Whale evolution

Cetaceans, or whales (a group which includes the animals commonly known as dolphins and porpoises), are interesting from an evolutionary perspective because they are so different from their ancestors. The ancestors of whales were fur-covered land mammals that rarely entered the water, whereas whales today are fully aquatic and thrive in the oceans, seas, and—in some instances—great rivers of the world. The ancestors were four-footed and hoofed for running on land, whereas whales today have forelimbs modified as flippers, lack external hindlimbs, and move by pushing themselves through water using a powerfully muscled tail with a broad terminal water-foil called a fluke. The ancestors were omnivorous to herbivorous; in contrast, whales today are piscivorous (fish-eating) and planktivorous (plankton-eating). The ancestors perceived their surroundings using their eyes and noses; however, whales today "see" their surroundings with their ears.

The origin of whales involved a macroevolutionary transition from a terrestrial to an aquatic way of life. And, compared with the general trend of vertebrate evolution from sea to land, the evolution of whales was backward, because they moved from land back to the sea. New fossil discoveries illuminate the origin and early evolution of whales.

Whale diversity and classification. Similarities and differences of whales are expressed in a classification (see **table**), which is also a reflection of their diversity. All whales are classified in the mammalian order Cetacea. Within Cetacea, there are two general kinds of whales living today: toothed whales in the suborder Odontoceti and baleen whales in the suborder Mysticeti. Odontocetes have simple teeth embedded in sockets of bone in the upper and lower jaws. This socketing is a general mammalian characteristic. Mysticetes have baleen, which is a keratinous tissue that frays into hairs. Hair, too, is a general characteristic of mammals. Living Odontoceti and Mysticeti go back some 35 million years in the fossil record to the Oligocene Epoch of geological time.

The third major group of whales is now extinct (or "pseudoextinct" in the sense that it includes ancestors of later whales, but has no representatives living today). This is the suborder Archaeoceti, known only from fossils in the Eocene Epoch, spanning an age range from about 53 to 35 million years before present. Archaeocetes have complex teeth with double-rooted molars, and this double-rooted condition is a diagnostic feature of mammals. Archaeoceti includes the earliest whales and can be shown to have given rise to later Odontoceti and Mysticeti through Oligocene intermediates. The transition from archaic to modern whales coincides with a major tectonic reorganization of ocean currents in the Oligocene that changed the distribution of heat on the surface of the Earth, leading to formation of ice caps at the Poles and causing cold nutrient-rich seawater to well up along the western coasts of continents. Whales responded by developing simplified

Summary classification of whales (order Cetacea)*

Suborder	Family	Common name	Number of genera	Geological epoch
Odontoceti	Delphinidae	Dolphins	17	Miocene–Recent
	Phocoenidae	Porpoises	8	Miocene–Recent
	Monodontidae	Narwhals	4	Miocene–Recent
	Platanistidae	Indian river dolphins	3	Miocene–Recent
	Pontoporiidae	South American river dolphins	6	Miocene–Recent
	Iniidae	Amazon river dolphins	6	Miocene–Recent
	Lipotidae	Chinese river dolphins	2	Miocene–Recent
	Kogiidae	Pygmy sperm whales	5	Miocene–Recent
	Acrodelphinidae	Acrodelphinids	5	Miocene
	Physeteridae	Sperm whales	17	Oligocene–Recent
	Hyperoodontidae	Beaked whales	23	Oligocene–Recent
	Squalodontidae	Squalodontids	15	Oligocene–Miocene
	Rhabdosteidae	Rhabdosteids	6	Oligocene–Miocene
	Kendriodontidae	Kendriodontids	11	Oligocene–Miocene
	Agorophiidae	Agorophids	1	Oligocene
Mysticeti	Eschrichtiidae	Grey whales	1	Pleistocene–Recent
	Balaenopteridae	Rorquals	8	Miocene–Recent
	Balaenidae	Right whales	6	Miocene–Recent
	Cetotheriidae	Cetotheres	29	Oligocene–Pliocene
	Aetiocetidae	Aetiocetids	1	Oligocene
	Mammalodontidae	Mammalodontids	1	Oligocene
	Llanocetidae	Llanocetids	1	Eocene–Oligocene
Archaeoceti	Basilosauridae	Basilosaurids	8	Middle–late Eocene
	Protocetidae	Protocetids	12	Middle Eocene
	Remingtonocetidae	Remingtonocetids	4	Middle Eocene
	Ambulocetidae	Ambulocetids	2	Middle Eocene
	Pakicetidae	Pakicetids	4	Early–middle Eocene

*Numbers of genera are approximate. Fossil whales are from the Cenozoic Era and range from early Eocene in age, approximately 53 million years ago, to the present.

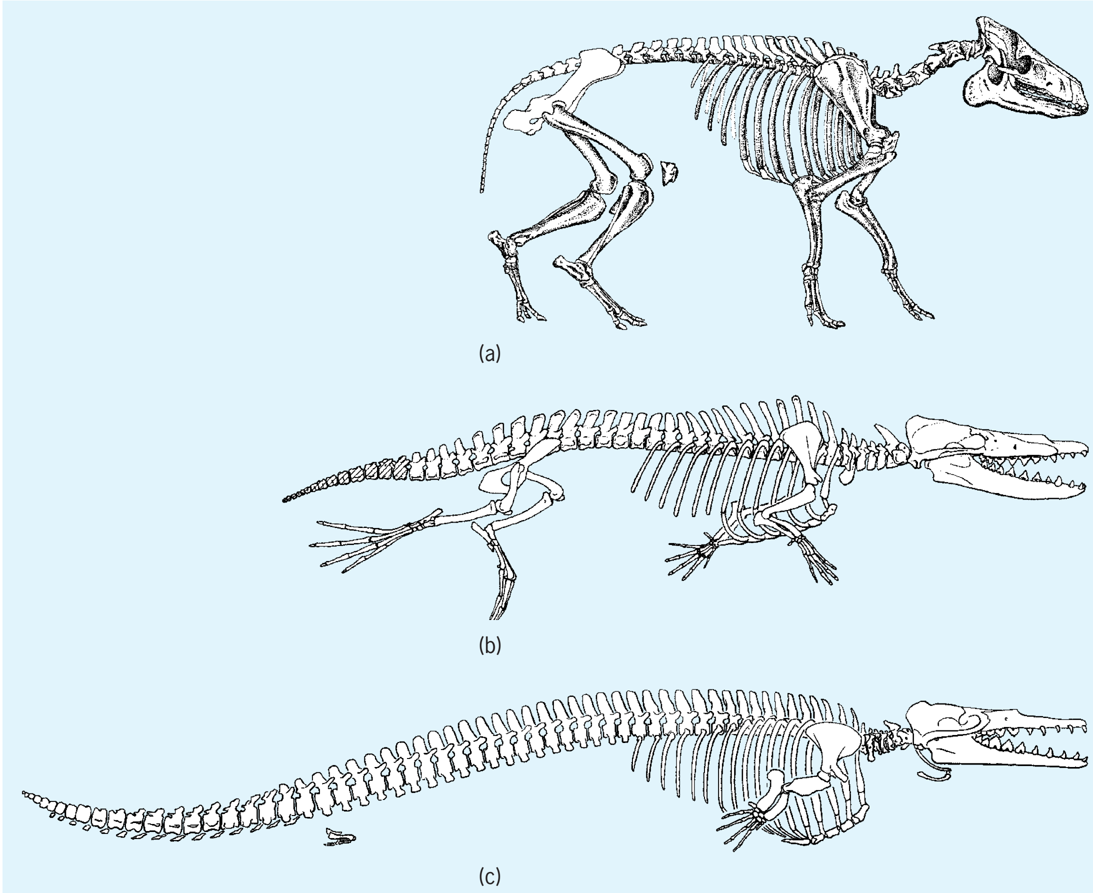

Fig. 1. **Comparison of skeletons showing the morphology of (*a*) a model ancestral land mammal (*Elomeryx*; skeleton is about 2 m or 6 ft in length); (*b*) a semiaquatic middle Eocene protocetid (*Rodhocetus*; 3 m or 10 ft in length); and (*c*) a fully aquatic middle-to-late Eocene basilosaurid (*Dorudon*; 6 m or 18 ft in length). All are standardized to approximately the same head and thorax size. Note that the archaeocete whales *Rodhocetus* and *Dorudon* have longer skulls and shorter necks, progressively shorter forelimbs, and progressively longer tails and more reduced hindlimbs compared with land-dwelling *Elomeryx*.**

teeth and high-frequency sonar to aid in feeding on fish (odontocetes) or by developing baleen to strain plankton from seawater directly, bypassing fish in the food chain altogether (mysticetes).

Fossil record. Whales have large bones, making them relatively easy to find as fossils. Whales are by definition water-dwelling animals, and watery environments are generally ideal for preserving bones as fossils. Whales thrive in shallow marine environments on the margins of continents, and the Cenozoic Era when whales lived is represented in the geological record by widespread shallow marine deposits. However, since whales reside at or near the top of the food chain (that is, they are rare compared with other animals), they have a good, but not yet great, fossil record. The fossil record is sufficiently dense and continuous, though, that broad lineages can be traced up and down through successive strata, moving forward and backward through earth history and evolutionary time.

The most interesting whales, in some respects, are those that document the transition from land to sea, and here an archaic whale from the Eocene named *Rodhocetus*, classified in the family Protocetidae, is crucially important. *Rodhocetus* is similar in some respects to the later Eocene basilosaurid *Dorudon* (**Fig. 1**). Both are known from nearly complete skeletons. Similarities include long tapering skulls with pointed incisors and canine teeth, complex puncturing and shearing premolar and molar teeth, necks of medium length, a narrow and deep chest or thorax, and mobile forelimbs modified to some degree for swimming. *Dorudon* is similar, in turn, to primitive mysticete and odontocete whales known from the subsequent Oligocene Epoch. Comparison between *Rodhocetus* and *Dorudon* shows a reduction of the neural spines rising above the thoracic vertebrae, great elongation of the vertebral column with addition of lumbar vertebrae, and great reduction of the hindlimbs in *Dorudon*.

Skeletons of primitive archaeocete whales with associated forelimbs and hindlimbs were discovered in 2000. The most complete of these, *Rodhocetus*, is important in showing that primitive archaeocetes had morphological characteristics of land mammals in general, and of the anthracotheriid group of artiodactyls in particular. Artiodactyls are hoofed animals with even numbers of toes; anthracotheriids are a group of artiodactyls that lived in the Eocene and Oligocene and are thought to have given rise to living

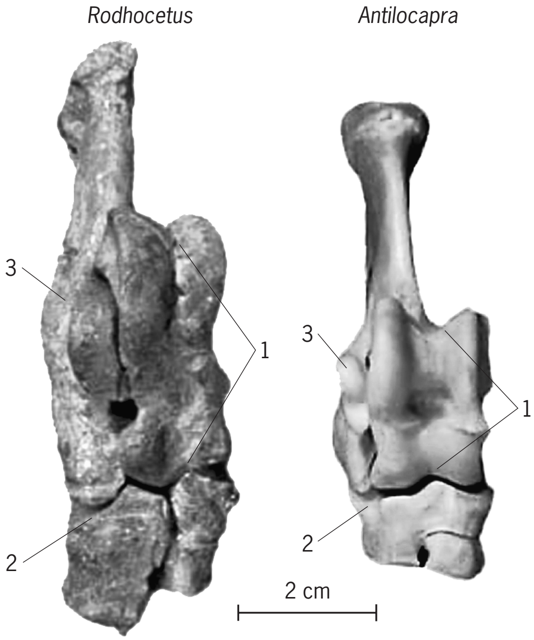

Fig. 2. Comparison of ankle bones of the middle Eocene protocetid *Rodhocetus* with those of an extant pronghorn *Antilocapra*. Note the presence of (1) a double-pulley astragalus bone; (2) a notch in the cuboid for insertion of the calcaneum; and (3) a large convex fibular facet on the calcaneum. This whole complex of characteristics unites early whales with artiodactyls, or even-toed hoofed mammals. Late Eocene basilosaurid whales have greatly simplified ankle bones, and later fossil and living whales lack these entirely.

Hippopotamus. The most important similarities between *Rodhocetus* and the anthracotheriids are those of the ankle bones, including a double-pulley astragalus, notched cuboid, and convex fibular facet of the calcaneum found only in artiodactyls (**Fig. 2**). Both *Rodhocetus* and *Elomeryx*, the best-known skeleton of the family Anthracotheriidae, retain five fingers on the hand, both are mesaxonic (having the central axis of the hand in or near the middle finger), and both have small hooves on the terminal phalanges of the second, third, and fourth digits. Compared with *Elomeryx*, *Rodhocetus* has an elongated skull, a shorter neck and forelimb, enlarged lumbar and caudal vertebrae, an elongated tail, and hindfeet that are modified into elongated, webbed flippers.

Artiodactyls were first convincingly linked to whales on the basis of their elevated mutual immune reactions compared with those of other pairs of mammals. Deoxyribonucleic acid sequencing has corroborated this relationship and, somewhat controversially, identified the hippo as the living artiodactyl closest to whales. Similarity of *Rodhocetus* to *Elomeryx* does not prove this connection because there is a lack of evidence of *Elomeryx*-like artiodactyls at the beginning of the Eocene; however, the new fossil evidence makes such a relationship to hippos more plausible than previously thought.

Transition from land to sea. *Elomeryx* is Oligocene in age, so it cannot be ancestral to *Rodhocetus*, but it nevertheless makes a good model for the kind of terrestrial artiodactyl thought to have given rise to whales about 55 million years ago at the beginning of the Eocene. The proportions of *Elomeryx*, *Rodhocetus*, and *Dorudon* are compared in Fig. 1. Here the relative sizes of the skull, neck, and thorax (rib cage) are standardized, making it easy to visualize how archaeocetes differ from *Elomeryx*: the archaeocetes have longer skulls and shorter necks, progressively shorter forelimbs, progressively longer tails, and more reduced hindlimbs (so small as to be vestigial for locomotion in *Dorudon*).

There are more than 100 species of semiaquatic mammals living today. These range from the more terrestrial tapirs, bears, and hippos to the more aquatic seals and sea lions. Comparison of the overall trunk, limb, and hand and foot proportions of *Rodhocetus* with a large sample of living semiaquatic mammals shows *Rodhocetus* to have been a desman-like foot-powered swimmer, and the presence of feet modified into elongated, webbed flippers is consistent with this. Thus it appears that descendents of hoofed terrestrial mammals such as *Elomeryx* passed through a foot-powered swimming stage before more whalelike tail-powered swimmers such as *Dorudon* evolved.

The oldest fossil whale known to date, *Himalayacetus*, is a pakicetid about 53 million years old that was found in marine strata of the lower Eocene of India. *Pakicetus* itself is a little younger and comes from riverine deposits of middle Eocene age in Pakistan. Skeletal remains of *Pakicetus* have been interpreted as being terrestrial, but these are much too fragmentary to interpret reliably. The bones that are complete enough to compare resemble those of semiaquatic Protocetidae, so it is doubtful that *Pakicetus* was terrestrial. Recovery of older *Himalayacetus* from marine deposits is powerful evidence, too, that the earliest whales known to date were already semiaquatic.

Conclusion. What we infer of whale evolution begins with an as yet unidentified early Eocene terrestrial artiodactyl ancestor (here represented provisionally by *Elomeryx*). The first stage documented in the fossil record is an early-to-middle Eocene pakicetid-protocetid stage represented by the semiaquatic foot-powered swimmer *Rodhocetus*. This is followed by a middle-to-late Eocene basilosaurid stage represented by the fully aquatic tail-powered swimmer *Dorudon*. Modern baleen and toothed whales differentiated in the latest Eocene or early Oligocene, giving rise to the diversity known today. Molecular evidence from living animals is consistent with this historical perspective in recognizing a close relationship of whales and artiodactyls.

For background information *see* ANIMAL EVOLUTION; ANIMAL SYSTEMATICS; ARTIODACTYLA; CETACEA; FOSSIL; MACROEVOLUTION in the McGraw-Hill Encyclopedia of Science & Technology.

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Bibliography. L. Bejder and B. K. Hall, Limbs in whales and limblessness in other vertebrates: Mechanisms of evolutionary and developmental transformation and loss, *Evol. Dev.*, 2002; F. E. Fish, in J.-M. Mazin and V. d. Buffrénil (eds.), *Secondary Adaptation of Tetrapods to Life in Water*, Friedrich Pfeil, Munich, 2001; R. E. Fordyce and C. de Muizon, in J.-M. Mazin and V. d. Buffrénil (eds.), *Secondary Adaptation of Tetrapods to Life in Water*, Friedrich Pfeil, Munich, 2001; J. E. Gatesy and M. A. O'Leary, Deciphering whale origins with molecules and fossils, *Trends Ecol. Evol.*, 2001; P. D. Gingerich et al., Origin of whales from early artiodactyls: Hands and feet of Eocene Protocetidae from Pakistan, *Science*, 2001; J. E. Heyning and G. M. Lento, in A. R. Hoelzel (ed.), *Marine Mammal Biology*, Blackwell Scientific, Oxford, 2002.