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CETACEA

GEORGE GAYLORD SIMPSON'S 1945 *CLASSIFICATION of Mammals* marks a turning point in the study of the origin and relationships of Cetacea. This is principally because Simpson so clearly characterized the state of knowledge at the time, but also because he unknowingly set the stage for a new approach to the study of whale relationships. First, Simpson (1945: 213) pointed out that the phylogenetic interpretation of the anatomy of cetaceans in comparison to that of other living mammals was ambiguous:

Because of their perfected adaptation to a completely aquatic life, with all its attendant conditions of respiration, circulation, dentition, locomotion, etc., the cetaceans are on the whole the most peculiar and aberrant of mammals. Their place in the sequence of cohorts and orders [of mammalian classification] is open to question and is indeed quite impossible to determine in any purely objective way.

And second, Simpson (1945: 214) noted that the fossil record known to him did little to constrain either the timing of whale origins or the relationships of suborders:

It is clear that the Cetacea are extremely ancient as such. . . . They probably arose very early and from a relatively undifferentiated eutherian ancestral stock. . . . Throughout the order Cetacea there is a noteworthy absence of annectent types, and nothing approaching a unified structural phylogeny can be suggested at present. Successive grades of structure appear in waves without any known origin for each. This is strikingly true in many orders, not only of

mammals but of all animals, but within the Mammalia it is perhaps most striking among the Cetacea. Thus the Archaeoceti . . . are definitely the most primitive of cetaceans, but they can hardly have given rise to the other suborders.

Reaction was swift, and five years later, Boyden and Gemeroy (1950: 150–151) published the first biochemical study of cetacean relationships, indicating “a greater similarity in the serum proteins of representative Cetacea and Artiodactyla than between the Cetacea and any other orders tested, all existing orders but the Lagomorpha being included in the comparisons” (lagomorphs being excluded because the antigens were tested in rabbits). Boyden and Gemeroy thus corroborated the much earlier comparative anatomy by John Hunter (1787) and William H. Flower (1883), who emphasized resemblances of cetaceans to ungulates rather than carnivores. Flower’s (1883: 376) scenario for the origin of Cetacea is particularly interesting:

We may conclude by picturing to ourselves some primitive generalised, marsh-haunting animals with scanty covering of hair like the modern hippopotamus, but with broad, swimming tails and short limbs, omnivorous in their mode of feeding, probably combining water-plants with mussels, worms, and freshwater crustaceans, gradually becoming more and more adapted to fill the void place ready for them on the aquatic side of the borderland on which they dwelt, and so by degrees being modified into dolphin-like creatures inhabiting lakes and rivers, and ultimately finding their way into the ocean.

Following Boyden and Gemeroy, Van Valen (1966: 90) reconciled both the newly hypothesized relationship of Cetacea to Artiodactyla and derivation of predaceous whales from herbivores by tracing the origin of whales through Paleocene members of the condylarth family Mesonychidae:

Only two known families need to be considered seriously as possibly ancestral to the archaeocetes and therefore to recent whales. These are the Mesonychidae and Hyaenodontidae (or just possibly some hyaenodontid-like palaeoryctid). No group that differentiated in the Eocene or later need be considered, since the earliest known archaeocete, *Protocetus atavus*, is from the early middle Eocene and is so specialized in the archaeocete direction that it is markedly dissimilar to any Eocene or earlier terrestrial mammal. It is also improbable that any strongly herbivorous taxon was ancestral to the highly predaceous archaeocetes.

In effect, Van Valen’s synthesis ranked Mesonychidae as the closer extinct sister taxon of Cetacea, and Artiodactyla as the more distant extant sister taxon of Cetacea.

Van Valen’s hypothesis deriving cetaceans from mesonychians initiated a slowly accelerating dance of disagreement between paleontologically trained morphologists committed to a carnivorous mesonychid origin on one hand, and biochemically trained systematists advocating direct derivation from or within herbivorous artiodactyls on the other. The principal cladistic studies of morphology favoring a relationship to mesonychids were by McKenna (1975), Pro-

thero et al. (1988), Thewissen (1994), Geisler and Luo (1998), O’Leary (1998), Luo and Gingerich (1999), O’Leary and Geisler (1999), and Geisler (2001). Some of the principal cladistic studies of molecular sequences favoring close a relationship to artiodactyls were by Irwin and Arnason (1994), Gatesy et al. (1996), Montgelard et al. (1997), Gatesy (1998), Milinkovitch et al. (1998), Liu and Miyamoto (1999), Nikaido et al. (1999), and Arnason et al. (2000). Thus, it was both a surprise and a relief when early archaeocete skeletons were discovered in 2000, enabling the issue to be resolved (Gingerich et al., 2001a; see below).

Here I review the general morphological characteristics of Cetacea, living and extinct. Tracing characteristics of living cetaceans back through geological time enables us to identify traits that are primitive in Cetacea and, hence, to recognize the origin of the order and its broader phylogenetic relationships. Relative likelihoods of various hypotheses of temporal distribution constrain a narrow range of credible times for the origin of whales. Finally, the stratigraphic record of early whale evolution enables discussion of the origin and diversification of Cetacea in a paleoenvironmental context.

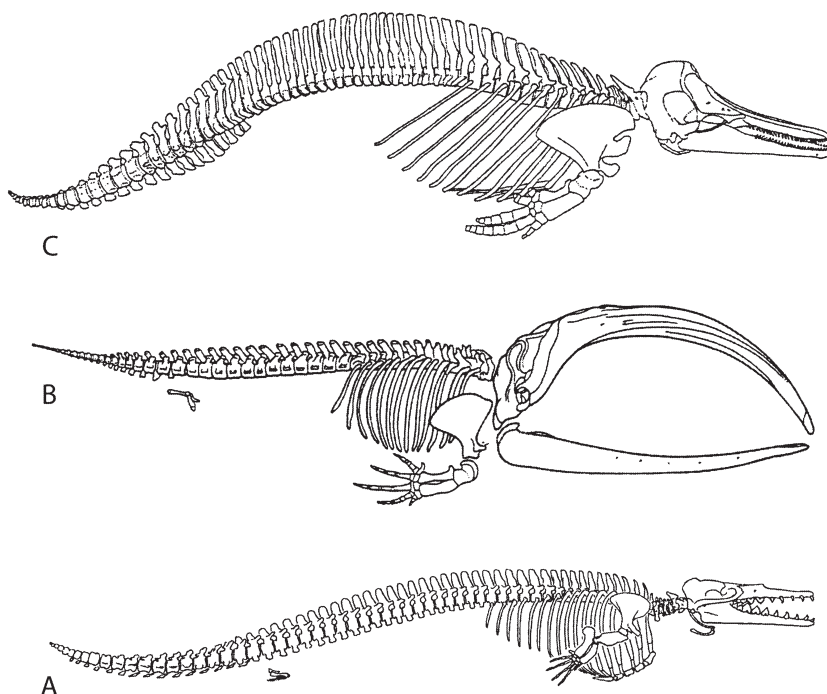
MORPHOLOGICAL CHARACTERIZATION

The mammalian order Cetacea is interesting from an evolutionary point of view, because it represents entry into and eventual mastery of a new aquatic adaptive zone markedly different from that of its terrestrial ancestors. It is true, as Simpson wrote in 1945, that adaptation to a predaceous aquatic life, with all its attendant modifications of morphology and physiology, has made living cetaceans markedly different from other mammals. This obscures phylogenetic relationships. However, on the positive side, life in water gives cetaceans excellent potential for preservation as fossils. Whale bones are large and hard to overlook, and remarkable progress has been made in recent years tracing modern groups of whales back through time in the fossil record.

Living cetaceans fall naturally into two groups, distinguished by their feeding apparatus. These are the baleen whales or Mysticeti (Fig. 15.1B), and the toothed whales or Odontoceti (Fig. 15.1C). Living odontocetes and mysticetes are so different from one another that distinguished authors argued for years that each evolved independently from a different terrestrial ancestor (e.g., Kükenthal, 1893, 1922; Miller, 1923; Slijper, 1936; Yablokov, 1964). Others argued that odontocetes and mysticetes are too similar not to be related (e.g., Flower and Lydekker, 1891; Weber, 1904; Winge, 1921; Kellogg, 1936; Simpson, 1945; Van Valen, 1968). Kellogg (1936: 339) summarized the controversy:

Contradictions of statement in regard to identical anatomical structures subserving the same function show how difficult it is even for such eminent experts as Kükenthal and Weber to come to some sort of an agreement in regard to the relative importance

Fig. 15.1. Comparison of skeletons in three suborders of Cetacea. Note the very different skull sizes and forms related to different modes of feeding, and retention of hindlimbs with feet and toes in the oldest suborder, represented by *Dorudon*. All skeletons are shown in right lateral view and drawn to approximately the same length (not to scale). (A) The middle-late Eocene archaeocete *Dorudon atrox*. (~5 m length). From Gingerich and Uhen (1996). (B) Modern mysticete *Balaena mysticetus* (~15 m). (C) Modern odontocete *Lagenorhynchus obscurus* (~3 m). B and C are modified from Fordyce and Muizon (2001).



to be assigned to similarities and dissimilarities, for by one the resemblances are classed as convergences (adaptive) and by the other as a demonstration of blood relationship (non-adaptive).

Fortunately, new fossils and more critical consideration of previously known fossils have resolved this issue, and there is no longer any question of separate origins (Van Valen, 1968; Barnes et al., 1985; Fordyce and Barnes, 1994; Fordyce and Muizon, 2001). A classification of Cetacea is listed in Table 15.1.

Odontoceti

Odontocetes can be traced back in the fossil record to the late Oligocene, where they are represented by a range of primitive forms, including *Agorophius* Cope (1895), *Patriocetus* Abel (1914), *Archaeodelphis* Allen (1921), *Xenorophus* Kellogg (1923), *Waipatia* Fordyce (1994), and *Simocetus* Fordyce (2002). An undescribed skull evidently carries the record of Odontoceti to or near the Eocene/Oligocene boundary (Barnes and Goedert, 2000). The first-named genera *Agorophius*, *Patriocetus*, and *Archaeodelphis* have been compared to Archaeoceti at one time or another, if not actually classified as archaeocetes. Skulls of *Agorophius* and *Simocetus* are shown in Fig. 15.2 to illustrate not only the anteroposterior foreshortening of the frontal region of the skull seen in mysticetes but also the distinct telescoping of the maxillae over the frontals characteristic of odontocetes. Morphological characteristics of Odontoceti are listed in Table 15.2. In spite of their more derived skulls, such primitive odontocetes as *Agorophius* and *Simocetus* retain teeth that are basically archaeocete in cusp arrangement (see, e.g., the teeth of *Simocetus* in Fordyce, 2002).

Mysticeti

Similarly, mysticetes can be traced back in the fossil record to the late Oligocene, where they are represented by a range of primitive forms, including *Cetotheriopsis* Brandt (1871), *Kekenodon* Hector (1881), *Mauicetus* Benham (1939), *Mammalodon* Pritchard (1939), *Aetiocetus* Emlong (1966), *Chonecetus* Russell (1968), *Ashorocetus* Barnes et al. (1995), *Micro-mysticetus* Sanders and Barnes (2002a), and *Eomysticetus* Sanders and Barnes (2002b). Here again, the first-named genera *Cetotheriopsis*, *Kekenodon*, *Mauicetus*, *Mammalodon*, *Aetiocetus*, and *Chonecetus* were compared to, or in several cases actually classified as, Archaeoceti at one time or another. *Phococetus* Gervais (1876) and *Llanocetus* Mitchell (1989) extend the range of mysticetes back into the early Oligocene or even possibly the latest Eocene (Fordyce, 2003). Skulls of *Aetiocetus* and *Eomysticetus* are shown in Fig. 15.2 to illustrate anteroposterior foreshortening of the intertemporal region of the skull compared to archaeocetes. Morphological characteristics of Mysticeti are listed in Table 15.3.

Archaeoceti

The best known archaeocetes can be divided into two distinct grades, a middle-to-late Eocene fully aquatic grade, classified as Basilosauridae, and a middle Eocene semiaquatic grade, classified as Protocetidae. Pakicetidae range back into the early Eocene and represent a slightly more primitive, but still poorly known grade (see below), whereas middle Eocene Ambulocetidae and Remingtonocetidae are divergently specialized and seemingly unrelated to later cetaceans. Early archaeocetes are known only from the eastern Tethys Sea, in what is now India and Pakistan, but later

Table 15.1 Outline classification of Cetacea at the family level

Suborder Archaeoceti	Superfamily Physeteroidea
Superfamily Protocetoidea	Physeteridae (sperm whales)
Pakicetidae	Kogiidae (pygmy sperm whales)
Protocetidae	Superfamily Ziphioidea
Ambulocetidae(?)	Ziphiidae (beaked whales)
Superfamily Remingtonocetoidea	Superfamily Platanistoidea
Remingtonocetidae	Squalodontidae
Superfamily Basilosauroidae	Squalodelphinidae
Basilosauridae	Waipatiidae
Suborder Mysticeti	Dalpiazinidae
Superfamily Aetiocetoidea	Platanistidae (river dolphins)
Aetiocetidae	Superfamily Eurhinodelphinoidea
Llanocetidae	Eurhinodelphinidae
Mammalodontidae	Eoplatanistidae
Superfamily Eomysticetoidea	Superfamily Iniioidea
Eomysticetidae	Iniidae (river dolphins)
Superfamily Balaenopteroidea	Pontoporiidae (river dolphins)
Cetotheriidae	Superfamily Lipotoidea
Balaenopteridae (fin whales)	Lipotidae (river dolphins)
Superfamily Eschrichtioidea	Superfamily Delphinoidea
Eschrichtiidae (gray whales)	Kentriodontidae
Superfamily Balaenoidea	Albireonidae
Neobalaenidae (pygmy right whales)	Delphinidae (dolphins)
Balaenidae (right whales)	Phocoenidae (porpoises)
Suborder Odontoceti	Monodontidae (white whales)
Superfamily Agorophioidea	Odobenocetopsidae
Agorophiidae	
Simocetidae	
Patriocetidae(?)	

Sources: Mysticeti follows Sanders and Barnes (2002b), Odontoceti follows Fordyce and Muizon (2001), with additions.

Notes: Common names are listed in parentheses for extant families. (?) indicates uncertainty of rank or placement.

Protocetidae and Basilosauridae are known from the eastern and western margins of the North Atlantic, and Basilosauridae are known from the South Pacific.

Basilosauridae include dorudontines, such as *Dorudon* Gibbes (1845), *Zygorhiza* True (1908), and *Saghacetus* Gingerich (1992), with normally proportioned vertebrae, and larger basilosaurines, such as *Basilosaurus* Harlan (1834) and *Basiloterus* Gingerich et al. (1997), with conspicuously inflated and elongated vertebrae. The best known basilosaurids are *Basilosaurus isis* (Gingerich et al., 1990) and *Dorudon atrox* (Uhen 1996, 2004), which are known from virtually complete skeletons. The skeleton of *Dorudon* is illustrated in Fig. 15.1A. Morphological characteristics of Basilosauridae are listed in Table 15.4.

Dorudon is the kind of generalized basilosaurid that might have given rise to later whales. It has multicusped cheek teeth that resemble those of primitive mysticetes and primitive odontocetes, and a well-developed fossa for the pterygoid sinus. Other salient characteristics of the skeleton are a vertebral formula (cervicals:thoracics:lumbar:sacrals:caudals) of 7:17:20:0:21, for a total of 65 vertebrae in the skeleton (Uhen 1996, 2004). Cervicals are short anteroposteriorly, neural spines on thoracics and lumbar are medium in length and robust, there is no sacrum, and the tail was evidently fluked (Uhen 1996, 2004). Forelimbs retain a mobile elbow joint, and the hindlimbs retain evidence

of *Basilosaurus*-like feet and toes. The hindlimbs are greatly reduced in size in relation to the rest of the skeleton, and the innominate did not contact the vertebral column, meaning that the hindlimbs could not have borne weight on land or have played any substantial role in locomotion.

The best known of the early middle Eocene protocetids are *Protocetus* Fraas (1904), *Rodhocetus* Gingerich et al. (1994), *Artiocetus* Gingerich et al. (2001a), and *Qaisracetus* Gingerich et al. (2001b), and the best known late middle Eocene protocetid is *Georgiacetus* Hulbert et al. (1998). Postcranial remains attributed to *Indocetus* by Gingerich et al. (1993) are now known to belong to *Remingtonocetus*. Skulls of *Artiocetus* and *Protocetus* are shown in Fig. 15.2 to illustrate their generalized mammalian form, with none of the anteroposterior foreshortening in the intertemporal region of the skull seen in mysticetes and odontocetes. Morphological characteristics of Protocetidae are listed in Table 15.5.

The skeleton of the early protocetid *Rodhocetus* is illustrated in Fig. 15.3B, based on the skull and axial skeleton of *Rodhocetus kasranii* (Gingerich et al., 1994) and fore- and hindlimbs of *R. balochistanensis* (Gingerich et al., 2001a). As a whole, the early protocetid skeleton retains more generalized mammalian proportions compared to those of later basilosaurids, mysticetes, and odontocetes. The vertebral formula is known from several individuals to be 7:13:6:4:x (the number of caudal vertebrae in the tail is not yet known).

Fig. 15.2. Comparison of skulls. Frontal bones are stippled. Note the foreshortening of frontals in mysticetes and the telescoping of maxillae over frontals in odontocetes. All skulls are shown in dorsal view, drawn to the same length (not to scale). (A) Early middle Eocene archaeocete *Artiocetus clavis*. Redrawn from Gingerich et al. (2001a). (B) Early middle Eocene archaeocete *Protocetus atavus*. Modified from Fordyce and Muizon (2001). (C) Late Oligocene mysticete *Aetiocetus cotylalveus*. Modified from Emlong (1966). (D) Late Oligocene mysticete *Eomysticetus whitmorei*. Modified from Sanders and Barnes (2002b). (E) Late Oligocene odontocete *Agorophius pygmaeus*. Modified from Whitmore and Sanders (1977) and Fordyce (1981). (F) Late Oligocene odontocete *Simocetus rayi*. Redrawn from Fordyce (2002).

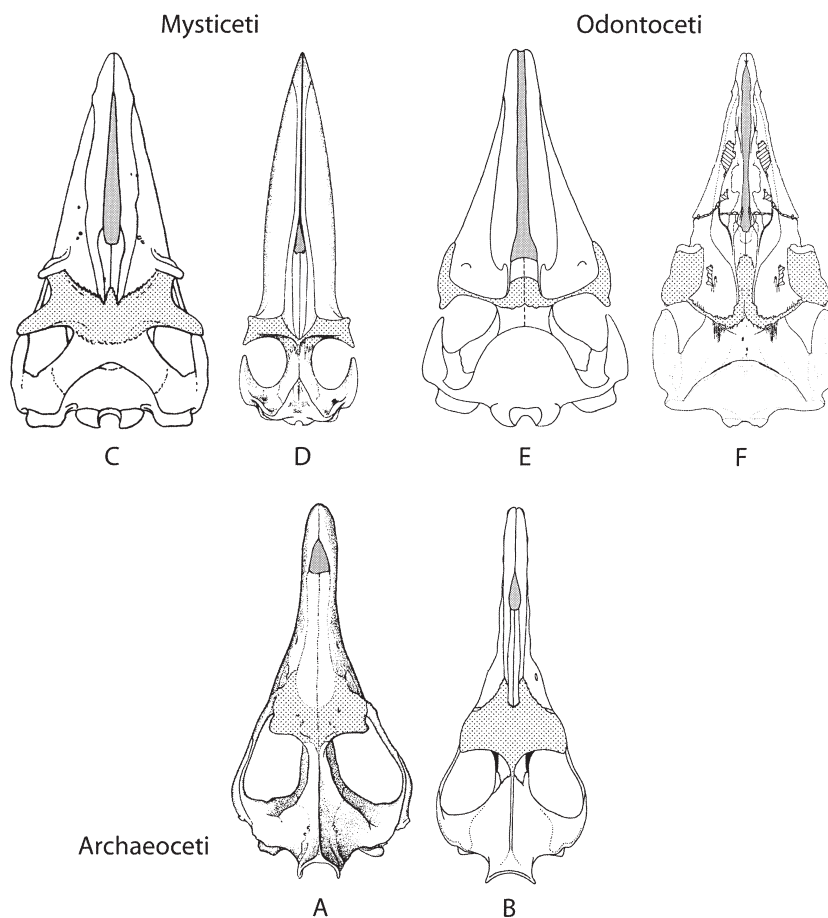


Table 15.2 Morphological characters of Oligocene-Recent Odontoceti as a group

Number	Character	Number	Character
1	Retention of heterodont dentition with some multicusped teeth (e.g., <i>Simocetus</i> ; primitive) to homodont dentition of simple conical teeth lacking accessory cusps (derived)	8	Dentaries relatively straight
2	Maxilla extends back over frontal, to or beyond orbit	9	Left and right sides of skull symmetrical in some taxa (primitive) to highly asymmetrical (derived)
3	Anteroposterior shortening of intertemporal region of skull (primitive) to shortened intertemporal region of skull with broad anteroposterior telescoping (derived)	10	Ability to echolocate inferred (primitive) to echolocation well developed (derived)
4	Dense tympanic bulla	11	Cervical vertebrae short (primitive) to highly compressed anteroposteriorly (derived)
5	Pterygoid sinus present	12	Immobile elbow articulation
6	Mandibular canal large	13	Sacrum lost entirely
7	Coronoid process retained on dentary (primitive) to coronoid process reduced (derived)	14	Innominate retained within body wall; femur and lower leg lacking
		15	Small-to-medium body size (primitive) to large body size (derived)

Source: Abstracted from Fordyce and Muizon (2001), with additions.

The neck is relatively long for a cetacean, and the anterior thoracic vertebrae retain high neural spines, like those of land mammals (e.g., *Elomeryx* in Fig. 15.3A). There are distinct anticlinal and diaphragmatic vertebrae in the posterior thoracic series. The centra of the sacrum are solidly co-ossified in some early protocetids and less so in others. The vertebrae at the base of the tail are robust, but neither the number of

caudals nor the length of the tail is known. The scapula is narrow, like that of land mammals. The humerus is relatively long, and bones of the forearm are relatively short. The manus retains five digits, of which the central three retain small, flattened, hooflike ungules (Gingerich et al., 2001a).

The hindlimb of *Rodhocetus* (Fig. 15.3B) has a large innominate articulating with the sacrum, but the ilium is short.

Table 15.3 Morphological characters of Oligocene-Recent Mysticeti as a group

Number	Character	Number	Character
1	Retention of multicusped teeth (e.g., <i>Aetiocetus</i> ; primitive) to filter-feeding with baleen (derived)	8	Coronoid process retained on dentary (primitive) to coronoid process on dentary reduced (derived)
2	Maxilla extends back under frontal, toward orbit	9	Dentaries relatively straight (primitive) to dentaries bowed (convex laterally; derived)
3	Palatal surface of maxilla flat (primitive), to palatal surface of maxilla flat and grooved for nutrient supply, to baleen (derived)	10	Cervical vertebrae short (primitive) to cervical vertebrae highly compressed anteroposteriorly (derived)
4	Anteroposterior shortening of intertemporal region of skull (primitive) to shortened intertemporal region of skull with conspicuous telescoping on midline (derived)	11	Immobile elbow articulation
5	Dense tympanic bulla	12	Sacrum lost entirely
6	Pterygoid sinus present	13	Innominate and femur retained within body wall
7	Mandibular canal large (primitive) to mandibular canal reduced (derived)	14	Small-to-medium body size (primitive) to medium-to-large body size (derived)

Source: Abstracted from Fordyce and Muizon (2001), with additions.

Table 15.4 Morphological characters of middle and late Eocene Basilosauridae as a group

Number	Character	Number	Character
1	Retention of heterodont dentition with multicusped cheek teeth	9	Coronoid process retained on dentary
2	Dental formula 3.1.4.2/3.1.4.3	10	Dentaries relatively straight
3	Maxilla-frontal contact largely in front orbit	11	Cervical vertebrae short anteroposteriorly
4	Long intertemporal region of skull; no telescoping	12	Mobile elbow articulation
5	Left and right sides of skull symmetrical	13	Sacrum lost entirely
6	Dense tympanic bulla	14	Innominate retained within body wall; femur, lower leg, and foot present
7	Pterygoid sinus present	15	Medium body size (primitive) to medium-to-large body size (derived)
8	Mandibular canal large		

Sources: Abstracted from Kellogg (1936), Luo and Gingerich (1999), and Uhen (1996, 2003), with additions.

Note: Based primarily on *Basilosaurus* and *Dorudon*.

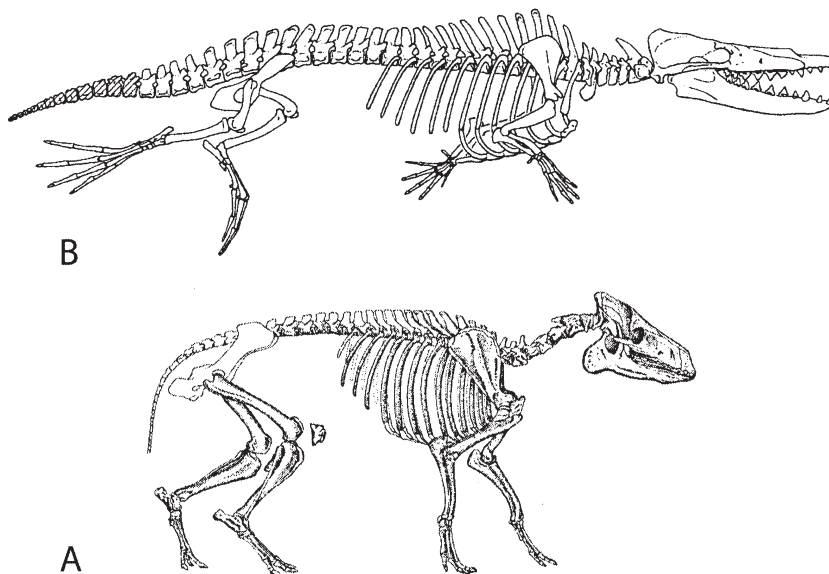
Table 15.5 Morphological characters of middle-late Eocene Protocetidae as a group

Number	Character	Number	Character
1	Retention of heterodont dentition with multicusped cheek teeth	11	Cervical vertebrae medium in length (primitive) to cervical vertebrae short anteroposteriorly (derived)
2	Dental formula 3.1.4.3/3.1.4.3	12	Mobile elbow articulation
3	Maxilla-frontal contact in front of orbit	13	Sacrum of four vertebrae, with anterior centra solidly fused (primitive) to sacrum reduced to a single centrum or lost entirely (derived)
4	Long intertemporal region of skull; no telescoping	14	Innominate articulates with sacrum; ilium short; lower leg and foot present (primitive) to innominate retained within body wall; ilium short; lower leg and foot present (?) (derived)
5	Left and right sides of skull symmetrical		
6	Dense tympanic bulla		
7	Pterygoid sinus absent (primitive) to anterior pterygoid sinus present (derived)		
8	Mandibular canal large		
9	Coronoid process retained on dentary	15.	Small-to-medium body size (primitive) to medium body size (derived)
10	Dentaries relatively straight		

Sources: Based primarily on *Rodhocetus* (Gingerich et al., 1994, 2001a), *Georgiacetus* (Hulbert, 1998; Hulbert et al., 1998), and *Eocetus* (Fraas, 1904; Uhen, 1999).

Note: (?) denotes a characteristic that has not been found in association with cranial or dental remains.

Fig. 15.3. Comparison of skeletons. (A) Early Oligocene anthracotheriid artiodactyl *Elomeryx armatus*. Redrawn from Scott (1894). (B) Early middle Eocene protocetid archaeocete *Rodhocetus balochistanensis* with an elongated skull, generalized mammalian vertebral formula with seven cervicals, 13 thoracics, six lumbar, and four sacral, shortened neck, retention of long neural spines on thoracic vertebrae, robust proximal caudal vertebrae (length of tail is not known), short forelimb (ulna and radius), short ilium relative to ischium, short femur, and elongated pes (see Fig. 15.4). From Gingerich et al. (2001a).



The femur is relatively short and robust, and the tibia and fibula are longer. The tarsus is known in *Artiocetus*, and the entire pes is known in *Rodhocetus*. The tarsal bones are interesting because of their general similarity to those of anthracotheriid artiodactyls. A comparison of the pes of *Rodhocetus* with that of the anthracothere *Elomeryx* is shown in Fig. 15.4. There are four notable points of resemblance: (1) the astragalus has a distal as well as a proximal trochlea, making it double-pulleyed; (2) the calcaneum has a prominent convex facet on its dorsal surface for articulation with the distal fibula; (3) the cuboid is distinctly stepped or notched to receive the distal process of the calcaneum; and (4) the entocuneiform is a relatively large, flat, platelike bone, with a small distal articular facet interpreted to indicate retention of metatarsal I. The first three tarsal traits are general artiodactyl characteristics (Gingerich et al., 2001a), but the fourth, conformation of the platelike entocuneiform, although possibly primitive, is a particular resemblance to anthracotheres. Scott (1894) described the entocuneiform of *Elomeryx* as resembling that of *Hippopotamus* (Scott, 1894: 485).

Comparison of the tarsus of *Rodhocetus* to that of *Elomeryx* shows many points of similarity, but proportions of the pes as a whole are very different in the two genera (Fig. 15.4). The metatarsals are longer and the proximal and medial phalanges are much longer in *Rodhocetus* than they are in *Elomeryx*. Both are drawn at the same calcaneum length in Fig. 15.4, and normalization to the same tarsus width would make these differences even more conspicuous.

Multivariate study of *Rodhocetus* and *Elomeryx* in a matrix of limb and trunk proportions for living semiaquatic mammals shows *Rodhocetus* to have been a desmanlike swimmer and *Elomeryx* to have been a more terrestrial, hippolike mammal (Gingerich, 2003b). More-aquatic semiaquatic mammals are distinguished from more-terrestrial semiaquatic mammals by the contrast between (1) long manual and pedal phalanges, combined with short femora and ilia in the former

(more aquatic), vs. (2) short manual and pedal phalanges, combined with long femora and ilia in the latter (more terrestrial). *Rodhocetus* has a more-aquatic suite of skeletal proportions, and *Elomeryx* has a more-terrestrial suite of proportions.

Pakicetid archaeocetes are known principally from cranial and dental specimens (Gingerich and Russell, 1981; Gingerich et al., 1983; Bajpai and Gingerich, 1998; Thewissen and Hussain, 1998; Thewissen et al., 2001). Some postcranial elements have been attributed to *Pakicetus*, including isolated vertebrae, a scapula, innominate, rare long bones and pieces of long bones, and astragali and calcanea (Gingerich, 1977; Thewissen et al., 1987, 2001). Some morphological characteristics of Pakicetidae are listed in Table 15.6. *Pakicetus* has generally been interpreted as a semiaquatic archaeocete (e.g., Gingerich et al., 1983; Thewissen and Hussain, 1993), but it has recently been reinterpreted as a “terrestrial mammal” with “running adaptations” that was “no more amphibious than a tapir” (Thewissen et al., 2001: 278). The presence of pointed anterior teeth in an elongated rostrum, dense auditory bullae, short cervical vertebrae, elongated caudal vertebrae, and an ilium no longer than the ischium all favor *Rodhocetus*-like semiaquatic habits for *Pakicetus* rather than terrestrial cursoriality. Definitive interpretation of *Pakicetus* will require associations of skeletal elements that have not yet been documented. The oldest pakicetid, early Eocene *Himalayacetus* Bajpai and Gingerich (1998), comes from marine strata, and it appears, as might have been expected, that the origin of whales goes hand-in-hand with aquatic adaptation.

ORIGIN OF CETACEA

Modern cetaceans, Mysticeti and Odontoceti, can be traced back in the fossil record to Oligocene times, when some genera in each group are seen to retain primitive characteristics,

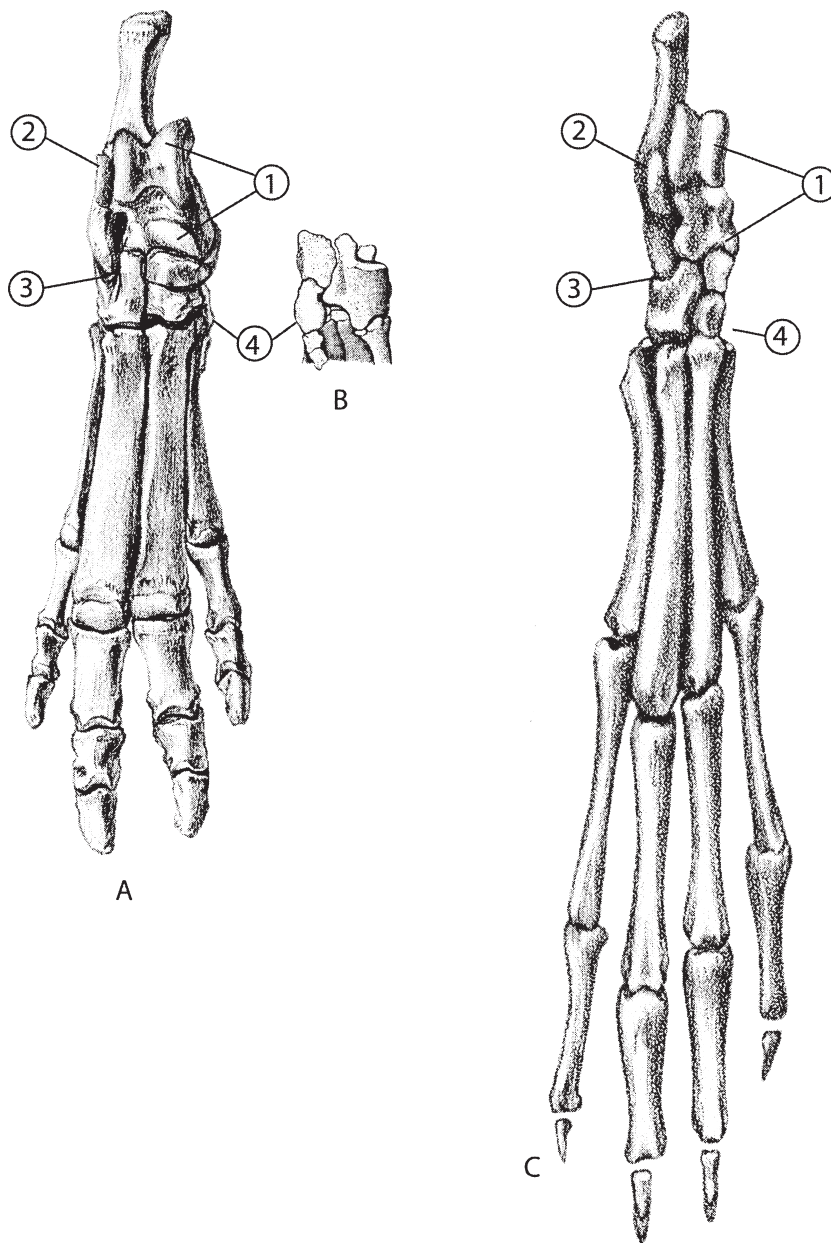


Fig. 15.4. Comparison of the pes. (A) Early Oligocene anthracotheriid artiodactyl *Elomeryx armatus*. Redrawn from Scott (1940). (B) Early Oligocene anthracotheriid artiodactyl *Elomeryx armatus*. From Scott (1894). (C) Early middle Eocene protocetid archaeocete *Rodhocetus balochistanensis*. From original specimen, drawn by B. Miljour. Both (A) and (C) are right feet, reduced to the same calcaneum length (52 and 54 mm, respectively; not to same scale). Characteristics of resemblance interpreted as synapomorphies of primitive Artiodactyla and early Cetacea are (1) double-pulley astragalus with a distal, as well as proximal, trochlea; (2) large convex fibular facet on the calcaneum; (3) stepped cuboid with distinct notch for calcaneum; and (4) large platelike entocuneiform with facet for metatarsal I. Note the much greater elongation of all metatarsals and proximal phalanges in the semiaquatic *Rodhocetus* relative to those of terrestrial *Elomeryx*.

Table 15.6 Morphological characters of middle-late Eocene Pakicetidae as a group

Number	Character	Number	Character
1	Retention of heterodont dentition with multicusped cheek teeth	9	Coronoid process retained on dentary
2	Dental formula 3.1.4.3/3.1.4.3	10	Dentaries relatively straight
3	Maxilla-frontal contact in front of orbit	11	Cervical vertebrae medium in length anteroposteriorly (?)
4	Long intertemporal region of skull; no telescoping	12	Mobile elbow articulation (?)
5	Left and right sides of skull symmetrical	13	Sacrum of four vertebrae, with anterior centra solidly fused (?)
6	Dense tympanic bulla	14	Innominate articulates with sacrum; ilium short; lower leg and foot present (?)
7	Pterygoid sinus absent	15	Small-to-medium body size
8	Mandibular canal small		

Sources: Based on Gingerich and Russell (1981), Gingerich et al. (1983), Thewissen and Hussain (1998), and Thewissen et al. (2001).

Notes: Based primarily on *Pakicetus*. (?) denotes a characteristic that has not been found in association with cranial or dental remains.

such as multicusped cheek teeth and a coronoid process on the dentary, linking them to late Eocene archaeocetes (Fordyce and Barnes, 1994; Fordyce and Muizon, 2001). Archaeoceti can, in turn, be traced back to middle Eocene times, when the protocetids *Artiocetus* and *Rodhocetus* are known from skulls and associated skeletons that retain such primitive characteristics as a double-pulley astragalus, convex fibular facet on the calcaneum, and a stepped cuboid, linking them to Artiodactyla among land mammals (Gingerich et al., 2001a).

Gingerich et al. (1990: 155) noted that a paraxonic pes in *Basilosaurus* “is consistent with serological evidence of relationship to Artiodactyla” but did not claim that this demonstrated such a relationship. Thewissen et al. (1998: 452) described an isolated “?pakicetid” astragalus and argued that the “absence of a trochleated astragalar head argues against . . . inclusion of Cetacea in Artiodactyla unless the flat head of the cetacean is interpreted as a secondary aquatic adaptation.” A year later, Thewissen and Madar (1999: 23, 28) described the same astragalus as “pakicetid” (without a query) and concluded that “new evidence of Eocene cetacean tarsal morphology is . . . consistent with inclusion of cetaceans in artiodactyls, if one assumes that the wide arc of rotation of the trochleated head was lost during the origin of Cetacea.” O’Leary and Geisler (1999) dismissed such claims about pakicetids, because the astragalus in question is fragmentary and was not associated with diagnostic cetacean material. After reading Gingerich et al. (2001a) in manuscript, Thewissen et al. (2001) acknowledged that the astragalus identified as “?pakicetid” and “pakicetid” was misidentified as cetacean, and Thewissen et al. (2001) then illustrated two new astragali as pakicetids that resemble astragali of *Artiocetus*, *Rodhocetus*, and artiodactyls. It is still true, as of this writing, that the only skeletons of archaeocetes that preserve associated ankle bones primitive enough and complete enough to demonstrate artiodactyl relationships are those of *Artiocetus* and *Rodhocetus* (Gingerich et al., 2001a). Now, knowing this association, it is possible to recognize that some astragali previously identified as representing artiodactyls are almost certainly from pakicetids (e.g., astragali described and illustrated as artiodactyls by Gingerich, 1977, and Thewissen et al. (1987, and those identified as *Pakicetus* and *Ichthyolestes* by Thewissen et al. (2001).

Fraas (1904) was clearly impressed by the upper molars of the early archaeocete *Protocetus*, when he removed Archaeoceti from Cetacea and included it as a subgroup of Creodonta (which, at the time, commonly included Mesonychidae). *Protocetus*, like *Pakicetus* and other primitive archaeocetes discovered later, retains much of the general mammalian tritubercular cusp pattern, with a large paracone and distinct remnants of a separate protocone and metacone positioned more or less like those of mesonychids. Van Valen (1966) transferred Mesonychidae to Condylarthra, and his inferences that archaeocetes evolved from mesonychid condylarths, while artiodactyls evolved from arctocyonid condylarths were both based on dental resemblances

of primitive archaeocetes and artiodactyls, respectively, to earlier condylarths. Dental resemblances of archaeocetes and mesonychids were analyzed in more detail by O’Leary (1998), who cautioned that similar morphology here does not translate directly into similar toothwear patterns. One interpretation might be that the dental similarities evolved convergently.

The tarsal characteristics of early archaeocetes (Fig. 15.4) are very informative of relationships because of the presence of detailed similarities in three different bones representing three different articulations of the ankle that are otherwise known in combination only in living and fossil artiodactyls (Schaeffer, 1947, 1948; Rose, 2001):

1. The bodies of the astragalus and calcaneum have large, hemicircular dorsal articular surfaces (paired with an intervening trochlea on the astragalus) for contact with the tibia and fibula, respectively, restricting movement at the upper ankle joint to a parasagittal plane;
2. The astragalus has a plantar surface dominated by a sustentacular facet elongated parallel to the long axis of the bone, whereas the calcaneum has a distal process guiding the astragalus laterally, so movement at the lower ankle joint is stable but permits both folding of the ankle and shortening and elongation of the tarsus, as a whole, as is characteristic of artiodactyls; and
3. The distal surface of the astragalus has a distinct trochlea for articulation with the navicular, whereas the calcaneum is elongated distally to contact and fit into a distinct step or notch in the cuboid—acting together, these stabilize the transverse tarsal joint and accommodate shortening and elongation at the lower ankle joint.

In mammals in general, this suite of characteristics is generally considered diagnostic of artiodactyls.

Rodhocetus and *Elomeryx* are illustrated here, but the evidence of relationship is based on more than this two-taxon comparison. The double-pulley astragalus, calcaneum with a convex fibular facet, and stepped cuboid are now known in all primitive pakicetid and protocetid archaeocetes for which such tarsal bones are known (Gingerich et al., 2001a; Thewissen et al., 2001; Zalmout et al., 2003), and these characteristics are known in all living and fossil artiodactyls for which the ankle is known (Schaeffer, 1947, 1948). It is not clear that pakicetids or protocetids retained a primitive mesonychid-like remnant of an astragalar canal (suggested by Rose, 2001), as the depressions present on different astragali are all shallow and blind, and these vary in position more like ligamentous pits.

Primitive fossil archaeocetes with diagnostically artiodactyl ankle characteristics corroborate other, much earlier, comparisons of soft anatomy, suggesting a relationship of Cetacea to Artiodactyla (Hunter, 1787; Flower, 1883)—an interpretation that could not really be taken seriously in the absence of a more complete fossil record exhibiting more continuity through time (e.g., Simpson, 1945; also Langer,

2001). Fossils linking early Cetacea to Artiodactyla also corroborate more recent biochemical and molecular evidence for the association of these two groups (Boyden and Gemeroy, 1950; Sarich, 1985, 1993; Graur and Higgins, 1994; Irwin and Arnason, 1994; Gatesy et al., 1996, 1999; Montgelard et al., 1997; Shimamura et al., 1997, 1999; Gatesy, 1998; Milinkovitch et al., 1998; Ursing and Arnason, 1998; Liu and Miyamoto, 1999; Nikaido et al., 1999; Arnason et al., 2000; Shedlock et al., 2000).

Many of the molecular studies just cited group not only Cetacea with Artiodactyla, but group Cetacea with Hippopotamidae within Artiodactyla. This may or may not be consistent with the fossil record. Early paleontological studies (e.g., Falconer and Cautley, 1847; Lydekker, 1884; Andrews, 1906; Colbert, 1935a,b; Scott, 1940; Simpson, 1945) linked Hippopotamidae to Anthracotheriidae. Anthracotheres are unusual among artiodactyls in retaining appendages with a five-fingered mesaxonic manus and some remnant of a fifth toe on the four-toed pes (Kowalevsky, 1873; Scott, 1894, 1940). These conformations of the hand and foot are similar to those of the primitive artiodactyl *Diacodexis* (Rose, 1982; Thewissen and Hussain, 1990) and to the protocetid archaeocete *Rodhocetus* (Gingerich et al., 2001a). If hippopotamids are derived from anthracotheres, then it appears plausible that hippopotamids may be the closest living relatives of whales. However, other paleontologists, including Matthew (1929), Pickford (1983, 1989), McKenna and Bell (1997), and Kron and Manning (1998), grouped hippopotamids with pigs and peccaries rather than anthracotheres. More work needs to be done to achieve a consensus on hippopotamid ancestry and evolution. As it stands, the record provides a permissive and plausible case for a relationship of Cetacea to hippopotamids within Artiodactyla through intermediate anthracotheriids.

The stratigraphic ranges and relationships of artiodactyls and whales are illustrated diagrammatically in the phylogeny of Fig. 15.5. The fossil record of Artiodactyla on the northern continents (Europe, Asia, and North America) extends to the beginning of the Eocene, and artiodactyls are one of the key index taxa marking the beginning of Eocene time (Sudre et al., 1983; Estravis and Russell, 1989; Gingerich, 1989, 2003a; Smith, 2000; Bowen et al., 2001, 2002). As an order, Cetacea has a similarly rich and continuous fossil record, extending from the present back into the early Eocene. Early Eocene archaeocetes are rare but are known from at least two sites: Kuthar Nala in Himachal Pradesh, India (Bajpai and Gingerich, 1998), and Panandhro in Gujarat, India (Bajpai and Thewissen, 2002). Pakicetids from the Kuldana Formation of Pakistan, previously thought to be early Eocene in age (e.g., Gingerich et al., 1983; Thewissen and Hussain, 1998), are more likely to come from the earliest middle Eocene (Gingerich, 2003c). Thus, there is a million-year-plus gap between the first appearance of artiodactyls in the fossil record at the beginning of the Eocene and the first appearance of the oldest known archaeocete cetaceans later in the early Eocene. However, in spite of this,

Cetacea is the last of the major orders of mammals to appear in the fossil record. Hence, we can expect that diversification of whales was probably one of the more profound and rapid adaptive radiations.

The fossil record indicates that Cetacea evolved in a Tethyan aquatic adaptive zone that was new for Artiodactyla and artiodactyl-like mammals. It is almost certain that the ancestor of the earliest archaeocetes would itself have been an artiodactyl, and it is therefore possible that Artiodactyla is a paraphyletic clade. This is true whether cetaceans evolved from an anthracotheriid or other stem lineage leading to hippopotamids, the plausible scenario favored by recent molecular studies, or from some other early and as yet unknown lineage. On a broader scale, the origin of Artiodactyla (or the greater Artiodactyla-Cetacea clade) is uncertain, but origin of this larger group from arctocyonid Condylarthra is suggested by the evidence at hand (Rose, 1996).

TIMING OF ORIGIN AND DIVERSIFICATION

Consideration of the timing of origin of a taxonomic or evolutionary group necessarily involves comparison of the likelihoods of alternative hypotheses (Strauss and Sadler, 1989). For any group that is reasonably well known in the fossil record, as cetaceans are, the group's stratigraphic or temporal range has been established. This is the range into which all known samples fall. It is possible to hypothesize a larger total range for a group than that observed, but any such new hypothesis has a quantifiable and smaller likelihood relative to the range now known, and the question then becomes whether the smaller relative likelihood of the hypothesized range lies within the bounds of credibility. To appreciate this, it is useful to construct a geometric model of the sample space. A uniform model was employed by Strauss and Sadler (1989), triangular and composite exponential models, respectively, were illustrated by Gingerich and Uhen (1994, 1998), and I develop a new composite exponential model here.

A temporal range can be thought of as a line of known length, symbolized by K (for "known"), or, equivalently, as the area under a unit uniform distribution of length K (and hence, area K). Any hypothesized extension can be represented by some additional length E (for "extension"). The known range K is established by a set of samples drawn from K , including N independently discovered samples (where $N = 2$, because a minimum of two independent records is required to establish a finite range). When a total range is hypothesized to be larger than the known range by some extension E , it is necessary to explain how, by chance, all samples drawn from a larger sample space $K + E$ (represented as a length, area, volume, or hypervolume) fall only in the known range K . This is easy to explain when the hypothesized extension is small and the number of independent

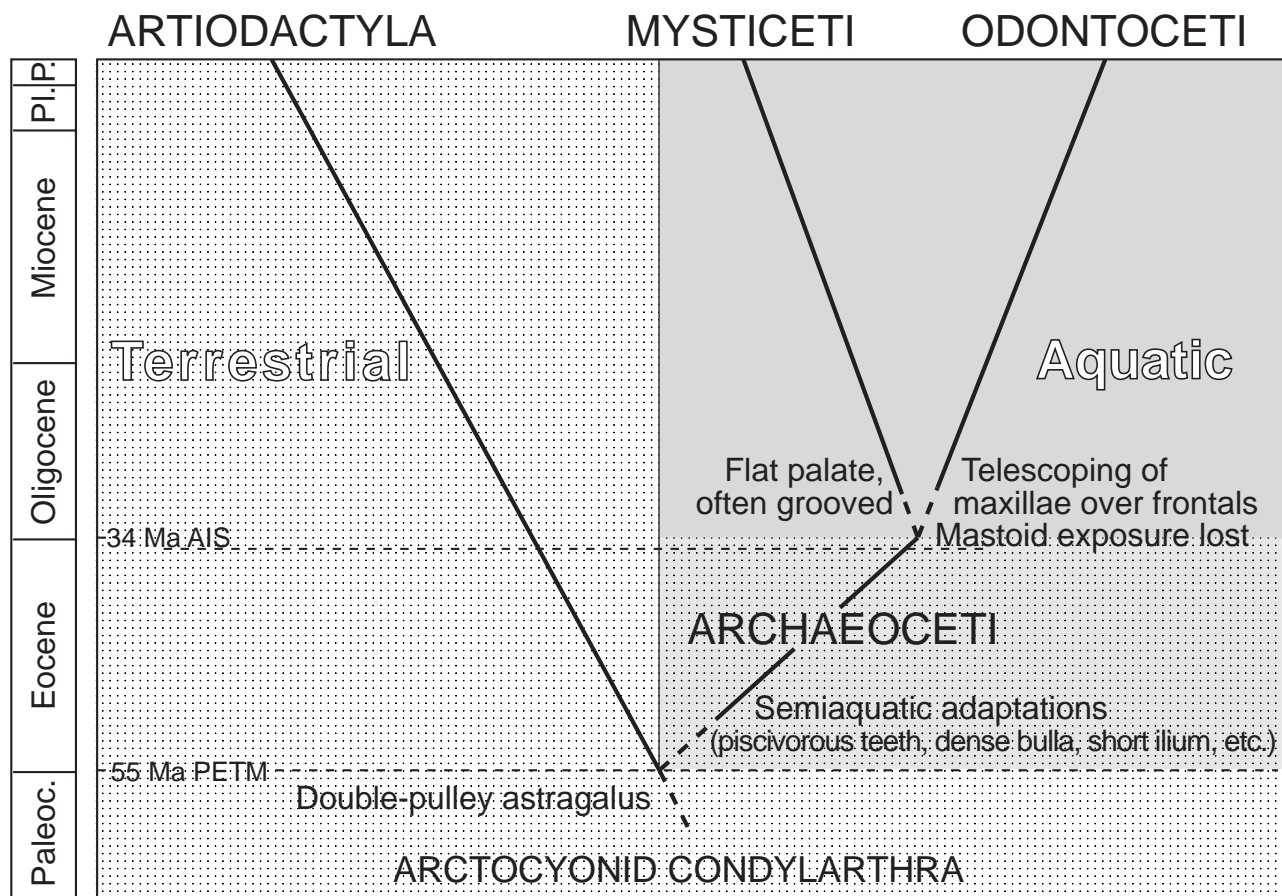


Fig. 15.5. Phylogeny of Archaeoceti, Mysticeti, and Odontoceti in the aquatic realm (darker shading), showing their hypothesized relationship to terrestrial Artiodactyla and arctocyonid Condylarthra. The common clade Artiodactyla-Cetacea is distinguished from earlier condylarths and other mammals by the presence of a double-pulley astragalus and other synapomorphies identified in Fig. 15.4. Archaeoceti and later Cetacea differ from Artiodactyla in sharing semiaquatic adaptations, including simple pointed anterior teeth, dense auditory bullae, and a short ilium. Mysticeti differ from other Cetacea in having a flat palate that is often grooved by nutrient canals associated with the presence of baleen. Odontoceti differ from other Cetacea in having the maxillae telescoped over the frontals. Note that semiaquatic-to-aquatic Archaeoceti appear in the fossil record following the Paleocene-Eocene thermal maximum at about 55 million years ago, and Mysticeti and Odontoceti appear in the fossil record with or following the reorganization of ocean circulation that led to Antarctic glaciation and the development of the Antarctic ice sheet (see Fig. 15.7). Removing the time axis, purely cladistic relationships in this figure could be expressed as: *Arctocyonia*-(*Artiodactyla*-(*Archaeoceti*-(*Mysticeti*-*Odontoceti*))). The phylogenetic history of early artiodactyls is poorly known, and it is possible that the branching order here was *Arctocyonia*-(*non-hippo Artiodactyla*-(*hippo Artiodactyla*-(*Archaeoceti*-(*Mysticeti*-*Odontoceti*))). (Extant taxa are italicized.) Abbreviations: AIS, Antarctic ice sheet; PETM, Paleocene-Eocene thermal maximum.

records is also small, because the associated probability is large. The probability that each independent sample falls in the smaller known range K when it was really drawn from a larger hypothesized range $K + E$ is the ratio $K / (K + E)$. This can be illustrated by a simple example: if K is assumed to be one unit in length, then one hypothesis might be that E is as large as K , meaning $E = K = 1$. Now the probability of a sample falling in K when it was drawn from $K + E$ is $K / (K + E) = 1 / 2 = 0.5$. Compare this to the probability of a sample falling in K when it was drawn from K , which is $K / K = 1$ (maximum likelihood). The relative likelihood is the ratio of probabilities of the two hypotheses, which is $0.5 / 1 = 0.5$, in this example. Hypotheses with such large relative likelihoods, or ratios of probabilities, are well within the bounds of reason.

In general, the relative likelihood L of a stratigraphic or temporal range extension depends on K , E , and N :

$$L = (K / [K + E])^{N-1}, \quad (\text{Equation 1})$$

which illustrates how the number of independent samples contributes to a calculation of relative likelihood. Any extension can be hypothesized, but the chance of it being reasonable or even credible, relative to the range we know, decreases as the size of the extension E becomes larger and decreases as the number of independent records N increases. A hypothesized extension can be one-tailed, meaning that E is an extension in one direction, or it can be two-tailed, meaning that E is partitioned to extend the range both forward and backward in time. Here we are only concerned with one-tailed range extensions backward in time.

An empirical example of such a comparison of likelihoods is shown graphically in Fig. 15.6A. The stratigraphic range of Archaeoceti is represented by the cross-hatched uniform distribution spanning much of the Eocene. The oldest archaeocete known to date is *Himalayacetus* (Bajpai and Gingerich, 1998) from low-latitude marine strata of the eastern Tethys, dated at about 53.5 million years ago (early

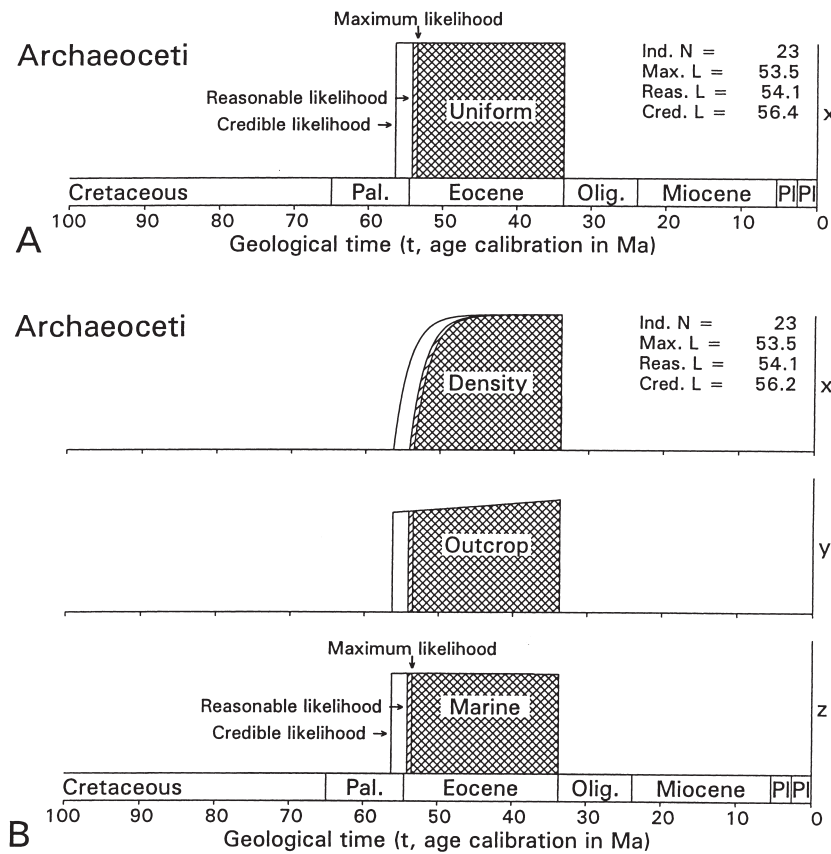


Fig. 15.6. Geometric models for understanding the relative likelihoods (L) of different times of origin of Archaeoceti. Abscissa in each model is time t . (A) Simple uniform x vs. t model, with ordinate x a unitary constant (Strauss and Sadler, 1989). (B) More complex and hence more representative x - y - z vs. t model, with increasing density of taxa or individuals during diversification on the x -axis, increasing outcrop area of sedimentary rocks in younger times (Blatt and Jones, 1975) on the y -axis, and changing marine area of the earth's surface (Smith et al., 1994) on the z -axis. Answers given by the two models are virtually identical, and it is not necessary to understand the complex model to appreciate the power of the statistical logic. Cross-hatched areas are a proportional representation of the difference on each axis over the known temporal range of the group. K is a simple $x \times t$ area in the uniform case (A), and an $x \times y \times z \times t$ four-dimensional hypervolume in the complex case (B). In this example, the number of independent records N is 23. Equation 1 is most easily solved iteratively, increasing E by small increments until reaching critical values of L .

Eocene). The youngest archeocetes are basilosaurids (e.g., *Saghacetus*; Gingerich, 1992) from low-latitude marine strata of the Tethys, extending near or to the end of the Eocene at 33.7 million years ago. Thus, archaeocetes have a known temporal range of about 19.8 million years. The number N of independent records can be estimated by counting the number of records coming from different geological formations, representing different temporal epochs in various geographic states or countries of the world. A survey of the Georef online database yields an estimate of $N = 23$ independent records. This N is conservative, because an ongoing compilation of published records now includes approximately twice as many independent records as are listed in the Georef database (see Gingerich and Uhen, 1998).

The relative likelihood of successive incremental extensions of the range of archaeocetes back in time can be explored by adding small increments to the first record at 53.5 million years ago. Each added increment represents a new hypothesis, with its own associated probability. We can stop adding increments when the likelihood ratio L of the total hypothesized range extension E reaches one-half of the maximum likelihood. This can be considered as a landmark of *reasonable likelihood*, because such an extension is half as likely as the known range, given what we know about the number and distribution of empirical records. Using a uniform model, our estimate of reasonable likelihood for the origin of archaeocetes is about 54.1 million years ago. Alternatively, we can continue adding increments until the

likelihood of the total hypothesized range extension E reaches 5% of the maximum likelihood. This can be considered a landmark of *credible likelihood*, because it is equivalent to the 95% confidence limit, in the sense that this or any greater hypothesized range extension is 5% or less likely compared to the known range. We ordinarily accept such a 95% confidence limit as marking the bounds of credibility. The maximum likelihood estimate for the time of origin of archaeocetes is about 53.5 million years ago, whereas the credible limit by this standard, based on the uniform distribution, is 56.4 million years ago.

It is possible to make the same calculations using a t : x : y : z four-dimensional hypervolume sample space to represent (1) the density of archaeocetes during their diversification (dimension x); (2) the declining availability of outcrop area for older sedimentary rocks (dimension y ; Blatt and Jones, 1975); and (3) the relative proportion of the earth's surface covered by oceans (dimension z ; Smith et al., 1994). This more complicated and hence more representative model, shown graphically in Fig. 15.6B, gives a slightly younger credible limit for the time of origin of archaeocetes (and cetaceans) of 56.2 million years ago (late Paleocene).

The oldest known mysticete is *Llanocetus* (Mitchell, 1989) from high-latitude marine strata of the Eocene/Oligocene boundary in Antarctica (Fordyce and Muizon, 2001). A survey of the Georef online database (Gingerich and Uhen, 1998: table 1) yields an estimate of $N = 34$ independent records of Mysticeti. This, like the survey of Archaeoceti

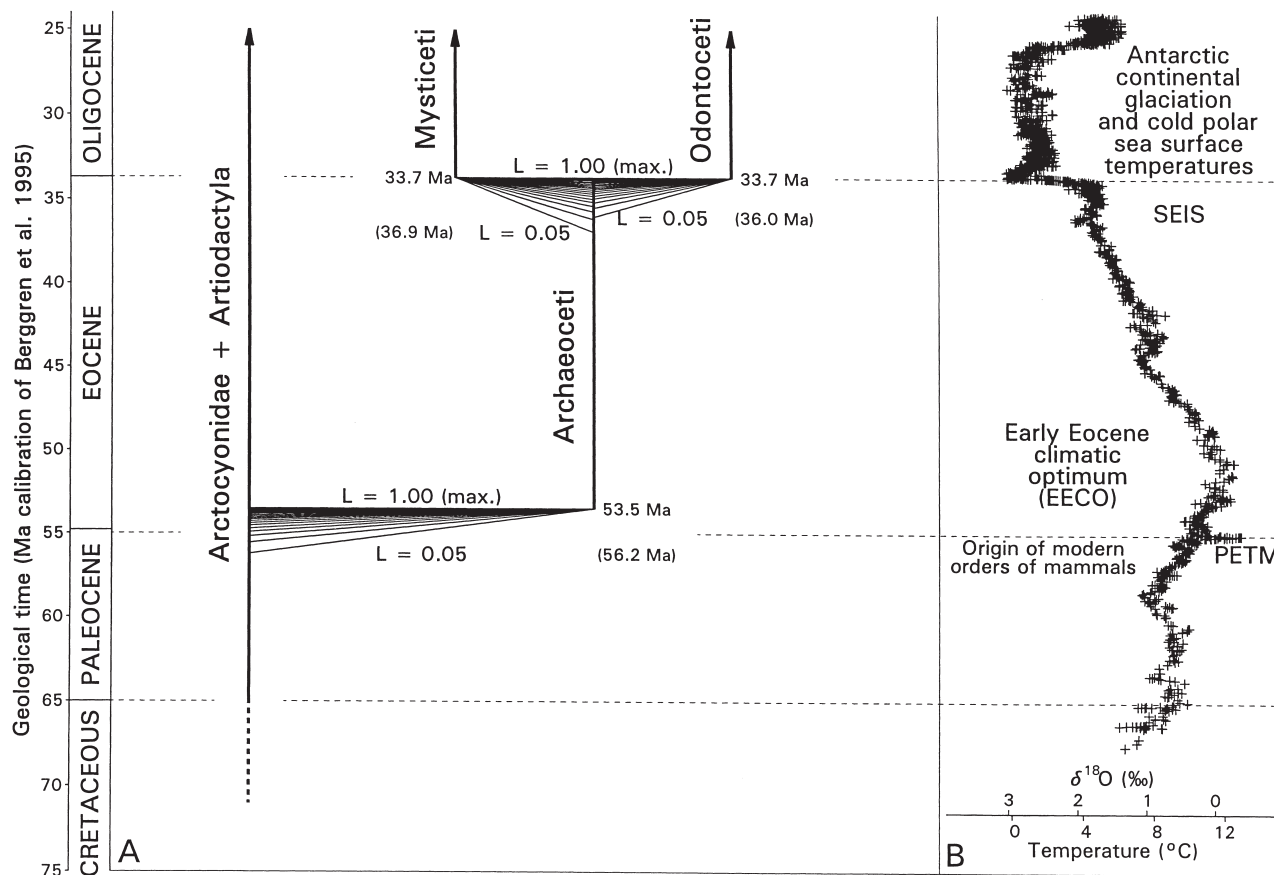


Fig. 15.7. Summary phylogeny of Artiodactyla and Cetacea in the context of environmental change in the world's oceans. (A) Range of credible times of origin of Archaeoceti, and credible times of divergence of Mysticeti and Odontoceti (calculated using the more complex model in Fig. 15.6). (B) Oxygen isotope record of temperature change preceding the onset of Antarctic ice sheets in the early Oligocene (data from Zachos et al., 2001). Note the coincidence of the origin of archaeocetes (and Cetacea) with the Paleocene-Eocene thermal maximum and the appearance of other modern orders at or near the Paleocene/Eocene boundary, and the divergence of Mysticeti and Odontoceti with the initiation of small ephemeral ice sheets in the southern oceans in the late Eocene, leading to full-scale Antarctic continental glaciation, cold polar sea-surface temperatures, and formation of cold bottom water in the oceans in the early Oligocene. Abbreviations: PETM, Paleocene-Eocene thermal maximum; SEIS, small ephemeral ice sheets.

described above, is undoubtedly conservative. Relative likelihoods calculated for Mysticeti, as in Fig. 15.6, yield a maximum likelihood estimate for the time of origin of about 33.7 million years ago and a credible limit of 37.0 million years ago.

The oldest known odontocete is an unnamed taxon from mid-latitude marine strata of the Eocene/Oligocene boundary in Washington state in western North America (Barnes and Goedert, 2000). A survey of the Georef online database (Gingerich and Uhen, 1998) gives an estimate of $N = 46$ independent records of Odontoceti; again, a conservative number. Relative likelihoods calculated for Odontoceti, as in Fig. 15.6, yield a maximum likelihood estimate for the time of origin of about 33.7 million years ago and a credible limit of 36.1 million years ago.

Ranges of possible divergence times for Archaeoceti from early Artiodactyla, Mysticeti from Archaeoceti, and Odontoceti from Archaeoceti are summarized graphically in Fig. 15.7A, based on these likelihood calculations. Credible estimates for the divergence of extant Cetacea from extant Artiodactyla are in the narrow range of 53.5–56.2 million

years ago, and credible estimates for the divergence of extant Odontoceti from Mysticeti within Cetacea lie in the restricted range of 33.7–36.9 million years ago.

This approach to estimating the time of origin requires that the whales included in a taxon be identifiable as such—in this case, identifiable to the suborders Archaeoceti, Mysticeti, or Odontoceti—but it does not require any assumption about the ancestral stock that gave rise to the taxon (i.e., the ancestral stock need not be known) or about the holophyly (non-paraphyly) of taxa in general. The alternative “ghost lineage” approach (O’Leary and Uhen, 1999; Gatesy and O’Leary, 2001) portrays all taxonomic groups as holophyletic, with sister taxa giving rise to one another only at the moment of their own conception. By this logic, the time of origin of a taxon of interest is not the time of its own origin, but at minimum, the time of appearance of its oldest sister taxon. Hence, the time of origin of Mysticeti and Odontoceti considered separately or the time of origin of the two considered together (“Neoceti”) would be, at a minimum, the time of appearance of Archaeoceti; the time of origin of Archaeoceti would be that of Artiodactyla; and the

time of origin of Artiodactyla would be that of Arctocyonidae plus Artiodactyla considered together.

All groups like Artiodactyla and Archaeoceti that were evolutionarily successful in the sense of giving rise to descendants outside the group itself are necessarily paraphyletic, and hence a ghost lineage approach to their times of origin is inappropriate. Furthermore, the limits of credible likelihood, calculated as in Fig. 15.6, show that many taxonomic groups (Mysticeti, Odontoceti [or Neoceti], and Archaeoceti included) cannot be as old as their putative sister taxa, and that paraphyly must be common.

ENVIRONMENTAL CONTEXT FOR THE ORIGIN OF CETACEA

The stratigraphic and temporal records summarized in Fig. 15.7A provide a framework for discussion of the origin and diversification of Cetacea in a broader paleoenvironmental context. Temperature is one of the most important components of paleoclimate and paleoenvironment. A deep-sea temperature proxy, the oxygen isotope record ($d^{18}O$) for the world's oceans, is shown on a matching time scale in Fig. 15.7B (Zachos et al., 2001). These oxygen isotope data provide constraints on the evolution of deep-sea temperatures and continental ice volumes. Deep-sea waters are derived primarily from the cooling and sinking of water in polar regions, so the deep-sea temperature record doubles as a time-averaged record of high-latitude sea-surface temperatures. Three events in this record are of particular interest:

1. The abrupt spike of climatic warming, known as the Paleocene-Eocene thermal maximum (PETM) right at the Paleocene/Eocene boundary (this is the event initially regarded as the late Paleocene thermal maximum [LPTM] by marine stratigraphers);
2. The early Eocene climatic optimum (EECO), when temperatures were the warmest known for the entire Cenozoic; and
3. The abrupt spike of cooling in the late Eocene, marking the first appearance of small, ephemeral ice sheets (SEIS) and leading to the first full-scale Antarctic continental glaciation in the early Oligocene, with cold polar sea-surface temperatures (Zachos et al., 2001).

Many of the modern orders of mammals, including Artiodactyla, appear abruptly in the fossil record at the PETM, a brief 80,000- to 200,000-year interval of abrupt global warming that coincides with the Paleocene/Eocene boundary (this is not really a coincidence, of course, because the epochs of the geological time scale generally reflect such substantial differences in faunas and floras). There is a 1.0- to 1.5-million-year lag in the appearance of archaeocetes, but the Paleocene/Eocene boundary at 55.0 million years ago lies within the range of credible estimates for the time of origin of whales. Thus, Cetacea, like other orders, probably originated directly or indirectly in response to global

warming during the PETM. Warm climates during the EECO would have facilitated adaptation to the marine realm; such conditions probably prevailed on the margins of the relatively warm, low-latitude Tethys Sea (where *Himalayacetus* and all later pakicetid fossils are found).

SEIS, the late Eocene cooling event, occurred at about the earliest credible time of origin of both Mysticeti and Odontoceti, anticipating the onset of Antarctic glaciation and cold polar sea-surface temperatures in the early Oligocene, when it appears that both mysticetes and odontocetes were already present in middle-to-high latitude waters. The result of SEIS was a reorganization of ocean circulation, with formation of cold bottom water and enhanced nutrient-rich upwelling (reviewed in Fordyce, 1980, 1989). These changes may well have affected life at high latitudes more than they did life in more equatorial areas; hence, it is not unreasonable to expect some temporal overlap of archaic and modern whales, even if they did not overlap geographically. It appears doubtful that Archaeoceti survived the abrupt ocean cooling recorded at the Eocene/Oligocene boundary. The great number of different kinds of both mysticetes and odontocetes present in the late Oligocene provides evidence that these modern groups continued to diversify during early Oligocene glaciation, although the fossil record is poor during this interval.

The origin of Cetacea and their diversification are both correlated in time with important environmental changes in the sea and on land. The environment changed abruptly at both the Paleocene/Eocene and Eocene/Oligocene boundaries, and there was a substantial pulse of resulting evolutionary turnover at or near both epoch boundaries. This is consistent with the "turnover pulse" hypothesis that environmental change drives evolution, as articulated by Vrba (1985). Whales illustrate how evolution is both stimulated and channeled by the physical environment.

RETROSPECTIVE

It is encouraging to see how much has been learned about whale evolution from the fossil record in the past sixty years, and we can thank George Gaylord Simpson for articulating so clearly how little was known in 1945. There are now remarkable "annectent types" connecting Artiodactyla to Archaeoceti and linking Archaeoceti to Mysticeti and Odontoceti. There is general agreement on a unified phylogeny of whales, with support from both paleontology and molecular biology. And finally, the appearance of successive grades of structure can be tied explicitly to environmental changes on land and in the sea. Simpson would write very differently today.

SUMMARY

Cetaceans are interesting from an evolutionary point of view, because they were able to colonize a new aquatic adaptive

zone markedly different from that of their terrestrial ancestors. Two suborders, Odontoceti and Mysticeti, are living today. Odontocetes can be traced back in the fossil record almost to the Eocene/Oligocene epoch boundary, and mysticetes can be traced back to the early Oligocene and possibly, to the latest Eocene. When they first appear in the fossil record, both modern groups resemble archaic whales, or Archaeoceti, in the form of their teeth and other characteristics. Archeocetes can be traced back from fully aquatic forms in the middle and late Eocene to amphibious, semi-aquatic forms in the early and middle Eocene. Among early archaeocetes, *Artiocetus* and *Rodhocetus* are particularly important, because they preserve ankle bones, (calcaneum, astragalus, and cuboid) in direct association with protocetid skulls and skeletons. The ankle bones are diagnostically artiodactyl in their form both as individual bones and in their articulation as a unit. Cetacea is very closely related to Artiodactyla, and the common ancestor of the two would almost certainly be considered a generalized artiodactyl if it were known. Derivation from an early anthracothere-like artiodactyl is a distinct possibility, in which case, a sister-group relationship of Cetacea to hippos within Artiodactyla, suggested by molecular comparisons of living animals, is also plausible in terms of the fossil record. The known fossil record of archaeocetes indicates a time of origin of Cetacea in the range of 53.5–56.2 million years ago (late part of the late Paleocene to the early part of the early Eocene). This interval includes the PETM event of global climate change, and it is likely that Cetacea originated in concert with other mammalian orders as part of the Paleocene-Eocene transition in earth history.

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