

Whale Origins as a Poster Child for Macroevolution

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Whales indisputably are mammals, which is clear from their means of oxygen intake (they breathe with lungs), their care of newborns (mothers nurse their calves with milk), and a host of other features. This implies that whales evolved from other mammals and, because ancestral mammals were land animals, that whales had land ancestors. What happened in the transition to life in the ocean has been hard to imagine for scientists and laypeople alike. In the first edition of the *Origin of Species* (1859), Darwin suggested that a bearlike animal swimming with an open mouth might be a precursor of a filter-feeding baleen whale. This statement attracted much ridicule; in a letter, Darwin observed, "It is laughable how often I have been attacked and misrepresented about this bear" (Gould 1995). In later editions, Darwin deleted this reference to evolution entirely and merely noted that a bear sifting water for insects is "almost like a whale."

Nearly 150 years later, we can fill in much of the gap that embarrassed Darwin. The last two decades have witnessed an explosive growth in the number of fossils documenting the origins of Cetacea (whales, dolphins, and porpoises). An excellent morphological series of transitional cetaceans is now available to document the transition from land to sea, and many sophisticated analyses detail the biology of these archaic cetaceans. The origin of whales now offers a spectacular example of evolutionary change, allowing us to chart changes in anatomy and physiology as whales first moved into the water and then gradually explored the open seas.

Although Darwin didn't have the details right—bears did not evolve into whales—his basic point was correct: We can now show that whales are in fact hooved mammals that took to sea. Yet in spite of the wealth of new evidence, certain segments of popular and creationist literature continue to use cetaceans as examples of animals that could not possibly have evolved through modified descent. Much of the blame for these misconceptions is the deliberate spread of misinformation by those who deny evolution, as well as simple

Editor's note: After this article went to press, Thewissen and colleagues published new whale fossil findings (Nature 413: 277–281).

FOSSILS COLLECTED IN THE LAST DECADE DOCUMENT THE WAYS IN WHICH CETACEA (WHALES, DOLPHINS, AND PORPOISES) BECAME AQUATIC, A TRANSITION THAT IS ONE OF THE BEST DOCUMENTED EXAMPLES OF MACROEVOLUTION IN MAMMALS

ignorance on the part of those unaware of published research. However, the sheer volume and pace of recent research also cause problems. For those outside of the circle of specialists actively studying whale origins, it is hard to keep up with all the new discoveries.

In this article, we first introduce the families of archaic cetaceans that lived in the Eocene (approximately 55 million to 34 million years ago), the oldest period from which cetaceans are known. After that, we discuss the several organ systems that underwent dramatic changes. Then, we put the functional morphology and evolution of two organ systems, locomotion and osmoregulation, in a broader perspective. We show that the differences among these extinct animals make sense only in the context of evolving adaptations to an aquatic environment. We cannot provide a comprehensive review of early cetacean evolution, as this would take up many pages. The two chosen organ systems make compelling examples of

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macroevolutionary change, showing a stepped transition from land to water for archaic cetaceans. From these beginnings, the order Cetacea expanded into a wide variety of aquatic groups, including mostly large, filter-feeding baleen whales (suborder Mysticeti), and predatory toothed whales (suborder Odontoceti, which includes, among others, dolphins, porpoises, sperm whales, beaked whales, and killer whales).

What we do know of early cetaceans amounts to an overwhelming and dramatic record of evolving adaptations. The field of whale origins is progressing quickly, and new finds will add new insights, so that this article cannot be the final synthesis of whale origins. But even as specialists continue to debate important questions such as that of the sister group of cetaceans and the age of the oldest whale, it is clear that we already know more than enough to trace the general outline of whale evolution. Though important, the remaining questions are essentially details of a broader story of adaptation to a new environment, and their eventual resolution will amplify the story described here without changing its essence.

The cast of Eocene cetaceans

The diversity of Eocene cetaceans can be summarized into six families that together document the transition from land to water. Their phylogenetic relations are uncontroversial (Luo 1998, Thewissen 1998, O'Leary and Uhen 1999): Pakicetids form the base group and may include some, but not all, descendants (i.e., they may be *paraphyletic*), followed by ambulocetids and then remingtonocetids. The next cluster is paraphyletic and is classified as protocetids. The youngest and most derived Eocene cetaceans are basilosaurids and dorudontids, the latter of which are the sister group to the modern suborders, mysticetes and odontocetes.

Pakicetid cetaceans are the most primitive and oldest cetaceans. They are about 50 million years old and only found in Pakistan and India (Figure 1). Some features of the pakicetid skull (Figure 2a) suggest an amphibious lifestyle; the eyes, for instance, are on top of the skull. The teeth suggest that they ate hard food and were carnivores. Pakicetids were small, varying from fox to wolf size, but no skeleton is known for them.

Ambulocetid cetaceans are slightly younger and more derived than pakicetid cetaceans. They were also much larger, similar in size to large sea lions. A nearly complete skeleton for *Ambulocetus* (Figure 3) shows that the animal had a large head, long muscular body, and a long tail. Its limbs were short but the feet long. In overall body shape, *Ambulocetus* looked somewhat like a crocodile, although its hind limbs and feet were considerably longer. It may have lived as an ambush predator of fish in shallow water. Ambulocetids lived in coastal environments such as bays and estuaries ap-

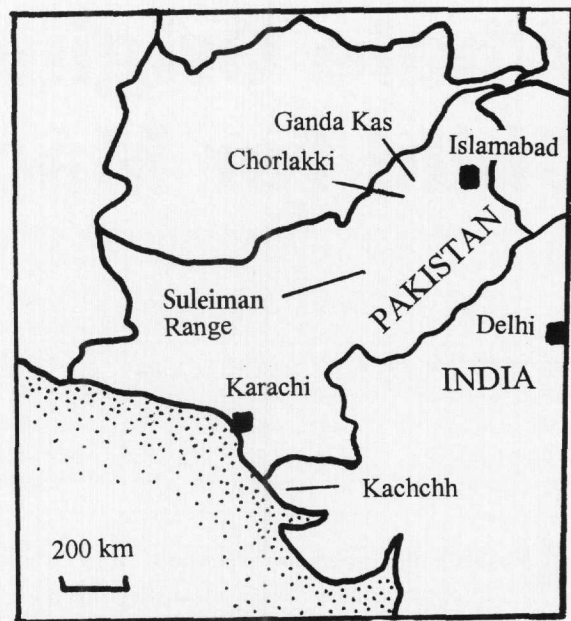


Figure 1. Map of Pakistan and western India showing important areas where archaic cetaceans have been found.

proximately 49 million years ago (mya) and are known only from India and Pakistan.

Remingtonocetid cetaceans (Figure 4) are more derived than pakicetids and ambulocetids in the shape of the teeth and the reduction of the limbs. They are only found in near-shore marine deposits of South Asia. Partial skeletons for remingtonocetids indicate that they had long snouts and small eyes (Figure 2b). Their (middle) ear was large, suggesting that they used hearing to detect prey (as do modern on-

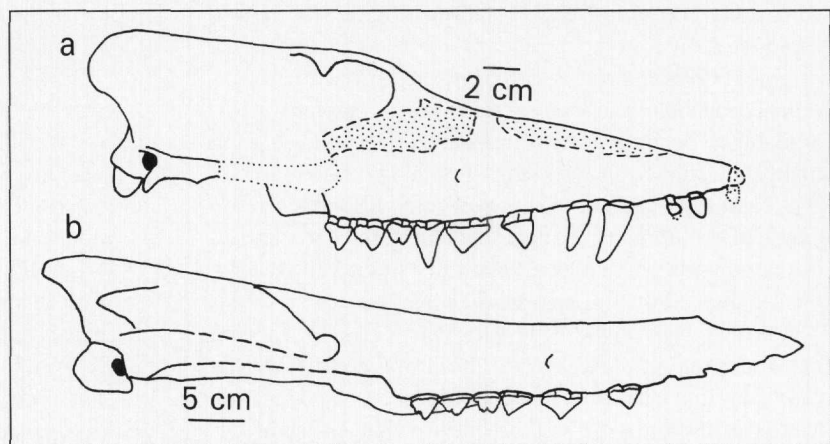


Figure 2. The skulls of *Pakicetus* and *Remingtonocetus*. (a) *Pakicetus* is based on specimens from the Ganda Kas area of Pakistan (Locality 62), consisting of a braincase with orbits, three fragments of the upper jaw, each with one or more teeth, and three isolated teeth. The stippled areas are not known. (b) The skull of *Remingtonocetus* is based on a single specimen, a skull that lost all teeth after death. The teeth are based on one other specimen. Front teeth are not known for this genus.

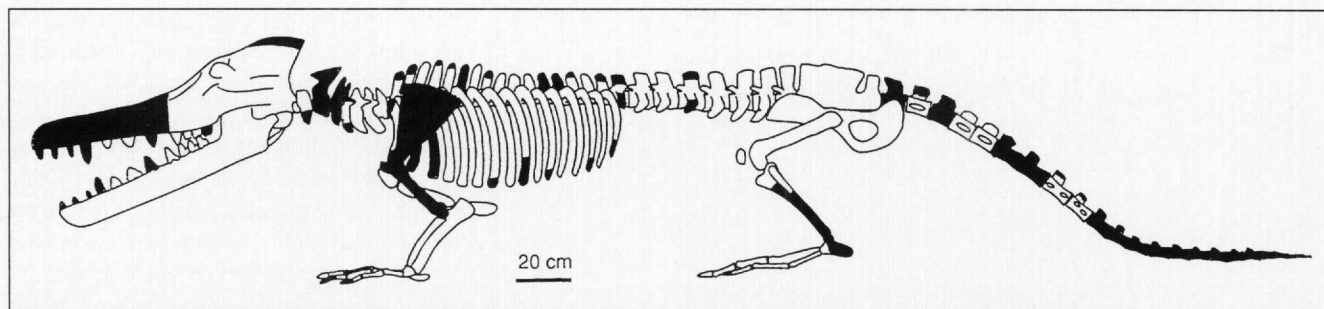


Figure 3. Reconstruction of the skeleton of the holotype, that is, the specimen that best represents the distinctive features of the species, of *Ambulocetus natans* (H-GSP 18507). Parts that are black are not known in the holotype and are reconstructed on the basis of other specimens or other archaic cetaceans.

tocetes). Known remingtonocetids had large and powerful tails and vertebral columns and relatively short legs, which were weight bearing. In this sense, they looked like long-snouted crocodiles. Remingtonocetids probably lived between 49 mya and 43 mya. They vary greatly in size; the smallest (*Kutchicetus*) are similar in size to *Pakicetus*, whereas the largest may have been as large as *Ambulocetus*.

Protocetids (Figure 5) are known from near-shore marine deposits, and they are the oldest cetaceans to have spread across the world. Several partial skeletons are known (e.g., *Rodhocetus* and *Georgiacetus*); they indicate that the limbs were short and not weight bearing in several taxa, implying that land locomotion was slow and cumbersome. These cetaceans may have lived like seals, spending most of their active time in the water but hauling ashore occasionally. Their eyes are large and oriented laterally, unlike remingtonocetids, but similar to dorudontids and basilosaurids. Most protocetids are relatively large, similar to small modern dolphins. The oldest protocetids are approximately 46 million years old; the youngest may be 39 million years old.

Basilosauridae and Dorudontidae reached their highest diversity in the late middle Eocene, around 35 mya. Skeletons of these animals (Figure 6) are unlike those of the other Eocene cetaceans in that they are immediately recognizable as cetaceans. As in modern cetaceans, basilosaurids and dorudontids have a streamlined form, short neck, forelimbs shaped like flippers, and strongly reduced hind limbs. Basilosaurids had long, snakelike bodies, around 20 m long, whereas dorudontids were dolphinlike in body shape and size. Both families are found in shallow marine environments.

Evolutionary change

In this section, we examine in more detail a few of the aspects of cetacean morphology that underwent dramatic change from the Eocene to the present. As the animals adapted to aquatic environments, changes occurred in most anatomical characters, from teeth

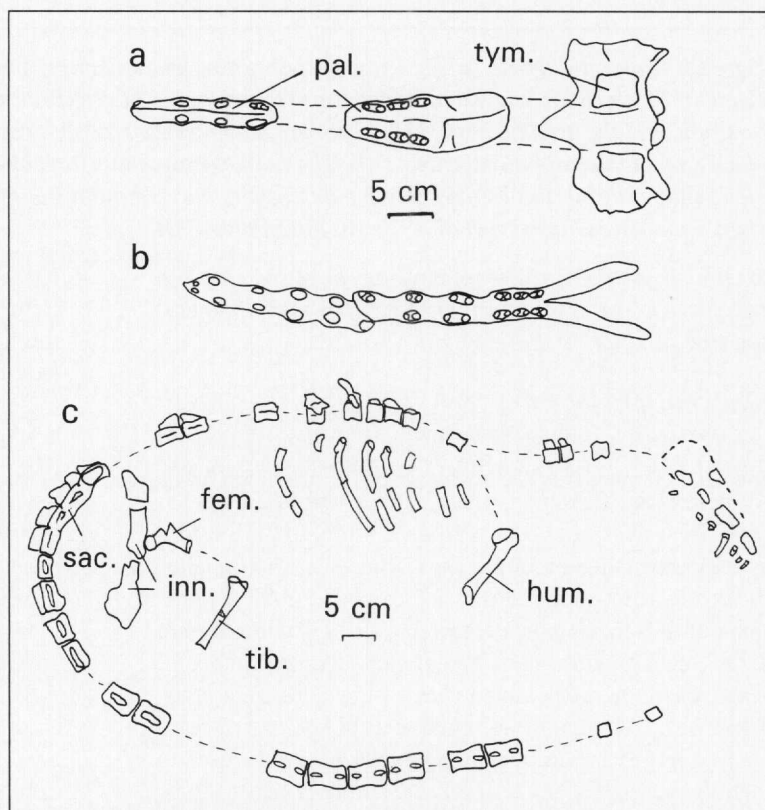


Figure 4. Remingtonocetid fossils. The skull of *Andrewsiphius* (a) in ventral view (Bajpai and Thewissen 1998) and (b) its lower jaw in occlusal view (looking down at the surface that held teeth). The skull of *Andrewsiphius* consists of three pieces that were found together. By articulating them with the lower jaw, it can be determined how much of the skull is missing (hatched lines). Note the narrow palate (pal.), large tympanic bone (tym.), and long crocodile-like lower jaw. Individual ovals represent positions of tooth roots. (c) The skeleton of *Kutchicetus* (Bajpai and Thewissen 2000), with stippled lines showing an approximate body template. Too little is known of this taxon to allow a full reconstruction, but important anatomical observations can be made: The tail was long and robust, and the preserved limb bones—humerus (hum.) and tibia (tib.)—were short in comparison. The sacrum (sac.) is large and consists of four vertebrae, and the innominate (inn.) is large. Only the proximal femur (fem.) is preserved.

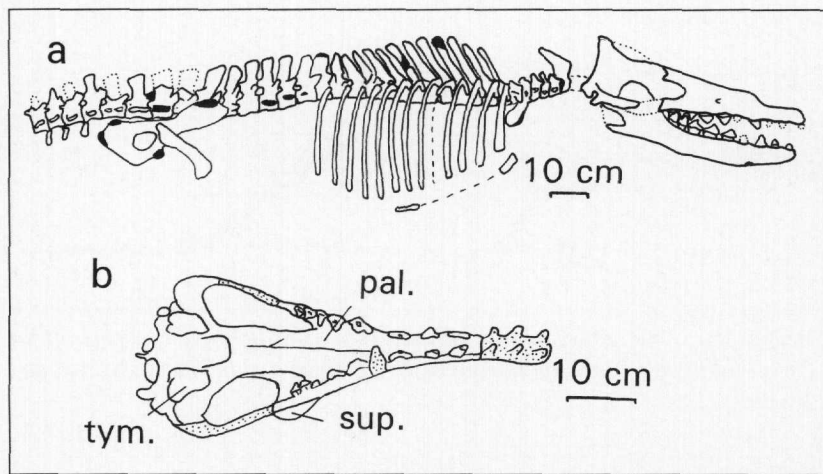


Figure 5. Protocetid fossils. (a) Skeleton of *Rodhocetus kasrani*, many skeletal elements of which are known, although the precise number of vertebrae, the forelimb, and the hind limb below the knee are not known. Areas that are black and stippled are reconstructed. (b) The skull of *Protocetus* (an oblique view) shows supraorbital shield (sup.), palate (pal.), and tympanic bone (tym.). (a) After Gingerich et al. 1994; (b) after Fraas 1904.

to tail. The fossil record documents many of these changes, and they can be explained in a functional morphological context.

Skull morphology. The Eocene families of cetaceans display remarkable differences in the shape of their skulls, and they show some consistent differences from land mammals. All mammals, including whales, have a middle ear that is partially walled in by the tympanic bone. In all modern cetaceans the tympanic bone has a thickened medial lip called the involucrum, and its lateral side has a fold of bone in the shape of an S, the sigmoid process (Figure 7). The involucrum and sigmoid process, whose functions are unknown, are present in all modern cetaceans and occur in no other mammal. These two characters are also present in all Eocene cetaceans for which the ear is known; these traits can thus be used to identify a cetacean. The only Eocene family of cetaceans for which the ear is insufficiently known is the Ambulocetidae. The only ear known for *Ambulocetus* shows that the involucrum is present, but the region of the sigmoid process is not preserved.

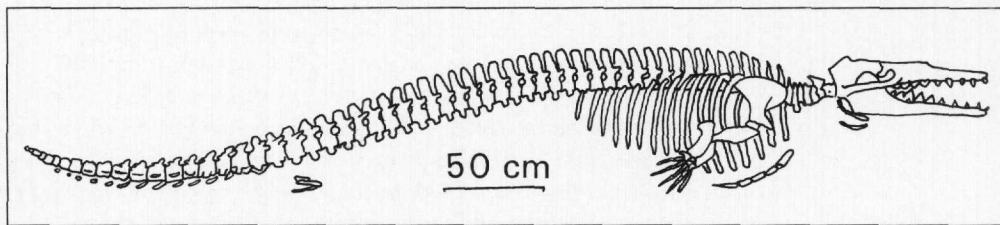


Figure 6. Skeleton of the protocetid *Dorudon atrox* (modified after reconstruction at the Exhibit Museum, University of Michigan). Dozens of skeletons of this species have been found in Egypt. Hind-limb elements known for this species are proximal femur, patella, and astragalus. Other elements are reconstructed based on closely related *Basilosaurus*.

The lower jaw of cetaceans offers another feature of evolutionary interest. In all mammals, including cetaceans, the nerves and blood vessels of the lower teeth travel through a canal called the mandibular foramen on the medial, or inner, side of the lower jaw. In odontocetes, this foramen covers the entire depth of the mandible and is much larger than is necessary for a simple conduit for nerve and vessels. Indeed the foramen has become part of the whale's hearing apparatus: It houses a fat pad, which extends posteriorly to the middle ear. Sounds are received by the lower jaw and are then transmitted by this fat pad to the middle ear. The posterior side of the mandible, with its fat pad, is the most sound-sensitive area of a modern odontocete, more sensitive than the area of the ear itself.

Land mammals, as well as the first whales, lack this method of hearing. In pakicetids, the mandibular foramen is small (Figure 8), similar in size to that of modern land mammals.

It did not house a fat pad and probably had no role in sound transmission. Later whales, however, show the beginnings of this hearing adaptation. The mandibular foramen of *Ambulocetus* is larger than in pakicetids, and it is larger yet in remingtonocetids and protocetids. The mandibular foramen of basilosaurids and dorudontids covers the entire depth of the mandible, as it does in modern odontocetes. It is likely that the mandible was involved in sound reception in basilosaurids and dorudontids as it is in modern toothed whales. Thus one can trace the evolutionary steps of this trait, from simple land-mammal-like foramen to the large conduit with presumed fat pad seen in modern odontocetes, over less than 15 million years.

The position of the orbits (eye sockets) also varies greatly among Eocene cetaceans. The skull of *Pakicetus* has orbits that are high on the side of the skull and face up, or dorsally (Figure 9). This placement is unique among cetaceans and is similar to that in crocodiles. Dorsally facing orbits help submerged crocodiles in watching potential prey items above the water. The orbits of *Ambulocetus* are also set high on the skull, but they face more laterally than in pakicetids (Figures 3 and 9). In remingtonocetids, the orbits are small, suggesting that vision was not an important sense. Remingtonocetid orbits face laterally and are not positioned on the dorsum of the skull (Figures 2b and 9).

The orbits of protocetids, dorudontids, and basilosaurids face laterally and are roofed dorsally by a large bony plate, the supraorbital process (Figure 9; Fraas 1904,

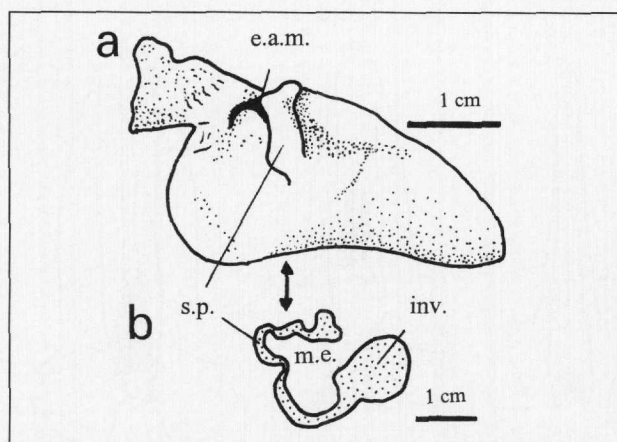


Figure 7. Lateral view of (a) right tympanic bone and (b) its cross section in *Tursiops truncatus* (bottle-nosed dolphin). The tympanic bone is a cup-shaped ear bone that houses the middle ear cavity (m.e.) and has two features that can be used to diagnose a cetacean; these features are present in all cetaceans and in no other vertebrate. First, the anterior process of the tympanic bone is folded into a curved shape called the sigmoid process (s.p.); its unusual folded shape can be seen in cross section (b). It is located anterior to the external auditory meatus (e.a.m.), the ear opening. Second, the medial lip of the tympanic bone is greatly inflated and consists of dense bone (involucrum, inv.). The cross section is based on a CT scan taken near the plane of the arrow (a). These features are discussed in detail by Luo 1998.

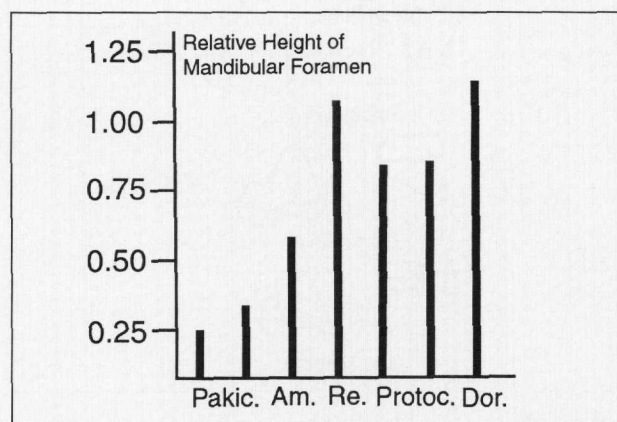


Figure 8. Relative height of the mandibular foramen for pakicetids (Pakic.; *Pakicetus*, *Ichthyolestes*), ambulocetids (Am.; *Ambulocetus*), remingtonocetids (Re.; *Dalanistes*), protocetids (Protoc.; *Georgiacetus*, *Rodhocetus*), and dorudontids (Dor.; *Zygorhiza*). Height of foramen is expressed as a fraction of the jaw depth below the last tooth. The mandibular foramen of modern land mammals is similar in size to that of pakicetids, whereas that of modern odontocetes (toothed whales) is similar to remingtonocetids and dorudontids. *Ambulocetus* is intermediate.

Kellogg 1937). In these families, the eyes face laterally and may be used to observe prey that live underwater. This is the orbital position in modern cetaceans, which hunt fish and other aquatic prey. The position of the eyes varies among early cetaceans; whereas the earliest ones have eyes typical of amphibious predators, those of later forms suggest they hunted underwater. This series is consistent with the acquisition of more aquatic habits in early cetaceans.

The position of the nasal opening changes dramatically in Eocene cetaceans. In modern cetaceans, the nasal opening is called the blowhole, and it is located on the forehead, allowing the animal to surface and breathe while in a horizontal position in the water (Figure 9). The first whales lacked such an adaptation. In *Pakicetus* the nasal opening is near the tip of the snout and is widest over the third incisor (the third tooth in the upper jaw; Figure 2a). The nasal opening is also in this position in the remingtonocetids *Andrewsiphius* and *Remingtonocetus* in spite of the long snouts of these animals. The nasal opening of *Protocetus* is large and opens over the canine, the fourth tooth of the upper jaw. In basilosaurids and dorudontids, the nasal opening is between the canine and the first premolar (the fifth tooth of the upper jaw). Fossil odontocetes and mysticetes have blowholes that are more caudal (toward the tail) than the Eocene cetaceans, but commonly not as caudal as in the modern species.

Dental morphology. Teeth frequently are preserved as fossils and thus are common markers of evolution. Specific dental morphologies can be used to determine phylogeny, and they correlate well with diet. Cetacean teeth reveal a series of evolutionary steps leading from the complex shape of the most ancient land mammals to the simple one-prong morphology of modern odontocetes.

In primitive land mammals, the basic pattern of each upper molar consists of three main cusps (elevated areas) arranged in a triangle. There are two cusps labially (on the side of the cheek), the paracone and the metacone, and one cusp lingually (on the tongue side), the protocone. Crests connect all three of these cusps. The upper molars of pakicetids and *Ambulocetus* (Figure 10) are based on the same blueprint as those of primitive land mammals, but the crests connecting the cusps are very weak. Lower molars of primitive mammals have a high anterior part (the trigonid) with three large cusps, and a low posterior part (the talonid) with two or three cusps. Lower molars of pakicetids and ambulocetids consist of a high trigonid and low talonid, but the trigonid bears only one large cusp (protoconid) and two (in pakicetids) or one (in ambulocetids) barely discernible cusp. In addition, two crests descend anteriorly from the protoconid in all Eocene cetaceans, making the anterior part of the tooth concave. Only one cusp is present on the talonid (hypoconid) of these archaic cetaceans. Unlike primitive terrestrial mammals, archaic cetaceans have no basins (depressed areas) on their lower molars.

Protocetid molars are more simple than those of pakicetids and ambulocetids and, thus, even less similar to primitive land

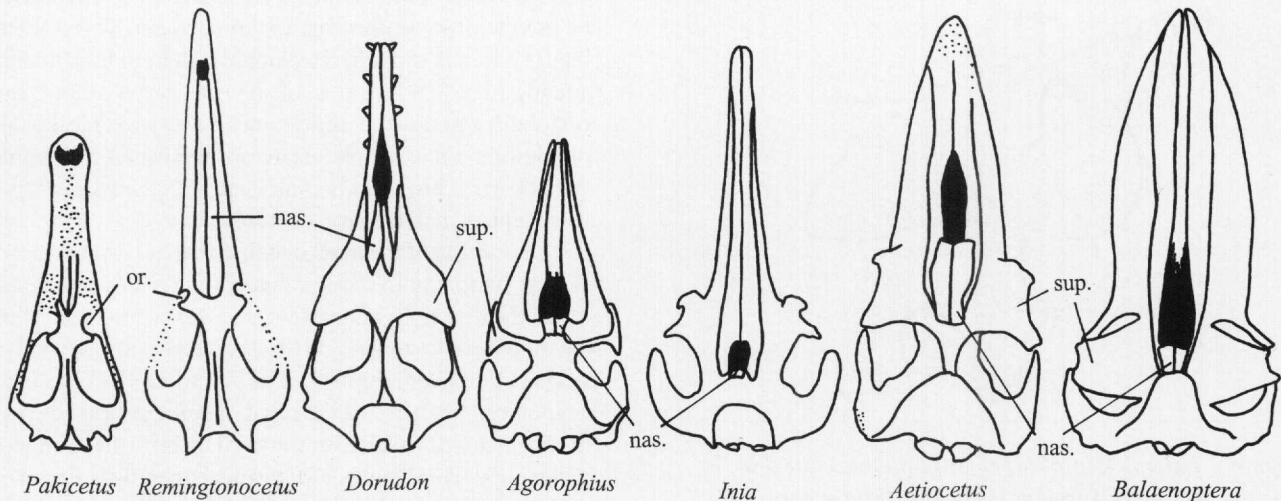


Figure 9. Dorsal view of cetacean skulls. From left are pakicetid *Pakicetus*; remingtonocetid *Remingtonocetus* (after Bajpai and Thewissen 1998); dorudontid *Dorudon* (after Kellogg 1937); Oligocene toothed whale *Agorophius* (after Kellogg 1928); modern Amazon River dolphin *Inia* (after Kellogg 1928); Oligocene mysticete *Aetiocetus* (after Barnes et al. 1994); and the modern mysticete *Balaenoptera musculus*, or blue whale (after Kellogg 1928). Note the varying position and size of the orbits (or.), which are covered by the supraorbital process (sup.) in dorudontids, odontocetes, and mysticetes. The nasal opening (black) shifted to a more posterior position on the skull as the nasals (nas.) became shorter. Drawings are not to scale; stippled areas are not known.

mammal teeth. The labial side of protoctetid upper molars (Figure 10) bears two large cusps, as in *Ambulocetus*. On the lingual side, the crown of the molar is expanded, but this expansion lacks a cusp. This is unlike molars of *Ambulocetus*, where this area bears the protocone. Lower molars of protoctetids are usually similar to those of ambulocetids, but there is only one cusp on the trigonid. The trend is continued in dorudontids and basilosaurids. The upper molars of these families have lost their lingual expansion altogether but have added a series of small cusps on the labial side. In the lower molars the distinction between trigonid and talonid disappears, and the tooth turns into a row of small cusps of descending heights. As in the earlier families, basilosaurids and dorudontids also have two crests extending from the anterior cusp to the base of the tooth.

In summary, the evolutionary trend in cetacean molar morphology is toward a reduction of crests and basins. Simple, pronglike cusps are lined up in a single row, which foreshadows the long rows of simple, pronglike teeth in most modern odontocetes.

Postcranial anatomy. Not surprisingly, the postcranial anatomy of modern cetaceans is spectacularly different from that of their terrestrial relatives. The fossils recovered in the past decade reveal much about how these differences evolved. As mentioned above, no partial skeletons are known for the most primitive cetaceans, pakicetids, but the skeletal morphology of *Ambulocetus* is intermediate in several respects between that of land mammals and that of modern cetaceans. Partial skeletons for the remingtonocetid *Kutchicetus* and several protoctetids fill in some details, and the virtually com-

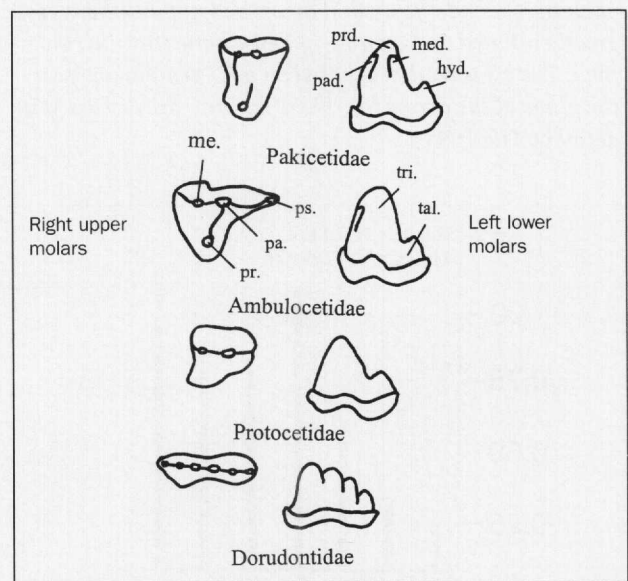


Figure 10. Fossil teeth of *Pakicetus*, *Ambulocetus*, the protoctetid *Babiocetus*, and the dorudontids *Pontogeneus* (upper molar) and *Zygorhiza* (lower molar). Right upper molars (left column) in occlusal (biting surface) view and left lower molars (right column) in lingual (tongue side) view. Cusps (elevated areas) on upper molars are indicated as circles: protocone (pr.), paracone (pa.), metacone (me.), and parastyle (ps.). The lower molars show the high trigonid (tri.), which may bear three cusps: protoconid (prd.), paraconid (pad.), and metaconid (med.). The lower part (talonid, tal.) only bears one cusp, the hypoconid (hyd.). Drawings are not to scale.

plete skeletons for dorudontids and basilosaurids show the final stages of how whales conquered the seas.

Modern cetaceans have a mobile shoulder but stiff elbow and wrist joints. Their skeleton includes bones that form five fingers, but these bones are embedded in a paddlelike flipper in which individual digits are not distinct externally and lack mobile joints. Unlike nearly all other mammals, the last bone of each digit lacks a dorsal cover of keratin (the finger nail of humans). In *Ambulocetus*, the radius, ulna, wrist, and much of the hand are preserved. They show that *Ambulocetus* had mobile joints at elbow, wrist, and fingers, and that the fingers were not embedded in a flipper. All of these features are similar to land mammals and unlike modern cetaceans. Indentations in the phalanges also indicate that the fingers had a dorsal keratin cover in the shape of a hoof. Hooves in an archaic whale are not surprising, as the closest living relatives of cetaceans are even-toed ungulates such as pigs and deer. Many critical features of the forelimb of remingtonocetids and protocetids are not known, but basilosaurids and dorudontids resemble modern cetaceans in having a fixed wrist and an elbow that can function only like a hinge joint. Their fingers, on the other hand, still retain the mobile joints of their ambulocetid relatives.

The pelvis (or hip girdle) is dramatically different in modern whales and land mammals (Figure 11). The pelvis in land mammals consists of sacrum and left and right innominate bones. The sacrum is a series of vertebrae (five in humans) that are fused to each other and connect to the innominates at the first (most anterior) of these vertebrae. The innominate is an elongated bone that bears the socket (acetabulum) for the femur, forming the hip joint, and has two branches posteriorly (ischium and pubis) that surround a foramen, or opening, and an anterior branch (ilium) that contacts the innominate from the other side. Sacrum and left and right innominates form a strong and rigid bony girdle that anchors the hind limbs and supports much of the body in locomotion. In modern whales, in contrast, the sacrum cannot be recognized, as there are no fused vertebrae and no vertebra has a joint for the innominate. In fact, the innominate in modern cetaceans is a tiny bar of bone lacking an acetabulum and distinct ischium, pubis, and ilium. The innominate is embedded in the ventral body wall where a few tiny muscles that are not involved in locomotion attach to it.

In *Ambulocetus* and *Kutchicetus*, the pelvis is much like that of a land mammal: The sacrum comprises four fused vertebrae, and these articulate with the innominate bones (Figure 11). Each innominate consists of ilium, ischium, and pubis and bears an acetabulum for the femur, as it does in land mammals. The femurs are long when compared with other whales, but shorter than most land mammals. *Ambulocetus* had large hind limbs and enormous feet. Feet are not known in remingtonocetids, but the sacral vertebrae of *Rodhocetus* are less strongly fused, and the femurs are shorter than in *Ambulocetus*. However, *Rodhocetus* innominates retain the deep acetabulum and the articulation with the sacrum. *Georgiacetus* is even more like modern whales, lacking a fused

series of sacral vertebrae as well as a contact between sacral vertebrae and innominates. Unlike modern whales, the sacral vertebrae of *Georgiacetus* differ from caudal and lumbar vertebrae, and each innominate is large and consists of ilium, ischium, and pubis. The femur of *Georgiacetus* is not known. In basilosaurids and dorudontids, the innominates are small bones, with ilia that are not distinct. However, they retain an acetabulum and foramen. The innominates are not connected to the vertebral column, but these whales retain femurs that are longer than in modern cetaceans. The entire hind limb (Figure 6) is smaller than in other Eocene cetaceans and barely protrude from the body wall.

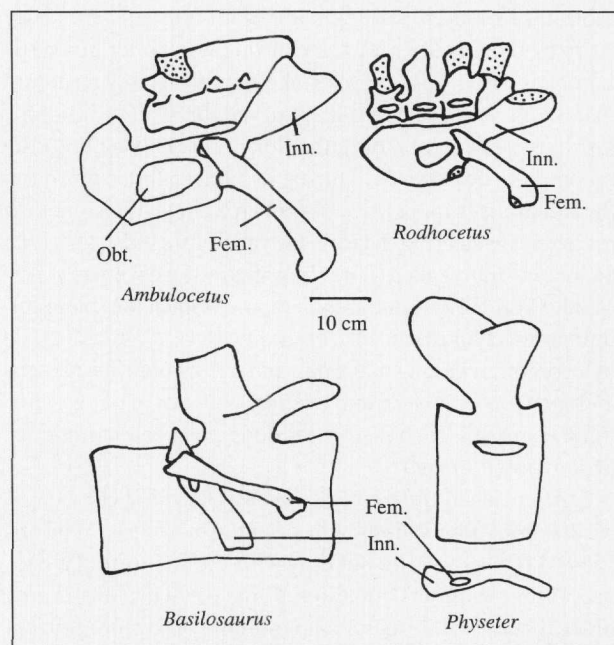


Figure 11. Sacrum, innominate, and femur of the ambulocetid *Ambulocetus*, the protocetid *Rodhocetus* (based on Gingerich et al. 1994), the basilosaurid *Basilosaurus* (based on Gingerich et al. 1983), and the odontocete *Physeter* (modern male sperm whale, based on Deimer 1977). In *Ambulocetus*, the sacrum consists of four vertebrae that are fused. The femur (Fem.) is substantial in size, and there is a strong, weight-bearing joint between sacrum and innominate (Inn.). In *Rodhocetus*, the fusion between vertebral bodies and spinous processes is reduced, and the innominate and femur are relatively short. However, the joint between innominate and sacrum is retained. In *Basilosaurus* and *Physeter*, there is no contact between sacrum and innominate, and the hind limb is not weight bearing. These two whales are large (as evidenced by their large vertebrae), and the sacrum consists of a single vertebra that is very similar to adjacent caudal and lumbar vertebrae. Innominate and femur in these two genera are on the ventral side of the animal, far removed from the spinal column, and they are not shown in their anatomical position. Stippled areas are unknown.

Together these pelvises form an excellent transitional series, in which ambulocetids and remingtonocetids retain all elements of land mammals, and protocetids lose the fused sacrum (*Rodhocetus*) and the iliosacral joints (*Georgiacetus*) and have short femurs (in known forms). Basilosaurids and dorudontids have greatly reduced hind limbs and reduced ilia, while still retaining the acetabulum and the foramen of the innominates. Only vestiges of these structures are present in modern whales.

Locomotor evolution

This detailed record of the locomotor anatomy of the ancient cetaceans allows us to analyze how they moved. The locomotion of modern cetaceans is elegant and efficient: They swim by moving their tail fluke through the water in a vertical plane. Their fluke consists of a flat, horizontal structure that is only supported by bone (tail vertebrae) in the midline. Just like the wing of a bird, the fluke causes lift on both the up- and the downstroke. During rectilinear, fast swimming, the forelimbs (flippers) are not involved in propulsion; they merely act as steering devices (Fish and Hui 1991). This type of locomotion, called caudal oscillation, uses energy efficiently (Fish 1993). Caudal oscillation, in which the spinal column moves at one point, like a standing wave, is rare as a mode of locomotion among mammals and occurs only in cetaceans and sirenians (manatees and relatives), but not in other swimming mammals (such as seals, sea lions, polar bears, muskrats, or star-nosed moles).

Efficiencies of different modes of swimming can be calculated from observations of locomoting mammals (Williams 1989). Efficiency varies not only with the anatomical attributes of the swimmers but also with the particular swimming mode that is used, as mammals commonly use more efficient modes at higher speeds (Fish 1993). Based on these considerations, Fish (1996) proposed a model of evolution of the cetacean locomotor pattern. The swimming mode of most terrestrial mammals, and presumably cetacean ancestors, is quadrupedal paddling, more familiarly known as the dog paddle. Fish (1996) proposed a series of intermediate locomotor modes between the extremes of modern cetaceans and terrestrial mammals' paddling, using modern mustelids (minks, otters, and so on) as analogues for these intermediate swimming modes.

In short, minks (*Mustela vison*) paddle quadrupedally (Figure 12), and freshwater otters (*Lontra canadensis*) swim mainly with their hind limbs (pelvic paddling), although they derive some additional lift from the tail (pelvic undulation). Sea otters (*Enhydra lutris*) use their highly asymmetrical feet as the propelling surfaces, but most of the power for the movements is not from the muscles of the hind limbs but rather from undulations of the vertebral column (pelvic undulation). The giant South American freshwater otter *Pteronura brasiliensis* uses caudal undulation: Sinusoidal motions of the vertebral column, like a wave moving through the entire spine, power a long and narrow tail that is dorsoventrally flat. No otter swims like a modern cetacean, but the

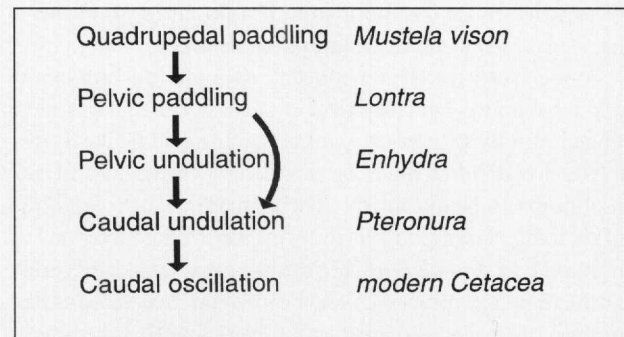


Figure 12. Hypothesis for the evolution of the caudal oscillation swimming mode of modern Cetacea, based on Thewissen and Fish (1997). Different swimming modes are listed in the left column, and arrows indicate transitions that can be predicted on the basis of efficiency considerations. Modern mustelids swim using various modes, and cetaceans probably went through these modes sequentially in their evolutionary history. Morphological study indicates that *Ambulocetus* was probably a pelvic paddler or caudal undulator and that *Kutchicetus* was mainly a caudal undulator.

swimming mode of *Pteronura* comes close. Modern cetaceans differ from *Pteronura* in having a rigid body with most of the movement concentrated at one point: Undulation became oscillation. In addition, modern cetaceans have a fluke.

Thewissen and Fish (1997) tested Fish's model with fossils by studying the anatomy of fossil cetaceans. They determined morphological correlates for the locomotor modes using modern swimmers as analogues and then attempted to identify these morphological correlates in *Ambulocetus*. Unlike quadrupedal paddlers, the feet of *Ambulocetus* are much longer than its hands. The long tail did not bear a fluke; hence, *Ambulocetus* was not a caudal oscillator. The feet are more or less symmetrical and have the shape of a paddle, not the shape of an asymmetrical hydrofoil, as in the foot of *Enhydra*. In its functional features, the morphology of *Ambulocetus* is closest to that of pelvic paddlers and caudal undulators, indicating that the animal displayed a mode of locomotion that is functionally intermediate between a land mammal and a modern whale. Most of the propulsion was provided by dorsoventral motions of the feet powered by the muscles of the hind limbs. Thus *Ambulocetus* presents a true intermediate stage in locomotion and serves as an evolutionary link between the quadrupedal paddling of the terrestrial ancestors of cetaceans and the efficient swimming of living cetaceans.

Kutchicetus may represent another step in this process. Its long and powerful tail appears to be more important in propulsion than its limbs. Although the detailed quantitative study has not been completed, it appears that caudal undulation was more important in the locomotor repertoire of *Kutchicetus* than it was for *Ambulocetus*. *Kutchicetus*'s locomotor behavior may have resembled that of *Pteronura*.

In dorudontids and basilosaurids, the succession of vertebrae underwent abrupt changes in morphology near the end of the tail (Buchholtz 1998), and one of the vertebrae has a rounded outline (Uhen 1998). A similar vertebra (the so-called ball vertebra) is found in modern cetaceans, located near the base of the fluke. This suggests that basilosaurids and dorudontids had a tail fluke and may have been caudal oscillators.

Osmoregulatory evolution

For most animals living offshore, life requires the ability to live without fresh water. In general, modern cetaceans have this ability. This is remarkable because most mammals of large body size require a source of fresh water and are unable to cope with the large salt load of seawater. Mammalian kidneys discharge excess salt by dissolving it in water and excreting the solution as urine. The osmoregulatory system of cetaceans is adapted to the high-ion levels of seawater, and modern cetaceans use water so sparingly that they do not need a source of fresh water and produce highly concentrated urine (Telfer et al. 1970). However, cetaceans evolved from large-bodied terrestrial mammals, and this suggests that the ability to live without fresh water evolved as cetaceans entered marine environments.

Drinking behaviors of early cetaceans can be investigated using stable oxygen isotopes (Roe et al. 1998). In a nutshell, the two most common isotopes of oxygen in nature are ^{16}O and ^{18}O , the former of which makes up well over 99% of naturally occurring oxygen. Ratios of these two isotopes are different for fresh water and seawater. The reason for this is simple: All fresh water is ultimately derived from meteoric water, and meteoric water is formed by evaporation. Heavier molecules are less likely to evaporate than lighter ones. Water with ^{18}O is heavier than water with ^{16}O , and thus oceanic waters have higher percentages of ^{18}O than fresh waters. Oxygen used in the calcium phosphate of mammalian bones is usually derived from drinking water. Mammals that drink seawater can thus be distinguished from those that drink fresh water. Thewissen and colleagues (1996) tested the theoretical predictions of this model for modern river dolphins and marine cetaceans, and Roe and colleagues (1998) present a more detailed and geochemically explicit explanation of this method, its limitations, and its results.

The transition from a freshwater-based osmoregulatory system to one that is independent of fresh water is documented in the fossil record (Figure 13; Thewissen et al. 1996, Roe et al. 1998). Oxygen isotopes of pakicetids, measured from fossil teeth, indicate that they drank fresh water. This is not surprising, as the sedimentological evidence shows that they did not live in the sea. *Remingtonocetus* and protocetids show values that are marine. This suggests that *Remingtonocetus* and protocetids did not ingest fresh water, which is consistent with their marine habitat. Apparently, cetaceans became independent of fresh water soon after their origin.

Most interesting are the ambulocetids and the remingtonocetid *Attockicetus*. In fossil teeth from the ambulocetids,

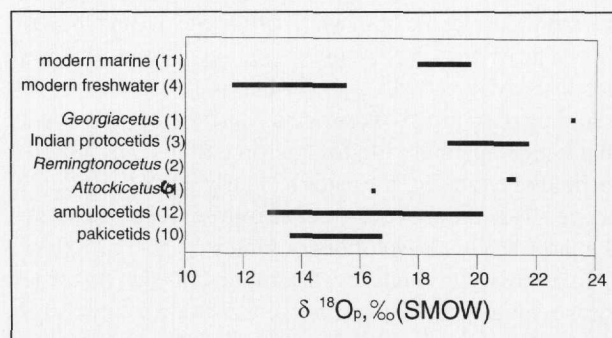


Figure 13. Stable oxygen isotopes in modern and fossil cetaceans. The ratio between ^{18}O and ^{16}O is indicated as $\delta^{18}\text{O}_p$ (SMOW), whereby higher values indicate more ^{18}O . Number of species represented in each group is indicated in parentheses. Note the clear separation of modern cetaceans with known water ingestion behaviors (modern freshwater dolphins and marine cetaceans). This difference is mirrored in the difference between freshwater pakicetids and marine protocetids and *Remingtonocetus*. *Ambulocetus* lived in a transitional habitat, and different individuals fall along a wide range of stable oxygen isotope ratios. Graph modified from Roe et al. 1998.

isotope ratios varied greatly, ranging from fresh water to marine. Although ambulocetids are found only in marine deposits, their isotope values indicate a range of water ingestion behaviors. These include specimens that show no evidence of seawater consumption. However, the data reflect the drinking behavior at the time that the animal was mineralizing its teeth (before they erupt). Hence, they are only a snapshot of the drinking behavior at one life stage, not a lifetime record or average. These numbers should therefore be interpreted with caution. It is possible that some individuals with freshwater values lived in fresh water as juveniles (where their isotope signature was established), but migrated to the sea when they were adults (where they were fossilized). It is also possible that these individuals lived most of their lives near river mouths and were in contact with fresh water and seawater. Some specimens of *Ambulocetus* show marine values, demonstrating that these individuals did not ingest fresh water at the time their teeth mineralized. Although several explanations are possible, it is clear that *Ambulocetus* tolerated a wide range of salt concentrations (that is, it was euryhaline). As such, it is a transitional form that makes sense in the context of osmoregulatory evolution.

Water ingestion behavior of *Attockicetus*, at present, is based on one specimen, so no firm conclusions can be drawn. It is interesting, though, that this primitive remingtonocetid has isotope values that indicate freshwater ingestion, contrasting with its marine habitat and with the values of more derived remingtonocetids.

Conclusion

Arriving at a scientific conclusion, particularly an evolutionary one, is not like watching a movie and relating its content.

It is more like a legal trial, in which all evidence is carefully scrutinized to arrive at the best interpretation of events that were not observed directly. In trials, the interpretation that prevails is supported by most of the evidence, and there is no evidence that is incompatible with this interpretation. Using a similar method of reasoning, the pattern of early whale evolution, as derived from the above discussion, only makes sense when it is interpreted in an evolutionary context.

In summary, the archaic cetaceans described in this article form a time-ordered sequence of transitional forms from terrestrial mammals to modern cetaceans. These transitional aspects pervade all aspects of cetacean morphology, ranging from dental morphology to osmoregulatory patterns and pelvic structure. Furthermore, geological evidence shows that cetaceans initially inhabited freshwater habitats, then moved to protected coastal environments near shore, and finally took to offshore living.

The function of most of the anatomical features we have discussed is known in modern cetaceans, and the differences seen in the fossil cetaceans are logically interpreted as emerging adaptations to an aquatic environment. Such an evolutionary interpretation of the fossil evidence is also supported by the study of phylogeny, embryology, and comparative anatomy of modern forms. As such, whale origins form one of the most compelling examples of macroevolutionary change in vertebrates.

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Appendix

Pakicetidae. Pakicetids were first found in 1979, when a team of paleontologists found a braincase at a locality called Chorlakki in northern Pakistan (Figure 1). The braincase showed a prominent sigmoid process and involucrum in the ear—telltale signs that this was a cetacean. Judging from its skull, the animal was approximately as large as a wolf, and it was named *Pakicetus* (Gingerich and Russell 1981). Partial skulls of pakicetids have now been found at other localities (Figure 2a; Luo and Gingerich 1999), and one of the best of these is called the Howard University–Geological Survey of Pakistan (H-GSP) Locality 62 in the Ganda Kas area.

At Locality 62, *Pakicetus* skulls were recovered with teeth and jaws similar in size to the original find. Nearly 100 fossils of the pakicetids *Pakicetus*, *Ichthyolestes*, and *Nalacetus* (Thewissen and Hussain 1998) have now been found, all within 250 km of the original site. At Locality 62, there is no association of elements; upper jaws are never found in occlusion with their lower jaws. Associations can still be determined, because upper and lower teeth have to interlock when occluded, and because molar morphology matches that of other, articulated early cetacean fossils. Moreover, the skulls, teeth, and jaws are all from mammals that are similar in size, and cetaceans are the only mammals of this size range that have ever been found in these beds. Many of the teeth are badly worn, implying that pakicetids ate hard food, and the system of valleys and hills on each tooth resembles that of modern meat eaters, not plant eaters.

Geology offers clues as to where this whale lived. The sediment at Locality 62 is a red conglomerate, a rock made up of small nodules in a homogeneous matrix, like cherries in a pie. Individual nodules are mostly less than 1 cm in diameter and consist of colorful concentric rings of calcium carbonate. In recent soils, such nodules form in dry climates that seasonally receive a great deal of rain (Aslan and Thewissen 1996). Other fossils in these conglomerates include the teeth of land mammals, such as opossums and rodents, as well as shells of land snails. Thus the sedimentological and fossil ev-

idence both suggest that these beds were deposited in a freshwater environment and that the animals found here did not live in the sea. This is confirmed geochemically by stable oxygen isotopes, which indicate a freshwater environment (Roe et al. 1998). The pakicetids lived in an ephemeral streambed.

Ambulocetidae. Ambulocetid cetaceans were discovered at another important early whale site, located 3 km north of H-GSP Locality 62 in the Ganda Kas area. This site, H-GSP Locality 9209, yielded a rare find—an associated skeleton of a single whale. More than 100 bones, all of matching sizes and many still in articular contact, were found together in a cluster about 3 m in diameter. The only other vertebrate fossil in the vicinity was a single scute (dermal bone fragment) of a crocodile. This cetacean skeleton was described as the holotype for the species *Ambulocetus natans* (Figure 3), whose name means the walking and swimming whale (Thewissen et al. 1994, 1996).

Since this first find, nearly 20 fossil ambulocetid specimens, all very fragmentary, have been found in northern Pakistan and adjacent India. Taken together, the holotype and additional specimens present a remarkably complete picture of this transitional whale. Most bones of *Ambulocetus* are known, including the skull, lower jaw, vertebrae, ribs, forelimb from the elbow down, and much of the hind limb. However, uncertainties remain about other parts of the skeleton of *Ambulocetus*. We do not know where the nose opening is, although we do know how long the snout was because it must have matched the lower jaw. We have only five tail vertebrae and hence do not know the length of its tail. However, the progressive changes in shape among the preserved vertebrae imply that the tail was much longer than in modern whales. The preserved tail vertebrae are similar to those of modern mammals with long powerful tails, suggesting that the tail of *Ambulocetus* was strong. No complete tibia is available, but the known length of femur and foot add up to an animal with large feet on stocky limbs. The forelimbs were short, and the hands were smaller than the feet.

The rock in which the holotype of *Ambulocetus* was found is a gray-green mudstone with numerous carbonized impressions of long, narrow leaves and marine invertebrates such as mollusks. Mollusk fossils are common, and several specimens of *Turritella*, a marine snail, were found in contact with the skeleton. Immediately adjacent to these deposits is a thick layer composed almost exclusively of oyster and other mollusk shells and the skeletons of large Foraminifera, a kind of protozoan. All of these invertebrates and protozoa indicate that *Ambulocetus* was buried in a near-shore marine environment. The plant leaves are similar to sea grasses in overall shape, which is consistent with this environment.

The rocks containing *Ambulocetus* were deposited on top of those harboring the pakicetids; therefore, *Ambulocetus* is younger. The benthic Foraminifera found in the rocks further bracket their ages, as biostratigraphers have documented that various species are restricted to certain time periods. Rocks below (older than) the pakicetids may be as old as 54 million

years (early Eocene), whereas rocks above *Ambulocetus* range somewhere between 42 million and 49 million years (late early or early middle Eocene). Hence, pakicetids and ambulocetids are not older than 54 million years and certainly not younger than 42 million years. Land mammal biostratigraphy, combined with analysis of the geological context, suggests that ages between 48 million and 52 million years are most likely.

Remingtonocetidae. A second cetacean, *Attockicetus*, is known from a site approximately 4 km from that of *Ambulocetus* (Thewissen and Hussain 2000). The sequence of sediments in this area is identical to that at the *Ambulocetus* site (e.g., oyster bed, mudstone with *Turritella*, overlain by a thick limestone with large benthic Foraminifera), indicating that the two sites are of the same age. *Attockicetus* is different from pakicetids and ambulocetids in the shape of its palate and the elongate shape of its tympanic bone (the bony shell of the middle ear), placing it in a family of cetaceans called Remingtonocetidae. These are well known from the Suleiman Range of central Pakistan (Gingerich et al. 1995) and District Kachchh (Bajpai and Thewissen 1998) in western India. In addition to *Attockicetus*, Remingtonocetidae also include *Remingtonocetus*, *Andrewsiphius*, *Dalanistes*, and *Kutchicetus*. In these cetaceans, the orbits are small (Figure 2b), the tympanic bone is disproportionately large and oval in ventral outline (Figure 4), and the snout is long and narrow. These features can be seen best in a complete skull of *Remingtonocetus* (Figure 2b). The strangest remingtonocetids are *Andrewsiphius* and *Kutchicetus*, in which the snout is very narrow, similar to a gavia or crocodile (Figure 4).

Although the cranial morphology of all genera of remingtonocetids is well known, associated skeletons are rare. One of the most complete skeletons was recently discovered in Kachchh, India, and was called *Kutchicetus* (Bajpai and Thewissen 2000). *Kutchicetus* is the smallest remingtonocetid and smaller than *Pakicetus*. No complete skull is known for *Kutchicetus*, but a snout fragment shows that the species was similar to *Andrewsiphius* and that the two were closely related.

Approximately 45 bones are known for *Kutchicetus* (Figure 4c), and some of the more important ones are known only from fragments. The distal humerus is missing, the tibia lacks part of the shaft, and only the proximal femur is known. The known long bones show that the limbs were short. The robust tail vertebrae with large processes indicate that the tail was long and muscular. The humerus was only slightly longer than two vertebrae from the middle of the tail, which is very unusual in mammals. The sacrum has four fused vertebrae that have a large contact with the pelvis.

Kutchicetus was found at the Locality Godhatad in Kachchh, where it was eroding out of a muddy limestone (Bajpai and Thewissen 2000), and its depositional environment is typical for that of other remingtonocetids. Other fossils at Godhatad include sirenians (manatees and their relatives) and oysters. Some of the mudstone is black with organic matter, showing that plants grew abundantly. In addition, there are thick lay-

ers of gypsum, a rock typically formed when seawater evaporates from a shallow basin. These factors together indicate that the cetaceans were living in a shallow and restricted part of the ocean. This basin had occasional connections to the open ocean, but sometimes closed off as a separate basin. An environment such as a bay or a tidal shelf protected by barrier islands is most consistent with these sedimentological data.

The assessment of the age of *Kutchicetus* mirrors that of other remingtonocetids. Benthic Foraminifera can be used to approximate the age. The foraminiferan *Asselina granulosa* is found in the layers underneath those with the cetaceans; the cetaceans are thus younger than *A. granulosa*. *Asselina granulosa* is also known from Pakistan, from the beds that contain *Ambulocetus*. Hence, *Kutchicetus* is younger than *Ambulocetus*. It is less easy to infer a more exact age for *Kutchicetus*. Some of the best evidence for this comes from the study of nanoplankton, the shells of organisms so small that they can only be studied with the scanning electron microscope. When combined with lithostratigraphy and foraminiferal biostratigraphy, an age of 43 million to 46 million years is most likely for *Kutchicetus*.

Protocetidae. Protocetids are named after *Protocetus atavus* (Figure 5b), which was discovered in Egypt at the beginning of the 20th century (Fraas 1904, Stromer 1908), long before any pakicetids, ambulocetids, or remingtonocetids were known. The skull and vertebral column were well preserved, but the specimen did not include limb bones. Its German discoverers realized that *Protocetus* was a cetacean, and for most of the past century *Protocetus* was the best model for what an archaic cetacean looked like. *Protocetus*, which became the type genus for the family Protocetidae, showed that early cetacean teeth were quite characteristic and were different from nearly all other mammals. Approximately 10 genera of protocetids are known from Indo-Pakistan, northern Africa, and the eastern United States (Bajpai and Thewissen 1998, Hulbert et al. 1998, Luo and Gingerich 1999, Uhen 1999), and it seems that this family of whales had a distribution that nearly circled the globe at low latitudes. Most protocetids are known from one or a few specimens, although some of these include relatively complete skeletons.

Some skulls of protocetids are associated with partial skeletons. Among these are *Rodhocetus* (Gingerich et al. 1994), a protocetid discovered in the Suleiman Range of Pakistan (Figure 5a), which may be the same animal as *Indocetus* from India (Sahni and Mishra 1975). *Georgiacetus* (Hulbert 1998, Hulbert et al. 1998) is a protocetid from the coastal plain of Georgia (United States). Not enough is known of the limb skeleton of these two cetaceans to allow a full reconstruction, but the parts preserved show some important differences from other cetacean families, mainly related to reduction of the hind limbs. In Indo-Pakistan, protocetids are found in the same layers as remingtonocetids, indicating that they inhabited similar environments and were of the same age. Protocetids such as *Georgiacetus*

are found in sedimentary deposits that are considerably younger than those with Indo-Pakistani protocetids. *Georgiacetus* comes from a geological unit (Hulbert et al. 1998) that contains microfossils (Foraminifera, nanoplankton) most consistent with an age of 40 mya to 43 mya. The unit with *Georgiacetus* can be traced geographically into South Carolina. The South Carolina deposits can be dated radiometrically, providing an independent age estimate. Potassium-argon dating of these rocks suggests ages of 38.1 million to 41.3 million years, and rubidium-strontium dating suggests 39.6 million to 41.2 million years. It is one of the latest protocetids.

The environment of *Protocetus* was different from that of most other non-Egyptian protocetids. *Protocetus* lived, according to sedimentological findings, in a shallow but offshore marine environment (Gingerich 1992, Williams 1998), as indicated for example by the presence of many echinoid (sea urchin) spines in these rocks; sea urchins are known to not tolerate brackish water. *Protocetus* has been dated using mollusks and planktonic foraminiferans to approximately between 43 million and 46 million years ago (see summary in Gingerich 1992).

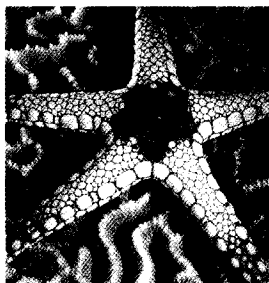
Basilosauridae and Dorudontidae. The genus *Basilosaurus* was described in 1834, based on a number of fossil fragments from the vicinity of Monroe, Louisiana. The initial collection consisted of incomplete fragments, but the vertebrae in this collection impressed its describer, Richard Harlan, who thought that they represented a giant lizard. Harlan called the animal *Basilosaurus*, meaning *king lizard*. Harlan took some of the bones to England, where he showed them to the comparative anatomist Richard Owen. Owen, who studied the fossils about two decades before Darwin published *Origin of Species*, recognized that the teeth, with their multiple roots, must represent a mammal.

Since then, whales similar to *Basilosaurus* have been discovered in many areas in the world, including India and Pakistan, New Zealand, and Africa. Several of these consist of virtually complete skeletons (Figure 6). Hundreds of specimens are known from Egypt (Uhen 1998). They are best classified as basilosaurids and dorudontids. Gingerich (1992) summarized much of the geology of the Egyptian sedimentary rocks,

explaining that biostratigraphy dates Egyptian dorudontids and basilosaurids to around 37 million years ago. This is consistent with radiometric dates of 24 million to 32 million years on volcanic rocks overlying (and thus younger than) the fossil-bearing layers. Study of the sediments of the Egyptian dorudontids and basilosaurids suggests that these were deposited in a near-shore marine environment, including mangrove swamps, sea-grass meadows, and bays with barrier islands, as well as offshore environments such as coral reefs. An abundance of marine invertebrate fossils is consistent with this interpretation (Gingerich 1992).

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