MARINE MAMMAL EVOLUTION AND TAXONOMY

J. E. Heyning, The Natural History Museum of Los Angeles County, Los Angeles, CA, USA

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Since Eocene times some 57 million years ago, several groups of land mammals have independently evolved adaptations for a marine existence. With just over 120 modern species (**Table 1**), marine mammals are not taxonomically diverse compared to other groups of marine organisms, yet they are important components of many ecosystems. Marine mammals have evolved from only two terrestrial groups, or clades, of mammals. The first is the Order Carnivora, which includes such familiar creatures as cats, dogs, and bears. From this order arose the pinnipeds (seals, sea lions, walruses), the sea otter, and the polar bear. The other clade is the Ungulata, a group that includes all the orders of modern hoofed animals. Evolving from this rank are the cetaceans (whales, dolphins, and porpoises), the sirenians (dugongs and manatees), and the extinct hippo-like desmostylians.

Table 1 Marine mammals

	Common name	*Number of living species*
Order Cetacea		
Suborder Mysticeti	Baleen whales	
Family Balaenidae	Right whales	4
Family Neobalaenidae	Pygmy right whale	1
Family Eschrichtiidae	Gray whale	1
Family Balaenopteridae	Rorqual whales	8
Suborder Odontoceti	Toothed whales	
Family Physeteridae	Sperm whale	1
Family Kogiidae	Pygmy sperm whales	2
Family Ziphiidae	Beaked whales	20
Family Platanistidae	Indian river dolphins	1
Family Iniidae	River dolphins	3
Family Monodontidae	Beluga and narwhal	2
Family Phocoenidae	Porpoises	6
Family Delphinidae	Oceanic dolphins	36
Order Carnivora	Carnivores	
Family Phocidae	Seals	19
Family Otariidae	Sea lions and fur seals	16
Family Odobenidae	Walruses	1
Order Sirenia	Sea cows	
Family Dugongidae	Dugongs	1
Family Trichechidae	Manatees	3

Systematics is the science of defining evolutionary relationships among organisms. A phylogeny is a hypothesis of those evolutionary relationships, and is the foundation for any evolutionary study. It is the distribution of characters on a phylogenetic tree that is used to evaluate whether similar features in two organisms are a result of inheritance from a common ancestor or evolved via convergence. No proposed phylogeny can be proven, as proof would require the unattainable knowledge of past evolutionary events. Hence, researchers today can only infer past events from phylogenetic reconstructions of evolutionary relationships.

Most modern systematists use a philosophical approach called cladistics. The basic tenets of cladistics are quite simple: organisms are deemed to be related based on shared derived characters called synapomorphies. Derived characters are defined as having arisen in the common ancestor of the taxa and are subsequently passed on to their descendant taxa. Groups of related taxa and their descendants are called clades regardless of taxonomic rank. Monophyletic groups are those that include the ancestor and all of its descendants. Paraphyletic groups are those which include the ancestor taxa, but not all the descendants. Paraphyletic groups often reflect a certain level of morphological organization or 'grade,' and exclude some or all of the more derived descendants. For example, in classical cetacean taxonomy, the suborder Archaeoceti is unquestionably paraphyletic, as this group of fossil cetaceans includes the most basal species, but not the descendant suborders Mysticeti and Odontoceti.

Order Carnivora

Several groups of carnivores have evolved to a partially aquatic existence, although all must return to land, at least to give birth. The polar bear, *Ursus maritimus*, appears to be a very recent evolutionary divergence of the brown bear, *Ursus arctos*, lineage. Analysis of molecular data suggests that polar bears are most similar to those brown bears from the islands off south-east Alaska. Fossils suggest that the two species diverged in the middle Pleistocene.

There are three species of marine carnivores in the weasel/otter family (Mustelidae). Along the north-east coast of North America, the extinct sea mink, *Mustela macrodon*, has been found primarily from Native American midden sites. The second is the chungungo or marine otter, *Lutra felina*, a poorly

known species inhabiting South American waters. Lastly, is the well-known sea otter, *Enhydra lutris*, of the temperate and subarctic North Pacific. These two otters are closely related to the fresh water otters. The sea otter appears to be related to the late Miocene to early Pliocene *Enhydritherium*, found along both coasts of North America and Europe.

Pinnipeds

The pinnipeds (from the Latin meaning 'fin-footed') are a group of the marine mammals, which includes the seals, sea lions, and walrus (**Figure 1**). Pinnipeds arose from the arctoid (bear, dogs, weasels, etc) lineage of carnivores. The pinnipeds consist of three living families, the Phocidae (true seals), the Otariidae (fur seals and sea lions), and the Odobenidae (walruses).

The terrestrial ancestor of the pinnipeds has been the subject of considerable debate. Two schools of thought exist. One, citing primarily biogeographical, and paleontological evidence, supports a diphyletic or dual origin, attributing the sea lions, fur seals, and walruses to an ursid (bear-like) ancestor evolving in the North Pacific and the true seals to a mustelid (weasels, otters, etc.) ancestor evolving in the North Atlantic. The other school, using molecular, karyological, and morphological evidence supports a monophyletic origin for all three pinniped families stemming from an unresolved arctoid ancestor. There is growing consensus that pinnipeds constitute a monophyletic group.

The extant true seals, Phocidae, are distinguished from the sea lions by the lack of external ear flaps, relatively short forelimbs with claws, backward directed hindlimbs that do not permit quadrupedal movement on land, and locomotion in water by sculling the hindlimbs. They are divided into two groups, the Monachinae ('southern' seals) and the Phocinae ('northern' seals). The oldest phocid fossils are from the late Oligocene of the North Atlantic.

The sea lions and fur seals (or 'eared' seals), Otariidae, can be distinguished from the phocids by the presence of external ear flaps, elongate flipper-like forelimbs, rotatable hindlimbs that allow quadrupedal locomotion on land, and locomotion in water by flapping of the fore-flippers. They are divided into two groups, the Arctocephalinae (fur seals) and the Otariinae (sea lions). The diagnostic feature is the presence of abundant underhair in the fur seals. The oldest fossil otariids are from the early Miocene of the North Pacific.

The walrus family includes mostly extinct species consisting of three groups. The most basal are archaic nontusked walruses referred to as

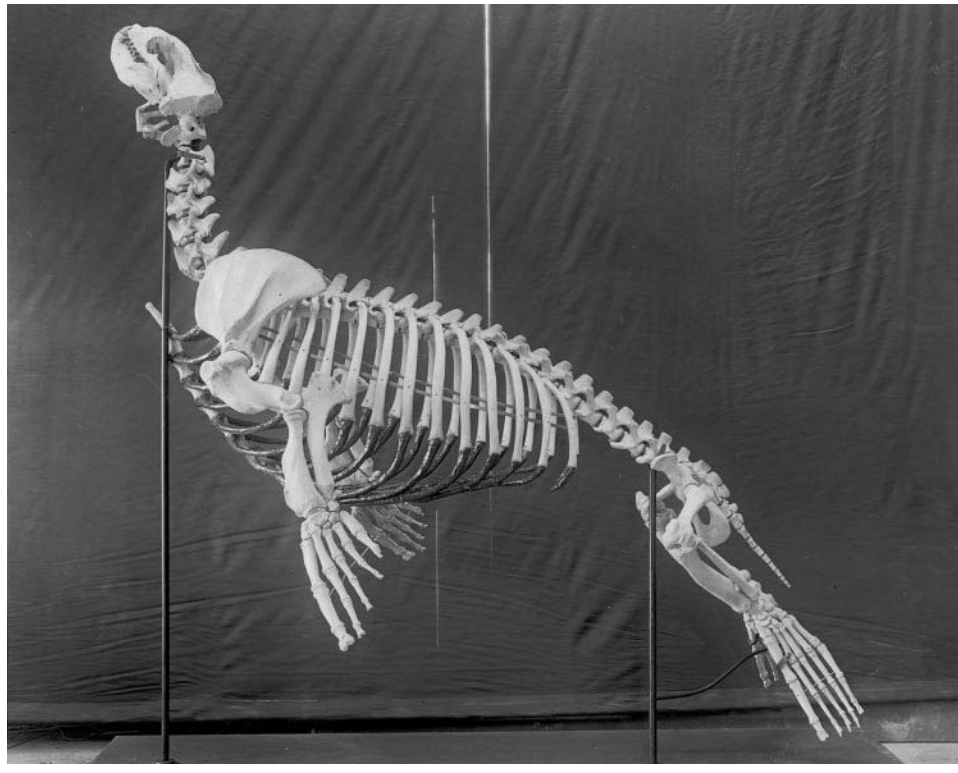

Figure 1 Skeleton of a modern southern sea lion (*Otaria flavescens*). Photo courtesy of the Natural History Museum of Los Angeles County.

imagotarines retaining the ancestral fish-eating diet of other pinnipeds whereas the Dusginathinae are an extinct group apparently specializing in squirt/suction feeding behavior for foraging on shellfish and/or crustaceans. Dusignathines have enlarged canines in both jaws providing a four-tusked image to the skull. These two groups are distinguished from the Odobeniinae that only develop tusks in the upper jaw and eventually gave rise to the modern walrus, *Odobenus rosmarus*, which feeds primarily by sucking bivalves out of their shells.

Order Cetacea

Until quite recently it was commonly asserted that whales were fish, and not mammals. Today, the cetaceans (whales, dolphins, and porpoises) are readily recognized as mammals. Their relationship to the ungulates (hoofed terrestrial mammals including horses, cows, pigs, camels, elephants, etc.) is generally accepted, though their closest relation among the living ungulates remains a topic of research. The Order Cetacea consists of three suborders: the Archaeoceti (an extinct group of archaic whales), the Odontoceti (toothed whales), and the Mysticeti (baleen whales).

The hypothesis that the order Cetacea is monophyletic is supported by an overwhelming amount of morphological, cytological, and molecular evidence. The karyotypes of cetaceans are amazingly conservative when compared to other groups of mammals. The typical chromosome count for most cetaceans is $2N = 44$. The exceptions are sperm whales (Physeteridae and Kogiidae), beaked whales (Ziphiidae), and right whales (Balaenidae). For right whales and beaked whales, the lower counts ($2N = 42$) are a result of the fusion of different chromosome pairs, respectively. The chromosome-banding pattern among cetaceans is also astonishingly conservative.

In modern cetaceans (**Figure 3**), the body shape is fish-like – streamlined with fin-like flippers and flukes. The hind limbs are but vestiges tucked within the body wall, and the nostrils are situated high on the head and termed blowholes. It is because cetaceans differ so strikingly from their terrestrial kin that it is difficult to discern intuitively which, among the other orders of ungulate mammals, are their closest kin.

There is now convincing fossil evidence that land-dwelling extinct mesonychians are closely related to the ancestor of whales; either they are the sister-taxon to the whale ancestor, or whales arose from within the paraphyletic extinct family Mesonychidae (**Figure 2**). There are many similarities between whales and at least some mesonychids in such features as the construction of the cheekteeth, the humerus, and the venous drainage of the skull. An analysis of the postcranial skeleton of the mesonychid *Pachyaena* suggests that this animal may have had a body form similar to tapirs, capybaras, or suids (pigs), many of which are excel-

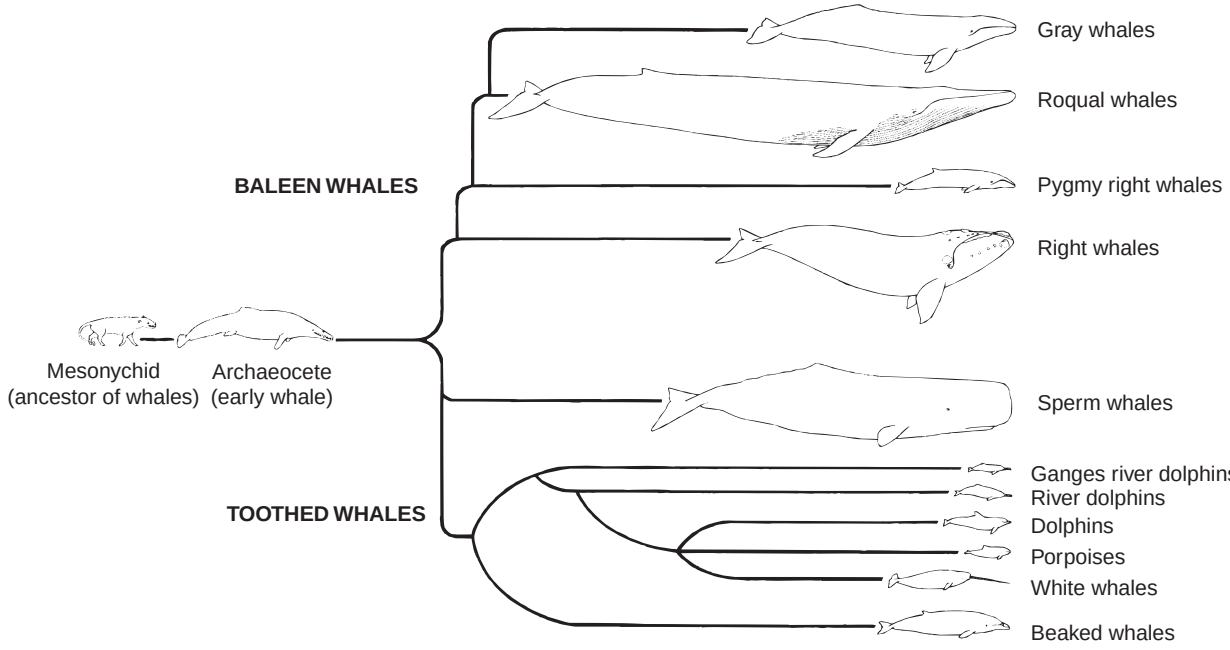

Figure 2 Phylogeny of the modern families of cetaceans based on morphological and molecular data (modified from Heyning, 1995).

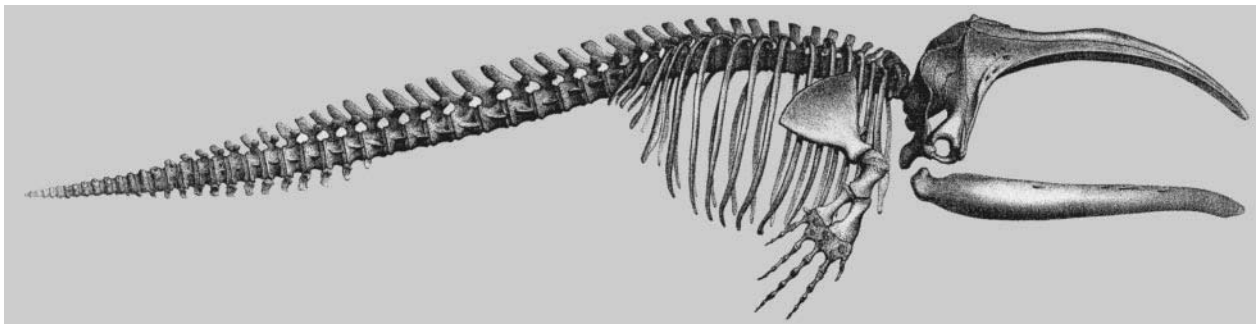

Figure 3 Skeleton of a modern baleen whale (*Balaena mysticetus*). (From Van Beneden and Gervais, 1880.)

lent swimmers. Some molecular studies indicate that the Cetacea may have actually evolved from within the order Artiodactyla.

Suborder Archaeoceti

Archaeocetes represent a primitive grade-level taxon that includes all cetaceans that lack the derived telescoped pattern of skull bones found in either mysticetes (baleen whales) or odontocetes (toothed whales). Archaeocetes are further characterized by an elongate snout, a narrow braincase, a skull with large temporal fossa and well-defined sagittal and lambdoidal crests, a broad supraorbital process of the frontal bone, and bony nares situated some distance posterior to tip of the snout. The archaeocete grade was 'extinct' by the end of the Eocene. The archaeocetes include five families: Pakicetidae, Ambulocetidae, Protocetidae, Remingtonocetidae, and Basilosaurocetidae.

Most Pakicetids have been unearthed from terrestrial, freshwater, or nearshore deposits of the eastern Tethys, a massive epicontinental sea that divided Eurasia from Africa/India. The oldest and most primitive whale, *Pakicetus inachus* was described from Pakistan. Many of these fossils from the eastern Tethys Sea, some with known hind limbs, are significant in that they serve as morphological transitions between land-dwelling mammals and fully aquatic cetaceans. The Ambulocetidae occupied tidal and estuary habitats. The enigmatic *Ambulocetus natans* differs from all other known archaeocetes in that its eyes are elevated above the overall profile of the skull, and its hind feet are elongate imparting a crocodile-like appearance. These hindlimbs were probably important for aquatic locomotion. The Protocetidae is defined by details of the orbits, teeth, and sacrum. In the eastern Tethys, protocetids are found in nearshore waters, whereas protocetids from the western Tethys died in shallow offshore regions and their North American kin have been found in shallow nearshore deposits. Remingtonocetidae have extremely long and narrow skulls with small eyes and are known from rock units from Pakistan and India. These archaeocetes are found in sediments indicating a coastal environment or nearshore shallow marine deposits. Though they are interpreted to be the most derived of the archaeocete families, the Basilosauridae were among the first archaeocete fossils to be discovered. Basilosaurids are typically divided into two subfamilies: the Durodontinae with unspecialized vertebrae and the Basilosauinae with extremely elongate vertebral bodies. It has been suggested that durodontines were ancestral to both mysticetes and odontocetes. However, further evidence suggests that the durodontines represent the sister taxa to the modern Cetacea clades.

One of the most dramatic morphological changes of early cetaceans was the shift from quadruped locomotion on land to the axial undulation of swimming in the ocean. These include changes of the vertebral column, limb structure, and of the tail flukes. One striking conclusion is how quickly these transitions occurred. At the dusk of the Early Eocene, *Pakicetus* and its contemporaries were quadruped animals that drank fresh water. A few million years later in the Middle Eocene, *Rodhocetus* and its kin were swimming with the aid of tail flukes and drinking sea water. By the Late Eocene, Basilosaurines possessed such exceedingly small hind limbs that it is unlikely that they were of much use in terrestrial locomotion. Hence, one can speculate that by the Late Eocene cetaceans had severed all links to the land.

One hypothesis is that archaeocetes first evolved in fluvial or estuarine environments of the eastern Tethys and subsequently dispersed as more morphologically and physiologically derived forms conquered the oceans. All of the most primitive and chronologically oldest fossil archaeocetes are found along the shores of the eastern Tethys, whereas the more morphologically derived and fully marine

protocetids and basilosaurids of the Middle and Late Eocene are found in rocks from Asia, North Africa, North America, New Zealand, and Antarctica.

Suborder Odontoceti

Some cetaceans possess teeth (odontocetes), whereas others have baleen for filtering out prey (mysticetes). There are numerous other synapomorphies that unite the Odontoceti such as the maxilla (upper jaw) which has telescoped back over the frontal bone of the skull. All living and all but the most basal fossil odontocetes have asymmetrical skulls, and all modern species have asymmetrical facial soft anatomy. This asymmetry results from an enlargement of the facial soft anatomy on the right side. All odontocetes have a complex series of air sacs off their nasal passages. All extant odontocetes possess an enlarged fatty melon in front of the nasal passages, which is distinctly different from the diminutive melon-like structure observed in mysticetes. Odontocetes are unique among all tetrapods in that the distal narial passages coalesce to form a single nostril or blowhole. The large melon, complex nasal anatomy, and asymmetry all appear to be correlated with the ability to echolocate.

The sperm whales are represented today by the giant sperm whale (Physeteridae) and the dwarf sperm whales (Kogiidae). This clade is the first to diverge from the lineage of living odontocetes. All sperm whales are recognized by the presence of a spermaceti organ in their head and very asymmetrical skulls. All living species are known or suspected to be deep divers. The beaked whales (Ziphiidae) are a very diverse group with at least 20 known living species. This group is typified by extreme sexual dimorphism in that males of most species have a one or two enlarged pairs of teeth used primarily for fighting other males, presumably for establishing breeding dominance. The river dolphin (genus *Platanista*) of the Indian subcontinent is the sole living representative of the family Platanistidae. The bone pattern of the palate and the elaborate crests of bone on top of the skull define this family. The other living river dolphins and their kin belong to the family Iniidae, with living representatives found in the waters of the Yanzee and Amazon river basins, and coastal waters of eastern South America. This clade is defined by the extreme asymmetry in the nasal sacs. The remaining odontocetes are the closely related families of the Monodontidae (narwhal and beluga), Phocoenidae (porpoises) and the taxonomically diverse oceanic dolphins (Delphinidae). This clade represents the vast majority of living species, and includes those most familiar to most people.

Suborder Mysticeti

The mysticetes, with their edentulous mouths lined with filtering baleen, are one of the distinct clades among the mammals. The evolutionary transition from capturing single prey to filtering numerous prey items out of mouthfuls of sea water has ramifications not only in the morphology, but also the behavioral ecology of these, the largest of all animals. Mysticetes evolved from cetaceans that possessed teeth. Certain cranial features predate the loss of teeth in the mysticete clade and, therefore, the most basal mysticetes retain teeth.

The oldest known mysticete is the toothed species *Llanocetus denticrenatus* from the Late Eocene of Seymour Island, Antarctica. The next oldest specimens are those of the Oligocene cetotheres whose wide, edentulous palates strongly imply the presence of baleen. As baleen is made of the protein keratin, it typically decomposes with the other soft tissues rarely leaving a fossil trace. These fossil discoveries now represent a moderately good morphological series from the archaeocetes to modern mysticetes.

Three families of extinct mysticetes are recognized. They are the Llancetidae, the Aetiocetidae, and the Cetotheridae. The family Llanocetidae is based on one species, *Llanocetus denticrenatus*, with an estimated total length of perhaps 10 m. Aetiocetids are relatively small toothed mysticetes known only from the shorelines of the North Pacific. *Chonecetus* and some species of *Aetiocetus* retain the primitive eutherian mammal tooth count. *Aetiocetus polydentatus* with its expanded toothcount exhibits an incipient stage of the derived feature of supernumerous teeth as seen in later cetaceans. The Cetotheriidae represent a phylogenetically heterogeneous assemblage that is truly a 'wastebasket' taxon with over 60 named species within 30 or so genera of unknown affinities. The rostrum is typically broad and flat, not dissimilar to that found in the primitive aetiocetids and modern balaenopterids. The oldest cetotheres are *Cetotheriopsis lintianus* from Austria and the relatively complete skull of *Mauicetus lophocephalus* from New Zealand, both from the Late Oligocene.

The modern mysticetes are divided into four families: the Balaenidae, Neobalaenidae, Eschrichtiidae, and Balaenopteridae. The systematics of these families are much less contentious than that for the modern odontocetes, though a few taxa remain elusive with regard to their relationship within and among other modern mysticete groups.

The right whales (Balaenidae) are heavy-bodied mysticetes with large arched heads and cavernous

mouths to accommodate the extremely large filtering surface formed by the extraordinarily long baleen plates. Balaenids lack throat grooves. There are two species of modern balaenids, the bowhead and the right whale. Balaenids have skulls that are narrow and highly arched. The baleen is long, narrow, with a fine fringe. The dorsal fin is absent. The oldest fossil of an extant mysticete family is the balaenid *Morenocetus parvus* from the earliest Miocene of Argentina.

The family Neobalaenidae is represented solely by the poorly known Southern Hemisphere pygmy right whale, *Caperea marginata*. Some workers have considered *Caperea* to be a balaenid. However, there is ever-growing consensus, based on morphology and molecular data, that *Caperea* is not an 'aberrant' right whale, but is instead more likely the sister group to the rorqual/gray whale clade. The dorsal fin is small, yet distinctive. The throat grooves of *Caperea* are highly variable in depth, and virtually absent in some individuals. The rostrum is only somewhat arched, intermediate between the conditions seen in gray whales (Eschrichtiidae) and right whales (Balaenidae). The ribs are unique among cetaceans, living or fossil, in that they are broad and overlap each other in profile.

The enigmatic gray whale, *Eschrichtus robustus*, is the sole member of the family Eschrichtiidae. The overall mottled gray color and small dorsal fin followed by a series of dorsal ridges characterize gray whales. The two to five throat grooves are well delineated and are confined to the gular region. The rostrum is attenuate and moderately arched. The yellowish to white baleen is relatively short and moderately wide. Gray whales have lost a digit in their flipper. The only fossil gray whale is a Late Pleistocene individual of superb preservation. However, this animal is indistinguishable from the modern species and its relative young age does not help to resolve the relationship between gray whales and other baleen whales.

The Balaenopteridae, also known as the rorquals, are immediately recognized by their numerous throat grooves. These distinctive throat grooves are numerous, ranging from 14–22 grooves in the humpback whale (*Megaptera novaengliae*) to 56–100 grooves in the fin whale (*Balaenoptera physalus*). Balaenopterids are the 'greyhounds of the sea.' Their bodies are the sleekest among living mysticetes. The dorsal fin is always present and tends to be inversely proportional to body size. The rostrum is extremely broad and flat. Rorqual whales have a very complex interdigitating pattern of bony sutures between the rostral bones and those of the braincase proper. Only four digits are present in the flippers. The humpback is unique among balaenopterids in that it has extremely elongate flippers.

There are three major cranial character suites that have been used to ascertain the phylogenetic position of fossil baleen-bearing whales. These are the position and shape of the occipital shield, the complexity of interdigitation between the bones of the rostrum (nasals, premaxillae, and maxillae) and the braincase proper, and slope of the supraorbital process of the frontal bone. Ancestrally, the occipital shield does not extend very far anteriorly providing dorsal midline exposure of the parietal and frontal bones. The most primitive character state of this feature is seen on the various toothed mysticetes. In the most advanced character state, the occipital is close to the nasals and premaxillae on the vertex. This condition is found in modern balaenopterids, neobalaenid, and also in some cetotheres. The complex interdigitation of the bony sutures is clearly derived. Incipient interdigitation of the rostrum and braincase is seen in cetotheres. Modern balaenopterids uniquely possess a supraorbital process of the frontal that is flat and horizontal until it reaches the braincase and then abruptly turns dorsally to the skull vertex. The result is a large region over the supraorbital process for the greatly enlarged temporalis muscle required to close the mouth after engulfing tons of water. The cetothere *Cetotherium* has distinct crests on the temporal ridge along the contact with the frontals which suggests a condition that foreshadows the state found in modern balaenopterids.

Although differing somewhat in detail, most morphologically based phylogenies of baleen whales as well as molecular-based studies suggest that the balaenids were the first clade to diverge, followed by the Neobalaenidae, then the Eschrichtiidae and Balaenopteridae as sister taxa. Several studies using molecular sequence data have implied that the ancestry of the gray whale (Eschrichtiidae) is located near or within the genus *Balaenoptera* (Balaenopteridae).

Order Sirenia

The sirenians, manatees, dugongs, and their extinct relatives, are a fully aquatic herbivorous group of mammals. The living species are restricted to tropical and subtropical waters; however, fossil species appear to have inhabited temperate waters and the range of the recently extinct Steller's sea cow extended into Arctic waters. Modern dugongs feed primarily on seagrasses, whereas the Steller's sea cow fed on brown algae, and manatees feed on a variety of freshwater aquatic plants. Sirenians are

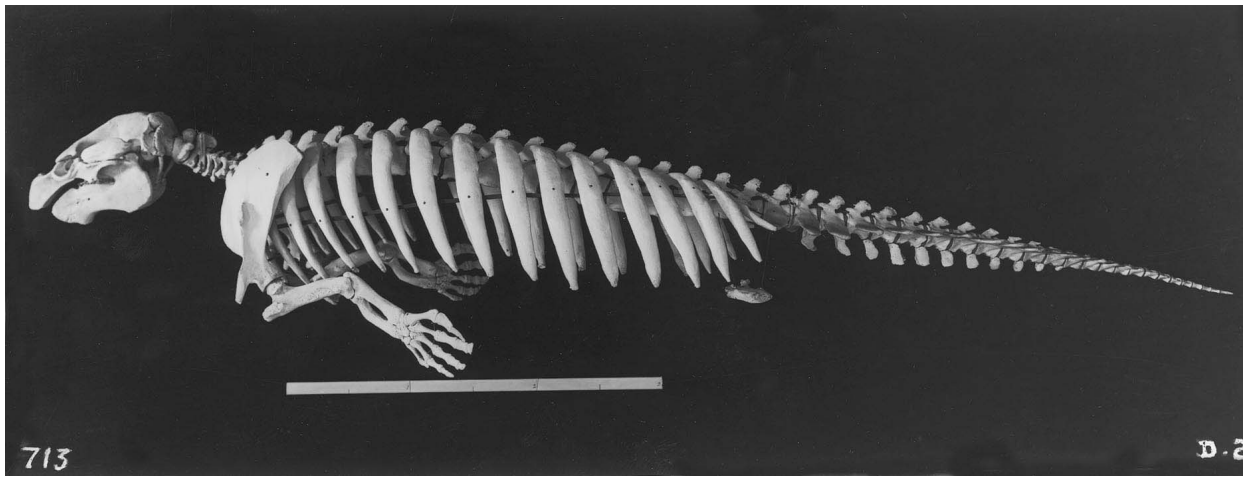

Figure 4 Skeleton of a modern manatee (*Trichechus manatus*). Photo courtesy of the Natural History Museum of Los Angeles County.

part of the ungulate clade called Tethytheria, which also includes the elephants and their extinct relatives, the extinct marine desmostylians, and in some classifications, the hyraxes. All living groups have a unique form of tooth replacement in which new teeth originate at the back of the toothrow, then slowly move forward, and finally the worn down tooth drops out of the front.

The oldest and most primitive sirenians are found in Eocene rocks; *Prorastomus* from the Early and Middle Eocene of Jamaica and *Protosiren* from the Middle Eocene of Pakistan, North Africa, and Europe. Ancient sirenians had four limbs and were amphibious, but as with the cetaceans, modern species have but vestiges of the pelvic girdle and are propelled entirely by tail flukes (**Figure 4**). There are two living groups of sirenians: the manatees (family Trichechidae) and the dugong (Dugongidae). The fossil record is rich with taxa, which is not the case for the living species.

There are but two species of recent dugongids: the dugong, *Dugong dugon*, of the Indo-Pacific and the recently extinct Steller's sea cow, *Hydrodamalis gigas*. Modern Dugongids have pointed flukes similar to cetaceans and are exclusively marine. The upper incisors are tusk-like in males. The Steller's sea cow was hunted to extinction in its last refugia of Commander Islands in 1768, but it occurred recently (19 000 years ago) as far south as Monterey, California. Dugongids were widespread in Miocene times and apparently spread from the Atlantic into the Pacific prior to the formation of the Isthmus of Panama. Dugongids subsequently became extinct in the Atlantic. There are three closely related species of manatees all distributed in the Atlantic: the West Indian manatee, *Trichechus manatus*; the African manatee, *T. senegalensis*; and the exclusively freshwater Amazon manatee, *T. inunguis*. Modern manatees have rounded tail flukes and are primarily found in fresh water although the West Indian manatees are not uncommonly found in marine waters. The fossil record for manatees is far sparser than that of dugongs.

See also

Baleen Whales. Seals. Sea Otters. Sirenians. Sperm Whales and Beaked Whales.

Further Reading

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