



In nature, many animals will meet a violent death. So the sad end of one small bandicoot seems hardly worth mention. The demise of this little fellow would, however, have surprised most modern onlookers. Its killer was a kangaroo—the Powerful-Toothed Giant Rat-kangaroo (Ekaltadeta ima), to be exact.

In 20th-century Australia, warm-blooded predators are few and far between. Among our natives, the largest carnivores are the Spotted-Tailed Quoll (Dasyurus maculatus) and the Tasmanian Devil (Sarcophilus harrisii). (The doglike dingo, which also eats flesh, did not originate in Australia but was introduced by humans between 5,000 and 4,000 years ago.) The Spotted-Tailed Quoll is a marsupial that weighs up to seven kilograms (15 pounds); it is also known as a native "cat" because of a passing resemblance to ordinary, placental cats. The Tasmanian Devil, another marsupial, is only slightly larger and looks like a lapdog with a fierce hyena's head. It is arguably the least fussy eater in the world and will devour an entire carcass, including the teeth. This odd pair is placed in the family Dasyuridae, which includes other native cats as well as far smaller, mostly insectivorous creatures called marsupial mice.

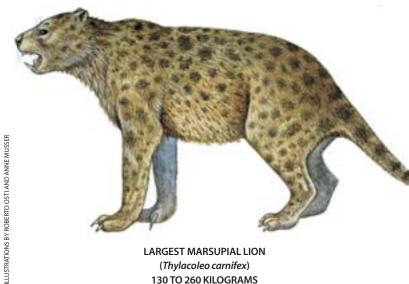
Some scientists have suggested that Australia has never supported a healthy contingent of large warmblooded carnivores. Most recently, Tim Flannery of Harvard University has argued that their evolution was constrained by poor soils and erratic climate for the past 20 million years or so. His rationale is that these constraints limited plant biomass, in turn restricting the size and abundance of potential prey animals. Instead, he and others have hypothesized, reptiles such as the seven-meter-long (23-foot-long) lizard Megalania prisca, which lived in Pleistocene times, took up the role of large terrestrial carnivores. Cold-blooded predators require less food than warm-blooded ones and so-the argument

goes—were more likely to survive difficult conditions. This claim is challenged by recent developments, notably spectacular fossil finds in Riversleigh, Queensland. A European naturalist, W. E. Cameron, first noted the presence of fossils at this remote site in 1900. But Cameron believed that the material he had seen was fairly young, less than two million years old. Moreover, Riversleigh's extreme inaccessibility-summer heat and monsoon rains allow excavations only in winter—persuaded paleontologists to neglect the locality for decades. In 1963, however, Richard Tedford of the American Museum of Natural History in New York City and Alan R. Lloyd of the Australian Bureau of Mineral Resources took a gamble and visited the site. They found the fossils intriguing and older than previously believed but fragmentary and hard to retrieve.

Still, their findings stimulated other expeditions to Riversleigh, and in 1983 my former supervisor Michael Archer, now director of the Australian Museum in Sydney, struck paleo pay dirt. In an idle moment at the site he looked down at his feet and saw a very large lump of rock that just happened to contain as many new species of Australian Tertiary mammals as had been described in previous centuries. Since then, new specimens, including large carnivores, have emerged at a prodigious rate. Many are exquisitely well preserved, so much so that some could be mistaken for the remains of animals that died only weeks ago.

Predator's Gallery

Formidable flesh-eaters from ancient Australia included a marsupial lion (below), a marsupial wolf (near right), a giant rat-kangaroo (far right) and an enormous lizard (below, right). The largest rat-kangaroo, Propleopus oscillans (which weighed 60 kilograms), the "lion" and the lizard survived until fairly recent times and may have even preyed on humans. -S.W.

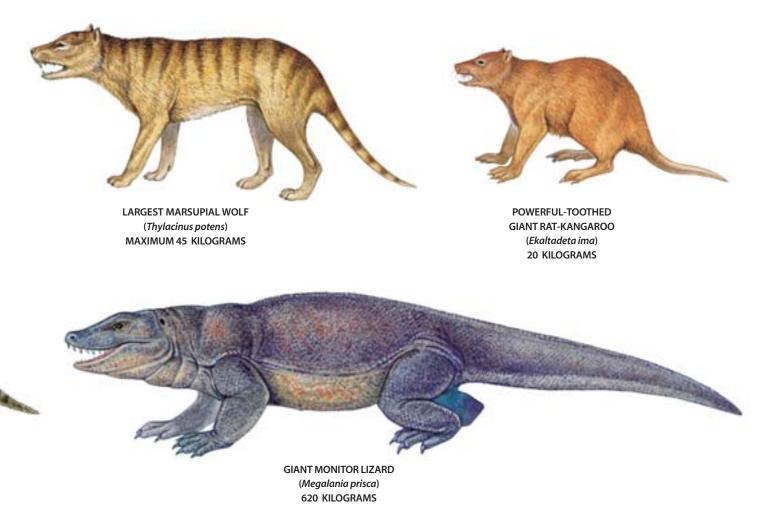


LARGEST MARSUPIAL LION (Thylacoleo carnifex) 130 TO 260 KILOGRAMS

The ancient creatures appear to have been mostly trapped in limestone caves. Their bones, which were quickly and perfectly preserved by water rich in calcium carbonate, testify to a lost menagerie of beasts that were every bit as deadly as, but far stranger than, anything known today. Since 1985 nine new species from Riversleigh, each the size of the Spotted-Tailed Quoll or bigger, have more than doubled the tally of large Australian carnivores at least five million years old. This bestiary now includes two kinds of giant rat-kangaroo, nine species of marsupial "wolf," five species of marsupial "lion" and one native cat.

The giant rat-kangaroos (propleopines) are closely related to the Musky Rat-kangaroo. This tiny animal, still found in the rain forests of Queensland, weighs less than a kilogram small enough to look like a rat. It eats a wide variety of plant stuffs and small animals, and alone among living kangaroos it cannot hop. A living fossil, it is the last and tiniest survivor of a family that included some fearsome, muscle-bound cousins. The giant rat-kangaroos ranged from around 15 to 60 kilograms in weight. Like their diminutive descendant, they probably walked on all fours.

The marsupial wolves (thylacinids) and marsupial lions (thylacoleonids) are so named because of their superficial physical resemblances to canines and felines, although they were more closely related to kangaroos. The last of the marsupial wolves, perhaps confusingly called the Tasmanian Tiger because of the stripes on its rump, was exterminated early in this century because of a largely undeserved reputation for preving on sheep. Like cats, the marsupial lions had short, broad, powerful skulls, and they probably filled simi-



lar ecological niches as well; their size ranged from that of a house cat to that of a lion. Although no fossils contain actual traces of a pouch, specialized features of the bones shared with living animals leave no doubt that all these creatures were marsupials.

Fearsome Forest

For much of the Miocene epoch (25 to five million years ago), Australia was carpeted in wall-to-wall green, and rain forest covered many areas that are now savanna or desert. These jungles were an evolutionary powerhouse, nurturing a far greater diversity of life than any modern Australian habitat does. A day trip through one of these forests would have been filled with surprises, many of them potentially dangerous.

One would have been the Powerful-Toothed Giant Ratkangaroo, among the most ancient of rat-kangaroos (another five species have been described from younger deposits). *E. ima* was also the smallest, weighing only about 10 to 20 kilograms. It is well represented by two nearly complete skulls. These fossils give us our best shot yet at understanding the feeding habits of the giant rat-kangaroos.

Because these animals descended from plant-eating marsupials, some controversy surrounds the interpretation of their biology. Nevertheless, all recent authors agree that these distinctly uncuddly kangaroos included meat in their diets. Evidence supporting this hypothesis comes from both their skulls and their teeth.

In popular imagination, ferocious meat-eaters usually come with large canines. In the main this holds true, but there are some exceptions. Many humans consume a good deal of flesh—more than some so-called carnivores—but we have small canines, whereas in gorillas, which are vegetarians, these teeth are large. The real hallmark of a terrestrial mammalian killer is a set of distinctive cheek teeth used for cutting and shearing.

In less specialized members of the placental carnivore, giant rat-kangaroo and marsupial lion clans, the last two to four teeth in the upper and lower jaws are broad molars, used primarily for crushing plant material. Immediately in front of these molars are vertical shearing blades, called carnassials, that can efficiently slice through muscle, hide and sinew. Within each of these three groups of animals, however, the carnassials of the most carnivorous species are greatly enlarged, whereas the plant-processing teeth are reduced, even lost. In the mouth of a domestic cat, for instance, can be found the cheek teeth of a highly specialized carnivore.

So the relative importance of the carnassial versus the crushing teeth in an animal's jaws offers a good indication of how much flesh it devoured. In this respect, the giant rat-kangaroos resembled canids such as foxes, which are opportunistic feeders and retain significant capacity to crush. But the skull of *E. ima* featured a number of other attributes typical of carnivores. Its robust architecture, for instance, undoubtedly supported the massive neck and jaw muscles that many predators need to subdue struggling prey. But it never evolved long canines in the lower jaw; instead its lower front incisors became daggerlike blades.

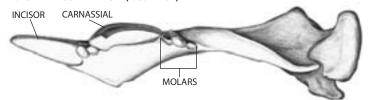
On these grounds, I and others have argued that giant ratkangaroos were generalists, taking flesh when available but

LARGEST MARSUPIAL LION (T. carnifex)

AFRICAN LION

INCISORS

CANINE



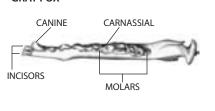
CARNASSIAL

MOLAR

INCISOR CARNASSIAL **MOLARS**

POWERFUL-TOOTHED GIANT RAT-KANGAROO

GRAY FOX



CARNASSIAL TEETH—vertical blades for slicing through meat and hide-are the hallmark of a terrestrial mammalian killer. In highly specialized carnivores such as the marsupial lion and the African lion shown, a single tooth on each side of the upper and

lower jaws has been modified for this task; all the molars behind this carnassial are reduced or lost. (Only the lower jaw is drawn.) Generalized carnivores, such as the giant rat-kangaroos and foxes, which consume much vegetation, retain their crushing molars.

supplementing their diet with a healthy variety of vegetable matter. These renegades of the kangaroo clan terrorized the Australian continent for at least 25 million years, going extinct only sometime over the past 40,000 years.

While keeping an eye open for meat-eating kangaroos, a human intruder in Miocene Australia would have done well to avoid low-slung branches. The trees were home to another unpleasant surprise: marsupial lions. Like the giant rat-kangaroos, the four species of Miocene "lions" evolved from peaceable, plant-eating types. The most primitive species have generalized molar teeth typical of omnivores, as well as carnassial blades. In other species the crushing molars are reduced or lost, and the flesh-shearing teeth become huge.

At least eight species of marsupial lions have been formally described, and two more are being studied by Anna Gillespie of the University of New South Wales in Sydney. Historically, the interpretation of marsupial lion biology has been contentious. As vombatomorphian marsupials, their closest living relatives are koalas and wombats. Some early paleontologists, prejudiced by the close relationship of these "lions" to herbivorous marsupials, refused to concede the possibility of a carnivorous way of life for them. They offered a variety of unlikely scenarios, culminating in the suggestion that the creatures were specialized melon munchers. (Because the teeth could barely grind, the food was assumed to have been rather soft!)

Nowadays scientists agree that marsupial lions were indeed killers. Many consider that the most recent species, Thylacoleo carnifex, was the most specialized mammalian carnivore ever known: it effectively dispensed with plantprocessing teeth, whereas the elaboration of its carnassials is unparalleled. It did not have big canines and must have used its long incisors to kill.

T. carnifex is also the only marsupial lion known from a complete skeleton. Many researchers have suggested that it was the size of a large wolf or leopard. Others, myself included, believe that such estimates have not accounted for the extreme robustness of the skeleton and that this frightening beast could have been as heavy as a modern lion. It was built for power, not endurance, and had tremendously muscular forelimbs. With teeth like bolt-cutters and a huge, sheathed, switchbladelike claw on the end of each semiopposable thumb, it would have been an awesome predator on any continent.

Pouched Pouncers

ndoubtedly, T. carnifex was adapted to take relatively large prey, probably much larger than itself. The exact purpose to which it put its thumb-claw is unclear, but one thing seems certain: once caught in the overpowering embrace of a large marsupial lion, few animals would have survived.

The kinds of marsupial lion known as Wakaleo were smaller, about the size of a leopard. Not designed for speed but immensely powerful, species of Wakaleo (and possibly Thylacoleo) may have specialized in aerial assault. Like the leopard, they could have launched themselves onto unsuspecting prey from trees. At the other end of the scale, at around the size of a domestic cat, Priscileo roskellyae may have concentrated on taking arboreal prey. Given their size and extreme predatory adaptations, I believe the larger marsupial lions most likely maintained a position at the top of the Australian food pyramid. And *T. carnifex* lived at least until 50,000 years ago—recently enough, perhaps, to have fed on humans.

On the forest floor, the marsupial wolves dominated. When Europeans arrived in Australia more than 200 years ago, they found only two marsupial families with carnivorous representatives. These were the "wolves"—only the Tasmanian Tiger remained—and a far more numerous group, the dasyurids. These mostly diminutive but pugnacious beasts are commonly measured in grams, not kilograms, and over 60 living species have been described.

Because in recent times dasyurids have clearly dominated in terms of species diversity, paleontologists had expected to find that they were also far more common than thylacinids in the distant past. We were wrong. Since 1990 seven new species of Miocene-age "wolves" have been found, bringing the total for the family to nine (including the Tasmanian Tiger). Descriptions of four more species are in the pipeline. On the other hand, only one definite dasyurid has been described from Miocene deposits. A few species known from fragmentary material may also turn out to be dasyurids. Even so, the proportion of marsupial wolf to dasyurid spe-



FOSSIL SKULL of the Powerful-Toothed Giant Rat-kangaroo displays the fearsome incisors and serrated carnassials (resembling cockleshells) that would have enabled it to kill and consume its prey efficiently. The skull measures 145 millimeters from end to end, and the lower jaw is 122 millimeters.

cies during the Miocene is in stark contrast to that of modern times.

The Tasmanian Tiger is the only thylacinid for which any firsthand accounts of biology and behavior are available. Most of these must be taken with a grain of salt. But the following is fairly certain: the Tasmanian Tiger was similar to most canids in that it was fully terrestrial, long-snouted and probably tended to take prey considerably smaller than itself. It differed in being relatively poorly adapted for running and probably was not a pack hunter. It further differed from the majority of canids in that its cheek teeth were adapted to a completely carnivorous diet.

In thylacinids and dasyurids the dental layout is different from that of most other flesh-eaters. These animals retain both a crushing and a vertical-slicing capacity on each individual molar. Thus, in meat-eating specialists of this type the crushing surfaces are reduced and the vertical shear is increased on each molar tooth.

Indeed, all the marsupial wolves were largely carnivorous, although the smaller, less specialized ones probably also ate insects. A number of these animals departed still further from the canid model. Some Miocene "wolves" were small compared with the Tasmanian Tiger, and one, *Wabulacinus ridei*, had a short, more catlike skull. We cannot even be sure that all Miocene-age thylacinids were terrestrial, because only fragments of the skulls and jaws are known for most. A magnificent exception is a 15-million-year-old individual recently discovered at Riversleigh; its skull and most of its skeleton are beautifully preserved. We can be reasonably certain that this animal at least lived on firm ground.

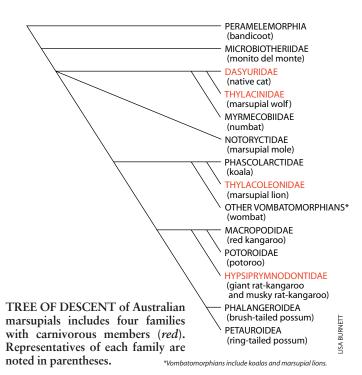
In the past few months Henk Godthelp of the University of New South Wales, Archer and I have described a mouse-size marsupial from deposits around 55 million years old in Murgon in southeastern Queensland. This new species has an extremely generalized dentition, so primitive in fact that its relation to other marsupials is very difficult to ascertain. It may represent an ancestor of thylacinids and dasyurids—or even of all Australian marsupials. An alternative possibility is that this new species does not belong to Australian marsupials) but instead to the mostly South American group Ameridelphia.

South America and Australia were once joined together in the continent of Gondwana, via Antarctica. And marsupials are believed to have arrived in Australia from South America. Some scientists have suggested that only Australidelphian mammals entered Australia before Gondwana completely broke up. In light of the new fossil finding, this conclusion could be premature.

Death to Killers

aving established that Australia's large marsupial carnivores were very diverse during the Miocene period, paleontologists are now faced with this question: What happened to them? The last of the marsupial lions and giant ratkangaroos (*T. carnifex* and *Propleopus oscillans*, respectively) died out not so long ago. In fact, they were probably around when the first Aborigines entered Australia, 50,000 or more years ago. Consequently, some scientists have maintained that it was the first humans who sounded their death knell.

Human culpability in this matter has been impossible to prove or disprove and remains a very contentious issue. No doubt the Aborigines helped to drive the Tasmanian Tiger to extinction by introducing the dingo, but their influence re-





A Killer Bird?

n November 1998 Peter Murray and Dirk Megirian of the Central Australian Museum described new fossil material from an extinct, terrestrial bird called *Bullockornis planei*. This species belongs to the Australian family Dromornithidae, also called Thunder Birds, known since 1839. Dromornithids could be huge, some weighing perhaps 500 kilograms or more. But with very limited skull material preserved, little that was certain could be said about their biology. Given the paucity of material and the generally accepted view that dromornithids were closely related to predominantly plant-eating birds, most scientists were of the view that these giants were herbivores. But Murray's excellent reconstruction of *B. planei* is startling, showing a massive head possibly more than half a meter long. Furthermore, the muscle attachment sites were enormous. What did a half-ton bird with military-grade jaw muscles and a beak that could hide a football eat?

In 1991 Lawrence M. Witmer, now at Ohio University's College of Osteopathic Medicine, and Kenneth D. Rose of the Johns Hopkins University School of Medicine convincingly argued that the massive beak and jaw musculature of *Diatryma*, an extinct bird from North America and Europe, would have constituted serious "overdesign" unless the bird was a carnivore. Following this line of reasoning, I have lately suggested that at least some dromornithids might similarly have eaten vertebrates, killed or scavenged. If so, Thunder Birds were the largest carnivores on two legs since the demise of the meat-eating dinosaurs.

—S.W.

garding other species is less clear-cut. These issues may never be completely resolved, but the fossil record makes one fact clear: marsupial carnivore diversity peaked by the early to middle Miocene and was already in steep decline long before humans arrived. For example, at least five marsupial wolves lived during the mid-Miocene, and two coexisted in the late

Obviously, some factor other than human influence was at

work; perhaps Aborigines simply accelerated an extinction process already long established. The most likely alternative candidate is drought. From mid-Miocene times onward, Australia was subject to increasingly severe ice age conditions as well as declining rainfall and sea levels. This trend peaked over the past two million years or so, with around 20 ice ages exposing the Australian fauna to great stress. The last of these was severe, though not the worst.

Many researchers believe some combination of climate change and pressure imposed by human arrivals extinguished most of the continent's surviving larger herbivores. With their favorite meat dishes gone, the clock began to run out on Australia's marsupial predators. It is now a sad fact that of the dozens of wondrous large marsupial carnivores that have existed, not only in Australia but in the Americas as well, only our own Spotted-Tailed Quoll and Tasmanian Devil remain. Nonindigenous Australians must accept full responsibility for the inexcusable loss of the Tasmanian Tiger, and posterity will surely never forgive us should we allow the same fate to befall our last two pouched killers.

The Author

Miocene, but only one was ever known to humans.

STEPHEN WROE recently received his Ph.D. in paleontology from the University of New South Wales in Sydney. He has published widely on the evolution of Australian marsupial carnivores, living and extinct. His areas of special interest include all aspects of the giant rat-kangaroo and dasyuromorphian marsupial radiations, as well as the biology of giant dromornithid birds and marsupial lions. The illustrations are based on reconstructions by Anne Musser of UNSW.

Further Reading

RIVERSLEIGH: THE STORY OF ANIMALS IN ANCIENT RAINFORESTS OF INLAND AUSTRALIA. M. Archer, S. Hand and H. Godthelp. Reed Books, 1994. KILLER KANGAROO. S. Wroe in *Australasian Science*, Vol. 19, No. 6, pages 25–28; July 1998.

THE GEOLOGICALLY OLDEST DASYURID, FROM THE MIOCENE OF RIVERS-LEIGH, NORTHWESTERN QUEENSLAND. S. Wroe in *Palaeontology* (in press). The Riversleigh Society Australian Paleontology site is at www.ozemail.com. au/~promote1/auspalaeo/index.html on the World Wide Web.