SPECIAL EDITION

SCIENTIFIC AMERICAN

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DINOSAURS
AND OTHER MONSTERS

T. rex Unleashed

Giant Predator Birds

Killer Kangaroos

Cretaceous Cockroaches

South Pole Survivors?

Rulers of the Jurassic Seas

Fierce Creatures

FLASHING A MOUTHFUL of 15-centimeter-long teeth like serrated knives, *Tyrannosaurus rex* ripped flesh from bone—and not just at mealtimes. In between entrées, the brute very likely battled its fellow tyrannosaurs over territory and mates. Ichthyosaurs, those fish-shaped lizards with sinuous bodies that measured twice the height of a human, chased lesser monsters through the open oceans. Some of the birds could have given Alfred Hitchcock fresh nightmares: two-meter-tall phorusrhacoids sprinted at 70 kilometers an hour and snapped their massive beaks on victims, beat them senseless against the ground and then swallowed them whole.

THE GOOD OLD DAYS? *Allosaurus* and its kin are best appreciated in retrospect.

ALFRED T. KAMAJIAN

Yes, from a purely self-interested standpoint, it's good that the dinosaurs and their ancient ilk are dead. Yet they live on in our imaginations and our intellectual pursuits, where they retain the power to puzzle, fascinate and startle us. How did they hunt (and what hunted them)? Were they orphans from birth, surviving on instinct and appetite alone, or did parents nurture them? Over millennia, how did their species evolve?

Studying the mineralized remains of prehistoric beasts from the comfortable distance of a few eons, scientists have learned a great deal about how these awesome creatures stalked and swam through the long-ago world. For instance, a mother lode of fossils—many of them nearly complete skeletons—baking in the Gobi Desert is giving paleontologists a broader and more vivid picture of Central Asia between 100 million and 75 million years ago. From what is now Australia, specimens with huge eyes and other adaptations reveal how dinosaurs endured months of darkness during frigid polar winters 100 million years ago. Rocks in Madagascar are divulging previously unknown assemblages of animals that foraged together 230 million years ago. Teeming bodies resembling pill bugs plucked from Canada's 600-million-year-old Burgess Shale illustrate the quirky, punctuated nature of evolutionary change.

This special edition from *Scientific American* presents articles about those and other discoveries in the field of paleontology, written by the experts who are leading the investigations. We invite you, in the pages that follow, to take an armchair safari into prehistory, to spend some quality time with the terrors of Earth's distant past.

John Rennie
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The history of life is not necessarily progressive; it is certainly not predictable. The earth's creatures have evolved through a series of contingent and fortuitous events.

Cover illustration by Alfred T. Kamajian.

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Fish-shaped reptiles called ichthyosaurs reigned over the oceans for as long as dinosaurs roamed the land, but only recently have paleontologists discovered why these creatures were so successful

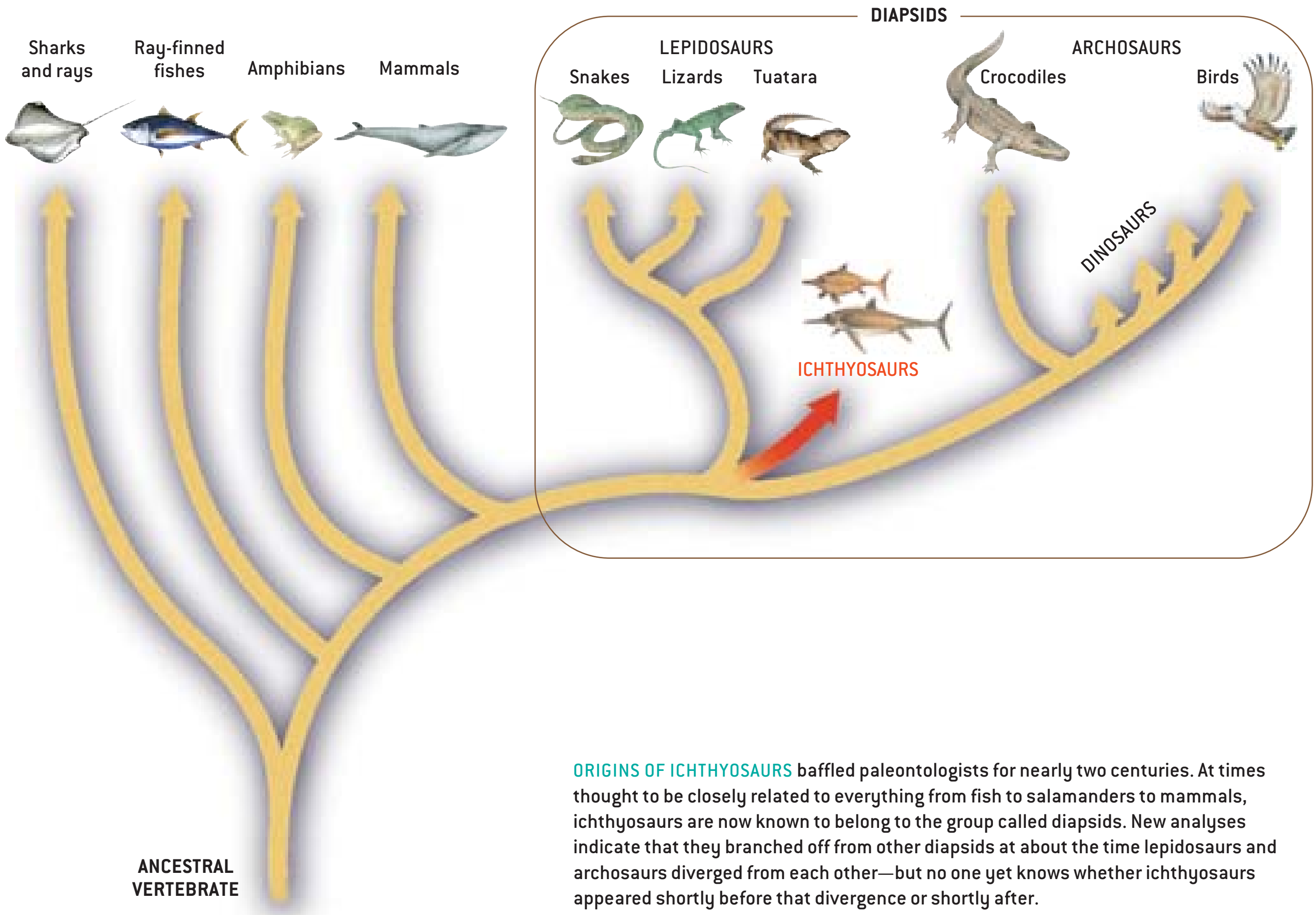
Picture a late autumn evening some 160 million years ago, during the Jurassic time period, when dinosaurs inhabited the continents. The setting sun hardly penetrates the shimmering surface of a vast blue-green ocean, where a shadow glides silently among the dark crags of a submerged volcanic ridge. When the animal comes up for a gulp of evening air, it calls to mind a small whale—but it cannot be. The first whale will not evolve for another 100 million years. The shadow turns suddenly and now stretches more than twice the height of a human being. That realization becomes particularly chilling when its long, tooth-filled snout tears through a school of squidlike creatures.

The remarkable animal is *Ophthalmosaurus,* one of more than 80 species now known to have constituted a group of sea monsters called the ichthyosaurs,

Rulers *of the* Jurassic Seas

By Ryosuke Motani

ICHTHYOSAURS patrolled the world's oceans for 155 million years.



ORIGINS OF ICHTHYOSAURS baffled paleontologists for nearly two centuries. At times thought to be closely related to everything from fish to salamanders to mammals, ichthyosaurs are now known to belong to the group called diapsids. New analyses indicate that they branched off from other diapsids at about the time lepidosaurs and archosaurs diverged from each other—but no one yet knows whether ichthyosaurs appeared shortly before that divergence or shortly after.

or fish-lizards. The smallest of these animals was no longer than a human arm; the largest exceeded 15 meters. *Ophthalmosaurus* fell into the medium-size group and was by no means the most aggressive of the lot. Its company would have been considerably more pleasant than that of a ferocious *Temnodontosaurus,* or "cutting-tooth lizard," which sometimes dined on large vertebrates.

When paleontologists uncovered the first ichthyosaur fossils in the early 1800s, visions of these long-vanished beasts left them awestruck. Dinosaurs had not yet been discovered, so every unusual feature of ichthyosaurs seemed intriguing and mysterious. Examinations of the fossils revealed that ichthyosaurs evolved not from fish but from land-dwelling animals, which themselves had descended from an ancient fish. How, then, did ichthyosaurs make the transition back to life in the water? To which other animals were they most related? And why did they evolve bizarre characteristics, such as backbones that looked like a stack of hockey pucks and eyes as big around as bowling balls?

Despite these compelling questions, the opportunity to unravel the enigmatic transformation from landlubbing reptiles to denizens of the open sea would have to wait almost two centuries. When dinosaurs such as *Iguanodan* grabbed the attention of paleontologists in the 1830s, the novelty of the fish-lizards faded away. Intense interest in the rulers of the Jurassic seas resurfaced only a few years ago, thanks to newly available fossils from Japan and China. Since then, fresh insights have come quickly.

Murky Origins

ALTHOUGH MOST PEOPLE forgot about ichthyosaurs in the early 1800s, a few paleontologists did continue to think about them throughout the 19th century and beyond. What has been evident since their discovery is that the ichthyosaurs' adaptations for life in water made them quite successful. The widespread ages of the fossils revealed that these beasts ruled the ocean from about 245 million until about 90 million years ago—roughly the entire era that dinosaurs dominated the continents. Ichthyosaur fossils were found all over the world, a sign that they migrated extensively, just as whales do today. And despite their fishy appearance, ichthyosaurs were obviously air-breathing reptiles. They did not have gills, and the configurations of their skull and jawbones were undeniably reptilian. What is more, they had two pairs of limbs (fish have none), which implied that their ancestors once lived on land.

Paleontologists drew these conclusions based solely on the exquisite skeletons of relatively late, fish-shaped ichthyosaurs. Bone fragments of the first ichthyosaurs were not found until 1927. Somewhere along the line, those early an-

KAREN CARR (*preceding pages*); TOMO NARASHIMA AND CLEO VILETT (*this page*)

FACT: The smallest ichthyosaur was no longer than a human arm;

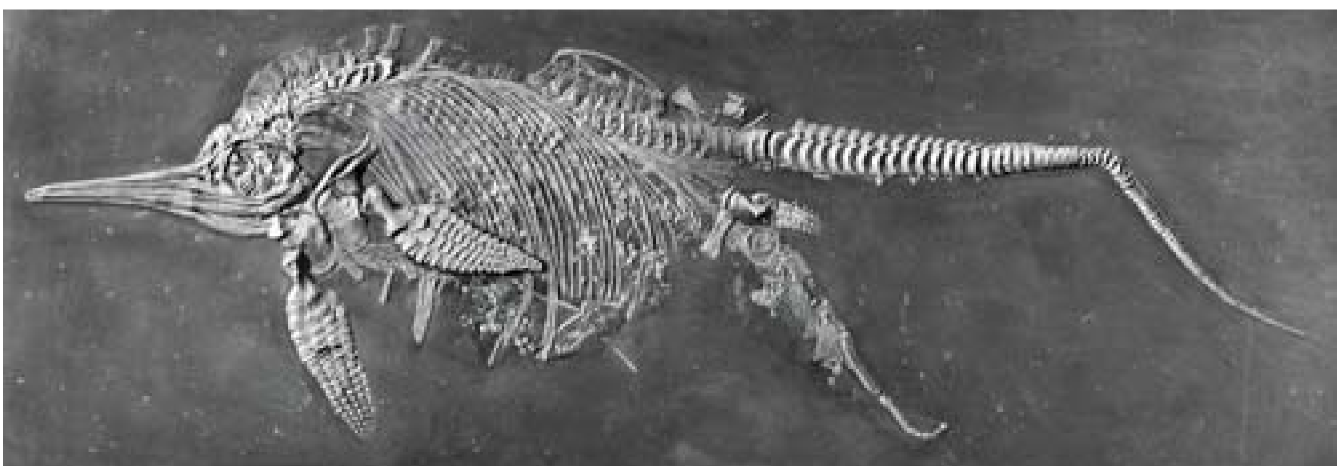
imals went on to acquire a decidedly fishy body: stocky legs morphed into flippers, and a boneless tail fluke and dorsal fin appeared. Not only were the advanced, fish-shaped ichthyosaurs made for aquatic life, they were made for life in the open ocean, far from shore. These extreme adaptations to living in water meant that most of them had lost key features—such as particular wrist bones and anklebones—that would have made it possible to recognize their distant cousins on land. Without complete skeletons of the very first ichthyosaurs, paleontologists could merely speculate that they must have looked like lizards with flippers.

The early lack of evidence so confused scientists that they proposed almost every major vertebrate group—not only reptiles such as lizards and crocodiles but also amphibians and mammals—as close relatives of ichthyosaurs. As the 20th century progressed, scientists learned better how to decipher the relationships among various animal species. On applying the new skills, paleontologists started to agree that ichthyosaurs were indeed reptiles of the group Diapsida, which includes snakes, lizards, crocodiles and dinosaurs. But exactly when ichthyosaurs branched off the family tree remained uncertain—until paleontologists in Asia unearthed new fossils of the world's oldest ichthyosaurs.

The first big discovery occurred on the northeastern coast of Honshu, the main island of Japan. The beach is dominated by outcrops of slate, the layered black rock that is often used for the expensive ink plates of Japanese calligraphy and that also harbors bones of the oldest ichthyosaur, *Utatsusaurus*. Most *Utatsusaurus* specimens turn up fragmented and incomplete, but a group of geologists from Hokkaido University excavated two nearly complete skeletons in 1982. These specimens eventually became available for scientific study, thanks to the devotion of Nachio Minoura and his colleagues, who spent much of the next 15 years painstakingly cleaning the slate-encrusted bones. Because the bones are so fragile, they had to chip away the rock carefully with fine carbide needles as they peered through a microscope.

As the preparation neared its end in 1995, Minoura, who knew of my interest in ancient reptiles, invited me to join the research team. When I saw the skeleton for the first time, I knew that *Utatsusaurus* was exactly what paleontologists had been expecting to find for years: an ichthyosaur that looked like a lizard with flippers. Later that same year my colleague You Hailu, then at the Institute for Vertebrate Paleontology and Paleoanthropology in Beijing, showed me a second, newly discovered fossil—the world's most complete skeleton of *Chaohusaurus,* another early ichthyosaur. *Chaohusaurus* occurs in rocks the same age as those harboring remains of *Utatsusaurus,* and it, too, had been found before only in bits and pieces. The new specimen clearly revealed the outline of a slender, lizardlike body.

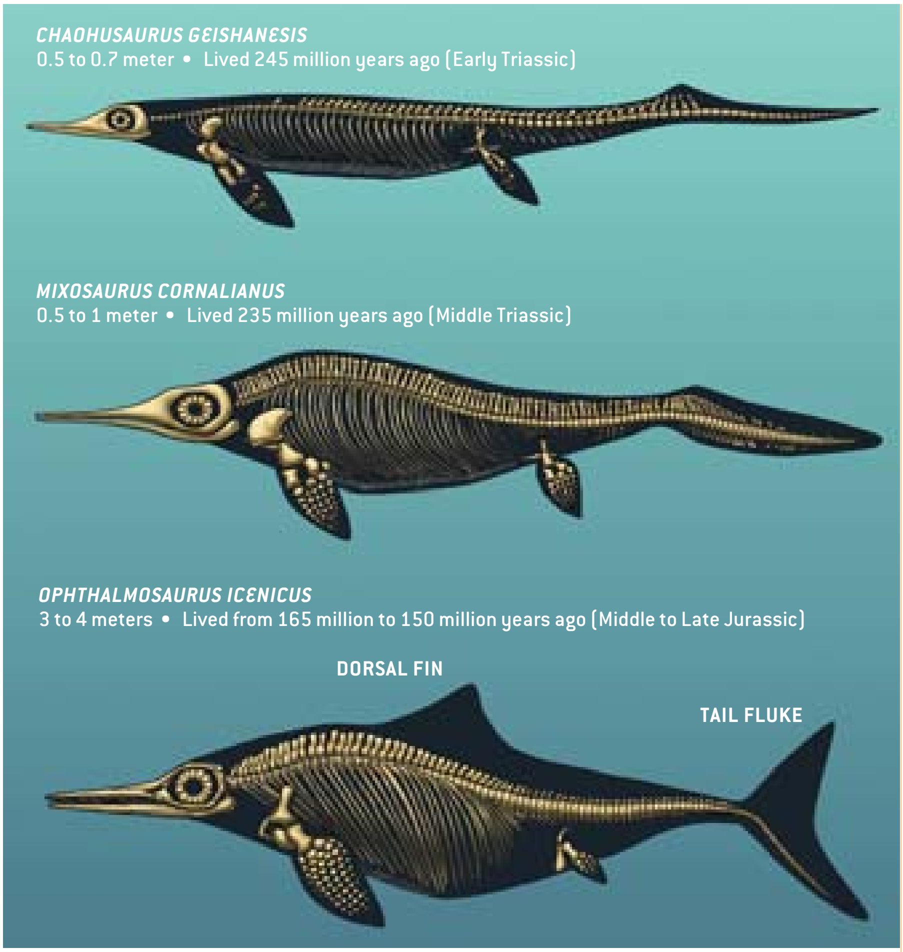
Utatsusaurus and *Chaohusaurus* illuminated at long last where ichthyosaurs belonged on the vertebrate family tree, because they still retained some key features of their land-dwelling ancestors. Given the configurations of the skull and limbs, my colleagues and I think that ichthyosaurs branched off from the rest of the diapsids near the separation of two major groups of living reptiles, lepidosaurs (such as snakes and lizards) and archosaurs (such as crocodiles and birds). Advancing the family-tree debate



NEW FOSSILS of the first ichthyosaurs, including *Chaohusaurus* (*right*), have begun to illuminate how these lizard-shaped creatures evolved into masters of the open ocean, such as *Stenopterygius,* shown below with a baby exiting the birth canal.

RYOSUKE MOTANI (*top*); STAATLICHES MUSEUM FÜR NATURKUNDE STUTTGART (*bottom*)

the largest was longer than a city bus



ANCIENT SKELETONS have helped scientists trace how the slender, lizardlike bodies of the first ichthyosaurs (*top*) thickened into a fish shape with a dorsal fin and a tail fluke.

was quite an achievement, but the mystery of the ichthyosaurs' evolution remained unsolved.

From Feet to Flippers

PERHAPS THE MOST exciting outcome of the discovery of these two Asian ichthyosaurs is that scientists can now paint a vivid picture of the elaborate adaptations that allowed their descendants to thrive in the open ocean. The most obvious transformation for aquatic life is the one from feet to flippers. In contrast to the slender bones in the front feet of most reptiles, all bones in the front "feet" of the fish-shaped ichthyosaurs are wider than they are long. What is more, they are all a similar shape. In most other four-limbed creatures it is easy to distinguish bones in the wrist (irregularly rounded) from those in the palm (long and cylindrical). Most important, the bones of fish-shaped ichthyosaurs are closely packed—without skin in between—to form a solid panel. Having all the toes enclosed in a single envelope of soft tissues would have enhanced the rigidity of the flippers, as it does in living whales, dolphins, seals and sea turtles. Such soft tissues also improve the hydrodynamic efficiency of the flippers because they are streamlined in cross section—a shape impossible to maintain if the digits are separated.

But examination of fossils ranging from lizard- to fish-shaped—especially those of intermediate forms—revealed that the evolution from fins to feet was not a simple modification of the foot's five digits. Indeed, analyses of ichthyosaur limbs reveal a complex evolutionary process in which digits were lost, added and divided. Plotting the shape of fin skeletons along the family tree of ichthyosaurs, for example, indicates that fish-shaped ichthyosaurs lost the thumb bones present in the earliest ichthyosaurs. Additional evidence comes from studying the order in which digits became bony, or ossified, during the growth of the fish-shaped ichthyosaur *Stenopterygius,* for which we have specimens representing various growth stages. Later, additional fingers appeared on both sides of the preexisting ones, and some of them occupied the position of the lost thumb. Needless to say, evolution does not always follow a continuous, directional path from one trait to another.

Built for Swimming

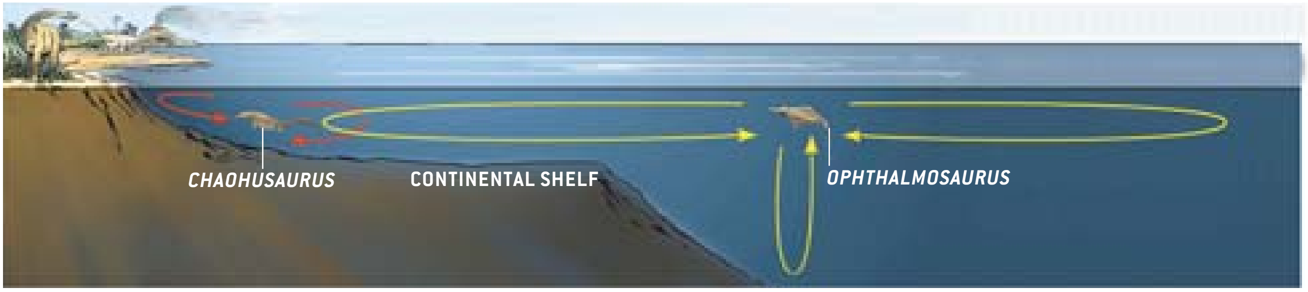
THE NEW LIZARD-SHAPED fossils have also helped resolve the origin of the skeletal structure of their fish-shaped descendants. The descendants have backbones built from concave vertebrae the shape of hockey pucks. This shape, though rare among diapsids, was always assumed to be typical of all ichthyosaurs. But the new creatures from Asia surprised paleontologists by having a much narrower backbone, composed of vertebrae more closely resembling canisters of 35-millimeter film than hockey pucks. It appeared that the vertebrae grew dramatically in diameter and shortened slightly as ichthyosaurs evolved from lizard- to fish-shaped. But why?

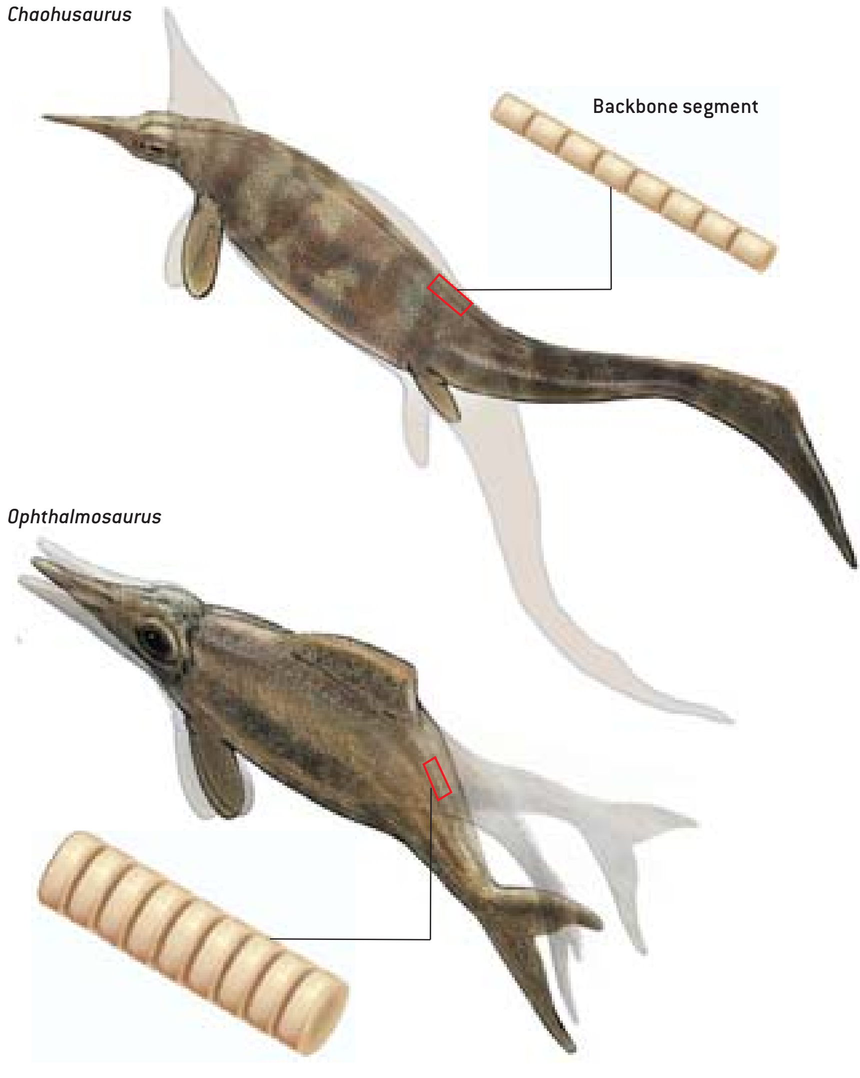
My colleagues and I found the answer in the swimming styles of living sharks. Sharks, like ichthyosaurs, come in various shapes and sizes. Cat sharks are slender and lack a tall tail fluke, also

THE AUTHOR

RYOSUKE MOTANI is assistant professor of paleontology at the University of Oregon and a former researcher at the Royal Ontario Museum in Toronto. As a child he thought ichthyosaurs "looked too ordinary in my picture books," but his view changed during his undergraduate years at the University of Tokyo, after a professor allowed him to study the only domestic reptilian fossil they had: an ichthyosaur. Motani explored ichthyosaur evolution for his doctoral degree from the University of Toronto in 1997 and did postdoctoral research at the University of California, Berkeley.

ED HECK





SWIMMING STYLES—and thus the habitats (*above*)—of ichthyosaurs changed as the shape of their vertebrae evolved. The narrow backbone of the first ichthyosaurs suggests that they undulated their bodies like eels (*right*). This motion allowed the quickness and maneuverability needed for shallow-water hunting. As the backbone thickened in later ichthyosaurs, the body stiffened so it could remain still as the tail swung back and forth (*bottom*). This stillness facilitated the energy-efficient cruising needed to hunt in the open ocean.

known as a caudal fin, on their lower backs, as did early ichthyosaurs. In contrast, mackerel sharks such as the great white have thick bodies and a crescent-shaped caudal fin similar to the later fish-shaped ichthyosaurs. Mackerel sharks swim by swinging only their tails, whereas cat sharks undulate their entire bodies. Undulatory swimming requires a flexible body, which cat sharks achieve by having a large number of backbone segments. They have about 40 vertebrae in the front part of their bodies—the same number scientists find in the first ichthyosaurs, represented by *Utatsusaurus* and *Chaohusaurus*. (Modern reptiles and mammals have only about 20.)

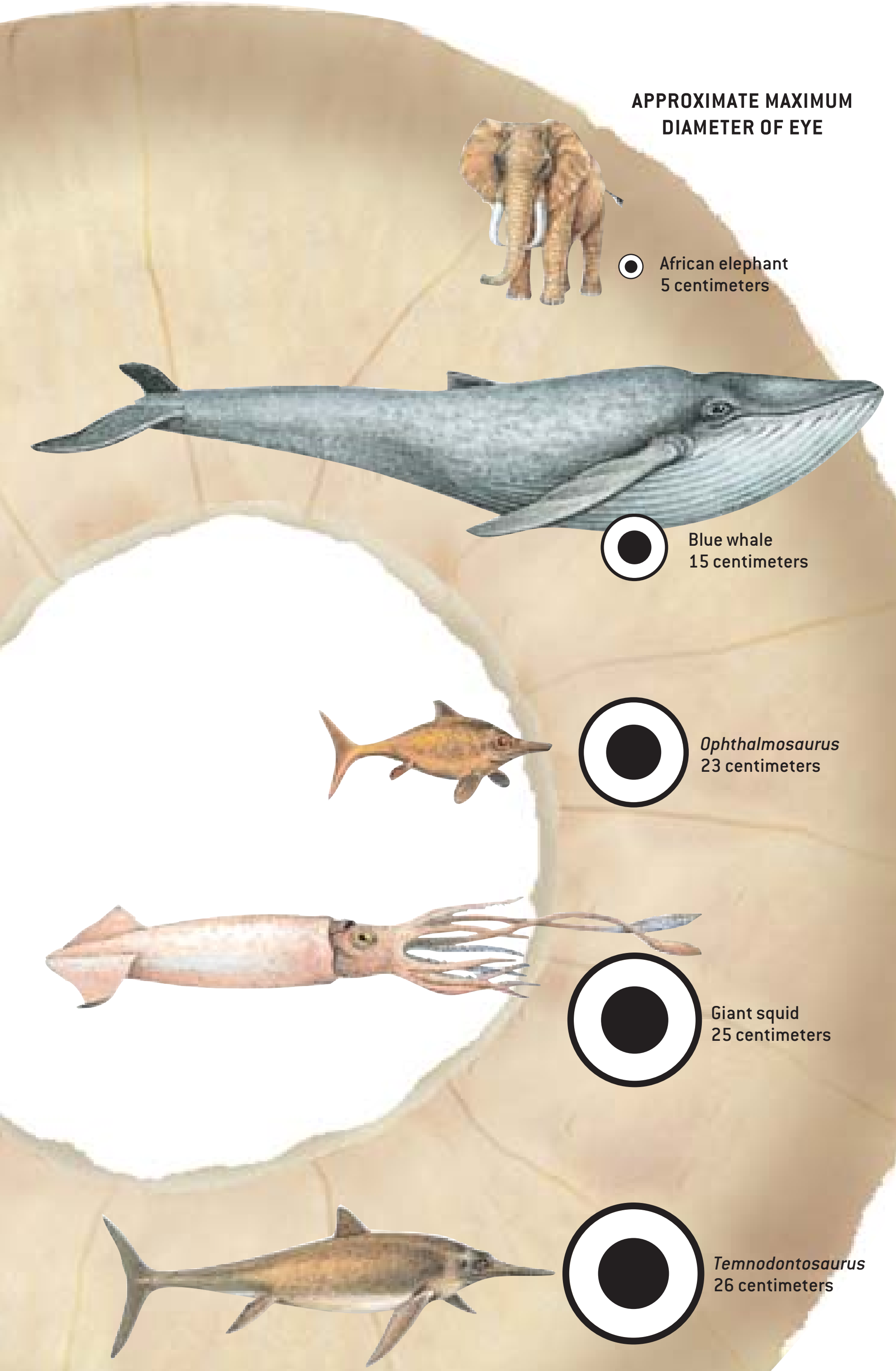
Undulatory swimmers, such as cat sharks, can maneuver and accelerate sufficiently to catch prey in the relatively shallow water above the continental shelf. Living lizards also undulate to swim, though not as efficiently. It is logical to conclude, then, that the first ichthyosaurs—which looked like cat sharks and descended from a lizardlike ancestor—swam in the same fashion and lived above the continental shelf.

Undulatory swimming enables predators to thrive near shore, where food is abundant, but it is not the best choice for an animal that has to travel long distances to find a meal. Offshore predators, which hunt in the open ocean where food is less concentrated, need a more energy-efficient swimming style. Mackerel sharks solve this problem by having stiff bodies that do not undulate as their tails swing back and forth. A crescent-shaped caudal fin, which acts as an oscillating hydrofoil, also improves their cruising efficiency. Fish-shaped ichthyosaurs had such a caudal fin, and their thick body profile implies that they probably swam like mackerel sharks.

Inspecting a variety of shark species reveals that the thicker the body from top

KAREN CARR (*top*); KAREN CARR; ADRIENNE SMUCKER (*vertebrae*) (*bottom*)

FACT: No other reptile group ever evolved a fish-shaped body



ICHTHYOSAUR EYES were surprisingly large. Analyses of doughnut-shaped eye bones called sclerotic rings reveal that *Ophthalmosaurus* had the largest eyes relative to body size of any adult vertebrate, living or extinct, and that *Temnodontosaurus* had the biggest eyes, period. The beige shape in the background is the size of an *Ophthalmosaurus* sclerotic ring. The photograph depicts a well-preserved ring from *Stenopterygius.*

to bottom, the larger the diameter of the vertebrae. It seems that sharks and ichthyosaurs solved the flexibility problem resulting from having high numbers of body segments in similar ways. As the bodies of ichthyosaurs thickened over time, the number of vertebrae stayed about the same. To add support to the more voluminous body, the backbone became at least one and a half times thicker than those of the first ichthyosaurs. As a consequence, the body became less flexible, and the individual vertebrae acquired their hockey-puck appearance.

Drawn to the Deep

THE ICHTHYOSAURS' invasion of open water also meant a deeper exploration of the marine environment. We know from the fossilized stomach contents of fish-shaped ichthyosaurs that they mostly ate squidlike creatures. Squid-eating whales hunt anywhere from about 100 to 1,000 meters deep and sometimes down to 3,000 meters. The great range in depth is hardly surprising considering that food resources are widely scattered below about 200 meters. But to hunt down deep, whales and other air-breathing divers have to go there and get back to the surface in one breath—no easy task. Reducing energy use during swimming is one of the best ways to conserve precious oxygen stored in their bodies. Consequently, deep divers today have streamlined body shapes that reduce drag—and so did the fish-shaped ichthyosaurs.

Characteristics apart from diet and body shape also indicate that at least some fish-shaped ichthyosaurs were deep divers. The ability of an air-breathing diver to stay submerged depends roughly on its body size: the heavier the diver, the more oxygen it can store in its muscles, blood and certain organs—and the slower the consumption of oxygen per

FACT: Their eyes were the largest of any animal, living or dead

TOMO NARASHIMA (*animals*); EDWARD BELL (*sclerotic ring*); RYOSUKE MOTANI (*photograph*)

SMALL ISLAND in northeast Japan harbored two almost complete skeletons of *Utatsusaurus,* the oldest ichthyosaur.

RYOSUKE MOTANI

unit of body mass. The evolution of a thick, stiff body increased the volume and mass of fish-shaped ichthyosaurs relative to their predecessors. Indeed, a fish-shaped ichthyosaur would have been up to six times heavier than a lizard-shaped ichthyosaur of the same length. Calculations based on the aerobic capacities of today's air-breathing divers (mostly mammals and birds) indicate that an animal the weight of fish-shaped *Ophthalmosaurus,* which was about 950 kilograms, could hold its breath for at least 20 minutes. *Ophthalmosaurus* could easily have dived to 600 meters—possibly even 1,500 meters—and returned to the surface in that time span.

Bone studies also indicate that fish-shaped ichthyosaurs were deep divers. Limb bones and ribs of four-limbed terrestrial animals include a dense outer shell that enhances the strength needed to support a body on land. But that dense layer is heavy. Because aquatic vertebrates are fairly buoyant, they do not need the extra strength it provides. Heavy bones can impede the ability of deep divers to return to the surface. A group of French biologists has established that modern deep-diving mammals solve that problem by making the outer shell of their bones spongy and less dense. The same type of spongy layer also encases the bones of fish-shaped ichthyosaurs, creating lighter skeletons.

Perhaps the best evidence for the deep-diving habits of later ichthyosaurs is their remarkably large eyes, up to 23 centimeters across for *Ophthalmosaurus*. Relative to a logarithmically corrected comparison of body size, that fish-shaped ichthyosaur had the biggest eyes of any animal ever known.

The size of their eyes also suggests that visual capacity improved as ichthyosaurs moved up the family tree. These estimates are based on measurements of the sclerotic ring, a doughnut-shaped bone that was embedded in their eyes. (Humans do not have such a ring, but most other vertebrates have bones in their eyes.) In the case of ichthyosaurs, the ring presumably helped to maintain the shape of the eye against the forces of water passing by as the animals swam.

The diameter of the sclerotic ring makes it possible to calculate the eye's minimum f-number—an index, used to rate camera lenses, for the relative-brightness-sensing ability of an optical system. Low-quality lenses have a value of f/3.5 and higher; high-quality lenses have values as low as f/1.0. The f-number for the human eye is about 2.1, whereas the number for the eye of a nocturnal cat is about 0.9. Calculations suggest that a cat would be capable of seeing at depths of 500 meters or greater in most oceans. *Ophthalmosaurus* also had a minimum f-number of about 0.9 but with its much larger eyes could probably outperform a cat.

Gone for Good

MANY CHARACTERISTICS of ichthyosaurs—including the shape of their bodies and backbones, the size of their eyes, their aerobic capacity, and their habitat and diet—seem to have changed in a connected way during their evolution. Such adaptations enabled ichthyosaurs to reign for 155 million years. New fossils of the earliest of these sea dwellers are now making it clear just how they evolved so successfully for aquatic life, yet still no one knows why ichthyosaurs went extinct.

Loss of habitat may have clinched the final demise of lizard-shaped ichthyosaurs, whose inefficient, undulatory swimming style limited them to near-shore environments. A large-scale drop in sea level could have snuffed out these creatures, along with many others, by eliminating their shallow-water niche. Fish-shaped ichthyosaurs, on the other hand, could make a living in the open ocean. Because their habitat never disappeared, something else must have eliminated them. The period of their disappearance roughly corresponds to the appearance of advanced sharks, but no one has found direct evidence of competition between the two groups.

Paleontologists may never fully explain the extinction of ichthyosaurs. But as we explore their evolutionary history, we are sure to learn a great deal more about how these fascinating creatures lived. SA

MORE TO EXPLORE

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Ryosuke Motani's Web site: **www.ucmp.berkeley.edu/people/motani/ichthyo/**

The Mammals That Conquered

New fossils and DNA analyses elucidate the remarkable evolutionary history of whales

"They say the sea is cold,
but the sea contains
the hottest blood of all,
and the wildest, the most urgent."

—D. H. Lawrence,
"Whales Weep Not!"

Dawn breaks over the Tethys Sea, 48 million years ago, and the blue-green water sparkles with the day's first light. But for one small mammal, this new day will end almost as soon as it has started.

ANCIENT WHALE *Rodhocetus* (*right* and *left front*) feasts on the bounty of the sea, while *Ambulocetus* (*rear*) attacks a small land mammal some 48 million years ago in what is now Pakistan.

the Seas

By Kate Wong

Tapir-like *Eotitanops* has wandered perilously close to the water's edge, ignoring its mother's warning call. For the brute lurking motionless among the mangroves, the opportunity is simply too good to pass up. It lunges landward, propelled by powerful hind limbs, and sinks its formidable teeth into the calf, dragging it back into the surf. The victim's frantic struggling subsides as it drowns, trapped in the unyielding jaws of its captor. Victorious, the beast shambles out of the water to devour its kill on terra firma. At first glance, this fearsome predator resembles a crocodile, with its squat legs, stout tail, long snout and eyes that sit high on its skull. But on closer inspection, it has not armor but fur, not claws but hooves. And the cusps on its teeth clearly identify it not as a reptile but as a mammal. In fact, this improbable creature is *Ambulocetus,* an early whale, and one of a series of intermediates linking the land-dwelling ancestors of cetaceans to the 80 or so species of whales, dolphins and porpoises that rule the oceans today.

Until recently, the emergence of whales was one of the most intractable mysteries facing evolutionary biologists. Lacking fur and hind limbs and unable to go ashore for so much as a sip of freshwater, living cetaceans represent a dramatic departure from the mammalian norm. Indeed, their piscine form led Herman Melville in 1851 to describe Moby Dick and his fellow whales as fishes. But to 19th-century naturalists such as Charles Darwin, these air-breathing, warm-blooded animals that nurse their young with milk distinctly grouped with mammals. And because ancestral mammals lived on land, it stood to reason that whales ultimately descended from a terrestrial ancestor. Exactly how that might have happened, however, eluded scholars. For his part, Darwin noted in *On the Origin of Species* that a bear swimming with its mouth agape to catch insects was a plausible evolutionary starting point for whales. But the proposition attracted so much ridicule that in later editions of the book he said just that such a bear was "almost like a whale."

The fossil record of cetaceans did little to advance the study of whale origins. Of the few remains known, none were sufficiently complete or primitive to throw much light on the matter. And further analyses of the bizarre anatomy of living whales led only to more scientific head scratching. Thus, even a century after Darwin, these aquatic mammals remained an evolutionary enigma. In fact, in his 1945 classification of mammals, famed paleontologist George Gaylord Simpson noted that whales had evolved in the oceans for so long that nothing informative about their ancestry was left. Calling them "on the whole, the most peculiar and aberrant of mammals," he inserted cetaceans arbitrarily among the other orders. Where whales belonged in the mammalian family tree and how they took to the seas defied explanation, it seemed.

Over the past two decades, however, many of the pieces of this once imponderable puzzle have fallen into place. Paleontologists have uncovered a wealth of whale fossils spanning the Eocene epoch, the time between 55 million and 34 million years ago when archaic whales, or archaeocetes, made their transition from land to sea. They have also unearthed some clues from the ensuing Oligocene, when the modern suborders of cetaceans—the mysticetes (baleen whales) and the odontocetes (toothed whales)—arose. That fossil material, along with analyses of DNA from living animals, has enabled scientists to paint a detailed picture of when, where and how whales evolved from their terrestrial forebears. Today their transformation—from landlubbers to leviathans—stands as one of the most profound evolutionary metamorphoses on record.

Guide to *Terminology*

CETACEA is the order of mammals that comprises living whales, dolphins and porpoises and their extinct ancestors, the archaeocetes. Living members fall into two suborders: the odontocetes, or toothed whales, including sperm whales, pilot whales, belugas, and all dolphins and porpoises; and the mysticetes, or baleen whales, including blue whales and fin whales. The term "whale" is often used to refer to all cetaceans.

ARTIODACTYLA is the order of even-toed, hoofed mammals that includes camels; ruminants such as cows; hippos; and, most researchers now agree, whales.

MESONYCHIDS are a group of primitive hoofed, wolflike mammals once widely thought to have given rise to whales.

EOCENE is the epoch between 55 million and 34 million years ago, during which early whales made their transition from land to sea.

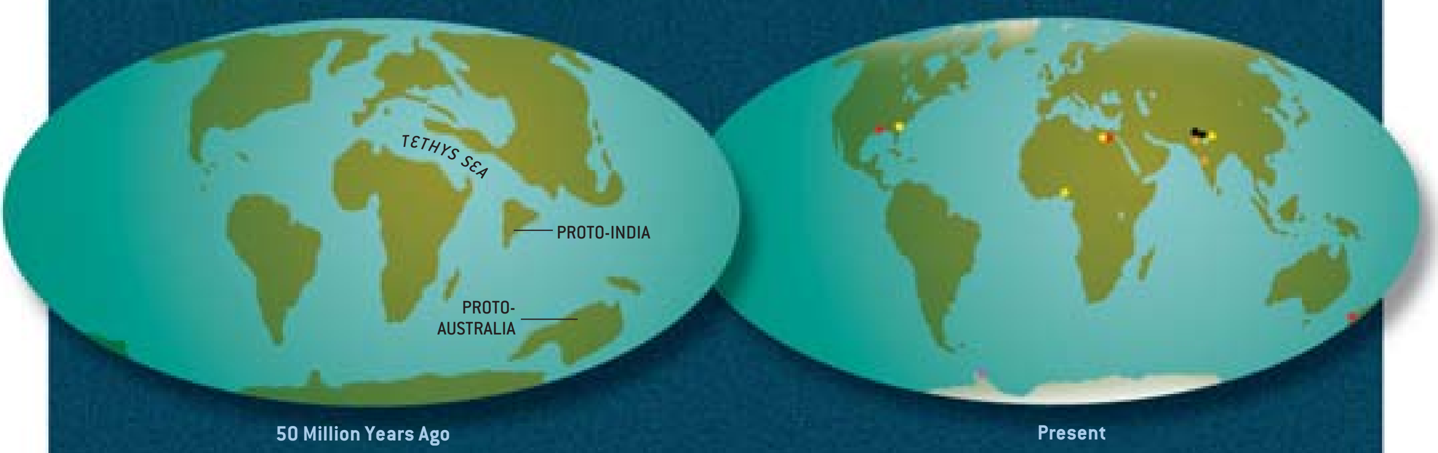
OLIGOCENE is the epoch between 34 million and 24 million years ago, during which odontocetes and mysticetes evolved from their archaeocete ancestors.

Evolving Ideas

AT AROUND THE SAME TIME that Simpson declared the relationship of whales to other mammals undecipherable on the basis of anatomy, a new comparative approach emerged, one that looked at antibody-antigen reactions in living animals. In response to Simpson's assertion, Alan Boyden of Rutgers University and a colleague applied the technique to the whale question. Their results showed convincingly that among living animals, whales are most closely related to the even-toed hoofed mammals, or artiodactyls, a group whose members include camels, hippopotamuses, pigs and ruminants such as cows. Still,

KAREN CARR (*preceding pages*)

THE WHALE'S CHANGING WORLD



It might seem odd that 300 million years after vertebrates first established a toehold on land, some returned to the sea. But the setting in which early whales evolved offers hints as to what lured them back to the water. For much of the Eocene epoch (roughly between 55 million and 34 million years ago), a sea called Tethys, after a goddess of Greek mythology, stretched from Spain to Indonesia. Although the continents and ocean plates we know now had taken shape, India was still adrift, Australia hadn't yet fully separated from Antarctica, and great swaths of Africa and Eurasia lay submerged under Tethys. Those shallow, warm waters incubated abundant nutrients and teemed with fish. Furthermore, the space vacated by the plesiosaurs, mosasaurs and other large marine reptiles that perished along with the dinosaurs created room for new top predators (although sharks and crocodiles still provided a healthy dose of competition). It is difficult to imagine a more enticing invitation to aquatic life for a mammal.

During the Oligocene epoch that followed, sea levels sank and India docked with the rest of Asia, forming the crumpled interface we know as the Himalayas. More important, University of Michigan paleontologist Philip Gingerich notes, Australia and Antarctica divorced, opening up the Southern Ocean and creating a south circumpolar current that eventually transformed the balmy Eocene Earth into the ice-capped planet we inhabit today. The modern current and climate systems brought about radical changes in the quantity and distribution of nutrients in the sea, generating a whole new set of ecological opportunities for the cetaceans.

As posited by paleontologist Ewan Fordyce of the University of Otago in New Zealand, that set the stage for the replacement of the archaeocetes by the odontocetes and mysticetes (toothed and baleen whales, respectively). The earliest known link between archaeocetes and the modern cetacean orders, Fordyce says, is *Llanocetus,* a 34-million-year-old protobaleen whale from Antarctica that may well have trawled for krill in the chilly Antarctic waters, just as living baleen whales do. Odontocetes arose at around the same time, he adds, specializing to become echolocators that could hunt in the deep.

Unfortunately, fossils documenting the origins of mysticetes and odontocetes are vanishingly rare. Low sea levels during the Middle Oligocene exposed most potential whale-bearing sediments from the Early Oligocene to erosive winds and rains, making that period largely "a fossil wasteland," says paleontologist Mark Uhen of the Cranbrook Institute of Science in Bloomfield Hills, Mich. The later fossil record clearly shows, however, that shortly after, by about 30 million years ago, the baleen and toothed whales had diversified into many of the cetacean families that reign over the oceans today. *—K.W.*

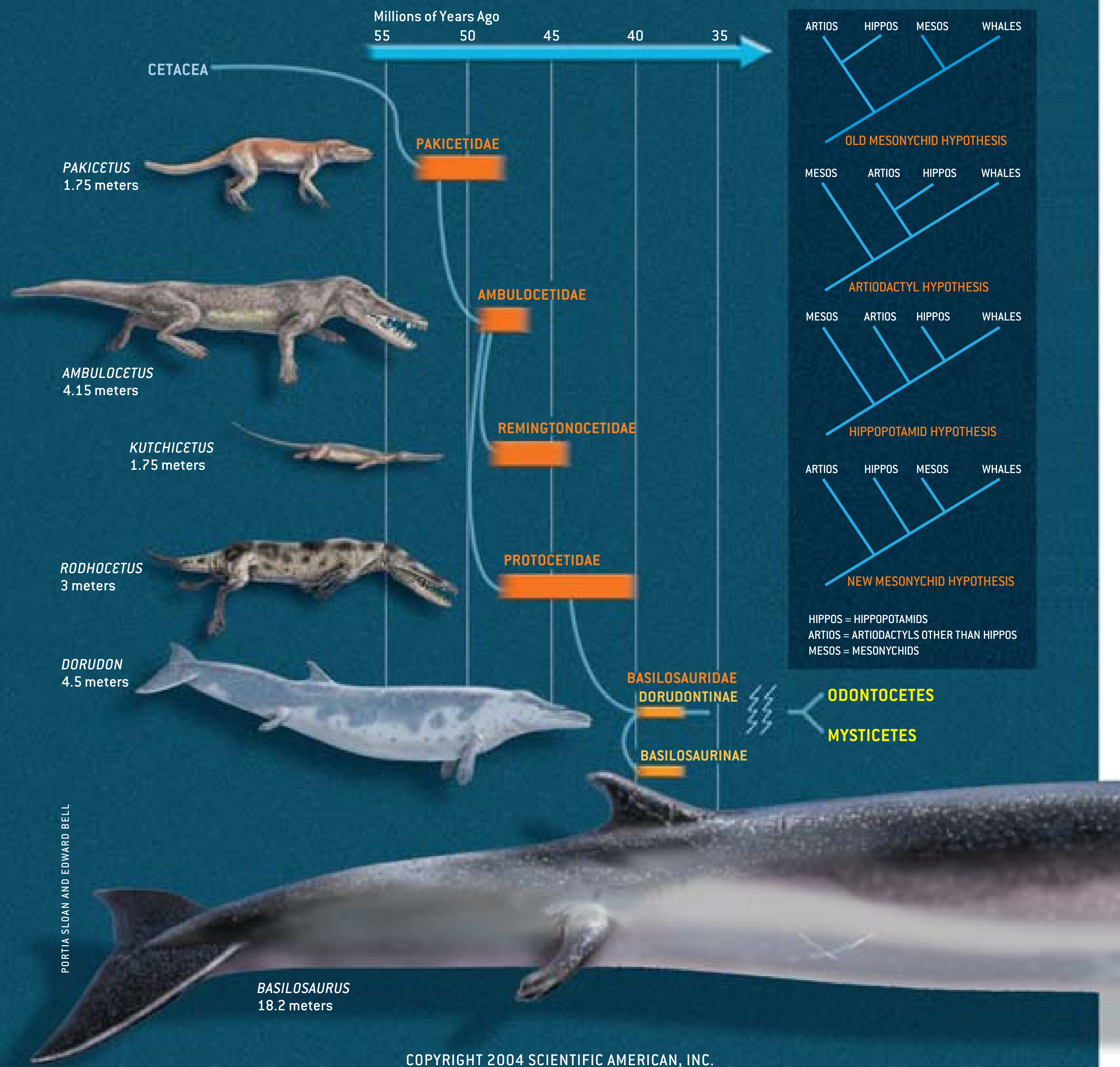
the exact nature of that relationship remained unclear. Were whales themselves artiodactyls? Or did they occupy their own branch of the mammalian family tree, linked to the artiodactyl branch via an ancient common ancestor?

Support for the latter interpretation came in the 1960s, from studies of primitive hoofed mammals known as condylarths that had not yet evolved the specialized characteristics of artiodactyls or the other mammalian orders. Paleontologist Leigh Van Valen, then at the American Museum of Natural History in New York City, discovered striking resemblances between the three-cusped teeth of the few known fossil whales and those of a group of meat-eating condylarths called mesonychids. Likewise, he found shared dental characteristics between artiodactyls and another group of condylarths, the arctocyonids, close relatives of the mesonychids. Van Valen concluded that whales descended from the carnivorous, wolflike mesonychids

SARA CHEN AND EDWARD BELL

CETACEAN RELATIONS

FAMILY TREE OF CETACEANS shows the descent of the two modern suborders of whales, the odontocetes and mysticetes, from the extinct archaeocetes. Representative members of each archaeocete family or subfamily are depicted (*left*). Branching diagrams illustrate various hypotheses of the relationship of whales to other mammals (*right*). The old mesonychid hypothesis, which posits that extinct wolflike beasts known as mesonychids are the closest relatives of whales, now seems unlikely in light of recent fossil whale discoveries. The anklebones of those ancient whales bear the distinctive characteristics of artiodactyl ankles, suggesting that whales are themselves artiodactyls, as envisioned by the artiodactyl hypothesis. Molecular studies indicate that whales are more closely related to hippopotamuses than to any other artiodactyl group. Whether the fossil record can support the hippopotamid hypothesis, however, remains to be seen. A fourth scenario, denoted here as the new mesonychid hypothesis, proposes that mesonychids could still be the whale's closest kin if they, too, were included in the artiodactyl order, instead of the extinct order Condylarthra, in which they currently reside. If so, they would have to have lost the ankle traits that characterize all known artiodactyls. —*K.W.*



PORTIA SLOAN AND EDWARD BELL

and thus appeared to be linked to artiodactyls through the condylarths.

Walking Whales

A DECADE OR SO PASSED before paleontologists finally began unearthing fossils close enough to the evolutionary branching point of whales to address Van Valen's mesonychid hypothesis. Even then the significance of these finds took a while to sink in. It started when University of Michigan paleontologist Philip D. Gingerich went to Pakistan in 1977 in search of Eocene land mammals. The expedition proved disappointing because just marine fossils turned up. Finding traces of ancient ocean life in Pakistan, far from the country's modern coast, is not surprising: during the Eocene, the vast Tethys Sea periodically covered great swaths of what is now the Indian subcontinent [*see box on page 15*]. Intriguingly, though, the team discovered among those ancient fish and snail remnants two pelvis fragments that appeared to have come from relatively large, walking beasts. "We joked about walking whales," Gingerich recalls with a chuckle. "It was unthinkable." Curious as the pelvis pieces were, the only fossil collected during that field season that seemed important at the time was a primitive artiodactyl jaw that had turned up in another part of the country.

Two years later, in the Himalayan foothills of northern Pakistan, Gingerich's team located another weird whale clue: a partial braincase from a wolf-size creature—found in the company of 50-million-year-old land mammal remains—that bore distinctive cetacean characteristics. All modern whales have features in their ears that do not appear in any other vertebrates. Although the fossil skull lacked the anatomy necessary for hearing directionally in water (a critical skill for living whales), it clearly had the diagnostic cetacean ear traits. The team had discovered the oldest and most primitive whale then known—one that must have spent some, if not most, of its time on land. Gingerich christened the creature *Pakicetus* for its place of origin and, thus hooked, began hunting for ancient whales in earnest.

Meanwhile another group recovered additional remains of *Pakicetus*—a lower jaw fragment and isolated teeth—that bolstered the link to mesonychids through strong dental similarities. With *Pakicetus* showing up around 50 million years ago and mesonychids known from around the same time in the same part of the world, it seemed increasingly likely that cetaceans had indeed descended from the mesonychids or something closely related to them. Still, what the earliest whales looked like from the neck down was a mystery.

Further insights from Pakistan would have to wait, however. By 1983 Gingerich was no longer able to work there because of the Soviet Union's invasion of Afghanistan. He decided to cast his net in Egypt instead, journeying some 95 miles southwest of Cairo to the Western Desert's Zeuglodon Valley, so named for early 20th-century reports of fossils of archaic whales—or zeuglodons, as they were then known—in the area. Like Pakistan, much of Egypt once lay submerged under Tethys. Today the skeletons of creatures that swam in that ancient sea lie entombed in sandstone. After several field seasons, Gingerich and his crew hit pay dirt: tiny hind limbs belonging to a 60-foot-long sea snake of a whale known as *Basilosaurus* and the first evidence of cetacean feet.

Earlier finds of *Basilosaurus,* a fully aquatic monster that slithered through the seas between about 40 million and 37 million years ago, preserved only a partial femur, which its discoverers interpreted as vestigial. But the well-formed legs and feet revealed by this discovery hinted at functionality. At less than half a meter in length, the diminutive limbs probably would not have assisted *Basilosaurus* in swimming and certainly would not have enabled it to walk on land, but they may well have helped guide the beast's serpentine body during the difficult activity of aquatic mating. Whatever their purpose, if any, the little legs had big implications. "I immediately thought, we're *10 million* years after *Pakicetus,*" Gingerich recounts excitedly. "If these things still have feet and toes, we've got 10 million years of history to look at." Suddenly, the walking whales they had scoffed at in Pakistan seemed entirely plausible.

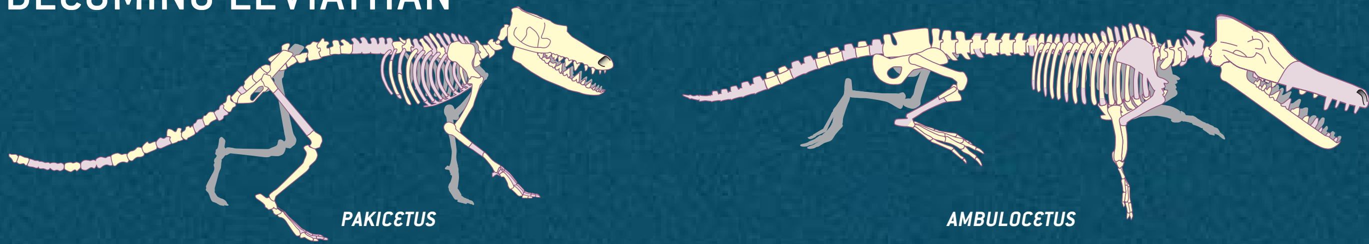
Just such a remarkable creature came to light in 1992. A team led by J.G.M. (Hans) Thewissen of the Northeastern Ohio Universities College of Medicine recovered from 48-million-year-old marine rocks in northern Pakistan a nearly complete skeleton of a perfect intermediate between modern whales and their terrestrial ancestors. Its large feet and powerful tail bespoke strong swimming skills, while its sturdy leg bones and mobile elbow and wrist joints suggested an ability to locomote on land. He dubbed the animal *Ambulocetus natans,* the walking and swimming whale.

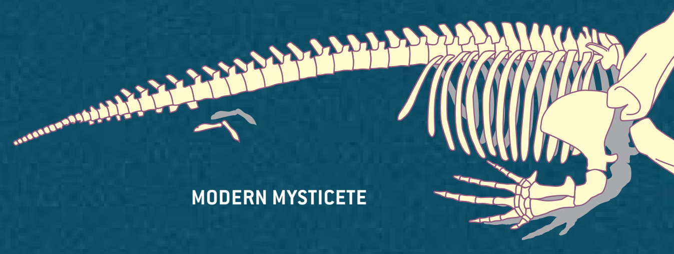
Shape Shifters

SINCE THEN, Thewissen, Gingerich and others have unearthed a plethora of fossils documenting subsequent stages of the whale's transition from land to sea. The picture emerging from those specimens is one in which *Ambulocetus* and its kin—themselves descended from the more terrestrial pakicetids—spawned needle-nosed beasts known as remingtonocetids as well as the intrepid protocetids, the first whales seaworthy enough to fan out from Indo-Pakistan across the globe. From the protocetids arose the dolphinlike dorudontines, the probable progenitors of the snakelike basilosaurines and modern whales [*see box on opposite page*].

In addition to furnishing supporting branches for the whale family tree, these discoveries have enabled researchers to chart many of the spectacular anatomical and

BECOMING LEVIATHAN





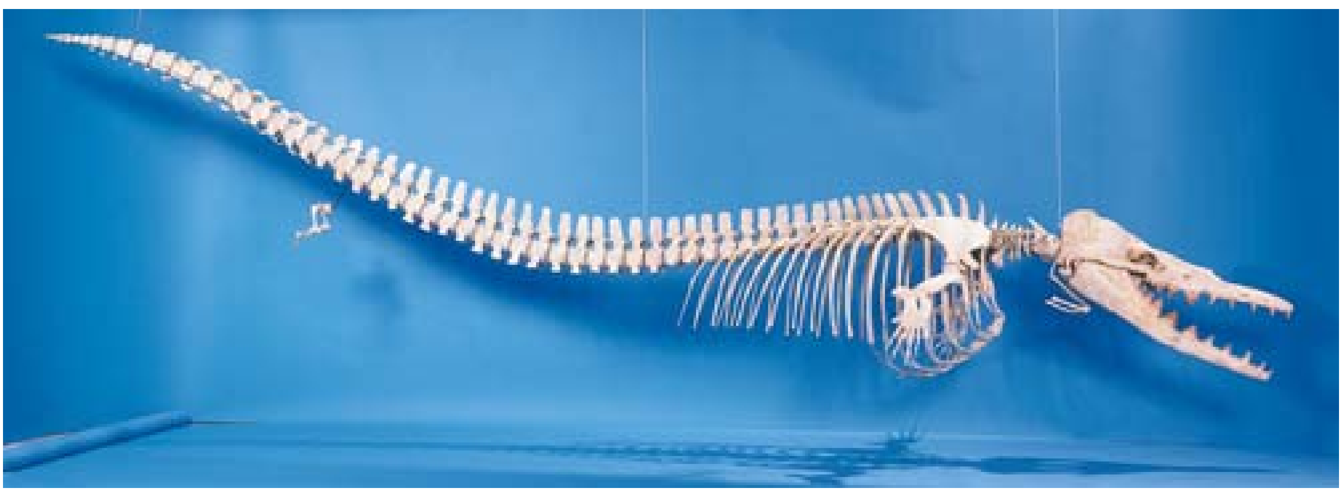
REPRESENTATIVE ARCHAEOCETES in the lineage leading to modern odontocetes and mysticetes trace some of the anatomical changes that enabled these animals to take to the seas (reconstructed bone appears in lavender). In just 15 million years, whales shed their terrestrial trappings and became fully adapted to aquatic life. Notably, the hind limbs diminished, the forelimbs transformed into flippers, and the vertebral column evolved to permit tail-powered swimming. Meanwhile the skull changed to enable underwater hearing, the nasal opening moved backward to the top of the skull, and the teeth simplified into pegs for grasping instead of grinding. Later in whale evolution, the mysticetes' teeth were replaced with baleen.

physiological changes that allowed cetaceans to establish permanent residency in the ocean realm. Some of the earliest of these adaptations to emerge, as *Pakicetus* shows, are those related to hearing. Sound travels differently in water than it does in air. Whereas the ears of humans and other land-dwelling animals have delicate, flat eardrums, or tympanic membranes, for receiving airborne sound, modern whales have thick, elongate tympanic ligaments that cannot receive sound. Instead a bone called the bulla, which in whales has become quite dense and is therefore capable of transmitting sound coming from a denser medium to deeper parts of the ear, takes on that function. The *Pakicetus* bulla shows some modification in that direction, but the animal retained a land mammal–like eardrum that could not work in water.

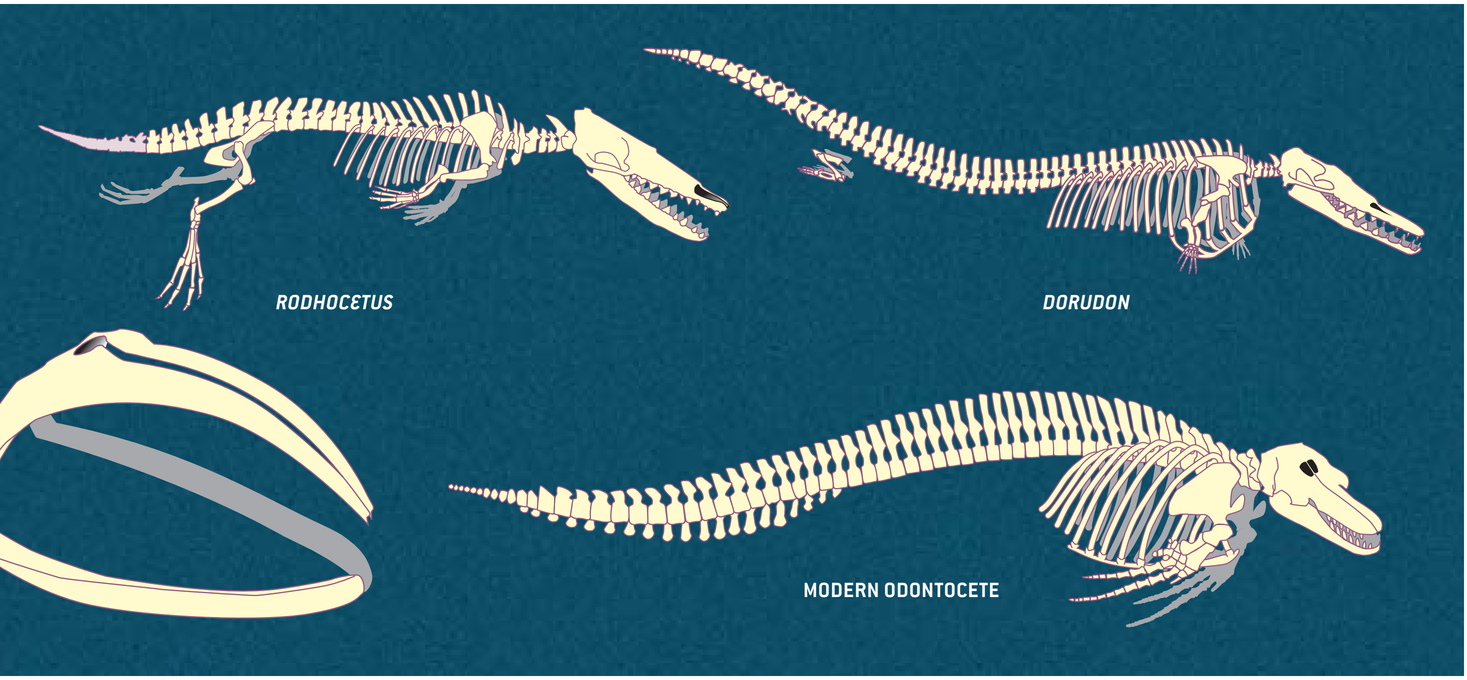
DORUDON, a 4.5-meter-long, dolphinlike archaeocete that roamed the seas between roughly 40 million and 37 million years ago, may be the ancestor of modern whales.

What, then, might *Pakicetus* have used its thickened bullae for? Thewissen suspects that, much as turtles hear by picking up vibrations from the ground through their shields, *Pakicetus* may have employed its bullae to pick up ground-borne sounds. Taking new postcranial evidence into consideration along with the ear morphology, he envisions *Pakicetus* as an ambush predator that may have lurked around shallow rivers, head to the ground, preying on animals that came to drink. *Ambulocetus* is even more likely to have used such inertial hearing, Thewissen says, because it had the beginnings of a channel linking jaw and ear. By resting its jaw on the ground—a strategy seen in modern crocodiles—*Ambulocetus* could have listened for approaching prey. The same features that allowed early whales to receive sounds from soil, he surmises, preadapted them to hearing in the water.

Zhe-Xi Luo of the Carnegie Museum of Natural History in Pittsburgh has shown that by the time of the basilosaurines and dorudontines, the first fully aquatic whales, the ropelike



PORTIA SLOAN (*illustrations*); UNIVERSITY OF MICHIGAN EXHIBIT MUSEUM OF NATURAL HISTORY (*photograph*)



tympanic ligament had probably already evolved. Additionally, air sinuses, presumably filled with spongy tissues, had formed around the middle ear, offering better sound resolution and directional cues for underwater hearing. Meanwhile, with the external ear canal closed off (a prerequisite for deep-sea diving), Luo adds, the lower jaw was taking on an increasingly important auditory role, developing a fat-filled canal capable of conducting sound back to the middle ear.

Later in the evolution of whale hearing, the toothed and baleen whales parted ways. Whereas the toothed whales evolved the features necessary to produce and receive high-frequency sounds, enabling echolocation for hunting, the baleen whales developed the ability to produce and receive very low frequency sounds, allowing them to communicate with one another over vast distances. Fossil whale ear bones, Luo says, show that by around 28 million years ago early odontocetes already had some of the bony structures necessary for hearing high-pitched sound and were thus capable of at least modest echolocation. The origin of the mysticete's low-frequency hearing is far murkier, even though the fossil evidence of that group now dates back to as early as 34 million years ago.

Other notable skull changes include movement of the eye sockets from a crocodilelike placement atop the head in *Pakicetus* and *Ambulocetus* to a lateral position in the more aquatic protocetids and later whales. And the nasal opening migrated back from the tip of the snout in *Pakicetus* to the top of the head in modern cetaceans, forming the blowhole. Whale dentition morphed, too, turning the complexly cusped, grinding molars of primitive mammalian ancestors into the simple, prong-shaped teeth of modern odontocetes, which grasp and swallow their food without chewing. Mysticetes lost their teeth altogether and developed plates of baleen that hang from their upper jaws and strain plankton from the seawater.

The most obvious adaptations making up the whale's protean shift are those that produced its streamlined shape and unmatched swimming abilities. Not surprisingly, some bizarre amphibious forms resulted along the way. *Ambulocetus,* for one, retained the flexible shoulder, elbow, wrist and finger joints of its terrestrial ancestors and had a pelvis capable of supporting its weight on land. Yet the creature's disproportionately large hind limbs and paddlelike feet would have made walking rather awkward. These same features were perfect for paddling around in the fish-filled shallows of Tethys, however.

Moving farther out to sea required additional modifications, many of which appear in the protocetid whales. Studies of one member of this group, *Rodhocetus,* indicate that the lower arm bones were compressed and already on their way to becoming hydrodynamically efficient, says University of Michigan paleontologist William J. Sanders. The animal's long, delicate feet were probably webbed, similar to the fins used by scuba divers. *Rodhocetus* also exhibits aquatic adaptations in its pelvis, where the fusion between the vertebrae that form the sacrum is reduced, loosening up the lower spine to power tail movement. These features, says Gingerich, whose team discovered the creature, suggest that *Rodhocetus* performed a leisurely dog paddle at the sea surface and a swift combination of otterlike hind-limb paddling and tail propulsion underwater. When it went ashore to breed or perhaps to bask in the sun, he proposes, *Rodhocetus* probably hitched itself around in the manner of a modern eared seal or sea lion.

By the time of the basilosaurines and dorudontines, whales were fully aquatic. As in modern cetaceans, the shoulder remained mobile while the elbow and wrist stiffened, forming flippers for steering and balance. Farther back on the skeleton, only tiny legs remained, and the pelvis had dwindled accordingly. Analyses of the vertebrae of *Dorudon,* conducted by Mark D.

Uhen of the Cranbrook Institute of Science in Bloomfield Hills, Mich., have revealed one tail vertebra with a rounded profile. Modern whales have a similarly shaped bone, the ball vertebra, at the base of their fluke—the flat, horizontal structure capping the tail. Uhen thus suspects that basilosaurines and dorudontines had tail flukes and swam much as modern whales do, using so-called caudal oscillation. In this energetically efficient mode of locomotion, motion generated at a single point in the vertebral column powers the tail's vertical movement through the water, and the fluke generates lift.

Exactly when whales lost their legs altogether remains unknown. In fact, a recent discovery made by Lawrence G. Barnes of the Natural History Museum of Los Angeles County hints at surprisingly well developed hind limbs in a 27-million-year-old baleen whale from Washington State, suggesting that whale legs persisted far longer than originally thought. Today, however, some 50 million years after their quadrupedal ancestors first waded into the warm waters of Tethys, whales are singularly sleek. Their hind limbs have shrunk to externally invisible vestiges, and the pelvis has diminished to the point of serving merely as an anchor for a few tiny muscles unrelated to locomotion.

WATER, WATER EVERYWHERE

MOST MAMMALS—big ones in particular—cannot live without freshwater. For marine mammals, however, freshwater is difficult to come by. Seals and sea lions obtain most of their water from the fish they eat (some will eat snow to get freshwater), and manatees routinely seek out freshwater from rivers. For their part, cetaceans obtain water both from their food and from sips of the briny deep.

When did whales, which evolved from a fairly large (and therefore freshwater-dependent) terrestrial mammal, develop a system capable of handling the excess salt load associated with ingesting seawater? Evidence from so-called stable oxygen isotopes has provided clues. In nature, oxygen mainly occurs in two forms, or isotopes: ^{16}O and ^{18}O. The ratios of these isotopes in freshwater and seawater differ, with seawater containing more ^{18}O. Because mammals incorporate oxygen from drinking water into their developing teeth and bones, the remains of those that imbibe seawater can be distinguished from those that take in freshwater.

J.G.M. (Hans) Thewissen of the Northeastern Ohio Universities College of Medicine and his colleagues thus analyzed the oxygen isotope ratios in ancient whale teeth to gain insight into when these animals might have moved from a freshwater-based osmoregulatory system to a seawater-based one. Oxygen isotope values for pakicetids, the most primitive whales, indicate that they drank freshwater, as would be predicted from other indications that these animals spent much of their time on land. Isotope measurements from amphibious *Ambulocetus,* on the other hand, vary widely, and some specimens show no evidence of seawater intake. In explanation, the researchers note that although *Ambulocetus* is known to have spent time in the sea (based on the marine nature of the rocks in which its fossils occur), it may still have had to go ashore to drink. Alternatively, it may have spent the early part of its life (when its teeth mineralized) in freshwater and only later entered the sea.

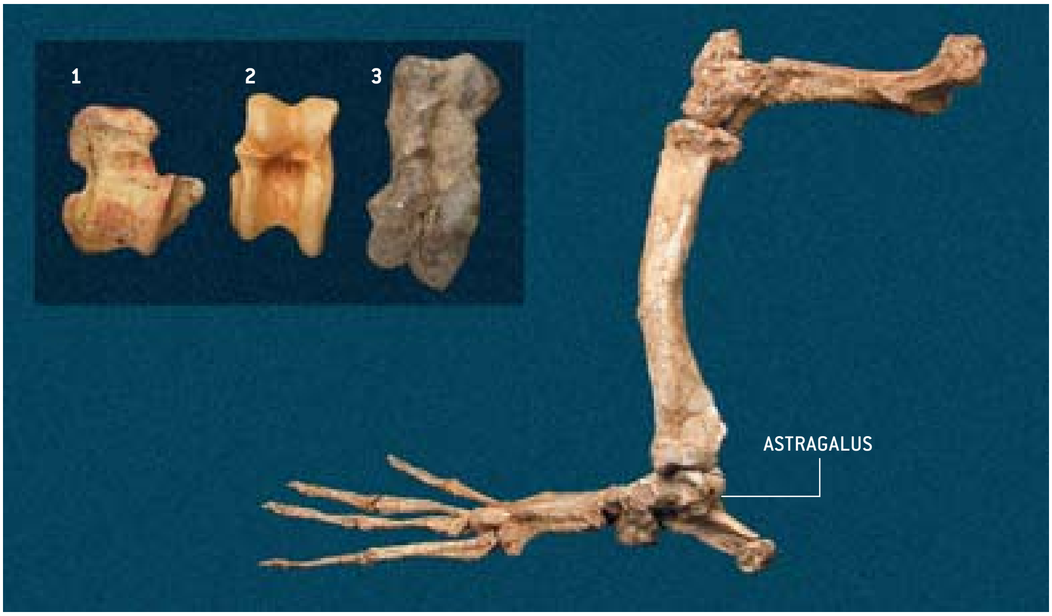
The protocetids, however, which show more skeletal adaptations to aquatic life, exhibit exclusively marine isotope values, indicating that they drank only seawater. Thus, just a few million years after the first whales evolved, their descendants had adapted to increased salt loads. This physiological innovation no doubt played an important role in facilitating the protocetids' dispersal across the globe. *—K.W.*

Making Waves

THE FOSSILS UNCOVERED during the 1980s and 1990s advanced researchers' understanding of whale evolution by leaps and bounds, but all morphological signs still pointed to a mesonychid origin. An alternative view of cetacean roots was gaining currency in genetics laboratories in the U.S., Belgium and Japan, however. Molecular biologists, having developed sophisticated techniques for analyzing the DNA of living creatures, took Boyden's 1960s immunology-based conclusions a step further. Not only were whales more closely related to artiodactyls than to any other living mammals, they asserted, but whales were themselves artiodactyls, one of many twigs on that branch of the mammalian family tree. Moreover, a number of these studies pointed to an especially close relationship between whales and hippopotamuses. Particularly strong evidence for this idea came in 1999 from analyses of snippets of noncoding DNA called SINES (short interspersed elements), conducted by Norihiro Okada and his colleagues at the Tokyo Institute of Technology.

The whale-hippo connection did not sit well with paleontologists. "I thought they were nuts," Gingerich recollects. "Everything we'd found was consistent with a mesonychid origin. I was happy with that and happy with a connection through mesonychids to artiodactyls." Whereas mesonychids appeared at the right time, in the right place and in the right form to be considered whale progenitors, the fossil record did not seem to contain a temporally, geographically and morphologically plausible artiodactyl ancestor for whales, never mind one linking whales and hippos specifically. Thewissen, too, had largely dismissed the DNA findings. But "I stopped rejecting it when Okada's SINE work came out," he says.

It seemed the only way to resolve the controversy was to find, of all things, an ancient whale anklebone. Morphologists have traditionally defined artiodactyls on the basis of certain features in one of their anklebones, the astragalus, that enhance mobility. Specifically, the unique artiodactyl astragalus has two grooved, pulleylike joint surfaces. One connects to the tibia, or shinbone; the other articulates with more distal anklebones. If whales descended from artiodactyls, researchers reasoned, those that had not yet fully adapted to life in the sea should exhibit this double-pulleyed astragalus.



HIND LIMB of an ancient whale, *Rodhocetus,* preserves a long-sought anklebone known as the astragalus (*at right*). Shown in the inset beside a mesonychid astragalus (*1*) and one from a modern artiodactyl (*2*), the *Rodhocetus* astragalus (*3*) exhibits the distinctive double-pulley shape that characterizes all artiodactyl astragali, suggesting that whales descended not from mesonychids, as previously thought, but from an ancient artiodactyl.

DAN ERICKSON

That piece of the puzzle appeared in 2001, when Gingerich and Thewissen both announced discoveries of new primitive whale fossils in Pakistan. In the eastern part of Baluchistan Province, Gingerich's team had found partially articulated skeletons of *Rodhocetus balochistanensis* and a new protocetid genus, *Artiocetus*. Thewissen and his colleagues recovered from a bone bed in Punjab much of the long-sought postcranial skeleton of *Pakicetus,* as well as that of a smaller member of the pakicetid family, *Ichthyolestes*. Each came with an astragalus bearing the distinctive artiodactyl characteristics.

The anklebones convinced both longtime proponents of the mesonychid hypothesis that whales instead evolved from artiodactyls. Gingerich has even embraced the hippo idea. Although hippos themselves arose long after whales, their purported ancestors—dog- to horse-size, swamp-dwelling beasts called anthracotheres—date back to at least the Middle Eocene and may thus have a forebear in common with the cetaceans. In fact, Gingerich notes that *Rodhocetus* and anthracotheres share features in their hands and wrists not seen in any other later artiodactyls. Thewissen agrees that the hippo hypothesis holds much more appeal than it once did. But he cautions that the morphological data still do not point to a particular artiodactyl, such as the hippo, being the whale's closest relative, or sister group. "We don't have the resolution yet to get them there," he remarks, "but I think that will come."

What of the evidence that seemed to tie early whales to mesonychids? In light of the recent ankle data, most workers now suspect that those similarities probably reflect convergent evolution rather than shared ancestry and that mesonychids represent an evolutionary dead end. But not everyone is convinced. Maureen O'Leary of Stony Brook University argues that until all the available evidence—both morphological and molecular—is incorporated into a single phylogenetic analysis, the possibility remains that mesonychids belong at the base of the whale pedigree. It is conceivable, she says, that mesonychids are actually ancient artiodactyls but ones that reversed the ankle trend. If so, mesonychids could still be whales' closest relative and hippos could be their closest living relative [*see box on page 16*]. Critics of that idea, however, point out that although folding the mesonychids into the artiodactyl order offers an escape hatch of sorts to supporters of the mesonychid hypothesis, it would upset the long-standing notion that the ankle makes the artiodactyl.

Investigators agree that determining the exact relationship between whales and artiodactyls will most likely require finding additional fossils—particularly those that can illuminate the beginnings of artiodactyls in general and hippos in particular. Yet even with those details still unresolved, "we're really getting a handle on whales from their origin to the end of archaeocetes," Uhen reflects. The next step, he says, will be to figure out how the mysticetes and odontocetes arose from the archaeocetes and when their modern features emerged. Researchers may never solve all the mysteries of whale origins. But if the extraordinary advances made over the past two decades are any indication, with continued probing, answers to many of these lingering questions will surface from the sands of time. SA

Kate Wong is editorial director of ScientificAmerican.com

MORE TO EXPLORE

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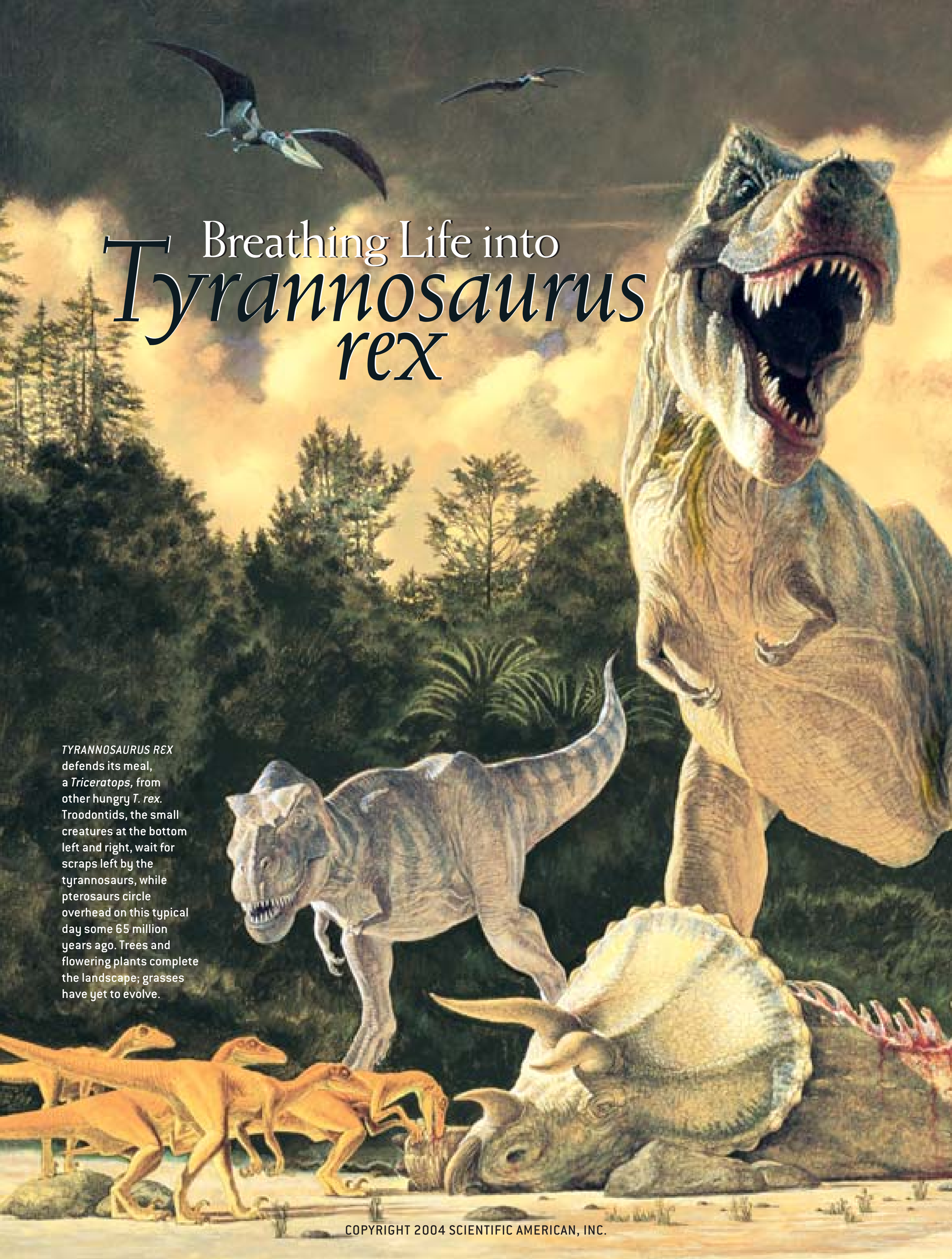
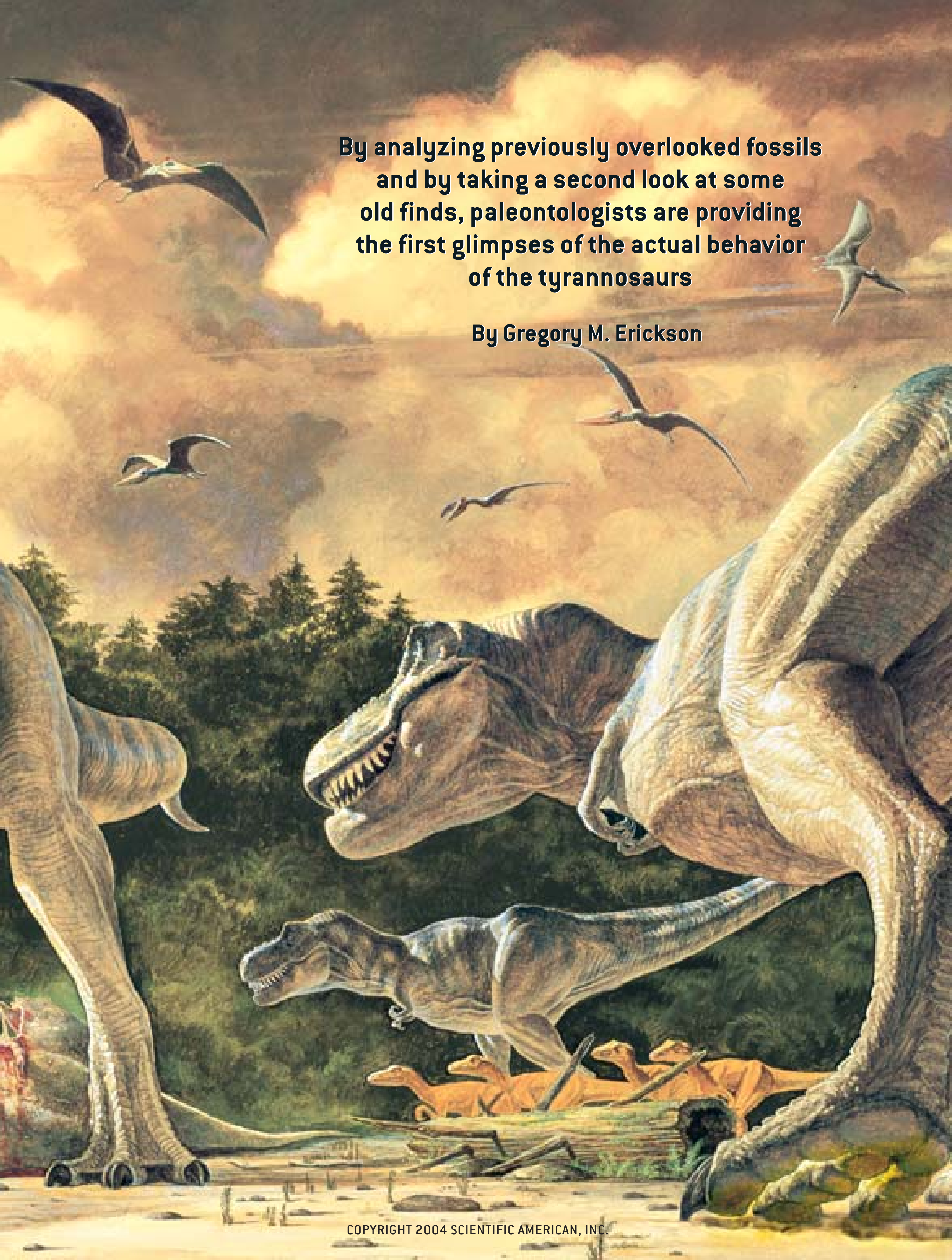


Breathing Life into *Tyrannosaurus rex*

TYRANNOSAURUS REX defends its meal, a *Triceratops,* from other hungry *T. rex.* Troodontids, the small creatures at the bottom left and right, wait for scraps left by the tyrannosaurs, while pterosaurs circle overhead on this typical day some 65 million years ago. Trees and flowering plants complete the landscape; grasses have yet to evolve.

By analyzing previously overlooked fossils and by taking a second look at some old finds, paleontologists are providing the first glimpses of the actual behavior of the tyrannosaurs

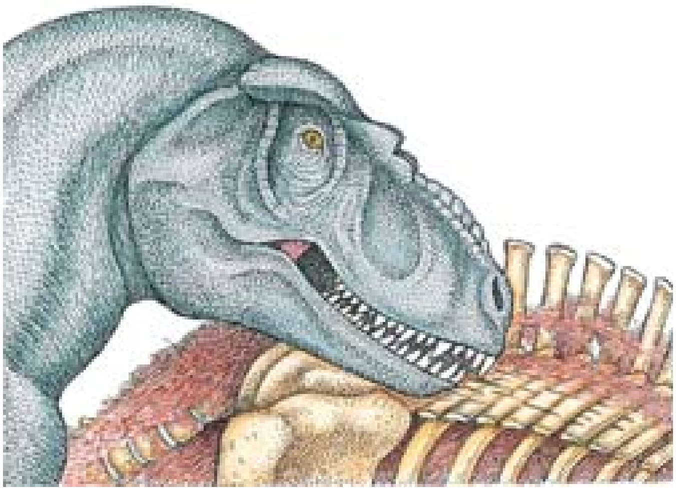
By Gregory M. Erickson



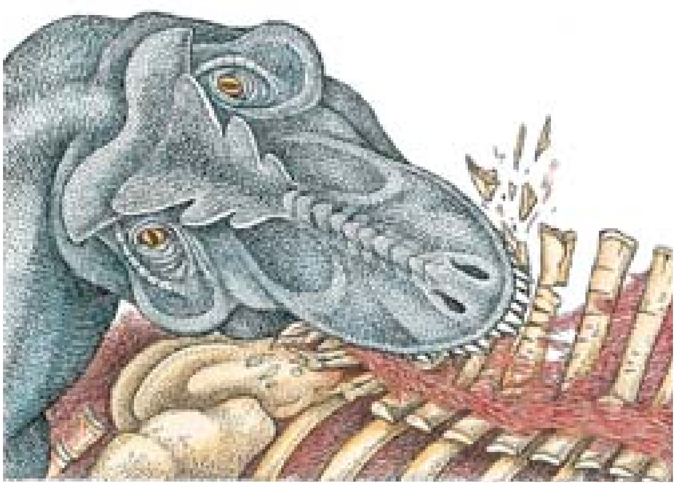
Dinosaurs ceased to walk the earth 65 million years ago, yet they still live among us. Velociraptors star in movies, and *Triceratops* toys clutter toddlers' bedrooms. Of these charismatic animals, however, one species has always ruled our fantasies. Children, filmmaker Steven Spielberg and professional paleontologists agree that the superstar was and is *Tyrannosaurus rex*.

The late Harvard University paleontologist Stephen Jay Gould said that every species designation represents a theory about that animal. The very name *Tyrannosaurus rex*—"tyrant lizard king"—evokes a powerful image of this species. John R. Horner of Montana State University and science writer Don Lessem wrote in their book *The Complete* T. Rex, "We're lucky to have the opportunity to know *T. rex,* study it, imagine it, and let it scare us. Most of all, we're lucky *T. rex* is dead." And paleontologist Robert T. Bakker of the Glenrock Paleontological Museum in Wyoming described *T. rex* as a "10,000-pound roadrunner from hell," a tribute to its obvious size and power.

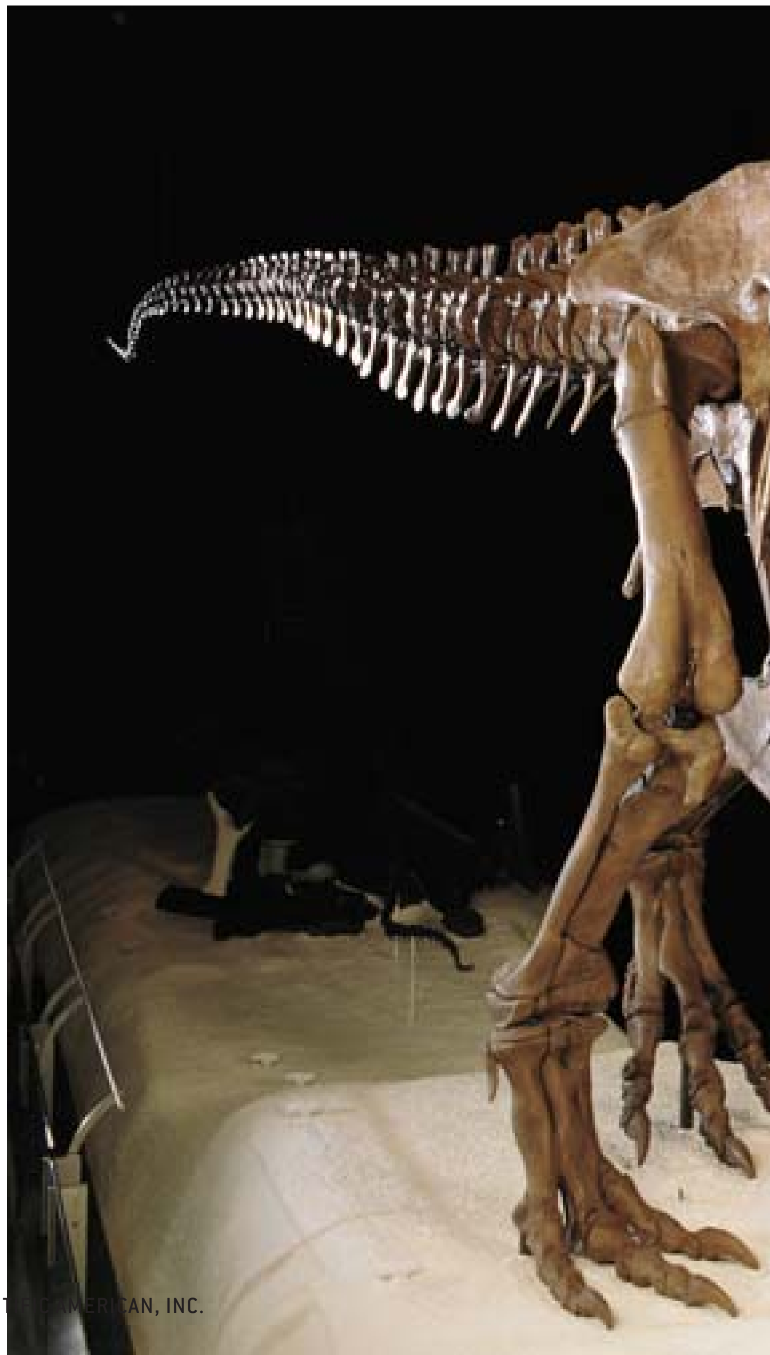
In Spielberg's *Jurassic Park,* which boasted the most accurate popular depiction of dinosaurs ever, *T. rex* was, as usual, presented as a killing machine whose sole purpose was aggressive, bloodthirsty attacks on helpless prey. *T. rex*'s popular persona, however, is as much a function of artistic license as of concrete scientific evidence. A century of study and the existence of 30 fairly complete *T. rex* specimens have generated substantial information about its anatomy. But inferring behavior from anatomy alone is perilous, and the true nature of *T. rex* continues to be largely shrouded in mystery. Whether it was even primarily a predator or a scavenger is still the subject of debate.



NIPPING STRATEGY enabled *T. rex* to remove strips of flesh in tight spots, such as between vertebrae, using only the front teeth.



MASSIVE FORCE generated by *T. rex* in the "puncture and pull" biting technique was sufficient to have created the huge furrows on the surface of the section of a fossil *Triceratops* pelvis shown in the inset at the right. The enormous body of the *T. rex* (*skeleton at right*) and its powerful neck musculature enabled the "pull" in "puncture and pull."



Over the past decade or so, a new breed of scientists has begun to unravel some of *T. rex*'s better-kept secrets. These paleobiologists try to put a creature's remains in a living context—they attempt to animate the silent and still skeleton of the museum display. *T. rex* is thus changing before our eyes as paleobiologists use fossil clues, some new and some previously overlooked, to develop fresh ideas about the nature of these magnificent animals.

Rather than draw conclusions about behavior based solely on anatomy, paleobiologists demand proof of actual activities. Skeletal assemblages of multiple individuals shine a light on the interactions among *T. rex* and between them and other species. In addition, so-called trace fossils reveal activities through physical evidence, such as bite marks on bones and wear patterns on teeth. Also of great value as trace fossils are coprolites, fossilized feces. (Remains of a herbivore, such as *Triceratops* or *Edmontosaurus,* in *T. rex* coprolites certainly provide smoking-gun proof of species interactions!)

One assumption that paleobiologists are willing to make is that closely related species may have behaved in similar ways. *T. rex* data are therefore being corroborated by comparisons with those of earlier members of the family Tyrannosauridae, including their cousins *Albertosaurus*, *Gorgosaurus* and *Daspletosaurus,* collectively known as albertosaurs.

Solo or Social?

TYRANNOSAURS are usually depicted as solitary, as was the case in *Jurassic Park*. (An alternative excuse for that film's loner is that the movie's genetic wizards wisely created only one.) Mounting evidence, however, points to gregarious *T. rex* behavior, at least for part of the animals' lives. Two *T. rex* excavations in the Hell Creek Formation of eastern Montana are most compelling.

KAZUHIKO SANO (*pages 22 and 23*); PATRICIA J. WYNNE (*illustrations on opposite page*); LOUIS PSIHOYOS *Matrix*; GREGORY M. ERICKSON (*inset on this page*)

In 1966 Los Angeles County Museum researchers attempting to exhume a Hell Creek adult were elated to find another, smaller individual resting atop the *T. rex* they had originally sought. This second fossil was identified at first as a more petite species of tyrannosaur. My examination of the histological evidence—the microstructure of the bones—now suggests that the second animal was actually a subadult *T. rex* [*see top illustration on page 28*]. A similar discovery was made during the excavation of "Sue," the largest and most complete fossil *T. rex* ever found. Sue is perhaps as famous for its $8.36-million auction price following ownership haggling as for its paleontological status [see "No Bones about It," by Karin Vergoth; News and Analysis, SCIENTIFIC AMERICAN, December 1997]. Remains of a subadult and a juvenile *T. rex* were later found in Sue's quarry by researchers from the Black Hills Institute of Geological Research in Hill City, S.D. Experts who have worked the Hell Creek Formation, myself included, generally agree that long odds argue against multiple, loner *T. rex* finding their way to the same burial. The more parsimonious explanation is that the animals were part of a group.

An even more spectacular find from 1910 further suggests gregarious behavior among the Tyrannosauridae. Researchers from the American Museum of Natural History in New York City working in Alberta, Canada, found a bone bed—a deposit with fossils of many individuals—holding at least nine of *T. rex*'s close relatives, albertosaurs.

Philip J. Currie and his team from the Royal Tyrrell Museum of Paleontology in Alberta have relocated the 1910 find and are conducting the first detailed study of the assemblage. Such aggregations of carnivorous animals can occur when one after another gets caught in a trap, such as a mud hole or soft sediment at a river's edge, in which a prey animal that has attracted them is already ensnared. Under those circumstances, however, the collection of fossils should also contain those of the hunted herbivore. The lack of such herbivore remains among the albertosaurs (and among the three–*T. rex* assemblage that included Sue) indicates that the herd most likely associated with one another naturally and perished together from drought, disease or drowning.

From examination of the remains collected so far, Currie estimates that the animals ranged from four to almost nine meters (13 to 29 feet) in length. This variation in size hints at a group composed of juveniles and adults. One individual is considerably larger and more robust than the others. Although it might have been a different species of albertosaur, a mixed bunch seems unlikely. I believe that if *T. rex* relatives did indeed have a social structure, this largest individual may have been the patriarch or matriarch of the herd.

Tyrannosaurs in herds, with complex interrelationships, are in many ways an entirely new species to contemplate. But science has not morphed them into a benign and tender collection of Cretaceous Care Bears: some of the very testimony for *T. rex* group interaction is partially healed bite marks that reveal nasty interpersonal skills.

A paper published by Currie and Darren Tanke, also at the Royal Tyrrell Museum, highlights this evidence. Tanke is a leading authority on paleopathology—the study of ancient injuries and disease. He has detected a unique pattern of bite marks among theropods, the group of carnivorous dinosaurs that encompasses *T. rex* and other tyrannosaurs. These bite marks consist of gouges and punctures on the sides of the snout, on the sides and bottom of the jaws, and occasionally on the top and back of the skull.

Interpreting these wounds, Tanke and Currie reconstructed how these dinosaurs fought. They believe that the animals faced off but primarily gnawed at one another with one side of their complement of massive teeth rather than snapping from the front. The workers also surmise that the jaw-gripping behavior accounts for peculiar bite marks found on the sides of tyrannosaur teeth. The bite patterns imply that the combatants maintained their heads at the same level throughout a confrontation. Based on the magnitude of some of the fossil wounds, *T. rex* clearly showed little reserve in battle and sometimes inflicted severe damage to its conspecific foe. One tyrannosaur studied by Tanke and Currie sports a souvenir tooth embedded in its own jaw, perhaps left by a fellow combatant.

Mounting evidence indicates that tyrannosaurs WERE NOT LONERS BUT MOVED IN GROUPS.

The usual subjects—food, mates and territory—may have prompted the vigorous clashes among tyrannosaurs. Whatever the motivation behind the fighting, the fossil record demonstrates that the behavior was repeated throughout a tyrannosaur's life. Injuries among younger individuals seem to have been more common, possibly because a juvenile was subject to attack by members of its own age group as well as by large adults. (Nevertheless, the fossil record may also be slightly misleading and simply contain more evidence of injuries in young *T. rex*. Nonlethal injuries to adults would have eventually healed, destroying the evidence. Juveniles were more likely to die from adult-inflicted injuries, and they carried those wounds to the grave.)

Bites and Bits

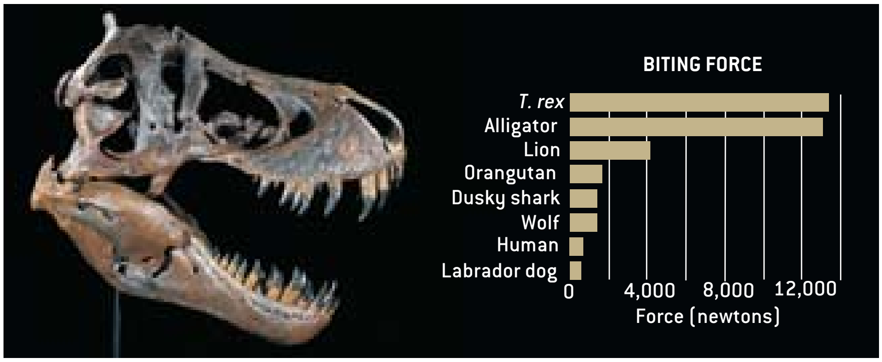
IMAGINE THE LARGE canine teeth of a baboon or lion. Now imagine a mouthful of much larger canine-type teeth, the size of railroad spikes and with serrated edges. Kevin Padian of the University of California at Berkeley has summed up the appearance of the huge daggers that were *T. rex* teeth: "lethal bananas."

Despite the obvious potential of such weapons, the general opinion among paleontologists had been that dinosaur bite marks were rare. The few published reports before 1990 consisted of brief comments buried in articles describing more sweeping new finds, and the clues in the marred remains concerning behavior escaped contemplation.

Some researchers have nonetheless speculated about the teeth. As early as 1973, Ralph E. Molnar, now at the Museum of Northern Arizona in Flagstaff, began musing about the strength of the teeth, based on their shape. Later, James O. Farlow of Indiana University–Purdue University Fort Wayne and Daniel L. Brinkman of Yale University performed elaborate morphological studies of tyrannosaur dentition, which made them confident that the "lethal bananas" were robust, thanks to their rounded cross-sectional configuration, and would endure bone-shattering impacts during feeding.

In 1992 I was able to provide material support for such speculation. Kenneth H. Olson, a Lutheran pastor and superb amateur fossil collector for the Museum of the Rockies in Bozeman, Mont., came to me with several specimens. One was a one-meter-wide, 1.5-meter-long partial pelvis from an adult *Triceratops*. The other was a toe bone from an adult *Edmontosaurus* (duck-billed dinosaur). I examined Olson's specimens and found that both bones were riddled with gouges and punctures up to 12 centimeters long and several centimeters deep. The *Triceratops* pelvis had nearly 80 such indentations. I documented the size and shape of the marks and used orthodontic dental putty to make casts of some of the deeper holes. The teeth that had made the holes were spaced some 10 centimeters apart. They left punctures with eye-shaped cross sections. They clearly included carinae, elevated cutting edges, on their anterior and posterior faces. And those edges were serrated. The totality of the evidence pointed to these indentations being the first definitive bite marks from a *T. rex*.

This finding had considerable behavioral implications. It confirmed for the first time the assumption that *T. rex* fed on its two most common contemporaries, *Triceratops* and *Edmontosaurus*.



BITE-FORCE graph shows that *T. rex* is the undisputed champion. The author, working with bioengineer Dennis R. Carter of Stanford University, simulated the production of feeding bite marks, which are typically less than full strength, using a cast of a *T. rex* tooth on cow pelvises. They made a conservative estimate of approximately 13,300 newtons (about 3,000 pounds) for one side of the mouth.

FRANÇOIS GOHIER *Photo Researchers, Inc.* (*photograph*); SARAH DONELSON (*graph*)

Furthermore, the bite patterns opened a window into *T. rex*'s actual feeding techniques, which apparently involved two distinct biting behaviors. *T. rex* usually used the "puncture and pull" strategy, in which biting deeply with enormous force was followed by drawing the teeth through the penetrated flesh and bone, which typically produced long gashes. In this way, a *T. rex* appears to have detached the pelvis found by Olson from the rest of the *Triceratops* torso. *T. rex* also employed a nipping approach in which the front (incisiform) teeth grasped and stripped the flesh in tight spots between vertebrae, where only the muzzle of the beast could fit. This method left vertically aligned, parallel furrows in the bone.

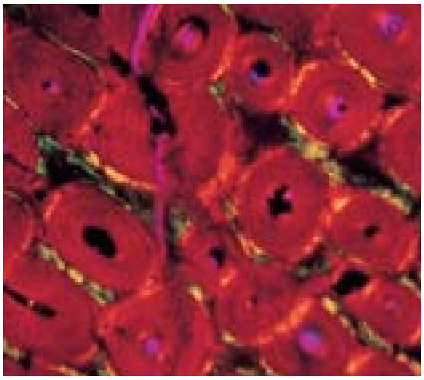
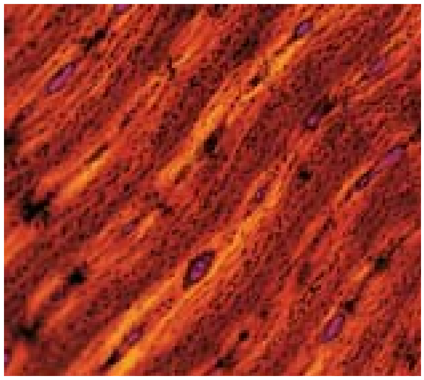
Many of the bites on the *Triceratops* pelvis were spaced only a few centimeters apart, as if the *T. rex* had methodically worked its way across the hunk of meat as we would nibble an ear of corn. With each bite, *T. rex* appears also to have removed a small section of bone. We presumed that the missing bone had been consumed, confirmation for which shortly came, and from an unusual source.

In 1997 Karen Chin, now at the University of Colorado, received a peculiar, tapered mass that had been unearthed by a crew from the Royal Saskatchewan Museum. The object, which weighed 7.1 kilograms and measured 44 by 16 by 13 centimeters, proved to be a *T. rex* coprolite [*see bottom illustration on next page*]. The specimen, the first ever confirmed from a theropod and more than twice as large as any previously reported meat eater's coprolite, was chock-full of pulverized bone. Once again making use of histological methods, Chin and I determined that the shattered bone came from a young herbivorous dinosaur. *T. rex* did ingest parts of the bones of its food sources and, furthermore, partially digested these items with strong enzymes or stomach acids.

Following the lead of Farlow and Molnar, Olson and I have argued vehemently that *T. rex* probably left multitudinous bite marks, despite the paucity of known specimens. Absence of evidence is not evidence of absence, and we believe two factors account for this toothy gap in the fossil record. First, researchers have never systematically

THE AUTHOR

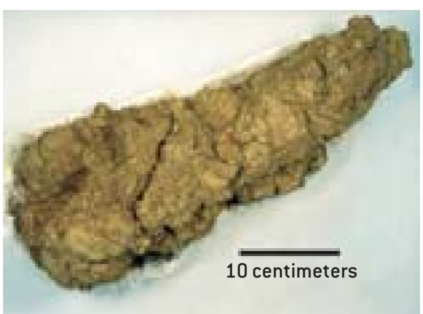
GREGORY M. ERICKSON is assistant professor of biological science at Florida State University and has studied dinosaurs since his first expedition to the Hell Creek Formation badlands of eastern Montana in 1986. He received his master's degree under John B. Horner in 1992 at Montana State University and a doctorate with Marvalee Wake in 1997 from the University of California, Berkeley. Erickson conducted postdoctoral research at Stanford and Brown universities aimed at understanding the form, function, development and evolution of the vertebrate skeleton, with *Tyrannosaurus rex* as one of his favorite study animals. He has won the Romer Prize from the Society of Vertebrate Paleontology, the Stoye Award from the American Society of Ichthyologists and Herpetologists, and the Davis Award from the Society for Integrative and Comparative Biology.

BONE MICROSTRUCTURE reveals the maturity of the animal under study. Older individuals have bone consisting of Haversian canals (*large circles, left*), bone tubules that have replaced naturally occurring microfractures in the more randomly oriented bone of juveniles (*right*). Microscopic examination of bone has shown that individuals thought to be members of smaller species are in fact juvenile *T. rex.*

searched for bite marks. Even more important, collectors have had a natural bias against finds that might display bite marks. Historically, museums desire complete skeletons rather than single, isolated parts. But whole skeletons tend to be the remains of animals that died from causes other than predation and were rapidly buried before being dismembered by scavengers. The shredded bits of bodies eschewed by museums, such as the *Triceratops* pelvis, are precisely those specimens most likely to carry the evidence of feeding.

Indeed, Aase Roland Jacobsen of the University of Århus in Denmark recently surveyed isolated partial skeletal remains and compared them with nearly complete skeletons in Alberta. She found that 3.5 times as many of the individual bones (14 percent) bore theropod bite marks as did the less disrupted remains (4 percent). Paleobiologists therefore



KING-SIZE COPROLITE, 44 centimeters long, is the largest of its kind from a carnivorous animal, more than twice the size of any previously reported. Its size, age, contents and geographic context rule out anything other than a tyrannosaur, and most likely a *T. rex,* as its producer.

view the majority of the world's natural history museums as deserts of behavioral evidence when compared with fossils still lying in the field waiting to be discovered and interpreted.

Hawk or Vulture?

SOME FEATURES of tyrannosaur biology, such as coloration, vocalizations or mating displays, may remain mysteries. But their feeding behavior is accessible through the fossil record. The collection of more trace fossils may finally settle a great debate in paleontology—the 80-year controversy over whether *T. rex* was a predator or a scavenger.

When *T. rex* was first found a century ago, scientists immediately labeled it a predator. But sharp claws and powerful jaws do not necessarily a predator make. For example, most bears are omnivorous and kill only a small proportion of their food. In 1917 Canadian paleontologist Lawrence Lambe examined a partial albertosaur skull and inferred that tyrannosaurs fed on soft, rotting carrion. He came to this conclusion after noticing that the teeth were relatively free of wear. (Future research would show that 40 percent of shed tyrannosaur teeth are severely worn and broken, damage that occurs in a mere two to three years, based on my estimates of their rates of tooth replacement.) Lambe thus established the minority view that the beasts were in fact giant terrestrial "vultures." The ensuing arguments in the predator-versus-scavenger dispute have centered on the anatomy and physical capabilities of *T. rex,* leading to a tiresome game of point-counterpoint.

Scavenger advocates adopted the "weak tooth theory," which maintained that *T. rex*'s elongate teeth would have failed in predatory struggles or in bone impacts. They also contended that its diminutive arms precluded lethal attacks and that *T. rex* would have been too slow to run down prey.

Predator supporters answered with biomechanical data. They cited my own bite-force studies that demonstrate that *T. rex* teeth were actually quite robust. (I personally will remain uncommitted in this argument until the discovery of direct physical proof.) They also noted that Kenneth Carpenter of the Denver Museum of Natural History and Matthew Smith, then at the Museum of the Rockies, estimated that the "puny" arms of a *T. rex* could curl nearly 180 kilograms. And they pointed to the work of Per Christiansen of the University of Copenhagen, who believes, based on limb proportion, that *T. rex* may have been able to sprint at 47 kilometers an hour (29 miles an hour). Such speed would be faster than that of any of *T. rex*'s contemporaries, although endurance and agility, which are difficult to quantify, are equally important in such considerations.

Even these biomechanical studies fail to resolve the predator-scavenger debate—and they never will. The critical determinant of *T. rex*'s ecological niche is discovering how and to what degree it utilized the animals living and dying in its environment, rather than establishing its presumed adeptness for killing. Both sides concede that predaceous animals, such as lions and spotted hyenas, will scavenge and that classic scavengers, such as vultures, will sometimes kill. And mounting physical evidence leads to the conclusion that tyrannosaurs both hunted and scavenged.

Within *T. rex*'s former range exist bone beds consisting of hundreds and sometimes thousands of edmontosaurs that died from floods, droughts and causes other than predation. Bite marks and shed tooth crowns in these edmontosaur assemblages attest to scavenging behavior by *T. rex*. Jacobsen has found com-

GREGORY M. ERICKSON (*top*); KAREN CHIN *University of Colorado* (*bottom*) parable evidence for albertosaur scavenging. Carpenter, on the other hand, has provided evidence that he considers solid proof of predaceous behavior in the form of an unsuccessful attack by a *T. rex* on an adult *Edmontosaurus*. The intended prey purportedly escaped with several broken tailbones that later healed. The only animal with the stature, proper dentition and biting force to account for this injury is *T. rex*.

Quantification of such discoveries could help determine the degree to which *T. rex* undertook each method of obtaining food, and paleontologists could avoid future arguments by adopting standard definitions of predator and scavenger. Such a convention is necessary, because a wide range of views pervades vertebrate paleontology as to what exactly makes for each kind of feeder. For example, some extremists contend that if a carnivorous animal consumes any carrion at all, it should be called a scavenger. But such a constrained definition negates a meaningful ecological distinction, because it would include nearly all the world's carnivorous birds and mammals.

In a definition more consistent with most paleontologists' commonsense categorization, a predatory species would be one in which most individuals acquire most of their meals from animals they or their peers killed. Most individuals in a scavenging species, on the other hand, would not be responsible for the deaths of most of their food.

Trace fossils could open the door to a systematic approach to the predator-scavenger controversy, and the resolution could come from testing hypotheses about entire patterns of tyrannosaur feeding preferences. For instance, Jacobsen has pointed out that evidence of a preference for less dangerous or easily caught animals supports a predator niche. Conversely, scavengers would be expected to consume all species equally.

Within this logical framework, Jacobsen has compelling data supporting predation. She surveyed thousands of dinosaur bones from Alberta and learned that unarmored hadrosaurs are twice as likely to bear tyrannosaur bite marks as are the more dangerous horned ceratopsians. Tanke, who participated in the collection of these bones, relates that no bite marks have been found on the heavily armored, tanklike ankylosaurs.

Jacobsen cautions, though, that other factors confuse this set of findings. Most of the hadrosaur bones are from isolated individuals, but most ceratopsians in her study are from bone beds. Again, these beds contain more whole animals that have been fossilized unscathed, creating the kind of tooth-mark bias discussed earlier. A survey of isolated ceratopsians would be enlightening. And analysis of more bite marks that reveal failed predatory attempts, such as those reported by Carpenter, could also turn up preferences, or the lack thereof, for less dangerous prey.

Jacobsen's finding that cannibalism among tyrannosaurs was rare—only 2 percent of albertosaur bones had albertosaur bite marks, whereas 14 percent of herbivore bones did—might also support predatory preferences instead of a scavenging niche for *T. rex,* particularly if these animals were in fact gregarious. Assuming that they had no aversion to consuming flesh of their own kind, it would be expected that at least as many *T. rex* bones would exhibit signs of *T. rex* dining as do herbivore bones. A scavenging *T. rex* would have had to stumble on herbivore remains, but if *T. rex* traveled in herds, freshly dead conspecifics would seem to have been a guaranteed meal.

Coprolites may also provide valuable evidence about whether *T. rex* had any finicky eating habits. Because histological examination of bone found in coprolites can give the approximate stage of life of the consumed animal, Chin and I have suggested that coprolites may reveal a *T. rex* preference for feeding on vulnerable members of herds, such as the very young. Such a bias would point to predation, whereas a more impartial feeding pattern, matching the normal patterns of attrition, would indicate scavenging. Meaningful questions may lead to meaningful answers.

Trace fossils may settle an 80-year debate: WAS *T. REX* A PREDATOR OR SCAVENGER?

In the past century, paleontologists have recovered enough physical remains of *Tyrannosaurus rex* to give the world an excellent idea of what these monsters looked like. The attempt to discover what *T. rex* actually *was* like relies on those fossils that carry precious clues about the daily activities of dinosaurs. Paleontologists now appreciate the need for reanalysis of finds that were formerly ignored and have recognized the biases in collection practices, which have clouded perceptions of dinosaurs. The intentional pursuit of behavioral data should accelerate discoveries of dinosaur paleobiology. And new technologies may tease information out of fossils that we currently deem of little value. The *T. rex,* still alive in the imagination, continues to evolve. SA

MORE TO EXPLORE

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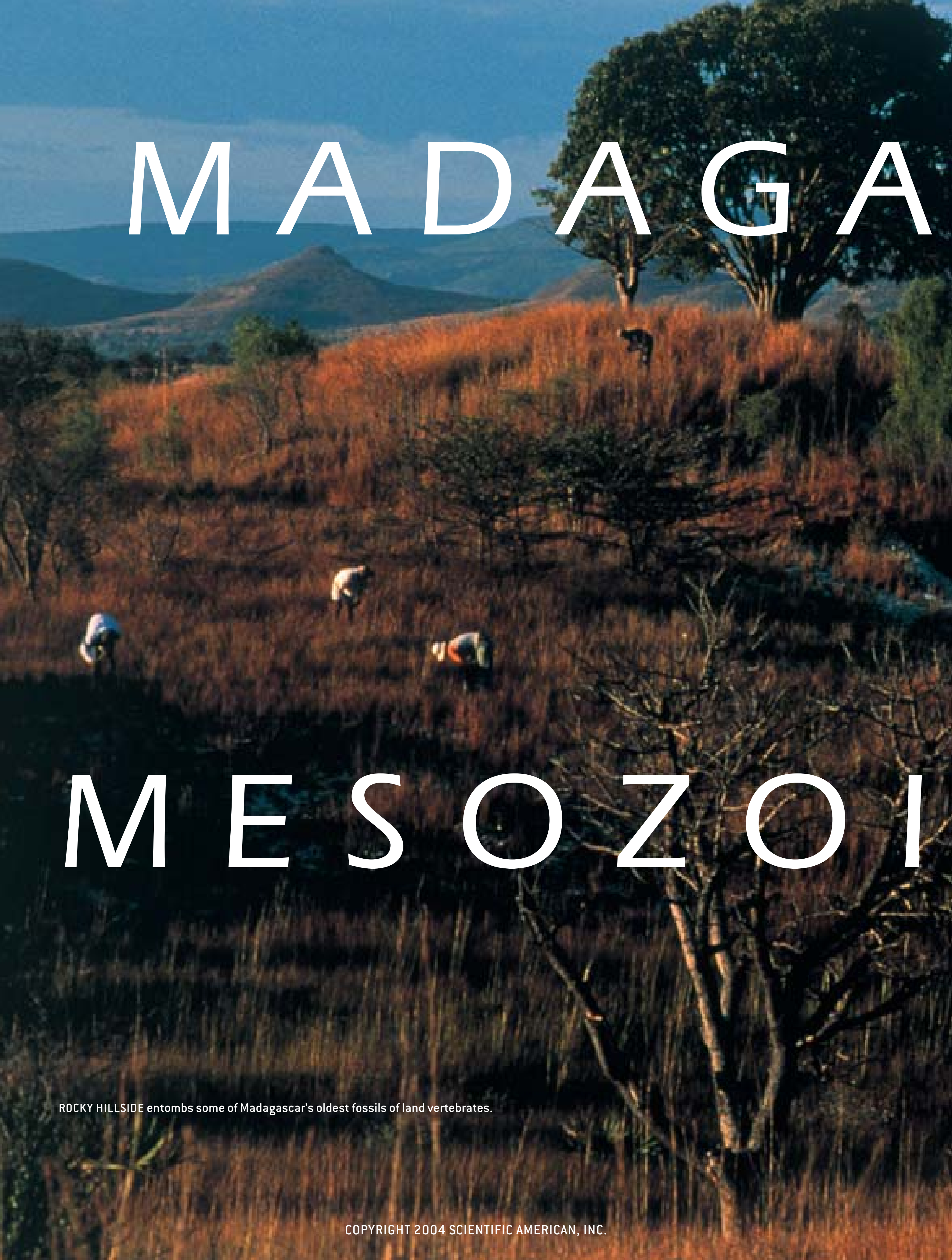
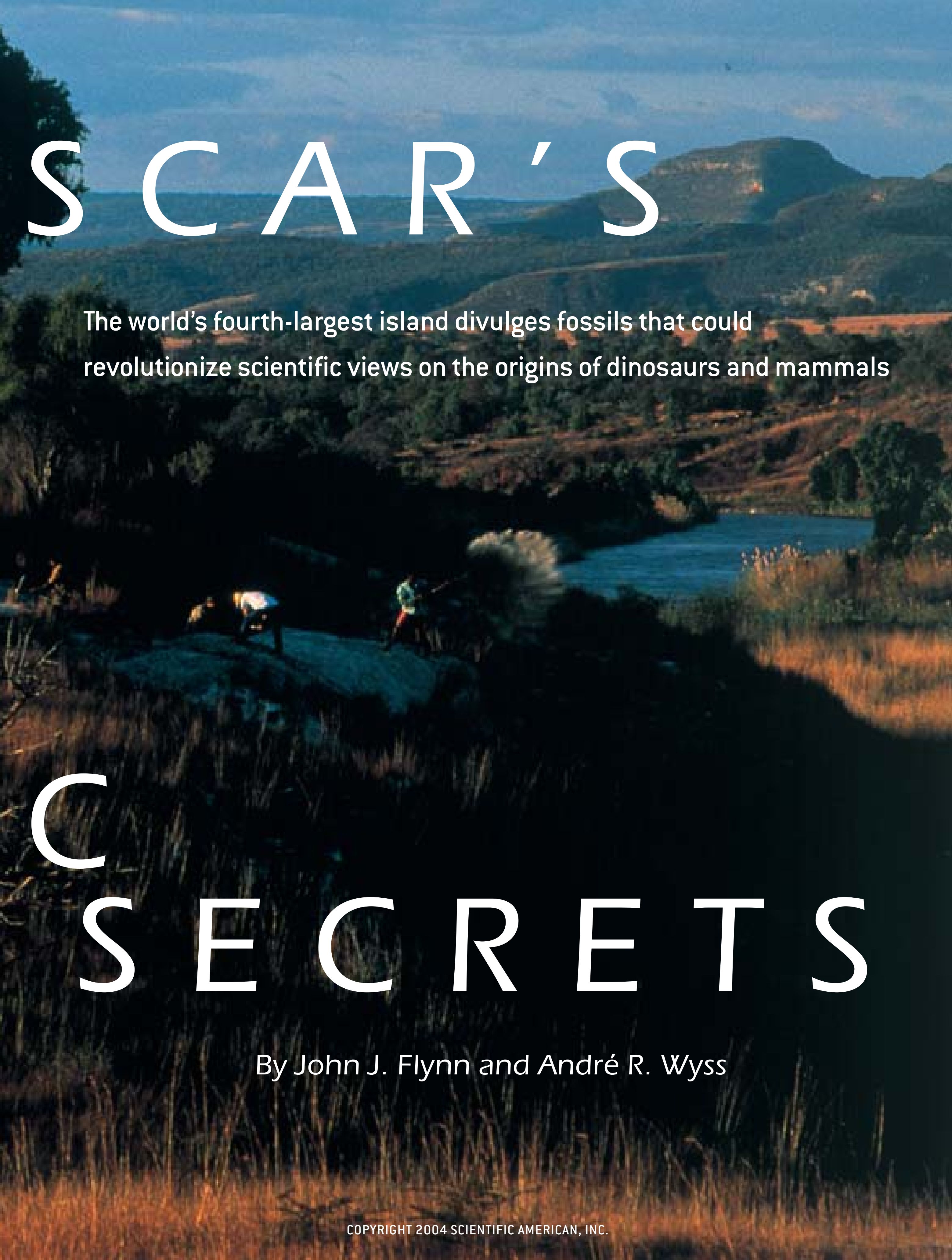


MADAGA

MESOZOI

ROCKY HILLSIDE entombs some of Madagascar's oldest fossils of land vertebrates.



SCAR'S C SECRETS

The world's fourth-largest island divulges fossils that could revolutionize scientific views on the origins of dinosaurs and mammals

By John J. Flynn and André R. Wyss

THREE WEEKS INTO our first fossil-hunting expedition in Madagascar in 1996, we were beginning to worry that dust-choked laundry might be all we would have to show for our efforts. We had turned up only a few random teeth and bones—rough terrain and other logistical difficulties had encumbered our search. With our field season drawing rapidly to a close, we finally stumbled on an encouraging clue in the southwestern part of the island. A tourist map hanging in the visitor center of Isalo National Park marked a local site called "the place of animal bones." We asked two young men from a neighboring village to take us there right away.

Our high hopes faded quickly as we realized that the bleached scraps of skeletons eroding out of the hillside belonged to cattle and other modern-day animals. This site, though potentially interesting to archaeologists, held no promise of harboring the much more ancient quarry we were after. Later that day another guide, accompanied by two dozen curious children from the village, led us to a second embankment similarly strewn with bones. With great excitement we spotted two thumb-size jaw fragments that were undoubtedly ancient. They belonged to long-extinct, parrot-beaked cousins of the dinosaurs called rhynchosaurs.

The rhynchosaur bones turned out to be a harbinger of a spectacular slew of prehistoric discoveries yet to come. Since then, the world's fourth-largest island has become a prolific source of new information about animals that walked the land during the Mesozoic era, the interval of the earth's history (from 250 million to 65 million years ago) when both dinosaurs and mammals were making their debut. We have unearthed the bones of what may be primitive dinosaurs that we suspect are older than any found previously. We have also stirred up controversy with the discovery of a shrewlike creature that seems to defy a prominent theory of mammalian history by being in the "wrong" hemisphere. These exquisite specimens, among numerous others collected over five field seasons, have enabled us to begin painting a picture of ancient Madagascar and have also shaped our strategy for a sixth expedition in 2003.

Much of our research over the past two decades has been aimed at unraveling the history of land-dwelling animals on the southern continents. Such questions have driven other paleontologists to fossil-rich locales in South Africa, Brazil, Antarctica and India. Rather than probing those established sites for additional finds, we were lured to Madagascar: the island embraces vast swaths of Mesozoic age rocks, but until recently only a handful of terrestrial vertebrate fossils from that time had been discovered there. Why? We had a hunch that no one had looked persistently enough to find them.

NEITHER REPTILE NOR MAMMAL, this leopard-size traversodontid, named *Menadon,* had the stout incisors and wide cheek teeth needed to grasp and grind vegetation as it browsed in Madagascar about 230 million years ago.

Persistence became our motto as we launched our 1996 expedition. Our team consisted of a dozen scientists and students from the U.S. and the University of Antananarivo in Madagascar. In addition to scientific and educational benefits, our partnership with the country's leading university facilitated the acquisition of collecting and exporting permits—requisite components of all paleontological fieldwork. Before long, however, we ran into logistical obstacles that surely contributed to earlier failures to find ancient fossils on the island. Mesozoic deposits in western Madagascar are spread over an area roughly the size of California. Generations of oxcarts and foot travel have carved the only trails into remote areas, and most of them are impassable by even the browniest four-wheel-drive vehicles. We had to haul most of our food, including hundreds of pounds of rice, beans and canned meats, from the capital. Fuel shortages sometimes seriously restricted mobility, and our work was even thwarted by wildfires, which occur frequently and rage unchecked. New challenges arose unexpectedly, requiring us to adjust our plans on the spot.

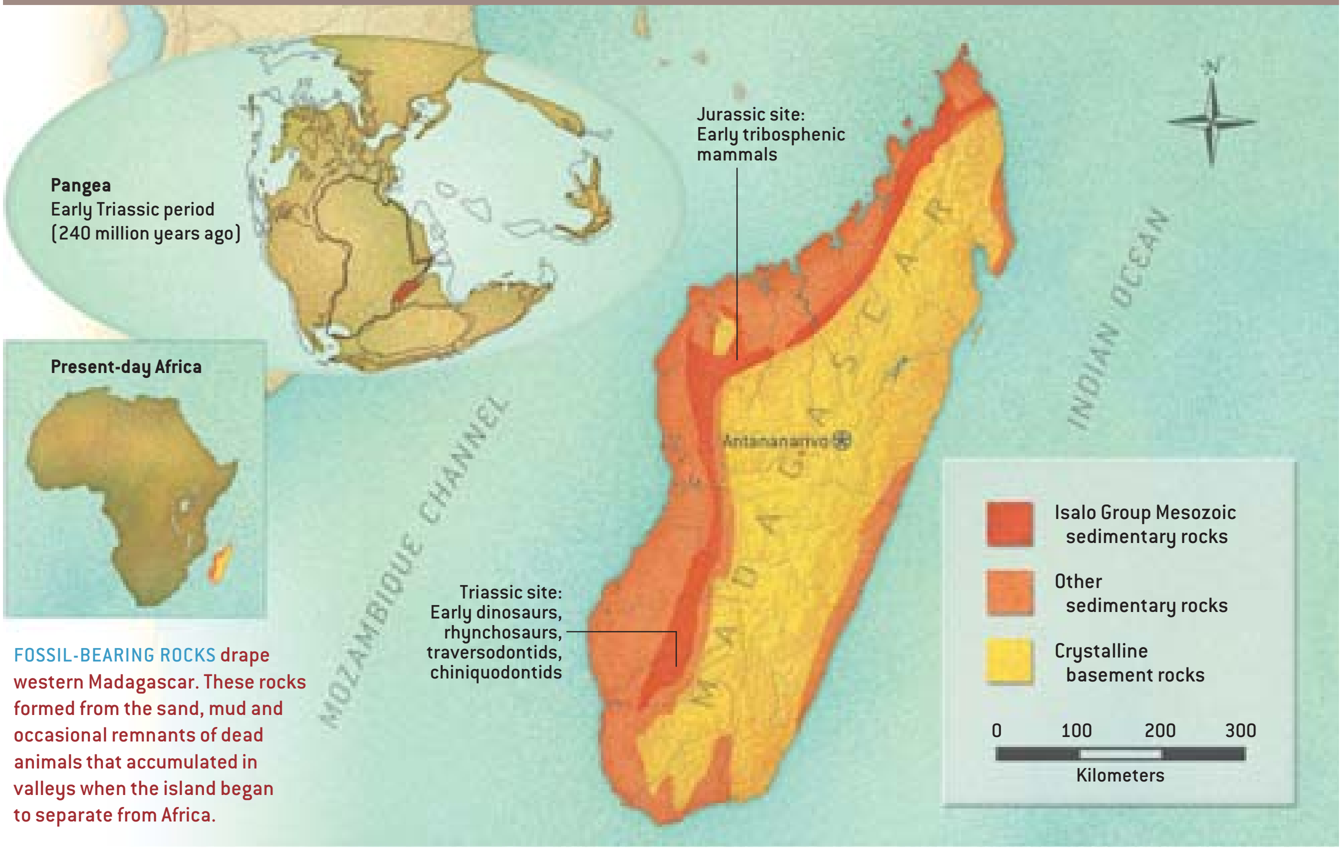
Ancient Luck

PERHAPS THE MOST DAUNTING obstacle we faced in prospecting such a large region was deciding where to begin. Fortunately, we were not planning our search blindly. The pioneering fieldwork of geologists such as Henri Besairie, who directed Madagascar's ministry of mines during the mid-1900s, provided us with large-scale maps of the island's Mesozoic rocks. From those studies we knew that a fortuitous combination of geologic factors had led to the accumulation of a thick blanket of sediments over most of Madagascar's western lowlands—and gave us good reason to believe that ancient bones and teeth might have been trapped and preserved there.

At the dawn of the Mesozoic era 250 million years ago, it would have been possible to walk from Madagascar to almost anywhere else in the world. All of the planet's landmasses were united in the supercontinent Pangea, and Madagascar was nestled between the western coast of what is now India and the eastern coast of present-day Africa [*see map on opposite page*]. The world was much warmer than at present—even the poles were free of ice. In the supercontinent's southern region, Gondwana, enormous rivers coursed into lowland basins that would

MARIA STENZEL *National Geographic Image Collection* (*preceding pages*); JOHN WEINSTEIN *The Field Museum* (*this page*)

MADAGASCAR THEN AND NOW



FOSSIL-BEARING ROCKS drape western Madagascar. These rocks formed from the sand, mud and occasional remnants of dead animals that accumulated in valleys when the island began to separate from Africa.

SARA CHEN

eventually become the Mozambique Channel, which today spans the 250 miles between Madagascar and eastern Africa.

These giant basins represent the edge of the geologic gash created as Madagascar began pulling away from Africa more than 240 million years ago. This seemingly destructive process, called rifting, is an extremely effective way to accumulate fossils. (Indeed, many of the world's most important fossil vertebrate localities occur in ancient rift settings.) The rivers flowing into the basins carried with them mud, sand, and occasionally the carcasses or bones of dead animals. Over time the rivers deposited this material as a sequence of vast layers. Continued rifting and the growing mass of sediment caused the floors of the basins to sink ever deeper. This depositional process persisted for nearly 100 million years, until the basin floors thinned to the breaking point and molten rock ascended from the planet's interior to fill the gap as new ocean crust.

Up to that point nature had afforded Madagascar three crucial ingredients required for fossil preservation: dead organisms, holes in which to bury them (rift basins), and material to cover them (sand and mud). But special conditions were also needed to ensure that the fossils were not destroyed during the subsequent 160 million years. Again, geologic circumstances proved fortuitous. As the newly separated landmasses of Africa and Madagascar drifted farther apart, their sediment-laden coastlines rarely experienced volcanic eruptions or other events that could have destroyed buried fossils. Also key for fossil preservation is that the ancient rift basins ended up on the western side of the island, which today is dotted with dry forests, grasslands and desert scrub. In a more humid environment, such deposits would have eroded away or would be hidden under dense vegetation like the kind that hugs much of the island's eastern coast.

Initially Madagascar remained attached to the other Gondwanan landmasses: India, Australia, Antarctica and South America. It did not attain islandhood until it split from India about 90 million years ago. Sometime since then, the island acquired its suite of bizarre modern creatures, of which lemurs are the best known. For more than a century, researchers have

THE AUTHORS

JOHN J. FLYNN and *ANDRÉ R. WYSS* have collaborated for 20 years on expeditions to the Rocky Mountains, Baja California, the Andes of Chile, and Madagascar. They also study the evolution of carnivores, including dogs, cats and seals. Flynn is MacArthur Curator of Fossil Mammals at the Field Museum in Chicago, associate chair of the University of Chicago's committee on evolutionary biology doctoral program, and adjunct professor at the University of Illinois at Chicago. Wyss is professor of geological sciences at the University of California, Santa Barbara, and a research associate at the Field Museum.

The authors thank the University of Antananarivo for its long-term collaboration and the National Geographic Society, the John C. Meeker family and the World Wildlife Fund for their exceptional support.

wondered how long these modern creatures and their ancestors have inhabited the island. Illuminating discoveries by another team of paleontologists indicate that almost all major groups of living vertebrates arrived on Madagascar since sometime near the end of the Mesozoic era 65 million years ago [*see box on page 38*]. Our own probing has focused on a more ancient interval of Madagascar's history—the first two periods of the Mesozoic era.

Pay Dirt

ONE OF THE JOYS of working in little-charted terrain has been that if we manage to find anything, its scientific significance is virtually assured. That's why our first discoveries near Isalo National Park were so exciting. The same evening in 1996 that we found the rhynchosaur jaw fragments, University of Antananarivo student Léon Razafimanantsoa spotted the six-inch-long skull of another interesting creature. We immediately identified the animal as a peculiar plant eater, neither mammal nor reptile, called a traversodontid cynodont [*see illustration on page 37*].

The rhynchosaur jaws and the exquisite traversodontid skull—the first significant discoveries of our ongoing U.S.-Malagasy project—invigorated our expedition. The first fossil is always the hardest one to find; now we could do the detailed collecting necessary to begin piecing together an image of the past. The white sandstones we were excavating had formed from the sand carried by the rivers that poured into lowlands as Madagascar unhinged from Africa. Within these prehistoric valleys rhynchosaurs and traversodontids, both four-legged creatures ranging from three to 10 feet in length, probably grazed together much the same way zebras and wildebeests do in Africa today. The presence of rhynchosaurs, which are relatively common in coeval rocks around the world, narrowed the date to sometime within the Triassic period (the first of three Mesozoic time intervals), which spans from 250 million to 205 million years ago. And because traversodontids were much more diverse and abundant during the first half of the Triassic than during the second, we thought initially that this scene played out before about 230 million years ago.

During our second expedition, in 1997, a third type of animal challenged our sense of where we were in time. Shortly after we arrived in southwestern Madagascar, one of our field assistants, a local resident named Mena, showed us some bones that he had found across the river from our previous localities. We were struck by the fine-grained red rock adhering to the bones—everything we had found until that point was buried in the coarse white sandstone. Mena led us about half a mile north of the rhynchosaur and traversodontid site to the bottom of a deep gully. Within a few minutes we spotted the bone-producing layer from which his unusual specimens had rolled. A rich concentration of fossils was entombed within the three-foot-thick layer of red mudstones, which had formed in the floodplains of the same ancient rivers that deposited the white sands. Excavation yielded about two dozen specimens of what seemed at first to be dinosaurs. Our team found jaws, strings of

TINY BONES TO PICK

Paleontologists brave wildfires, parasites and scorching temperatures in search of ancient mammal fossils

By Kate Wong

THE THREE LAND ROVERS pause while John Flynn consults the device in his hand. "Is the GPS happy?" someone asks him. Flynn concludes that it is, and the caravan continues slowly through the bush, negotiating trails usually traversed by oxcart. We have been driving since seven this morning, when we left Madagascar's capital city, Antananarivo. Now, with the afternoon's azure sky melting into pink and mauve, the group is anxious to locate a suitable campsite. A small cluster of thatched huts comes into view, and Flynn sends an ambassador party on foot to ask the inhabitants whether we may camp in the area. By the time we reach the nearby clearing, the day's last light has disappeared and we pitch our tents in the dark. Tomorrow the real work begins.

The expedition team of seven Malagasies and six Americans, led by paleontologists Flynn and André Wyss of the Field Museum in Chicago and the University of California at Santa Barbara, respectively, has come to this remote part of northwestern Madagascar in search of fossils belonging to early mammals. Previous prospecting in the region had revealed red and buff-colored sediments dating back to the Jurassic period—the ancient span of time (roughly 205 million to 144 million years ago) during which mammals made their debut. Among the fossils unearthed was a tiny jaw fragment with big implications.

Conventional wisdom holds that the precursors of modern placental and marsupial mammals arose toward the end of the Jurassic in the Northern Hemisphere, based on the ages and locations of the earliest remains of these shrewlike creatures, which are characterized by so-called tribosphenic molars. But the Malagasy jaw, which Flynn and Wyss have attributed to a new genus and species, *Ambondro mahabo,* possesses tribosphenic teeth and dates back some 167 million years to the Middle Jurassic. As such, their fossil suggests that tribosphenic mammals arose at least 25 million years earlier than previously thought and possibly in the south rather than the north.

No one has disputed the age of *A. mahabo,* but not everyone agrees that the finding indicates that tribosphenic mammals originated in the south. Fossil-mammal expert Zhexi Luo of the Carnegie Museum

FOUR-INCH-LONG MAMMAL *Ambondro mahabo* lived in Madagascar about 167 million years ago.

of Natural History in Pittsburgh and several of his colleagues recently suggested that *A. mahabo* and a similarly surprising fossil beast from Australia named *Ausktribosphenos nyktos* might instead represent a second line of tribosphenic mammals—one that gave rise to the egg-laying monotremes. But Flynn and Wyss counter that some of the features that those researchers use to link the Southern tribosphenic mammals to monotremes may be primitive resemblances and therefore not indicative of an especially close evolutionary relationship.

As with so many other debates in paleontology, much of the controversy over when and where these mammal groups first appeared stems from the fact that so few ancient bones have ever been found. With luck, this season's fieldwork will help fill in gaps in the fossil record. And recovering more specimens of *A. mahabo* or remains of previously unknown mammals could bolster considerably Flynn and Wyss's case for a single, Southern origin for the ancestors of modern placentals and marsupials.

The next morning, after a quick breakfast of bread, peanut butter and coffee, we are back in the vehicles, following the GPS's trail of electronic bread crumbs across the grassland to a fossil locality the team found at the end of its previous expedition. Stands of doum palms and thorny Mokonazy trees dot the landscape, which the dry season has left largely parched. By the time we reach our destination, the morning's pleasant coolness has given way to a rather toastier temperature. "When the wind stops, it cooks," remarks William Simpson, a collections manager for the Field Museum, coating his face with sunscreen. Indeed, noontime temperatures often exceed 90 humid degrees Fahrenheit.

Flynn instructs the group to start at the base of the hillside and work up. Meanwhile he and Wyss will survey the surrounding area, looking for additional exposures of the fossil-bearing horizon. "If it's something interesting, come back and get me," he calls. Awls in hand and eyes inches from the ground, the workers begin to scour the gravel-strewn surface for small bones, clues that delicate mammal fossils are preserved below. They crawl and slither in pursuit of their quarry, stopping only to swig water from sun-warmed bottles. Because early mammal remains are so minute (*A. mahabo*'s jaw fragment, for example, measures a mere 3.6 millimeters in length), such sleuthing rarely leads to instant gratification. Rather the team collects sediments likely to contain such fossils and ships that material back to the U.S. for closer inspection. Within a few hours, a Lilliputian vertebra and femur fragment turn up—the first indications that the fossil hunters have hit pay dirt. "It's a big Easter egg hunt," Wyss quips. "The eggs are hidden pretty well, but we know they're out there."

By the third day the crew has identified a number of promising sites and bagged nearly a ton of sediment for screen washing. Members head for a dammed-up stream that locals use to water their animals. Despite the scorching heat, those working in the water must don heavy rubber boots and gloves to protect against the parasites that probably populate the murky green pool. They spend the next few hours sifting the sediments through screen-bottomed baskets and buckets. Wyss spreads the resulting concentrate on a big blue plastic tarp to dry. Volunteers at the Field Museum will eventually look for fossils in this concentrate under a microscope, one spoonful at a time, but Wyss has a good feeling about the washed remains already.

JURASSIC AGE jaw fragment of *A. mahabo* features specialized molars that are unique to tribosphenic mammals.

"You can actually see bone in the mix," he observes. The haul that yielded *A. mahabo,* in contrast, offered no such hints to the naked eye.

Hot and weary from the screen washing, the researchers eagerly break for lunch. Under the shade of a Mokonazy tree, they munch their sardine, Gouda and jalapeño sandwiches, joking about the bread, which, four days after leaving its bakery in Antananarivo, has turned rather tough. Wyss ceremoniously deposits a ration of jelly beans into each pair of upturned palms. Some pocket the treats for later, others trade for favorite flavors, and a few ruefully relinquish their sweets, having lost friendly wagers made earlier.

Usually lunch is followed by a short repose, but today nature has a surprise in store. A brushfire that had been burning off in the distance several hours ago is now moving rapidly toward us from the northeast, propelled by an energetic wind. The crackling sound of flames licking bone-dry grass crescendos, and ashen leaf remnants drift down around us. We look on, spellbound, as cattle egrets collect in the fire's wake to feast on toasted insects, and birds of prey circle overhead to watch for rodents flushed out by the flames. Only the stream separates us from the blaze, but reluctant to abandon the screen washing, Flynn and Wyss decide to wait it out. Such fires plague Madagascar. Often set by farmers to encourage new grass growth, they sometimes spread out of control, especially in the tinderbox regions of the northwest. Indeed, the explorers will face other fires that season, including one that nearly consumes their campsite.

An hour later the flames have subsided, and the team returns to the stream to finish the screening quickly. Banks once thick with dry grass now appear naked and charred. Worried that the winds might pick up again, we pack up and go to one of the team's other fossil localities to dig for the rest of the afternoon.

Following what has already become the routine, we return to camp by six. Several people attend to the filtering of the drinking water, while the rest help to prepare dinner. During the "cocktail hour" of warm beer and a shared plate of peanuts, Flynn and Wyss log the day's events and catalogue any interesting specimens they have collected. Others write field notes and letters home by the light of their headlamps. By nine, bellies full and dishes washed, people have retired to their tents. Camp is silent, the end of another day's efforts to uncover the past.

Kate Wong is editorial director of ScientificAmerican.com

FRANK IPPOLITO (*opposite page*); JOHN J. FLYNN AND SUSANA MAGALLON *The Field Museum* (*above*) vertebrae, hips, claws, an articulated forearm with some wrist bones, and other assorted skeletal elements. When we examined the jawbones more closely, we realized that we had uncovered remains of two different new reptile species (not yet formally named), one of which appears to resemble a prosauropod dinosaur from Morocco called *Azendohsaurus*. Prosauropods, which typically appear in rocks between 225 million and 190 million years old, are smaller-bodied precursors of the long-necked sauropod dinosaurs, including such behemoths as *Brachiosaurus*. Much to our surprise, however, as the other bones were later cleaned from the rock, and as we found additional bones over subsequent field seasons, we began to wonder whether we were dealing with an entirely new kind of ancient reptile, rather than a true dinosaur. These mysterious animals have teeth and some skull features that look just like those of typical prosauropod dinosaurs, but the rest of their skeleton is strikingly more primitive than any known dinosaur. We have not yet completely analyzed the unexpected combination of bones and teeth, but this evolutionary chimera—mixing characteristics of distantly related reptile groups—is even leading us to question whether certain features long believed to characterize dinosaurs might have evolved much earlier in their archosaur ancestry. If so, it is likely that *Azendohsaurus,* the new Malagasy fossil, and other animals long assumed to be dinosaurs might be something else entirely.

When we discovered that dinosaurlike animals were foraging among rhynchosaurs and traversodontids, it became clear that we had unearthed a collection of fossils not known to coexist anywhere else. In Africa, South America and other parts of the world, traversodontids are much less abundant and less diverse once dinosaurs appear. Similarly, the most common type of rhynchosaur we found, *Isalorhynchus,* lacks advanced characteristics and thus is inferred to be more ancient. What is more, the Malagasy fossil assemblage lacks remains of several younger reptile groups usually found with the earliest dinosaurs, including the heavily armored, crocodilelike phytosaurs and aetosaurs. The mixture of ancient kinds of animals found alongside our enigmatic reptile, plus the lack of younger creatures, suggests that the Malagasy fossil deposit is as old as any dinosaur ever discovered, if not older.

We had unearthed a collection of fossils NOT KNOWN TO COEXIST ANYWHERE ELSE.

INSPECTING THE ROCKS UP CLOSE, author Flynn (*right*) and William F. Simpson work to ensure that no scraps of bone have been overlooked.

Just one early dinosaur site—at Ischigualasto, Argentina—contains a rock layer that has been dated directly; all other early dinosaur sites with similar fossils are thus estimated to be no older than its radioisotopic age of about 228 million years. (Reliable radioisotopic ages are obtainable only from rock layers produced by contemporaneous volcanoes. The Malagasy sediments accumulated with no volcanoes nearby.) Based on the fossils present, we have tentatively concluded that our fossil-bearing rocks slightly predate the Ischigualasto time span. And because prosauropods represent a major branch of the dinosaur evolutionary tree, the common ancestor of all dinosaurs must be older still. Rocks from before about 245 million years ago have been moderately well sampled around the world, but none of them has yielded dinosaurs. That means the search for the common ancestor of all dinosaurs must focus on a relatively poorly known and ever narrowing interval of Middle Triassic rocks, between about 240 million and 230 million years old.

Mostly Mammals

DINOSAURS NATURALLY ATTRACT considerable attention, being the most conspicuous land animals of the Mesozoic. Less widely appreciated is the fact that mammals and dinosaurs sprang onto the evolutionary stage at nearly the same time. At least two factors account for the popular misconception that mammals arose only after dinosaurs became extinct: Early mammals were all chipmunk-size or smaller, so they don't grab the popular imagination. In addition, the fossil record of early mammals is sparse. To our delight, Madagascar has once again filled in two mysterious gaps in the fossil record. The traversodontid cynodonts from the Isalo deposits reveal new details about close mammalian relatives, and a younger fossil from the northwest side of the island poses controversial questions about where and when a key advanced group of mammals got its start.

The Malagasy traversodontids, the first known from the island, include some of the best-preserved representatives of early cynodonts ever discovered. (Cynodontia is a broad group of land animals that includes mammals and their nearest relatives.) Accordingly, these bones provide a wealth of new ana-

MARIA STENZEL *National Geographic Image Collection* (*this page*); FRANK IPPOLITO (*opposite page*)

LIVING IN MIXED COMPANY

PALEONTOLOGISTS DID NOT KNOW until recently that the unusual group of ancient animals shown above—possible prosauropods (*1*), traversodontids (*2*), rhynchosaurs (*3*) and chiniquodontids (*4*)—once foraged together. In the past eight years, southwestern Madagascar has become the first place where bones of each particular type of animal have been unearthed alongside the others, in this case from Triassic rocks about 230 million years old. Then the region was a lush, lowland basin that was forming as the supercontinent Pangea began to break up. The long-necked possible prosauropods here, which may represent some of the oldest dinosaurs yet discovered, browse on conifers while a parrot-beaked rhynchosaur prepares to sip from a nearby pool. The prosauropodlike teeth were spear-shaped and serrated—good for slicing vegetation; rhynchosaurs were perhaps the most common group of plant eaters in the area at that time. Foraging among these large reptiles are the peculiar traversodontids and chiniquodontids—early members of the Cynodontia, a broad group that includes today's mammals. The grinding cheek teeth of the traversodontids suggest that they were herbivores; the chiniquodontids sport the sharp, pointed teeth of carnivores. —*J.J.F. and A.R.W.*

tomical information. These cynodonts are identified by, among other features, a simplified lower jaw dominated by a single bone, the dentary. Some specimens include both skulls and skeletons. Understanding the complete morphology of these animals is crucial for resolving the complex evolutionary transition from the large cold-blooded, scale-covered animals with sprawling limbs (which dominated the continents prior to the Mesozoic) to the much smaller warm-blooded, furry animals with an erect posture that are so plentiful today.

Many kinds of mammals, with many anatomical variations, now inhabit the planet. But they all share a common ancestor marked by a single, distinctive suite of features. To determine what these first mammals looked like, paleontologists must examine their closest evolutionary relatives within the Cynodontia, which include the traversodontids and their much rarer cousins, the chiniquodontids (also known as probainognathians), both of which we have found in southwestern Madagascar. Traversodontids almost certainly were herbivorous, because their wide cheek teeth are designed for grinding—evidence of which we and our colleagues recently documented with scanning electron microscope analyses of microwear features on the teeth. One of our four new Malagasy traversodontid species also has large, stout, forward-projecting incisors for grasping vegetation. The chiniquodontids, in contrast, were undoubtedly carnivorous, with sharp, pointed teeth. Most paleontologists agree that some chiniquodontids share a more recent common ancestor with mammals than the herbivorous traversodontids do. The chiniquodontid skulls and skeletons we found in Madagascar will help reconstruct the bridge between early cynodonts and true mammals.

Not only are Madagascar's Triassic cynodonts among the best preserved in the world, they also sample a time period that is poorly known elsewhere. The same is true for the youngest fossils our expeditions have uncovered—those from a region of the northwest where the sediments are about 165 million years in age. (That date falls within the middle of the Jurassic, the second of the Mesozoic's three periods.) Because these sediments were considerably younger than our Triassic rocks, we allowed ourselves the hope that we might find remains of an ancient mammal. Not a single mammal had been recorded from Jurassic rocks of a southern landmass at that point, but this did nothing to thwart our motivation.

Madagascar's Triassic cynodonts are among the BEST PRESERVED IN THE WORLD.

Once again, persistence paid off. During our 1996 field season, we had visited the village of Ambondromahabo after hearing local reports of abundant large fossils of the sauropod dinosaur *Lapparentosaurus*. Sometimes where large animals are preserved, the remains of smaller animals can also be found—though not as easily. We crawled over the landscape, eyes held a few inches from the ground. This uncomfortable but time-tested strategy turned up a few small theropod dinosaur teeth, fish scales and other bone fragments, which had accumulated at the surface of a small mound of sediment near the village.

These unprepossessing fossils hinted that more significant items might be buried in the sediment below. We bagged about

MODERN-DAY MYSTERY

MADAGASCAR IS FAMOUS for its 40 species of lemurs, none of which occurs anywhere else in the world. The same is true for 80 percent of the island's plants and other animals. This biotic peculiarity reflects the island's lengthy geographic isolation. Madagascar has not been connected to another major landmass since it separated from India nearly 90 million years ago, and it has not been joined with its nearest modern neighbor, Africa, since about 160 million years ago. But scant fossil evidence meant that little was known about the origin of these unique creatures.

While our research group was probing Madagascar's Triassic and Jurassic age rocks, teams led by David W. Krause of Stony Brook University were unearthing a wealth of younger fossils in the island's northwestern region. These specimens, which date back some 70 million years, include more than three dozen species, none of which is closely related to the island's modern animals. This evidence implies that most modern vertebrate groups must have immigrated to Madagascar after this point.

The best candidate for a Malagasy motherland is Africa, and yet the modern faunas of the two landmasses are markedly distinct. Elephants, cats, antelope, zebras, monkeys and many other modern African mammals apparently never reached Madagascar. The four kinds of terrestrial mammals that inhabit the island today—rodents, lemurs, carnivores and the hedgehoglike tenrecs—all appear to be descendants of more ancient African beasts. The route these immigrants took from the mainland remains unclear, however. Small clinging animals could have floated from Africa across the Mozambique Channel on "rafts" of vegetation that broke free during severe storms. Alternatively, when sea level was lower these pioneers might have traveled by land and sea along a chain of currently submerged highlands northwest of the island.

Together with Anne D. Yoder of Northwestern University Medical School and others, we are using the DNA structure of modern Malagasy mammals to address this question. These analyses have recently revealed that the ancestor of Madagascar's modern carnivores arrived at a different time than the island's other mammal groups, each of which colonized the island in separate, long-distance dispersal events rather than a single episode. *—J.J.F. and A.R.W.*

200 pounds of sediment and washed it through mosquito-net hats back in the capital, Antananarivo, while waiting to be granted permits for the second leg of our trip—the leg to the southwest that turned up our first rhynchosaur jaws and traversodontid skull.

During the subsequent years back in the U.S., while our studies focused on the exceptional Triassic material, the tedious process of sorting the Jurassic sediment took place. A dedicated team of volunteers at the Field Museum in Chicago—Dennis Kinzig, Ross Chisholm and Warren Valsa—spent many a weekend sifting through the concentrated sediment under a microscope in search of valuable flecks of bone or teeth. We didn't think much about that sediment again until 1998, when Kinzig relayed the news that they had uncovered the partial jawbone of a tiny mammal with three grinding teeth still in place. We were startled not only by the jaw's existence but also by its remarkably advanced cheek teeth. The shapes of the teeth document the earliest occurrence of Tribosphenida, a group encompassing the vast majority of living mammals. We named the new species *Ambondro mahabo,* after its place of origin.

The discovery pushes back the range of this group of mammals by more than 25 million years and offers the first glimpse of mammalian evolution on the Southern continents during the latter half of the Jurassic period. It shows that this subgroup of mammals may have evolved in the Southern Hemisphere rather than the Northern, as is commonly supposed. The information does not resolve the debate, but it does point out the precarious nature of long-standing assumptions rooted in a fossil record historically biased toward the Northern Hemisphere [*see box on page 34*].

Planning Persistently

ALTHOUGH OUR TEAM has recovered a broad spectrum of fossils in Madagascar, scientists are only beginning to describe the Mesozoic history of the Southern continents. The number of species of Mesozoic land vertebrates known from Australia, Antarctica, Africa and South America is probably on an order of magnitude smaller than the number of contemporaneous findings from the Northern Hemisphere. Clearly, Madagascar now ranks as one of the world's top prospects for adding important insights to paleontologists' knowledge of the creatures that once roamed Gondwana.

Often the most significant hypotheses about ancient life on the earth can be suggested only after these kinds of new fossil discoveries are made. Our team's explorations provide two cases in point: the fossils found alongside the Triassic reptiles indicate that dinosaurs may have debuted earlier than previously recorded, and the existence of the tiny mammal at our Jurassic site implies that tribosphenic mammals may have originated in the Southern, rather than Northern, Hemisphere. The best way to bolster these proposals (or to prove them wrong) is to go out and uncover more bones. That is why the primary goal of our August-September 2003 expedition was the same as it has been for our past five expeditions: find as many fossils as possible.

Our agenda typically includes digging deeper into known sites and surveying new regions, blending risky efforts with sure bets. No matter how carefully formulated, however, our plans are always subject to last-minute changes, dictated by such things as road closures. In 2003 our most daunting challenge was the appearance of frenzied boomtowns.

During our first three expeditions, we never gave a second thought to the gravels that overlay the Triassic rock outcrops in the southwestern part of the island. Little did we know that those gravels contain sapphires. By 1999 tens of thousands of people were scouring the landscape in search of these gems. The next year all our Triassic sites fell within sapphire-mining claims. Those areas are now off-limits to everyone, including paleontologists, unless they get permission from both the claim holder and the government. Leaping that extra set of hurdles was one of our foremost tasks.

Even without such logistical obstacles slowing our progress, it would require uncountable lifetimes to carefully survey all the island's untouched rock exposures. But now that we have seen a few of Madagascar's treasures, we are inspired to keep digging—and to reveal new secrets. SA

INTO THE SUNSET: Authors Flynn (*right*) and Wyss ride back to camp after a long day's digging in southwestern Madagascar.

MARIA STENZEL *National Geographic Image Collection*

MORE TO EXPLORE

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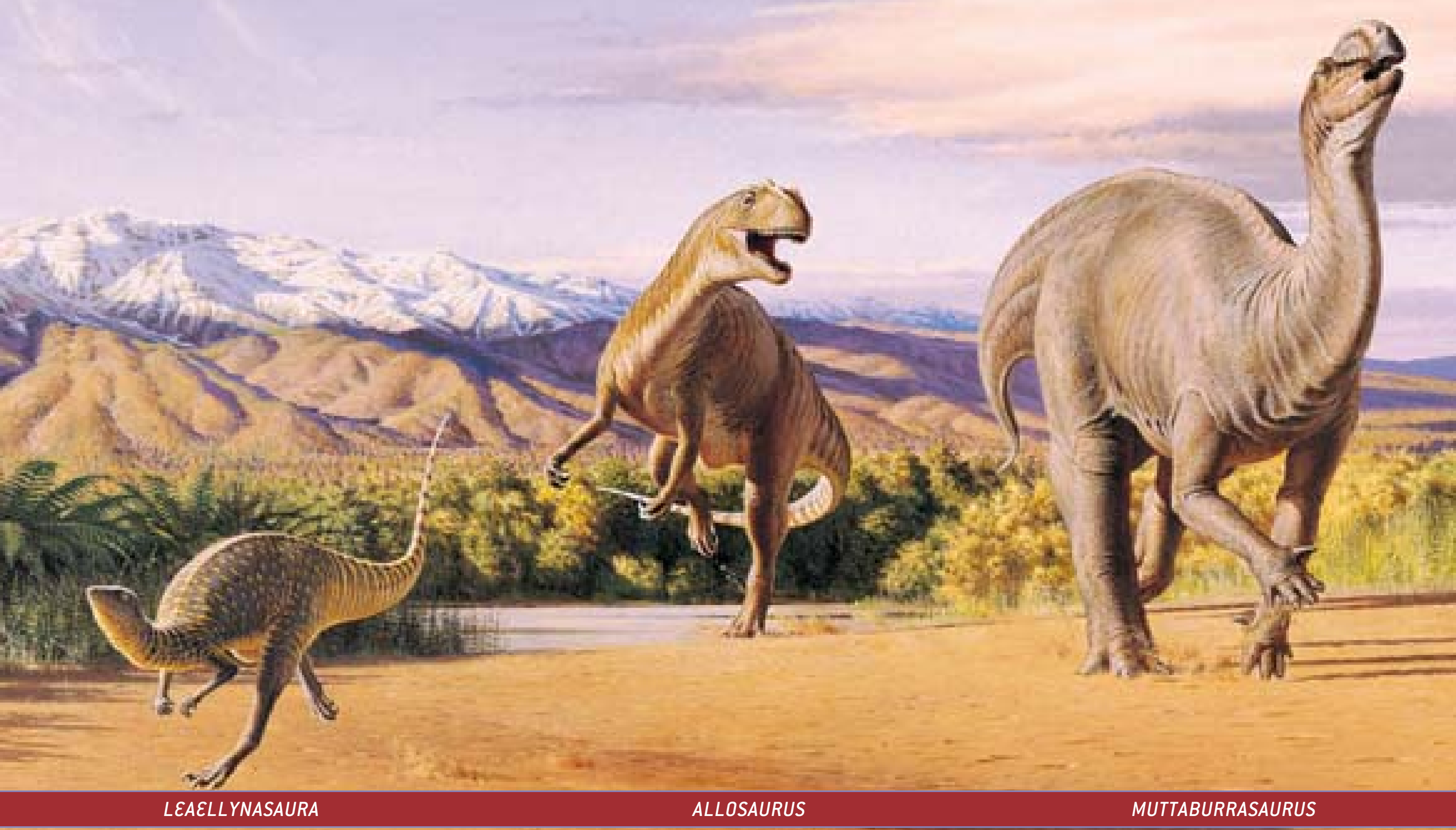
Dinosaurs of

Their excellent night vision and apparent warm blood raise a question: Could they have survived icehouse conditions at the end of the Cretaceous period?

By Patricia Vickers-Rich and Thomas Hewitt Rich



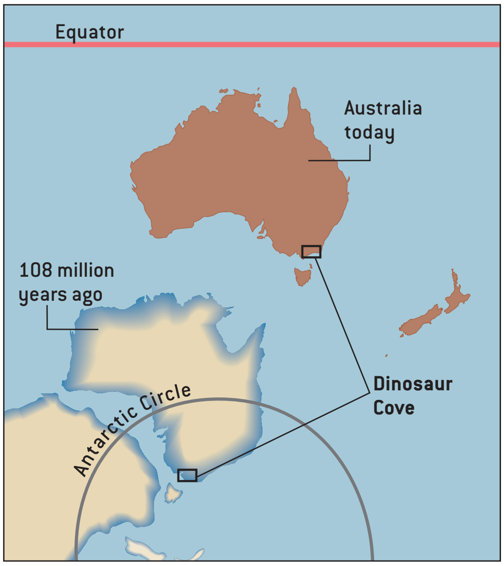
AUSTRALIAN DINOSAURS flourished in southeastern Victoria during the Early Cretaceous, when the region lay within the Antarctic Circle. This mural depicts six species that left fossils there and a seventh—the large iguanodontid *Muttaburrasaurus*—that has been found only in Queensland,

the Antarctic

IN THE EARLY CRETACEOUS PERIOD, about 100 million years ago, Australia lay alongside Antarctica, which straddled the South Pole as it does today. Australia's south-eastern corner, now the state of Victoria, lay well inside the Antarctic Circle. At that time, the region hosted an assemblage of animals and plants that lived under climate conditions having no modern analogue. The average temperature appears to have ranged from frigid to low temperate. Through the long winter, the sun did not shine for weeks or months at a time.

far to the north. The paucity of large polar dinosaurs may reflect a real absence or merely the selective preservation of small bones.

Peter Trusler painted the mural of the creatures, which was created for an Australia Post stamp issue entitled "Australia's Dinosaur Era."



SOUTHERN SUPERCONTINENT known as Gondwana began to break up more than 100 million years ago, when a rift valley formed between what would become Australia and Antarctica (*left*). Stream channels in the valley received bones gathered by floodwaters that periodically swept these broad plains. The bones, together with clay and silt, created the fossil-bearing formations of Dinosaur Cove (*right*).

Many dinosaur lineages survived in this strange environment after they had died out in other places. At least one member of the group evolved an adaptation to the cold and to the dark that is interesting both in itself and for what it tells of the passing of a biological epoch. If global cooling indeed killed the dinosaurs, as many paleontologists have suggested, then Australia's species were the ones most likely to have survived the longest. Did their adaptations to an already marginal climate help them survive a sharp cooling trend, one that caught species living on other continents unprepared?

Although the Cretaceous fossil plants of southeastern Australia have been studied for more than a century, the animals remained mostly hidden until recently. In 1903 geologist William Hamilton Ferguson found two bones that have had a bearing on later paleontological work—the tooth of a lungfish and the claw of a carnivorous dinosaur, assigned to the theropod genus *Megalosaurus*. For the next 75 years, as no further finds joined them, these bones lay neglected in a cabinet in Museum Victoria. Then, in 1978, two graduate students at Monash University, Tim F. Flannery and John A. Long, discovered near Ferguson's original site the first specimens of a trove of dinosaur bones embedded in hard sandstones and mudstones from the Early Cretaceous.

These discoveries—only an hour and a half's drive southeast of Melbourne—encouraged paleontologists to prospect other coastal sites. In 1980 we struck a rich lode in the Otway ranges, which the Victorian government, at our suggestion, has since named Dinosaur Cove. There, for a decade—with the help of Earthwatch and other volunteers, the National Geographic Society, the Australian Research Council, and Atlas Copco, a manufacturer of mining equipment—we spent three months out of every year chiseling, hammering and on occasion blasting tunnels into the fossil-bearing strata. With Dinosaur Cove worked out in 1994, effort has since been concentrated at a site about 300 kilometers east, called Flat Rocks. The rocks there are about 10 million years older than those at Dinosaur Cove.

Flat Rocks, Dinosaur Cove and other sites of similar character were formed when violent, seasonal streams swept broad floodplains of their accumulated bones and plant life, depositing this flotsam and jetsam at the bottom of shallow stream channels. These deposits appear along the southern Victorian shore because only there could gnawing waves expose the sediments laid down in the rift valley that formed when Australia and Antarctica went their separate ways, as did the other fragments of Gondwana, an ancient supercontinent [*see illustration above*]. Only two fossil sites from the same period have been found inland, one in sediments laid down under far quieter conditions at the bottom of an ancient lake. This inland site has therefore yielded some uncommonly well preserved specimens.

It must be noted that southeastern

THE AUTHORS

PATRICIA VICKERS-RICH and *THOMAS HEWITT RICH* collaborate on the study of fossils. Vickers-Rich holds a personal chair in paleontology at Monash University in Melbourne, Australia. She is interested in reconstructing ancient environments, especially those without modern analogues, and in analyzing rapid biotic change. Rich is curator of vertebrate paleontology at Museum Victoria in Melbourne. He conducts research on the evolutionary patterns of Mesozoic vertebrates, specializing in primitive mammals and ornithischian dinosaurs. The Riches received undergraduate degrees in paleontology from the University of California, Berkeley, and doctorates in geology from Columbia University. They live near Melbourne and have two children.

Updated from the July 1993 issue

Australia's dinosaurs are known from a mere 8,000 individual bones and two partial skeletons. Only a few hundred of the bones can be assigned to a given species or genus. What they lack in number, however, they make up for in scientific interest.

All efforts at interpretation revolve around the estimation of temperature, for which three methods have been tried. Robert T. Gregory of Southern Methodist University and his associates infer Australian paleoclimate from the ratio of oxygen 18 to oxygen 16 trapped in concretions in ancient rocks. They find that mean annual temperatures probably approached zero degrees Celsius but might have reached as high as eight degrees C. Such values occur today in Hudson Bay, Saskatchewan (zero degrees C), and in Minneapolis and Toronto (eight degrees C).

Work by Andrew Constantine of Origin Energy on structures preserved in the rocks in which the dinosaur bones are buried reveals evidence for the former existence of permafrost and ice wedging as well as patterned ground and hummocky ground. Such features are formed today in regions with mean annual temperatures of three degrees C below zero to three degrees C above zero. These structures are not as commonly encountered as the concretions, yet they are most obvious only three meters stratigraphically below the Flat Rocks locality where dinosaurs, mammals and associated fauna have been found. Evidence for the occurrence of permafrost had never before been reported in association with dinosaurs.

Robert A. Spicer of the Open University in the U.K. and Judith Totman Parrish of the University of Idaho instead deduce temperature from the structure of ancient plants, arriving at the somewhat higher mean annual temperature of 10 degrees C. Their research with colleagues has demonstrated that polar Australia supported conifers, ginkgoes, ferns, cycads, bryophytes and horsetails but only a few angiosperms, or flowering plants, identifiable by a sprinkling of pollen. The angiosperms were then just beginning to spread into new niches. Perhaps they got their start by exploiting weedy ecological systems in the rift valleys that formed as the supercontinent split apart.

Spicer and Parrish noticed that evergreens, which provided forage in all seasons, had thick cuticles and other structural features that indicate adaptation to cold or dryness (perhaps brought on by winter freezing). Deciduous plants offer another climatic clue: they seem to have lost all their leaves at once. These mass falls may have been triggered by darkness or cold. Drought, however, probably did not serve as a constant cue—the sedimentary record and the abundance of ferns and bryophytes argue for conditions that were moist in all seasons except perhaps winter.

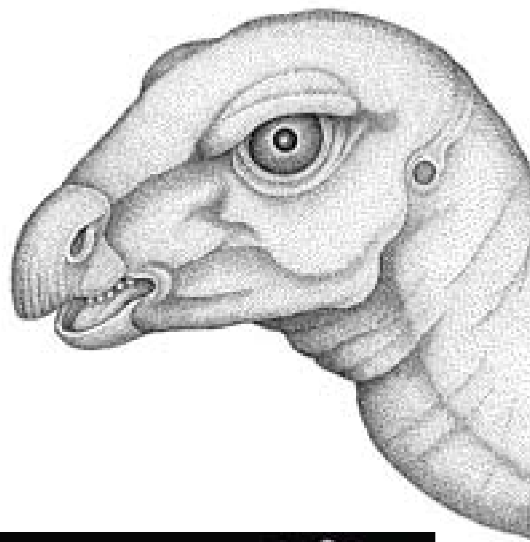
Surviving the Cold

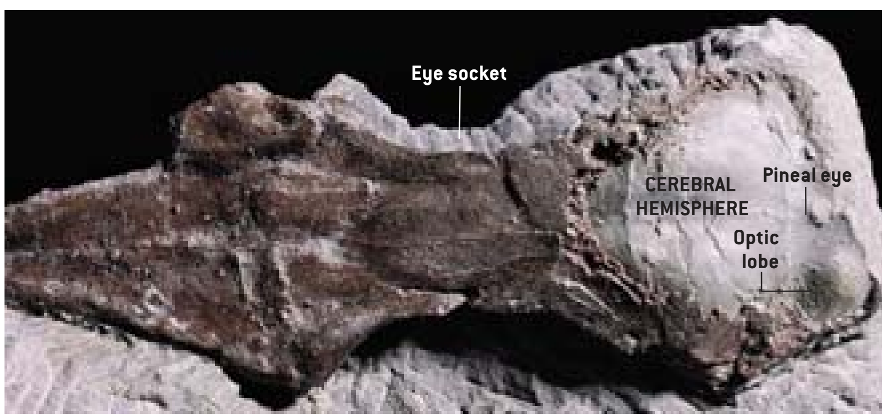
IF THE HIGHER ESTIMATE of mean temperature is correct, Australia was both temperate and subject to a period of continuous darkness every year—a combination with absolutely no modern counterpart. The winter night lasted between six weeks and four and a half months, depending on the true paleolatitude. Because the lower extreme of temperature would then have fallen well below the mean, most of the vertebrates preserved as fossils must have lived quite close to their thermal limits. Some, such as lungfish, cannot now breed in waters colder than 10 degrees C.

If, on the other hand, the lower mean temperature is correct, it becomes more than a typical scientific challenge to understand how this paleocommunity functioned at all. Before seriously attacking this problem, scientists will first have to demonstrate that it exists. To refine the estimate of the average annual temperature, a multidisciplinary team is comparing floral, geochemical and other forms of evidence.

Nothing in this fauna is quite so peculiar to the region as the koala is today, for although the species and genera were local, they belonged to cosmopolitan families. Yet their adaptations are striking, as is the fact that some survived beyond the time of demise for their families elsewhere.

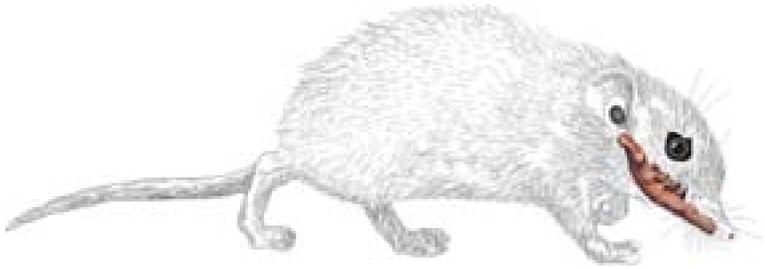
Among such anachronisms—or relicts—are the labyrinthodont amphibians, ancestors of modern amphibians





ACUTE NIGHT VISION is suggested by the eyes and brain of *Leaellynasaura amicagraphica,* a hypsilophodontid shown here at life size (*top*). The large eyes were common to all hypsilophodontids and may have helped the group dominate an environment marked by seasonal darkness. This hypothesis may also explain the huge optic lobes, of which the left one can be seen at the rear of this natural brain cast (*bottom, enlarged*), formed when silt solidified in the skull.

PATRICIA J. WYNNE (*top*); STEVE MORTON *Monash University* (*bottom*)



WHEN ALIVE during the Cretaceous, *Ausktribosphenos* from southeastern Australia may have resembled this modern-day spineless hedgehog from China. The jaw, superimposed on a sketch of the hedgehog, shows what is known of the fossil.

and reptiles. Most paleontologists had thought this group went extinct by the Jurassic, some 160 million years ago. In the past 25 years, however, Michael Cleeland and Lesley Kool of Monash University found three jaws from this group in Victorian sediments dating from the Early Cretaceous. Two of the jaws were unmistakable, because their teeth had the labyrinthine infolding of the enamel that gives this group its name. At least one large species of labyrinthodonts lived in polar Australia 115 million years ago, several million years after the group had died out elsewhere.

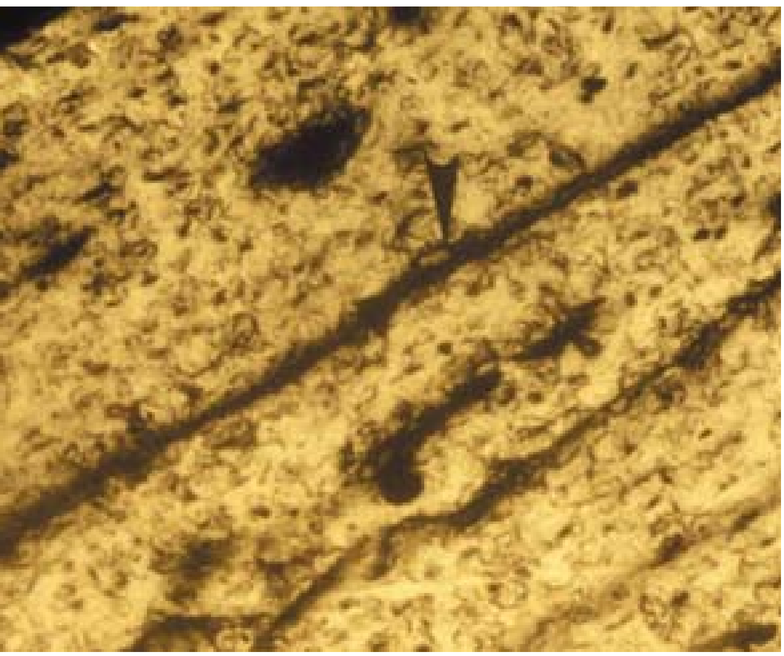
How did they survive? We suspect that the cool weather preserved the animals from competition with crocodiles, which were probably poorly adapted to the conditions prevailing in southeastern Australia until the onset of climatic warming during the last five million years of the Early Cretaceous. The hypothesis rests on the fact that contemporary crocodilians now live in waters no colder than 10 degrees C, whereas some modern frogs and salamanders can be active in meltwater from snow.

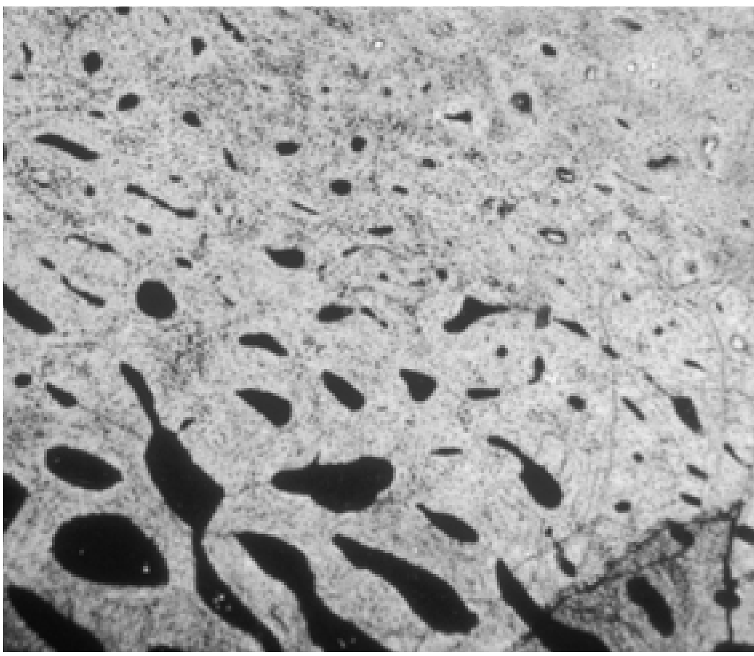
Another late survivor was a close relative of the familiar *Allosaurus,* a carnivorous theropod. Elsewhere in the world this animal ranged up to five meters in height, but the southeastern Australian specimen stood no more than two meters high—hardly taller than a human. This "pygmy," presumably a juvenile, is the latest-surviving allosaur that has yet been found. It remains unclear whether this species also owed its longevity to some niche that cold climate may have carved out for it. The discovery of juvenile forms (but no eggshells so far) does suggest that these dinosaurs were not just casual visitors but lived near the pole for much of the year, using the area as a nursery during the period of maximum sunlight.

Unlike the allosaurs, many dinosaurs of Australia were not the last in their lineage; some may have been the first. At least two and perhaps as many as four families of dinosaurs have been recognized that include forms which are either the oldest or among the oldest of their kind. For instance, the ornithomimosaurs, carnivores of ostrichlike size and appearance, are manifestly primitive and among the oldest within this group. The elongated, slender hind limbs of the Australian species made them the gazelles of the dinosaur world, able to escape from predators and to run down prey. The ornithomimosaurs probably originated in Gondwana and spread northward to join the later Cretaceous faunas of North America and Eurasia, where they enjoyed wide success.

Two very small theropods remain unidentified, but one seems to resemble

DRAGA GELT *Monash University* (*top*); ANUSUYA CHINSAMY *South African Museum, Cape Town* (*bottom*)





TRANSVERSE SECTION of the femora from the ornithomimosaur *Timimus hermani* (*left*) shows prominent lines of arrested growth (*arrow*), indicating severe slowing of metabolism during prolonged winter night. But in a similar section from the hypsilophodontid *L. amicagraphica* (*right*) from Dinosaur Cove, such lines are absent, meaning the polar creature remained active during the dark season.

an egg-eating oviraptosaur, known until now exclusively from the younger Cretaceous rocks of North America and Asia. These groups may also have an origin in Gondwana.

Yet another dinosaur group that has recently been identified belongs to the neoceratopsians, or horned dinosaurs. Identification is tentative, because it is based on just two ulnae (part of the lower arm), but the similarity to *Leptoceratops,* a browser the size of a sheep, is uncanny. Previously, all neoceratopsian records dated from the Late Cretaceous and, with the exception of a few bones from Argentina, came from the Northern Hemisphere. Recent reports indicate the existence of Early Cretaceous neoceratopsians in Utah and China. This dinosaur family may also have arisen in the southern supercontinent.

In addition to dinosaurs, the region provides evidence for mammals that appear to be among the earliest members of their groups. The minuscule *Ausktribosphenos* resembles the living spineless hedgehog *Neotetracus*. This animal may have been a placental. If so, it is as old as the oldest placentals reported from the Northern Hemisphere and twice the age of the oldest marsupial yet found in Australia. This age is surprising because the domination of Australia by marsupials is typically explained as the result of land-dwelling placentals reaching the continent long after the marsupials.

Another mammalian group, whose presence is no surprise, is the monotremes. An isolated limb bone of one of them has a structure suggestive of a more upright stance than either the echidna or the platypus. A second species is by far the smallest monotreme, weighing only 1 percent as much as any other living or fossil member of the group.

The Australian Early Cretaceous also reshaped forms that continued to flourish in other regions. By far the most successful such group consisted of the hypsilophodontid dinosaurs. These animals, most of them hardly larger than a chicken, were bipeds built for speed, with large hind legs, small but well-developed hands, substantial tails and—for the most part—herbivorous habits. They thus resembled wallabies in both shape and ecological role.

The family Hypsilophodontidae was common throughout the world from the Middle Jurassic to Late Cretaceous times, but its prominence reaches an absolute and relative peak in the Victorian sediments. Not only do hypsilophodontids constitute most of the dinosaur remains, they are also represented by four to five genera, depending on the taxonomic criteria one uses, and five to six species. Other areas, some much more richly endowed with dinosaur species, never harbored more than three kinds of hypsilophodontids at a time. Something clearly favored the diversification of this group in polar Australia.

Big-Eyed Foragers

A PARTICULARLY intriguing adaptation of at least one species of polar hypsilophodontid is suggested by the magnificently preserved brain cast of *Leaellynasaura amicagraphica* (named after our daughter, along with friends of the Museum of Victoria and the National Geographic Society). The brain, unusually large for a dinosaur of this size, bears the marks of optic lobes the relative size of which is easily the greatest ever documented in a hypsilophodontid.

How is one to interpret these enlarged lobes? We hypothesize that they enhanced the animals' ability to see in the dark, enabling them to forage effectively during the long winter months. There would have been no lack of food then, for those capable of seeing it: the herbivores could have lived off evergreens and deciduous leaf mats, and the carnivores could have hunted the herbivores.

This hypothesis also explains why this group came to dominate the polar environment in the first place. Hypsilophodontids everywhere in the world had large eyes and, presumably, acute vision. That trait could have given them their foothold in polar Australia. Once established in this "protected" environment, the hypsilophodontids could have competed with one another to produce the observed diversity of genera and species, perhaps all sharing hypertrophied optic lobes.

These animals, so SUPERBLY ADAPTED to the cold and dark, could not have been driven to extinction BY AN ARTIFICIAL WINTER.

If the animals foraged at night, they must have been active at freezing or subfreezing temperatures. This feat goes far beyond the cold tolerance of any modern reptile, even the New Zealand tuatara, *Sphenodon punctatus,* which can remain active at five degrees C provided it can sun itself. *Leaellynasaura* could have survived solely by maintaining a constant body temperature, eating frequently, as birds do in wintertime.

More evidence that the hypsilophodontids remained active during the prolonged winter night is found in the microscopic structure of their bones, deciphered by Anusuya Chinsamy-Turan of the South African Museum. So-called lines of arrested growth form when terrestrial vertebrates markedly slow down or cease their growth. The markings appear as dark lines of dense bone against a background of lighter bone. The lines can be laid during a period of lack of food or water or when an animal estivates or hibernates. The hypsilophodontids from polar southeastern Australia, as well as from elsewhere, all lack such lines, unlike the majority of dinosaurs. So they seem to have maintained relatively uniform metabolic activity year round.

Pterosaurs—the flying reptiles—and the heavily armored ankylosaurs also appear in the Gondwana fossil record, but the remains are so fragmented that they tell us little about the animals' lives. Much can be gleaned from one handful of teeth, however, for they come from plesiosaurs. These long-necked reptiles, not themselves dinosaurs, generally paddled the seas, but here they inhabited fresh water in the ancient valley between Australia and Antarctica. They thus recall the Ganges River dolphin, one of the few cetaceans that live in fresh water.

The sauropods are one of the few major dinosaur groups that are absent. These giants, familiar from the example of *Apatosaurus* (or *Brontosaurus*, as it is more popularly known), lived at that time in Australia's lower latitudes. Not one, however, has been found farther south nor, indeed, in any of the nine Cretaceous polar dinosaur sites so far identified in both hemispheres. The only polar sauropod yet discovered is the much older (Early Jurassic) *Rhoetosaurus* from northeastern Australia.

The apparent restriction of these large dinosaurs to lower latitudes in the Cretaceous of Australia may be real or merely an artifact of sampling. We worry about this question because the floodwaters that broke out of rain-swollen rivers would have collected small and medium-size bones but left large ones. The body of a sauropod would have stayed put rather than floating to a place where many specimens were concentrated in the small flood channels, which were no more than five to 10 meters in width and 20 to 30 centimeters in depth.

Yet we suspect there was an underlying tendency toward small body size in these polar environs. None of the hypsilophodontids, it must be remembered, stood taller than a human, and most were barely knee-high. The dwarf allosaurid matches the smallest we have examined in the North American collections. The

PETER TRUSLER, COURTESY OF *WILDLIFE OF GONDWANA*, © REED BOOKS INTERNATIONAL, 1993

BONE TURNS TO STONE: *Leaellynasaura* as it might have appeared in the process of becoming a fossil. A bone assemblage from an individual could have fossilized in this way only if the stream channel was choked off, forming an oxbow or billabong.

HARD ROCK made hard work for these volunteer paleontologists at Dinosaur Cove in Australia. Full-scale mining techniques (*left*) and rock saws (*right*) are used to extract fossil-bearing slabs, which tend to fracture along the planes containing the largest treasures.

ornithomimosaur is equally unprepossessing, and the protoceratopsid and the ankylosaur are each no bigger than a sheep. A single fragment of a claw constitutes our sole record of a large dinosaur—a carnivore, apparently similar to *Baryonyx* of England—which may have measured up to eight meters in length.

This pattern contradicts the classic scaling laws formulated by Carl Bergmann and Joel Allen in the 19th century. According to these laws, animals in a given lineage tend to become larger and more compact as the average temperature of their environment falls. This trend is exemplified by the comparison of mountain lions in Canada with pumas of Central America and of human populations in the subarctic and tropical zones.

Other factors also determine body dimensions, especially the size of the territory in which a population lives. Individuals found on islands are often smaller than their mainland counterparts. For example, there were dwarf elephants on the ancient Mediterranean islands, and pygmy mammoths were recently found in 4,000-year-old sediments on islands off the north coast of Siberia. Dwarfism may be a response to selective pressure to increase the number of individuals so as to ensure a gene pool diverse enough for the species to survive in a restricted area. This effect has also been observed on peninsulas—and ancient southeast Australia was a peninsula of the Gondwana landmass.

The dinosaurs on that peninsula were trapped virtually at the ends of the earth. Their direct path north was blocked by a vast inland sea, which they could have passed only by going hundreds of kilometers to the west before wheeling about to the north. At the end of such labors, they would have been able to catch, at most, an hour of sun a day in winter. Migration would have made little sense for such small animals.

Less formidable barriers sealed in the dinosaurs of the one other polar site that has yielded large quantities of fossils: the North Slope of Alaska. The dinosaurs there had a clear north-south corridor along which they could migrate with ease. It is significant that those dinosaurs were big—at least equal in size to caribou, wildebeest and other modern animals that migrate.

Safe Haven in Gondwana

ONE MUST QUESTION whether animals so superbly adapted to the cold and the dark could have been driven to extinction by an artificial winter, such as is supposed to have followed a cataclysmic event at the boundary between the Cretaceous and Tertiary formations. It is proposed that the cataclysm, perhaps a collision with a comet or asteroid or a series of volcanic eruptions, suffused the atmosphere with a blanket of dust, excluding sunlight and freezing or starving most animals to death.

We suspect, however, that no such artificial winter could have killed the dinosaurs unless it lasted for a long time, certainly more than a few months. Otherwise at least a few of the polar dinosaurs would have survived the cataclysm. Of course, it is possible that a different development had already ended the reign of southern Australia's dinosaurs by the end of the Cretaceous.

English writer Arthur Conan Doyle once dreamed of a plateau in South America that time forgot, where dinosaurs continued to reign. Reports in the early 1990s that dwarf mammoths survived to early historical times, on islands off the coast of Siberia, give force to such speculation. If dinosaurs found a similar haven in which they outlived the rest of their kind, then we think polar Gondwana, including southeastern Australia, is a likely place to look. SA

MORE TO EXPLORE

The Hypsilophodontidae from Southeastern Australia. Thomas H. Rich and Patricia Vickers-Rich in *Proceedings of the Second Gondwana Dinosaur Symposium.* Edited by Y. Tomada, T. H. Rich and P. Vickers-Rich. National Science Museums Monographs, Tokyo, Vol. 15, pages 167–180; 1999.

Dinosaurs of Darkness. Thomas H. Rich and Patricia Vickers-Rich. Indiana University Press, 2000.

A Century of Australian Dinosaurs. Thomas H. Rich and Patricia Vickers-Rich. Queen Victoria Museum and Art Gallery and the Monash Science Center, 2003.

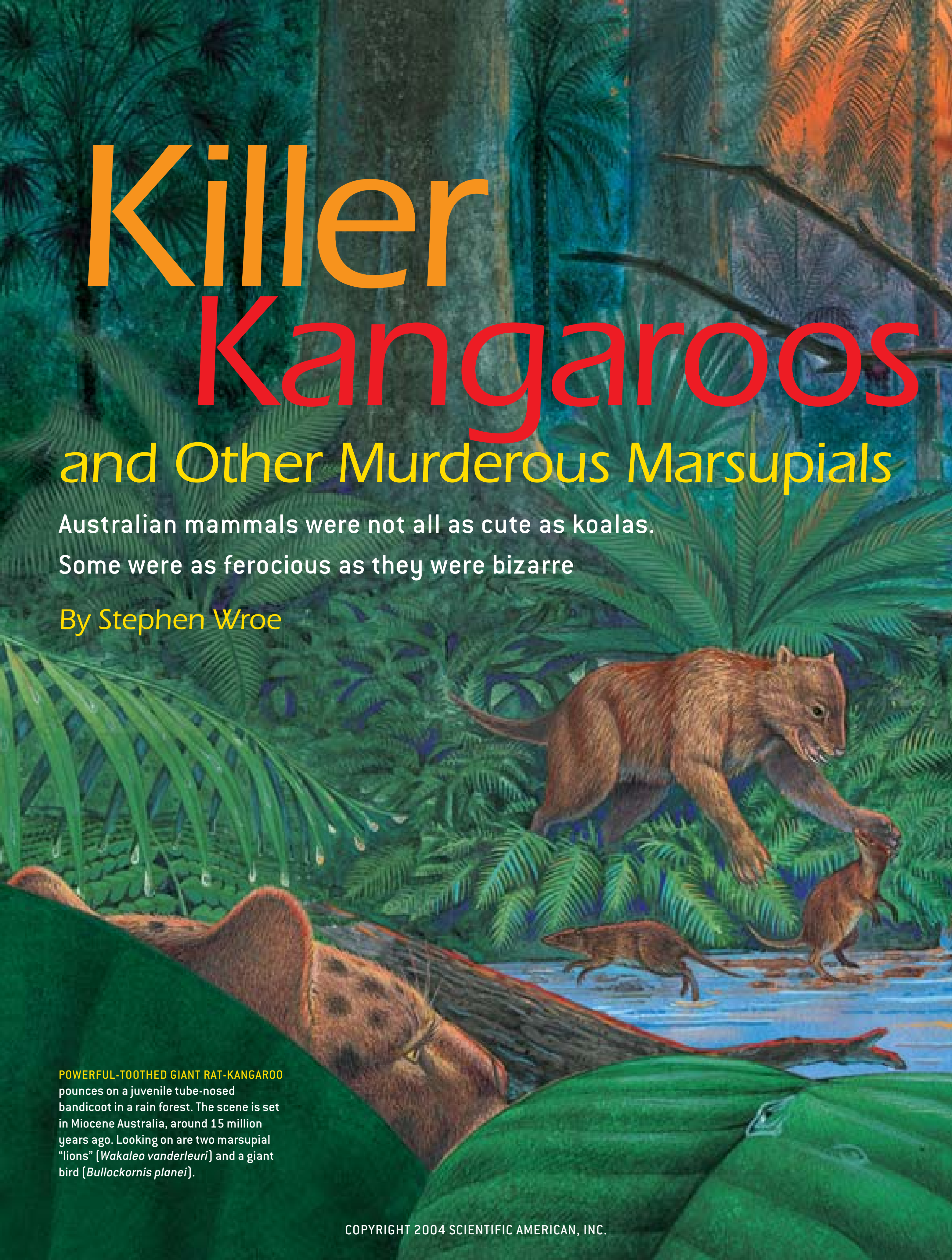
PETER MENZEL, COURTESY OF NATIONAL GEOGRAPHIC SOCIETY (*left*); FRANK COFFA (*right*)

Killer Kangaroos

and Other Murderous Marsupials

Australian mammals were not all as cute as koalas. Some were as ferocious as they were bizarre

By Stephen Wroe



POWERFUL-TOOTHED GIANT RAT-KANGAROO pounces on a juvenile tube-nosed bandicoot in a rain forest. The scene is set in Miocene Australia, around 15 million years ago. Looking on are two marsupial "lions" (*Wakaleo vanderleuri*) and a giant bird (*Bullockornis planei*).

ROBERTO OSTI

DAWN MIST BLANKETS THE RAIN FOREST

in northeastern Australia, 15 million years ago. A bandicoot family emerges to dip snouts warily into a shallow freshwater pool. Their ears swivel, ever alert to a sudden crack or rustle in the undergrowth: drinking is always a dangerous activity. Suddenly, a dark, muscular form explodes from behind a bush, colliding with a young bandicoot in one bound. The shaggy phantom impales its victim on long, daggerlike teeth, carrying the carcass to a quiet nook to be dismembered and eaten at leisure. 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 21st-century Australia, large warm-blooded predators are few and far between. Among the natives, the biggest 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 nearly twice this size 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 warm-blooded carnivores. Most recently, Tim F. Flannery of the South Australian Museum in Adelaide 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 giant 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.

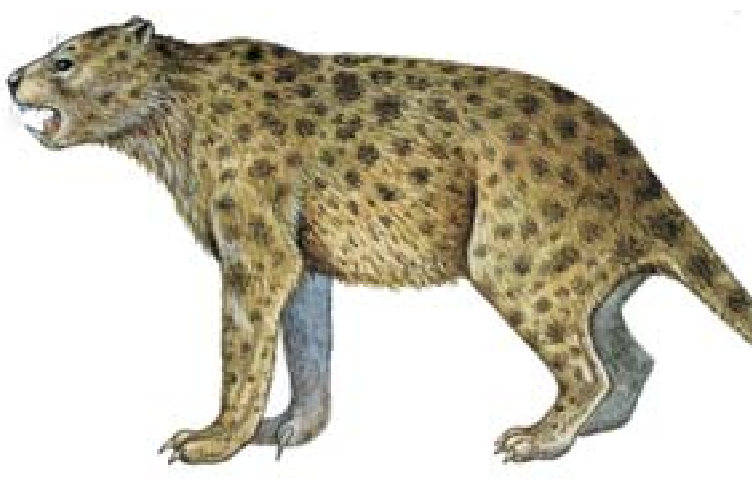
This claim is challenged by recent finds at various Australian sites, notably in Riversleigh, Queensland. A European naturalist, W. E. Cameron, first noted the presence of fossils at this remote site in 1900. But Cameron believed that the material he had seen was fairly young, less than two million years old. Moreover, Riversleigh's extreme inaccessibility—summer heat and monsoon rains allow excavations only in winter—caused paleontologists to neglect the locality for decades. In 1963, however, Richard H. 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 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 the previous century. 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.

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, 15 new spe-

PREDATOR'S GALLERY

FORMIDABLE FLESH-EATERS from ancient Australia included a marsupial lion, a marsupial wolf, a giant rat-kangaroo and an enormous lizard. 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.*



ILLUSTRATIONS BY ROBERTO OSTI AND ANNE MUSSER

LARGEST MARSUPIAL LION
(*Thylacoleo carnifex*)
Average weight: 100 kilograms

cies, including nine from Riversleigh, have more than doubled the tally of large Australian fossil carnivores. This bestiary now includes six kinds of giant rat-kangaroo, 12 species of marsupial "wolf," eight species of marsupial "lion" and three native cats.

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 formidable, 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.

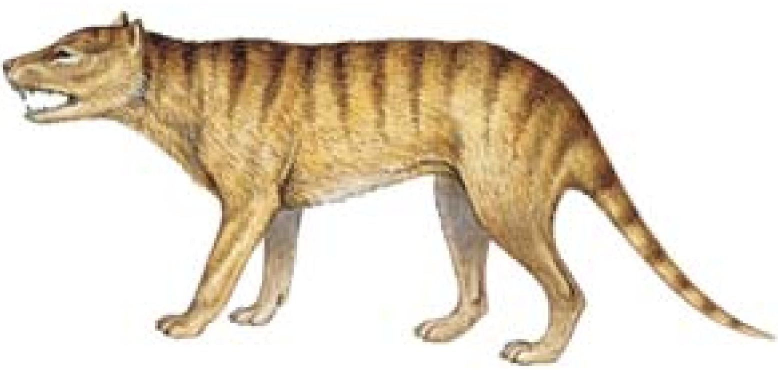
The marsupial wolves (thylacinids) and marsupial lions (thylacoleonids) are so named because of their passing physical resemblances to canids and felids, although they were more closely related to kangaroos. The last of the marsupial wolves, perhaps confusingly called the Tasmanian Tiger because of the stripes on its rump, was exterminated early in the 20th century because of a largely undeserved reputation for preying on sheep. Like cats, the marsupial lions had short, broad, powerful skulls, and they probably filled similar ecological niches as well; their size ranged from that of a house cat to that of a female lion. Although no fossils contain actual traces of a pouch, specialized features of the skeleton shared with living animals leave no doubt that all these creatures were marsupials.

Fearsome Forest

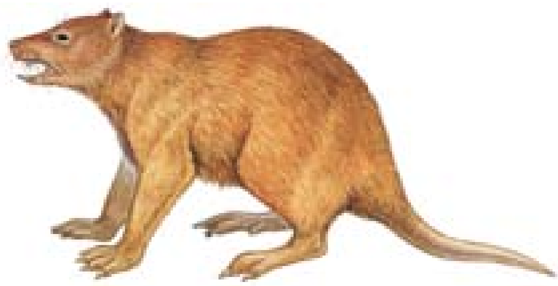
FOR MUCH of the Miocene epoch (25 million to five million years ago), Australia was carpeted in wall-to-wall green, and rain forest covered many areas that are now savanna or desert. These jungles were an evolutionary powerhouse, nurturing a far greater diversity of life than any modern Australian habitat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

One would have been the Powerful-Toothed Giant Rat-kangaroo, among the most ancient of its kind. *Ekaltadeta ima* was also the smallest, weighing only about 15 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.

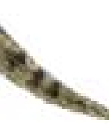
Because these "killer kangaroos" descended from plant-eating marsupials, some controversy surrounds the interpretation of their biology. Nevertheless, all recent authors agree that these distinctly uncuddly kangaroos included meat in their diets. Ev-

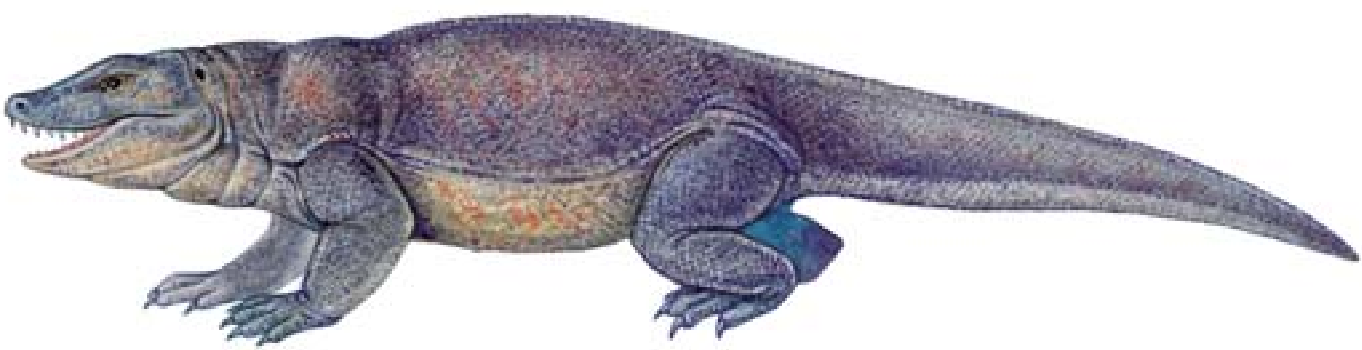


LARGEST MARSUPIAL WOLF
(*Thylacinus potens*)
45 kilograms



POWERFUL-TOOTHED GIANT RAT-KANGAROO
(*Ekaltadeta ima*)
15 kilograms





GIANT MONITOR LIZARD
(*Megalania prisca*)
160 kilograms

idence supporting this hypothesis comes from both their skulls and their teeth.

In the 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 many 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 indicates how much flesh it devoured. In this respect, the giant rat-kangaroos resembled opportunistic feeders such as foxes and retained significant capacity to process plants and invertebrates. Nevertheless, 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 rat-kangaroos were generalists, taking flesh when available but 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, pouched "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.

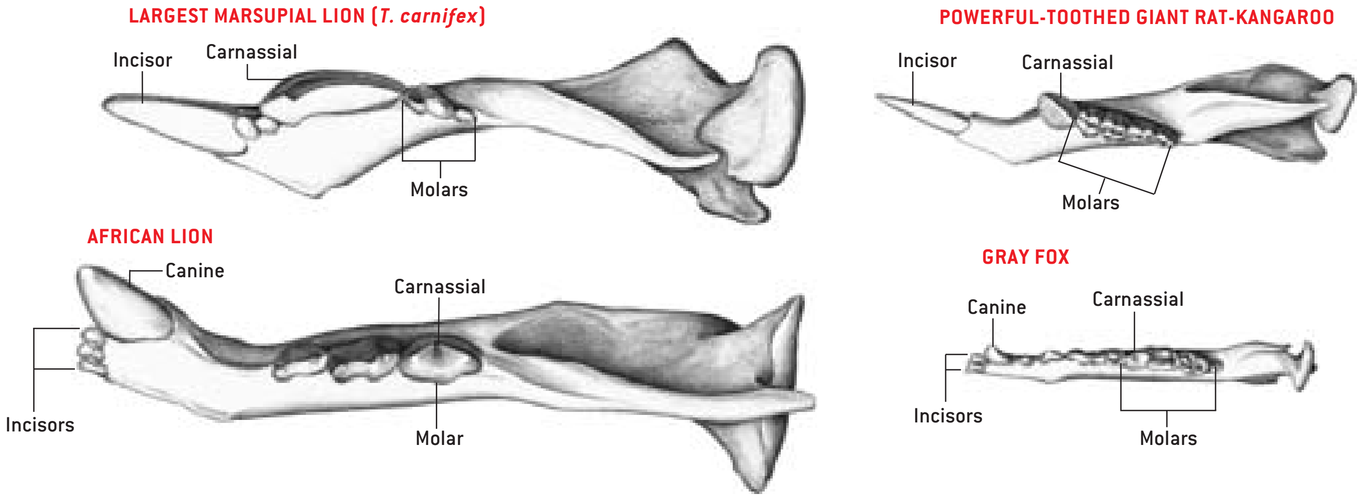
Eight species of marsupial lions have been described, and two more are being studied at the University of New South Wales in Sydney by Anna Gillespie. The interpretation of marsupial lion biology has been contentious. As diprotodont marsupials, their closest living relatives are either koalas, wombats or opossums. 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.

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

The Pleistocene marsupial lion is the only member of its family known from a complete skeleton. Historically, *T. carnifex* was compared in size to a wolf or leopard. But such esti-

LAST REMNANTS of a once extensive menagerie of Australian predators, such as the Tasmanian Devil (*left*), do not lack in ferocity. The Spotted-Tailed Quoll (*right*) is a native "cat," whereas the Musky Rat-kangaroo (*below*) is the end of a line reaching back to the carnivorous giant rat-kangaroos.

NORMAN O. TOMALIN *Bruce Coleman Inc.* (*left*); JOHN CANCALOSI *Peter Arnold, Inc.* (*center*); ERWIN AND PEGGY BAUER *Bruce Coleman Inc.* (*right*)



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.

mates have not accounted for the extreme robustness of the skeleton. At more than 100 kilograms, this frightening beast was comparable to a modern lioness. It was built for power, not endurance, and had tremendously muscular forelimbs. With massive jaws, 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. Preliminary analyses that I have conducted with Colin McHenry of the University of Newcastle in Australia suggest that it could exert a bite force more than two and a half times that of the spotted hyena. Once caught in the jaws of a marsupial lion, few animals could have survived.

Pouched Pouncers

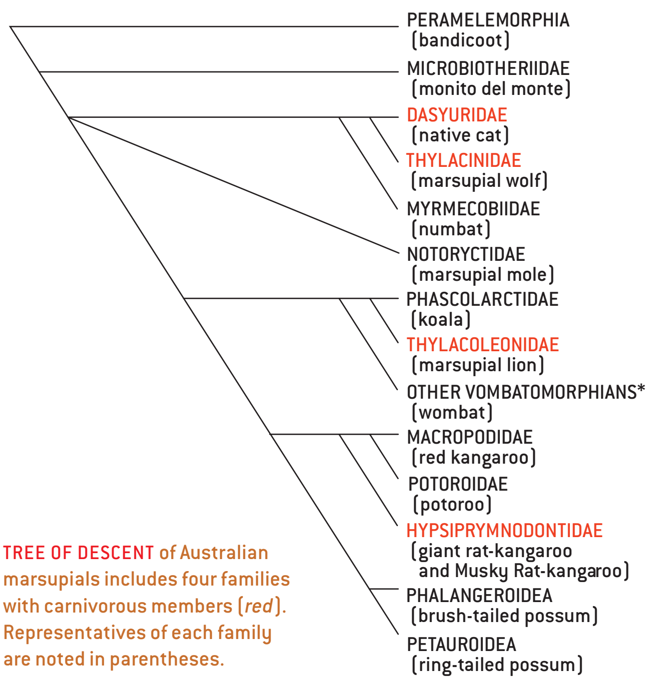
UNDOUBTEDLY, *T. carnifex* was adapted to take large prey. The kinds of marsupial lion known as *Wakaleo* were smaller, about the size of a leopard. Not designed for speed but immensely powerful, species of *Wakaleo* (and possibly *Thylacoleo*) may have used trees to stash kills. Their prey was most likely terrestrial, however, and taken by stealth that culminated in an explosive pounce. At the other end of the scale, at around the size of a domestic cat, *Priscileo roskellyae* may have concentrated on 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.

Next to marsupial lions, the marsupial "wolves" were the most voracious of Australia's now extinct predators. When Europeans arrived in Australia more than 200 years ago, they found just 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 more than 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, 10 new species of

THE AUTHOR

STEPHEN WROE is a biologist at the University of Sydney and received his Ph.D. in paleontology from the University of New South Wales. He has published widely on the evolution and biology of marsupial carnivores, both fossil and living, as well as megafaunal extinction. Illustrations for this article are based on reconstructions by Anne Musser of the Australian Museum.



TREE OF DESCENT of Australian marsupials includes four families with carnivorous members (*red*). Representatives of each family are noted in parentheses.

**Vombatomorphians include koalas and marsupial lions.*

ANNE MUSSER (*illustrations*)

Miocene-age wolves have been found, bringing the total for the family to 13 (including the Tasmanian Tiger). On the other hand, just one definite dasyurid has been described from Miocene deposits. Clearly, the proportion of marsupial wolf to dasyurid species 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 one thing is fairly certain: the Tasmanian Tiger was similar to most canids in that it was terrestrial, long-snouted and probably tended to take prey smaller than itself. It differed from placental wolves in being relatively poorly adapted for running and probably was not a pack hunter. Moreover, the morphology of its cheek teeth suggests that unlike most canids it was hypercarnivorous—almost completely dependent on vertebrate flesh. Indeed, a tendency toward hypercarnivory is common to most large marsupial carnivores but not the majority of placental carnivores. This distinction should be kept in mind when comparing the two groups.

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.

Myth of Reptilian Domination

WHILE EVIDENCE for an unexpected diversity of once large marsupial carnivores in Australia grows, it is also becoming apparent that the presumed diversity of former big terrestrial reptiles has been exaggerated. For example, estimates of maximum body mass in the giant lizard, *Megalania prisca,* were extrapolated from a single toe bone. This case was always flimsy, a fact that has been further highlighted by a recent revelation from Ralph Molnar of the Queensland Museum (now retired) that this bone probably did not belong to *M. prisca*. More important, average sizes, not maxima, are the critical numbers in assessing ecological significance. My estimate for mean body mass in *M. prisca* is less than 160 kilograms—still a very big lizard but far short of the 1,000 kilograms commonly cited. Add the perspective that *M. prisca* was much better adapted to a scavenging role than marsupial lions, ate around 90 percent less per unit body weight and was less widely distributed, and the argument for reptilian domination in Australia looks weak.

Marsupial lions had MASSIVE JAWS and a switchbladelike claw on each semiopposable thumb.

Similar problems undermine the credibility of the two other reptiles offered as contenders in the big terrestrial carnivore stakes: the giant snake *Wonambi naracoortensis* and the "terrestrial" crocodile *Quinkana fortirostrum*. It remains uncertain that either was actually terrestrial, and if large nonterrestrial reptiles are brought into the equation, then Australia is no standout. In modern South America, for instance, eight species of crocodile and a giant semiaquatic snake commonly take terrestrial prey.

It is true that *Thylacoleo carnifex* was smaller than the biggest of contemporaneous mammalian carnivores elsewhere in the world. And at least in the Pleistocene, there were fewer species of large warm-blooded predators in Australia than in arbitrarily defined regions of similar size in North America or Africa. But attempts to explain this situation as a product of low productivity overlook a more obvious difference: Australia is an island. Fundamental principles of biogeography invalidate comparisons that do not account for the isolation of the island continent. Consider South America, which until three million years ago was also isolated and dominated by marsupial carnivores. In the two million years preceding species interchange with North America, no more than three large, truly carnivorous mammals are known to have existed in South America. The biggest was the 60-kilogram marsupial sabertooth, *Thylacosmilus atrox*. But after formation of the Panama land bridge, circumstances changed dramatically. There have been at least 12 large hypercarnivorous mammals in South America in just the past 65,000 years, some more than five times as heavy as *T. atrox,* and all have descended from North American immigrants. It is difficult to escape the conclusion that isolation and immigration were the key factors behind this turnaround.

Previous projections of Australia as the island where low productivity produced a biotically stunted mammalian carnivore fauna were wrong. Fossil diversity has been underestimated, and the effects of isolation have not been properly considered.

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; the lower jaw is 122 millimeters.

STEPHEN WROE

A KILLER BIRD?

IN NOVEMBER 1998 Peter Murray of the Museum of Central Australia and Dirk Megirian of the Museum and Art Gallery of the Northern Territory described new fossil material from an extinct, terrestrial bird called *Bullockornis planei.* This species belongs to the Australian family Dromornithidae, known since 1839. Dromornithids could be huge, some weighing perhaps 500 kilograms. 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 nearly 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 the Ohio University 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 suggested that at least some dromornithids might similarly have eaten vertebrates. Although it is highly unlikely that these birds ran down big prey, their exceptionally well developed sense of smell (derived from olfactory lobes and seen only in turkey vultures today) suggests that carrion was a regular feature of their diet. If so, *B. planei* was the largest carnivore on two legs since the demise of the meat-eating dinosaurs. —*S.W.*

B. planei

Death to Killers

HAVING ESTABLISHED that Australia's large marsupial carnivores were far more diverse during the Miocene period, paleontologists are now faced with this question: What happened to them? Because the last of the marsupial lions and giant rat-kangaroos probably died out after Aborigines colonized Australia earlier than 42,000 years ago, some researchers have maintained that it was the first humans who sounded their death knell. Human culpability remains contentious, but the fossil record makes one fact clear: marsupial carnivore diversity peaked by the Middle Miocene and was already in steep decline long before humans arrived. For example, at least six marsupial wolves lived during the Middle Miocene, and three coexisted in the Late Miocene, but only one was ever known to humans.

Obviously, some factor other than human influence was at work, most likely climate. From Middle 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 successive ice ages exposing the Australian fauna to great stress. The last of these may have been the most severe.

Some researchers believe that pressure imposed by human arrivals extinguished most of the continent's larger herbivores. But for many reasons, Judith Field and other investigators at the University of Sydney and I have recently concluded that the last round of megafaunal extinction in Australia was unlikely to have been driven by a hunting blitzkrieg. Most obvious is a complete lack of both megafaunal kill sites and the technologies typically associated with systematic big-game hunting, such as stone-tipped spear points and spear-throwers. An ever strengthening case for megafauna in younger sites such as Cuddie Springs, at ages of 28,000 years or less, suggests a human-megafaunal overlap of at least 14,000 years. If humans did play a role in the extinction of Australia's last surviving mega-herbivores, the process was certainly complex and protracted and occurred against a backdrop of climatic disintegration.

With their favorite meat dishes on the decline, Australia's big marsupial predators were running out of time. It is now a sad fact that of the dozens of wondrous large marsupial carnivores that have existed, not just in Australia but in the Americas as well, only the Down Under continent's Spotted-Tailed Quoll and Tasmanian Devil remain. Nonindigenous Australians must accept full responsibility for the final, 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.

Three years ago the red fox was introduced to Tasmania in an act of senseless environmental vandalism. As if that is not bad enough, a mysterious disease is devastating devil populations. Now more than ever, these last survivors of a once proud heritage, as well as the precious natural communities they live in, desperately need our help. SA

MORE TO EXPLORE

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Stephen Wroe's Web site: **www.bio.usyd.edu.au/staff/swroe/swroe.htm**

ROBERTO OSTI AND ANNE MUSSER

FRED CONRAD

Fossils of the FLAMING CLIFFS

By Michael J. Novacek, Mark Norell, Malcolm C. McKenna and James Clark

The Gobi Desert of Central Asia is one of the earth's desolate places. Its million square kilometers of sand dunes, sculpted badlands and saw-toothed mountains are alternately scorched by summer's high-latitude sun and frozen by winter's Siberian winds. It is not a place to explore unprepared: crossing vast, uninhabited areas between a sprinkling of oases requires careful planning akin to the siege tactics for scaling a Himalayan peak or traversing the Antarctic continent. There are few maps, and satellite navigation is of limited help to a traveler trying to choose among deeply rutted, wildly crisscrossing roads that wander as unpredictably as the nomadic settlements they connect. Even a modern expedition runs the risk of water, fuel and food shortages. Getting lost is not merely frustrating but a matter of serious danger.

Yet the Gobi is a paradise for paleontologists. Its eroding terrain exposes nearly complete skeletons of creatures hitherto known only through painstaking reconstructions from a few scattered bones. Our expeditions, jointly sponsored by the Mongolian Academy of Sciences and the American Museum of Natural History, have excavated dinosaurs, lizards and small mammals in an unprecedented state of preservation. Freshly exposed skeletons sometimes look more like the recent remains of a carcass than like an 80-million-year-old fossil. The skeletons and skulls we have found are often complete or nearly complete, in sharp contrast to the fragments typically recovered elsewhere.

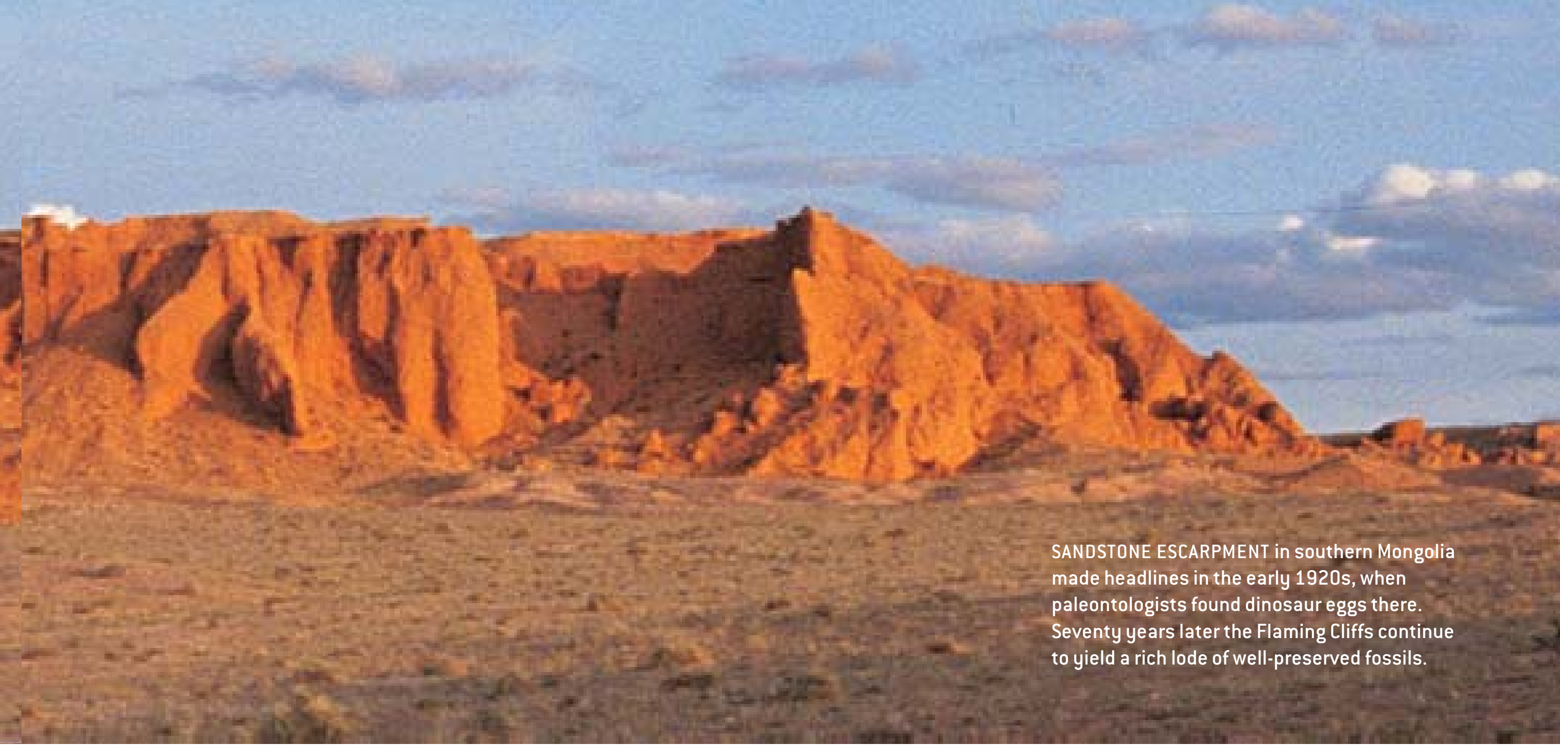
No one knows why fossils in the Gobi are so well preserved. In other specimen-rich areas, such as the one that became the Rocky Mountains, streams or rivers carried animal remains to fossil sites, disarranging them along the way. The Late Cretaceous environment in the Gobi, however, may have been much as it is today: open valleys of sand dunes and cliffs, sparsely watered by small, seasonal lakes or streams. Indeed, indications of ancient sand dunes can be observed in rock sections there.

It is also apparent that the animals were buried very soon after their death, before scavengers or weather had much time to get at them. Poorly sorted layers of sandstone in the Cretaceous rock formations suggest deposits of the kind one would expect in violent sandstorms. In the early 1990s Tomasz Jerzykiewicz of the Geological Survey of Canada in Calgary and his colleagues studied fossil beds in Chinese Inner Mongolia and found that vertebrate fossils are often embedded in these layers. Such storms might not have merely buried carcasses but killed animals as well. Entombed in a matter of minutes or hours, their remains emerge some 80 million years later, almost undisturbed.

Stumbling Upon Protoceratops

MONGOLIA WAS NOT ALWAYS recognized for its bounty of prehistoric material. During the late 19th and early 20th centuries, the Rocky Mountain region of western North America was the mecca for vertebrate paleontologists. Then, in 1922, Roy Chapman Andrews, a scientist from the American Museum of Natural History, led an expedition into the heart of the Gobi and changed the geography of the fossil world. Andrews chronicled his five expeditions in a remarkable narrative entitled *The New Conquest of Central Asia.* The romance and excitement of the enterprise foreshadowed the exploits of the movie character Indiana Jones. En route, the explorers were challenged by track-

 Updated from the December 1994 issue



SANDSTONE ESCARPMENT in southern Mongolia made headlines in the early 1920s, when paleontologists found dinosaur eggs there. Seventy years later the Flaming Cliffs continue to yield a rich lode of well-preserved fossils.

Mongolia's Gobi Desert contains one of the richest assemblages of dinosaur remains ever found. Paleontologists are uncovering much of the region's history

less dune fields, raging sandstorms and marauding bandits. Andrews's caravan of camels and spindly-wheeled Dodge motorcars was a logistic nightmare across the moonscape of the Gobi.

One of the most important discoveries in the history of scientific exploration came in the midst of such difficulties. Late in the first field season of 1922, the expedition got off track. Team photographer J. B. Shackleford wandered toward an unassuming rock rim at the edge of a field. There he was startled to find a fantasy of red cliffs and spires—and fossils.

Within 10 minutes he had uncovered the first known skull of the *Protoceratops,* a parrot-beaked, shield-headed dinosaur that has since become a reference fossil of the Late Cretaceous of Central Asia. The crew recovered more bones and even a small egg, which they mistook for that of a bird. They returned the next summer to find an extravagance of dinosaurs, ancient mammals and other vertebrates, as well as the first known cluster of dinosaur eggs. Their findings, particularly the eggs, became front-page news. Andrews named the place the Flaming Cliffs, inspired by their magnificent red-orange glow in the late afternoon sun.

By the beginning of the 1930s Andrews, frustrated by a volatile political scene in Mongolia, gave up his exploration. The Gobi was inaccessible to Western interests for more than 60 years, leaving Soviet-bloc scientists to extend the work Andrews had begun. Between 1946 and 1949, joint Russian-Mongolian expeditions penetrated the Nemegt basin and uncovered rich badlands of Cretaceous and Cenozoic fossils there.

Zofia Kielan-Jaworowska, a world-renowned fossil-mammal specialist at the Institute of Paleontology in Warsaw, led a highly skilled and energetic Polish-Mongolian team to the Nemegt and other areas between 1963 and 1971. She and her colleagues produced a series of classic monographs and a magnificent display of dinosaurs and other fossil vertebrates at the Natural History Museum in the Mongolian capital of Ulaanbaatar. Since the 1960s Mongolian paleontologists have conducted extensive fieldwork both independently and in collaboration with Soviet (now Russian) scientists.

Westerners first returned after the development of Mongolian democracy in 1990. That summer our colleagues at the Mongolian Academy of Sciences invited us for a reconnaissance that paved the way for more ambitious expeditions during succeeding years. Japanese, German and other American parties have since conducted field projects. Soon Mongolia may be trampled by a stampede of bone hunters, but meanwhile we feel fortunate to be the first Westerners to resume the adventure that Andrews inaugurated.

Rockies of the Desert

IF ANYTHING, the contrast between the Gobi and other, more accessible fossil areas has increased since Andrews's time. A century ago, in the glory days of dinosaur hunting in the American West, prospectors encountered valleys and canyons where skeletons were exposed like corpses on a deserted battlefield, but today many prime dinosaur hunting grounds appear nearly exhausted.

The cumulative activities in Mongolia over the past 70 years, in comparison, do not approach those in the Americas. Erosion is still exposing a wealth of fossils even at sites well mined by

OVIRAPTORID, a large predatory dinosaur, stands near its nest by the bodies of two young troodontids (another fleet-footed predator). At the Gobi Desert's Ukhaa Tolgod site, the authors found an oviraptorid nest that contained two skulls of infant dinosaurs of the same family as *Troodon;* the interlopers might have been raiding the nest, they might have been brought by a parent oviraptorid to feed its young, or they might even have been laid in the nest surreptitiously (as the cuckoo does today) and incubated there.

ALFRED T. KAMAJIAN

Andrews and others. Moreover, the very difficulty and unexplored nature of the Gobi increases the chance that paleontologists may yet stumble onto wholly unexplored pockets of badlands.

Early in the 1993 season, with our Mongolian colleague, Demberelyin Dashzeveg of the Mongolian Academy of Sciences, our field party struck out for an undistinguished set of red-brown sandstones on the north side of the Nemegt Valley, near the base of a jagged mountain range called Gilbent Uul. Previous expeditions, Dashzeveg said, had ignored this region in their rush to reach the more dramatic badlands of the western Nemegt Valley. We arrived at the area, struggled for a few kilometers along a wash, and established a bivouac where our heavy gasoline tanker and trailer buried itself in the sand.

The next morning we started prospecting the hills and gullies nearest camp. Within hours it was clear that we had come across one of the richest concentrations of fossils ever recovered from the age of the dinosaurs. In a basin less than two kilometers across, we found scores of dinosaur skeletons and egg nest sites weathering on gentle slopes. Intermixed with the dinosaur fossils were abundant smaller vertebrates—lizards and mammals—that were also key members of the ancient Cretaceous ecosystem.

The local name for the site of this bonanza is Ukhaa Tolgod ("Brown Hills"). Its natural amphitheater contained roughly 100 readily visible dinosaur skeletons, many of them in nearly pristine condition. During subsequent field seasons we selected the most desirable specimens. Among them are 25 skeletons of theropod dinosaurs. This group of agile carnivores runs the gamut from the enormous *Tyrannosaurus* and *Allosaurus* through fast-running dromaeosaurs such as *Velociraptor* (the villainous predator of *Jurassic Park,* a title some 60 million years out of date) to smaller birdlike creatures such as the oviraptorids. We also gathered an unprecedentedly rich collection of small vertebrates: more than 200 skulls of mammals—many with their associated skeletons—and an even greater number of lizard skulls and skeletons.

Cretaceous Treasure Trove

AS THE VARIETY of our specimens makes clear, the flowering of terrestrial life during the Cretaceous of Central Asia was not limited to dinosaurs. The Gobi of 80 million years ago supported a wide variety of lizards, crocodilians and mammals. We have found specimens representing more than 30 species of lizards; some are extremely well preserved and display anatomical features that offer clues to the relations among major lizard families.

Probably the most spectacular of these is *Estesia*. Early one morning during a reconnaissance, we came across an exquisite, 20-centimeter-long skull with knife-edged teeth half embedded, like a bas-relief, in a vertical slab of sandstone. At the time we thought it belonged to a small carnivorous dinosaur, but later examination determined that the skull was that of a wholly new kind of large predatory lizard, closely resembling the Komodo dragon of today. We named the species after the late Richard Estes of San Diego State University, the world's foremost authority on fossil lizards.

Estesia is a very primitive animal and as such is significant for understanding the family tree of the varanoid lizards (the group that includes the Komodo). The skull has an unusual series of canals at the base of the teeth that suggests *Estesia* injected poison into its prey. This lethal weapon is not common to living varanoids but is found in the Gila monster of the southwestern U.S. and northern Mexico.

We have since uncovered fragments of *Estesia* in other sites where smaller lizards, tiny mammals and dinosaur eggshells are common. Modern varanoids are noted for their voracious and wide-ranging appetites. It is likely that *Estesia* ate smaller vertebrates, small dinosaurs and possibly dinosaur eggs.

Although much of the Cretaceous Gobi was dry, water must have been abundant in at least a few places and times. We found occasional fossils of turtles, usually associated with aquatic habitats. At one site, in chromatic badlands west of the Nemegt Valley, a small depression roughly the size of a wading pool held shells and skeletal parts of more than 50 individuals representing two turtle genera.

Some of the greatest treasures of the Cretaceous Gobi are easy to miss when scanning the slopes and gullies: the tiny skulls and skeletons of mammals. These fossils represent important precursors of the great mammalian radiation that followed the extinction of the dinosaurs at the end of the Mesozoic.

The bulk of scientific information on

these earlier mammals comes from North American fossils, which are mostly fragmentary jaws and teeth. In fact, there are virtually no complete skulls of these Cretaceous mammals from North America. As a result, the Gobi assemblage, including our finds and those of earlier expeditions, surely represents the world's reference collection for Late Cretaceous mammals.

A small block recovered from Ukhaa Tolgod revealed six shrewlike placental mammals, each only a few centimeters long. Amazingly, the fossils consist of complete skulls attached to skeletons; such tiny bones are usually highly vulnerable to disarticulation and breakage. These small creatures were probably buried rapidly after they had died.

We have found two basic groups of mammals. The first is the multituberculates, or "multis," as paleontologists call them. They are a curious array of animals with long front incisors and molars with a complex of bumps (tubercles) on the tooth crowns. The Mongolian Cretaceous multis offer by far the best accumulation of skeletal material for examining the relations of these creatures with other mammal lineages.

Multis can be thought of as the rodents of their time, even though they are in fact only distantly related to modern groups of mammals. Their rodentlike adaptations are a sign of convergent evolution with the rats, mice and squirrels familiar today. The multis thrived through the first several million years of the Tertiary period, after the dinosaurs had died out. They then dwindled in number and disappeared, replaced by more recent groups of similar habits.

The second group is the therians, ancestors of both marsupials and modern placental mammals (a category ranging from whales to bats, aardvarks and humans). These early therians consist of half a dozen shrewlike forms whose traits offer clues to the origins of later members of the group. Fossils from the genus *Deltatheridium,* for example, seem to straddle the line between marsupials and placentals.

Other species point to a more primitive age of placental mammals. Modern species have at most four premolar teeth on each side of the jaw, but certain Mongolian specimens of placental mammals, such as juvenile individuals of the genus *Kennalestes,* have at least five. Another group, *Zalambdalestes,* is interesting because it has rabbitlike or rodentlike incisors and a skeleton adapted for running and hopping, also like that of living rabbits. Paleontologists are divided on whether *Zalambdalestes* might be an early rabbit ancestor or simply an example of convergent evolution.

One of the most spectacular prizes of our expeditions is a beautifully preserved skull of *Zalambdalestes.* In collaboration with Timothy Rowe of the University of Texas at Austin, we examined it using a very high resolution computed tomography scanner. The three-dimensional x-ray images allowed us to reconstruct the paths of arteries, veins and even nerves. The CT images confirm an earlier hypothesis by Kielan-Jaworowska: the carotid arteries, the main channels supplying blood to the brain and the eye, enter the skull along the midline rather than at the sides, as they do in most living mammals.

Mammals, lizards and other vertebrates are crucial to reconstructing the past environment of the Gobi and to tracing the main lines of evolution. But dinosaurs still occupy center stage in the public eye. The Cretaceous Gobi is unquestionably one of the world's great dinosaur hunting grounds. The fossils range from complete skeletons of *Tarbosaurus*—a fierce carnivore closely related to the North American *Tyrannosaurus*—to giant sauropods, duck-billed dinosaurs, armored ankylosaurs, frilled ceratopsian dinosaurs such as *Protoceratops* and a magnificent assemblage of smaller carnivores. Birdlike oviraptorids and dromaeosaurs such as *Velociraptor* are better represented in the stratified rocks of the Gobi than anywhere else in the world.

These remains have given rise to controversies but also to some definitive conclusions. Artists often depict *Velociraptor* hunting in packs like African wild dogs, for example, but there is no definitive proof that it was capable of such cooperative behavior. The predator's taste for *Protoceratops,* however, is more than a matter of speculation. In the late 1960s a group of Polish and Mongolian scientists at Tugrugeen, a white sandstone escarpment about 80 kilometers west of the Flaming Cliffs, excavated one of the most remarkable pair of specimens in the history of paleontology. Two nearly complete skeletons—a *Protoceratops* and a *Velociraptor*—are preserved locked in mortal combat. *Velociraptor* clutches the lowered head of *Protoceratops* with its forelimbs and raises the killing hooks of its hind claws high against its prey's flanks. The "fighting dinosaurs," which may have met their end in one of the Gobi's sandstorms, are one of the great exhibits of the Natural History Museum in Ulaanbaatar.

Velociraptor skeletons are not only fascinating for the image they convey of intelligent, swift and lethal terrors. They offer

ADULT OVIRAPTORID SKULL was found at Ukhaa Tolgod in the western Gobi. This birdlike family of dinosaurs bore a resemblance to modern ostriches. Some oviraptorids (perhaps only one of the sexes) grew a large bony crest after they matured.

MARK NORELL; SPECIMEN PREPARED BY WILLIAM AMAREL clues to the evolutionary connection between birds and dinosaurs. *Velociraptor* and its relatives have many birdlike features, including the construction of the bony case of the brain and the design of the elongated limbs and digits. A nearly complete skeleton of *Velociraptor* unearthed at Tugrugeen in 1991 has a nearly complete braincase; in its details the architecture of the braincase is surprisingly similar to that of modern birds.

An unexpected discovery at Tugrugeen further amplified the proposed connection between dinosaurs and birds. We found a delicate skeleton that was identical, except for its smaller size, to one discovered by Mongolian scientists some years earlier. The animal, roughly the size of a turkey, has a remarkably gracile frame with long legs. In addition, the keel of the breastbone is extremely well developed. In modern birds, strong pectoral muscles that power the downstroke of the beating wing attach to this keel. Instead of long wing bones, however, this creature has stubby, massive forelimbs somewhat like those of a digging mole. The end of the arm and hand is appointed with a single, very large claw; hence, the scientific name bestowed on the animal is *Mononykus*—literally, "single claw."

Mononykus is a bizarre creature. Although it has no wings, it has features that suggest a closer relation to modern birds than the famous primitive bird *Archaeopteryx*. A detailed analysis of *Mononykus* favors the view that this creature was a flightless relative of modern birds.

That argument has drawn some criticism. Certain specialists claim *Mononykus* is simply a small dinosaur whose birdlike features are a product of convergent evolution. The weight of the evidence, however, does not favor convergence. The history of birds is marked by species (such as ostriches, emus and kiwis) that have lost their capacity for flight. Our *Mononykus* fossils do not show evidence of feathers, but it is only by some miracle of preservation that the fine Jurassic limestone entombing *Archaeopteryx* leaves impressions of tiny feathers. *Mononykus,* like most fossils, is not preserved in such unusual rock.

We have detected remains of this animal at many localities. Among the skeletons recovered from Ukhaa Tolgod is a nearly complete specimen that includes a well-preserved skull. This fossil shows evidence of an elongated head. What we can see is much different from previous reconstructions, which were extrapolated from partial fragments of the braincase.

Egg Hunter or Incubator?

EGGS OF BOTH dinosaurs and birds, found in various parts of the Gobi, add another dimension to the fossil record. Some of the eggs contain small embryonic skeletons of the bird *Gobipteryx,* and others preserve the skeletal remains of a small embryonic dinosaur. In some places, several nests may be clustered on a hillside, and we infer that these nests mark a congregation of dinosaurs, much like a colony of seabirds today.

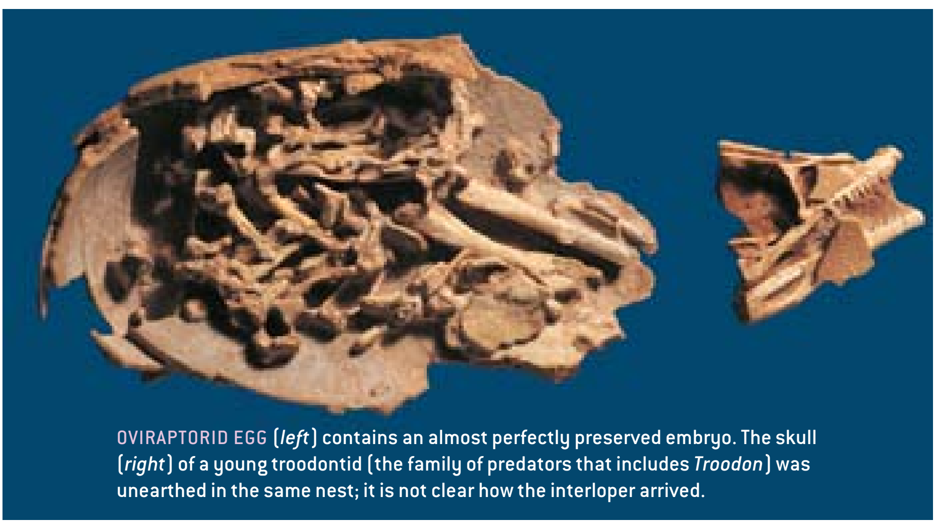
At Tugrugeen Shireh, we found 12 jumbled skeletons of *Protoceratops* on a flat not much larger than a putting green. A Sino-Canadian team also reported such accumulations of *Protoceratops* in Cretaceous rocks of northern China.

The *Protoceratops* sample includes several growth stages, providing a glimpse of this largely unknown aspect of dinosaur biology. Adults typically measure two meters long; in 1994 our team recovered some *Protoceratops* less than nine centimeters long. These skeletons are obviously those of very young individuals, possibly newborns.

As we make such discoveries, however, the picture of dinosaur life that emerges becomes more complex. Because *Protoceratops* is the most common dinosaur fossil in the region, paleontologists have long assumed that the many shells and egg aggregates found at the Flaming Cliffs and elsewhere belong to it. Yet evidence for this supposition has been unsatisfactory. None of the hundreds of dinosaur eggs collected have clearly identifiable *Protoceratops* embryos within them. Even the tiny skulls of *Protoceratops* we discovered cannot be positively linked with an egg of a particular type.

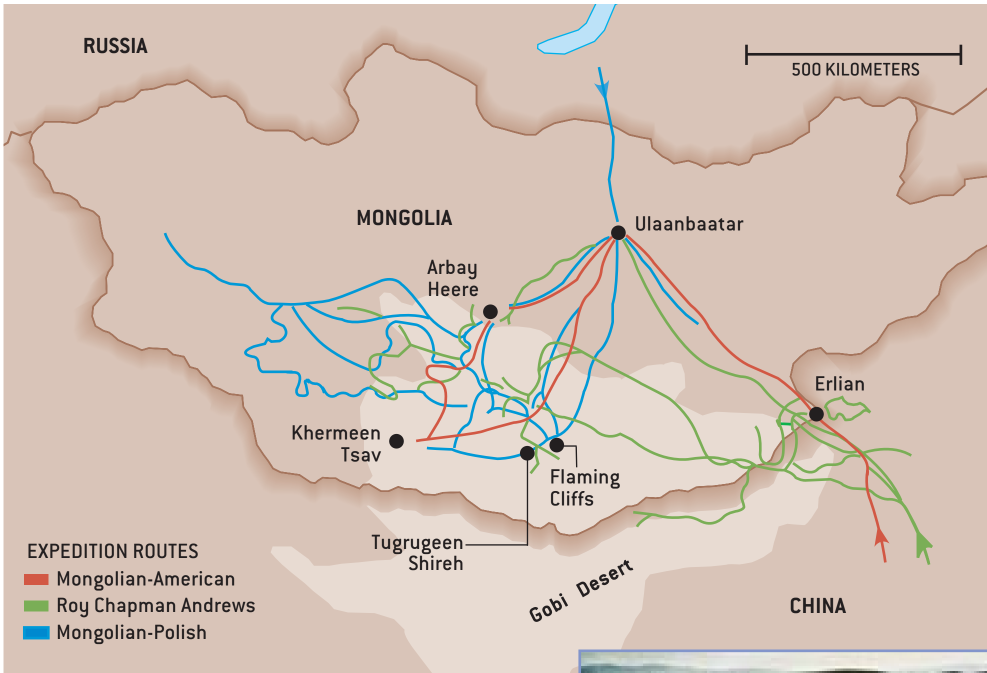
A find from Ukhaa Tolgod suggests that this assumption may have been wrong. The examination of a clutch of eggs containing dinosaur embryos found on our first day there revealed that an oblong, somewhat wrinkly egg usually at-

MARK NORELL; SPECIMEN PREPARED BY AMY DAVIDSON



OVIRAPTORID EGG (*left*) contains an almost perfectly preserved embryo. The skull (*right*) of a young troodontid (the family of predators that includes *Troodon*) was unearthed in the same nest; it is not clear how the interloper arrived.

SPECIMEN of the oviraptorid *Citipati* atop a nest of eggs.



ROY CHAPMAN ANDREWS (*at left, below*) led the first fossil-hunting expedition to the Gobi Desert in 1922. His group, which included camels and primitive cars, got lost several times; one such episode sparked the discovery of the Flaming Cliffs. Current expeditions can rely on satellite navigation aids, but they face no less arduous conditions. Although paleontologists have mapped many rich fossil territories, much of the Gobi remains unexplored.

JOHNNY JOHNSON (*map*); AMNH PHOTOGRAPHIC ARCHIVES (*photograph*)

tributed to *Protoceratops* held a nearly perfect oviraptorid skeleton. It appears likely that many of the eggs found at Ukhaa Tolgod (and possibly elsewhere) belong to these small carnivores rather than to the parrot-beaked, herbivorous Protos.

The Ukhaa Tolgod "nest" contained other fossils of great intrigue. Two tiny skulls of a troodontid (possibly *Byronosaurus*) were found in the clump of eggs; bits of oviraptorid eggshell were associated with their bones. This curious coincidence of eggs, an oviraptorid embryo, and two very young or newborn troodontids has several plausible explanations.

Perhaps the young dromaeosaurs were honing their skills at an early age by raiding dinosaur nests. Alternatively, the parent oviraptorid may have been feeding the dromaeosaurs to her offspring, or the dromaeosaurs might have been interlopers, their eggs placed in the oviraptorid nest in much the same way that cuckoo birds place their eggs in the nests of other bird species. Although the mystery cannot be resolved, these fossils suggest ways of life and nesting behaviors for theropod dinosaurs that had thus far not been tied to hard paleontological data.

This discovery also puts an ironic twist on nomenclatural history. The Andrews expeditions applied the name *Oviraptor* to a skeleton at the Flaming Cliffs because it was found atop a clutch of eggs. They assumed that the eggs belonged to the common *Protoceratops* and that *Oviraptor* (literally, "egg hunter") was raiding a nest. Our find demonstrates that *Oviraptor* may not have been devouring eggs but rather incubating them. The name will stick because of nomenclatural rules, but it hardly befits the true circumstances behind the discovery of the first known skeleton.

Time Eludes

NESTING SITES and skeletons of birds, dinosaurs, mammals and other vertebrates all make up a fairly detailed picture of life in the Gobi during the Late Cretaceous. The evidence contributed by the Mongolian Academy–American Museum expeditions has been gathered by logging thousands of kilometers over a wide stretch of the Gobi rather than concentrating for a prolonged period on a single or a few sites. This method not only increases the chance of finding new fossil sites, it conveys a better sense of the rock sequence through comparison of fossil-bearing strata over a broad area. Thus, we can try to determine whether assemblages of animals and sediments representing a particular environment and time interval are widespread or confined to isolated outcrops.

For example, paleontologists have generally believed that the community of fossils in the Djadokhta Formation (a Central Gobi bed of brilliant red sandstones named for the Flaming Cliffs) is slightly older than that of the Barun Goyot Formation (which gets its name from an ancient settlement in the Nemegt Valley) in the western Nemegt. Both our findings at Ukhaa Tolgod and our broad survey, however, suggest that the two formations preserve contemporary, virtually identical fauna. We found an extension of this community in the magnificent red and vermilion beds of Khermeen Tsav, an isolated set of badlands in the arid desert west of the Nemegt region that strongly resembles the canyon lands of southern Utah.

We have also found fossils from the Djadokhta community, including the fa-

THE AUTHORS

MICHAEL J. NOVACEK, MARK NORELL, MALCOLM C. McKENNA and *JAMES CLARK* have together explored fossil sites in the Gobi Desert under the auspices of the American Museum of Natural History and the Mongolian Academy of Sciences. Novacek is the museum's senior vice president for science, Norell is chair of the paleontology division, and McKenna is curator emeritus of vertebrate paleontology there and adjunct curator at the University of Colorado Museum. Clark, who worked at the American Museum for three years, is now professor of biology at George Washington University.

DINOSAUR AND MAMMAL FOSSILS from the Gobi are remarkably well preserved. The newly discovered troodontid (*life-size photograph of skull and sketch*) was a small carnivore closely related to birds. The multituberculated skeleton (*opposite page*) is almost completely intact even though some of its

miliar *Protoceratops,* in an area called Khugene Tsavkhlant, near the eastern railway. These discoveries are particularly significant because the sandstones there appear to be the result of stream or river action, a situation more typical of North American sites than of the Gobi. It is slowly becoming clear that the animal community once thought to be localized at the Flaming Cliffs may have occupied a range of habitats.

The wide geographic separation of many sites, however, impedes these comparisons of fossil localities. In addition, Gobi rock sequences are entirely sedimentary, without even traces of volcanic rocks. Thus, geologists cannot determine the age of these strata by analyzing their proportions of radioactive isotopes. Estimates of the age of various formations must rely on the similarity of the vertebrates to those of reference faunas on other continents and on correlations with invertebrate fossils from Cretaceous marine rocks in Central and East Asia.

We have sampled representative rock sequences in the hope of obtaining paleomagnetic signals, but results have not yet come in. These signals track the orientation of the earth's magnetic field at the time the rock and its minerals are deposited. The "frozen" paleomagnetic signals can then be matched against a chronology of reversals in the earth's field. Paleomagnetic data would therefore provide an independent source for estimating the age of the Gobi rocks.

In yet another ironic twist, the rocks of the Gobi appear to be missing precisely those strata that currently hold the greatest public interest: no sections found thus far include the Cretaceous-Tertiary (K-T) boundary, when the dinosaurs became extinct. Although the Gobi is richly endowed with early Tertiary mammal faunas, there seems to be a gap of at least several million years between these and the Late Cretaceous dinosaur faunas. Whatever cataclysm wiped out the dinosaurs (and many other species then on the earth), its mark on Central Asia has apparently been erased. If a continuous sequence could be located somewhere in the desert's vastness, it would make a formidable contribution to our knowledge concerning the dinosaur extinction and the subsequent rise of mammals.

The notion of finding the K-T boundary in the Gobi is not just wishful thinking. Satellite navigation has already made a tremendous difference in the effectiveness of our work. We can plot the precise location of fossil sites and the routes that lead to them. We have also used *LANDSAT* and *SPOT* satellite images as a prospecting tool. After we returned from Ukhaa Tolgod in 1993, Evan Smith of the Yale University Center for Earth Observation enhanced red and brown spectral bands on computer-based satellite images by matching colors from photographs of the rocks there. The result is a map that shows with high precision the extent and contours of fossil-bearing strata.

During the 1994 season, we used these images as a field guide and simply drove to the latitude and longitude of a telltale cluster of red pixels. Some of these computer-targeted spots proved productive. Satellite and computer technology have provided us with a useful paleontological atlas in a region where detailed topographic or geologic maps are virtually lacking. We now also have something that might have cost Andrews his most important but serendipitous discoveries: a fairly decent road map of the Gobi.

Despite our new technology and the decades of insights into the evolution of vertebrates, exploration of the Gobi has much the same quality that Andrews experienced 82 years ago. The Flaming Cliffs we encountered on that first joyful day in 1990 were as Andrews described them—imposing, brilliant red in color and replete with fossils. Sandstorms that engulfed the 1920s expeditions returned to wreak havoc on our fragile campsites.

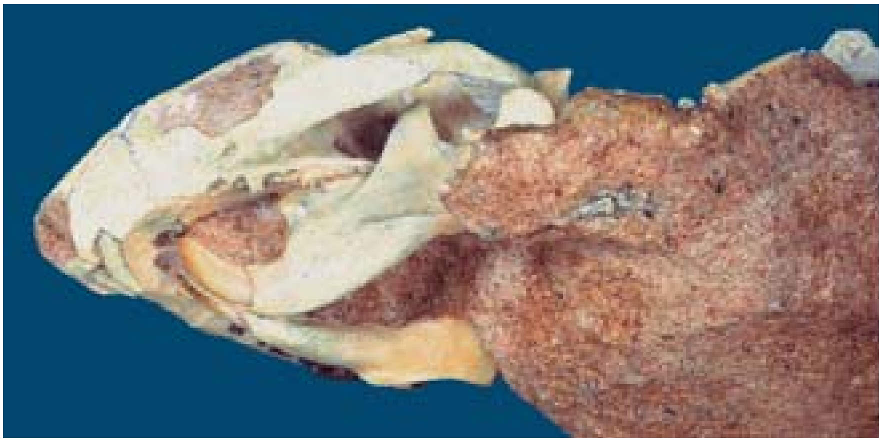
When the sandstorms clear, one can see from the top of the cliffs the mauve, furrowed mountains of the Gurvan Saichan. Beyond the mountains are hundreds of square kilometers of fossil-rich badlands whose existence Andrews could only have imagined. The Gobi is and will be for some time a great wilderness. It will continue to hold many secrets of prehistory, of the rise and fall of dinosaurs and other biological empires.

Epilogue

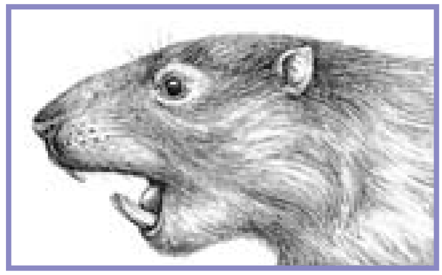
By Mark Norell and Michael J. Novacek

Many discoveries have been made since we wrote our 1994 article on the Gobi fossil hunt. Our summer 2004 expedition will mark the 15th consecutive year of joint journeys by the Mongolian Academy of Sciences and the American Museum of Natural History. During the past decade the important Ukhaa area has continued to yield many new and exciting fossils, including those in older rocks, in Lower Cretaceous beds in the north-central Gobi, and, during 2002 and 2003, in Cretaceous sequences in the poorly explored reaches of the eastern Gobi near the Trans-Siberian Railway. This cumulative effort has revealed a broader and more graphic picture of life

MICHAEL J. NOVACEK; SPECIMENS PREPARED BY WILLIAM AMAREL (*photographs*); MICHAEL ELLISON *AMNH* (*left drawing*); ED HECK *AMNH* (*right drawing*)



bones are barely half a millimeter thick; the skull is about 2.5 centimeters long. Multis, recognizable by the many bumps (tubercles) on the crowns of their teeth, were small mammals whose habits presaged those of rodents such as squirrels and mice.



and death in Central Asia between 100 million and 75 million years ago.

Ukhaa Tolgod remains as perhaps the most significant discovery. It is a small, shallow drainage area of about four square kilometers, bordered by a serpentine line of low bluffs and adjacent flats where red rocks of the Djadoktha Formation are exposed. Geologic work has prompted reinterpretation of the accepted view that animals there were buried by gargantuan sandstorms. Based on detailed studies of sediments, our geologists David Loope and Lowell Dingus noted that the fossils at Ukhaa Tolgod are mostly restricted to beds that have no structure, suggesting that the dunes were stationary and possibly crowned with plants whose roots disrupted sand layers below the surface. This process of bioturbation was aided by the burrowing of small subterranean invertebrates, such as worms and insects, as well as larger burrowing mammals and lizards.

Loope and Dingus also observed that Ukhaa fossil beds contain streamers of pebbles too big to be windblown. Moreover, the sand has a high clay content, and the Mesozoic dunes are intercalated with water-resistant caliche layers. Hence, the dunes could not drain during heavy rainstorms; they instead acted as giant sandy sponges. At some point they became oversaturated and collapsed in large debris flows that covered sedentary animals, such as nesting dinosaurs, along with more active animals, making for phenomenal fossil preservation. Sometimes every bone in a body is preserved.

Many dinosaurs, lizards and mammals have been found at Ukhaa Tolgod. Most of them are fairly small, but there are hints (like shed dinosaur teeth and footprints) that very large dinosaurs at least passed through. Some of the most common Ukhaa dinosaurs, such as ankylosaurs, were 4.5 meters long, and adult oviraptorids were a respectable three meters long. The remarkable dinosaurs also include groups of immature armored ankylosaurs, which may well have been gregarious, because multiple skeletons are often encountered together.

Some of the most dramatic specimens are of the oviraptorid *Citipati,* which have been recovered sitting on their nests of eggs. Named after the Himalayan protector god of the funeral pyre, the creatures are the first nonavian dinosaurs known to exhibit avianlike brooding behavior. Additional specimens of the bizarre dinosaur *Shuvuuia* (previously called *Mononykus*) indicate that this animal is not a close relative of early birds but more primitive. Surprisingly, however, with one *Shuvuuia* specimen we found structural and biochemical evidence of feathers.

More than 600 mammal skulls, many with skeletons, have been recovered. This rich collection is critical to understanding the origins of modern mammal groups. Noteworthy is a form we named *Ukhaatherium,* which resembles the shrewlike species of the modern placental mammals but also retains primitive features such as the splintlike epipubic bones extending from the pelvis. The site has also yielded some of the best skeletons of *Deltatheridium,* an early relative of the marsupials, a group that includes opossums and kangaroos. Forms such as *Deltatheridium* and even more primitive species from the Early Cretaceous of northern China suggest that important branching events leading to the marsupial lineage occurred in the Mesozoic of Central Asia.

For the past two seasons we have concentrated our efforts in the eastern Gobi, near our field operations of 1991. Additional study at Khugene Tsavkhlant, where we had earlier reported the ubiquitous *Protoceratops,* has indicated that this form is a much more primitive relative. We have also found interesting remains of mammals with low-crowned teeth. Right now we think this group is a distinct lineage that branched off just before the radiation of the modern placental mammals. These new animals seem to be closely related to the previously described zhelestid mammals from the Cretaceous beds of Uzbekistan.

Research progress has been aided by the technological trappings of 21st-century field exploration. Global Positioning System units, satellite phones and satellite imaging, portable computers, and digital cameras are standard equipment. We even have a solar-powered refrigerator to make camp life a little easier. The Gobi will doubtless continue to yield spectacular finds. SA

MORE TO EXPLORE

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New Limb on the Avian Family Tree. Mark Norell, Luis Chiappe and James Clark in *Natural History,* Vol. 102, No. 9, pages 38–43; September 1993.

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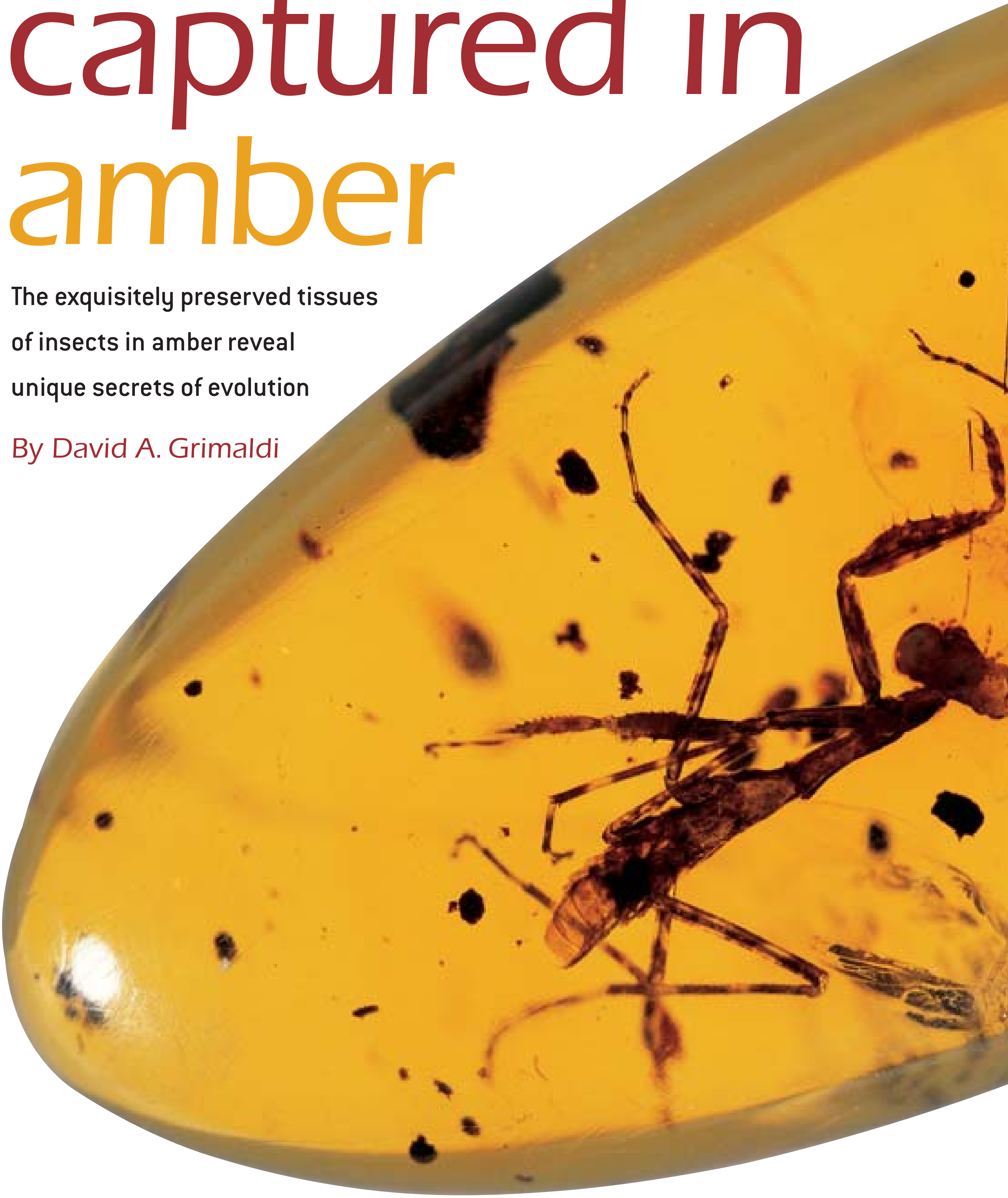
captured in amber

The exquisitely preserved tissues of insects in amber reveal unique secrets of evolution

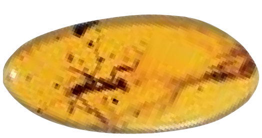
By David A. Grimaldi



Updated from the April 1996 issue

PRAYING MANTIS preserved in Dominican amber—most of which is 25 million years old—is related to cockroaches and termites. This one was probably caught while stalking prey along the trunk of a tree that exuded the amber-producing resin.

ACTUAL SIZE



ED BRIDGES *American Museum of Natural History*

A hurricane had savaged the forest of giant *Hymenaea* trees along a Central American coastline. Yellow streams of resin oozed from mangled branches and gashed trunks, while insects bred in the wreckage. One termite happened to brush against the resin and stuck fast, ultimately becoming enveloped in its flow. Terpenes and other fragrant vapors from the resin penetrated the termite's tissues, replacing the water and killing bacteria.

Air, along with light and heat from the sun, induced chemical reactions in the resin so that the carbon atoms in its long molecules began to link up. The chunk of hardening sap fell to the ground, one among thousands. Tides from tropical storms of a later year washed the resin fragments and rotting logs into a lagoon, where coastal sediments covered them. Twenty-five million years of subterranean pressure polymerized the resin even further, making it solid and chemically inert. Tectonic movements eventually lifted the coastline into steep mountains

3,000 feet high, to become the island of Hispaniola in the Caribbean.

Wandering in those hills some years ago, a Dominican miner came across a small landslide that revealed a black vein of fossilized wood. Digging for hours along the seam, he unearthed a pile of nuggets and the glassy glint of amber. Within one piece lay a very large termite, wings slightly parted and legs splayed.

The amber piece with its embalmed *Mastotermes electrodominicus* found its way to the American Museum of Natural History in New York City. Entomologists have long been intrigued by these primitive insects, which share features with cockroaches and were thought to connect the latter with modern termites. Relatives of *Mastotermes* extinct for 130 million to 30 million years show up in rocks and amber around the world. One species, *M. darwiniensis,* survives to this day in Australia, an evolutionary relic.

In 1992 I worked with Rob DeSalle, Ward Wheeler and John Gatesy at the museum. The Hispaniola specimen was sliced open, allowing us to extract tissues from the termite. The sample contained exquisitely preserved cells, many with even the mitochondria intact. The tissues were dehydrated, yet they had not shrunk, as one would expect with the water gone. The process by which resin "fixes" tissue so that it retains its original size is still a mystery.

The dehydration was critical to the success of our experiment. After death, DNA degrades in the presence of water; the desiccation had allowed large segments of DNA to survive unaltered. We isolated snippets of the 18s and 16s ribosomal DNA genes. Mapping the sequence of bases on a DNA fragment, we compared it with corresponding sections from living termites, cockroaches and praying mantises, which constitute the group Dictyoptera.

The physical similarity between *Mastotermes* and roaches, it turned out, was a vestige of an even more ancient ancestry. The extinct and living *Mastotermes* were very closely related, both being purely termites. The two species differed by nine base pairs in a segment

DENIS FINNIN *American Museum of Natural History* c

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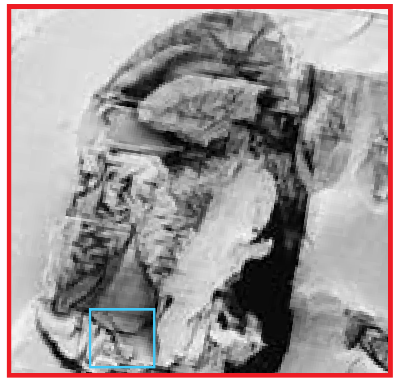

American Museum of Natural History (a–i)

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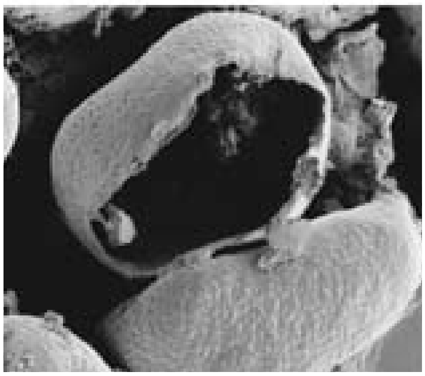
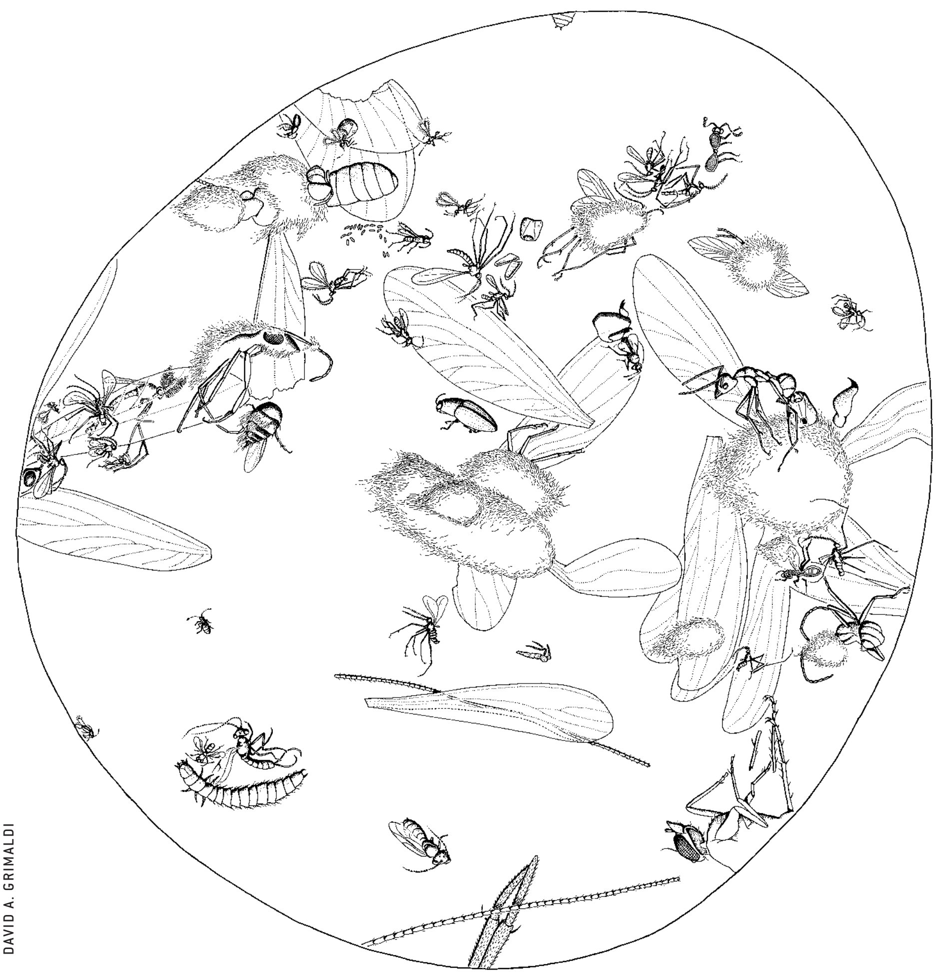


SCANNING ELECTRON MICROGRAPHS of a stingless bee, *Proplebeia dominicana,* attest to the astonishing preservation of tissues in amber. The polished piece (*a*) is sawed to within a hair's breadth of the insect, cleaned and gently pried open. The left half of the specimen (*b*) contains parts of the head (*top*), thorax (*middle*) and abdomen (*bottom*). Within the head (*c*) lie the brain (*top middle*) and the long muscles used for sucking (*left*), along with the bee's small tongue (*bottom*). The scales on the tongue (*d*) are each about 10 microns long. The thorax (*e*) contains folded air sacs and, among other structures, a small bundle of muscles (*f*), each fiber of which is about 15 microns thick. The right half of the specimen (*g*) holds another part of the abdomen (*lower right*), along with pollen grains (*h*) that the bee had ingested. A single grain (*i*), viewed here from a different angle, is about 30 microns across. Stingless bees are common in Dominican amber: while harvesting the resin to construct their nests, the bees were often trapped instead.



DAVID A. GRIMALDI

MENAGERIE IN AMBER (*far left*) contains 62 whole and partial insects, all within a piece just 2.8 centimeters across. A map of the specimen (*left*), drawn by the author, depicts insects belonging to five orders and 14 families. Among them are several gall midges, ants, adult and larval beetles, and parasitoid wasps—including one that has just deposited her eggs (*top left*). Termite wings and antennae float across the scene; parts of three termites are sticking out of fuzzy mold. (Some of the insects were probably only partially trapped at first. The exposed parts decomposed, became moldy and were then covered by another layer of resin.)

of the 16s gene with 100 base pairs. The extinct DNA enabled us to reconstruct the evolutionary tree for the group and helped to clarify the relation of *M. darwiniensis* to other termites.

Since that study, DNA has been reported from a *Drosophila* fruit fly, a stingless bee, a wood gnat, a fungus gnat, and tree leaf and chrysomelid beetles, all preserved in Dominican amber. Raul J. Cano and his colleagues at California Polytechnic State University reported sequenced DNA from a weevil in Lebanese amber; at 125 million years old it would be the most ancient DNA known.

Thorough work on putatively ancient DNA from amber was done in 1998 at the University of Illinois and the Natural History Museum in London. Ancient DNA was not recovered from any specimens, though, suggesting that DNA in earlier reports may have been contaminated by DNA from living insects being studied simultaneously in laboratories. Nevertheless, the tissue preservation observed continues to astound. In 2001, working with Lynn Margulis and Michael Dolan of the University of Massachusetts at Amherst, my laboratory unearthed microscopic remains of symbiotic protists and bacteria-like spirochetes in the gut of an extinct termite. Modern termites require such microbes to digest cellulose. Our work proves that ancient relatives were similarly dependent.

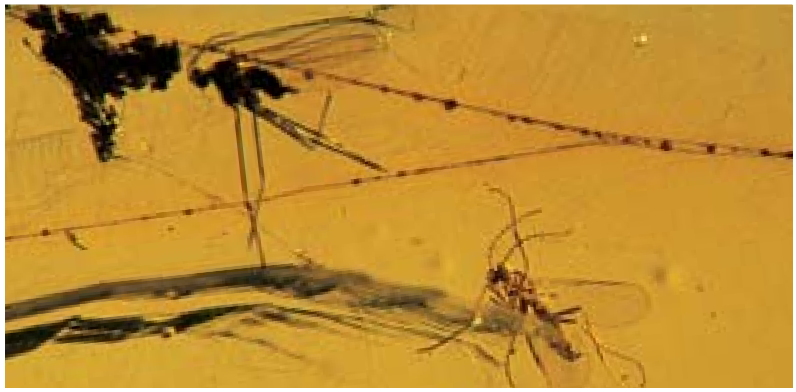
Right now amber from the Cretaceous period of 140 million to 65 million years ago is attracting scientists' attention. Dinosaurs died out at the end of this period; more important, the landscape transformed during its tenure. Flowering plants blossomed onto the scene. Many modern groups of insects evolved: ants, termites, bees, moths, butterflies, beetles and other creatures associated with flowering plants.

One of the most important deposits of Cretaceous amber, from 94 million to 90 million years old, was discovered in central New Jersey in 1992. This trove has yielded some extraordinary fossils. Among the startling finds is a bird feather—the oldest terrestrial record of a bird in North America—and the oldest definitive bee and ants. In addition, we have uncovered the only flower in Cretaceous amber, a small inflorescence of the most primitive known oak.

The New Jersey amber has yielded the oldest fossil tardigrade—a minute animal closely related to arthropods—and it is extremely similar to modern species, indicating that remarkably little has changed in 90 million years. Other significant finds include 100-million-year-old amber from northern Myanmar (Burma) that contains diverse organisms. We are eager to learn more. SA

CAUGHT IN THE ACT

INSECT TABLEAUX sealed in Dominican amber have demonstrated that some familiar behaviors are at least 25 million years old.



STRANDS OF A SPIDER'S WEB snag one of two delicate gall midges, in the family Cecidomyidae.

THREE ANTS ATTACK a nymphal praying mantis, evidence of cooperative hunting—or, possibly, defense—among ants.

DAVID A. GRIMALDI (*top*); JACKIE BECKETT *American Museum of Natural History* (*bottom*)

LOVE AND DEATH unite two mating gall midges, providing specimens of both sexes. The female would have laid about 100 eggs, the larvae of which feed on fungi.

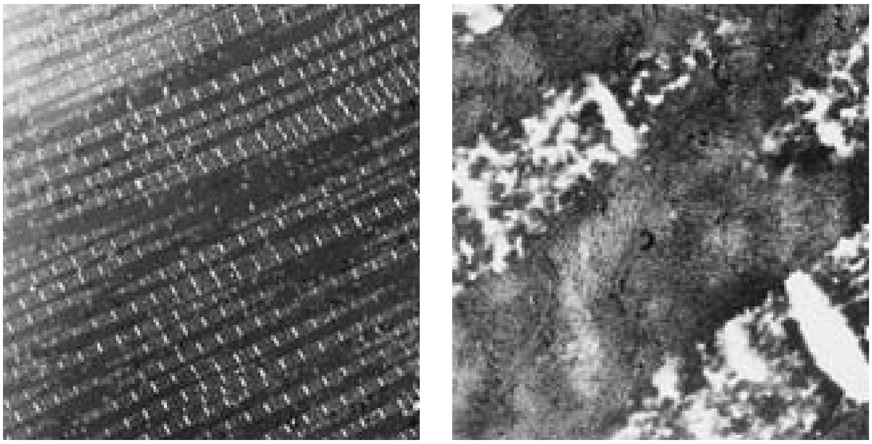
LAYING EGGS as it dies, a moth demonstrates a reflexive action observed in many insects. Larvae of this moth (family unknown, probably Tineoid) are thought to have fed on hard, woody bracket fungi that infected *Hymenaea* trees.

QUEEN ANT of the genus *Acropyga* carries a scale insect in her jaws, in an exceptional example of symbiosis. Some ants tend colonies of such insects, from which they harvest a sugary secretion called honeydew. (Some modern-day relatives of scale insects are common garden pests, such as whiteflies.) As the queen departs her old colony, she takes a scale insect along on her nuptial flight to start her new nest.

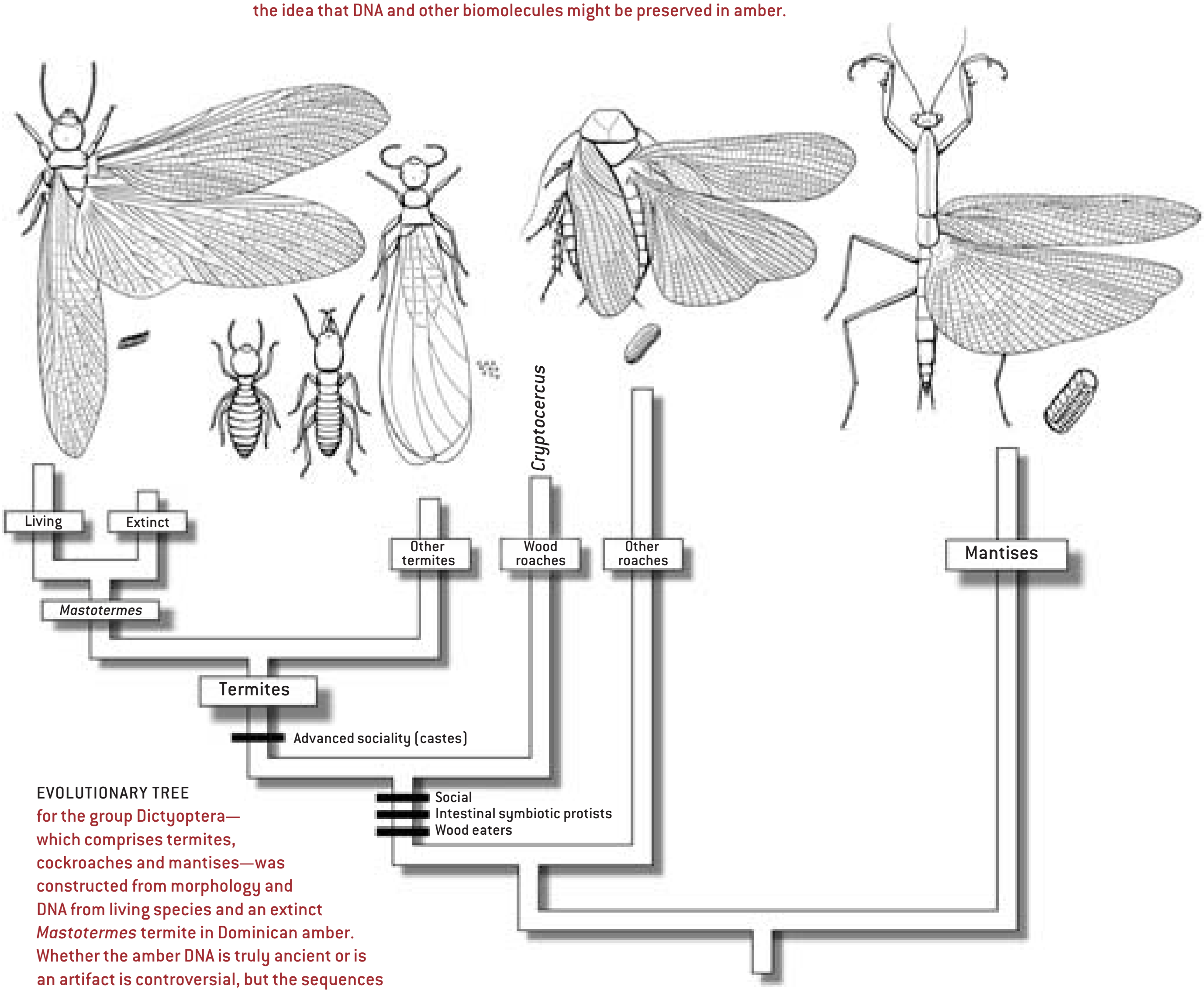
MITE CLINGS to the abdomen of a chironomid midge. These midges live in water or very damp soil during their larval stages, picking up the mites.

BITING MIDGE (family Ceratopogonidae) is bloated after a blood meal. Popular culture holds that blood from similar midges in Cretaceous amber was ingested from dinosaurs. This midge, however, lived 40 million years after the dinosaurs had vanished.

DAVID A. GRIMALDI



FLIGHT MUSCLES of a fossilized stingless bee (*left*) are magnified to reveal banded muscle fibers. Each fiber is up to one micron across. Between the strands are packed the folded membranes of mitochondria, which, when sliced through, look like fingerprints (*right*). Such preservation led to the idea that DNA and other biomolecules might be preserved in amber.



EVOLUTIONARY TREE for the group Dictyoptera—which comprises termites, cockroaches and mantises—was constructed from morphology and DNA from living species and an extinct *Mastotermes* termite in Dominican amber. Whether the amber DNA is truly ancient or is an artifact is controversial, but the sequences do indicate that the extinct species is closely related to the one living species of *Mastotermes,* in Australia. *Mastotermes* is the most primitive living genus of termites. (The illustration is by the author.)

STEPHEN DOBERSTEIN AND MICHAEL DELANNOY *Johns Hopkins University* (*micrographs*); DAVID A. GRIMALDI (*drawings*)

NEW JERSEY AMBER, between 94 million and 90 million years old, has yielded many of the most exciting fossils. Among the most beautifully preserved is a cluster of oaklike flowers (*left*) found in 1994 and an as yet unidentified flower discovered in 2003 (*right*). The feather (*top center*) is the oldest record of a terrestrial bird in North America. The amber also contains the oldest specimens of several insect families and of mushrooms, as well as the oldest true member of the phylum Tardigrada (*bottom center*). Tardigrades are minute creatures (this one is barely one millimeter long) that are the closest relatives of arthropods and can remain dormant under extreme conditions. This tardigrade is remarkably similar to a widespread, living species, indicating that scarcely any change has occurred in this lineage for 90 million years.

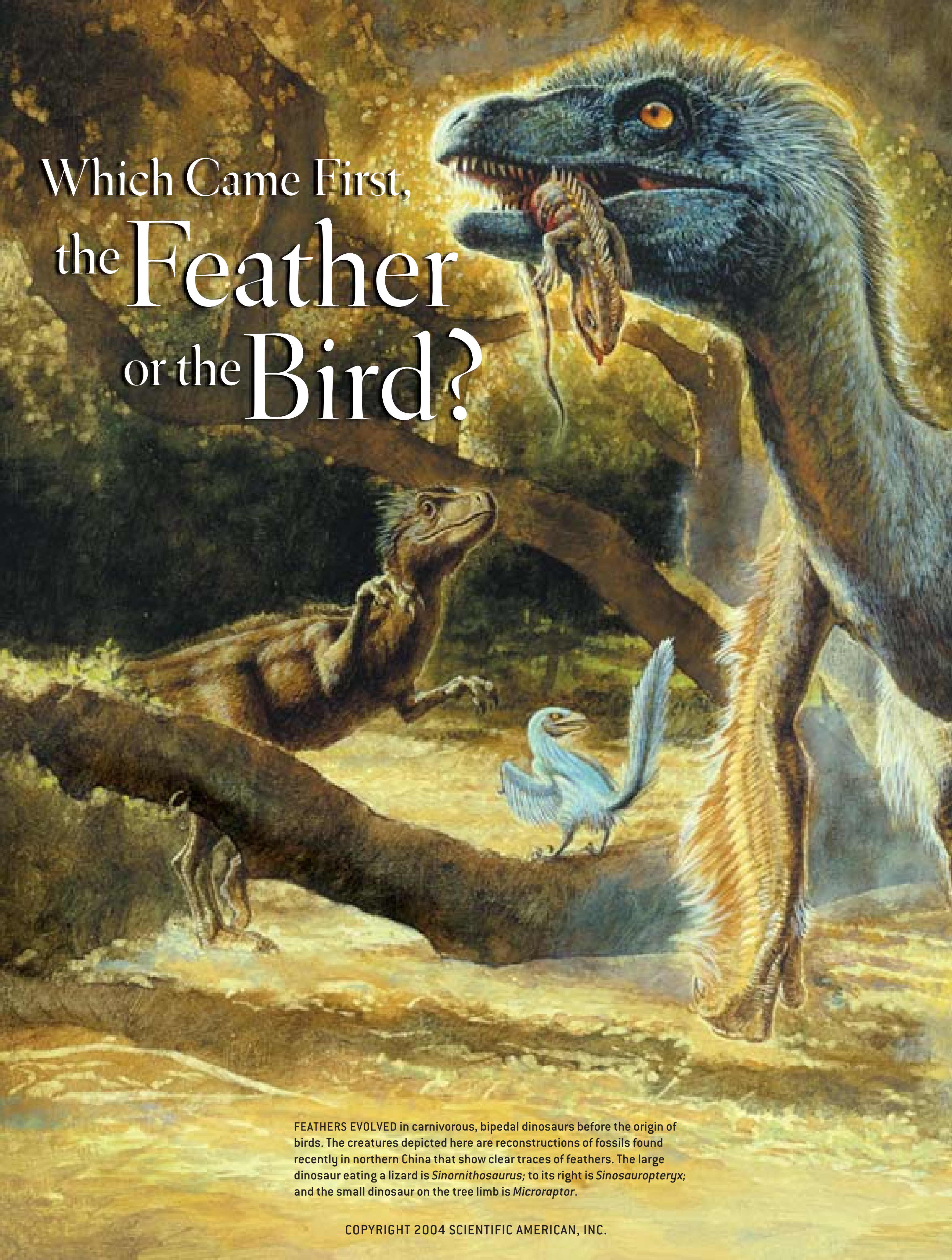
ELEUTHERODACTYLUS FROG (*left*) and *Sphaerodactylus* gecko (*right*) are trapped in pieces of Dominican amber 5.8 and 4.3 centimeters in size, respectively. Poised above the frog is the decayed carcass of another one, surrounded by fly larvae. The gecko's back is broken, perhaps because it struggled to escape from the resin; the leaf adjoining it has been chewed, most likely by a leaf-cutter bee. Dominican amber is renowned for the variety of life it embalms, including these rare vertebrates.

DAVID A. GRIMALDI (*top*); JACKIE BECKETT *American Museum of Natural History* (*bottom*)

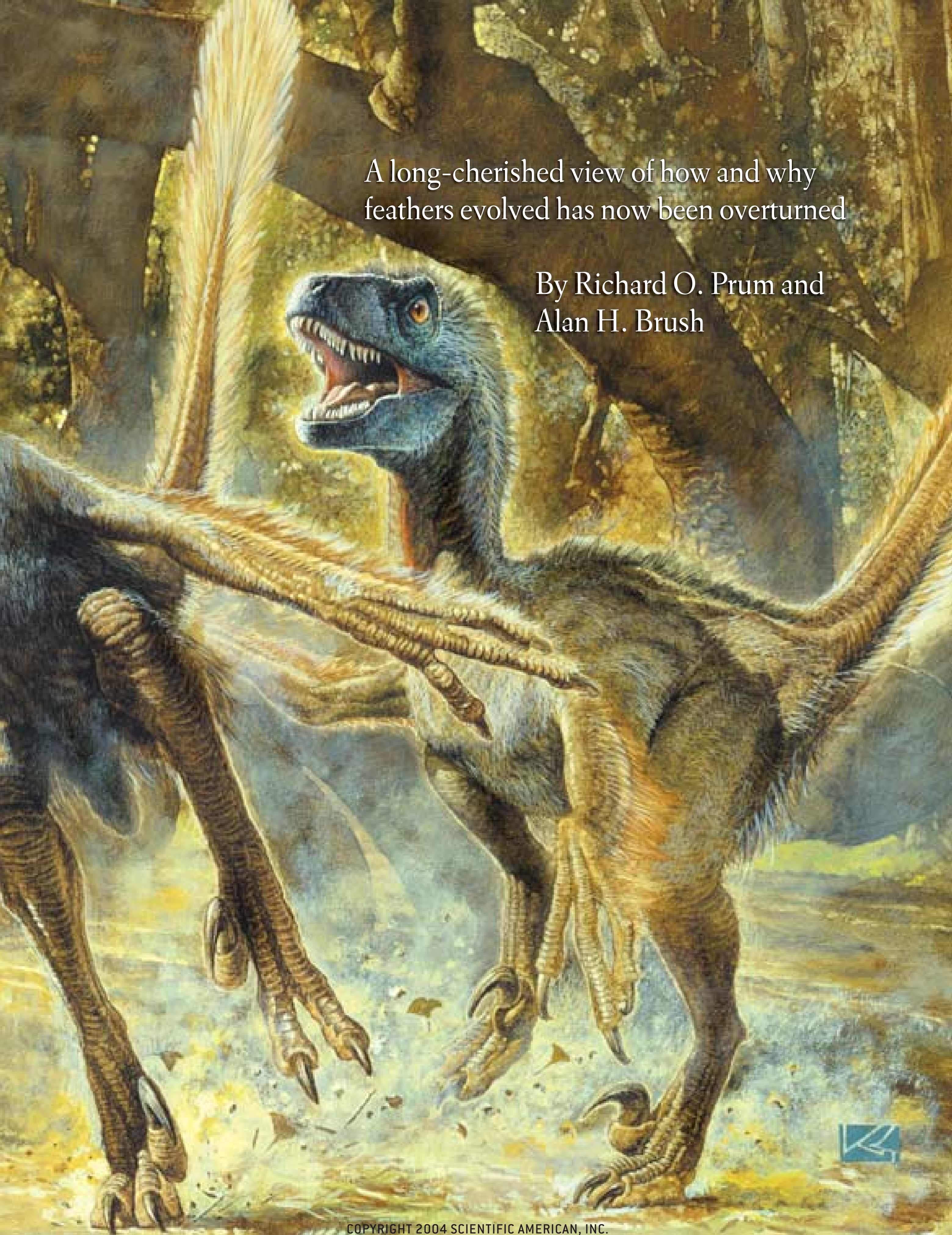
THE AUTHOR

DAVID A. GRIMALDI is curator of invertebrate zoology at the American Museum of Natural History in New York City. He obtained his Ph.D. in 1986 from Cornell University, where he is now adjunct professor of entomology. He is also adjunct professor of ecology and evolutionary biology at the City University of New York and at Columbia University. Grimaldi's main interests are systematics, paleontology and biogeography, the science of why lifeforms are where they are. Trained also as an artist, he is known in scientific circles for his illustrations. Grimaldi is author of *Amber: Window to the Past* (Harry N. Abrams, 1996) and, with Michael S. Engel, *Evolution of the Insects* (Cambridge University Press, 2004).

Which Came First, the Feather or the Bird?



FEATHERS EVOLVED in carnivorous, bipedal dinosaurs before the origin of birds. The creatures depicted here are reconstructions of fossils found recently in northern China that show clear traces of feathers. The large dinosaur eating a lizard is *Sinornithosaurus;* to its right is *Sinosauropteryx;* and the small dinosaur on the tree limb is *Microraptor*.



A long-cherished view of how and why feathers evolved has now been overturned

By Richard O. Prum and Alan H. Brush

HAIR, SCALES, FUR, FEATHERS. Of all the body coverings nature has designed, feathers are the most various and the most mysterious. How did these incredibly strong, wonderfully lightweight, amazingly intricate appendages evolve? Where did they come from? Only in the past six years have we begun to answer this question. Several lines of research have recently converged on a remarkable conclusion: the feather evolved in dinosaurs before the appearance of birds.

The origin of feathers is a specific instance of the much more general question of the origin of evolutionary novelties—structures that have no clear antecedents in ancestral animals and no clear related structures (homologues) in contemporary relatives. Although evolutionary theory provides a robust explanation for the appearance of minor variations in the size and shape of creatures and their component parts, it does not yet give as much guidance for understanding the emergence of entirely new structures, including digits, limbs, eyes and feathers.

Progress in solving the particularly puzzling origin of feathers has also been hampered by what now appear to be false leads, such as the assumption that the primitive feather evolved by elongation and division of the reptilian scale, and speculations that feathers evolved for a specific function, such as flight. A lack of primitive fossil feathers hindered progress as well. For many years the earliest bird fossil has been *Archaeopteryx lithographica,* which lived in the Late Jurassic period (about 148 million years ago). But *Archaeopteryx* offers no new insights on how feathers evolved, because its own feathers are nearly indistinguishable from those of today's birds.

Recent contributions from several fields have put these traditional problems to rest. First, biologists have begun to find fresh evidence for the idea that developmental processes—the complex mechanisms by which an individual organism grows to its full size and form—can be a window into the evolution of a species' anatomy. This idea has been reborn as the field of evolutionary developmental biology, or "evo-devo." It has given us a powerful tool for probing the origin of feathers. Second, paleontologists have unearthed a trove of feathered dinosaurs in China. These animals have a diversity of primitive feathers that are not as highly evolved as those of today's birds or even *Archaeopteryx*. They are critical clues to the structure, function and evolution of modern birds' intricate appendages.

Together these advances have produced an extremely detailed and revolutionary picture: feathers originated and diversified in carnivorous, bipedal theropod dinosaurs before the origin of birds or the origin of flight.

The Totally Tubular Feather

THIS SURPRISING PICTURE was pieced together thanks in large measure to a new appreciation of exactly what a feather is and how it develops in modern birds. Like hair, nails and scales, feathers are integumentary appendages—skin organs that form by controlled proliferation of cells in the epidermis, or outer skin layer, that produce the keratin proteins. A typical feather features a main shaft, called the rachis [*see box on opposite page*]. Fused to the rachis are a series of branches, or barbs. In a fractal-like reflection of the branched rachis and barbs, the barbs themselves are also branched: a series of paired filaments called barbules are fused to the main shaft of the barb, the ramus. At the base of the feather, the rachis expands to form the hollow tubular calamus, or quill, which inserts into a follicle in the skin. A bird's feathers are replaced periodically during its life through molt—the growth of new feathers from the same follicles.

Variations in the shape and microscopic structure of the barbs, barbules and rachis create an astounding range of feathers. But despite this diversity, most feathers fall into two structural classes. A typical pennaceous feather has a prominent rachis and barbs that create a planar vane. The barbs in the vane are locked together by pairs of specialized barbules. The barbules that extend toward the tip of the feather have a series of tiny hooklets that interlock with grooves in the neighboring barbules. Pennaceous feathers cover the bodies of birds, and their tightly closed vanes create the aerodynamic surfaces of the wings and tail. In dramatic contrast to pennaceous feathers, a plumulaceous, or downy, feather has only a rudimentary rachis and a jumbled tuft of barbs with long barbules. The long, tangled barbules give these feathers their marvelous properties of lightweight thermal insulation and comfortable loft. Feathers can have a pennaceous vane and a plumulaceous base.

In essence, all feathers are variations on a tube produced by proliferating epidermis with the nourishing dermal pulp in the center. And even though a feather is branched like a tree, it grows from its base like a hair. How do feathers accomplish this?

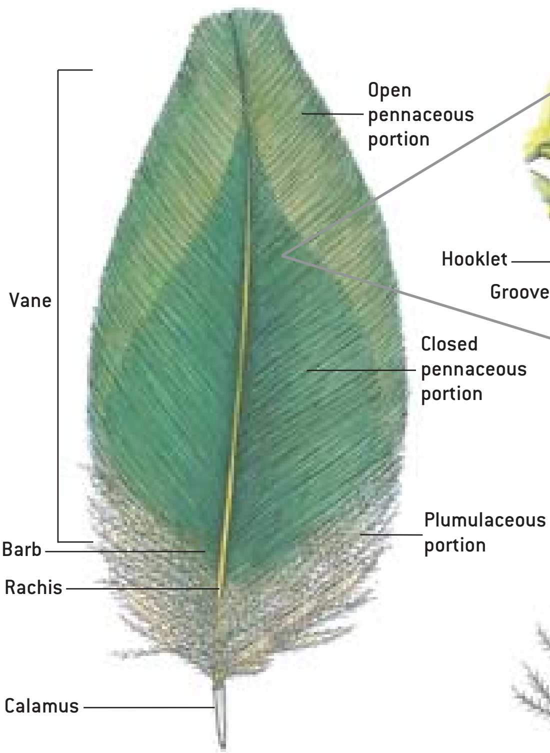
Feather growth begins with a thickening of the epidermis called the placode, which elongates into a tube—the feather germ [*see illustration on page 76*]. Proliferation of cells in a ring around the feather germ creates a cylindrical depression, the follicle, at its base. The growth of keratin cells, or keratinocytes, in the epidermis of the follicle—the follicle "collar"—forces older cells up and out, eventually generating the entire feather in an elaborate choreography that is one of the wonders of nature.

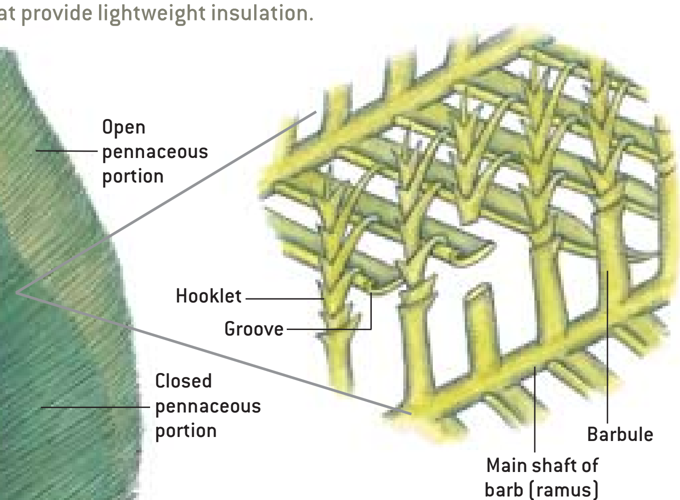
As part of that choreography, the follicle collar divides into a series of longitudinal ridges—barb ridges—that create the separate barbs. In a pennaceous feather, the barbs grow helically around the tubular feather germ and fuse on one side to form the rachis. Simultaneously, new barb ridges form on the other side of the tube. In a plumulaceous feather, barb ridges grow straight without any helical movement. In both types of feather, the barbules that extend from the barb ramus grow from a single layer of cells, called the barbule plate, on the periphery of the barb ridge.

KAZUHIKO SANO (*preceding pages*)

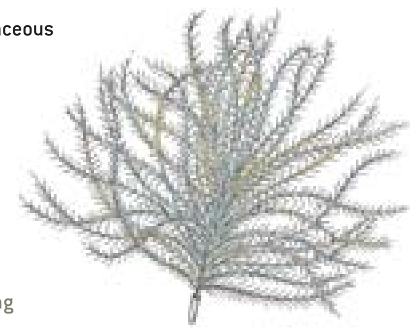
THE NATURE OF FEATHERS

FEATHERS DISPLAY AN AMAZING DIVERSITY and serve almost as wide a range of functions, from courtship to camouflage to flight. Variations in the shapes of a feather's components—the barbs, barbules and rachis—create this diversity. Most feathers, however, fall into two basic types. The pennaceous is the iconic feather of a quill pen or a bird's wing. The plumulaceous, or downy, feather has soft, tangled plumes that provide lightweight insulation.





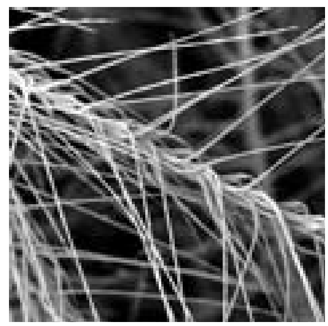
PENNACEOUS FEATHER
Paired barbs fused to the central rachis create the defining vane of a pennaceous feather. In the closed pennaceous portion of the vane, tiny hooklets on one barbule interlock with grooves in the neighboring barbule (*detail* and *middle micrograph*) to form a tight, coherent surface. In the open pennaceous portion, the barbules do not hook together. Closed pennaceous feathers are essential for avian flight.



PLUMULACEOUS (DOWNY) FEATHER
A plumulaceous feather has no vane. It is characterized by a rudimentary rachis and a jumbled tuft of barbs with elongated barbules.

Open pennaceous vane

Closed pennaceous vane



Plumulaceous (downy) feather

DOWNY FEATHER
Fluffy structure provides insulation.

CONTOUR FEATHER
Planar vane helps form the outline of the body.

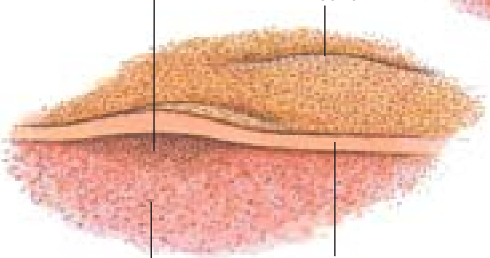
FLIGHT FEATHER
Asymmetrical vane creates aerodynamic forces.

PINFEATHERS
Newly emerged, incompletely developed feathers are visible on two species of cockatoo.

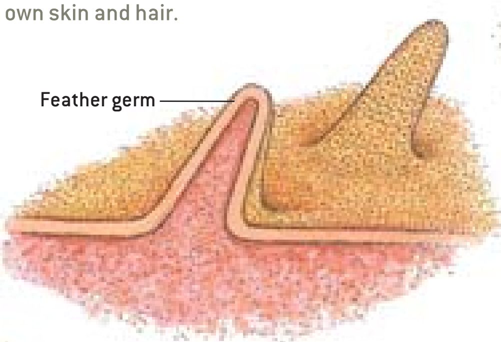
ILLUSTRATIONS BY PATRICIA J. WYNNE; MICROGRAPHS BY TIM LEE QUINN; FEATHER PHOTOGRAPHS BY TINA WEST; COCKATOOS PHOTOGRAPH BY GAIL J. WORTH *Aves International*

HOW FEATHERS GROW

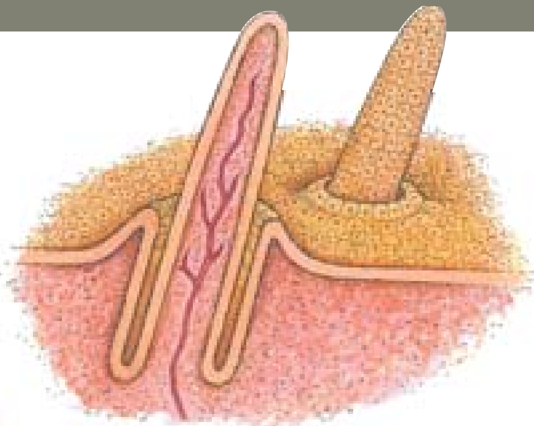
AS IN HAIR, NAILS AND SCALES, feathers grow by proliferation and differentiation of keratinocytes. These keratin-producing cells in the epidermis, or outer skin layer, achieve their purpose in life when they die, leaving behind a mass of deposited keratin. Keratins are filaments of proteins that polymerize to form solid structures. Feathers are made of beta-keratins, which are unique to reptiles and birds. The outer covering of the growing feather, called the sheath, is made of the softer alpha-keratin, which is found in all vertebrates and makes up our own skin and hair.



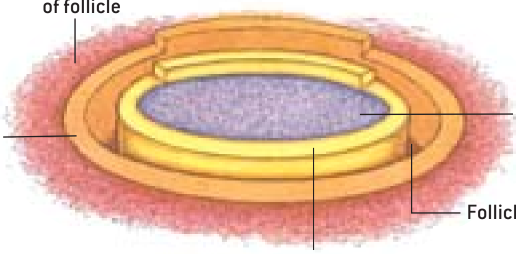
Feather growth begins with the placode, a thickening of the epidermis over a condensation of cells in the dermis.



The placode then forms a unique elongated tube, the feather germ.



Proliferation of cells in a ring around the feather germ creates the follicle (*detail below*), the organ that generates the feather. At the base of the follicle, in the follicle collar, the continuing production of keratinoctyes forces older cells up and out, eventually forming the entire, tubular feather.



Evo-Devo Comes to the Feather

TOGETHER WITH VARIOUS COLLEAGUES, we think the process of feather development can be mined to reveal the probable nature of the primitive structures that were the evolutionary precursors of feathers. Our developmental theory proposes that feathers evolved through a series of transitional stages, each marked by a developmental evolutionary novelty, a new mechanism of growth. Advances at one stage provided the basis for the next innovation [*see box on pages 78 and 79*].

In 1999 we proposed the following evolutionary scheme. Stage 1 was the tubular elongation of the placode from a feather germ and follicle. This yielded the first feather—an unbranched, hollow cylinder. Then, in stage 2, the follicle collar, a ring of epidermal tissue, differentiated (specialized): the inner layer became the longitudinal barb ridges, and the outer layer became a protective sheath. This stage produced a tuft of barbs fused to the hollow cylinder, or calamus.

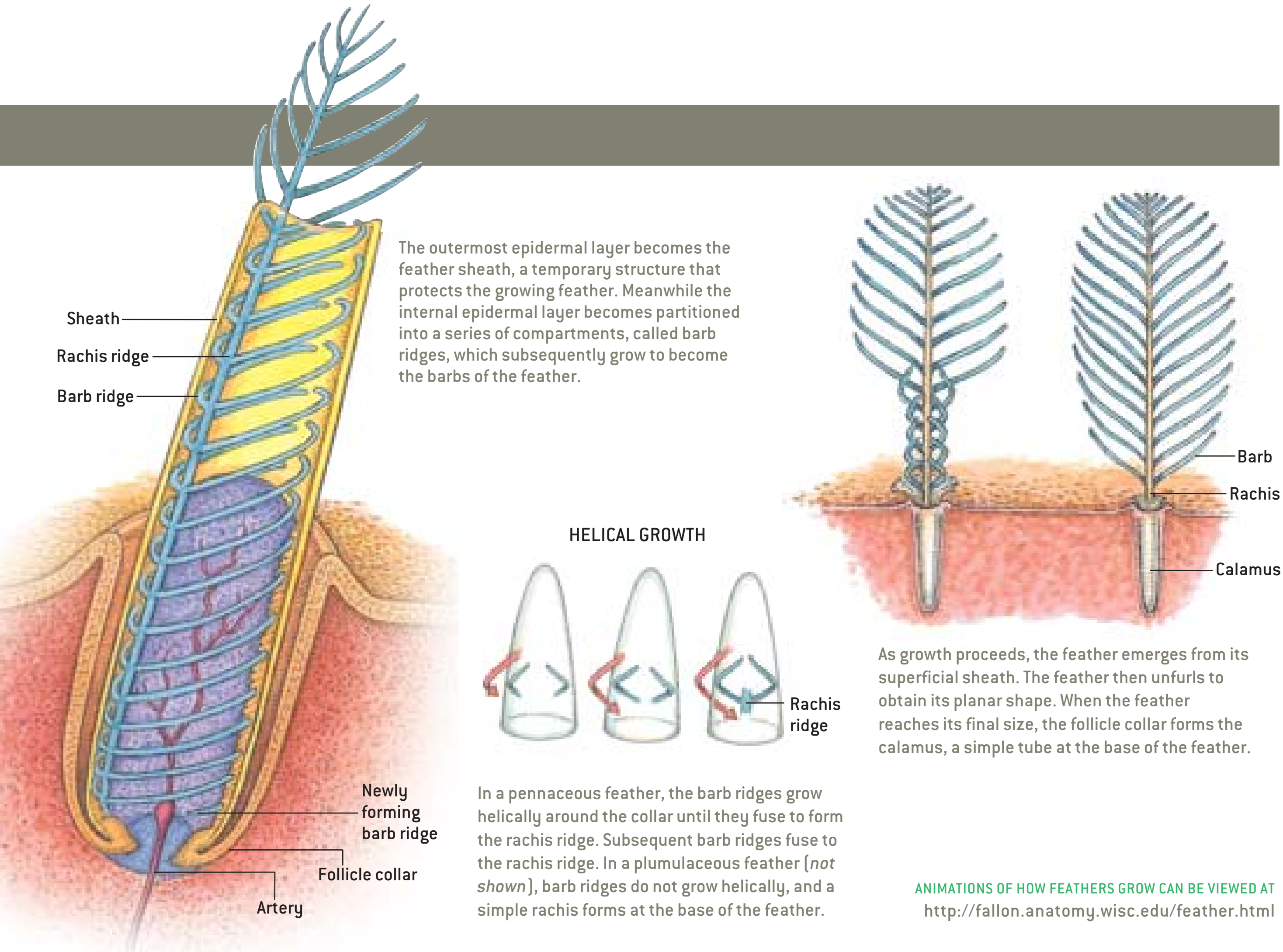
The model has two alternatives for the next stage—either the origin of helical growth of barb ridges and formation of the rachis (stage 3a) or the origin of the barbules (3b). The ambiguity about which came first arises because feather development does not indicate clearly which event occurred before the other. A stage 3a follicle would produce a feather with a rachis and a series of simple barbs. A stage 3b follicle would generate a tuft of barbs with branched barbules. Regardless of which stage came first, the evolution of both these features, stage 3a+b, would yield the first double-branched feathers, exhibiting a rachis, barbs and barbules. Because barbules were still undifferentiated at this stage, a feather would be open pennaceous—that is, its vane would not form a tight, coherent surface in which the barbules are locked together.

In stage 4 the capacity to grow differentiated barbules evolved. This advance enabled a stage 4 follicle to produce hooklets at the ends of barbules that could attach to the grooved barbules of the adjacent barbs and create a pennaceous feather with a closed vane. Only after stage 4 could additional feather variations evolve, including the many specializations seen at stage 5, such as the asymmetrical vane of a flight feather.

The Supporting Cast

INSPIRATION FOR THE THEORY came from the hierarchical nature of feather development itself. The model hypothesizes, for example, that a simple tubular feather preceded the evolution of barbs because barbs are created by the differentiation of the tube into barb ridges. Likewise, a plumulaceous tuft of barbs evolved before the pennaceous feather with a rachis because the rachis is formed by the fusion of barb ridges.

PATRICIA J. WYNNE



The outermost epidermal layer becomes the feather sheath, a temporary structure that protects the growing feather. Meanwhile the internal epidermal layer becomes partitioned into a series of compartments, called barb ridges, which subsequently grow to become the barbs of the feather.

In a pennaceous feather, the barb ridges grow helically around the collar until they fuse to form the rachis ridge. Subsequent barb ridges fuse to the rachis ridge. In a plumulaceous feather (*not shown*), barb ridges do not grow helically, and a simple rachis forms at the base of the feather.

As growth proceeds, the feather emerges from its superficial sheath. The feather then unfurls to obtain its planar shape. When the feather reaches its final size, the follicle collar forms the calamus, a simple tube at the base of the feather.

ANIMATIONS OF HOW FEATHERS GROW CAN BE VIEWED AT http://fallon.anatomy.wisc.edu/feather.html

Similar logic underlies each of the hypothesized stages of the developmental model.

Support for the theory comes in part from the diversity of feathers among modern birds, which sport feathers representing every stage of the model. Obviously, these feathers are recent, evolutionarily derived simplifications that merely revert back to the stages that arise during evolution, because complex feather diversity (through stage 5) must have evolved before *Archaeopteryx*. These modern feathers demonstrate that all the hypothesized stages are within the developmental capacity of feather follicles. Thus, the developmental theory of feather evolution does not require any purely theoretical structures to explain the origin of all feather diversity.

Support also comes from exciting molecular findings that have confirmed the first three stages of the evo-devo model. Recent technological advances allow us to peer inside cells and identify whether specific genes are expressed (turned on so that they can give rise to the products they encode). Several laboratories have combined these methods with experimental techniques that investigate the functions of the proteins made when their genes are expressed during feather development. Matthew Harris and John F. Fallon of the University of Wisconsin–Madison and one of us (Prum) have studied two important pattern formation genes—*sonic hedgehog* (*Shh*) and *bone morphogenetic protein 2* (*Bmp2*). These genes play a crucial role in the growth of vertebrate limbs, digits, and integumentary appendages such as hair, teeth and nails. We found that Shh and Bmp2 proteins work as a modular pair of signaling molecules that, like a general-purpose electronic component, is reused repeatedly throughout feather development. The Shh protein induces cell proliferation, and the Bmp2 protein regulates the extent of proliferation and fosters cell differentiation.

The expression of Shh and Bmp2 begins in the feather placode, where the pair of proteins is produced in a polarized anterior-posterior pattern. Next, Shh and Bmp2 are both expressed

THE AUTHORS

RICHARD O. PRUM and *ALAN H. BRUSH* share a passion for feather biology. Prum, who started bird-watching at the age of 10, is now professor of ecology and evolutionary biology at Yale University and curator of ornithology at the Peabody Museum of Natural History there. His research has focused on avian phylogeny, avian courtship and breeding systems, the physics of structural colors, and the evolution of feathers. He has conducted field studies in Central and South America, Madagascar and New Guinea. Brush is emeritus professor of ecology and evolutionary biology at the University of Connecticut. He has worked on feather pigment and keratin biochemistry and the evolution of feather novelties. He was editor of *The Auk*.

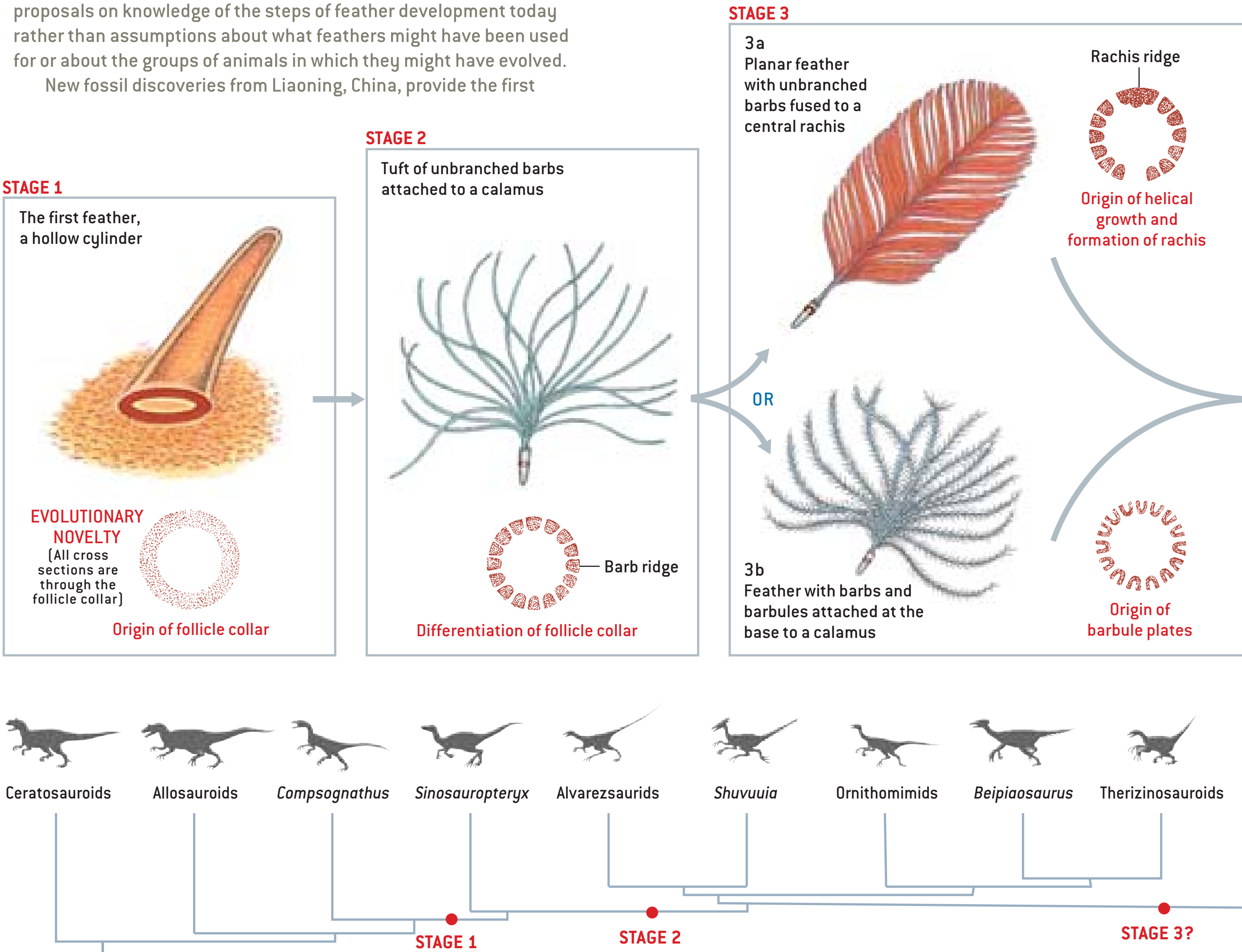
at the tip of the tubular feather germ during its initial elongation and, following that, in the epithelium that separates the forming barb ridges, establishing a pattern for the growth of the ridges. Then, in pennaceous feathers, the Shh and Bmp2 signaling lays down a pattern for helical growth of barb ridges and rachis formation, whereas in plumulaceous feathers the Shh and Bmp2 signals create a simpler pattern of barb growth. Each stage in the development of a feather has a distinct pattern of Shh and Bmp2 signaling. Again and again the two proteins perform critical tasks as the feather unfolds to its final form.

These molecular data confirm that feather development is composed of a series of hierarchical stages in which subsequent events are mechanistically dependent on earlier stages. For example, the evolution of longitudinal stripes in Shh-Bmp2 expression is contingent on the prior development of an elongate tubular feather germ. Likewise, the variations in Shh-Bmp2 patterning during pennaceous feather growth are contingent on the prior establishment of the longitudinal stripes. Thus, the molec-

EVO-DEVO AND THE FEATHER

THE AUTHORS' THEORY of feather origin grew out of the realization that the mechanisms of development can help explain the evolution of novel features—a field dubbed evo-devo. The model proposes that the unique characteristics of feathers evolved through a series of evolutionary novelties in how they grow, each of which was essential for the appearance of the next stage. Thus, the theory bases its proposals on knowledge of the steps of feather development today rather than assumptions about what feathers might have been used for or about the groups of animals in which they might have evolved.

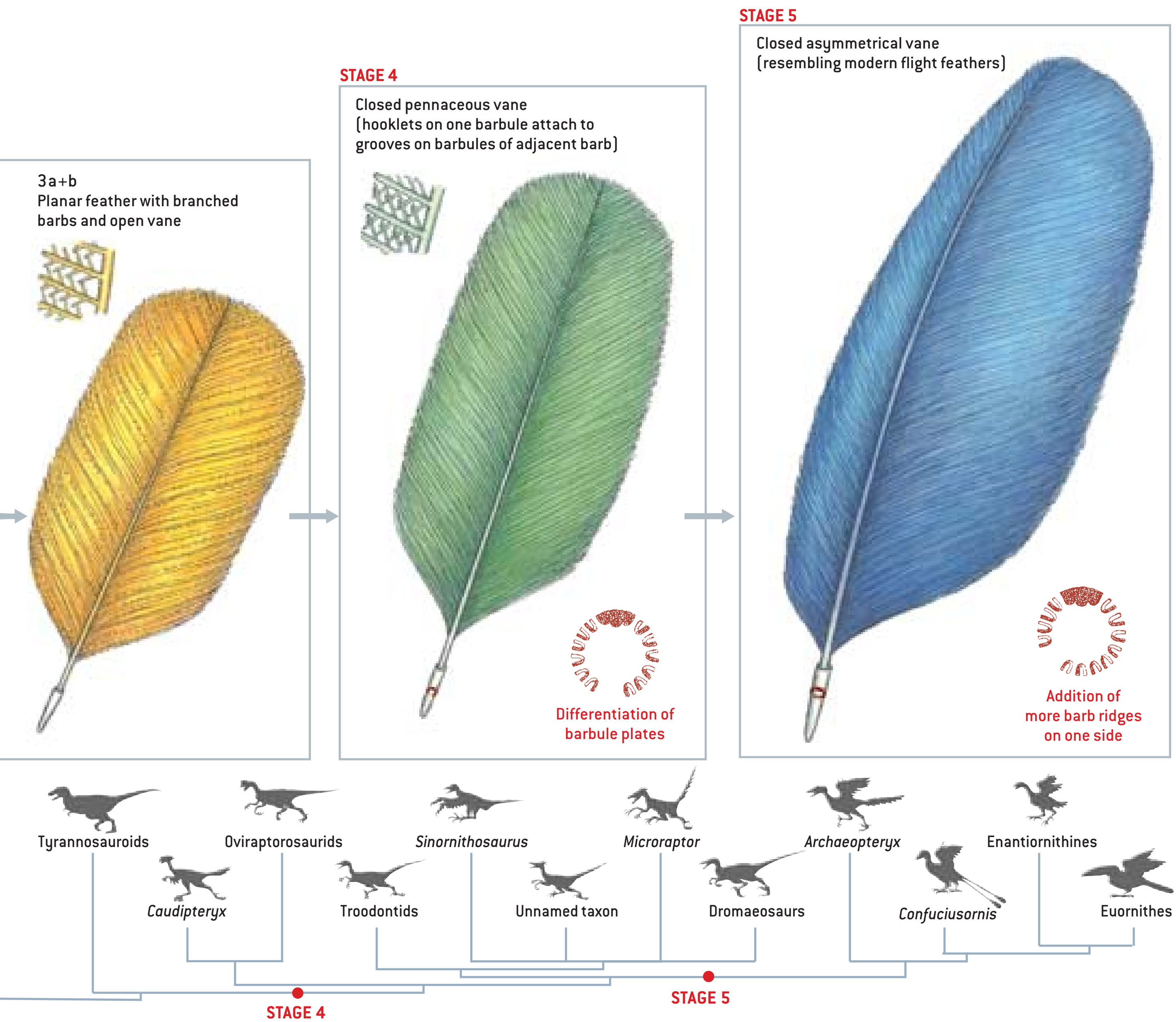
New fossil discoveries from Liaoning, China, provide the first insights into which theropod dinosaurs evolved the feathers of each hypothesized stage. Based on the similarities between the primitive feather predictions of the model and the shapes of the fossil skin appendages, the authors suggest that each stage evolved in a particular group of dinosaurs.



ular data are beautifully consistent with the scenario that feathers evolved from an elongate hollow tube (stage 1), to a downy tuft of barbs (stage 2), to a pennaceous structure (stage 3a).

The Stars of the Drama

NEW CONCEPTUAL THEORIES have spurred our thinking, and state-of-the-art laboratory techniques have enabled us to eavesdrop on the cell as it gives life and shape to a feather. But plain old-fashioned detective work in fossil-rich quarries in northern China has turned up the most spectacular evidence for the developmental theory. Chinese, American and Canadian paleontologists in Liaoning Province have unearthed a startling trove of fossils in the Early Cretaceous Yixian Formation (124 million to 128 million years old). Excellent conditions in the formation have preserved an array of ancient organisms, including the earliest placental mammal, the earliest flowering plant, an explosion of ancient birds [see "The Origin of Birds and Their Flight," by Kevin Padian and Luis M.



PATRICIA J. WYNNE

Chiappe; SCIENTIFIC AMERICAN, February 1998] and a diversity of theropod dinosaur fossils with sharp integumentary details. Various dinosaur fossils clearly show fully modern feathers and a variety of primitive feather structures. The conclusions are inescapable: feathers originated and evolved their essentially modern structure in a lineage of terrestrial, bipedal, carnivorous dinosaurs before the appearance of birds or flight.

The first feathered dinosaur found there, in 1997, was a chicken-size coelurosaur (*Sinosauropteryx*); it had small tubular and perhaps branched structures emerging from its skin. Next the paleontologists discovered a turkey-size oviraptoran dinosaur (*Caudipteryx*) that had beautifully preserved, modern-looking pennaceous feathers on the tip of its tail and forelimbs. Some skeptics have claimed that *Caudipteryx* was merely an early flightless bird, but many phylogenetic analyses place it among the oviraptoran theropod dinosaurs. Subsequent discoveries at Liaoning have revealed pennaceous feathers on specimens of dromaeosaurs, the theropods that are hypothesized to be most closely related to birds but that clearly are not birds. In all, investigators found fossil feathers from more than a dozen nonavian theropod dinosaurs, among them the ostrich-size therizinosaur *Beipiaosaurus* and a variety of dromaeosaurs, including *Microraptor* and *Sinornithosaurus*.

FOSSILS FOUND IN QUARRIES in Liaoning Province, China, over the past five years, such as this *Caudipteryx* forelimb, reveal feathered appendages. This dinosaur, which was roughly the size of a turkey, has excellently preserved pennaceous feathers on its tail as well as its forelimbs.

The heterogeneity of the feathers found on these dinosaurs is striking and provides strong direct support for the developmental theory. The most primitive feathers known—those of *Sinosauropteryx*—are the simplest tubular structures and are remarkably like the predicted stage 1 of the developmental model. *Sinosauropteryx*, *Sinornithosaurus* and some other nonavian theropod specimens show open tufted structures that lack a rachis and are strikingly congruent with stage 2 of the model. There are also pennaceous feathers that obviously had differentiated barbules and coherent planar vanes, as in stage 4 of the model.

These fossils open a new chapter in the history of vertebrate skin. We now know that feathers first appeared in a group of theropod dinosaurs and diversified into essentially modern structural variety within other lineages of theropods before the origin of birds. Among the numerous feather-bearing dinosaurs, birds represent one particular group that evolved the ability to fly using the feathers of its specialized forelimbs and tail. *Caudipteryx*, *Protopteryx* and dromaeosaurs display a prominent "fan" of feathers at the tip of the tail, indicating that even some aspects of the plumage of modern birds evolved in theropods.

The consequence of these amazing fossil finds has been a simultaneous redefinition of what it means to be a bird and a reconsideration of the biology and life history of the theropod dinosaurs. Birds—modern birds and the group that includes all species descended from the most recent common ancestor of *Archaeopteryx*—used to be recognized as the flying, feathered vertebrates. Now we must acknowledge that birds are a group of the feathered theropod dinosaurs that evolved the capacity of powered flight. New fossil discoveries have continued to close the gap between birds and dinosaurs and ultimately make it more difficult even to define birds. Conversely, many of the most charismatic and culturally iconic dinosaurs, such as *Tyrannosaurus* and *Velociraptor,* are very likely to have had feathered skin but were not birds.

Dinosaur or Bird? The Gap Narrows

THE DISTINCTIONS between birds and dinosaurs continue to diminish with every new discovery. In 2003 Xing Xu and Zhonghe Zhou of the Institute of Vertebrate Paleontology and Paleoanthropology at the Chinese Academy of Sciences described some remarkable new specimens of *Microraptor gui,* a dromaeosaur in the group of theropods that are most closely related to birds. The creatures have asymmetrical feathers on both their arms and legs. In living birds, feathers with asymmetrical vanes function in flight. *Microraptor* had four wings—two on its arms and two on its legs—that apparently had an aerodynamic function. Xu and colleagues hypothesize that *Microraptor* was an advanced glider, and because *Microraptor* is in the group that is most closely related to birds, they further propose that the two-winged powered flight of birds evolved through a similar four-winged gliding ancestor.

The debate on the origin of bird flight has focused on two competing hypotheses: flight evolved from the trees through a

MICK ELLISON

gliding stage, or flight evolved from the ground through a powered running stage. The trees-down theory gets some additional new support with the discovery of a functional glider in the theropod dinosaurs most closely related to birds. Many questions remain, of course, including how *Microraptor* actually used its four wings.

For thousands of years, humans have believed that feathers and feather-powered flight were unique to birds. But we have learned that feathers evolved and diversified in theropod dinosaurs before the origin of birds and discovered that even some aspects of avian flight may not be unique to birds. Both of the historical claims to the status of the birds as a special class of vertebrates—feathers and flight—have evaporated. Although this realization may disappoint some people, the disappearance of large gaps in our knowledge about the tree of life represents a great success for evolutionary biology.

A Fresh Look

THANKS TO THE DIVIDENDS provided by the recent findings, researchers can now reassess the various earlier hypotheses about the origin of feathers. The new evidence from developmental biology is particularly damaging to the classical theory that feathers evolved from elongate scales. According to this scenario, scales became feathers by first elongating, then growing fringed edges, and finally producing hooked and grooved barbules. As we have seen, however, feathers are tubes; the two planar sides of the vane—the front and the back—are created by the inside and outside of the tube only after the feather unfolds from its cylindrical sheath. In contrast, the two planar sides of a scale develop from the top and bottom of the initial epidermal outgrowth that forms the scale.

The fresh evidence also puts to rest the popular and enduring theory that feathers evolved primarily or originally for flight. Only highly evolved feather shapes—namely, the asymmetrical feather with a closed vane, which did not occur until stage 5—could have been used for flight. Proposing that feathers evolved for flight now appears to be like hypothesizing that fingers evolved to play the piano. Rather feathers were "exapted" for their aerodynamic function only after the evolution of substantial developmental and structural complexity. They evolved for some other purpose and were then exploited for a different use.

Numerous other proposed early functions of feathers remain plausible, including insulation, water repellency, courtship, camouflage and defense. Even with the wealth of new paleontological data, though, it seems unlikely that we will ever gain sufficient insight into the biology and natural history of the specific lineage in which feathers evolved to distinguish among these hypotheses. Instead our theory underscores that feathers evolved by a series of developmental innovations, each of which may have evolved for a different original function. We do know, however, that feathers emerged only after a tubular feather germ and follicle formed in the skin of some species. Hence, the first feather evolved because the first tubular appendage that grew out of the skin provided some kind of survival advantage.

XING XU

NEWLY DISCOVERED *Microraptor gui* had asymmetrical feathers, blurring the distinction between birds and dinosaurs.

Creationists and other evolutionary skeptics have long pointed to feathers as a favorite example of the insufficiency of evolutionary theory. There were no transitional forms between scales and feathers, they have argued. Further, they asked why natural selection for flight would first divide an elongate scale and then evolve an elaborate new mechanism to weave it back together. Now, in an ironic about-face, feathers offer a sterling example of how we can best study the origin of an evolutionary novelty: focus on understanding those features that are truly new and examine how they form during development in modern organisms. This new paradigm in evolutionary biology is certain to penetrate many more mysteries. Let our minds take wing. SA

MORE TO EXPLORE

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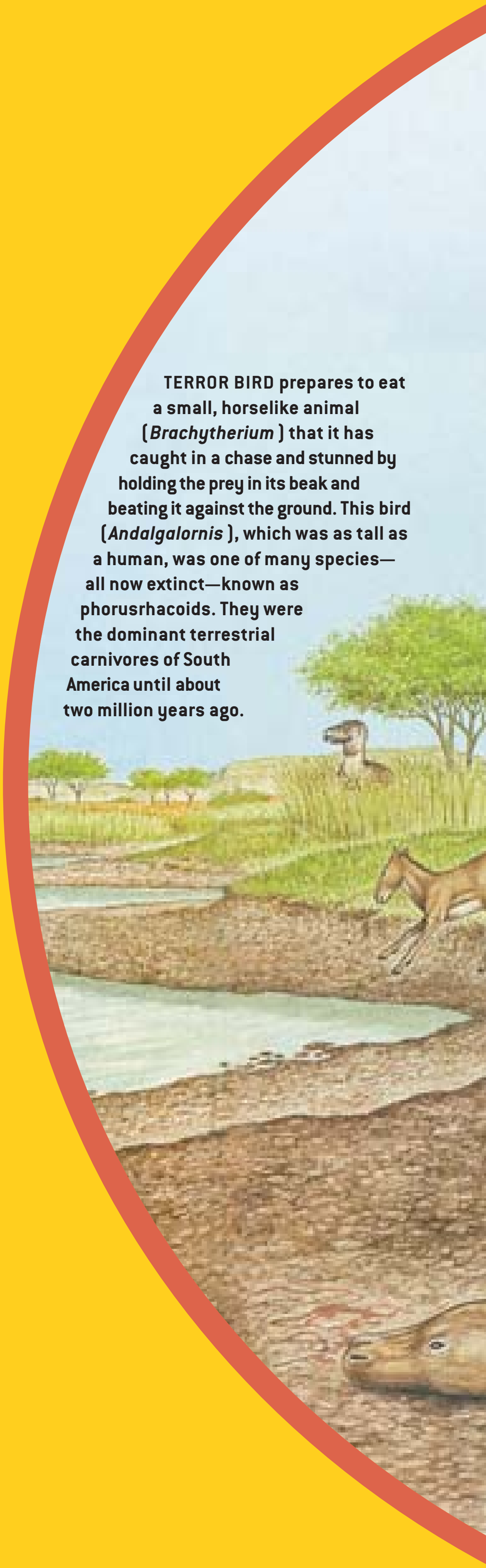
the Terror Birds of South America

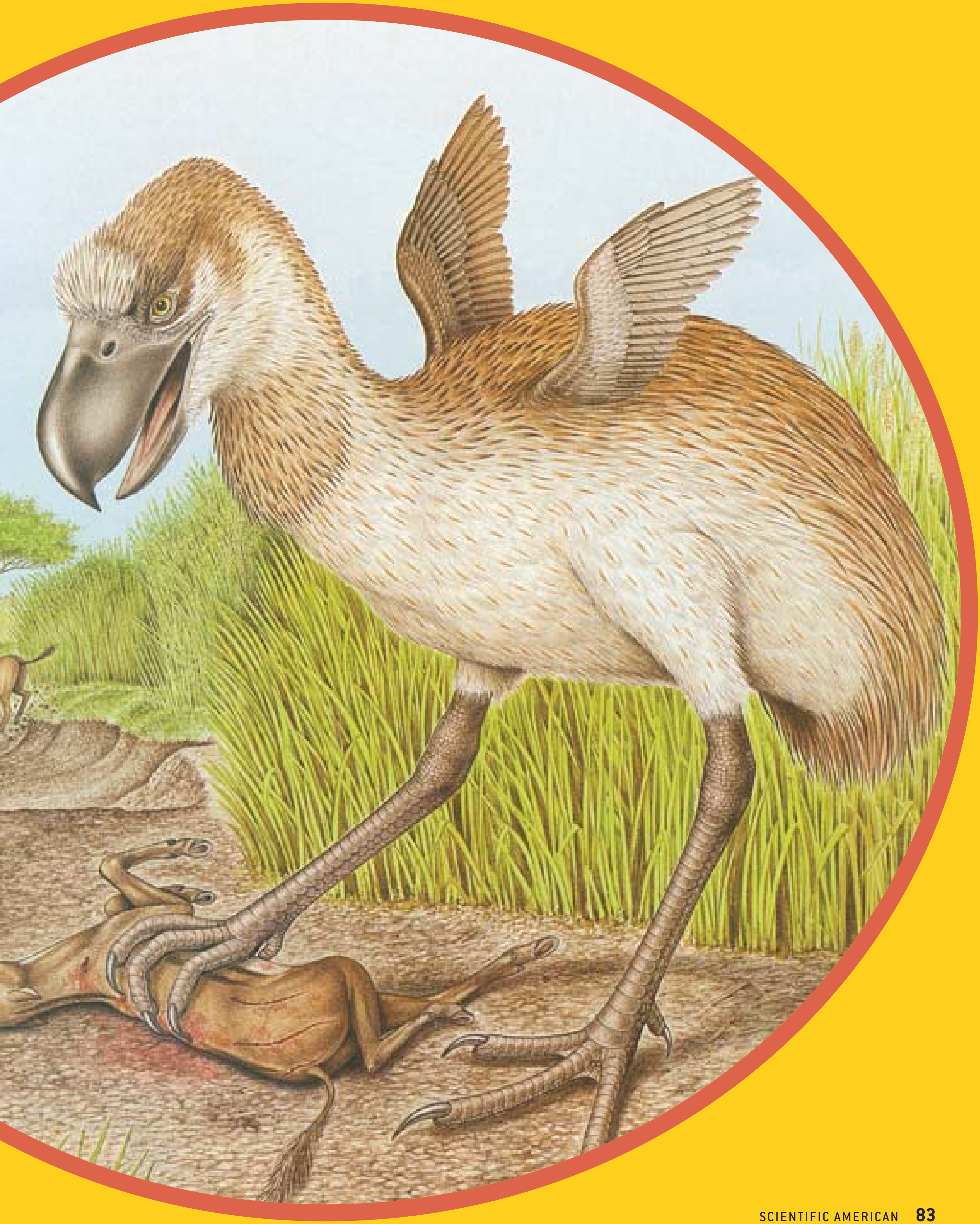
These huge, swift creatures were the dominant carnivores of the continent for millions of years, until competitors drove them into extinction

By Larry G. Marshall



TERROR BIRD prepares to eat a small, horselike animal (*Brachytherium*) that it has caught in a chase and stunned by holding the prey in its beak and beating it against the ground. This bird (*Andalgalornis*), which was as tall as a human, was one of many species—all now extinct—known as phorusrhacoids. They were the dominant terrestrial carnivores of South America until about two million years ago.

Updated from the February 1994 issue

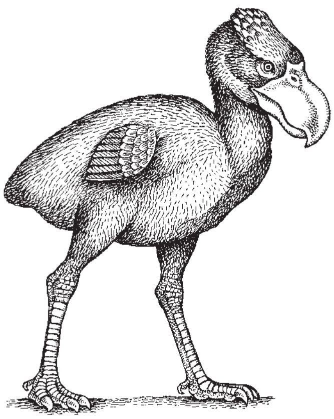


It is a summer day on the pampas of central Argentina some five million years ago. A herd of small, horselike mammals are grazing peacefully in the warm sun. None of the animals is aware of the tall, vigilant creature standing 50 meters away in the high grass. Most of the watcher's trim, feathered body is concealed by the vegetation. Its eyes, set on the sides of a disproportionately large head perched on a long and powerful neck, are fixed on the herd. The head moves from side to side in short, rapid jerks, permitting a fix on the prey without the aid of stereoscopic vision.

Soon the head drops to the level of the grass, and the creature moves forward a few meters, then raises its head again to renew the surveillance. At a distance of 30 meters, the animal is almost ready to attack. In preparation, it lowers its head to a large rock close to its feet, rubbing its deep beak there to sharpen the bladelike edges.

Now the carnivore bristles its feathers and springs. Propelled by two long, muscular legs, it dashes toward the herd. Within a few seconds it is moving at 70 kilometers an hour. Its small wings, useless for flight, are extended to the sides in aid of balance and maneuverability.

The herd, stricken with fright, bolts in disarray as the predator bears down. The attacker fixes its attention on an old male lagging behind the fleeing animals and quickly gains on it. Although the old male runs desperately, the attacker is soon at its side. With a stunning sideswipe of its powerful left foot, it knocks the prey off balance, seizes it in its massive beak and, with swinging motions of its head, beats it on the ground until it is unconscious. Now the attacker can swallow the limp body whole—an easy feat, given the creature's meter-long head and half-meter gape. Content, the gorged predator returns to its round nest of twigs in the grass nearby and resumes the incubation of two eggs the size of basketballs.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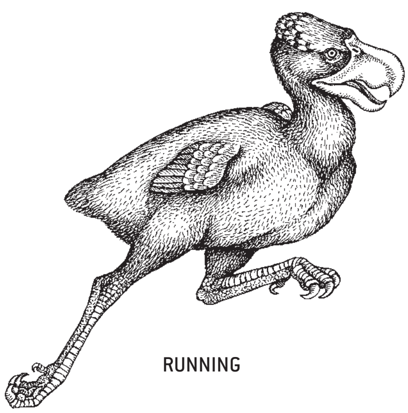
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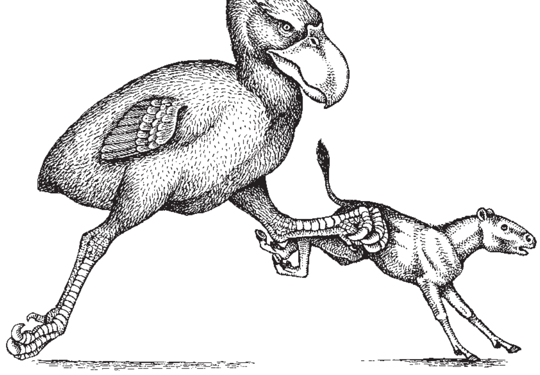
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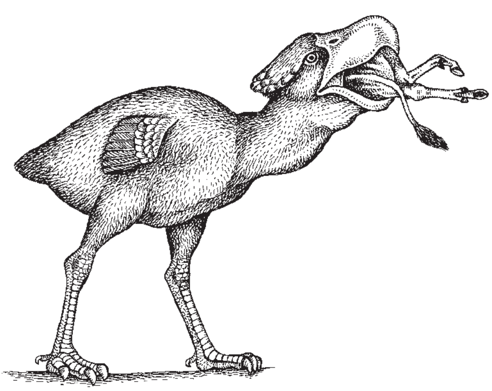
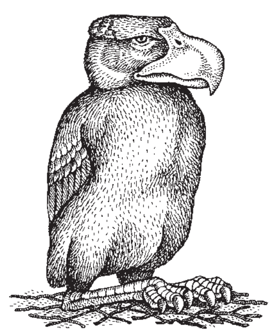

EATING


GORGED

HUNTING TECHNIQUE of a terror bird was focused and deadly. Living on the pampas of South America, the bird could stay hidden in the grass until it had drawn close to its prey. It would then dash toward its victim at speeds close to 70 kilometers an hour, seize the catch in its beak and stun it. It often ate its catch whole. Having no natural predators itself, it could then feed at leisure before returning to its nest.

ROBERTO OSTI (*preceding pages*); PATRICIA J. WYNNE (*this page*)

LIVING RELATIVES of the phorusrhacoids are the seriema birds of South America: the red-legged (*Cariama cristata*) (*left*) and the black-legged, or Burmeister's, seriema (*Chunga burmeisteri*) (*below*). The seriemas, considerably smaller at about 0.7 meter, hunt much as the terror birds did. Seriema nests are in low trees, but the terror birds built nests on the ground.

RONALD ORENSTEIN *Animals Animals* (*top*); FRANCISCO ERIZE *Bruce Coleman, Inc.* (*bottom*)

Eating Machines

MEET THE TERROR BIRDS, the most spectacular and formidable group of flightless, flesh-eating birds that ever lived. They are all extinct now, but they were once to the land what sharks are to the seas: engines of destruction and awesome eating machines. In their time, from 62 million years to about 2.5 million years ago, these creatures became the dominant carnivores of South America. Yet they ultimately declined as a result of competition from other carnivores.

The terror birds are members of a group ornithologists call phorusrhacoids. The first phorusrhacoid to be described scientifically—in 1887 by Argentine paleontologist Florentino Ameghino—was a fossil that he named *Phorusrhacos longissimus*. (*Phorusrhacos* is the genus; *longissimus* the species. Taxonomists go on to classify living and extinct organisms in increasingly larger groups: family, order, class, phylum, kingdom and, sometimes, domains.) The fossil came from the Santa Cruz Formation in Patagonia, the southernmost region of Argentina; the formation is about 17 million years old.

Ameghino and other researchers reconstructed the appearance of the birds from their fossil remains and their behavior from what creatures that might be living relatives do. The investigators initially interpreted the flesh-eating habits of the phorusrhacoids as an indication that they were related to modern eagles and hawks. Not all paleontologists agreed, and the issue was debated over the next 12 years. Charles W. Andrews of the British Museum resolved the controversy in 1899, concluding that among all living and extinct groups, the phorusrhacoids were most closely related to the South American seriema birds, which could also be regarded as the structural ancestors of the phorusrhacoids. Seriemas live today in the grasslands of northern Argentina, eastern Bolivia, Paraguay, and central and eastern Brazil. Seriemas and phorusrhacoids are classified as members of the order Gruiformes, which includes cranes and rails and their kin.

There are two living seriema species, the red-legged seriema (*Cariama cristata*) and the black-legged, or Burmeister's, seriema (*Chunga burmeisteri*). These birds reach a height of 0.7 meter. They are light-bodied, long-legged and long-necked. Their wings are small relative to their body, and the birds resort to spurts of short-distance flight only when pressed. They are excellent runners, able to attain speeds in excess of 60 kilometers an hour. Seriemas build twig nests, four to six meters above the ground, in low trees. The young, usually two, become fledglings in about a month, whereupon they leave the nest to live and hunt in the nearby grasslands. Like most carnivorous animals, seriemas are territorial. Their call has been described as eerie and piercing.

Seriemas eat insects, reptiles, small mammals and other birds. Under favorable conditions, they will attack larger game. They seize their prey in their beaks and beat the animal on the ground until it is limp enough to be swallowed whole. This feeding strategy is also practiced today by the roadrunner (*Geococcyx californianus*) of the southwestern U.S. and the secretary bird (*Sagittarius serpentarius*) of Africa.

Seriemas are placed in the family Cariamidae, which now is restricted to South America. About 10 fossil species have been found there, the oldest being from the Middle Paleocene epoch (some 62 million years ago) of Brazil. Relatives of this group are represented by two fossil families: the Bathornithidae, which appear in beds 40 million to 20 million years old in North America, and the Idiornithidae, found in certain European rock formations 40 million to 30 million years old. Some scientists believe these families are so closely related that they should all be grouped in the family Cariamidae.

Trading Flight for Speed

MOST OF THE TERROR birds were considerably larger than their living relatives. The creatures ranged in height from one to three meters (just shy of 10 feet). The earliest known members are virtually as specialized as the latest, indicating that they originated before their first appearance in the fossil record.

About a dozen genera and 25 species of terror birds have been recognized. The relation among them is still not clear. They were classified in 1960 by Bryan Patterson of the Museum of Comparative Zoology at Harvard University and Jorge L. Kraglievich of the Municipal Museum of Natural and Traditional Sciences of Mar del Plata in Argentina. This classification ordered the terror birds in three families that, in comparison to families of mammals, include animals of medium, large and gigantic size. Other workers, basing their view on the period of greatest diversity among terror birds, achieved between five million and three million years ago, recognize two families—gigantic and medium—as well as two subfamilies. Some researchers place all the fossils in one family.

In the three-family system the gigantic forms are members of the family Brontornithidae. Fossils of this family have been found in beds ranging in age from 27 million to 17 million years. A heavy, ponderous build characterized the birds; the leg bones were fairly short, the beaks massive. This evidence suggests that the birds were cumbersome runners, slower afoot than the members of the other two families.

Next comes the family Phorusrhacidae. Its members ranged between two and three meters in height. Fossils have been found in rocks ranging in age from 27 million to three million years. The third family, Psilopteridae, comprised quite small members; most of them stood no more than one meter in height. Their known fossils range from 62 million to two million years in age. Within this family is the oldest known phorusrhacoid, *Paleopsilopterus,* which was found in Brazil. Members of these last two families were lightly built, swift runners. They were the members that became the dominant running carnivores of their time, and they held that status for millions of years.

The fact that phorusrhacoids came in several sizes indicates that the adults were capable of preying on a wide variety of animals, from rodents to large herbivores. Although some of the adult herbivores were as big as some adult phorusrhacoids, the birds could easily have preyed on the young ones. Phorusrhacoids newly out of the nest would certainly have had different food needs because they were smaller; they probably hunted rodents and other small vertebrates, much as their living seriema relatives still do.

During most of the age of mammals (the past 66 million years or so), phorusrhacoids thus occupied the role of fleet-footed carnivores in South America. They were able to assume this role by giving up the greatest virtue of being a bird—the power of flight. The door to dominance as carnivores opened to the phorusrhacoids when their predecessors in that role—small, bipedal dinosaurs known as coelurosaurs—disappeared in the dinosaur extinction 66 million years ago. Paleobiologists call such a transition an evolutionary relay.

The forms of the terror birds and the coelurosaurs were quite similar: trim, elongated bodies; long, powerful hind limbs; long necks; large heads. Many coelurosaurs had reduced anterior limbs,

The terror bird's unusual feeding strategy is PRACTICED TODAY BY THE U.S. ROADRUNNER and the African secretary bird.

THE AUTHOR

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indicating that the animals captured, killed and processed prey primarily with the hind limbs and mouth, as the phorusrhacoids did. Coelurosaurs apparently used their long tail as a balance while running; phorusrhacoids probably used their reduced wings for the same purpose. Different strategies and appendages were thus employed to serve the same functional purpose.

Land Bridges Taken

TERROR BIRDS and their relatives are also known outside South America. Their distribution is the key to the intriguing biogeographic history that accounts for the gradual ending of the terror birds' reign as South America's primary carnivores.

In rocks from 55 million to 45 million years old in North America, Europe and Asia, large carnivorous birds are represented by the family Diatrymatidae—which, according to my colleague Herculano M. F. Alvarenga of the University of São Paulo in Brazil, developed characteristics similar to those of the phorusrhacoids. Diatrymatidae family members attained heights of about two meters. Like the phorusrhacoids, they had massive skulls and large claws. Their legs, however, were relatively shorter and sturdier, suggesting that they were more methodical and cumbersome in their movements, much as the brontornithids were.

A reported phorusrhacoid, *Ameghinornis,* is known from the Phosphorites du Quercy rocks, 38 million to 35 million years old, in France. This animal was the size of a living seriema and was apparently capable of brief flight.

The Antarctic is also the scene of similar fossils. Two isolated footprints, 18 centimeters in length, are known in rocks about 55 million years old on the Fildes Peninsula of King George Island in West Antarctica. The three-toed bird was big, broad and elongated, either a ratite (a rhea or an ostrich or one of their relatives) or a phorusrhacoid.

The anterior part of a phorusrhacoid's beak was collected from rocks (dated to 40 million years ago) of the La Meseta Formation on Seymour Island, which is on the south side of the Antarctic Peninsula. The proportions of the beak indicate that the bird was more than two meters tall.

Finally, a formidable phorusrhacoid named *Titanis walleri* is known from rocks in northern Florida aged 2.5 million to 1.5 million years. The estimated height of the bird is more than three meters. This record is the youngest yet found and represents the last of the known terror birds.

A scenario for this pattern of phorusrhacoid distribution can be constructed from the premises that these flightless birds required overland routes for dispersal and that the fossil record accurately reflects their occurrence in space and time.

Both biological and geologic evidence show that a continuously dry land bridge united North and South America about 59 million years ago. It ran by way of the Greater and Lesser Antilles, providing an opportunity for dispersal for various groups of terrestrial vertebrates. Among them were a seriema and a phorusrhacoid (probably a Psilopteridae) that dispersed north.

Fifty-five million to 45 million years ago a land corridor between North America and Europe that included what is now Ellesmere Island provided another route by which the phorusrhacoids could steadily disperse. One group that appeared to have used the route was indeed *Ameghinornis.* A note of caution is in order here: the supposition presumes that the phorusrhacoid group was al-

DECLINE OF TERROR BIRDS began when the Panamanian land bridge (*red*) formed between North and South America some 2.5 million years ago, allowing North American mammals that could outhunt the terror birds to enter South America. Fossils of animals that migrated south or north have been found on both continents (*green dots*). Terror bird fossils (*orange dots*) are mostly in South America. A tip of a jaw (*bottom*) was found in Antarctica.

MICHAEL O. WOODBURNE *University of California, Riverside (jaw)* ready present in North America. No fossils of that age have yet been found there.

From at least 45 million years ago, perhaps as much as 70 million, a body of land united southernmost South America and West Antarctica. The supposition of a land connection at this time is supported by a group of marsupials, an armadillo and the southern beech in the same rock beds as the phorusrhacoid on Seymour Island. Together the land bridge and the cool, temperate climate of the time account for the presence of terror birds in West Antarctica 40 million years ago.

Eventually the land bridges uniting South America with North America and Antarctica disappeared. South America remained an island continent until the appearance of the Panamanian land bridge 2.5 million years ago. The bridge formed as a result of the continued tectonic uplift of the northern Andes region, probably associated with a worldwide drop in sea level of as much as 50 meters resulting from the buildup of the polar ice caps. The final connection of the bridge was completed in the area of what has become southern Panama and northern Colombia.

A cooling of world climates at the time shrank tropical habitats and expanded the savannas. Grassland environments were established on the land bridge. After a time, a continuous corridor of savannas extended from Argentina to Florida. The reciprocal dispersal of terrestrial fauna made possible by these conditions is now known as the Great American Interchange. It represents the best-documented example in the fossil record of the intermingling of two long-separated continental biotas. Among the participants were the terror birds. One phorusrhacoid lineage survived beyond 2.5 million years ago in South America, and individuals dispersed north to give rise to *Titanis* in Florida.

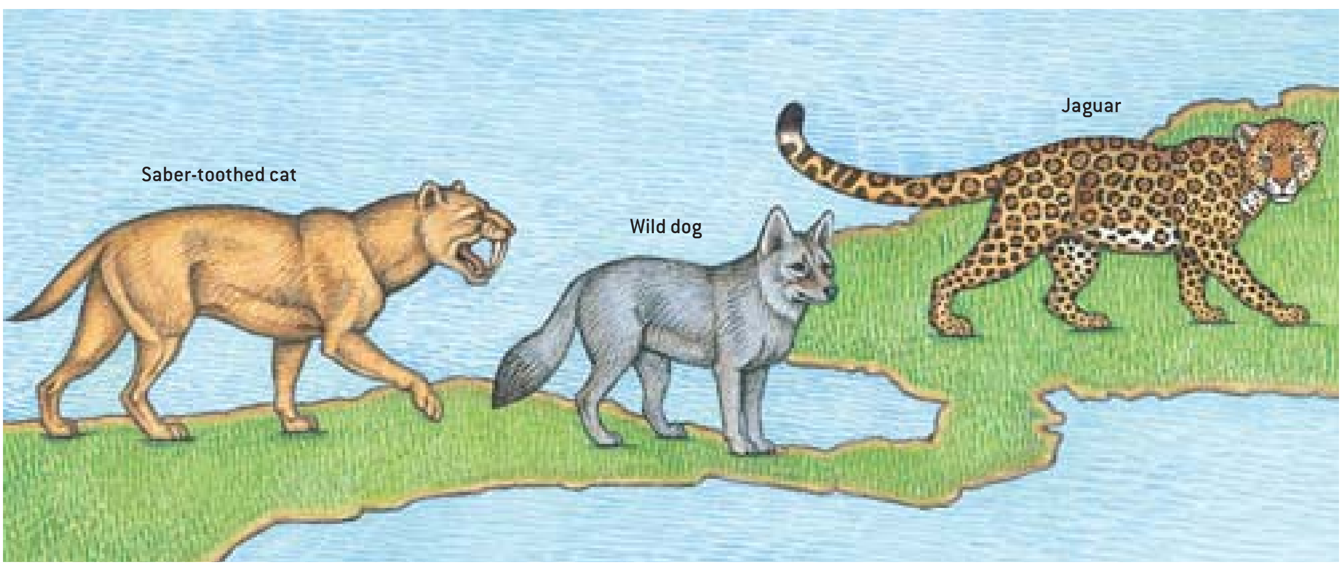
Against this background, one can begin to see why a group of large, flightless birds rose to the top of the food pyramid in South America and why they finally lost that position. The answer lies in the historical development of the terrestrial fauna of South America.

Recall that for most of the past 66 million years South America was, as Australia is today, an island continent. As a consequence of the groups that inhabited each of these continents 66 million years ago, the role of terrestrial mammal carnivores was filled in South America by marsupials and the role of large herbivores by placentals. This marsupial-placental combination was unique among continental faunas; both roles were filled by marsupials in Australia and by placentals in North America, Europe and Asia.

The group of South American marsupials that evolved to fill the place that placental dogs and cats eventually held on the northern continents is called borhyaenoid. Its doglike members are further grouped into three families. They ranged in size from that of a skunk to that of a bear. One specialized family, the thylacosmilids, had characteristics similar to those of the placental saber-toothed cats. It is particularly significant that all these animals were relatively short-legged and that none showed marked adaptation to running. These were the mammal occupants of the carnivore niche in South America.

Gone to the Dogs

ALSO IN THIS NICHE were large terrestrial or semiterrestrial crocodiles of the family Sebecidae. They had deep skulls; their limbs were positioned more under the body than those of aquatic, flat-skulled crocodiles, and their laterally compressed teeth had serrated cutting edges, much like those of carnivorous dinosaurs. The other occupants of the carnivore niche were the terror birds. Thus, from about 66 million to about 2.5 million years ago, the role of terrestrial carnivores in South America was shared at various times, but not equally, by mar-



PATRICIA J. WYNNE

DOWNFALL OF THE TERROR BIRDS was apparently caused by the influx of many species of carnivores, particularly large dogs and cats, that crossed the Panamanian land bridge into South America. Greater intelligence, more speed and agility, or the ability to prey on terror bird eggs and hatchlings could explain how these migrants from North America displaced the long-established terror birds.

supial mammals, sebecid crocodiles and phorusrhacoid birds.

From about 27 million to 2.5 million years ago, the fossil record shows a protracted decrease in the size and diversity of the doglike borhyaenoids and a concurrent increase in the size and diversity of the phorusrhacoids. Consequently, by about five million years ago, phorusrhacoids had completely replaced rusrhacoids. It proved to be a losing battle for the birds.

The Riddle Remains

THUS IT WAS that the phorusrhacoids reached their peak in size and diversity just before the interchange, gradually declining thereafter because of the competition with the dogs and cats. Only one lineage survived beyond 2.5 million years in

The terror birds thus flourished in the absence of advanced placental carnivores, which have repeatedly shown themselves to be better competitors. The marsupial borhyaenoids and placental creodonts were, in essence and in comparison with the terror birds, second rate.

Though plausible, this argument is speculative. One cannot identify with certainty a single factor that explains the

Competing with big dogs and cats that crossed THE PANAMANIAN LAND BRIDGE PROVED TO BE a losing battle for the large birds.

the large carnivorous borhyaenoids on the savannas of South America. (The smaller ones, which were not competitive with the terror birds anyway, also became extinct before the Panamanian land bridge appeared.) This transition demonstrates another relay in the evolutionary history of the phorusrhacoids whereby they successfully replaced their marsupial counterparts, the borhyaenoids. Just why the phorusrhacoids were able to do so is unclear, but their superior running ability would certainly have been an advantage for capturing prey in the savanna environments that first came into prominence about 27 million years ago.

After the emergence of the Panamanian land bridge, placental dogs and cats of the families Canidae and Felidae dispersed into South America from North America. Because all the large marsupial carnivores of South America were by then long extinct, the only competition the dogs and cats had was from the pho-

South America; it is the one that dispersed to Florida, where it is represented by *Titanis*. This was the only South American carnivorous animal to disperse northward. Its success there at coexisting with the advanced placental carnivores was brief. Why that was so is a major riddle. Perhaps the resident placental carnivores were too well established for the phorusrhacoids to find a permanent niche.

The fate of the phorusrhacoid relatives in North America and Europe between 55 million and 45 million years ago is also linked to the appearance of advanced placental carnivores. During that time on the northern continents, the large mammalian carnivores were the creodonts. This primitive group of placentals resembled the marsupial borhyaenoids in that they lacked special running abilities and had rather small brains. The phorusrhacoid relatives on these continents disappeared with the appearance of advanced placental mammals beginning about 45 million years ago.

extinction of any group of animals now found only as fossils. In the case of the terror birds, their disappearance on two occasions in time correlates directly with the appearance of advanced placental carnivores. Were the advanced placentals more intelligent than the terror birds and so better adapted to capturing the prey that the birds had had to themselves? Did the fact that they had four legs give them an advantage over the two-legged phorusrhacoids in speed or agility? Did the placentals eat the phorusrhacoids' eggs, which were readily accessible in ground nests because of the birds' large size? Did the placentals prey on the vulnerable hatchlings?

It is intriguing to think what might happen to the mix of fauna if all big carnivorous mammals were suddenly to vanish from South America. Would the seriemas again give rise to a group of giant flesh-eating birds that would rule the savannas as did the phorusrhacoids and their bygone allies? SA

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the evolution of life on earth

The history of life is not necessarily progressive; it is certainly not predictable. The earth's creatures have evolved through a series of contingent and fortuitous events

By Stephen Jay Gould

Some creators announce their inventions with grand éclat. God proclaimed, "*Fiat lux,*" and then flooded his new universe with brightness. Others bring forth great discoveries in a modest guise, as did Charles Darwin in defining his new mechanism of evolutionary causality in 1859: "I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection."

Natural selection is an immensely powerful yet beautifully simple theory that has held up remarkably well, under intense and unrelenting scrutiny and testing, for 135 years. In essence, natural selection locates the mechanism of evolutionary change in a "struggle" among organisms for reproductive success, leading to improved fit of populations to changing environments. (Struggle is often a metaphorical description and need not be viewed as overt combat, guns blazing. Tactics for reproductive success include a variety of nonmartial activities such as earlier and more frequent mating or better cooperation with partners in raising offspring.) Natural selection is therefore a principle of local adaptation, not of general advance or progress.

Yet powerful though the principle may be, natural selection is not the only cause of evolutionary change (and may, in many cases, be overshadowed by other forces). This point needs emphasis because the standard misapplication of evolutionary theory assumes that biological explanation may be equated with devising accounts, often speculative and conjectural in practice, about the adaptive value of any given feature in its original environment (human aggression as good for hunting, music and religion as good for tribal cohesion, for example). Darwin himself strongly emphasized the multifactorial nature of evolutionary change and warned against too exclusive a reliance on natural selection, by placing the following statement in a maximally conspicuous place at the very end of his introduction: "I am convinced that Natural Selection has been the most important, but not the exclusive, means of modification."

Reality versus Conceit

NATURAL SELECTION is not fully sufficient to explain evolutionary change for two major reasons. First, many other causes are powerful, particularly at levels of biological organization both above and below the traditional Darwinian focus on organisms and their struggles for reproductive success. At the lowest level of substitution in individual base pairs of DNA, change is often effectively neutral and therefore random. At higher levels, involving entire species or faunas, punctuated equilibrium can produce evolutionary trends by selection of species based on their rates of origin and extirpation, whereas mass extinctions wipe out substantial parts of biotas for reasons unrelated to adaptive struggles of constituent species in "normal" times between such events.

Second, and the focus of this article, no matter how adequate our general theory of evolutionary change, we also yearn to document and understand the actual pathway of life's history. Theory, of course, is relevant to explaining the pathway (nothing about the pathway can be inconsistent with good theory, and theory can predict certain general aspects of life's geologic pattern). But the actual pathway is strongly *underdetermined* by our general theory of life's evolution. This point needs some belaboring as a central yet widely misunderstood aspect of the world's complexity. Webs and chains of historical events are so intricate, so imbued with random and chaotic elements, so unrepeatable in encompassing such a multitude of unique (and uniquely interacting) objects, that standard models of simple prediction and replication do not apply.

SLAB CONTAINING SPECIMENS of *Pteridinium* from Namibia shows a prominent organism from the earth's first multicellular fauna, called Ediacaran, which appeared some 600 million years ago. The Ediacaran animals died out before the Cambrian explosion of modern life. These thin, quilted, sheetlike organisms may be ancestral to some modern forms but may also represent a separate and ultimately failed experiment in multicellular life. The history of life tends to move in quick and quirky episodes, rather than by gradual improvement.

History can be explained, with satisfying rigor if evidence be adequate, after a sequence of events unfolds, but it cannot be predicted with any precision beforehand. Pierre-Simon Laplace, echoing the growing and confident determinism of the late 18th century, once said that he could specify all future states if he could know the position and motion of all particles in the cosmos at any moment, but the nature of universal complexity shatters this chimerical dream. History includes too much chaos, or extremely sensitive dependence on minute and unmeasurable differences in initial conditions, leading to massively divergent outcomes based on tiny and unknowable disparities in starting points. And history includes too much contingency, or shaping of present results by long chains of unpredictable antecedent states, rather than immediate determination by timeless laws of nature.

Homo sapiens did not appear on the earth, just a geologic second ago, because evolutionary theory predicts such an outcome based on themes of progress and increasing neural complexity. Humans arose, rather, as a fortuitous and contingent outcome of thousands of linked events, any one of which could have occurred differently and sent history on an alternative pathway that would not have led to consciousness. To cite just four among a multitude: (1) If our inconspicuous and fragile lineage had not been among the few survivors of the initial radiation of multicellular animal life in the Cambrian explosion 530 million years ago, then no vertebrates would have inhabited the earth at all. (Only one member of our chordate phylum, the genus *Pikaia,* has been found among these earliest fossils. This small and simple swimming creature, showing its allegiance to us by possessing a notochord, or dorsal stiffening rod, is among the rarest fossils of the Burgess Shale, our best preserved Cambrian fauna.) (2) If a small and unpromising group of lobe-finned fishes had not evolved fin bones with a strong central axis capable of bearing weight on land, then vertebrates might never have become terrestrial. (3) If a large extraterrestrial body had not struck the earth 65 million years ago, then dinosaurs would still be dominant and mammals insignificant (the situation that had prevailed for 100 million years previously). (4) If a small lineage of primates had not evolved upright posture on the drying African savannas just two to four million years ago, then our ancestry might have ended in a line of apes that, like the chimpanzee and gorilla today, would have become ecologically marginal and probably doomed to extinction despite their remarkable behavioral complexity.

Therefore, to understand the events and generalities of life's pathway, we must go beyond principles of evolutionary theory to a paleontological examination of the contingent pattern of life's history on our planet—the single actualized version among millions of plausible alternatives that happened not to occur. Such a view of life's history is highly contrary both to conventional deterministic models of Western science and to the deepest social traditions and psychological hopes of Western culture for a history culminating in humans as life's highest expression and intended planetary steward.

Science can, and does, strive to grasp nature's factuality, but all science is socially embedded, and all scientists record prevailing "certainties," however hard they may be aiming for pure objectivity. Darwin himself, in the closing lines of *On the Origin of Species,* expressed Victorian social preference more than

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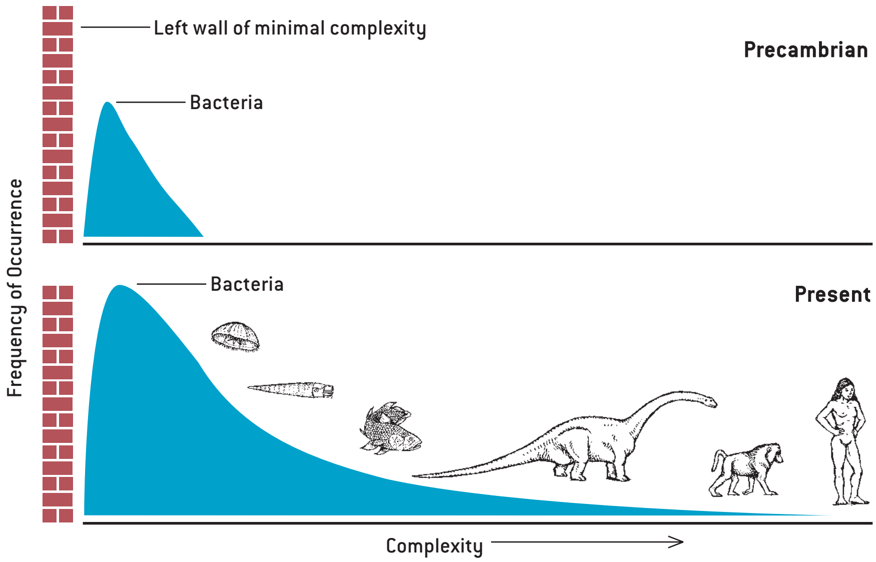

PROGRESS DOES NOT RULE (and is not even a primary thrust of) the evolutionary process. For reasons of chemistry and physics, life arises next to the "left wall" of its simplest conceivable and preservable complexity. This style of life (bacterial) has remained most common and most successful. A few creatures occasionally move to the right, thus extending the right tail in the distribution of complexity. Many always move to the left, but they are absorbed within space already occupied. Note that the bacterial mode has never changed in position, but just grown higher.

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nature's record in writing: "As natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection."

Life's pathway certainly includes many features predictable from laws of nature, but these aspects are too broad and general to provide the "rightness" that we seek for validating evolution's particular results—roses, mushrooms, people and so forth. Organisms adapt to, and are constrained by, physical principles. It is, for example, scarcely surprising, given laws of gravity, that the largest vertebrates in the sea (whales) exceed the heaviest animals on land (elephants today, dinosaurs in the past), which, in turn, are far bulkier than the largest vertebrate that ever flew (extinct pterosaurs of the Mesozoic era).

Predictable ecological rules govern the structuring of communities by principles of energy flow and thermodynamics (more biomass in prey than in predators, for example). Evolutionary trends, once started, may have local predictability ("arms races," in which both predators and prey hone their defenses and weapons, for example—a pattern that Geerat J. Vermeij of the University of California at Davis has called "escalation" and documented in increasing strength of both crab claws and shells of their gastropod prey through time). But laws of nature do not tell us why we have crabs and snails at all, why insects rule the multicellular world and why vertebrates rather than persistent algal mats exist as the most complex forms of life on the earth.

Relative to the conventional view of life's history as an at least broadly predictable process of gradually advancing complexity through time, three features of the paleontological record stand out in opposition and shall therefore serve as organizing themes for the rest of this article: the constancy of modal complexity throughout life's history; the concentration of major events in short bursts interspersed with long periods of relative stability; and the role of external impositions, primarily mass extinctions, in disrupting patterns of "normal" times. These three features, combined with more general themes of chaos and contingency, require a new framework for conceptualizing and drawing life's history, and this article therefore closes with suggestions for a different iconography of evolution.

The Lie of "Progress"

THE PRIMARY paleontological fact about life's beginnings points to predictability for the onset and very little for the particular pathways thereafter. The earth is 4.6 billion years old, but the oldest rocks date to about 3.9 billion years because the earth's surface became molten early in its history, a result of bombardment by large amounts of cosmic debris during the solar system's coalescence and of heat generated by radioactive decay of short-lived isotopes. These oldest rocks are too metamorphosed by subsequent heat and pressure to preserve fossils (although some scientists interpret the proportions of carbon isotopes in these rocks as signs of organic production). The oldest rocks sufficiently unaltered to retain cellular fossils—African and Australian sediments dated to 3.5 billion years old—do preserve prokaryotic cells (bacteria and cyanophytes) and stromatolites (mats of sediment trapped and bound by these cells in shallow marine waters). Thus, life on the earth evolved quickly and is as old as it could be. This fact alone seems to indicate an inevitability, or at least a predictability, for life's origin from the original chemical constituents of atmosphere and ocean.

No one can doubt that more complex creatures arose sequentially after this prokaryotic beginning—first eukaryotic cells, perhaps about two billion years ago, then multicellular animals about 600 million years ago, with a relay of highest complexity among animals passing from invertebrates, to marine vertebrates and, finally (if we wish, albeit parochially, to honor neural architecture as a primary criterion), to reptiles, mammals and humans. This is the conventional sequence represented in the old charts and texts as an "age of invertebrates," followed by an "age of fishes," "age of reptiles," "age of mammals," and "age of man" (to add the old gender bias to all the other prejudices implied by this sequence).

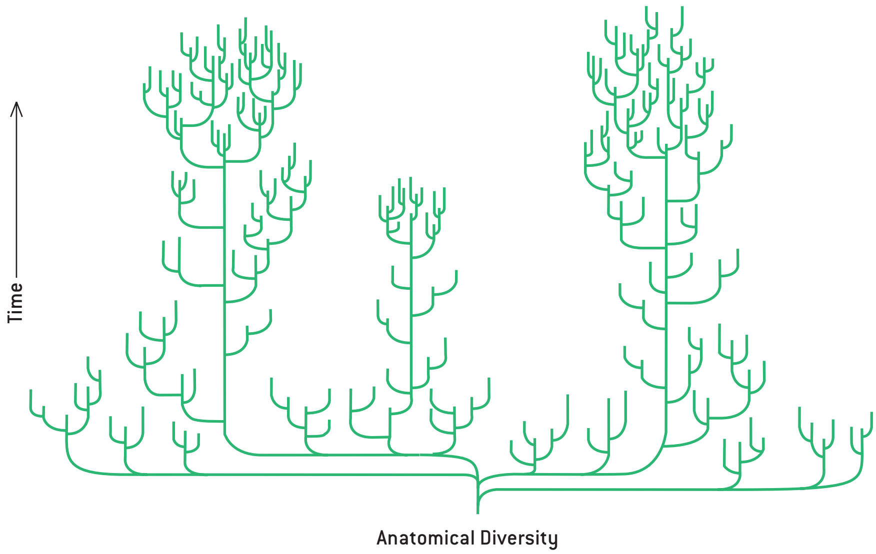
I do not deny the facts of the preceding paragraph but wish to argue that our conventional desire to view history as progressive, and to see humans as predictably dominant, has grossly distorted our interpretation of life's pathway by falsely placing in the center of things a relatively minor phenomenon that arises only as a side consequence of a physically constrained starting point. The most salient feature of life has been the stability of its bacterial mode from the beginning of the fossil record until today and, with little doubt, into all future time so long as the earth endures. This is truly the "age of bacteria"—as it was in the beginning, is now and ever shall be.

For reasons related to the chemistry of life's origin and the physics of self-organization, the first living things arose at the lower limit of life's conceivable, preservable complexity. Call this lower limit the "left wall" for an architecture of complexity. Because so little space exists between the left wall and life's initial bacterial mode in the fossil record, only one direction for future increment exists—toward greater complexity at the right. Thus, every once in a while, a more complex creature evolves and extends the range of life's diversity in the only available direction. In technical terms, the distribution of complexity becomes more strongly right skewed through these occasional additions.

But the additions are rare and episodic. They do not even constitute an evolutionary series but form a motley sequence of distantly related taxa, usually depicted as eukaryotic cell, jellyfish, trilobite, nautiloid, eurypterid (a large relative of horseshoe crabs), fish, an amphibian such as *Eryops*, a dinosaur, a mammal and a human being. This sequence cannot be construed as the major thrust or trend of life's history. Think rather of an occasional creature tumbling into the empty right region of complexity's space. Throughout this entire time, the bacterial mode has grown in height and remained constant in position. Bacteria represent the great success story of life's pathway. They occupy a wider domain of environments and span a broader range of biochemistries than any other group. They are adaptable, indestructible and astoundingly diverse. We cannot even imagine how anthropogenic intervention might threaten their extinction, although we worry about our impact on nearly every other form of life. The number of *Escherichia coli* cells in the gut of each human being exceeds the number of humans that has ever lived on this planet.

One might grant that complexification for life as a whole represents a pseudotrend based on constraint at the left wall but still hold that evolution within particular groups differentially favors complexity when the founding lineage begins far enough from the left wall to permit movement in both directions. Empirical tests of this interesting hypothesis are just beginning (as concern for the subject mounts among paleontologists), and we do not yet have enough cases to advance a generality. But the first two studies—by Daniel W. McShea of the University of Michigan on mammalian vertebrae and by George F. Boyajian of the University of Pennsylvania on ammonite suture lines—show no evolutionary tendencies to favor increased complexity.

Moreover, when we consider that for each mode of life involving greater complexity, there probably exists an equally advantageous style based on greater simplicity of form (as often found in parasites, for example), then preferential evolution toward complexity seems unlikely a priori. Our impression that life evolves toward greater complexity is probably only a bias inspired by parochial focus on ourselves, and consequent overattention to complexifying creatures, while we ignore just as many lineages adapting equally well by becoming simpler in form. The morphologically degenerate parasite, safe within its host, has just as much prospect for evolutionary success as its gorgeously elaborate relative coping with the slings and arrows of outrageous fortune in a tough external world.



NEW ICONOGRAPHY OF LIFE'S TREE shows that maximal diversity in anatomical forms (not in number of species) is reached very early in life's multicellular history. Later times feature extinction of most of these initial experiments and enormous success within surviving lines. This success is measured in the proliferation of species but not in the development of new anatomies. Today we have more species than ever before, although they are restricted to fewer basic anatomies.

Steps, Not Inclines

EVEN IF COMPLEXITY is only a drift away from a constraining left wall, we might view trends in this direction as more predictable and characteristic of life's pathway as a whole if increments of complexity accrued in a persistent and gradually accumulating manner through time. But nothing about life's history is more peculiar with respect to this common (and false) expectation than the actual pattern of extended stability and rapid episodic movement, as revealed by the fossil record.

Life remained almost exclusively unicellular for the first five sixths of its history—from the first recorded fossils at 3.5 billion years to the first well-documented multicellular animals less than

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600 million years ago. (Some simple multicellular algae evolved more than a billion years ago, but these organisms belong to the plant kingdom and have no genealogical connection with animals.) This long period of unicellular life does include, to be sure, the vitally important transition from simple prokaryotic cells without organelles to eukaryotic cells with nuclei, mitochondria and other complexities of intracellular architecture—but no recorded attainment of multicellular animal organization for a full three billion years. If complexity is such a good thing, and multicellularity represents its initial phase in our usual view, then life certainly took its time in making this crucial step. Such delays speak strongly against general progress as the major theme of life's history, even if they can be plausibly explained by lack of sufficient atmospheric oxygen for most of Precambrian time or by failure of unicellular life to achieve some structural threshold acting as a prerequisite to multicellularity.

More curiously, all major stages in organizing animal life's multicellular architecture then occurred in a short period beginning less than 600 million years ago and ending by about 530 million years ago—and the steps within this sequence are also discontinuous and episodic, not gradually accumulative. The first fauna, called Ediacaran to honor the Australian locality of its initial discovery but now known from rocks on all continents, consists of highly flattened fronds, sheets and circlets composed of numerous slender segments quilted together. The nature of the Ediacaran fauna is now a subject of intense discussion. These creatures do not seem to be simple precursors of later forms. They may constitute a separate and failed experiment in animal life, or

1. *Vauxia* (gracile)
2. *Branchiocaris*
3. *Opabinia*
4. *Amiskwia*
5. *Vauxia* (robust)
6. *Molaria*
7. *Aysheaia*
8. *Sarotrocercus*
9. *Nectocaris*
10. *Pikaia*
11. *Micromitra*
12. *Echmatocrinus*
13. *Chancelloria*
14. *Pirania*
15. *Choia*
16. *Leptomitus*
17. *Dinomischus*
18. *Wiwaxia*
19. *Naraoia*
20. *Hyolithes*
21. *Habelia*
22. *Emeraldella*
23. *Burgessia*
24. *Leanchoilia*
25. *Sanctacaris*
26. *Ottoia*
27. *Louisella*
28. *Actaeus*
29. *Yohoia*
30. *Peronochaeta*
31. *Selkirkia*
32. *Ancalagon*
33. *Burgessochaeta*
34. *Sidneyia*
35. *Odaraia*
36. *Eiffelia*
37. *Mackenzia*
38. *Odontogriphus*
39. *Hallucigenia*
40. *Elrathia*
41. *Anomalocaris*
42. *Lingulella*
43. *Scenella*
44. *Canadaspis*
45. *Marrella*
46. *Olenoides*

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they may represent a full range of diploblastic (two-layered) organization, of which the modern phylum Cnidaria (corals, jellyfishes and their allies) remains as a small and much altered remnant.

In any case, they apparently died out well before the Cambrian biota evolved. The Cambrian then began with an assemblage of bits and pieces, frustratingly difficult to interpret, called the "small shelly fauna." The subsequent main pulse, starting about 530 million years ago, constitutes the famous Cambrian explosion, during which all but one modern phylum of animal life made a first appearance in the fossil record. (Geologists had previously allowed up to 40 million years for this event, but an elegant study, published in 1993, clearly restricts this period of phyletic flowering to a mere five million years.) The Bryozoa, a group of sessile and colonial marine organisms, do not arise until the beginning of the subsequent, Ordovician period, but this apparent delay may be an artifact of failure to discover Cambrian representatives.

Although interesting and portentous events have occurred since, from the flowering of dinosaurs to the origin of human consciousness, we do not exaggerate greatly in stating that the subsequent history of animal life amounts to little more than variations on anatomical themes established during the Cambrian explosion within five million years. Three billion years of unicellularity, followed by five million years of intense creativity and then capped by more than 500 million years of variation on set anatomical themes can scarcely be read as a predictable, inexorable or continuous trend toward progress or increasing complexity.

We do not know why the Cambrian explosion could establish all major anatomical designs so quickly. An "external" explanation based on ecology seems attractive: the Cambrian explosion represents an initial filling of the "ecological barrel" of niches for multicellular organisms, and any experiment found a space. The barrel has never emptied since; even the great mass extinctions left a few species in each principal role, and their occupation of ecological space forecloses opportunity for fundamental novelties. But an "internal" explanation based on genetics and development also seems necessary as a complement: the earliest multicellular animals may have maintained a flexibility for genetic change and embryological transformation that became greatly reduced as organisms "locked in" to a set of stable and successful designs.

Either way, this initial period of both internal and external flexibility yielded a range of invertebrate anatomies that may have exceeded (in just a few million years of production) the full scope of animal form in all the earth's environments today (after more than 500 million years of additional time for further expansion). Scientists are divided on this question. Some claim that the anatomical range of this initial explosion exceeded that of modern life, as many early experiments died out and no new phyla have ever arisen. But scientists most strongly opposed to this view allow that Cambrian diversity at least equaled the modern range—so even the most cautious opinion holds that 500 million subsequent years of opportunity have not expanded the Cambrian range, achieved in just five million years. The Cambrian explosion was the most remarkable and puzzling event in the history of life.

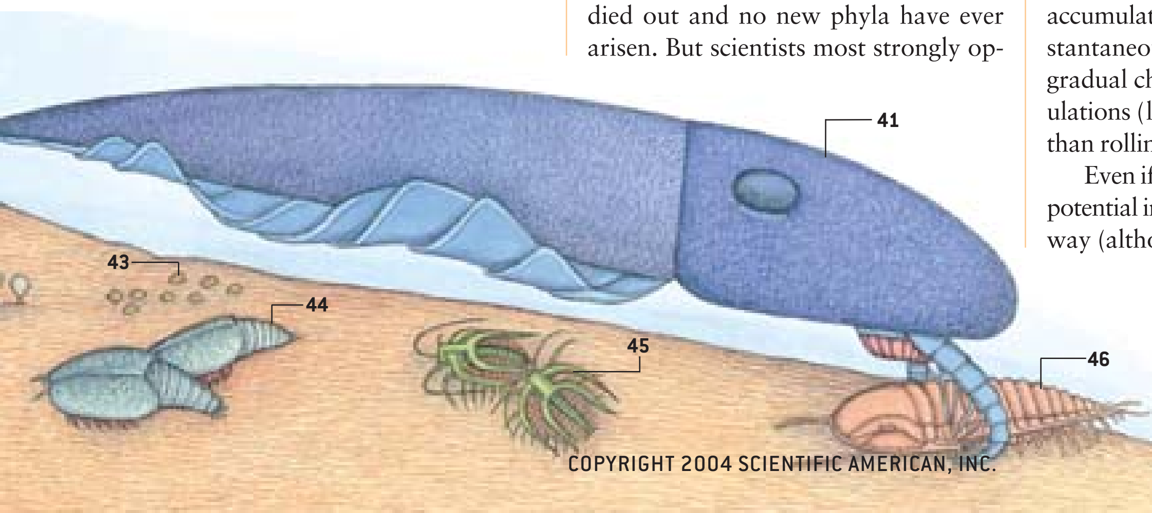
Dumb Luck

MOREOVER, WE DO NOT know why most of the early experiments died, while a few survived to become our modern phyla. It is tempting to say that the victors won by virtue of greater anatomical complexity, better ecological fit or some other predictable feature of conventional Darwinian struggle. But no recognized traits unite the victors, and the radical alternative must be entertained that each early experiment received little more than the equivalent of a ticket in the largest lottery ever played out on our planet—and that each surviving lineage, including our own phylum of vertebrates, inhabits the earth today more by the luck of the draw than by any predictable struggle for existence. The history of multicellular animal life may be more a story of great reduction in initial possibilities, with stabilization of lucky survivors, than a conventional tale of steady ecological expansion and morphological progress in complexity.

Finally, this pattern of long stasis, with change concentrated in rapid episodes that establish new equilibria, may be quite general at several scales of time and magnitude, forming a kind of fractal pattern in self-similarity. According to the punctuated equilibrium model of speciation, trends within lineages occur by accumulated episodes of geologically instantaneous speciation, rather than by gradual change within continuous populations (like climbing a staircase rather than rolling a ball up an inclined plane).

Even if evolutionary theory implied a potential internal direction for life's pathway (although previous facts and argu-

GREAT DIVERSITY quickly evolved at the dawn of multicellular animal life during the Cambrian period (530 million years ago). The creatures shown here are all found in the Middle Cambrian Burgess Shale fauna of Canada. They include some familiar forms (sponges, brachiopods) that have survived. But many creatures (such as the giant *Anomalocaris,* at the lower right, largest of all the Cambrian animals) did not live for long and were so anatomically peculiar (relative to survivors) that we cannot classify them among known phyla.



CLASSICAL REPRESENTATIONS OF LIFE'S HISTORY reveal the severe biases of viewing evolution as embodying a central principle of progress and complexification. In these paintings by Charles R. Knight from a 1942 issue of *National Geographic,* the first panel shows invertebrates of the Burgess Shale. But as soon as fishes evolve, no subsequent scene ever shows another invertebrate, although they did not go away or stop evolving. When land vertebrates arise (*panel 2*), we never see another fish, even though return of land vertebrate lineages to the sea may be depicted (*panel 3*). The sequence always ends with mammals—even though fishes, invertebrates and reptiles are still thriving—and, of course, humans.

CHARLES R. KNIGHT, COURTESY OF *NATIONAL GEOGRAPHIC*

ments in this article cast doubt on such a claim), the occasional imposition of a rapid and substantial, perhaps even truly catastrophic, change in environment would have intervened to stymie the pattern. These environmental changes trigger mass extinction of a high percentage of the earth's species and may so derail any internal direction and so reset the pathway that the net pattern of life's history looks more capricious and concentrated in episodes than steady and directional.

Mass extinctions have been recognized since the dawn of paleontology; the major divisions of the geologic time scale were established at boundaries marked by such events. But until the revival of interest that began in the late 1970s, most paleontologists treated mass extinctions only as intensifications of ordinary events, leading (at most) to a speeding up of tendencies that pervaded normal times. In this gradualistic theory of mass extinction, these events really took a few million years to unfold (with the appearance of suddenness interpreted as an artifact of an imperfect fossil record), and they only made the ordinary occur faster (more intense Darwinian competition in tough times, for example, leading to even more efficient replacement of less adapted by superior forms).

The reinterpretation of mass extinctions as central to life's pathway and radically different in effect began with the presentation of data by Luis and Walter Alvarez in 1979, indicating that the impact of a large extraterrestrial object (they suggested an asteroid seven to 10 kilometers in diameter) set off the last great extinction at the Cretaceous-Tertiary boundary 65 million years ago. Although the Alvarez hypothesis initially received very skeptical treatment from scientists (a proper approach to highly unconventional explanations), the case now seems virtually proved by discovery of the "smoking gun," a crater of appropriate size and age located off the Yucatán peninsula in Mexico.

This reawakening of interest also inspired paleontologists to tabulate the data of mass extinction more rigorously. Work by David M. Raup, J. J. Sepkoski, Jr., and David Jablonski of the University of Chicago has established that multicellular animal life experienced five major (end of Ordovician, late Devonian, end of Permian, end of Triassic and end of Cretaceous) and many minor mass extinctions during its 530-million-year history. We have no clear evidence that any but the last of these events was triggered by catastrophic impact, but such careful study leads to the general conclusion that mass extinctions were more frequent, more rapid, more extensive in magnitude and more different in effect than paleontologists had previously realized. These four properties encompass the radical implications of mass extinction for understanding life's pathway as more contingent and chancy than predictable and directional.

Mass extinctions are not random in their impact on life. Some lineages succumb and others survive as sensible outcomes based on presence or absence of evolved features. But especially if the triggering cause of extinction be sudden and catastrophic, the reasons for life or death may be random with respect to the original value of key features when first evolved in Darwinian struggles of normal times. This "different rules" model of mass extinction imparts a quirky and unpredictable character to life's pathway based on the evident claim that lineages cannot anticipate future contingencies of such magnitude and different operation.

To cite two examples from the impact-triggered Cretaceous-Tertiary extinction 65 million years ago: First, an important study published in 1986 noted that diatoms survived the extinction far better than other single-celled plankton (primarily coccoliths and radiolaria). This study found that many diatoms had evolved a strategy of dormancy by encystment, perhaps to survive through seasonal periods of unfavorable conditions (months of darkness in polar species as otherwise fatal to these photosynthesizing cells; sporadic availability of silica needed to construct their skeletons). Other planktonic cells had not evolved any mechanisms for dormancy. If the terminal Cretaceous impact produced a dust cloud that blocked light for several months or longer (one popular idea for a "killing scenario" in the extinction), then diatoms may have survived as a fortuitous result of dormancy mechanisms evolved for the entirely different function of weathering seasonal droughts in ordinary times. Diatoms are not superior to radiolaria or other plankton that succumbed in far greater numbers; they were simply fortunate to possess a favorable feature, evolved for other reasons, that fostered passage through the impact and its sequelae.

Second, we all know that dinosaurs perished in the end Cretaceous event and that mammals therefore rule the vertebrate world today. Most people assume that mammals prevailed in these tough times for some reason of general superiority over dinosaurs. But such a conclusion seems most unlikely. Mammals and dinosaurs had coexisted for 100 million years, and mammals had remained rat-sized or smaller, making no evolutionary "move" to oust dinosaurs. No good argument for mammalian prevalence by general superiority has ever been advanced, and fortuity seems far more likely. As one plausible argument, mammals may have survived partly as a result of their small size (with much larger, and therefore extinction-resistant, populations as a consequence, and less ecological specialization with more places to hide, so to speak). Small size may not have been a positive mammalian adaptation at all, but more a sign of inability ever to penetrate the dominant domain of dinosaurs. Yet this "negative" feature of normal times may be the key reason for mammalian survival and a prerequisite to my writing and your reading this article today.

Sigmund Freud often remarked that great revolutions in the history of science have but one common, and ironic, feature: they knock human arrogance off one pedestal after another of our previous conviction about our own self-importance. In Freud's three examples, Copernicus moved our home from center to periphery; Darwin then relegated us to "descent from an animal world"; and, finally (in one of the least modest statements of intellectual history), Freud himself discovered the unconscious and exploded the myth of a fully rational mind.

In this wise and crucial sense, the Darwinian revolution remains woefully incomplete because, even though thinking humanity accepts the fact of evolution, most of us are still unwilling to abandon the comforting view that evolution means (or at least embodies a central principle of) progress defined to render the appearance of something like human consciousness either virtually inevitable or at least predictable. The pedestal is not smashed until we abandon progress or complexification as a central principle and come to entertain the strong possibility that *H. sapiens* is but a tiny, late-arising twig on life's enormously arborescent bush—a small bud that would almost surely not appear a second time if we could replant the bush from seed and let it grow again.

Parochial Evolution

PRIMATES ARE VISUAL ANIMALS, and the pictures we draw betray our deepest convictions and display our current conceptual limitations. Artists have always painted the history of fossil life as a sequence from invertebrates, to fishes, to early terrestrial amphibians and reptiles, to dinosaurs, to mammals and, finally, to humans. There are no exceptions; all sequences painted since the inception of this genre in the 1850s follow the convention.

Yet we never stop to recognize the almost absurd biases coded into this universal mode. No scene ever shows another invertebrate after fishes evolved, but invertebrates did not go away or stop evolving! After terrestrial reptiles emerge, no subsequent scene ever shows a fish (later oceanic tableaux depict only such returning reptiles as ichthyosaurs and plesiosaurs). But fishes did not stop evolving after one small lineage managed to invade the land. In fact, the major event in the evolution of fishes, the origin and rise to dominance of the teleosts, or modern bony fishes, occurred during the time of the dinosaurs and is therefore never shown at all in any of these sequences—even though teleosts include more than half of all species of vertebrates. Why should humans appear at the end of all sequences? Our order of primates is ancient among mammals, and many other successful lineages arose later than we did.

We will not smash Freud's pedestal and complete Darwin's revolution until we find, grasp and accept another way of drawing life's history. J.B.S. Haldane proclaimed nature "queerer than we can suppose," but these limits may only be socially imposed conceptual locks rather then inherent restrictions of our neurology. New icons might break the locks. Trees—or rather copiously and luxuriantly branching bushes—rather than ladders and sequences hold the key to this conceptual transition.

We must learn to depict the full range of variation, not just our parochial perception of the tiny right tail of most complex creatures. We must recognize that this tree may have contained a maximal number of branches near the beginning of multicellular life and that subsequent history is for the most part a process of elimination and lucky survivorship of a few, rather than continuous flowering, progress and expansion of a growing multitude. We must understand that little twigs are contingent nubbins, not predictable goals of the massive bush beneath. We must remember the greatest of all biblical statements about wisdom: "She is a tree of life to them that lay hold upon her; and happy is every one that retaineth her." SA

MORE TO EXPLORE

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The Book of Life. Edited by Stephen Jay Gould. W. W. Norton, 1993.

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