaves bristly with stiff hairs. Its germination is shown in Fig. 3, p. 10. Its inflorescence is a raceme, but with the bracts abortive (Fig. 179 *C*). The flower, which is of radial symmetry, consists of:

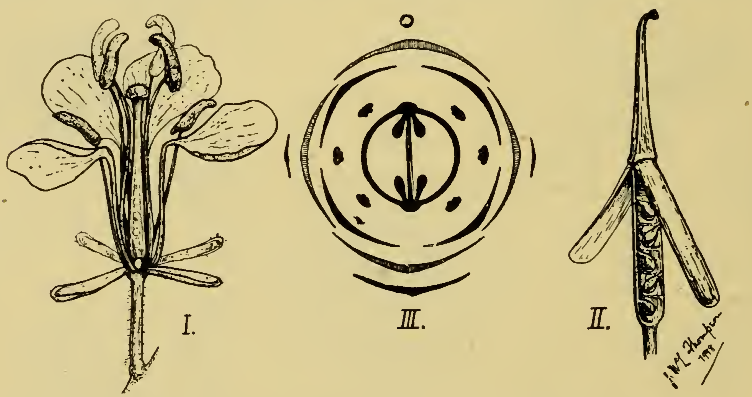

Fig. 477.
Charlock (*Brassica Sinapis,* Visiani). I. flower, with parts slightly displaced. II. ripe and dehiscent fruit. III. floral diagram.

Calyx, sepals 4, polysepalous, inferior; in two pairs, the outermost being antero-posterior, the inner lateral.

Corolla, petals 4, polypetalous, inferior, with a long basal claw. They are cruciform, and alternate with the sepals.

Androecium, stamens 6, free, hypogynous: two are short and lateral, opposite the lateral sepals: four are longer in two pairs, opposite the antero-posterior sepals.

Gynoecium, carpels 2, syncarpous, superior; ovary bilocular, with many ovules; an ill-defined style, and a stigma with antero-posterior lobes. The ovules are curved, and seeds ex-albuminous (Fig. 477, I. II.). *Fruit*, a "siliqua" which is a dry capsule, the lateral carpellary walls of which split from the base upwards, leaving the two placentas as a frame with the transparent septum stretched between them (Fig. 101). The septum is called "false" because it is formed late, by ingrowths from the two opposite placentas, the ovary being originally unilocular, as it is in the Poppies and in the Capers.

Pollination. The flowers being grouped are conspicuous, and are visited for their pollen, and for honey. The honey-secretion is by glands at the insertion of the short lateral stamens. Insects passing from flower to flower and inserting their proboscis, will probably effect intercrossing; but self-pollination is possible, and it is even provided for by the longer stamens coming in contact with the stigma as the style elongates. It is not a highly specialised type of flower. It is very constant in the Cruciferae, and may be equally well studied in the Wallflower (20). The structure is probably dimerous throughout, but with a fission of the median petals to form divergent pairs, and of the median inner stamens to form the four longer. This is expressed in the floral formula:—S. $2+2$, P. $2_2\times$, A. $2+2_2$, G. $\underline{(2)}$.

The construction of the flower would then be theoretically as follows:

Two antero-posterior sepals.

Two lateral sepals.

Two antero-posterior petals (by fission resulting in the four oblique petals).

Two lateral stamens, short.

Two antero-posterior stamens (by fission resulting in the four long stamens).

Two lateral carpels.

Comparison with the Poppies and the Caper Family shows this to be the probable interpretation of the Cruciferous Flower, and that it is thus referable to a dimerous origin, with regularly alternating whorls.

The Cruciferae provide a large proportion of garden vegetables, such as Cabbage, Cress, Turnip, Horse-radish, etc.

ORDER: GERANIALES.

Family: GERANIACEAE. *Example:* THE FIELD GERANIUM.

(21) The Field Geranium (*Geranium pratense*, L.) is a strong-growing herb with opposite, palmate, and stipulate leaves. The inflorescences are lax cymose panicles (Fig. 478). Each flower consists of:

Calyx, sepals 5, polysepalous, inferior.

Corolla, petals 5, polypetalous, inferior, alternating with the sepals.

Androecium, stamens 10, free, perigynous, with filaments widened at the base. The five petaline stamens are external, the five sepaline are internal, a condition described as "obdiplostemonous," and notable as an apparent departure from the rule of alternation of successive whorls.

Gynoecium, carpels 5, syncarpous, superior, with single style bearing five distinct stigmas. Ovary with five loculi, each containing two ovules, of which only one usually matures.

The dry *fruit* is characteristic. The style remains as a firm woody beak. At ripeness each carpel suddenly splits away longitudinally from the beak and curving sharply, hurls out its seed to a distance (Fig. 243, p. 324).

The floral formula is S. 5, P. 5, And. $5+5$, G. 5.

Pollination. The flower is showy, and attracts also by honey secretion outside the bases of the stamens. It is markedly protandrous. The five outer stamens open first, followed by the five inner, but the stigmas remain closely appressed together (III.), and expand only after the pollen is shed, when the anthers curve away from them (IV.). This separation of the sexes both in time and space makes self-pollination highly improbable, and the plant depends upon cross-pollination resulting from insect visits. In other species of *Geranium*, especially the smaller-flowered, self-pollination occurs, the separation of the sexes being less marked. On the other hand in the Scarlet Geranium of gardens (*Pelargonium*) (22), the flowers are slightly zygomorphic, and there is a deep honey-gland sunk in the pedicel opposite to the posterior sepal, a specialisation still more perfected in the Nasturtium (*Tropaeolum*).

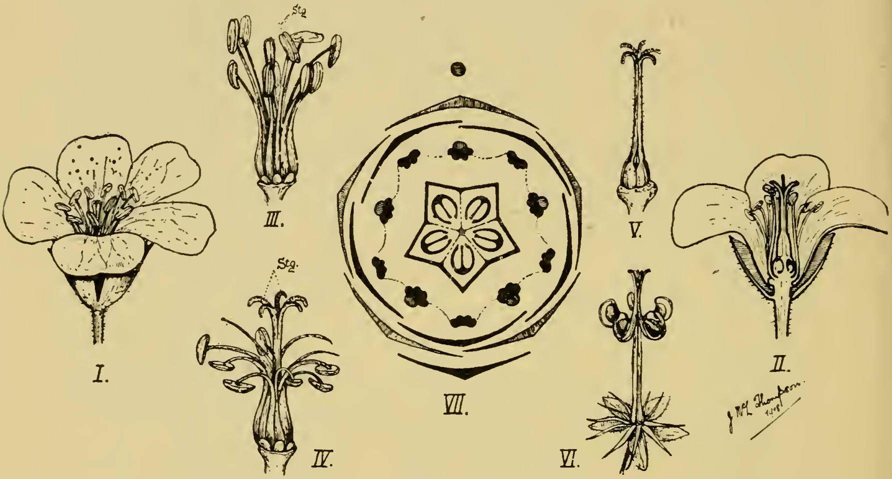

FIG. 478.

Geranium pratense, L. I. whole flower. II. the same in section. III. the stamens at time of dehiscence, the stigmas (*stg*) still closely appressed. IV. later stage with stigmas (*stg*) recurved. V. gynoecium at same stage as IV. VI. ripe fruit dehisced. VII. floral diagram.

ORDER: TRICOCCAE.

Family : EUPHORBIACEAE. *Example :* THE CAPER-SPURGE, OR OTHER SPECIES.

The Euphorbiaceae, or Spurges, are a very large Family, of which the genus *Euphorbia* is an extreme type. They have reduced, unisexual flowers, which are sometimes isolated, with their floral envelopes developed, as in *Phyllanthus*; but in *Euphorbia* and others the flowers are closely grouped together, so that a whole inflorescence may appear, and even functionate as a single flower. The less reduced types indicate that their relation is with the Geraniales, from which they may be regarded as an interesting reduction-series.

(23) *Euphorbia* is represented in the British Flora by many species. They are herbs or small shrubs with smooth surface, and milky juice. Their leaves

are exstipulate, but that is not general for the Family. The inflorescence is very complicated, the apparent unit being the flower-like *cyathium*, which is itself a very compact, compound spike (Fig. 479, I. II.). These units are borne like flowers on an inflorescence, which is usually a cymose umbel. The cyathium itself consists of an external cup, which looks like a calyx, but is really formed of five coalescent *bracts*, forming an *involucre*. On its margin four, or occasionally five, yellowish *glands* are borne, a blank space being left on one side ; there two teeth of the bracts are found, where the missing gland might be. Within the cyathium a single stalked *female flower* occupies the centre : it projects from the cup, and hangs over the side between the two bracts which are not separated by a gland. It consists of a gynoecium of three syncarpous carpels, having three styles with bifid stigmas. It is trilocular, and one pendulous, anatropous ovule lies in each : the upward-directed micropyle is covered by a fleshy outgrowth known as the caruncle, which is characteristic. At the base of the ovary is a distended ring, held to represent the abortive perianth. The gynoecium is thus superior.

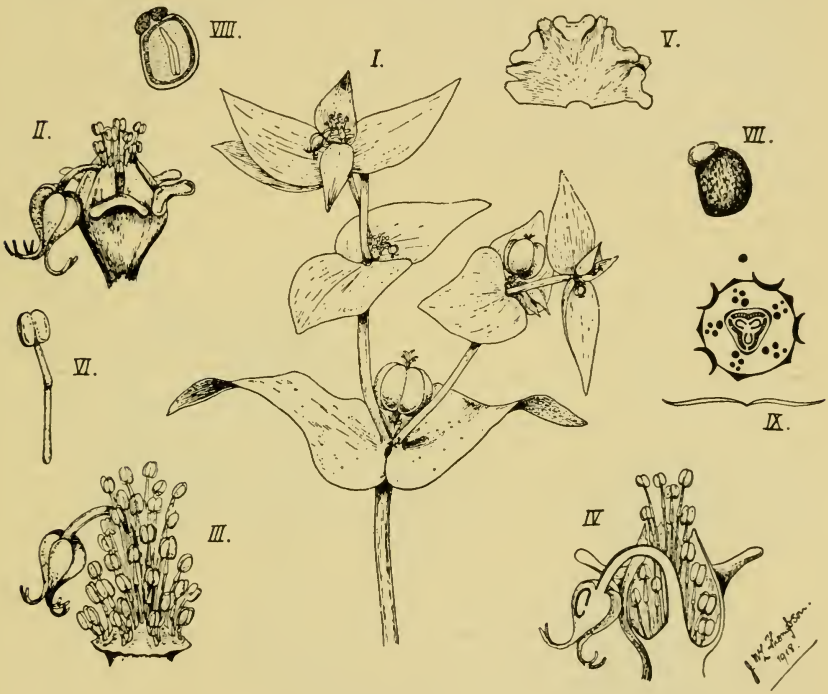

Fig. 479.

Euphorbia Lathyrus, L. I. flowering shoot. II. a single cyathium. III. Cyathium with involucre removed. IV. same in section. V. the involucre. VI. a single male flower. VII. ripe seed with caruncle. VIII. same in section. IX. diagram of a cyathium.

Around the female flower are a number of structures which look like stamens : they are associated with minute hairy bracts. Each of these is a *male flower* (vi.), consisting of a single stamen with a bilobed anther. The stalk which looks like a filament bears about half way down a constricted joint, which is believed to mark the place of an abortive perianth. The part below it would then be a pedicel, above it the filament. In *Anthostema* the perianth is better developed (Fig. 178, iii. p. 256). If these conclusions be correct, then the Cyathium is properly regarded as a condensed inflorescence.

The *fruit* is a capsule ; when it is ripe the carpels separate elastically from a central column. This type of carpel, though in larger number, is seen in *Hura* (Fig. 102, p. 166), another member of the Family. This type of carpel is known as a coccus, hence the name Trococcae, for the number is usually three. The similarity to the fruit of the Geraniaceae is striking.

Pollination. The stigmas in any Cyathium have as a rule ceased to be receptive before the pollen of the same cyathium is shed. Thus the inflorescences are *protogynous.*

Important Rubber-yielding plants belong to this Family (*e.g. Manihot*), and some drugs, *e.g. Ricinus.*

ORDER : SAXIFRAGALES.

The Saxifragales probably represent a type from which a number of derivative groups have sprung. A general floral formula for them is S. n, P. n, And. $n+n$, G. n, with the ovary superior, and in the simplest examples, such as *Astilbe,* the carpels are separate and many-seeded pods. This type may be varied by increase in number of the stamens, or of the carpels ; by the sinking of the carpels more or less completely into the receptacle, so as to give a half-inferior or an inferior ovary ; and in some cases by reduction of the number of the carpels to two or only one. The number of ovules may also be reduced. But still the main framework of the flower remains the same. Most of the related plants bear stipulate leaves.

Family : Saxifragaceae. *Example :* Meadow Saxifrage.

(24) The White Meadow Saxifrage (*Saxifraga granulata,* L.) is a frequent herb of grass-land, and banks. It bears at its base pink bulbils, by which it multiplies vegetatively, associated with radical leaves. The flowering stem bears leaves below, and a definite cymose inflorescence above, with few large flowers. The whole plant has glandular hairs. The flower-stalk widens out into a green hemispherical region : this encloses the base of the ovary, which is thus half-inferior ; while the other floral parts are inserted on its margin (Fig. 480). The flower consists of :

Calyx, sepals 5, polysepalous, seated on the margin of the receptacle ; the odd sepal is posterior.

Corolla, petals 5, polypetalous, alternating with the sepals.

Androecium, stamens $5+5$, the petaline outermost (obdiplostemonous) inserted round the half-sunk carpels, *i.e.* half-epigynous.

Gynoecium, carpels 2, half-inferior, oblique ; united in their lower part, but separate above, with distinct styles and capitate stigmas (half-syncarpous). Ovary bilocular, ovules numerous, placentation axile.

Fruit, a dry capsule, with longitudinal dehiscence.

Pollination. The flowers are protandrous, the inner series of stamens ripening first; then the outer. Nectar is secreted at the upper surface of the ovary. The flowers are visited by flies and small bees, and repeated visits will give a high probability of cross-pollination. But the flower is not highly specialised, and self-pollination is possible.

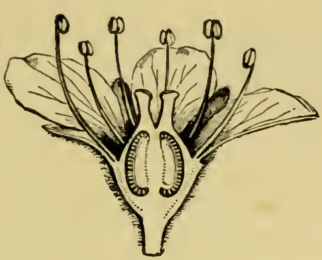

FIG. 480.
Median section of the flower of Saxifrage, showing the carpels half sunk in the receptacle, and coherent for the greater part of their length. (After Figuier.)

The London Pride (*Saxifraga umbrosa*, L.) will serve as an alternative example, though the flowers are smaller and more numerous, and the carpels are not so deeply sunk. It is pollinated by small flies.

(25) The Red-Flowering Currant (*Ribes sanguineum*, Pursh) is native in North America, and is commonly grown in gardens. It serves as an example of the Ribesiaceæ, which are usually grouped with the Saxifragaceæ, notwithstanding their inferior ovary, and five stamens. The Gooseberry or Currant of gardens would serve equally well.

FIG. 481.
Inflorescence of Currant: a raceme. (After Figuier.)

FIG. 482.
Berries of the Currant.
(After Figuier.)

The Inflorescence is a pendulous raceme (Fig. 481), arising in the axil of a foliage leaf of the previous season. The flowers are hermaphrodite and actinomorphic, composed as follows:

Calyx, sepals 5, polysepalous, superior, crimson, ; odd sepal posterior.

Corolla, petals 5, polypetalous, alternating with sepals, paler coloured.

Androecium, stamens 5, alternating with petals; seated on rim of receptacular tube.

Gynoecium, carpels 2, syncarpous, ovary inferior, unilocular, with numerous ovules seated on lateral placentas, ovules anatropous.

Fruit, an inferior berry (Fig. 482).

Pollination. The flowers are attractive by colour, and by grouping in racemes. Honey is secreted at the base of the receptacular tube. The flowers are very slightly protogynous, and are pollinated chiefly by bees ; but self-pollination is also possible.

ORDER: ROSALES.

The Rosales are herbs, shrubs, and trees, with alternate stipulate leaves. They are widely distributed, especially in temperate zones, and are largely represented among cultivated flowers and fruits. The flowers are actinomorphic, and usually pentamerous ; but the stamens are often numerous. The Order is specially instructive from the variability in development of the receptacle, so that it includes perigynous and epigynous types. There is also great variability in the number of the carpels. But still it is a very natural group, the flowers being referable to the same fundamental construction as the Saxifragaceae, to which they are closely allied.

Family : Rosaceae. *Examples :* Apple, Strawberry, Rose, Cherry.

(26) The Apple (*Pyrus Malus,* L.) is a small tree with long vegetative shoots and short spurs, upon which the flowers are borne. The leaves are stipulate. The flowers appear in groups, one terminal on the spur, the rest in the axils of the bracts below it. Each flower, together with two bracteoles, is

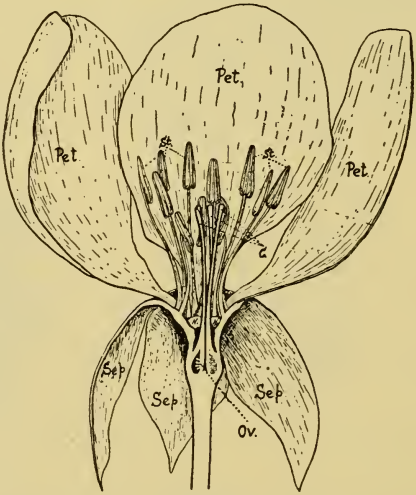

Fig. 483.

Vertical section through a flower of the Quince (*Cydonia*). *sep*=sepals. *pet*=petals. *st*=stamens. *c*=apices of the carpels, elongated into styles. *ov*=ovules. *n*=nectaries. The receptacle is here hollowed out, so that the carpels appear sunk down into a cavity. (After Church.)

borne on an elongated stalk, which swells immediately below the calyx into the enlarged *inferior ovary*. It is thus *epigynous* (Fig. 212, *B*, p. 290), and consists of :

Calyx, sepals 5, polysepalous, superior ; the odd sepal is posterior.

Corolla, petals 5, polypetalous, superior, alternating with the sepals.

Androecium, stamens indefinite, free, epigynous.

Gynoecium, carpels 5, syncarpous, inferior ; five distinct stigmas are borne on styles separate above, but more or less distinct below. Ovary with five loculi, and several ovules in each (Fig. 484, *A*).

Fruit, consists of the inferior ovary crowned by the persistent calyx. The five carpels are sunk in the succulent tissue of the receptacle, from which they are not distinctly marked off. Their inner cartilaginous wall forms the " core," and one or more " pips," or seeds, are contained in each.

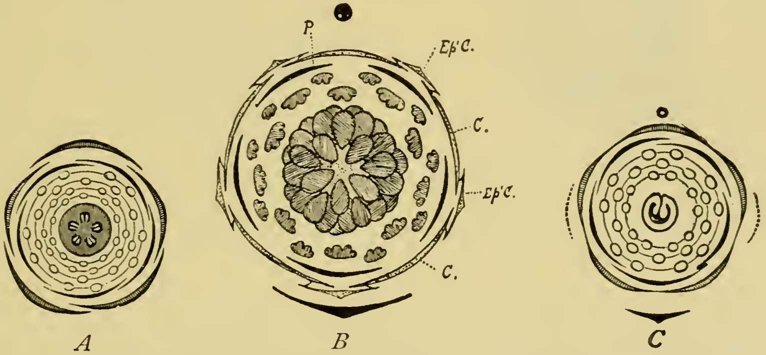

FIG. 484.

A, diagram of Apple. (After Eichler.) *B*, diagram of *Potentilla Comarum*. *C*, diagram of Cherry. (After Eichler.)

Pollination. The flowers are attractive by colour, and by easily accessible honey secreted on the concave surface within the stamens. They are slightly protogynous, but are not highly specialised. Insects collecting honey and pollen will carry out cross-pollination, but self-pollination is also possible.

(27) The Wild Strawberry (*Fragaria vesca*, L.) is a perennial herb with ternate, stipulate leaves, borne upon a sympodial rhizome. The apex of the leafy shoot of the preceding year grows up into the inflorescence of the current year, while it is upon a lateral bud from it that the foliage leaves are borne. The inflorescence is cymose. *Potentilla Comarum* will serve as an alternative example (Fig. 484, *B*). The flower consists of :

Calyx, sepals 5, polysepalous, seated at the margin of the widened receptacle. Between the sepals are five additional green lobes, forming what is called an *epicalyx*, believed to represent the fused pairs of stipules of the sepals, the vegetative leaves being stipulate. (The number of sepals in cultivated strawberries may be more than five.)

Corolla, petals 5, polypetalous, alternating with the sepals.

Androecium, stamens indefinite, free, perigynous. They are arranged with some regularity in whorls ; the outermost is of 10, representing five stamens which have undergone fission.

Gynoecium, carpels indefinite, apocarpous superior, seated on the spherical receptacle. Style springing from the side of each ovary, which contains only one ovule.

Fruit. A number of dry nuts seated on the receptacle, which has become distended and succulent, while the calyx is persistent as the " hull " (Fig. 485).

Pollination. The flowers are conspicuous by their white petals, and honey is secreted on the receptacular cup between stamens and carpels. They are slightly protogynous. The result of repeated insect visits will thus be a probability of cross-pollination, though self-pollination is also possible.

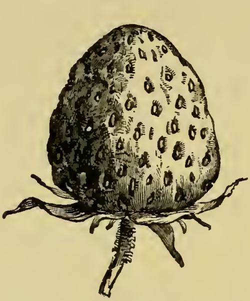

FIG. 485.
Succulent receptacle of Strawberry. (After Figuier.)

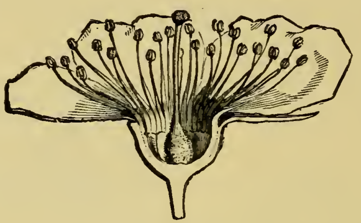

FIG. 486.
Vertical section of flower of the Peach, as an example of a perigynous flower. (After Figuier.)

(28) The flower of the Dog Rose (*Rosa canina*, L.) is constructed on a plan similar to that of the Strawberry, but without the epicalyx. The chief difference is in the receptacle, which instead of being convex with the carpels carried up on the hemispherical axis, is hollowed into a sunken cavity. This encloses the numerous bristly carpels, while their stigmas project above. When mature the receptacle becomes succulent as in the Strawberry, forming the " hip," with the nutlets or true fruits within.

(29) The Cherry (*Prunus Cerasus*, L.) has a construction of the flower like that of the Rose, but with only one carpel borne in the hollow, cup-like receptacle (Fig. 484, *C*). It consists of :

Calyx, sepals 5, inserted upon the margin of the cup-like receptacle. The odd sepal is posterior.

Corolla, petals 5, polypetalous, alternating with the sepals.

Androecium, stamens indefinite, free, perigynous, *i.e.* inserted on the margin of the receptacular cup.

Gynoecium, carpel 1, superior. The swollen ovary contains two ovules.

Fruit, a drupe. The receptacular cup here dries up, and falls away. The wall of the ovary differentiates into a superficial skin, a middle region of succulent pulp, and an inner stony layer. The stone of the mature cherry contains as a rule only one kernel, which is the exalbuminous seed, developed from one of the ovules. Sometimes, however, both are matured. The *Drupe* thus constructed is the type of fruit of Plums, Apricots, Peaches, etc. (Fig. 487).

Pollination. The Cherry flower is not highly specialised. Anthers and stigmas ripen simultaneously. Honey is secreted on the hollow surface of the cup. It is visited by various short-lipped insects.

The variability of Rosaceous flowers is illustrated by such examples. A striking feature is the diversity of origin of the succulent pulp, which gives value to their fruits. In the Strawberry it arises from the convex receptacle; in the Rose from the concave receptacle; in the Apple and Pear partly from the receptacle, partly from the carpels; in the Raspberry it is from the middle layer of the tissue of the very numerous carpels (Fig. 488); in the Cherry and Plum from the corresponding tissue of the single carpel. The Almond of shops is the seed taken from the drupe of *Amygdalus*.

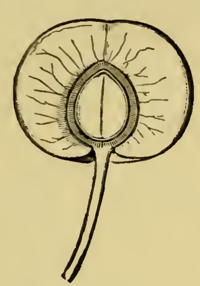

Fig. 487.
Drupe of Cherry. (After Figuier.)

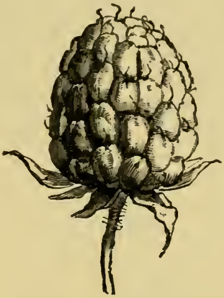

Fig. 488.
Grouped drupels of the Raspberry. (After Figuier.)

ORDER: LEGUMINALES.

This is one of the largest and most important Orders of Plants, and it is cosmopolitan. It is characterised by its gynoecium, which consists of a single carpel, ripening as a Legume, or Pod, as in the Pea. It is divided into three Families: the *Mimoseae*, which are the most primitive, having flowers of radial symmetry, as in *Mimosa* and *Acacia*; the *Caesalpineae*, which have zygomorphic flowers, as in the Tamarind, or *Cassia*; and the *Papilionaceae*, or Pea-flowers. The last of these only are represented in the British Flora. The Order yields most varied products of importance: food-stuffs, timbers, drugs, and dyes, etc.

Family: Papilionaceae. *Examples:* Trefoil, Pea.

(30) The Bird's Foot Trefoil (*Lotus corniculatus*, L.) forms many straggling branches from a central root-stock. The leaves have green "stipules" which are really basal pinnae, and three distal lobes, hence its name. The flowering branches are leafless, but bear distally a leafy bract and a radiating group of flowers. Each flower is strongly zygomorphic, its plane of symmetry being vertical and median, as it is in all of the Papilionaceae (Fig. 489). It is composed thus:

Calyx, sepals 5, gamosepalous, inferior, the odd sepal being anterior. The calyx-tube gives mechanical support to the internal parts, and is slightly widened in a perigynous manner.

Corolla, petals 5, polypetalous, inserted separately on the slightly widened receptacle, *i.e.* perigynous. The petals alternate with the sepals. The posterior petal is the large vexillum or standard; the two lateral are the alae or wings, which invest the anterior carina, or keel. The latter is formed from two obliquely anterior petals, inserted by separate stalks, but fused distally, so as to enclose the stamens and carpel.

Androecium, stamens 10, perigynous: nine are united by their stalks into a tube; the tenth, which is posterior, is separate to its base. The anthers are completely enclosed in the carina.

Gynoecium, carpel 1, apocarpous, superior. It is a pod, containing numerous ovules, with placentation on the posterior margins. The style is longer than the stamens, and bears a capitate stigma. The pod is almost surrounded by the united filaments, but access to the honey-secretion, which is on the enlarged receptacle round its base, is gained through the slits right and left of the separate stamen. The fruit when ripe is a dry pod, splitting longitudinally into halves.

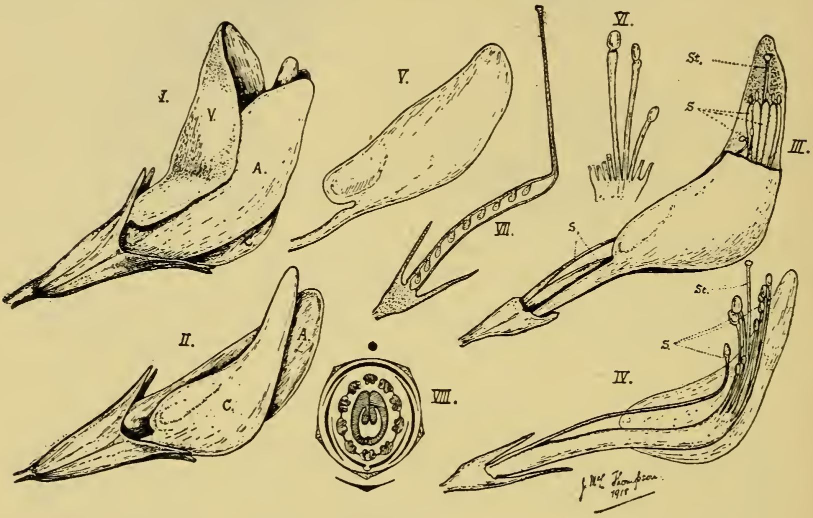

FIG. 489.
Flower of *Lotus corniculatus*, L. I. flower complete. II. with vexillum removed. III. with alae and part of carina removed. IV. carina slit longitudinally. V. one of the alae. VI. stamens of different length. VII. carpel in section. VIII. floral diagram. *s*=sepals; *v*=vexillum; *A*=alae; *e*=carina; *s*=stamens; *st*=stigma.

Pollination. The mechanism of the flower is elaborate, and secures cross-pollination notwithstanding the close relation of anthers and stigma, which are both enclosed in the funnel-like carina. For the stigma is not receptive until it has been rubbed, and remains infertile till the insect-visitors, which are bees, arrive. Searching for nectar, and guided by the converging red lines on the standard, the bee alights on the projecting wings; its weight is transmitted by their interlocking surfaces to the keel, which is thus depressed, and yields. The stiff stamens and carpel do not yield, and so first the stigma, and then the anthers with their pollen project through a pore which is left open at the tip of the keel. When the weight of the bee is removed the keel rises, and the stamens and stigma are again enveloped, and are ready for a fresh insect visit. The effect of such visits will be, *first*, to rub the stigma, and make it receptive, while as it emerges first from the keel it receives any pollen brought from other flowers by the bee ; *second*, to deposit a fresh supply of pollen on the insect. A cross-pollination is thus a virtual certainty.

(31) The flower of the Garden Pea (*Pisum sativum*), may be taken as an alternative type, the construction being essentially the same as in *Lotus*, though differing slightly in details of its mechanism. The weight of the visiting-insect depresses the interlocking wings and keel as before ; but the latter is closed only along the anterior margin, so that when it is depressed the stiffer stamens and carpel rise out of the boat-like keel, and come in contact with the lower surface of the insect. The style bears a brush of hairs, which, as it rises, sweeps out the pollen on to the insect's body ; but the stigma reaches its body first, and receives thus such pollen as it may have brought. The flower is elastic and recovers, making successive visits possible. The mechanism is less precise than in *Lotus*, but still very effective. It requires a strong insect, and in absence of cross-pollination self-pollination is possible.

These examples serve to illustrate the exact mechanism of the Papilionaceous flower, and the way in which slight differences may affect the process of their pollination.

ORDER : UMBELLALES.

Family : UMBELLIFERAE. *Example :* COW PARSNIP.

(32) The Cow Parsnip (*Heracleum Sphondylium*, L.) is a coarse perennial herb, with massive storage stock, which sends up the annual leafy and flowering shoot. The stem is hollow and fluted, and bears alternate leaves with broad sheathing base, and irregularly cut lamina. The main inflorescence is terminal, but others may arise in the axils of the upper leaves. It is a compound umbel (p. 262, Fig. 185). The flowers are individually small, but many being grouped together, and all at the same level, the aggregate inflorescence becomes a conspicuous feature. Each flower is borne upon a slender hairy stalk, which widens out just below the flower itself into a flattened green body. This is the inferior ovary, and the flower is *epigynous* (Fig. 490). Care should be taken to select perfect flowers for observation, as the parts fall away early. The flower consists of :

Calyx, sepals 5, superior, present as minute teeth visible between the petals. The odd sepal is posterior.

Corolla, petals 5, polypetalous, free, superior. Each is notched at the free edge. In the marginal flowers the petals are unequal, the outermost being the largest.

Androecium, stamens 5, free, epigynous, alternating with the petals ; bent inward in bud, but straightening when mature.

Gynoecium, carpels 2, syncarpous ; stigmas 2, styles widening downwards into two yellowish green nectaries. Ovary inferior, bilocular, with one pendulous ovule in each loculus.

Fruit, a flattened oval body, which matures dry. When ripe it splits into two halves (mericarps), attached at first by a slender middle column, from which they later break away, and are readily carried by the wind. Each mericarp contains a single albuminous seed, and is marked by elongated oil-glands, four on the outer and two on the inner flattened sides.

Pollination. The aggregate inflorescence attracts the attention of insects from a distance : the slight zygomorphy increases its effect. It is visited by various insects, the exposed honey being accessible alike to short-tongued and long-tongued. The individual flowers are *protandrous*, the stamens often falling before the stigmas are mature. Cross-pollination is probably by insects crawling from flower to flower, but self-pollination is still possible.

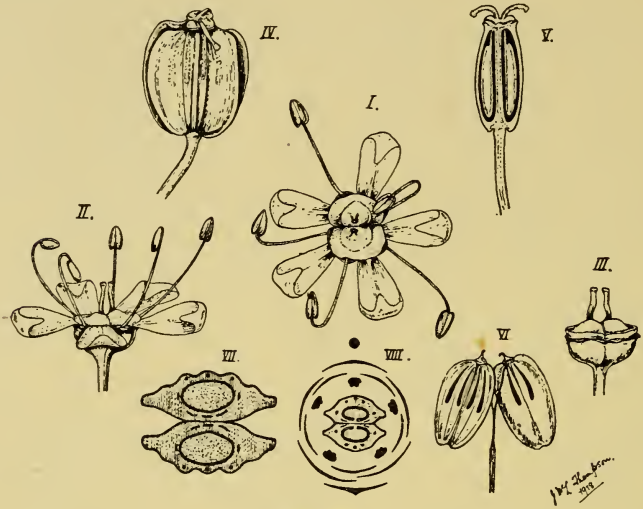

FIG. 490.

Heracleum Sphondylium. I. whole flower seen from above. II. the same seen from the side. III. gynoecium. IV. fruit. V. ditto in section. VI. mature fruit with mericarps separate. VII. fruit in transverse section. VIII. floral diagram.

There is in the Cow Parsnip, but still more in other Umbelliferae, a partial separation of the sexes in space as well as in time ; since the pistil is degenerate in the later-formed flowers, they are practically male. That is seen markedly in *Astrantia* and in *Myrrhis*. The condition is described as *andro-diclinous*, and clearly it will promote cross-pollination, while it also secures the pollination of those hermaphrodite flowers which are formed late, and are protandrous.

The Umbelliferae are a numerous and wide-spread Family of herbs, often strong-smelling, and poisonous. But it includes cultivated plants, such as Carrot, Parsley, Celery, Caraway. Some yield drugs (*Asafœtida*), and oils.

DICOTYLEDONEAE—SYMPETALAE.

Those Dicotyledons which have their petals united, that is sympetalous or gamopetalous, are held to show in this respect a position in advance of the Polypetalous types. A further character which they have in marked degree is that their flowers are strongly cyclic, and the number of parts more definite than in flowers of more primitive construction. They are divided into two series on the broad feature of the number of the whorls in which their parts are arranged. Those with five whorls have the general formula, S. n, P. n, A. $n+n$, G. $n-$, and they are styled the *Pentacyclicae*. Those with only four whorls have the general formula, S. n, P. n, A. n, G. $n-$, and they are styled the *Tetracyclicae*. The number of the carpels is usually below the typical number (n). The number of the stamens is also frequently less than (n) or $n+n$, especially in those flowers where the pollination-mechanism is specialised.

(*a*) *PENTACYCLICAE.*

ORDER: BICORNES.

Family : Ericaceae. *Example :* Cross-leaved Heath.

(33) The Cross-leaved Heath (*Erica Tetralix*, L.) is a shrubby moorland plant, mycorhizic like the rest of the family, bearing minute stiff leaves, studded with red, stalked glands. The margins of the leaves are reflexed, so that the lower stomatal area is concave, and more or less closed. All these features are xerophytic.

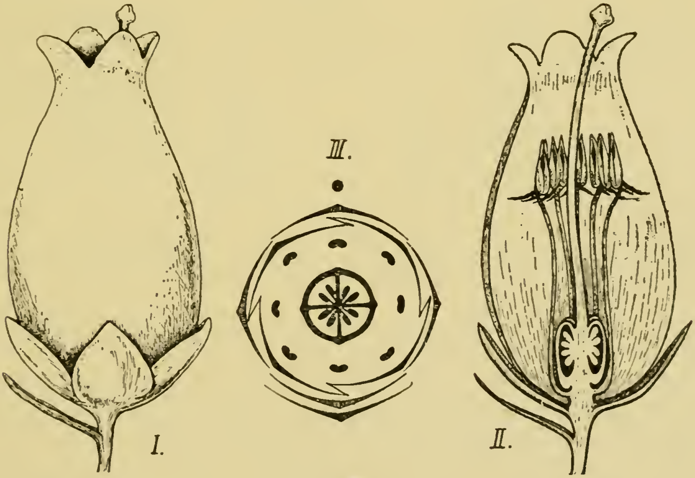

Fig. 491.
Erica Tetralix. I. whole flower from outside. II. flower in section. III. floral diagram.

The flowers are borne in dense racemes, and are pendulous on pedicels bearing two bracteoles (Fig. 491). They consist of:

Calyx, sepals 4, polysepalous, inferior, glandular.

Corolla, petals 4, gamopetalous, inferior, globose, with a narrow opening, through which the capitate stigma projects.

Androecium, stamens 4+4, free, hypogynous, with curved filaments; anthers dehiscing by two distal pores, which face downwards. From the base of each anther two divergent spurs project outwards to the inner surface of the corolla.

Gynoecium, carpels 4, syncarpous, superior, style elongated, with capitate stigma. Ovary with 4 loculi, ovules minute, numerous, on an enlarged axile placenta. Honey-disc round the base of the hairy ovary.

Fruit, a loculicidal capsule, from which the minute seeds are shaken by wind.

Pollination is by bees, which hang on to the pendent flowers. The bee first touches the sticky stigma, depositing pollen it may have brought from another flower; then inserting the proboscis, it collides with the spurred stamens, shaking out a shower of dry pollen. Thus there is a high probability of cross-pollination, though self-pollination is possible by some falling upon the stigma of the same flower. The gamopetalous corolla with narrow mouth, and the spurred stamens exclude small thieving insects.

(34) Compare the Bilberry (*Vaccinium Myrtillus*, L.), in which the floral structure is essentially the same, but the ovary is here inferior. In this genus, and in the Ericaceae generally, there is frequent *meristic variation*, the flowers being either tetra-merous or penta-merous.

ORDER: PRIMULALES.

Family: PRIMULACEAE. *Example:* COMMON PRIMROSE.

(35) The Primrose (*Primula vulgaris*, Huds.) is a perennial with its stock covered with old leaf-bases, and ending in a rosette of leaves of the current year. The flowers are borne singly in the axils of bracts, which succeed the foliage leaves. There are two types of flower which are borne on distinct plants: "pin-eyed," with the stigma occupying the centre of the flower, and "thrum-eyed," where its place is taken by five anthers. It will be seen, however, that in number and arrangement of the parts both are alike: the difference is one of proportion of development of the parts (Fig. 492). For convenience a "pin-eyed" flower may be taken; it consists of:

Calyx, sepals 5, gamosepalous, inferior, forming a tube supporting the corolla. The odd sepal is posterior.

Corolla, petals 5, gamopetalous, inferior, alternating with the sepals, and forming a long narrow tube below, with five lobes diverging at right angles from it.

Androecium, stamens 5, epipetalous, inserted with very short filaments half-way up the tube of the corolla, and opening inwards (Fig. 492, II.). Note that the stamens are opposite the petals (anti-petalous).

Gynoecium, carpels 5, syncarpous, superior; style elongated so as to carry the pin-headed stigma to the throat of the corolla. Ovary turgid, unilocular; ovules numerous, placentation axile.

Fruit, a capsule opening distally by ten teeth, which become reflexed. The number five of the carpels is inferred from comparison with other flowers, and from the parts of the Primrose itself. The ten teeth of the fruit support this view. The anti-petalous position of the stamens, and the number (n), instead of ($n + n$), suggests that five sepaline stamens have disappeared: this conclusion is supported by the fact that in *Samolus*, *Lysimachia*, etc., five small staminodes are present in the place where the missing stamens should be. The family shows meristic variation, the whorls varying in number of parts from four to nine. *Trientalis* and *Lysimachia* are specially variable.

Pollination. Compare first the "thrum-eyed" type of flower. The parts are numerically the same as in the "pin-eyed"; but the style carries the stigma only half-way up the corolla-tube, corresponding in level to the stamens of the "pin-eyed." The stamens are inserted at the throat of the corolla, corresponding in level to the stigma of the "pin-eyed." The effect of this "dimorphism" is to increase the probability of intercrossing as a consequence of repeated visits from bees to the two types of flower, which are borne on different plants. The sticky pollen deposited on the proboscis of the bee from the "pin-eyed" type will correspond in level to the stigma of the "thrum-eyed," and the pollen of the latter to the stigma of the former. These are what have been called "legitimate" crosses, and they have been shown to be more prolific than the "illegitimate" crosses, between parts of unequal length. But self-pollination is not precluded. The gamopetalous corolla is effective in excluding smaller insects, while bees are attracted by honey, colour, and scent.

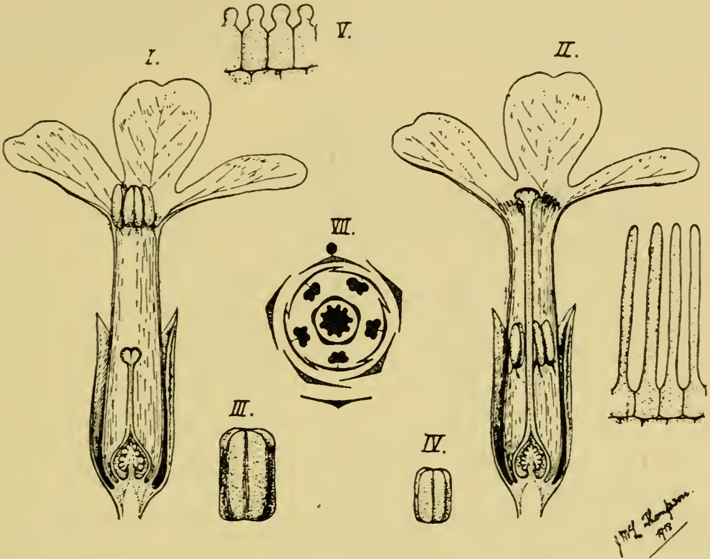

FIG. 492.

Primula vulgaris. I. short-styled type of flower (thrum-eyed) in section. II. long-styled type (pin-eyed). III. pollen of short-styled. IV. of long-styled types. V. stigmatic papillae of short-styled. VI. of long-styled type. VII. floral diagram.

(*b*) *TETRACYCLICAE.*

ORDER: PERSONATAE.

This Order includes a large number of showy plants of temperate and tropical climates, with tetracyclic, gamopetalous flowers, having the general formula S. 5, P. (5), A. 5, G. $(\underline{2})$. The ovary is superior, and bilocular, and the number of ovules borne on the axile placenta is usually large.

Family : Solanaceae. *Examples :* Nightshade, Potato.

(36) The Deadly Nightshade (*Atropa Belladonna*, L.) is a perennial herb of shrubby habit, with entire leaves having a clammy glandular surface. It bears its flowers solitary in the axils of leafy bracts. The whole inflorescence, which is cymose, starts with a single terminal flower : below this strong branches develop, the ultimate branchings of which are complicated by adhesions. The flower consists of :

Calyx, sepals 5, gamosepalous, inferior ; the odd sepal is posterior.

Corolla, petals 5, gamopetalous, inferior, alternating with the sepals ; very slightly zygomorphic.

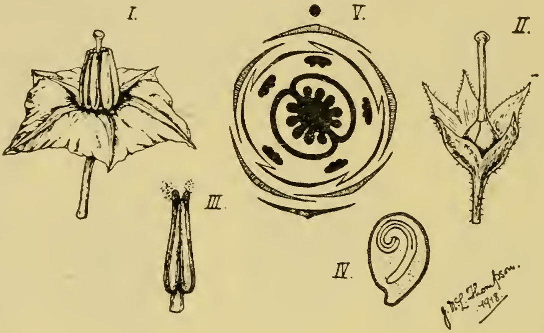

Fig. 493.
Solanum tuberosum. I. flower. II. pistil, and persistent calyx. III. stamen with porous dehiscence. IV. seed in median section. V. floral diagram.

Androecium, stamens 5, hypogynous, epipetalous ; filaments curved.

Gynoecium, carpels 2, syncarpous, superior, placed obliquely to the median plane ; style elongated, stigma capitate, ovary bilocular, ovules numerous, placentation axile. A honey-disc surrounds the base of the ovary.

Fruit, a large black berry, surrounded by the persistent green calyx. Seeds albuminous, embryo curved.

Pollination. The colour and honey-secretion offer attractions to bees, especially humble-bees, while the gamopetalous corolla and the stiff hairs at the base of the filaments tend to exclude small crawling insects. The stigma and anthers mature almost simultaneously. The stigma projects beyond the curved stamens, thus there is a probability of cross-pollination from visits from humble-bees, but the flower is not highly specialised.

(37) The Potato (*Solanum tuberosum*, L.) is an herbaceous plant that reproduces itself by tubers (Fig. 147, p. 218). But it commonly flowers also in cymose inflorescences, which are without bracts. The flowers of the cultivated varieties are apt to show abnormalities. The normal structure is like *Atropa* in number and arrangement of parts. But the corolla is wheel-shaped, and expanded in a vertical plane, while the five projecting stamens open by terminal pores (Fig. 493, III.). The stigma projects beyond them. There is no honey-secretion. The native habitat is South America. The arrangement of the flower might lead to crossing if the suitable insects were present, but here insects rarely visit the flowers. Self-pollination is possible, and fruit is often set. The fruit is a berry.

ORDER: PERSONATAE.

Family: SCROPHULARIACEAE. *Examples:* FIGWORT, SPEEDWELL.

(38) The Figwort (*Scrophularia nodosa*, L.) is a common plant of moist soil, with upright four-angled stems bearing decussate leaves, and terminating in lax cymose panicles of tawny purplish flowers. They are zygomorphic, and strongly protogynous (Fig. 494). Each flower consists of:

Calyx, sepals 5, slightly gamosepalous, inferior. The odd sepal is posterior.

Corolla, petals 5, gamopetalous, inferior; two-lipped.

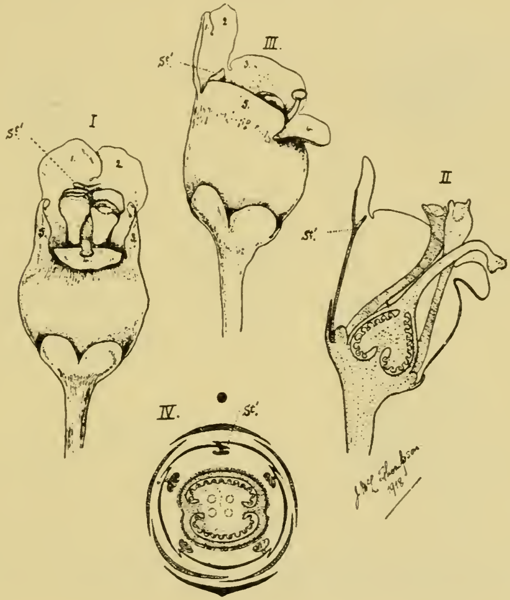

FIG. 494.

Scrophularia nodosa. I. flower in anterior view with stigma recurved, and the stamens dehiscent (late stage). II. same in section. III. flower seen laterally with projecting stigma (early stage). IV. floral diagram.

Androecium, stamens 4, epipetalous; the fifth posterior stamen represented by a prominent staminode below the upper lip.

Gynoecium, carpels 2, syncarpous, superior, antero-posterior; style elongated stigma capitate. Ovary bilocular, with numerous ovules on an enlarged axile placenta. A yellow honey-disc surrounds the base of the ovary. Fruit a dry capsule, which splits septicidally, and liberates the numerous albuminous seeds, with straight embryos.

Pollination. The tawny colour of the flower attracts wasps, which are the pollinating agents. The flowers are strongly protogynous. While the stamens are still tightly packed in the globose corolla, the stigma protrudes so as to meet any visiting insect, and receives any pollen she may bring (III.).

Later it is strongly recurved, and the stamens then straighten their filaments, carrying their anthers outwards, partly blocking the lower side of the corolla-tube (I. II.). They will thus deposit their pollen on the ventral surface of the visiting insect, conveniently for transfer to the stigma of flowers in the earlier female stage. The posterior stamen from its position could not do this : it is superfluous, and is reduced to a staminode. Cross-pollination is thus highly probable, but self-pollination is possible by pollen falling from the anthers upon the still receptive stigma.

The Foxglove (*Digitalis purpurea*, L.) has a similar structure, but its wide bell is suitable for humble bees, the pollen being deposited on their backs.

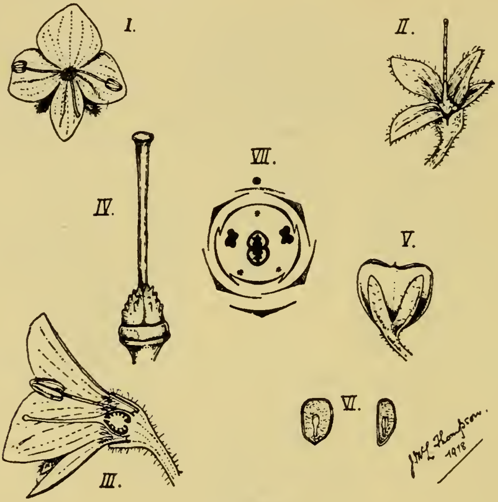

Fig. 495.

Flower of *Veronica Chamaedrys*, typically pentamerous : but the posterior sepal is abortive : the two obliquely posterior petals are fully fused to form apparently one ; only the two obliquely posterior stamens are developed.

The flowers are here protandrous. Cross-pollination is probable, but self-pollination is still possible. Comparison of the Foxglove with the Figwort shows how, with the same plan of floral construction, there may be differences in the detail and in the agent of cross-pollination.

(39) The Germander Speedwell (*Veronica Chamaedrys*, L.) is a common perennial of road-sides and banks. It has long ascending shoots bearing decussate leaves. The racemose inflorescences arise in the axils of the upper leaves. Each flower has a slender stalk, and consists of the following parts

Calyx, sepals 4, slightly gamosepalous, inferior. Though the number appears to be four, comparison with other species of *Veronica*, and with other related plants, such as the Foxglove, shows that a fifth sepal, which should be median and posterior, is here wanting (Fig. 495, II.).

Corolla, petals apparently four, gamopetalous, inferior, alternating with the sepals and forming a wheel-shaped (rotate) corolla, which readily falls away in one piece. Comparison with related plants shows that the large posterior petal is really the equivalent of two obliquely posterior petals fused together. In front view the petals are marked by lines, or honey-guides, converging to the centre of the flower (Fig. 495, I.).

Androecium, stamens 2, epipetalous, diverging widely right and left. Comparison shows that these correspond to the two obliquely posterior stamens, while those obliquely anterior are abortive, as well as the median posterior stamen (Fig. 495, I., III., VII.).

Gynoecium, carpels 2, antero-posterior, syncarpous, superior. The single style projects between the diverging stamens, and bears a capitate stigma. Ovary bilocular, ovules numerous, placentation axile.

Fruit, a dry capsule.

Pollination. The flower is a specialised and reduced example of the Scrophulariaceae. The change from a pentamerous to an apparently tetramerous type follows from the abortion of the posterior stamen, which leads to abortion of the posterior sepal and fusion of the two obliquely posterior petals. The obliquely anterior stamens are also abortive, not being necessary for effective pollination by flies. The rotate corolla is expanded in a vertical plane, with the style and two stamens projecting horizontally. The insect alighting on the flower gains a foothold by grasping the stamens, drawing them together so that they deposit pollen on the under surface of his body. On going to another flower the stigma receives this, before an additional supply from that flower can be deposited. The result is a high certainty of cross-pollination, with high improbability of self-pollination ; and it is effectively carried out without the three stamens that are abortive.

ORDER : VERBENALES.

Family : LABIATAE. *Examples :* DEAD-NETTLE, SAGE.

(40) The LABIATAE are a very large Family including herbs and shrubs spread through warm and temperate regions, and characterised by their four-angled stamens and decussate leaves. They have often an aromatic smell : Mint, Sage, and Lavender are examples. Their floral structure is very constant. The flowers are either solitary or in axillary cymes. The White Dead Nettle (*Lamium album*, L.) illustrates the leading features. Its flowers, which are in crowded " verticillasters," show their cymose arrangement by the fact that the flower directly in the axil of the leafy bract opens first, and those right and left successively later. Each flower is strongly zygomorphic, with its median plane vertical (Fig. 496). It consists of :

Calyx, sepals 5, gamosepalous, inferior, odd sepal posterior.

Corolla, petals 5, gamopetalous, inferior ; strongly two-lipped. One large petal forms the anterior lower lip, two smaller petals guard the entrance to the tube laterally, the upper lip forms a hood, composed of two obliquely posterior petals. The corolla is easily removed in one piece, its tube is narrow below, but widens upwards.

Androecium, stamens 4, epipetalous. The fifth posterior stamen is absent, its place being inconveniently behind the style. The anthers, of unequal length and opening downwards, lie below the hood of the corolla. In this Family sometimes the outer, sometimes the inner pair are the longer.

Gynoecium, carpels 2, syncarpous, superior, antero-posterior ; style elongated ; stigma two-lipped, lying between the pairs of anthers, with lobes widely divergent, the anterior lobe directed downwards. The ovary 4-partite, with one anatropous ovule in each. It is really bilocular, with two ovules in each loculus ; but it becomes "falsely" quadrilocular by intrusion of a septum between each pair of ovules. Nectaries are found at the anterior base of the ovary. The nectar accumulates in the narrow lower part of the corolla-tube, protected by a fringe of hairs which grow inwards from the tube of the corolla just above the ovary.

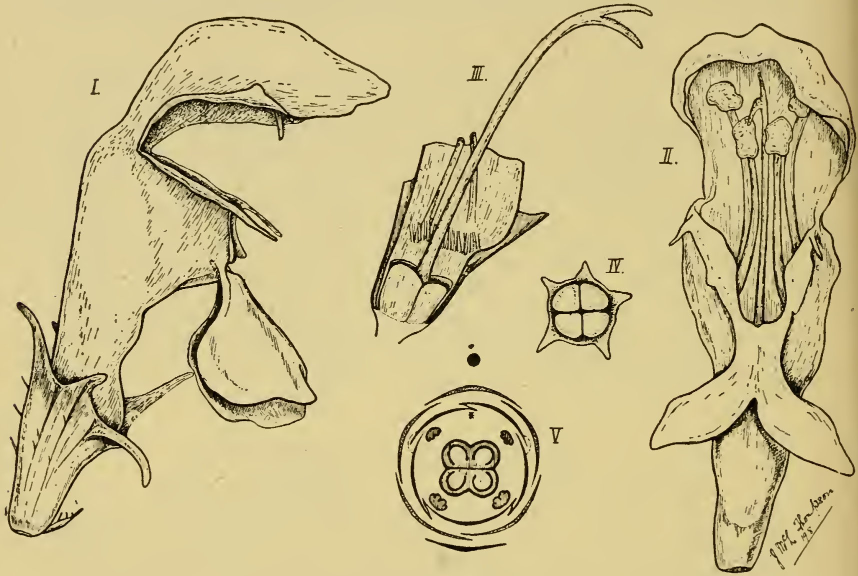

Fig. 496.
Lamium album. I. flower seen laterally. II. same in frontal view. III. dissection showing ovary and style, and the base of the corolla-tube, with insertion of stamens and fringe of hairs. IV. ovary as seen from above. V. floral diagram.

Fruit, four dry nutlets, two being derived from each carpel. They remain till shed, enclosed by the persistent calyx.

Pollination is by bees, which alight on the lower lip of the corolla and insert the proboscis into the tube. The bee's body fills the space between the upper and lower lips, so that its back presses against the stamens and stigma. The anterior lobe of the stigma projects further downwards than the stamens, so that it first touches the back of the bee, receiving pollen if she has brought any from another flower. She then receives pollen from the anthers which open downwards. The flower is homogamous, that is, the stigma is receptive at the time when the pollen is shed. Self-pollination is therefore possible, but there is a high probability of cross-pollination.

(41) The Dead Nettle is highly specialised, and deposits the pollen on a limited area of the insect's body ; but a still higher degree of specialisation is seen in *Salvia pratensis*, or other species. The plan of the flower is the same as

in *Lamium*, but, as the mechanism is more precise, sufficient probability of pollination can be secured with greater economy of pollen than in other Labiatae (Fig. 497). Only the two obliquely anterior stamens are matured, the posterior are represented by minute staminodes, or are quite abortive. The anthers of the two well-developed stamens have the "connectives" between the anther-lobes elongated, so that they are separated by about half an inch. Each anther is affixed midway on the short stout filament of the stamen by a flexible joint, so as to be able to move like the lever of an Egyptian well. One of the lobes is directed forwards, and this develops normal pollen; the other is directed backwards and develops as a sterile knob. This is so placed as to block the entrance to the corolla-tube, while the fertile lobe rests under the hood of the corolla. The flower is strongly protandrous, the style being hidden, and the stigma-lobes appressed at the time of shedding of the pollen.

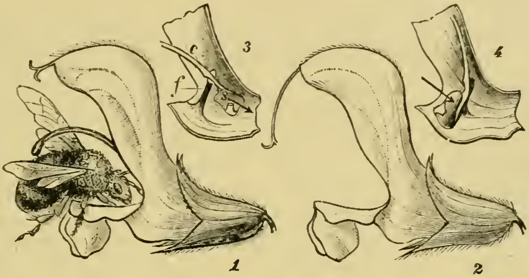

FIG. 497.

Pollination of *Salvia pratensis*. 1, Flower visited by Humble Bee, showing the projection of the curved connective from the helmet-shaped upper lip, and the deposit of the pollen on the back of the Bee. 2, older flower, with connective withdrawn and elongated style. 4, the staminal apparatus at rest, with connective enclosed within the upper lip. 3, the same when disturbed by the entrance of the proboscis of the Bee in the direction of the arrow. *f*=filament. *c*=connective. *s*=the obstructing half of the anther, which produces no pollen. (After Strasburger.)

If a large insect, perching on the lower lip of the flower of *Salvia*, inserts its proboscis, the sterile lobes will be pressed upwards, and this will cause the fertile lobes to descend, depositing the pollen over a definite area of the insect's back. In older flowers that have already shed their pollen, the style elongates: its lobes diverge and take such a position that the stigma touches that region of the insect's body which received the pollen from the younger flowers. Cross-pollination thus follows on repeated visits to flowers of various ages; and it is effected with a high degree of certainty, though in each flower only two half-anthers are fertile. Economy of pollen follows on perfection of the mechanism.

ORDER: SYNANDRAE.

Family: COMPOSITAE. *Examples:* OX-EYE, DANDELION, CORNFLOWER.

The Family of the Compositae consists mostly of herbs. It is of world-wide distribution, and is the largest Family of Flowering Plants. It is characterised by having the gamopetalous flowers collected into capitula, or heads.

Each *head* is surrounded by a common *involucre* of protective bracts. The whole head is equivalent biologically to a single flower, and behaves as such, though morphologically it is a *closely packed, spicate inflorescence.* The Dandelion and Daisy are familiar examples (Fig. 498). The structure of the individual flower is already known in the case of the Sunflower, by the study of its development (Chapter XIV., p. 273, Fig. 198). Each flower is there seen in the normal position, *i.e.* in the axil of a bract; it consists of 5 petals, 5 stamens, and 2 carpels. The transverse section of the flower approaching maturity shows these parts arranged as in a floral diagram. The odd petal is anterior; the stamens alternate with the petals, and the carpels are antero-posterior (Fig. 198, viii.). The ovary is inferior, unilocular, and contains one ovule. This structure is fundamental for all Compositae (Fig. 499).

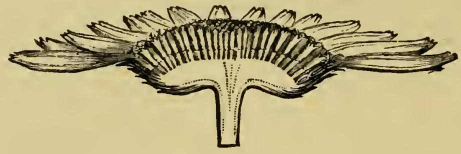

FIG. 498.
Inflorescence of Daisy: a capitulum. (After Figuier.)

FIG. 499.
Floral diagram for Compositae. (After Eichler.)

As in similarly crowded inflorescences (for instance the cyathium of the Spurges, p. 629), the crowding brings with it reduction of the individual flowers, but it does not go so far in the Compositae as in the Spurges. The most usual modification is the reduction of the calyx, its protective function having devolved upon the involucre. Sometimes it is absent, as in the Daisy; or it may be represented by two or three teeth, as in *Bidens* (Fig. 251, *E*). But most frequently it is replaced by a number of bristles composing what is called the "pappus," which serves as a means of fruit-dispersal, taking the form of a "pappus" composed of bristles, which spread like a parachute (Fig. 247, p. 326). The bract subtending each flower is often abortive, as in the Dandelion and Daisy. The flowers themselves though typically hermaphrodite are liable to become unisexual by abortion. These are all features of reduction, following on the aggregation of the flowers in the compact inflorescence.

The flowers may develop in three different ways, though all are fundamentally of the same construction, having the general formula, S, (5, or less, or 0, or x), $\underbrace{\text{P. }5,\ \text{A. }5,}$ G. $\overline{(2)}$. The first type is radially symmetrical, with five equal petals. This is probably the original type, and is characteristic of the *florets of the disc* (Fig. 500, III., IV.). A second type is seen in the *ray-florets* (Fig. 500, V.), in which the corolla is tubular below, but the three anterior petals are elongated into a long strap-shaped ray, as shown by the three distal teeth; the two obliquely posterior are reduced or absent. These ray-florets are frequently female, or neuter. A third type is the *ligulate floret*, in which the corolla is split on one side, and all the five petals, as shown by the five distal teeth, are elongated into a strap-shaped ray ; but here all five join in its formation (Fig. 502). According to the type of flower the Family is divided into two Sub-families : (i) The *Tubuliflorae*, in which the flowers are all tubular, or the outer may be developed as ray-florets (Fig. 500). They have watery juice. Examples are the Groundsel, Daisy, Sunflower, and Cornflower. (ii) The *Liguliflorae*, in which all the flowers are ligulate (Fig. 502). They have milky juice. Examples are Dandelion or Hawk-weed.

(i) *Tubuliflorae.*

(42) The Common Groundsel (*Senecio vulgaris*, L.) is one of the commonest weeds of cultivated ground. It is annual and herbaceous, with branched leafy stem, bearing a few heads drooping when young, erect when old. The single head, examined in full flower, shows a green involucre of bracts, the outer short, the inner long, with black tips. These surround numerous tubular disc-florets. Ray-florets are usually absent. The single disc-floret consists of :

Calyx, replaced by numerous bristles (pappus), rising from the top of the inferior ovary.

Corolla, petals 5, gamopetalous, superior, rather longer than the pappus. The five equal teeth are borne at the end of the corolla-tube, which is narrower below and widens upwards into a bell.

Androecium, stamens 5, epipetalous, alternating with the petals, inserted by five distinct filaments on the throat of the corolla-tube at the point where it dilates. Anthers united into a tube (syngenesious).

Gynoecium, carpels 2, syncarpous, ovary inferior, unilocular, with one ascending, anatropous ovule. Style elongated, bearing in fully matured flowers two antero-posterior lobes, which diverge beyond the tube of the anthers.

Fruit, a brown striated nut, bearing the wide-spread pappus at the tip, by means of which it is distributed by the wind.

Pollination. If several flowering heads be examined from above it will be seen that the flowers mature in *acropetal succession*, the oldest being outside. The corolla bursts, the syngenesious and introrse anthers protrude, and the pollen is driven out of them by the elongating style, the stigmatic lobes being still appressed ; later these expand, exposing their inner receptive surfaces. The flowers are thus *protandrous*. There is honey-secretion in the corolla-tube, but the flowers are rarely visited by insects and self-pollination is certainly common.

(43) The Ox-Eye Daisy (*Chrysanthemum Leucanthemum*, L.), belonging also to the Tubuliflorae, is a common perennial of dry ground (Fig. 500). The capitulum is solitary on the end of a stem, which widens out to form the *general receptacle*. From its margin arises the involucre of bracts, with membranous margins. Within are numerous florets inserted on the receptacle, but without any bracts subtending them. Centrally are the yellow florets of the disc, peripherally the white ray-florets. Each disc-floret consists of :

Calyx, represented only by a rim round the upper limit of the inferior ovary. There is no pappus.

Corolla, petals 5, gamopetalous, superior.

Androecium, stamens 5, alternating with the petals, epipetalous, inserted by separate filaments upon the throat of the corolla, but with the anthers united laterally into a tube (syngenesious).

Gynoecium, carpels 2, antero-posterior, syncarpous. Ovary inferior, unilocular, containing a single anatropous ovule. Style elongated, and bearing up through the tube of the anthers the two lobes of the stigma, which diverge beyond it in the later stages of flowering (Fig. 500, vii.).

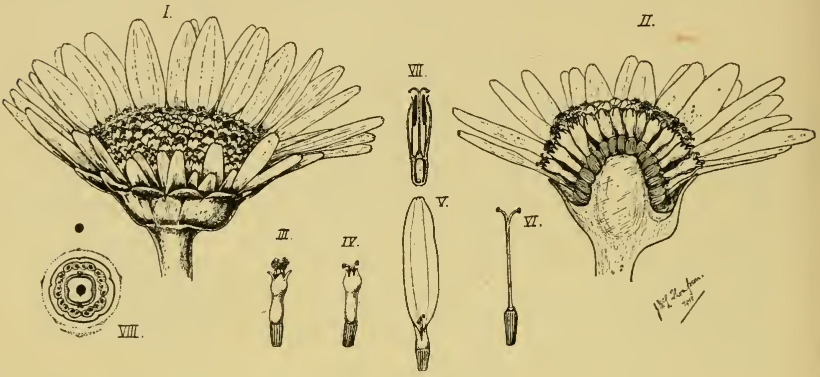

Fig. 500.

I. Whole capitulum of *Chrysanthemum*. II. same in median section. III. disc-floret in earlier (male) condition. IV. same in later (female) condition. V. ray-floret. VI. style and stigma. VII. disc-floret in section. VIII. floral diagram.

The white ray-floret consists of:

Calyx, as before.

Corolla, petals 5, gamopetalous; tubular below, elongated above into a narrow strap-shaped ray representing the three anterior petals, the two posterior being here obsolete.

Androecium, absent.

Gynoecium, as before (Fig. 500, v., vi.).

Fruit. Each flower produces a dry achene, which at maturity is shaken out from the protecting involucre. There is no pappus.

Pollination. The mechanism is here essentially the same as in Groundsel, but with addition of the attractive ray-florets. In the first flowering stage the disc-florets offer pollen, in the second stage the expanded stigmas to the insects that are attracted by the colour and honey (iii. iv.). Any crawling insect will effect crossing. But if this fails self-pollination is also possible.

(44) A third more elaborate type is seen in Cornflower (*Centaurea Cyanus*, or *C. montana* will serve). The general structure is the same, but the ovoid head is tightly enclosed by the appressed bracts with brown margins. The receptacle is flat and bristly. The flowers are all tubular, but the *outermost are neuter*, and coloured, with long tubular two-lipped and 5-lobed corolla, and abortive stamens and ovary. The *inner* florets are *hermaphrodite*, and of the usual type, with pappus of short unequal bristles. The lower part of the corolla-tube is tubular and narrow, the upper is globose, bearing five

distal lobes. The syngenesious anthers form a dark purple tube, with a terminal beak. The style bears below the stigma-lobes a ring of bristles, which acts like a sweep's brush upon the pollen. The flowers are protandrous as before. The *filaments* are curved and *sensitive, contracting on the stimulus of touch.* This is received by hairs radiating out from them ; honey is secreted at the base of the corolla (Fig. 501).

The insect visitors are most commonly bees. Inserting the proboscis into the tube of a floret with stigma not yet receptive, the filaments are stimulated ; they straighten and contract, drawing the anther-tube downwards. The bristles of the style thus brush out the pollen at the moment the insect is there, and it is deposited on his body. If he then passes to a floret with stigmas expanded cross-pollination is ensured. But self-pollination is also possible by curvature of the stigmas to touch the pollen carried on the stylar brush. These examples show how differences of detail in the florets of the Tubuliflorae may be effective in pollination : the fundamental facts being a protandrous condition, and an aggregated inflorescence.

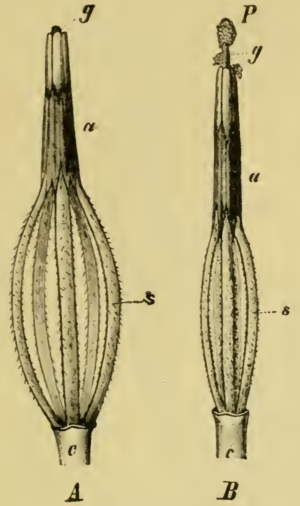

FIG. 501.

Stamens and style of *Centaurea*. *A*, in the unstimulated, *B*, in the stimulated state. The style in the latter projects beyond the anthers, and the pollen has been brushed out. (After Strasburger.)

(ii) *Liguliflorae.*

(45) The Common Dandelion, or any Hawk-weed, will serve as an example. The Dandelion (*Taraxacum officinale*, Web.) is a perennial herb, with massive storage root, a rosette of radical leaves, and solitary, long-stalked heads. The tissues are traversed by branched latex-tubes containing milky-juice. The head consists of an involucre of bracts (Fig. 502, *i*), seated at the margin of a naked, pitted general receptacle (*gr.*). Within are numerous *ligulate florets*, which are all alike, and have the same number and relation of parts as in the Tubuliflorae. But the split ligulate corolla shows by its five teeth at the distal end that it is composed of five petals.

The *pollination-mechanism* is founded on protandry. The elongating style sweeps out the pollen during the first stage of flowering ; the stigma then expands and is receptive during the second stage. The heads expand in sunshine, and intercrossing is possible by many different insects. Self-pollination is also possible by the recurved stigmas coming in contact with pollen adhering to the style. It has, however, been found that in certain cases the fruit of the Dandelion can be matured without any pollination at all, even in buds from which the anthers and stigmas have been all cut away before flowering.

The *fruiting head* is the well-known Dandelion "clock," a type which is characteristic for many of the Compositae. The individual fruit is a dry inferior achene or nut, attached by a long beak to the parachute-like pappus.

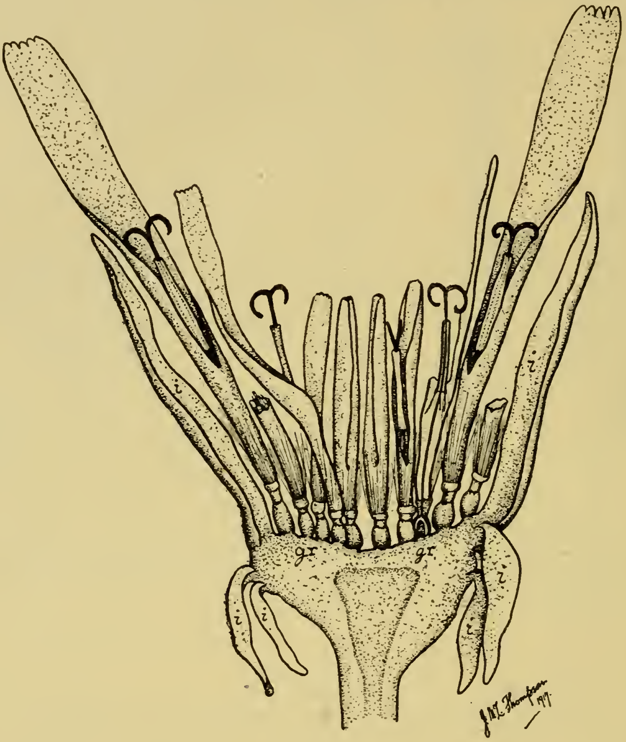

Fig. 502.
Head of Dandelion in vertical section. *i*=involucre. *gr*=general receptacle.
See Text.

These fruits are easily detached by wind, being exposed on the convex growth of the receptacle, owing to the curving back of the involucre (Fig. 247, p. 326). They are thus scattered long distances by the wind. The success of the Compositae as a Family depends largely upon the certainty of each floret producing a good fruit, and on the effective dispersal of the fruit by the wind.

APPENDIX B.

VEGETABLE FOOD-STUFFS.

The Plant-body, containing as it does digestible proteins, carbohydrates, and fats, together with certain mineral salts, is a natural food for Man. Primitive Man used what Nature supplied. But with civilisation came cultivation of the selected plants which best met his needs. Continued cultivation led to improvement in quantity and quality of the crop; and though certain supplies are still drawn from natural sources, it is the cultivated plants that yield by far the greater proportion of the vegetable foods. They are so varied in origin, and in the parts used, that an exact scientific classification is difficult. They may be roughly grouped for practical study under four heads: as (i) Roots and Shoots, (ii) Legumes, (iii) Fruits, and (iv) Cereal grains. Naturally the parts where the material is stored compactly for the use of the Plant itself are those which are of most value to Man. It is to the roots and tubers, and to the fruits and seeds that he looks for his best supplies of food. On the other hand, in the kitchen garden profuse vegetation is encouraged so as to obtain in the shortest possible time a large quantity of succulent tissue, with the least proportion of woody fibre. Halophytes have provided many of the original stocks from which garden vegetables have sprung. The original sources of Cabbage, Sea-Kale, Beet, Asparagus, and Spinach were all coastal plants, while the Potato and Carrot are at home on marine sands.

The analysis of average samples affords some knowledge of the feeding value of each. The results of such analyses for a few of the vegetable foods in common use are given in the following tables, which have been extracted from König's *Die menschlichen Nährungs- und Genuss-Mittel*, and other sources. But there may be considerable variation from sample, and the figures should be held as a guide to an estimate of feeding-value rather than as any exact statement applicable to all cases.

The Potato (*Solanum tuberosum*, L. Solanaceae) grows abundantly on the sand of the sea-shore in the archipelago of S. Chili (Fig. 147, p. 218). At the time of the discovery of America its cultivation was practised with every appearance of ancient usage from Chili to New Grenada. It was introduced probably in the latter half of the sixteenth century into Virginia and North Carolina, and imported into Europe at the time of Raleigh's Virginian voyages, between 1580 and 1585, first by the Spaniards and afterwards by the English. The tubers, which are axillary buds specialised for storage and propagation, are deficient in fats, and contain little proteins. More than four-fifths of the organic substance is in the form of starch. Hence potatoes are used with meat and fats to make a well-balanced meal. Some of the protein is in the form of cubical crystalloids, located near to the corky rind, and thus liable to be removed by peeling the potato (Fig. 82, p. 124).

The Beet (*Beta vulgaris* and *B. maritima*, L. Chenopodiaceae) grows wild on sandy shores in the Mediterranean region, extending northwards to our own coasts. Its originally slender root became fleshy from the effects of soil and cultivation, and Vilmorin has shown that it is one of the plants most easily improved by selection. It has been cultivated since before the Christian era. The fleshy root, characterised by repeated cycles of separate vascular strands, as seen in transverse section, contains cane-sugar in its sappy parenchyma. The analysis shows, for garden Beet, over 14 per cent. ; but in specially selected and cultivated sugar-beets the percentage is higher. It has long been grown as a garden vegetable for winter use ; but latterly it has become the chief European source of Sugar.

The Parsnip (*Pastinaca sativa*, L. Umbelliferae) ranks high as a nutritious vegetable. The original type is native in Britain ; it has been cultivated since Roman times. The root, distended by cultivation, is apt to be fibrous on poor soils ; but when well grown it contains a high percentage of digestible carbohydrates.

The Onion (*Allium cepa*, L. Liliaceae) was used as a condiment by the Egyptians, Greeks, and Romans. It appears to have originated from a wild species of the Middle East. The distended leaf-bases form a bulb containing a large deposit of sugar. But it is as a condiment that it is specially valued. Other species of *Allium* give Garlic, Shallots, Chives, etc.

The Carrot (*Daucus Carota*, L. Umbelliferae) is the enlarged root of the species native in Britain.

The Cabbage, Kale, Cauliflower, and Turnip (Cruciferae) are represented by many varieties. They may all be attributed to one or another of four Linnaean species, viz. *Brassica oleracea*, *napus*, *rapa*, and *campestris*. Some varieties are cultivated for their leaves, as Cabbages ; or for their crowded inflorescences, as Cauliflower ; or for the oil in their seeds, as Colza and Rape ; others again for the fleshy swellings of the root, or lower part of the stem. In Turnips and Swedes the hypocotyl is swollen ; in Kohl-rabi the epicotyl. All of these were ultimately of European or Siberian origin, and some of their ancestral forms grow wild on our coasts. Their cultivation was diffused in Europe before the Aryan invasion. The analyses show that their value as foods is not high, though they contain a fair proportion of digestible proteins and carbohydrates.

Celery (*Apium graveolens*, L. Umbelliferae) is derived from the wild species widely spread from Sweden through Europe and the Near East. It was known to the Greeks. In cultivation it is blanched by earthing up, so as to diminish its bitterness. The feeding value is about equivalent to Winter Kale.

Spinach (*Spinacia oleracea*, L. Chenopodiaceae) was not known to the ancients. It was new to Europe in the sixteenth century, being introduced from the Near East. It is not known in the wild state. The feeding value of its leaves is below that of Kale.

The Garden Lettuce (*Lactuca Scariola* : var. *sativa*, Compositae) is derived from the wild species native in temperate and southern Europe. It was used by the Greeks and Romans as a salad, and several varieties were already known to them. It is notable for its high water-content.

TABLE OF ANALYSES OF ROOTS AND SHOOTS.

N.B.—Vegetables used in the fresh state have a very high water-content. This must be taken fully into account in considering their value as foods.

Name.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash
Potato	74·98	2·08	0·15	21·01	0·69	1·09
Beetroot	82·25	1·27	0·12	14·40	1·14	0·82
Parsnip	79·31	1·32	—	16·36	1·73	1·28
Onion	85·99	1·68	0·10	10·82	0·71	0·70
Carrot	86·79	1·23	0·30	9·17	1·49	1·02
Turnip	87·80	1·54	0·21	8·22	1·32	0·91
Cauliflower	90·89	2·48	0·34	4·55	0·91	0·83
Winter Kale	80·03	3·99	0·90	11·63	1·88	1·57
Celery	84·09	1·48	0·39	11·80	1·40	0·84
Spinach	88·47	3·49	0·58	4·44	0·93	2 09
Lettuce	94·33	1·41	0·31	2·19	0·73	1·03

TABLE OF ANALYSES OF LEGUMES.

The Legumes are notable for the high protein-content of their seeds. The water-content of the parched seeds averages about 13 per cent. Consequently the percentage of the other constituents appears to stand high as compared with the previous table, and with the analyses of Green Peas and French Beans.

Name.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Bean	13·49	25·31	1·68	48·33	8·06	3·13
Parched Peas	13·92	23·15	1·89	52·68	5·68	2·68
Lentils	12·33	25·94	1·93	52·84	3·92	3·04
Soya Beans	12·71	38·18	14·03	31·97	4·40	4·71
Arachis	7·71	31·12	46·56	9·39	2·16	3·06
Green Peas	78·44	6·35	0·53	12·00	1·87	0·81
French Beans	88·75	2·72	0·14	6·60	1·18	0·61

The Broad Bean (*Vicia Faba*, L.) was cultivated in Europe in prehistoric times. It was probably introduced during the earliest Aryan migrations, its wild habitat having been south of the Caspian, while a related species (*V. narbonensis*) is still wild in the Mediterranean region. The large percentage of protein in the Bean is represented by numerous small aleurone grains, and the protoplasmic matrix in the cotyledonary cells, while large starch-grains account for most of the digestible carbohydrates. The thick cell-walls make up 8 per cent., while the ash is unusually high. Beans are difficult of digestion, but very nutritious.

The Garden Pea (*Pisum sativum*, L.) was introduced into Europe by the Aryans from the Near East, but it no longer exists in a wild state. It has been found among the relics of the Bronze Age, and even of the Stone Age. In point of analysis it corresponds nearly to the Bean. It is, however, commonly used in the immature state, as " green peas " ; but the analysis of these, putting aside the high water-content, corresponds in essential feeding-value to that of dried peas, while they are more readily digestible.

The Lentil (*Ervum lens*, L.) was cultivated from prehistoric times in western Asia, and in Egypt, and it has been found in the remains of the Swiss lake-dwellings, but it is no longer known in the wild state. Its analysis corresponds to that of Beans, but notably with a smaller proportion of cellulose and lignin.

The most important of all the Legumes for the future may be the Soya Bean (*Glycine soja*, Sieb. et Luce, and other species), which is of very early cultivation in the Far East. The analysis shows that while the protein content is extremely high, oil replaces a considerable proportion of the digestible carbohydrate. The chief supply was formerly from Manchuria, but its cultivation has now spread to many other countries, some effort having been made to introduce the crop to Britain ; as, with the exception of Rape and Linseed, no oleaginous seeds are grown in this country.

The Pea-nut, or Monkey-nut (*Arachis hypogaea*, L.) is believed to have originated in Brazil. Seeds have been found in Peruvian tombs. Thence it was conveyed to Africa and Asia, and it is now cultivated in all hot countries, either for the seed or for the oil which they contain in so large a proportion, replacing most of the digestible carbohydrates.

The French Bean, or Haricot (*Phaseolus vulgaris*, Savi) was probably of American origin, its seeds having been found in Peruvian tombs. There is no evidence that it has been long cultivated in Europe or Asia. In its qualities and uses it resembles the Pea and Bean. Its immature pods, used as a vegetable, are inferior in food-value to green Peas.

FRUITS.

The chief interest in Fresh Fruits, apart from their high water-content, lies in the proportion of sugar and of free acids (but see p. 662). Upon the former depends their value for the production of wines, in which the Grape takes precedence. The Vine (*Vitis vinifera*, L. Vitaceae) grows wild in W. Asia, S. Europe, and N. Africa. Both Semitic and Aryan nations knew the use of wine, and Egyptian records carry back the cultivation of the grape to 4000 B.C. The grape-sugar, of which it contains over 14 per cent., is the starting-point for alcoholic fermentation. But it is also important in the dried state, giving their value to raisins, and to dried currants, which are small dried grapes. The Apple (sugar 7·22 per cent.) and Pear (8·26 per cent.) give respectively Cider and Perry, while the Currant (6·38 per cent.) and the Gooseberry (7·03 per cent.) are also used in the preparation of British wines. But the relatively large proportion of free acids in these detracts from their value.

TABLE OF ANALYSES OF FRESH FRUITS.

Name.	Water.	Nitrogenous substances	Free acids.	Sugar.	Other digestible carbohydrates.	Cellulose and lignin.	Ash.
Apples - -	84·79	0·36	0·82	7·22	5·81	1·51	0·49
Pears - - -	83·03	0·36	0·20	8·26	3·54	4·30	0·31
Plums - - -	84·86	0·40	1·50	3·56	4·68	4·43	0·66
Peaches - -	80·03	0·65	0·92	4·48	7·17	6·06	0·69
Apricots - -	81·22	0·49	1·16	4·69	6·35	5·27	0·82
Cherries - -	79·82	0·67	0·91	10·24	1·76	6·07	0·73
Grapes - -	78·17	0·59	0·79	14·36	1·96	3·60	0·53
Strawberries -	87·66	0·54	0·93	6·28	1·46	2·32	0·81
Raspberries -	85·74	0·40	1·42	3·86	0·66	7·44	0·48
Blackberries -	86·41	0·51	1·19	4·44	1·76	5·21	0·48
Gooseberries -	85·74	0·47	1·42	7·03	1·40	3·52	0·42
Currants - -	84·77	0·51	2·15	6·38	0·90	4·57	0·72

The actual nutritive value of fresh fruits is usually small. But in the dried state those which contain sugar, and the kernels of oily nuts, are of high value, as shown by the following table:

ANALYSES OF DRIED FRUITS.

Name.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Almond - -	6·02	23·49	53·02	7·84	6·51	3·12
Hazel Nut - -	7·11	17·41	62·60	7·22	3·17	2·49
Walnut - -	7·18	15·77	57·43	13·03	4·59	2·00
Raisins - -	32·02	2·42	0·59	62·04	1·72	1·21
Dried Figs - -	31·20	4·01	—	49·79	—	2·86

A comparison of the constituents of kernels such as the Almond, and of dried fruits such as the Raisin or Fig, shows that together they supply in suitable proportions the proteins, fats, and digestible carbohydrates required for food.

CEREAL GRAINS.

By far the most important vegetable foods are the Cereal Grains, which are the fruits of various Grasses (Gramineae). The general construction of all of these grains is the same, and the structure of the grain of Wheat will serve to illustrate it for them all.

The Wheat-Grain is oval, and hairy at the apical end, but smooth at the base where is the scar of attachment. A lateral groove running longitudinally marks the posterior side; the anterior side is convex, and shows near its base an area which is depressed and wrinkled when dry. This marks the position of the *germ*, which is thus basal and faces the anterior side of the grain (Fig. 503). The greater part of the grain is made up of a mass of *endosperm*: this together with the germ is covered by the fruit-coat (pericarp) and seed-coat (testa), which jointly form a hard brittle shell, separated in milling from the inner parts as *Bran.*

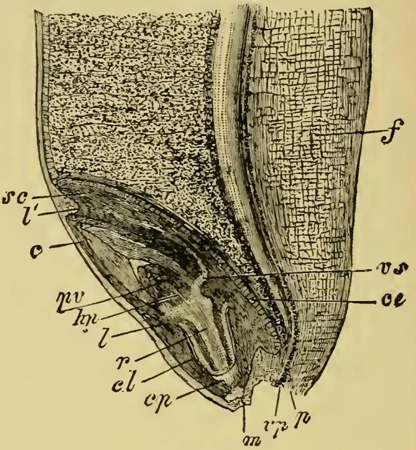

FIG. 503.

Part of a median longitudinal section of a grain of Wheat, showing embryo and scutellum (*sc*). *vs*=vasc. bundle of scutellum; *ce*=its columnar epithelium; *l'*=ligule; *c*=sheathing part of cotyledon; *pv*=vegetative cone of stem; *hp*=hypocotyl; *l*=epiblast; *r*=radicle; *cl*=root-sheath; *m*=micropyle; *p*=funiculus; *vp*=vascular bundle of funiculus; *f*=lateral wall of groove; *cp*=pericarp. (× 14.) (After Strasburger.)

A microscopic examination shows that the *germ* consists of thin-walled tissue densely stored with oily protoplasm, but with *no starch.* The *endosperm* is also thin-walled, but contains *much starch* closely packed (Fig. 482, *am*); but a superficial layer of its cells is distinguished by the absence of starch, while as it contains numerous aleurone grains it is recognised as the *aleurone-layer* (*al*). The *Bran* consists of compressed and thickened cell-walls of *woody texture,* containing a deposit of silica. The outer band (*p*) represents the fruit-coat or pericarp: the inner (*t*) represents the seed-coat or testa.

The constitution of the Wheat-Grain as shown by analysis may vary considerably according to sample. This is shown even in so important a feature as the proportion of nitrogenous substances. "Soft Wheat" may contain only 10·80 per cent. of protein, while "Hard Wheat" has been found to contain 13·83 per cent. In some Russian Wheats it may even rise above 17 per cent. These facts are mentioned to show that the results of analysis must be taken as a general guide rather than as a statement of constant fact.

It is important as a basis for judgment of the results of milling to know by analysis the distribution of the constituent substances in the Wheat-Grain. This is shown by the subjoined table, taken from Dr. Hutcheson's book on *Food* :

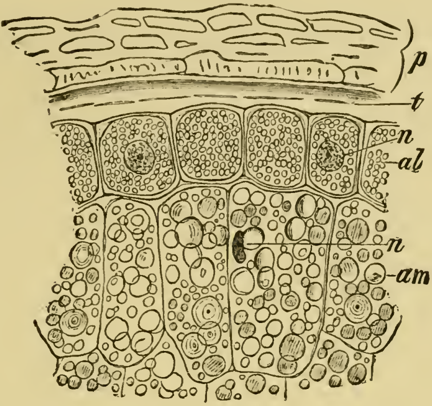

FIG. 504.

Part of a section of a grain of Wheat. *p*=pericarp; *t*=seed-coat, internal to which is the endosperm; *al*=aleurone grains; *am*=starch grains; *n*=nucleus. (× 240.) (After Strasburger.)

Wheat.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Whole Grain, 100% -	14·5	11·0	1·2	69·0	2·6	1·7
Bran, 13·5% -	12·5	16·4	3·5	43·6	18·0	6·0
Endosperm, 85% -	13·0	10·5	0·8	74·3	0·7	0·7
Germ, 1·5% -	12·5	35·7	13·1	31·2	1·8	5·7

A large portion of the grain (85 per cent.) is endosperm ; the bran amounts to 13·5 per cent., and the germ only to 1·5 per cent. The latter is, however, important, for it contains a high proportion of proteins, of fats, and of ash. Since the *germ* flattens in roller-milling, it can be sifted out. The highly nitrogenous and fatty body thus extracted may then be added to ordinary flour in varying proportions, giving different kinds of germ-bread. *Bran* is characterised by its large proportion of cellulose and lignin (18 per cent.), which is indigestible by man, but more available for herbivorous animals. There is in it, however, a large quantity of nitrogenous substance, owing to the adherence of the aleurone-layer of the endosperm to the flaky scales of the fruit-coat ; the silica in the latter accounts for the large percentage of ash in bran (6 per cent.). Thus bran contains an undue proportion of proteins in which the grain as a whole is deficient. Its value in bran-mash for horses is therefore easily understood. The *endosperm*, which forms 85 per cent. of the grain, is broken down in the process of milling into fine flour, semolina, and other products. Its analysis shows that, while about three-quarters of it consists of starch, there still remains in it about 10 per cent. of protein, which, as " gluten," forms the basis of the dough of bread when moistened with water.

The purpose of milling of grain was in the first instance simply to grind it into small parts. The bread of primitive Man was doubtless " wholemeal " bread. But even in the old stone-grinding the products were usually graded roughly as bran, pollard, sharps, middlings, and fine flour. Sometimes the coarser products were reground, and the fine flour again extracted from them ; but mostly they were regarded as " offals," and were fed to stock in various forms. More recently in the process of roller-milling the grain is comminuted more accurately by successive stages, being passed through rollers with successively finer ridges. The products of these successive " breaks " are sifted partly by screens, partly by air-blasts, so arranged that their various grading can be very perfectly carried out. The end-product of greatest importance is the flour. The finer this flour is graded the less percentage of it will be yielded from the milled grain, but the whiter will be the flour and the bread made from it. In practice the highest percentage of finest white flour that can be obtained is about 70 per cent. of the weight of the whole grain. Higher extraction results in a flour showing some degree of brownness owing to the inclusion of a proportion of bran. In deciding the type of flour that is to be produced, various aspects have to be considered, such as nutritional value and acceptability, and there has been some difference of opinion on the matter. In war-time the need for economy gives added importance to a relatively high extraction. During the 1939-45 War, British national flour has been based on an extraction of 80-85 per cent. of the wheat grain.

A comparison of the analyses of average samples of the grains in common use by Man gives a basis for estimating their relative values as foods. The average of a large number of different samples of each is given in the subjoined table :

TABLE OF ANALYSES OF CEREAL GRAINS.

Name.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Wheat - -	13·37	12·04	1·91	69·07	1·90	1·71
Rye - - -	13·37	10·81	1·77	70·21	1·78	2·06
Barley - -	14·05	9·66	1·93	66·99	4·95	2·42
Oats, average from all lands - -	12·11	10·66	4·99	58·37	10·58	3·29
Oats, England and Scotland - -	12·11	13·05	6·15	53·16	11·89	3·64
Maize - - -	13·35	10·17	4·78	68·63	1·67	1·40
Rice (not cleaned)	11·99	6·48	1·65	70·07	6·48	3·33

Wheat (*Triticum vulgare*, Villars) has been cultivated from prehistoric times in Europe and Egypt, and in China records of it go back to 2700 B.C. It is represented by numerous varieties. Those in which the ripened grain detaches itself naturally from the husk are referred to one species (*Triticum vulgare*, Villars); those in which the ripe grain is closely contained in the husk are distinguished as Spelts (*T. Spelta*, L.). The separation of these was probably prehistoric. There is no certain evidence of the place of origin of wheat, for it is not found wild, but its probable home was in the Near East. It is the chief staple food of the white races.

Rye (*Secale cereale*, L.) probably had its origin in the countries north of the Danube, and its cultivation was hardly earlier than the Christian era. It does not greatly differ in its nutritive qualities from wheat, and is largely grown in central and northern Europe.

Barley (*Hordeum distichon*, L., *vulgare*, L., and *hexastichon*, L.) is among the most ancient of cultivated plants. It has been found wild in the Caspian region. It is chiefly used for malting and brewing, for which its low content of proteins is suitable.

The Oat (*Avena sativa*, L.) is not now found wild, but it was probably derived from a form native in Eastern Temperate Europe. It was cultivated anciently in Italy and Greece, and its grains have been found in Swiss lake-dwellings, and in early German tombs. Though a coarse grain with much cellulose and lignin in its outer coats (10 to 12 per cent.), its high percentage of fats (5 to 6 per cent.), proteins (12-13 per cent.), and ash (3 to 4 per cent.), mark it as superior to any other Cereal as a staple food. Moreover, a comparison of the average of analyses of Oats from all sources with those from England and Scotland shows that these stand the highest of all; a fact which justifies, and should encourage, the prevalent use of porridge and oat-cake.

Maize (*Zea Mays*, L.) is of American origin. At the time of the discovery of the New World it was found to be one of the staples of widespread agriculture from Peru northwards, but it has not been found in the wild state. Its large grain is very hard, by reason of the close packing of the starch-grains in the endosperm. Starch is also present in the relatively large germ. Its analysis shows a rather high percentage of fats; but the hardness of the endosperm gives a gritty texture to its products, and makes thorough cooking necessary.

Rice (*Oryza sativa*, L.) is indigenous in India, and perhaps also in China. It is a more widespread staple food than any other, supporting about one-third of the human race. It has a rough husk, which represents 6 per cent. of the grain, and is cleaned off before exportation. This tends to remove the aleurone layer also, and to carry off a proportion of the proteins from a grain that is already deficient in them (6.48 per cent.). The analysis of cleaned rice, *i.e.* after removal of the husk, shows a very high percentage of digestible carbohydrates, with a marked deficiency of proteins and fats. This justifies its use in curries and puddings, in the preparation of which fats and proteins are added. But as a staple food without additions it leaves much to be desired.

FOOD VALUES. VITAMINS.

The relative values of the various vegetable food-stuffs of which analyses have been given above, may be assessed in the first instance by considering their " fuel values ", *i.e.* the number of " Calories " which each produces when completely oxidised (one [large] Calorie is the amount of heat required to raise the temperature of one kilogram of water by one degree C.—or that of one lb. of water by 4 degrees F.). It has been calculated by physiologists that an average healthy man, weighing 70 kg. (11 stone) and doing a moderate amount of physical work, requires each day food with a total fuel value of 3300 Calories. Assuming each gram of protein or carbohydrate to provide 4 Calories and each gram of fat 9 Calories, the normal metabolic requirements of the average man will be met by a diet comprising 100 grams of protein, 100 grams of fat and 500 grams of carbohydrate per day.

The fuel value of any substance is however only one aspect of its suitability for human food. As regards proteins, in particular, quality is quite as important as quantity. Digestibility and palatability of the food must likewise be taken into account. Among the drawbacks of a purely vegetarian diet is the monotonous and unpalatable character of many vegetable staple foods. Rice, for example, quite apart from its very low fat and protein content, makes an insipid dish and hence an unsatisfactory staple diet unless seasoned by the addition of highly flavoured condiments such as curry or soy. The widespread instinctive preference for a mixed diet is moreover biologically justified, not only by the need for a proper balance between protein, fat and carbohydrate, but also because adherence to such a diet is the natural way of ensuring a sufficient and regular supply of the essential mineral salts and of the no less indispensable *vitamins*.

Vitamins are " accessory food factors ". Though they are not themselves food substances in the ordinary sense, a certain amount of each vitamin must be supplied to the human body if full health is to be maintained. That amount is very small ; perhaps not more than one millionth part of the daily food ration ; but, on the other hand, a minimum supply of every vitamin is absolutely necessary, since lack of any one results in a characteristic " deficiency disease ". The best known of these ailments are *scurvy* and *rickets*.

Scurvy has been known for centuries, especially among seafaring peoples. Its connection with a diet lacking fresh vegetables and fruit was first clearly demonstrated by Lind in 1757. Captain Cook was able to keep his crews free of the disease by making them eat fresh food as often as possible. It is now known that the active principle in fresh foods which prevents the development of scurvy is the " anti-scorbutic vitamin " or " Vitamin C ".

Rickets is ordinarily caused by lack of sunlight aggravated by a diet poor in natural fats. The specific " anti-rachitic " agent is " Vitamin D ", one of the richest sources of which is cod-liver oil (and similar fish oils). Most other natural foods contain comparatively little of this vitamin, hence the importance of sufficient sunlight, the ultra-violet rays in which transform any inactive " provitamin " present in the body into the active vitamin.

Certain eye-troubles (such as night-blindness) and an unhealthy condition of the mucous membranes result from a deficiency of " Vitamin A ". This vitamin is readily obtained from fresh green vegetables (*e.g.* spinach or cabbage) and from *yellow* root vegetables (*e.g.* carrot), in fact from all foods rich in the chromatophore pigment *carotene*, which is the provitamin. The vitamin is also present in fish-liver oils and in ox-liver. In this case the provitamin is synthesised solely by plants; the transformation of carotene into the active vitamin, on the other hand, takes place so far as is known only within the animal body.

Other serious diseases due to vitamin deficiency, but less familiar in Europe, are " beri-beri " (" Vitamin B_1 " deficiency) and " pellagra " (deficiency of the " P.P. Vitamin ").

At the time when the vitamin theory of deficiency diseases was first put forward (1912) and for many years afterwards, little or nothing was known about the chemical nature of vitamins, which were indeed long regarded as mysterious if not as miraculous agents. More recently, however, most of them have been isolated in the pure state, analysed and their constitution determined; several have even been synthesised. It has already been noted that " Vitamin A" is a derivative of the complex hydrocarbon *carotene*. " Vitamin C " is *ascorbic acid*, $C_6H_8O_6$ and " Vitamin D " is a modification, under the influence of ultra-violet radiation, of *ergosterol*, $C_{28}H_{44}O$.

We are, in fact, now in a position to administer all the principal vitamins in the pure form as curative or preventive agents, if need be. The first line of defence against deficiency diseases, however, should be a good mixed diet, including daily supplies of fresh vegetables and fruit; in addition, ample sunlight is essential, or, where sunlight is deficient, regular doses of cod-liver or halibut oil.

INDEX AND GLOSSARY

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