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PREHISTORIC BEASTS



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Feathered dinosaurs, walking whales, killer kangaroos—these are but a few of the fantastic creatures that roamed the planet before the dawn of humans. For more than 200 years, scientists have studied fossil remnants of eons past, painstakingly piecing together the history of life on earth. Through their efforts, not only have long-extinct beasts come to light, but the origins of many modern animals have been revealed.

In this exclusive online issue, *Scientific American* authors ponder some of the most exciting paleontological discoveries made in recent years. Gregory Erickson reexamines *T. rex* and reconstructs how the monster lived. Ryosuke Motani describes the reign of fishlike reptiles known as ichthyosaurs. Kevin Padian and Luis Chiappe trace today's birds back to their carnivorous, bipedal dinosaur forebears. And Stephen Wroe presents the menacing relatives of Australia's beloved pouched mammals. Other articles document the descent of whales from four-legged landlubbers and recount the challenges and rewards of leading fossil-collecting expeditions to uncharted locales. —the Editors

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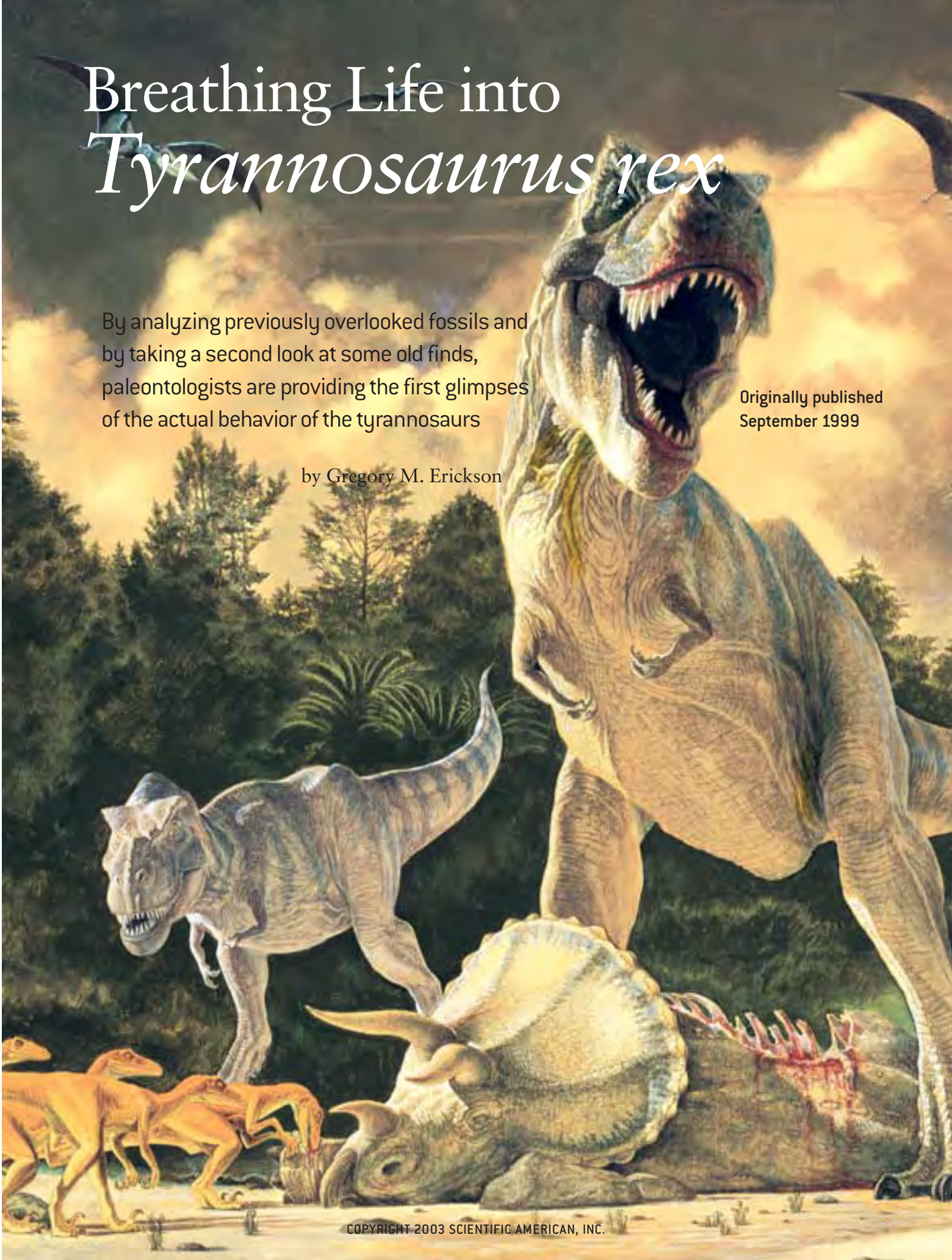
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Breathing Life into *Tyrannosaurus rex*

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

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by Gregory M. Erickson





KAZUHIKO SANO

TYRANNOSAURUS REX defends its meal, a *Triceratops*, from other hungry *T. rex*. Troodontids, the small velociraptors at the bottom left, 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.

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

Harvard University paleontologist Stephen Jay Gould has 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 [4,500-kilogram] 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 22 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.

Over the past decade, 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 solely based 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 in bones and wear patterns in 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 certainly 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.

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*. 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 her \$8.36-million auction price following ownership haggling as for her paleontological status [see "No Bones about It," News and Analysis, SCIENTIFIC AMERICAN, De-

cember 1997]. Remains of a second adult, a juvenile and an infant *T. rex* were later found in Sue's quarry. Researchers 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.

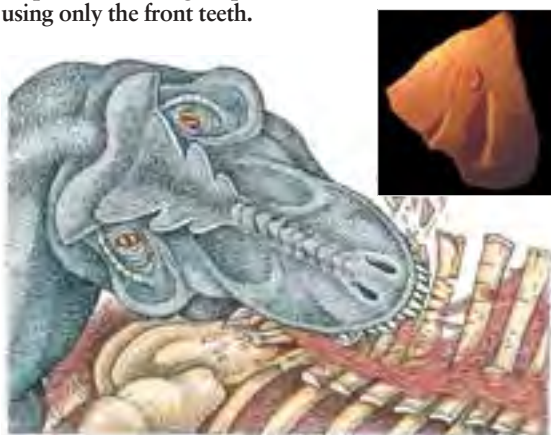
Philip J. Currie and his team from the Royal Tyrrell Museum of Paleontology in Alberta recently relocated the 1910 find and are conducting the first detailed study of the assemblage. Such aggregations of carnivorous animals can occur when one after another gets caught in a trap, such as a mud hole or 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 four-*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



NIPPING STRATEGY (above) 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 (above) was sufficient to have created the huge furrows on the surface of the section of a fossil *Triceratops* pelvis (inset)

healed bite marks that reveal nasty interpersonal skills. A paper just 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 com-

batants 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 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.

The usual subjects—food, mates and territory—may have prompted the vigorous disagreements 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 his 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.

Nevertheless, some researchers specu-

lated about the teeth. As early as 1973, Ralph E. Molnar of the Queensland Museum in Australia 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 carinas, 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*. 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 his 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 of the U.S. Geological Survey 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. 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 indeed 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 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 Royal Tyrrell Museum 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 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 ascertained 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.

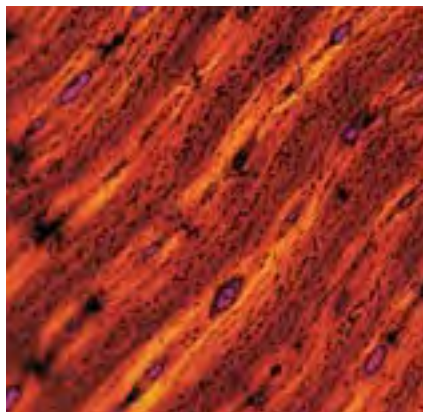
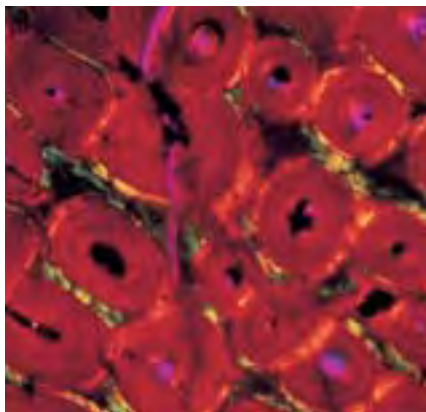
Predator supporters answered with biomechanical data. They cited my own bite-force studies that demonstrate that *T. rex* teeth were actually quite robust. (I personally will remain uncommitted in this argument until the discovery of direct physical proof.) They also note that Kenneth Carpenter of the Denver Museum of Natural History and Matthew

Smith, then at the Museum of the Rockies, estimate that the “puny” arms of a *T. rex* could curl nearly 180 kilograms. And they point 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 per 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 comparable evidence for albertosaur scavenging. Carpenter, on the other hand, has provided solid proof of predaceous behavior, in the form of an unsuccessful attack by a *T. rex* on an adult *Edmontosaurus*. The intended prey 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 can help determine the degree to which *T. rex* undertook each method of obtaining food, and paleontologists can avoid future arguments by adopting standard definitions of predator and scavenger. Such a convention is necessary, as 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, as it would include nearly all the world's carnivorous birds and mammals.



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*.

In a definition more consistent with most paleontologists' common-sense 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 reveal 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.

Over this 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.

The Author

GREGORY M. ERICKSON 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 Jack Horner in 1992 at Montana State University and a doctorate with Marvalee Wake in 1997 from the University of California, Berkeley. Erickson is currently conducting postdoctoral research at Stanford and Brown universities aimed at understanding the form, function, development and evolution of the vertebrate skeleton. *Tyrannosaurus rex* has been one of his favorite study animals in this pursuit. 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. He will shortly become a faculty member in the department of biological science at Florida State University.

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The Teeth of the Tyrannosaurs

by William L. Abler

Their teeth reveal aspects of their hunting and feeding habits

Understanding the teeth is essential for reconstructing the hunting and feeding habits of the tyrannosaurs. The tyrannosaur tooth is more or less a cone, slightly curved and slightly flattened, so that the cross section is an ellipse. Both the narrow anterior and posterior surfaces bear rows of serrations. Their presence has led many observers to assume that the teeth cut meat the way a serrated steak knife does. My colleagues and I, however, were unable to find any definitive study of the mechanisms by which knives, smooth or serrated, actually cut. Thus, the comparison between tyrannosaur teeth and knives had meaning only as an impetus for research, which I decided to undertake.

Trusting in the logic of evolution, I began with the assumption that tyrannosaur teeth were well adapted for their biological functions. Although investigation of the teeth themselves might appear to be the best way of uncovering their characteristics, such direct study is limited; the teeth cannot really be used for controlled experiments. For example, doubling the height of a fossil tooth's serrations to monitor changes in cutting properties is impossible. So I decided to study steel blades whose serrations or sharpness I could alter and then com-

pare these findings with the cutting action of actual tyrannosaur teeth.

The cutting edges of knives can be either smooth or serrated. A smooth knife blade is defined by the angle between the two faces and by the radius of the cutting edge: the smaller the radius, the sharper the edge. Serrated blades, on the other hand, are characterized by the height of the serrations and the distance between them.

To investigate the properties of knives with various edges and serrations, I created a series of smooth-bladed knives with varying interfacial angles. I standardized the edge radius for comparable sharpness; when a cutting edge was no longer visible at 25 magnifications, I stopped sharpening the blade. I also produced a series of serrated edges.

To measure the cutting properties of the blades, I mounted them on a butcher's saw operated by cords and pulleys, which moved the blades across a series of similarly sized pieces of meat that had been placed on a cutting board. Using weights stacked in baskets at the ends of the cords, I measured the downward force and drawing force required to cut each piece of meat to the same depth. My simple approach gave consistent and provocative results, including this important and perhaps unsurprising

one: smooth and serrated blades cut in two entirely different fashions.

The serrated blade appears to cut meat by a "grip and rip" mechanism. Each serration penetrates to a distance equal to its own length, isolating a small section of meat between itself and the adjacent serration. As the blade moves, each serration rips that isolated section. The blade then falls a distance equal to the height of the serration, and the process repeats. The blade thus converts a pulling force into a cutting force.

A smooth blade, however, concentrates downward force at the tiny cutting edge. The smaller this edge, the greater the force. In effect, the edge crushes the meat until it splits, and pulling or pushing the blade reduces friction between the blade surface and the meat.

After these discoveries, I mounted actual serrated teeth in the experimental apparatus, with some unexpected results. The serrated tooth of a fossil shark (*Carcharodon megalodon*) indeed works exactly like a serrated knife blade does. Yet the serrated edge of even the sharpest tyrannosaur tooth cuts meat more like a smooth knife blade, and a dull one at that. Clearly, all serrations are not alike. Nevertheless, serrations are a major and dramatic feature of tyrannosaur teeth. I therefore began to

wonder whether these serrations served a function other than cutting.

The serrations on a shark tooth have a pyramidal shape. Tyrannosaur serrations are more cubelike. Two features of great interest are the gap between serrations, called a cella, and the thin slot to which the cella narrows, called a diaphysis. Seeking possible functions of the cellae and diaphyses, I put tyrannosaur teeth directly to the test and used them to cut fresh meat. To my knowledge, this was the first time tyrannosaur teeth have ripped flesh in some 65 million years.

I then examined the teeth under the microscope, which revealed striking characteristics. (Although I was able to inspect a few *Tyrannosaurus rex* teeth, my cutting experiments were done with teeth of fossil albertosaurs, which are true tyrannosaurs and close relatives of *T. rex*.) The cellae appear to make excellent traps for grease and other food debris. They also provide access to the deeper diaphyses, which grip and hold filaments of the victim's tendon. Tyrannosaur teeth thus would have harbored bits of meat and grease for extended periods. Such food particles are receptacles for septic bacteria—even a nip from a tyrannosaur, therefore, might have been a source of a fatal infection.

Another aspect of tyrannosaur teeth encourages contemplation. Neighboring serrations do not meet at the exterior of the tooth. They remain separate inside it down to a depth nearly equal to the exterior height of the serration. Where they finally do meet, the junction, called the ampulla, is flask-shaped rather than V-shaped. This ampulla seems to have protected the tooth from cracking when force was applied. Whereas the narrow opening of the diaphysis indeed put high pressure on trapped filaments of tendon, the rounded ampulla distributed pressure uniformly around its sur-

face. The ampulla thus eliminated any point of concentrated force where a crack might begin.

Apparently, enormously strong tyrannosaurs did not require razorlike teeth but instead made other demands on their dentition. The teeth functioned less like knives than like pegs, which gripped the food while the *T. rex* pulled it to pieces. And the ampullae protected the teeth during this process.

An additional feature of its dental anatomy leads to the conclusion that *T. rex* did not chew its food. The teeth have no occlusal, or articulating, surfaces and rarely touched one another. After it removed a large chunk of carcass, the tyrannosaur probably swallowed that piece whole.

Work from an unexpected quarter also provides potential help in reconstructing the hunting and feeding habits of tyrannosaurs. Herpetologist Walter Auffenberg of the University of Florida spent more than 15 months in Indonesia studying the largest lizard in the world, the Komodo dragon [see "The Komodo Dragon," by Claudio Ciofi; SCIENTIFIC AMERICAN, March]. (Paleontologist James O. Farlow of Indiana University–Purdue University Fort Wayne has suggested that the Komodo dragon may serve as a living model for the behavior of the tyrannosaurs.) The dragon's teeth are remarkably similar in structure to those of tyrannosaurs, and the creature is well known to inflict a dangerously septic bite—an animal that escapes an attack with just a flesh wound is often living on borrowed time. An infectious



PHOTOGRAPH COURTESY OF WILLIAM L. ABLER

EXPERIMENTAL DEVICE (above) for measuring cutting forces of various blades: weights attached to cords at the sides and center cause the blade to make a standard cut of 10 millimeters in a meat sample (represented here by green rubber).

bite for tyrannosaurs would lend credence to the argument that the beasts were predators rather than scavengers. As with Komodo dragons, the victim of what appeared to be an unsuccessful attack might have received a fatal infection. The dead or dying prey would then be easy pickings to a tyrannosaur, whether the original attacker or merely a fortunate conspecific.

If the armamentarium of tyrannosaurs did include septic oral flora, we can postulate other characteristics of its anatomy. To help maintain a moist environment for its single-celled guests, tyrannosaurs probably had lips that closed tightly, as well as thick, spongy gums that covered the teeth. When tyrannosaurs ate, pressure between teeth and gums might have cut the latter, causing them to bleed. The blood in turn may have been a source of nourishment for the septic dental bacteria. In this scenario, the horrific appearance of the feeding tyrannosaur is further exaggerated—their mouths would have run red with their own bloodstained saliva while they dined.

The Author

WILLIAM L. ABLER received a doctorate in linguistics from the University of Pennsylvania in 1971. Following a postdoctoral appointment in neuropsychology at Stanford University, he joined the faculty of linguistics at the Illinois Institute of Technology. His interests in human origins and evolution eventually led him to contemplate animal models for human evolution and on to the study of dinosaurs, particularly their brains. The appeal of dinosaurs led him to his current position in the Department of Geology at the Field Museum, Chicago.

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MADAGASCAR'S MESOZOIC 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 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 rhynchosaur.

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 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 to shape our strategy for a sixth expedition this summer.

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.

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. Among other 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 headlong 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 more remote areas, and most of them are impassable by even the brawniest 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 often arose unexpectedly, requiring us to adjust our plans on the spot.

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.

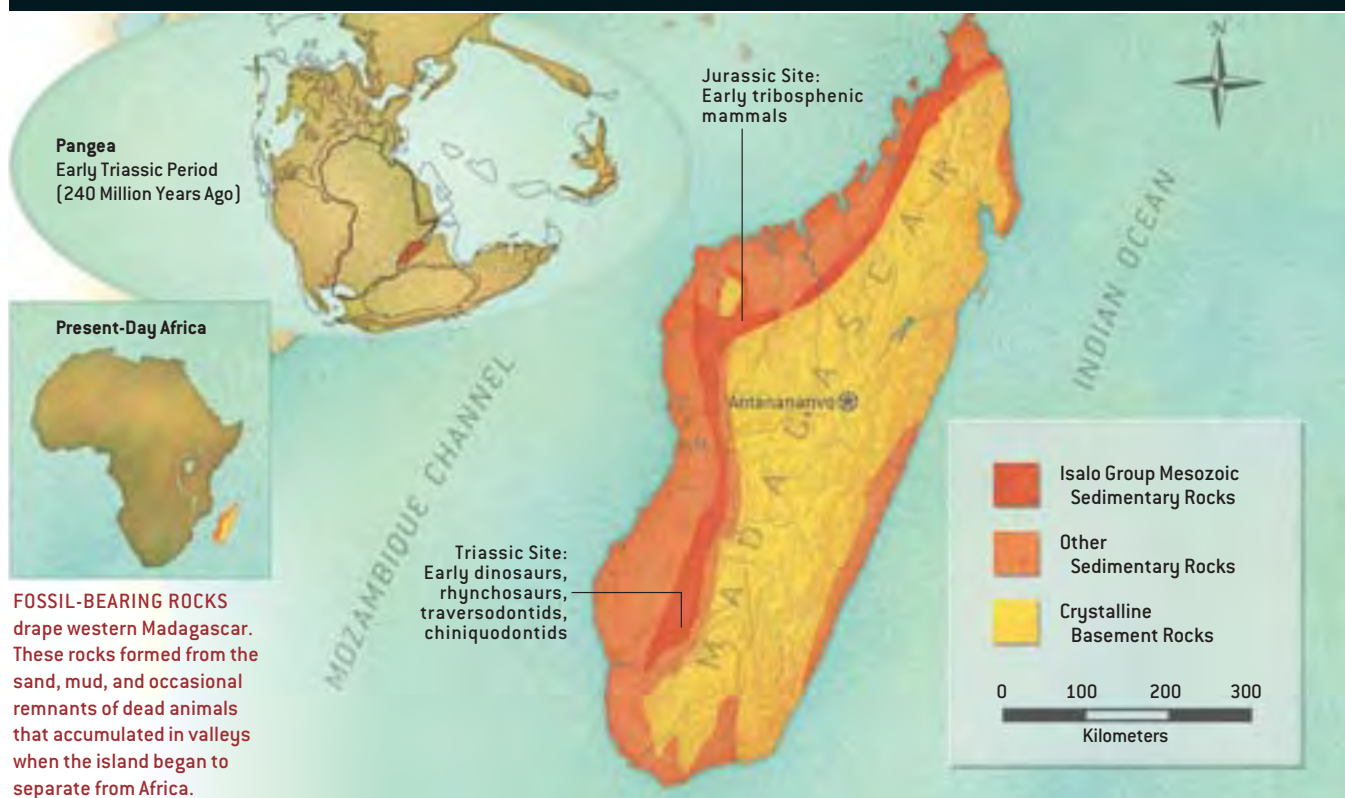
Mostly Mammals

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 west coast of what is now India and the east coast of present-day Africa (*see map*). The world was a good deal warmer than at present—even the poles were free of ice. In the supercontinent's southern region, called Gondwana, enormous rivers coursed into lowland basins that would 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—including the famous record of early human evolution in the much younger rift basins of east Africa.) 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

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.

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 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 "Modern-Day Mystery," on page 17]. 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.

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 hunker down and do the detailed collecting work 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 of this picture 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

THE AUTHORS

JOHN J. FLYNN and **ANDRÉ R. WYSS** have collaborated for nearly 20 years. Their expeditions have taken them to the Rocky Mountains, Baja California, the Andes of Chile, and Madagascar. Together they also study the evolutionary history of carnivores, including dogs, cats, seals, and their living and fossil relatives. 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 a professor of geological sciences at the University of California, Santa Barbara, and a research associate at the Field Museum. The authors thank the National Geographic Society, the John C. Meeker family and the World Wildlife Fund for their exceptional support of this research.

than during the second, we thought initially that this scene played out sometime 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 appeared to be dinosaurs. Our team found jaws, strings of vertebrae, hips, claws, an articulated forearm with some wrist bones, and other assorted skeletal elements. When we examined these and other bones more closely, we realized that we had uncovered remains of two different species of prosauropods (not yet formally named), one of which appears to resemble a species from Morocco called *Azendohsaurus*. These 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*.

When we discovered that dinosaurs 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 than the group of rhynchosaurs that is found with other early dinosaurs. 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 occurrence of dinosaurs with more ancient kinds of animals, plus the lack of younger groups, suggests that the Malagasy prosauropods are as old as any dinosaur ever discovered, if not older.

Only 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 for fossils are obtainable only from rock layers produced by contemporaneous volcanoes. The Malagasy sediments accumulated in a rift basin with no volcanoes nearby.) Based on the fossils present, we have tentatively concluded that our dinosaur-bearing rocks slightly predate the Ischigualasto time span. And because prosauropods represent one of the major branches of the dinosaur evolu-

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



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

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 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 some of the 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 last year's 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. Awns 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. "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've 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 a writer and editor for ScientificAmerican.com

tionary tree, we know that 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 yet 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 all were chipmunk-size or smaller, so they don't grab the popular imagination in the way their giant Mesozoic contemporaries do. In addition, the fossil record of early mammals is quite sparse, apart from very late in the Mesozoic. 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 some 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 the name applied to a broad group of land animals that includes mammals and their nearest relatives.) Accordingly, these bones provide a wealth of anatomical information previously un-

documented for these creatures. These cynodonts are identified by, among other diagnostic features, a simplified lower jaw that is 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. 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

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 for decades the scant fossil evidence of land-dwelling animals from the island meant that little was known about the origin and evolution of these unique creatures.

While our research group was probing Madagascar's Triassic and Jurassic age rocks, teams led by David W. Krause of the State University of New York at Stony Brook 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 the potential to reveal whether the ancestors of Madagascar's modern mammals arrived in multiple, long-distance dispersal events or in a single episode of "island hopping." —J.J.F. and A.R.W.



LIVING IN MIXED COMPANY

PALEONTOLOGISTS DID NOT KNOW until recently that the unusual group of ancient animals shown above—prosauropods [1], traversodontids [2], rhynchosaurs [3] and chiniquodontids [4]—once foraged together. In the past six 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 prosauropods here, which represent some of the oldest dinosaurs

yet discovered, browse on conifers while a parrot-beaked rhynchosaur prepares to sip from a nearby pool. The prosauropod 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. Both types of creatures are early members of the Cynodontia, a broad group that includes today's mammals. The grinding cheek teeth of the traversodontids suggest they were herbivores; the chiniquodontids sport the sharp, pointed teeth of carnivores.

—J.J.F. and A.R.W.

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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.

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 *Lapperentosaurus*. 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 beneath. We bagged about 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 geologic 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 last 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. Although the available information does not conclusively resolve the debate, this important addition to the record of early fossil mammals does point out the precarious nature of long-standing assumptions rooted in a fossil record historically biased toward the Northern Hemisphere [see "Tiny Bones to Pick," by Kate Wong, on page 13].

Although our team has recovered a broad spectrum of fossils in Madagascar, scientists are only beginning to de-

scribe 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 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 insight to paleontologists' knowledge of the creatures that once roamed Gondwana.

Planning Persistently

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 prosauropods indicate that dinosaurs 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 our primary goal this summer will be the same as it has been for our past five expeditions: find as many fossils as possible.

Our agenda includes digging deeper into known sites and surveying new regions, blending risky efforts with sure bets. No matter how carefully formulated, however, our plans will be subject to last-minute changes, dictated by such things as road closures and our most daunting challenge to date, 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 will be one of our foremost tasks this year.

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.

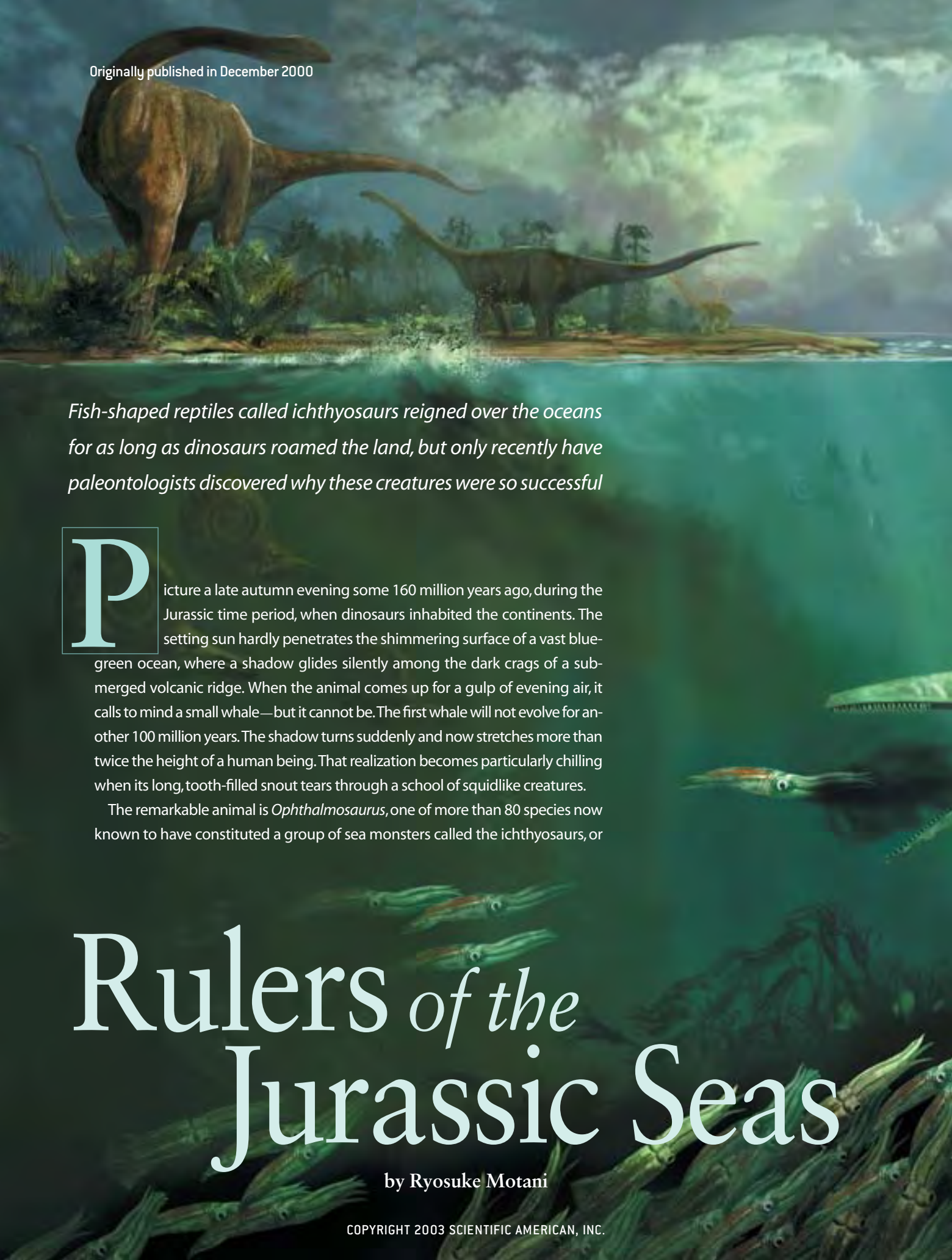
MORE TO EXPLORE

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Originally published in December 2000

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

P

icture 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, or

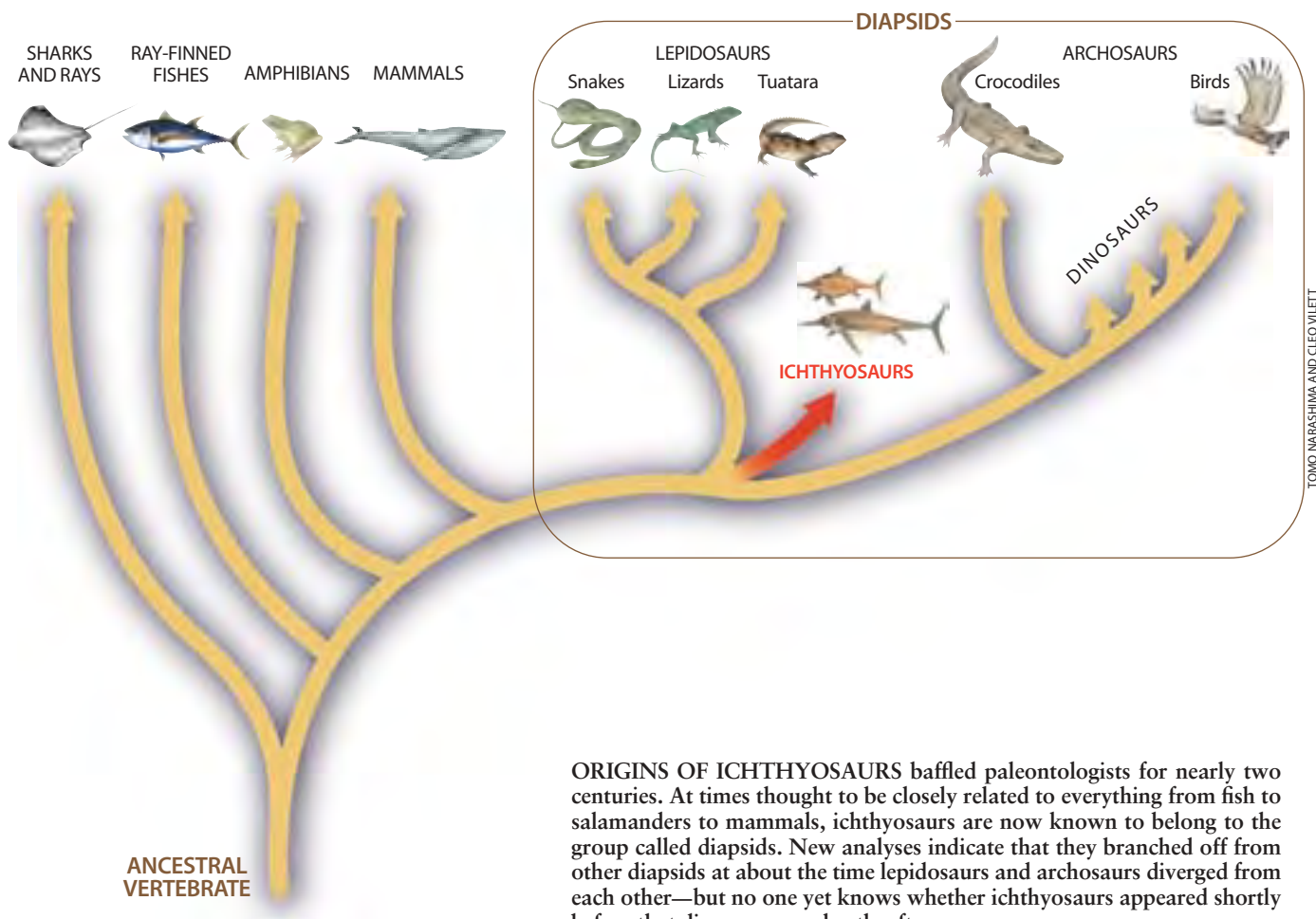
Rulers of the Jurassic Seas

by Ryosuke Motani

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



TONO NARASHIMA AND CLEO VILETT

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.

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 look 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 *Iguanodon* 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 ev-

ident 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

FACT: The smallest ichthyosaur was shorter than a human arm;

animals 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 and ankle bones—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 recently 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 was a great 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

NEW FOSSILS of the first ichthyosaurs, including *Chaohusaurus*, have illuminated how these lizard-shaped creatures evolved into masters of the open ocean.

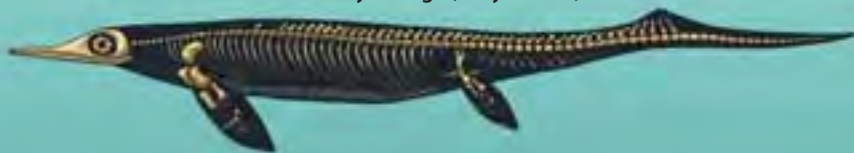


RYOSUKE MOTANI

the largest was longer than a typical city bus

Chaohusaurus geishanensis

0.5 to 0.7 meter • Lived 245 million years ago (Early Triassic)



Mixosaurus cornalianus

0.5 to 1 meter • Lived 235 million years ago (Middle Triassic)



Ophthalmosaurus icenicus

3 to 4 meters • Lived from 165 million to 150 million years ago (Middle to Late Jurassic)



vertebrae shaped more like 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 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 as creatures that spend all their time at sea. 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 in the environment 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 ich-

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.

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 spec-

imens 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.

Backbones 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

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



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 for the quickness and maneuverability needed for shallow-water hunting. As the backbone thickened in later ichthyosaurs, the body stiffened and so 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.

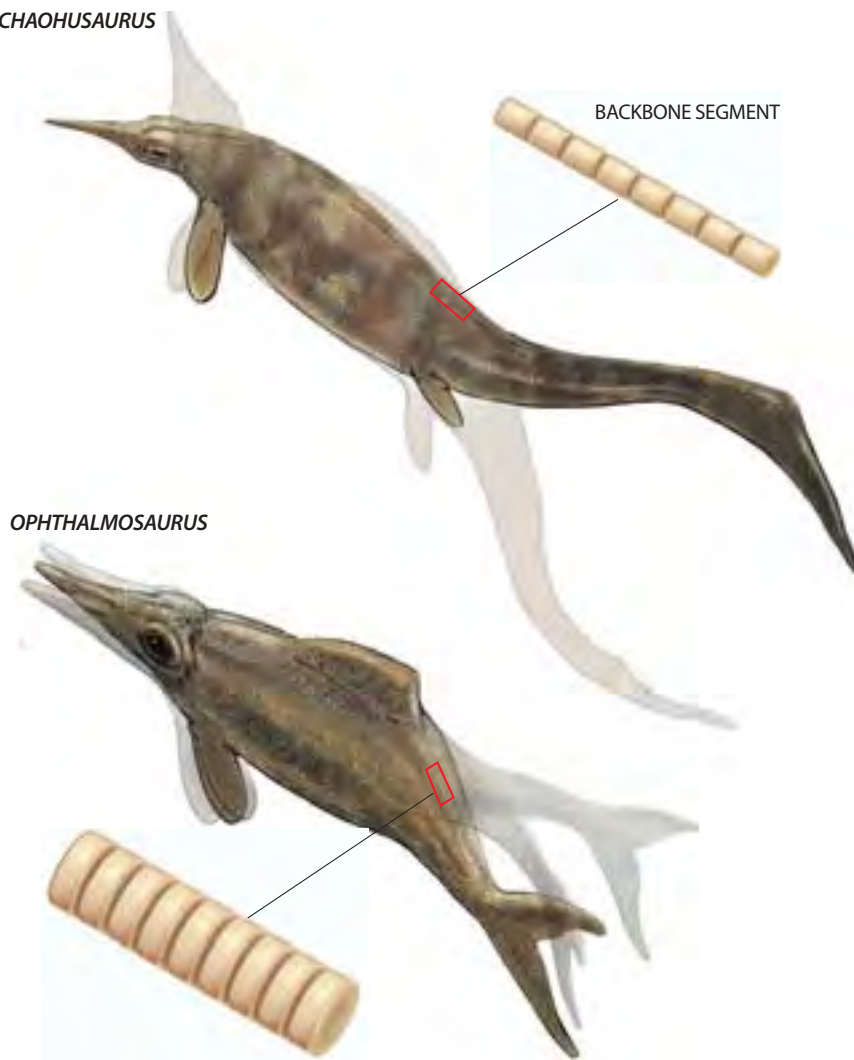
thyosaurs had such a caudal fin, and their thick body profile implies that they probably swam like mackerel sharks.

Inspecting a variety of shark species reveals that the thicker the body from top to bottom, the larger the diameter of the vertebrae in the animal's trunk. 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 of this thickening, the body became less flexible, and the individual vertebrae acquired their hockey-puck appearance.

Drawn to the Deep

The ichthyosaurs' invasion of open water meant not only a wider coverage of surface waters but also a deeper exploration of the marine environment. We know from the fossilized stomach contents of fish-shaped ichthyosaurs that they mostly ate squidlike creatures known as dibranchiate cephalopods. 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

CHAOHUSAURUS



OPHTHALMOSAURUS

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 shapes that reduce drag—and so did 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 other organs—and the slower the consumption of oxygen per 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 body length. Fish-shaped ichthyosaurs also grew longer, further augmenting their bulk. Calculations based on the aerobic capacities of today's air-breathing divers (mostly mammals and

APPROXIMATE MAXIMUM
DIAMETER OF EYE:



AFRICAN ELEPHANT
5 CENTIMETERS



BLUE WHALE
15 CENTIMETERS



OPHTHALMOSAURUS
23 CENTIMETERS



GIANT SQUID
25 CENTIMETERS



TEMNODONTOSAURUS
26 CENTIMETERS



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*.

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. A conservative estimate suggests, then, that *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 in water, they do not need the extra strength it provides. In fact, heavy bones (which are little help for oxygen storage) 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, which implies that they, too, benefited from lighter skeletons.

Perhaps the best evidence for the deep-diving habits of later ichthyosaurs is their remarkably large eyes, up to 23 centimeters across in the case of *Ophthalmosaurus*. Relative to 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

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

that was embedded in their eyes. (Humans do not have such a ring—it was lost in mammalian ancestors—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, regardless of depth.

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 of an optical system. The lower the number, the brighter the image and therefore the shorter the exposure time required. 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, it probably could 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, although it is not possible to judge what is the cause and what is the effect. Such adaptations enabled ichthyosaurs to reign for 155 million years. New fossils of the earliest of



RYOSUKE MOTANI

SMALL ISLAND in northeast Japan turned out to harbor two almost complete skeletons of *Utatsusaurus*, the oldest ichthyosaur.

these sea dwellers are now making it clear just how they evolved so successfully for aquatic life, but 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, where they would have had a

better chance of survival. 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.

Scientists may never fully explain the extinction of ichthyosaurs. But as paleontologists and other investigators continue to explore their evolutionary history, we are sure to learn a great deal more about how these fascinating creatures lived.

The Author

RYOSUKE MOTANI, who was born in Tokuyama, Japan, is a researcher in the department of paleobiology at the Royal Ontario Museum in Toronto. As a child he found ichthyosaurs uninteresting. ("They looked too ordinary in my picture books," he recalls.) But his view changed during his undergraduate years at the University of Tokyo, after a paleontology professor allowed him to study the only domestic reptilian fossil they had: an ichthyosaur. "I quickly fell in love with these noble beasts," he says. Motani went on to explore ichthyosaur evolution for his doctoral degree from the University of Toronto in 1997. A fellowship from the Miller Institute then took him to the University of California, Berkeley, for postdoctoral research. He moved back to Canada in September 1999.

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

The Origin of Birds and Their Flight

Originally published in
February 1998

Anatomical and aerodynamic analyses of fossils and living birds show that birds evolved from small, predatory dinosaurs that lived on the ground

by Kevin Padian and Luis M. Chiappe

Sinornis



ILLUSTRATIONS BY ED HECK

Until recently, the origin of birds was one of the great mysteries of biology. Birds are dramatically different from all other living creatures. Feathers, toothless beaks, hollow bones, perching feet, wishbones, deep breastbones and stumplike tailbones are only part of the combination of skeletal features that no other living animal has in common with them. How birds evolved feathers and flight was even more imponderable.

In the past 20 years, however, new fossil discoveries and new research methods have enabled paleontologists to determine that birds descend from ground-dwelling, meat-eating dinosaurs of the group known as theropods. The work has also offered a picture of how the earliest birds took to the air.

Scientists have speculated on the evolutionary history of birds since shortly after Charles Darwin set out his theory of evolution in *On the Origin of Species*. In 1860, the year after the publication of Darwin's treatise, a solitary feather of a bird was found in Bavarian limestone deposits dating to about 150 million years ago (just before the Jurassic period gave way to the Cretaceous). The next year a skeleton of an animal that had birdlike wings and feathers—but a very unbirdlike long, bony tail and toothed jaw—turned up in the same region. These finds became the first two specimens of the blue jay-size *Archaeopteryx lithographica*, the most archaic, or basal, known member of the birds [see “*Archaeopteryx*,” by Peter Wellnhofer; *SCIENTIFIC AMERICAN*, May 1990].

Archaeopteryx's skeletal anatomy provides clear evidence that birds descend from a dinosaurian ancestor, but in 1861 scientists were not yet in a position to make that connection. A few years later, though, Thomas Henry Huxley, Darwin's staunch defender, became the first person to connect birds to dinosaurs. Comparing the hind limbs of *Megalosaurus*, a giant theropod, with those of the ostrich, he noted 35 features that the two groups shared but that

EARLY BIRDS living more than 100 million years ago looked quite different from birds of today. For instance, as these artist's reconstructions demonstrate, some retained the clawed fingers and toothed jaw characteristic of nonavian dinosaurs. Fossils of *Sinornis* (left) were uncovered in China; those of *Iberomesornis* and *Eoalulavis* (below) in Spain. All three birds were about the size of a sparrow. *Eoalulavis* sported the first known alula, or “thumb wing,” an adaptation that helps today's birds navigate through the air at slow speeds.



Iberomesornis



Eoalulavis



Tracking the Dinosaur Lineage Leading to Birds

The family tree at the right traces the ancestry of birds back to their early dinosaurian ancestors. This tree, otherwise known as a cladogram, is the product of today's gold standard for analyzing the evolutionary relations among animals—a method called cladistics.

Practitioners of cladistics determine the evolutionary history of a group of animals by examining certain kinds of traits. During evolution, some animal will display a new, genetically determined trait that will be passed to its descendants. Hence, paleontologists can conclude that two groups uniquely sharing a suite of such novel, or derived, traits are more closely related to each other than to animals lacking those traits.

Nodes, or branching points (*dots*), on a cladogram mark the emergence of a lineage possessing a new set of derived traits. In the cladogram here, the Theropoda all descend from a dinosaurian ancestor that newly possessed hollow bones and had only three functional toes. In this scheme, the theropods are still dinosaurs; they are simply a subset of the saurischian dinosaurs. Each lineage, or clade, is thus nested within a larger one (*colored rectangles*). By the same token, birds (*Aves*) are maniraptoran, tetanuran and theropod dinosaurs.

—K.P. and L.M.C.



Titanosaurus

DINOSAUR LINEAGES
THAT DID NOT LEAD
TO BIRDS

DINOSAURIA

SAURISCHIA

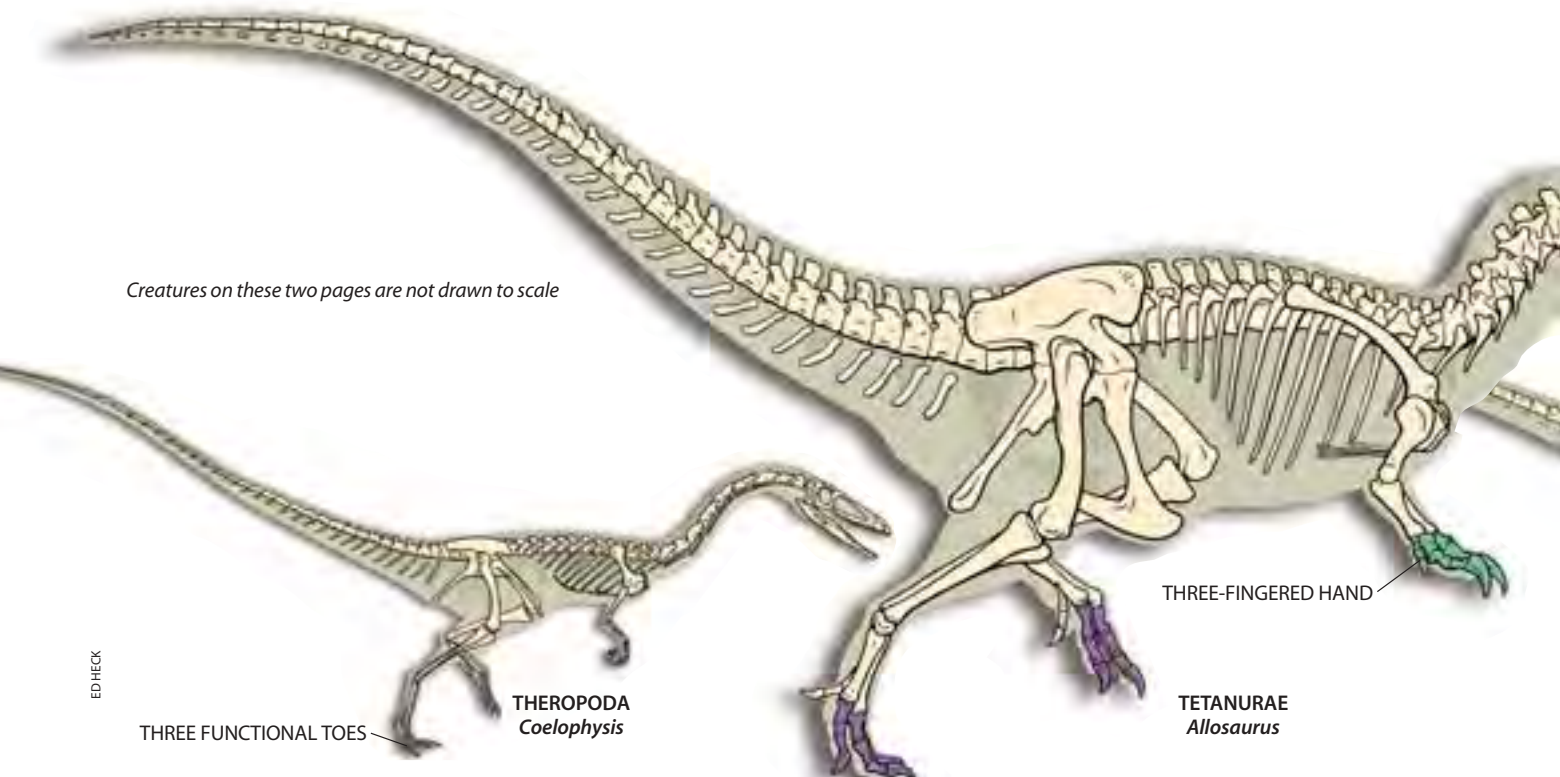
did not occur as a suite in any other animal. He concluded that birds and theropods could be closely related, although whether he thought birds were cousins of theropods or were descended from them is not known.

Huxley presented his results to the Geological Society of London in 1870, but paleontologist Harry Govier Seeley contested Huxley's assertion of kinship between theropods and birds. Seeley suggested that the hind limbs of the ostrich

and *Megalosaurus* might look similar just because both animals were large and bipedal and used their hind limbs in similar ways. Besides, dinosaurs were even larger than ostriches, and none of them could fly; how, then, could flying birds have evolved from a dinosaur?

The mystery of the origin of birds gained renewed attention about half a century later. In 1916 Gerhard Heilmann, a medical doctor with a penchant for paleontology, published

Creatures on these two pages are not drawn to scale



THREE FUNCTIONAL TOES

THEROPODA
Coelophysis

THREE-FINGERED HAND

TETANURAE
Allosaurus

THEROPODA Three functional toes; hollow bones

TETANURAE Three-fingered hand

MANIRAPTORA Half-moon-shaped wristbone

AVES Reversed first toe;
fewer than 26 vertebrae in tail

Coelophysis

Allosaurus

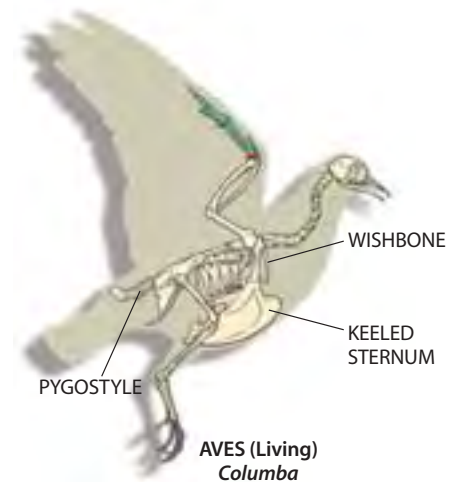
Velociraptor

Archaeopteryx

Columba (pigeon)

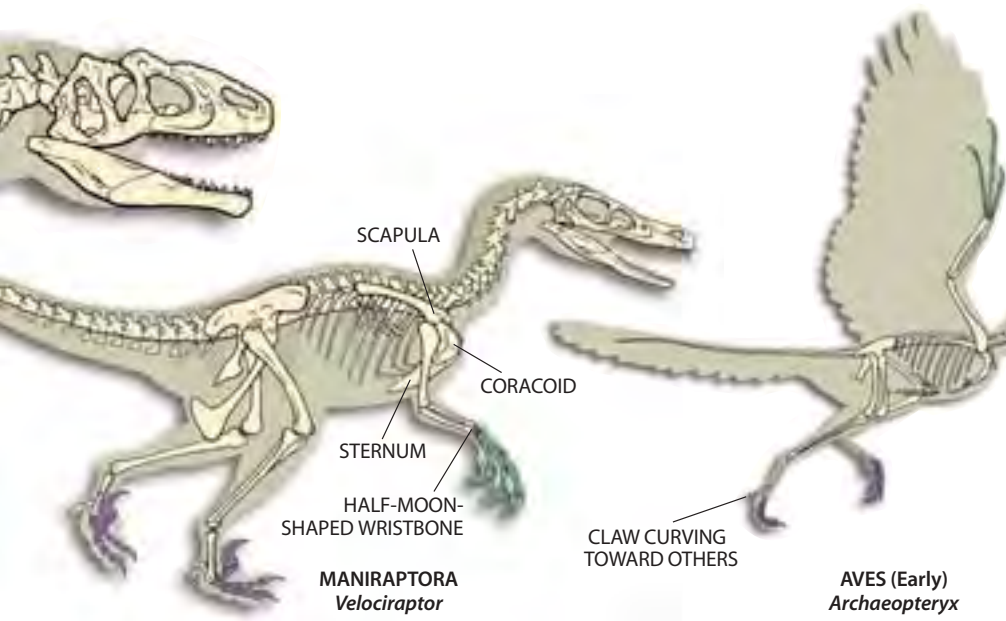
TOMO NARASHIMA

(in Danish) a brilliant book that in 1926 was translated into English as *The Origin of Birds*. Heilmann showed that birds were anatomically more similar to theropod dinosaurs than to any other fossil group but for one inescapable discrepancy: theropods apparently lacked clavicles, the two collarbones that are fused into a wishbone in birds. Because other reptiles had clavicles, Heilmann inferred that theropods had lost them. To him, this loss meant birds could not have evolved from theropods, because he was convinced (mistakenly, as it turns out) that a feature lost during evolution could

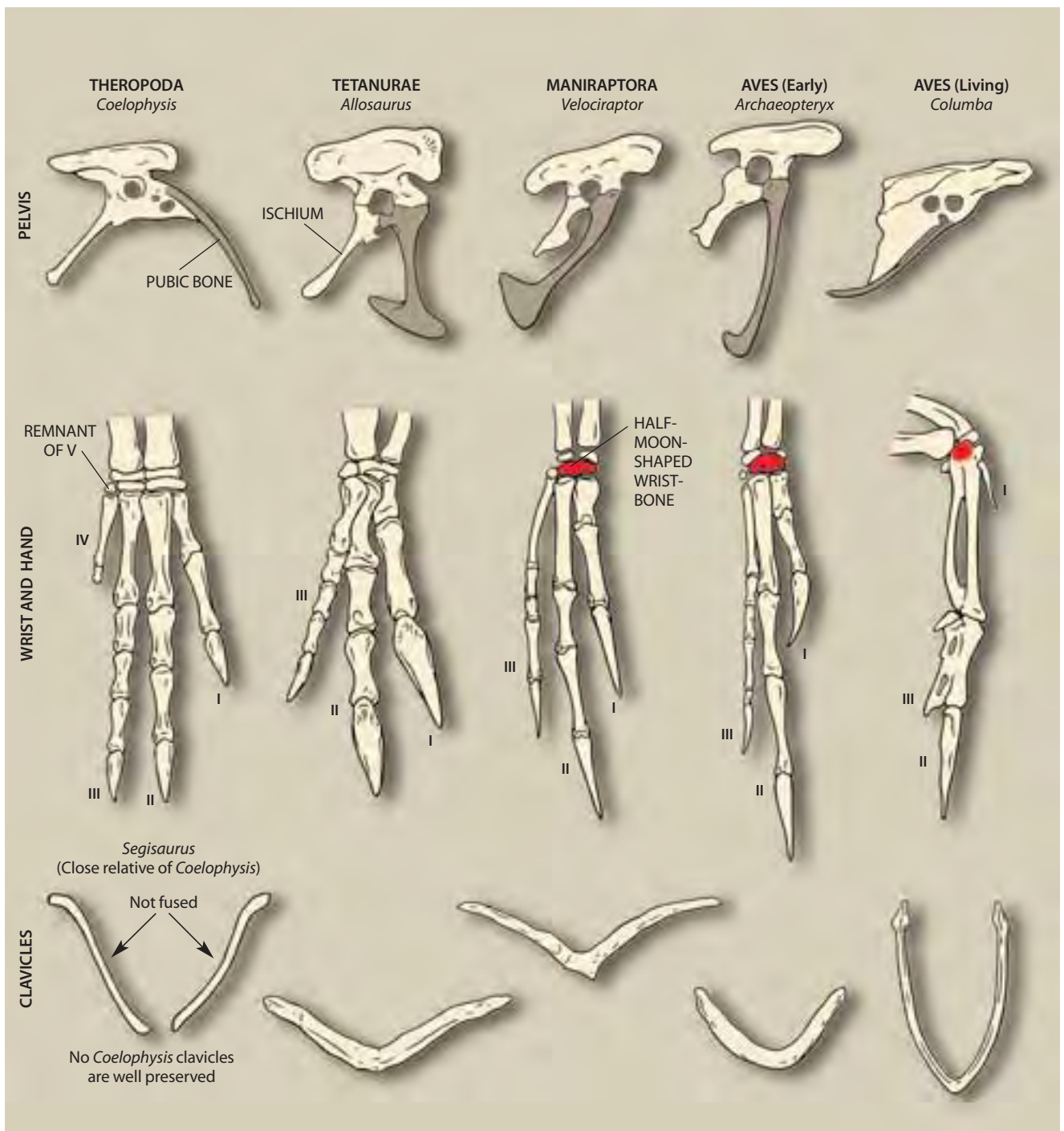


AVES (Living)
Columba

REPRESENTATIVE THEROPODS in the lineage leading to birds (Aves) display some of the features that helped investigators establish the dinosaurian origin of birds—including, in the order of their evolution, three functional toes (*purple*), a three-fingered hand (*green*) and a half-moon-shaped wristbone (*red*). *Archaeopteryx*, the oldest known bird, also shows some new traits, such as a claw on the back toe that curves toward the claws on the other toes. As later birds evolved, many features underwent change. Notably, the fingers fused together, the simple tail became a pygostyle composed of fused vertebrae, and the back toe dropped, enabling birds' feet to grasp tree limbs firmly.



AVES (Early)
Archaeopteryx



EDHECK

COMPARISONS OF ANATOMICAL STRUCTURES not only helped to link birds to theropods, they also revealed some of the ways those features changed as dinosaurs became more birdlike and birds became more modern. In the pelvis (*side view*), the pubic bone (*brown*) initially pointed forward (toward the right), but it later shifted to be vertical or pointed backward. In the hand (*top view*), the relative proportions of the bones re-

mained quite constant through the early birds, but the wrist changed. In the maniraptoran wrist, a disklike bone took on the half-moon shape (*red*) that ultimately promoted flapping flight in birds. The wide, boomerang-shaped wishbone (fused clavicles) in tetanurans and later groups compares well with that of archaic birds, but it became thinner and formed a deeper U shape as it became more critical in flight.

not be regained. Birds, he asserted, must have evolved from a more archaic reptilian group that had clavicles. Like Seeley before him, Heilmann concluded that the similarities between birds and dinosaurs must simply reflect the fact that both groups were bipedal.

Heilmann's conclusions influenced thinking for a long time,

even though new information told a different story. Two separate findings indicated that theropods did, in fact, have clavicles. In 1924 a published anatomical drawing of the bizarre, parrot-headed theropod *Oviraptor* clearly showed a wishbone, but the structure was misidentified. Then, in 1936, Charles Camp of the University of California at Berkeley

found the remains of a small Early Jurassic theropod, complete with clavicles. Heilmann's fatal objection had been overcome, although few scientists recognized it. Recent studies have found clavicles in a broad spectrum of the theropods related to birds.

Finally, a century after Huxley's disputed presentation to the Geological Society of London, John H. Ostrom of Yale University revived the idea that birds were related to theropod dinosaurs, and he proposed explicitly that birds were their direct descendants. In the late 1960s Ostrom had described the skeletal anatomy of the theropod *Deinonychus*, a vicious, sickle-clawed predator about the size of an adolescent human, which roamed in Montana some 115 million years ago (in the Early Cretaceous). In a series of papers published during the next decade, Ostrom went on to identify a collection of features that birds, including *Archaeopteryx*, shared with *Deinonychus* and other theropods but not with other reptiles. On the basis of these findings, he concluded that birds are descended directly from small theropod dinosaurs.

As Ostrom was assembling his evidence for the theropod origin of birds, a new method of deciphering the relations among organisms was taking hold in natural history museums in New York City, Paris and elsewhere. This method—called phylogenetic systematics or, more commonly, cladistics—has since become the standard for comparative biology, and its use has strongly validated Ostrom's conclusions.

Traditional methods for grouping organisms look at the similarities and differences among the animals and might exclude a species from a group solely because the species has a trait not found in other members of the group. In contrast, cladistics groups organisms based exclusively on certain kinds of shared traits that are particularly informative.

This method begins with the Darwinian precept that evolution proceeds when a new heritable trait emerges in some organism and is passed genetically to its descendants. The precept indicates that two groups of animals sharing a set of such new, or "derived," traits are more closely related to each other than they are to groups that display only the original traits but not the derived ones. By identifying shared derived traits, practitioners of cladistics can determine the relations among the organisms they study.

The results of such analyses, which generally examine many traits, can be represented in the form of a cladogram: a treelike diagram depicting the order in which new characteristics, and new creatures, evolved. Each branching point, or node, reflects the emergence of an ancestor that founded a group having derived characteristics not present in groups that evolved earlier. This ancestor and all its descendants constitute a "clade," or closely related group.

Ostrom did not apply cladistic methods to determine that birds evolved from small theropod dinosaurs; in the 1970s the approach was just coming into use. But about a decade later Jacques A. Gauthier, then at the University of California at Berkeley, did an extensive cladistic analysis of birds, dinosaurs and their reptilian relatives. Gauthier put Ostrom's comparisons and many other features into a cladistic framework and confirmed that birds evolved from small theropod dinosaurs. Indeed, some of the closest relatives of birds include the sickle-clawed maniraptoran *Deinonychus* that Ostrom had so vividly described.

Today a cladogram for the lineage leading from theropods to birds shows that the clade labeled Aves (birds) consists of the ancestor of *Archaeopteryx* and all other descendants of

Bones of Contention

Although many lines of evidence establish that birds evolved from small, terrestrial theropod dinosaurs, a few scientists remain vocally unconvinced. They have not, however, tested any alternative theory by cladistics or by any other method that objectively analyzes relationships among animals. Here is a sampling of their arguments, with some of the evidence against those assertions.

Bird and theropod hands differ: theropods retain fingers I, II and III (having lost the "pinky" and "ring finger"), but birds have fingers II, III and IV. This view of the bird hand is based on embryological research suggesting that when digits are lost from the five-fingered hand, the outer fingers (I and V) are the first to go. No one doubts that theropods retain fingers I, II and III, however, so this "law" clearly has exceptions and does not rule out retention of the first three fingers in birds. More important, the skeletal evidence belies the alleged difference in the hands of birds and nonavian theropods. The three fingers that nonavian theropods kept after losing the fourth and fifth have the same forms, proportions and connections to the wristbones as the fingers in *Archaeopteryx* and later birds [see middle row of illustration on previous page].

Theropods appear too late to give rise to birds. Proponents of this view have noted that *Archaeopteryx* appears in the fossil record about 150 million years ago, whereas the fossil remains of various nonavian maniraptors—the closest known relatives of birds—date only to about 115 million years ago. But investigators have now uncovered bones that evidently belong to small, nonavian maniraptors and that date to the time of *Archaeopteryx*. In any case, failure to find fossils of a predicted kind does not rule out their existence in an undiscovered deposit.

The wishbone (composed of fused clavicles) of birds is not like the clavicles in theropods. This objection was reasonable when only the clavicles of early theropods had been discovered, but boomerang-shaped wishbones that look just like that of *Archaeopteryx* have now been uncovered in many theropods.

The complex lungs of birds could not have evolved from theropod lungs. This assertion cannot be supported or falsified at the moment, because no fossil lungs are preserved in the paleontological record. Also, the proponents of this argument offer no animal whose lungs could have given rise to those in birds, which are extremely complex and are unlike the lungs of any living animal.

—K.P. and L.M.C.

that ancestor. This clade is a subgroup of a broader clade consisting of so-called maniraptoran theropods—itsself a subgroup of the tetanuran theropods that descended from the most basal theropods. Those archaic theropods in turn evolved from nontheropod dinosaurs. The cladogram shows that birds are not only *descended* from dinosaurs, they *are* dinosaurs (and reptiles)—just as humans are mammals, even though people are as different from other mammals as birds are from other reptiles.

Early Evolutionary Steps to Birds

Gauthier's studies and ones conducted more recently demonstrate that many features traditionally considered "birdlike" actually appeared before the advent of birds, in their preavian theropod ancestors. Many of those properties undoubtedly helped their original possessors to survive as terrestrial dinosaurs; these same traits and others were eventually used directly or were transformed to support flight and an arboreal way of life. The short length of this article does not allow us to catalogue the many dozens of details that combine to support the hypothesis that birds evolved from small theropod dinosaurs, so we will concentrate mainly on those related to the origin of flight.

The birdlike characteristics of the theropods that evolved prior to birds did not appear all at once, and some were present before the theropods themselves emerged—in the earliest

reduced fingers disappeared altogether in tetanuran theropods, and the remaining three (I, II, III) became fused together sometime after *Archaeopteryx* evolved.

In the first theropods, the hind limbs became more birdlike as well. They were long; the thigh was shorter than the shin, and the fibula, the bone to the side of the shinbone, was reduced. (In birds today the toothpicklike bone in the drumstick is all that is left of the fibula.) These dinosaurs walked on the three middle toes—the same ones modern birds use. The fifth toe was shortened and tapered, with no joints, and the first toe included a shortened metatarsal (with a small joint and a claw) that projected from the side of the second toe. The first toe was held higher than the others and had no apparent function, but it was later put to good use in birds. By the time *Archaeopteryx* appeared, that toe had rotated to lie behind the others. In later birds, it descended to become opposable to the others and eventually formed an important part of the perching foot.

More Changes

Through the course of theropod evolution, more features once thought of as strictly avian emerged. For instance, major changes occurred in the forelimb and shoulder girdle; these adjustments at first helped theropods to capture prey and later promoted flight. Notably, during theropod evolution, the arms became progressively longer, except in such gi-

Birds are not only *descended* from dinosaurs, they *are* dinosaurs

dinosaurs. For instance, the immediate reptilian ancestor of dinosaurs was already bipedal and upright in its stance (that is, it basically walked like a bird), and it was small and carnivorous. Its hands, in common with those of early birds, were free for grasping (although the hand still had five digits, not the three found in all but the most basal theropods and in birds). Also, the second finger was longest—not the third, as in other reptiles.

Further, in the ancestors of dinosaurs, the ankle joint had already become hingelike, and the metatarsals, or foot bones, had become elongated. The metatarsals were held off the ground, so the immediate relatives of dinosaurs, and dinosaurs themselves, walked on their toes and put one foot in front of the other, instead of sprawling. Many of the changes in the feet are thought to have increased stride length and running speed, a property that would one day help avian theropods to fly.

The earliest theropods had hollow bones and cavities in the skull; these adjustments lightened the skeleton. They also had a long neck and held their back horizontally, as birds do today. In the hand, digits four and five (the equivalent of the pinky and its neighbor) were already reduced in the first dinosaurs; the fifth finger was virtually gone. Soon it was completely lost, and the fourth was reduced to a nubbin. Those

ant carnivores as *Carnotaurus*, *Allosaurus* and *Tyrannosaurus*, in which the forelimbs were relatively small. The forelimb was about half the length of the hind limb in very early theropods. By the time *Archaeopteryx* appeared, the forelimb was longer than the hind limb, and it grew still more in later birds. This lengthening in the birds allowed a stronger flight stroke.

The hand became longer, too, accounting for a progressively greater proportion of the forelimb, and the wrist underwent dramatic revision in shape. Basal theropods possessed a flat wristbone (distal carpal) that overlapped the bases of the first and second palm bones (metacarpals) and fingers. In maniraptorans, though, this bone assumed a half-moon shape along the surface that contacted the arm bones. The half-moon, or semilunate, shape was very important because it allowed these animals to flex the wrist sideways in addition to up and down. They could thus fold the long hand, almost as living birds do. The longer hand could then be rotated and whipped forward suddenly to snatch prey.

In the shoulder girdle of early theropods, the scapula (shoulder blade) was long and straplike; the coracoid (which along with the scapula forms the shoulder joint) was rounded, and two separate, S-shaped clavicles connected the shoulder to the sternum, or breastbone. The scapula soon became longer

and narrower; the coracoid also thinned and elongated, stretching toward the breastbone. The clavicles fused at the midline and broadened to form a boomerang-shaped wishbone. The sternum, which consisted originally of cartilage, calcified into two fused bony plates in tetanurans. Together these changes strengthened the skeleton; later this strengthening was used to reinforce the flight apparatus and support the flight muscles. The new wishbone, for instance, probably became an anchor for the muscles that moved the forelimbs, at first during foraging and then during flight.

In the pelvis, more vertebrae were added to the hip girdle, and the pubic bone (the pelvic bone that is attached in front of and below the hip socket) changed its orientation. In the first theropods, as in most other reptiles, the pubis pointed down and forward, but then it began to point straight down or backward. Ultimately, in birds more advanced than *Archaeopteryx*, it became parallel to the ischium, the pelvic bone that extends backward from below the hip socket. The benefits derived from these changes, if any, remain unknown, but the fact that these features are unique to birds and other maniraptorans shows their common origin.

Finally, the tail gradually became shorter and stiffer throughout theropod history, serving more and more as a balancing organ during running, somewhat as it does in today's road-runners. Steven M. Gatesy of Brown University has demonstrated that this transition in tail structure paralleled another change in function: the tail became less and less an anchor for the leg muscles. The pelvis took over that function, and in maniraptorans the muscle that once drew back the leg now mainly controlled the tail. In birds that followed *Archaeopteryx*, these muscles would be used to adjust the feathered tail as needed in flight.

In summary, a great many skeletal features that were once thought of as uniquely avian innovations—such as light, hollow bones, long arms, three-fingered hands with a long second finger, a wishbone, a backward-pointing pelvis, and long hind limbs with a three-toed foot—were already present in theropods before the evolution of birds. Those features generally served different uses than they did in birds and were only later co-opted for flight and other characteristically avian functions, eventually including life in the trees.

Evidence for the dinosaurian origin of birds is not confined to the skeleton. Recent discoveries of nesting sites in Mongolia and Montana reveal that some reproductive behaviors of birds originated in nonavian dinosaurs. These theropods did not deposit a large clutch of eggs all at once, as most other reptiles do. Instead they filled a nest more gradually, laying one or two eggs at a time, perhaps over several days, as birds do. Recently skeletons of the Cretaceous theropod *Oviraptor* have been found atop nests of eggs; the dinosaurs were apparently buried while protecting the eggs in very birdlike fashion. This find is ironic because *Oviraptor*, whose name means "egg stealer," was first thought to have been raiding the eggs of other dinosaurs, rather than protecting them. Even the structure of the eggshell in theropods shows features otherwise seen only in bird eggs. The shells consist of two layers of calcite, one prismatic (crystalline) and one spongy (more irregular and porous).

As one supposedly uniquely avian trait after another has been identified in nonavian dinosaurs, feathers have continued to stand out as a prominent feature belonging to birds alone. Some intriguing evidence, however, hints that even feathers might have predated the emergence of birds.

In 1996 and 1997 Ji Qiang and Ji Shu'an of the National Geological Museum of China published reports on two fossil animals found in Liaoning Province that date to late in the Jurassic or early in the Cretaceous. One, a turkey-size dinosaur named *Sinosauropteryx*, has fringed, filamentous structures along its backbone and on its body surface. These structures of the skin, or integument, may have been precursors to feathers. But the animal is far from a bird. It has short arms and other skeletal properties indicating that it may be related to the theropod *Compsognathus*, which is not especially close to birds or other maniraptorans.

The second creature, *Protarchaeopteryx*, apparently has short, true feathers on its body and has longer feathers attached to its tail. Preliminary observations suggest that the animal is a maniraptoran theropod. Whether it is also a bird will depend on a fuller description of its anatomy. Nevertheless, the Chinese finds imply that, at the least, the structures that gave rise to feathers probably appeared before birds did and almost certainly before birds began to fly. Whether their original function was for insulation, display or something else cannot yet be determined.

The Beginning of Bird Flight

The origin of birds and the origin of flight are two distinct, albeit related, problems. Feathers were present for other functions before flight evolved, and *Archaeopteryx* was probably not the very first flying theropod, although at present we have no fossils of earlier flying precursors. What can we say about how flight began in bird ancestors?

Traditionally, two opposing scenarios have been put forward. The "arboreal" hypothesis holds that bird ancestors began to fly by climbing trees and gliding down from branches with the help of incipient feathers. The height of trees provides a good starting place for launching flight, especially through gliding. As feathers became larger over time, flapping flight evolved, and birds finally became fully airborne.

This hypothesis makes intuitive sense, but certain aspects are troubling. *Archaeopteryx* and its maniraptoran cousins have no obviously arboreal adaptations, such as feet fully adapted for perching. Perhaps some of them could climb trees, but no convincing analysis has demonstrated how *Archaeopteryx* would have climbed and flown with its forelimbs, and there were no plants taller than a few meters in the environments where *Archaeopteryx* fossils have been found. Even if the animals could climb trees, this ability is not synonymous with arboreal habits or gliding ability. Most small animals, and even some goats and kangaroos, can climb trees, but that does not make them tree dwellers. Besides, *Archaeopteryx* shows no obvious features of gliders, such as a broad membrane connecting forelimbs and hind limbs.

The "cursorial" (running) hypothesis holds that small dinosaurs ran along the ground and stretched out their arms for balance as they leaped into the air after insect prey or, perhaps, to avoid predators. Even rudimentary feathers on forelimbs could have expanded the arm's surface area to enhance lift slightly. Larger feathers could have increased lift incrementally, until sustained flight was gradually achieved. Of course, a leap into the air does not provide the acceleration produced by dropping out of a tree; an animal would have to run quite fast to take off. Still, some small terrestrial animals can achieve high speeds.

The cursorial hypothesis is strengthened by the fact that

the immediate theropod ancestors of birds were terrestrial. And they had the traits needed for high liftoff speeds: they were small, active, agile, lightly built, long-legged and good runners. And because they were bipedal, their arms were free to evolve flapping flight, which cannot be said for other reptiles of their time.

Although our limited evidence is tantalizing, probably neither the arboreal nor the cursorial model is correct in its extreme form. More likely, the ancestors of birds used a combination of taking off from the ground and taking advantage of accessible heights (such as hills, large boulders or fallen trees). They may not have climbed trees, but they could have used every available object in their landscape to assist flight.

More central than the question of ground versus trees, however, is the evolution of a flight stroke. This stroke generates not only the lift that gliding animals obtain from moving their wings through the air (as an airfoil) but also the thrust that enables a flapping animal to move forward. (In contrast, the “organs” of lift and thrust in airplanes—the wings and jets—are separate.) In birds and bats, the hand part of the wing generates the thrust, and the rest of the wing provides the lift.

Jeremy M. V. Rayner of the University of Bristol showed in the late 1970s that the down-and-forward flight stroke of birds and bats produces a series of doughnut-shaped vortices that propel the flying animal forward. One of us (Padian) and Gauthier then demonstrated in the mid-1980s that the movement generating these vortices in birds is the same action—sideways flexion of the hand—that was already present in the maniraptorans *Deinonychus* and *Velociraptor* and in *Archaeopteryx*.

As we noted earlier, the first maniraptorans must have used this movement to grab prey. By the time *Archaeopteryx* and other birds appeared, the shoulder joint had changed its angle to point more to the side than down and backward. This alteration in the angle transformed the forelimb motion from a prey-catching one to a flight stroke. New evidence from Argentina suggests that the shoulder girdle in the closest maniraptorans to birds (the new dinosaur *Unenlagia*) was already angled outward so as to permit this kind of stroke.

Recent work by Farish A. Jenkins, Jr., of Harvard University, George E. Goslow of Brown University and their colleagues has revealed much about the role of the wishbone in flight and about how the flight stroke is achieved. The wishbone in some living birds acts as a spacer between the shoulder girdles, one that stores energy expended during the flight stroke. In the first birds, in contrast, it probably was less elastic, and its main function may have been simply to anchor the forelimb muscles. Apparently, too, the muscle most responsible for rotating and raising the wing during the recovery stroke of flight was not yet in the modern position in *Archaeopteryx* or other very early birds. Hence, those birds were probably not particularly skilled fliers; they would have been unable to flap as quickly or as precisely as today’s birds can. But it was not

long—perhaps just several million years—before birds acquired the apparatus they needed for more controlled flight.

Beyond *Archaeopteryx*

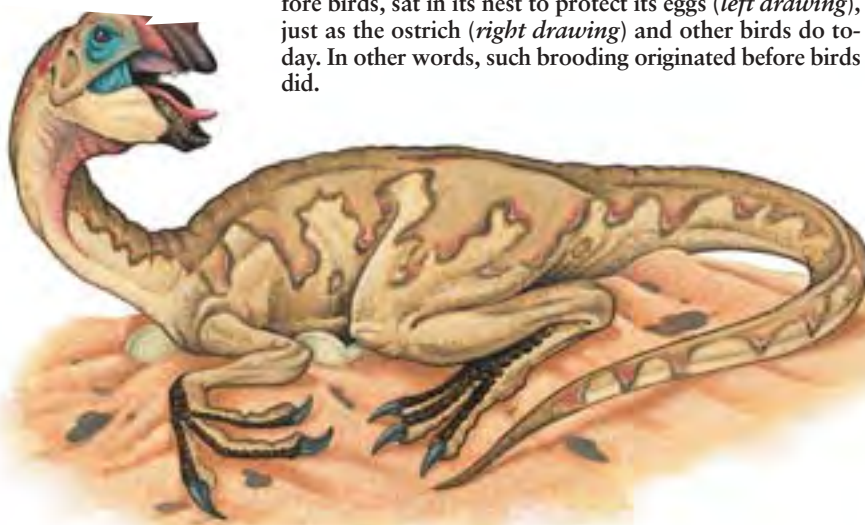
More than three times as many bird fossils from the Cretaceous period have been found since 1990 than in all the rest of recorded history. These new specimens—uncovered in such places as Spain, China, Mongolia, Madagascar and Argentina—are helping paleontologists to flesh out the early evolution of the birds that followed *Archaeopteryx*, including their acquisition of an improved flying system. Analyses of these finds by one of us (Chiappe) and others have shown that birds quickly took on many different sizes, shapes and behaviors (ranging from diving to flightlessness) and diversified all through the Cretaceous period, which ended about 65 million years ago.

A bird-watching trek through an Early Cretaceous forest would bear little resemblance to such an outing now. These early birds might have spent much of their time in the trees and were able to perch, but there is no evidence that the first birds nested in trees, had complex songs or migrated great distances. Nor did they fledge at nearly adult size, as birds do now, or grow as rapidly as today’s birds do. Scientists can only imagine what these animals looked like. Undoubtedly, however, they would have seemed very strange, with their clawed fingers and, in many cases, toothed beaks.

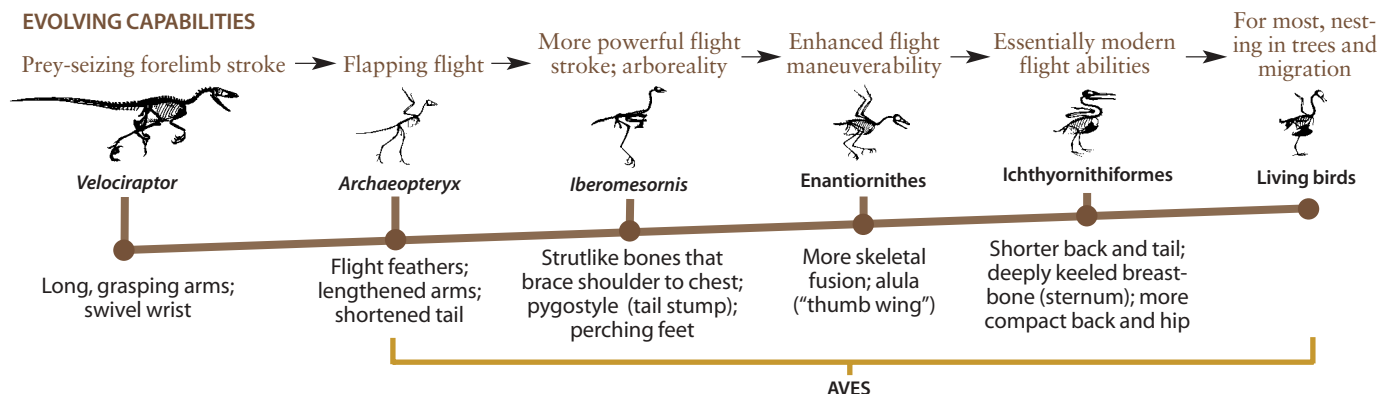
Underneath the skin, though, some skeletal features certainly became more birdlike during the Early Cretaceous and enabled birds to fly quite well. Many bones in the hand and in the hip girdle fused, providing strength to the skeleton for flight. The breastbone became broader and developed a keel down the midline of the chest for flight muscle attachment. The forearm became much longer, and the skull bones and vertebrae became lighter and more hollowed out. The tailbones became a short series of free segments ending in a fused stump (the familiar “parson’s nose” or “Pope’s nose” of roasted birds) that controlled the tail feathers. And the alula, or “thumb wing,” a part of the bird wing essential for flight control at low speed, made its debut, as did a long first toe useful in perching.

Inasmuch as early birds could fly, they certainly had higher

OVIRAPTOR, a maniraptoran theropod that evolved before birds, sat in its nest to protect its eggs (*left drawing*), just as the ostrich (*right drawing*) and other birds do today. In other words, such brooding originated before birds did.



EVOLVING CAPABILITIES



ED HECK

CLADOGRAM OF BIRD EVOLUTION indicates that birds (Aves) perfected their flight stroke gradually after they first appeared approximately 150 million years ago. They became ar-

boreal (able to live in trees) relatively early in their history, however. Some of the skeletal innovations that supported their emerging capabilities are listed at the bottom.

metabolic rates than cold-blooded reptiles; at least they were able to generate the heat and energy needed for flying without having to depend on being heated by the environment. But they might not have been as fully warm-blooded as today's birds. Their feathers, in addition to aiding flight, provided a measure of insulation—just as the precursors of feathers could have helped preserve heat and conserve energy in nonavian precursors of birds. These birds probably did not fly as far or as strongly as birds do now.

Bird-watchers traipsing through a forest roughly 50 million years later would still have found representatives of very primitive lineages of birds. Yet other birds would have been recognizable as early members of living groups. Recent research shows that at least four major lineages of living birds—including ancient relatives of shorebirds, seabirds, loons, ducks and geese—were already thriving several million years before the end of the Cretaceous period, and new paleontological and molecular evidence suggests that forerunners of other modern birds were around as well.

Most lineages of birds that evolved during the Cretaceous died out during that period, although there is no evidence that they perished suddenly. Researchers may never know whether the birds that disappeared were outcompeted by newer forms, were killed by an environmental catastrophe or were just unable to adapt to changes in their world. There is no reasonable doubt,

however, that all groups of birds, living and extinct, are descended from small, meat-eating theropod dinosaurs, as Huxley's work intimated more than a century ago. In fact, living birds are nothing less than small, feathered, short-tailed theropod dinosaurs.

The Authors

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Further Reading

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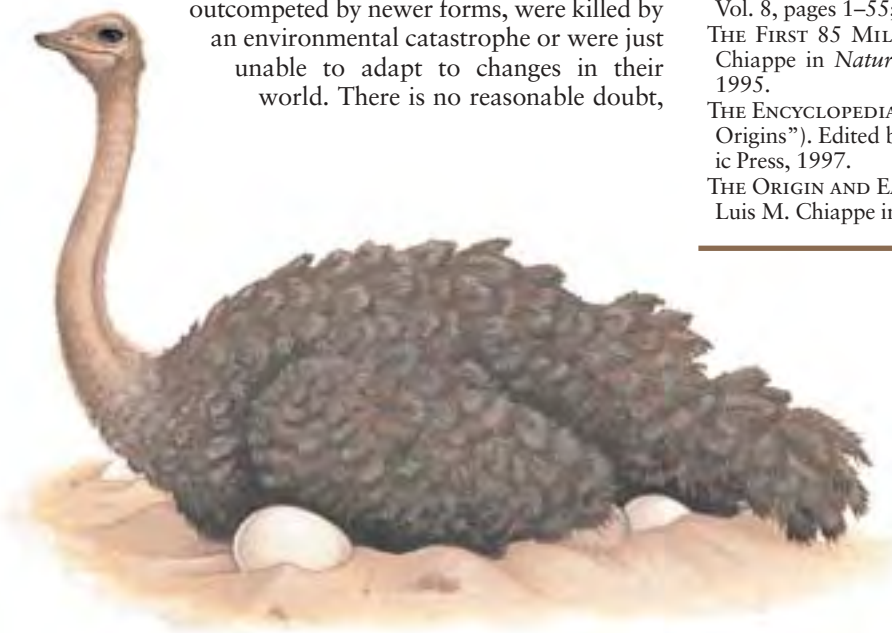
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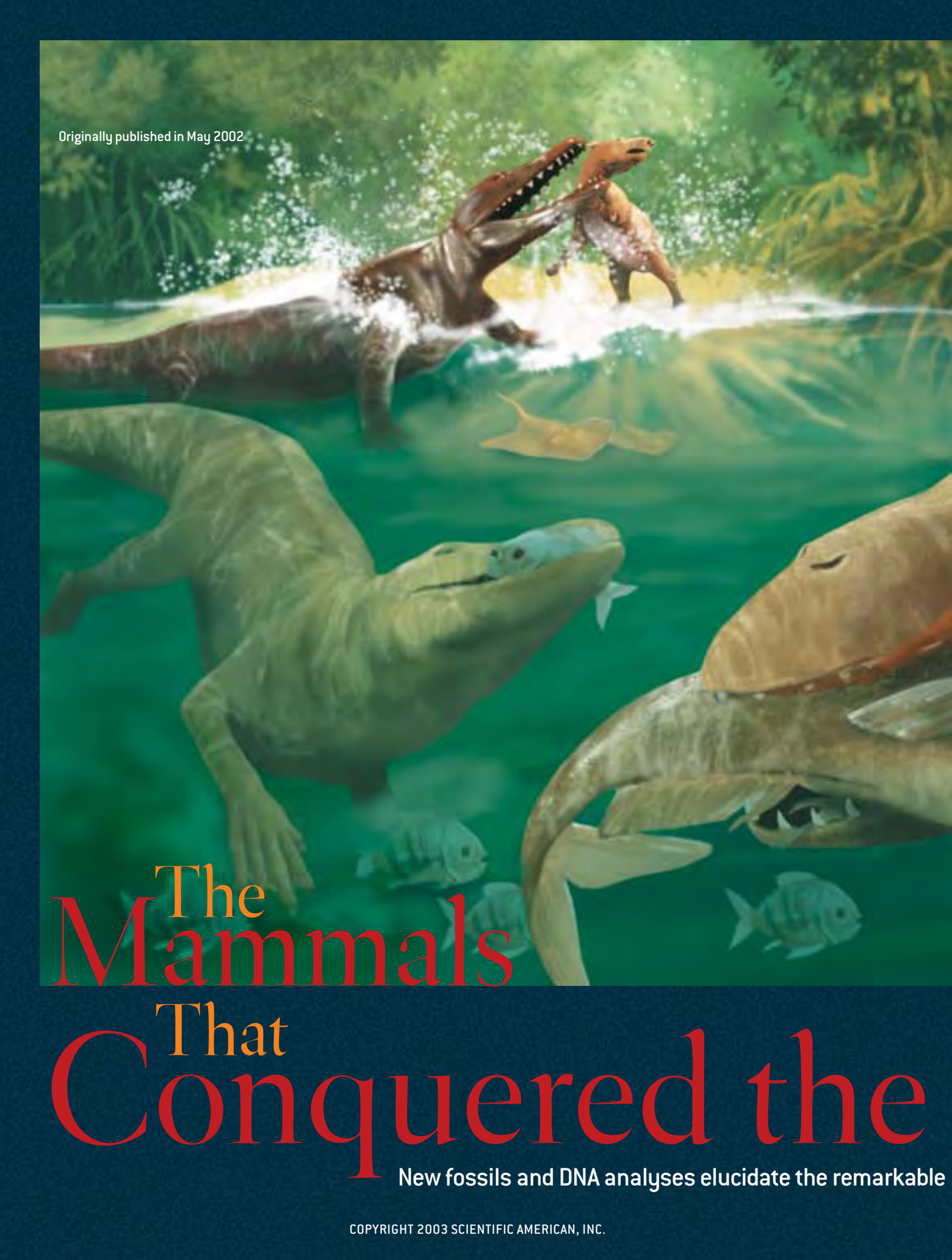
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ILLUSTRATIONS BY ED HECK





Originally published in May 2002

The Mammals That Conquered the

New fossils and DNA analyses elucidate the remarkable

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“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.

Seas

evolutionary history of whales

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 viselike 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 remained. 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.

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, 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 and thus were linked to artiodactyls through the condylarths.

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.

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

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

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.

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 Gingerich went to Pakistan in 1977 in search of Eocene land mammals, visiting an area previously reported to shelter such remains. The expedition proved disappointing because the spot turned out to contain only marine fossils. Finding traces of ancient ocean life in Pakistan, far from the coun-

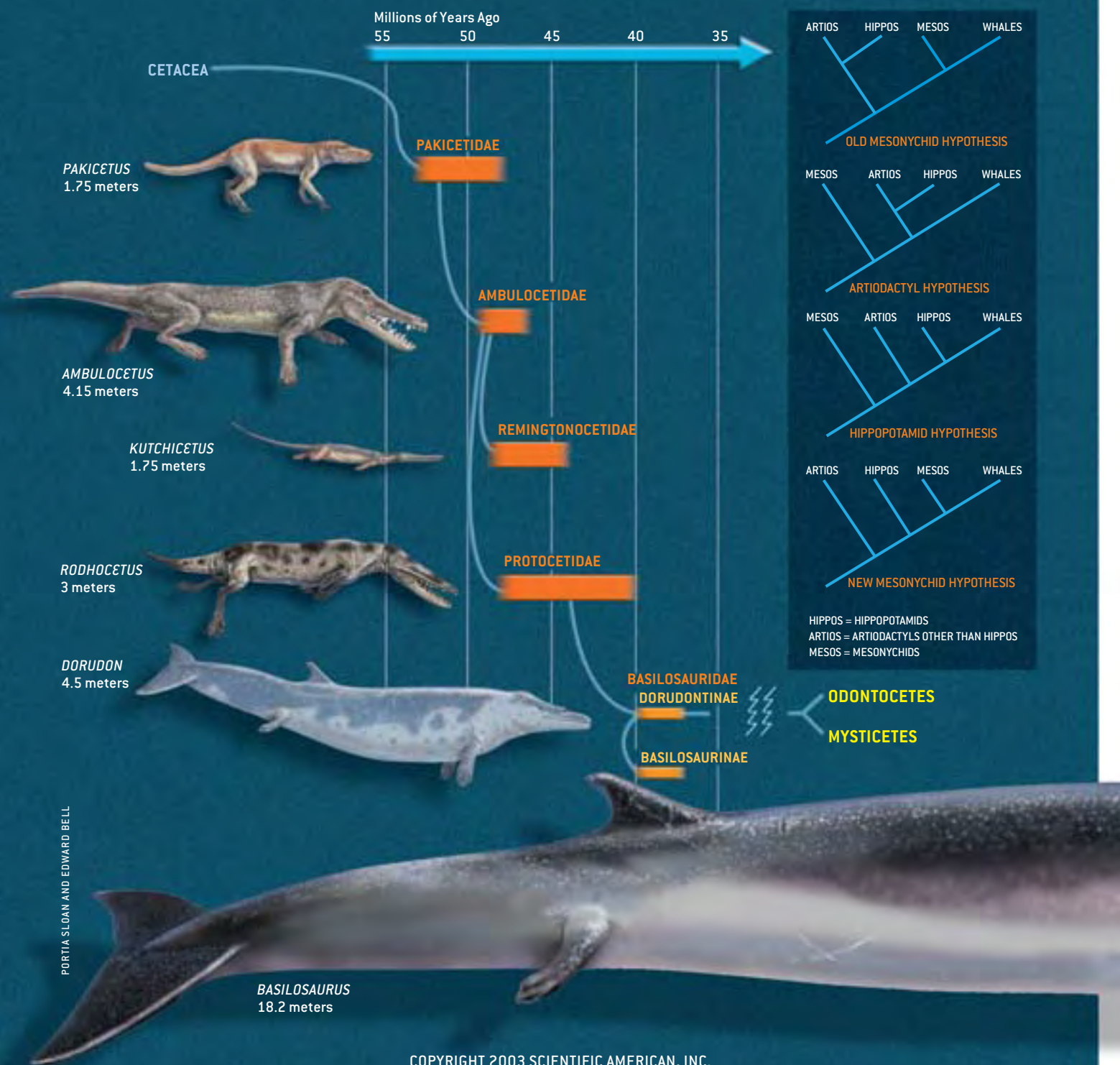
try's modern coast, is not surprising: during the Eocene, the vast Tethys Sea periodically covered great swaths of what is now the Indian subcontinent. Intriguingly, though, the team discovered among those ancient fish and snail remnants two pelvis fragments that appeared to have come from relatively 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 found another weird whale clue: a par-

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 new 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.



tial braincase from a wolf-size creature—found in the company of 50-million-year-old land mammal remains—that bore some 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.

At around the same time, another group recovered additional remains of *Pakicetus*—a lower jaw fragment and some 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 looked 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 zeuglodonts, 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 some 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. Although 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, they may well have helped guide the beast's serpentine body during the difficult ac-

tivity 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 and 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 previous 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 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.

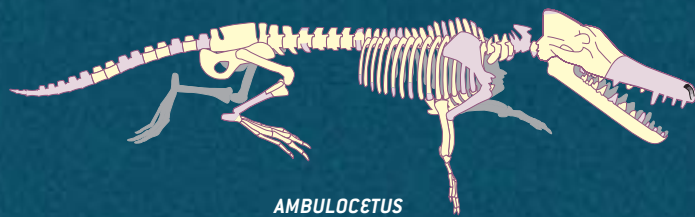
What, then, might *Pakicetus* have used its thickened bullae for? Thewissen suspects that much as turtles hear by picking up vibrations from the ground through their shields, *Pakicetus* may have employed its bullae to pick up ground-borne sounds. Taking new postcranial evidence into consideration along 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



BECOMING LEVIATHAN

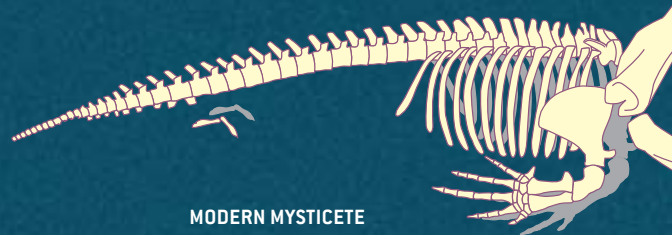


PAKICETUS



AMBULOCETUS

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.



MODERN MYSTICETE

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 tympanic ligament had probably already evolved. Additionally, air sinuses, presumably filled with spongelike 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), he 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.

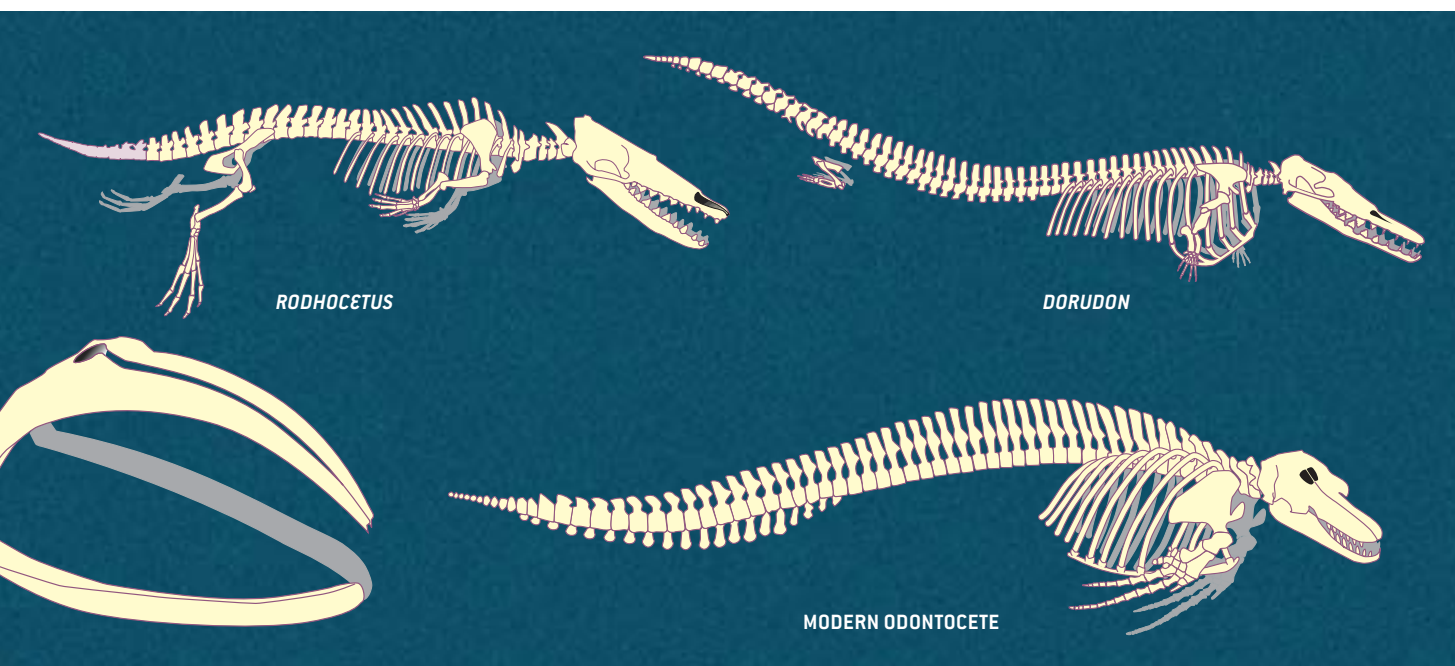
Other notable skull changes include movement of the eye sockets from a crocodilelike placement atop the head in *Pakicetus* and *Ambulocetus* to a lateral position in the more aquatic protocetids and later whales. And the nasal opening migrated back from the tip of the snout in *Pakicetus* to the top of the head in modern cetaceans, forming the blowhole. Whale dentition morphed, too, turning the complexly cusped, grind-

ing molars of primitive mammalian ancestors into the simple, pronglike teeth of modern odontocetes, which grasp and swallow their food without chewing. Mysticetes lost their teeth altogether and developed comblike 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 somewhat 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 Bill Sanders. The animal's long, delicate feet were probably webbed, like the fins used by scuba divers. *Rodhocetus* also exhibits aquatic adaptations in its pelvis, where 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 somewhat like 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.

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 taking wing 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 in fact 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 seas should exhibit this double-pulleyed astragalus.

That piece of the puzzle fell into place last fall, when Gingerich and Thewissen both announced discoveries of new primitive whale fossils. 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 the Kala Chitta Hills of Punjab, Pakistan, 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.

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 some 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.

Thewissen agrees that the hippo hypothesis holds much more appeal than it once did. But he cautions that the morphological data do not yet 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 new 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 the State University of New York at Stony Brook 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 the whales' closest relative, and hippos could be their closest living relative. 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 figuring out 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 unravel 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.

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MORE TO EXPLORE

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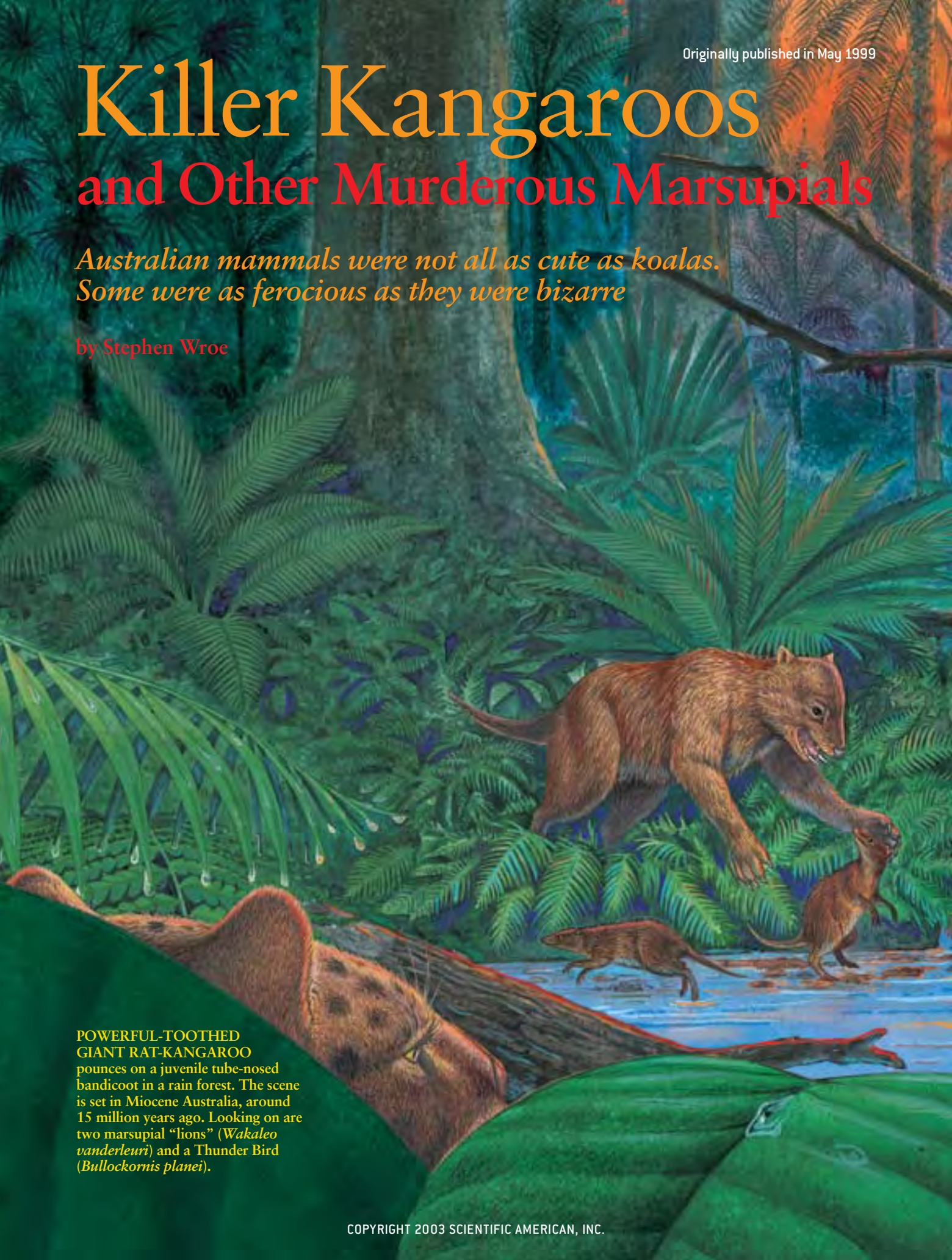
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Killer Kangaroos and Other Murderous Marsupials

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

by Stephen Wroe

A detailed illustration of a prehistoric rainforest scene. In the foreground, a large, brown, furry marsupial with a long tail is pouncing on a smaller, brown, tube-nosed marsupial. In the background, another similar marsupial is running through a stream. The forest is lush with green ferns and trees, with rain falling. A large, brown, furry marsupial is visible in the lower left foreground, partially obscured by a large green leaf.

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 Thunder Bird
(*Bullockornis planei*).



Dawn mist blankets the rain forest of Riversleigh 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 nearby 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.

ROBERTO OSTI

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

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

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

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

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

Predator’s Gallery

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



ILLUSTRATIONS BY ROBERTO OSTI AND ANNE MUSSER

LARGEST MARSUPIAL LION
(*Thylacoleo carnifex*)
130 TO 260 KILOGRAMS

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

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

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



LARGEST MARSUPIAL WOLF
(*Thylacinus potens*)
MAXIMUM 45 KILOGRAMS



**POWERFUL-TOOTHED
GIANT RAT-KANGAROO**
(*Ekaltadeta ima*)
20 KILOGRAMS



GIANT MONITOR LIZARD
(*Megalania prisca*)
620 KILOGRAMS

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

Fearsome Forest

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

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

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

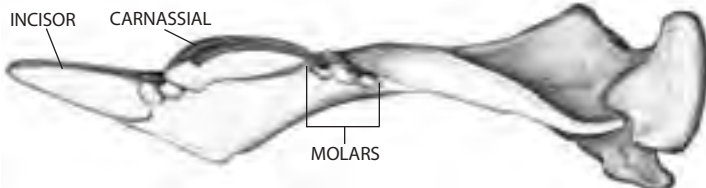
In popular imagination, ferocious meat-eaters usually come with large canines. In the main this holds true, but

there are some exceptions. Many humans consume a good deal of flesh—more than some so-called carnivores—but we have small canines, whereas in gorillas, which are vegetarians, these teeth are large. The real hallmark of a terrestrial mammalian killer is a set of distinctive cheek teeth used for cutting and shearing.

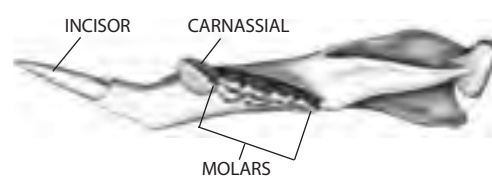
In less specialized members of the placental carnivore, giant rat-kangaroo and marsupial lion clans, the last two to four teeth in the upper and lower jaws are broad molars, used primarily for crushing plant material. Immediately in front of these molars are vertical shearing blades, called carnassials,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

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

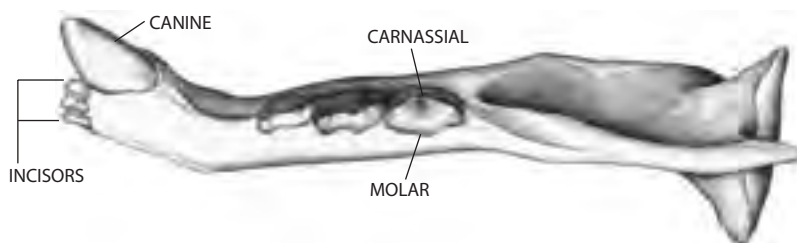
On these grounds, I and others have argued that giant rat-kangaroos were generalists, taking flesh when available but

LARGEST MARSUPIAL LION (*T. carnifex*)

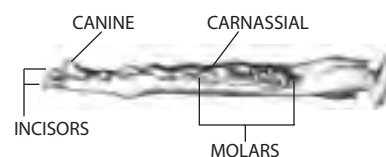
POWERFUL-TOOTHED GIANT RAT-KANGAROO



AFRICAN LION



GRAY FOX



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

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

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

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

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

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

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

posable thumb, it would have been an awesome predator on any continent.

Pouched Pouncers

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

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

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

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

ANNE MÜSSER



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

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

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

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

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

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

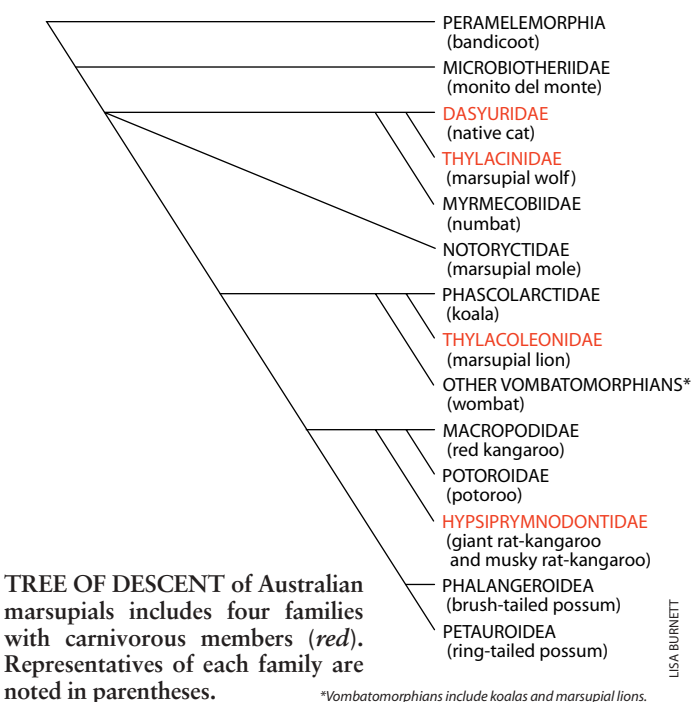
South America and Australia were once joined together in the continent of Gondwana, via Antarctica. And marsupials are believed to have arrived in Australia from South America. Some scientists have suggested that only Australidelphian mammals entered Australia before Gondwana completely

broke up. In light of the new fossil finding, this conclusion could be premature.

Death to Killers

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

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



A Killer Bird?

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

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



ROBERTO OSTI AND ANNE MUSSER

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

Obviously, some factor other than human influence was at

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

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

The Author

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

Further Reading

RIVERSLEIGH: THE STORY OF ANIMALS IN ANCIENT RAINFORESTS OF INLAND AUSTRALIA. M. Archer, S. Hand and H. Godthelp. Reed Books, 1994.
KILLER KANGAROO. S. Wroe in *Australasian Science*, Vol. 19, No. 6, pages 25–28; July 1998.
THE GEOLOGICALLY OLDEST DASYURID, FROM THE MIOCENE OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND. S. Wroe in *Palaeontology* (in press).
The Riversleigh Society Australian Paleontology site is at www.ozemail.com.au/~promote1/auspaleo/index.html on the World Wide Web.