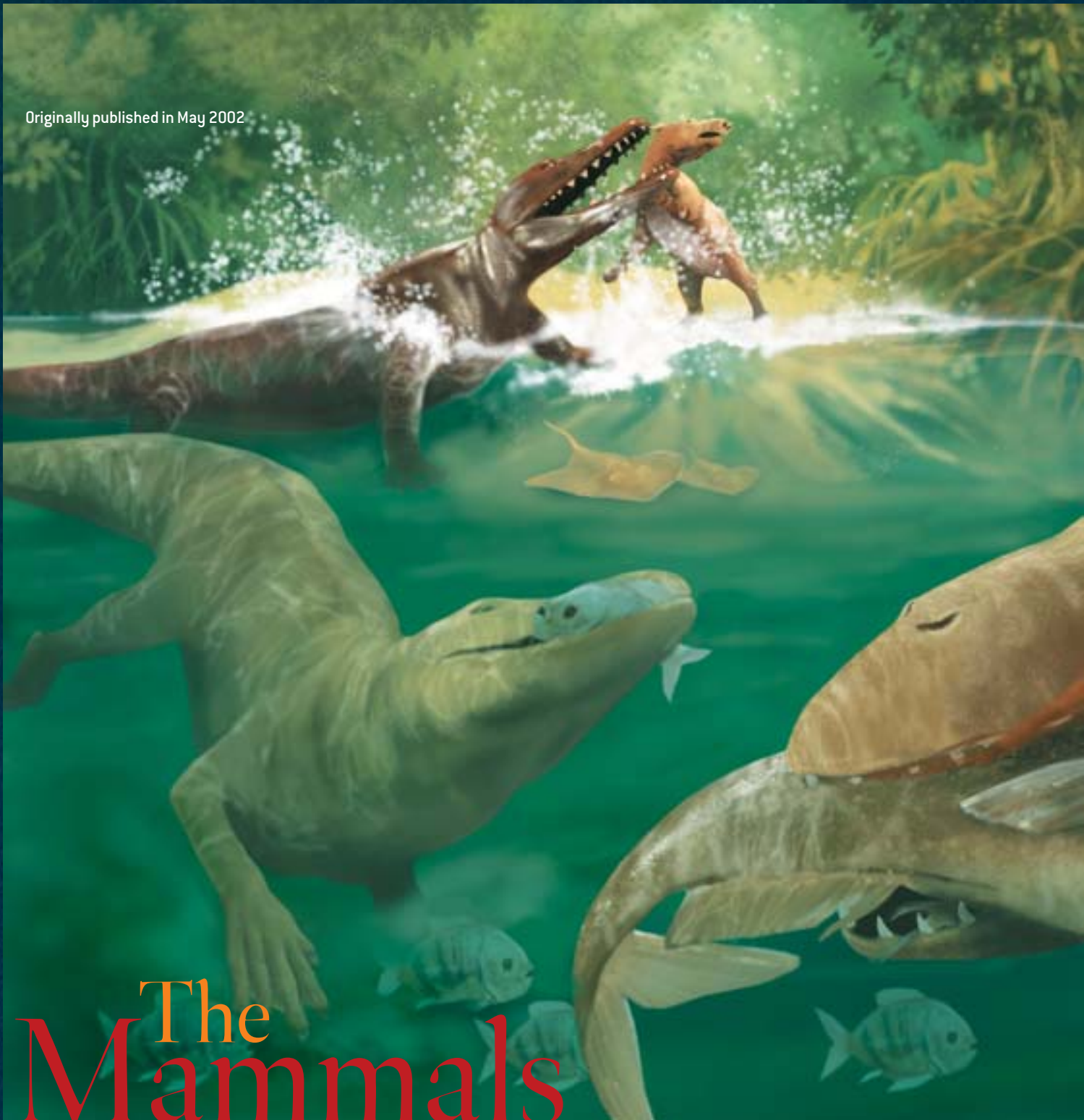


Originally published in May 2002



# The Mammals That Conquered the

New fossils and DNA analyses elucidate the remarkable



“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!”

**D**awn 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-

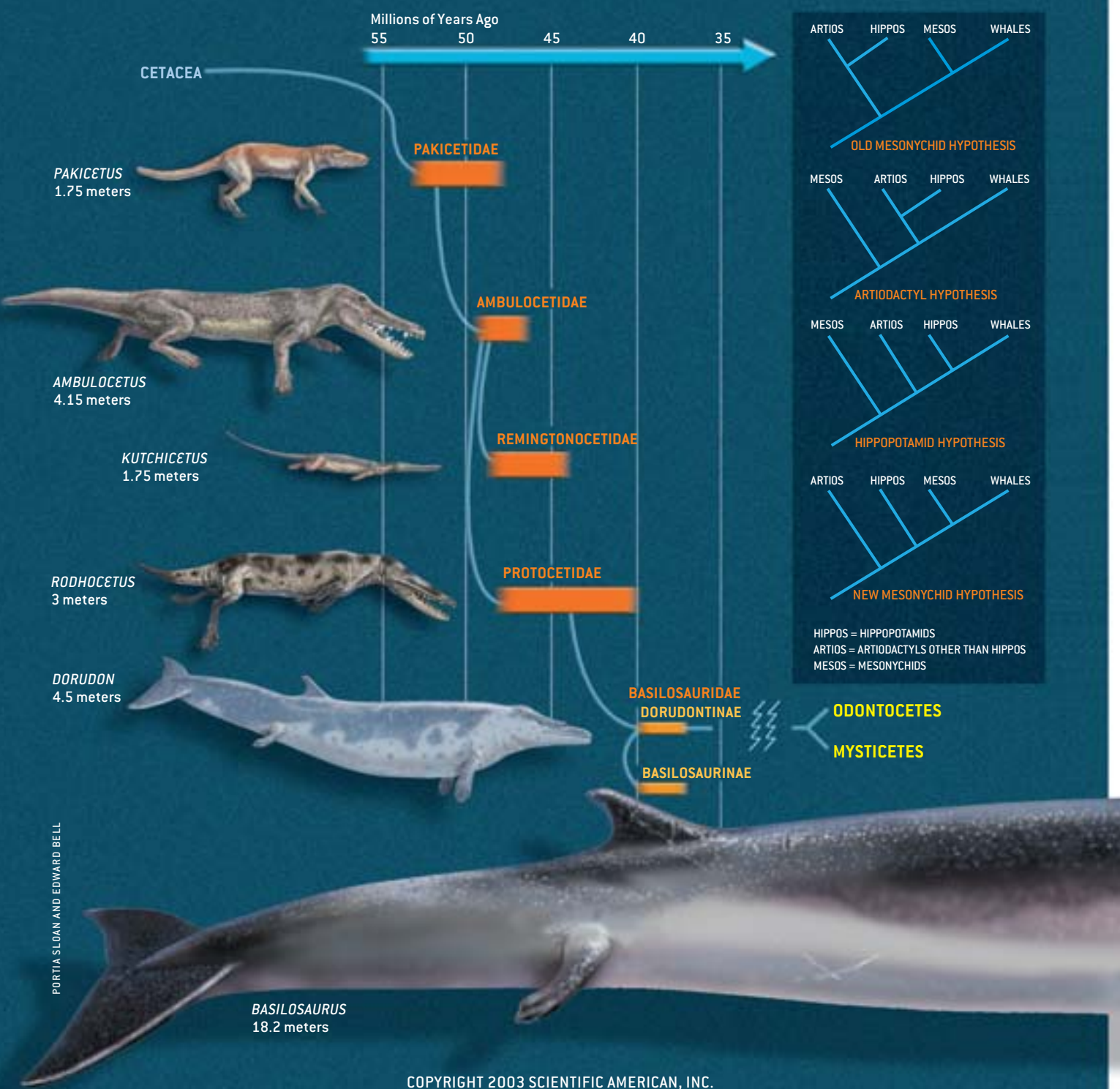
try's modern coast, is not surprising: during the Eocene, the vast Tethys Sea periodically covered great swaths of what is now the Indian subcontinent. Intriguingly, though, the team discovered among those ancient fish and snail remnants two pelvis fragments that appeared to have come from relatively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



PORTIA SLOAN AND EDWARD BELL

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 zeuglodon, 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 scooped 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.

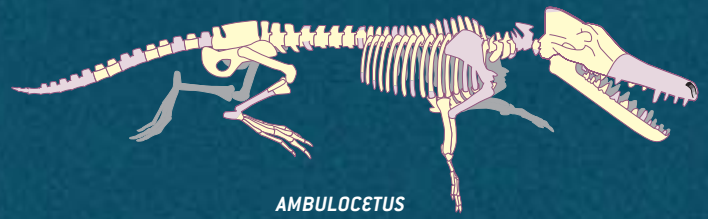
What, then, might *Pakicetus* have used its thickened bullae for? Thewissen suspects that much as turtles hear by picking up vibrations from the ground through their shields, *Pakicetus* may have employed its bullae to pick up ground-borne sounds. Taking new postcranial evidence into consideration along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

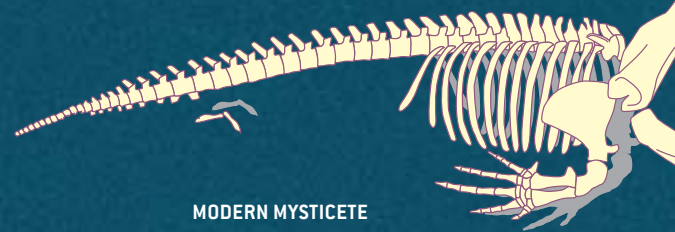


PAKICETUS



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.

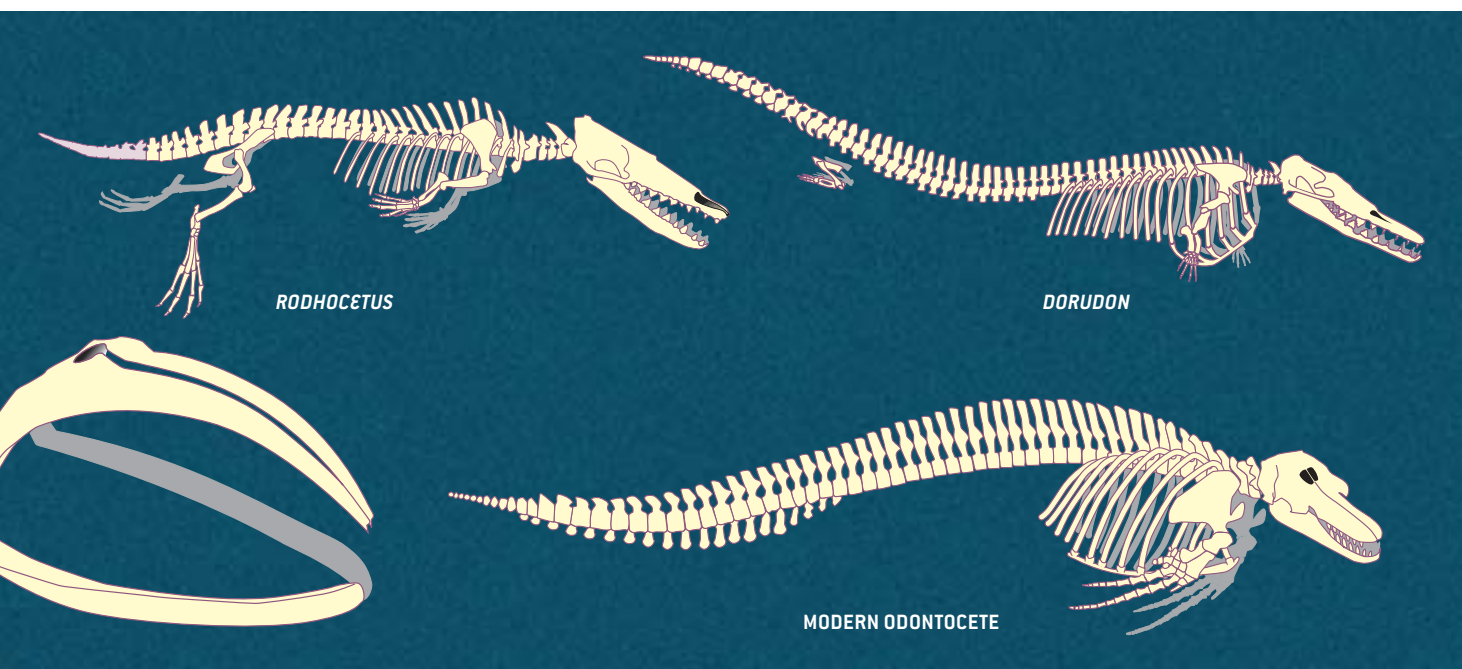
Other notable skull changes include movement of the eye sockets from a crocodilelike placement atop the head in *Pakicetus* and *Ambulocetus* to a lateral position in the more aquatic protocetids and later whales. And the nasal opening migrated back from the tip of the snout in *Pakicetus* to the top 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-pulleys 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:  $^{16}\text{O}$  and  $^{18}\text{O}$ . The ratios of these isotopes in freshwater and seawater differ, with seawater containing more  $^{18}\text{O}$ . 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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*Kate Wong is a writer and editor for ScientificAmerican.com*

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