The Origin(s) of Whales

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Abstract

Whales are first found in the fossil record approximately 52.5 million years ago (Mya) during the early Eocene in Indo-Pakistan. Our knowledge of early and middle Eocene whales has increased dramatically during the past three decades to the point where hypotheses of whale origins can be supported with a great deal of evidence from paleontology, anatomy, stratigraphy, and molecular biology. Fossils also provide preserved evidence of behavior and habitats, allowing the reconstruction of the modes of life of these semiaquatic animals during their transition from land to sea. Modern whales originated from ancient whales at or near the Eocene/Oligocene boundary, approximately 33.7 Mya. During the Oligocene, ancient whales coexisted with early baleen whales and early toothed whales. By the end of the Miocene, most modern families had originated, and most archaic forms had gone extinct. Whale diversity peaked in the late middle Miocene and fell thereafter toward the Recent, yielding our depauperate modern whale fauna.

INTRODUCTION

Whales represent one of the most aberrant forms of mammals to have evolved in their long history, in terms of both morphology and ecology. The earliest mammals that show some of the morphological hallmarks of whales lived in Indo-Pakistan approximately 52.5 million years ago (Mya). These earliest whales were primarily terrestrial animals, with some adaptations for feeding in the water (Uhen 2007a), hearing in the water (Gingerich & Russell 1981, Luo & Gingerich 1999), and walking in the water (Madar 2007).

Whales also represent a recent iteration of the pattern of reinvasion of the aquatic environment by tetrapods (Uhen 2007a). Many different tetrapod groups have returned to the aquatic environment at different times in Earth's history. These groups include, but are not restricted to, placodonts approximately 245 Mya, ichthyosaurs approximately 245 Mya (Shikama et al. 1978), turtles approximately 220 Mya (Li et al. 2008), plesiosaurs from 199 Mya (O'Keefe 2001), mosasaurs from 99 Mya (Polcyn et al. 1999), penguins from 62 Mya (Slack et al. 2006), sirenians from 49 Mya (Domning 2001, Savage et al. 1994), pinnipeds from 28 Mya (Berta 1991), and aquatic sloths from 8 Mya (de Muizon et al. 2003). In addition, these tetrapod groups include the many partially aquatic vertebrates that exist today and undoubtedly existed in the past, as well as undiscovered extinct fossil aquatic tetrapods. Whales, along with their unrelated herbivorous counterparts the sirenians, are the only known fully aquatic mammals. No other mammalian groups have completely abandoned the terrestrial environment. Interestingly, both Cetacea and Sirenia appear to have originated at approximately the same time in the Eocene; they followed similar patterns of change in their trunks and limbs but different patterns of change in their heads and dentitions.

WHAT IS A WHALE?

Before discussing the origins of the mammalian order Cetacea, it is critical to clarify what is meant by the term. Different groups of researchers use completely different sets of data to analyze this problem, and have also used completely different (but overlapping) concepts for Cetacea at the same time. Although this point has been made before (Gingerich & Uhen 1998), it is very much worth repeating.

When molecular biologists discuss the origin of Cetacea, they mean the origin of living cetaceans, or crown group Cetacea (see **Figure 1**). This crown group includes the two living clades the Mysticeti and Odontoceti, usually referred to as suborders (see Living Clades sidebar). Crown group Cetacea has also been termed Autoceta (Geisler & Sanders 2003, Haeckel 1866) or Neoceti (Fordyce 2008, Fordyce & de Muizon 2001).

When paleontologists discuss Cetacea, they usually include a host of additional forms often grouped in the paraphyletic suborder Archaeoceti. These wholly extinct taxa form the stem to

LIVING CLADES

Mysticeti is the clade of living baleen whales and its corresponding stem taxa, exclusive of archaeocetes. All mysticetes today have baleen and lack teeth as adults, but many stem mysticetes had teeth and at least some potentially had both teeth and baleen. Neoceti is the clade of living whales and its corresponding stem taxa, exclusive of archaeocetes; it includes Mysticeti plus Odontoceti. Odontoceti is the clade of living toothed whales and its corresponding stem taxa, exclusive of archaeocetes. All living and fossil odontocetes have the bony hallmarks associated with echolocation. Pelagiceti is the clade of cetaceans that are fully aquatic; it includes Neoceti plus Basilosauridae.
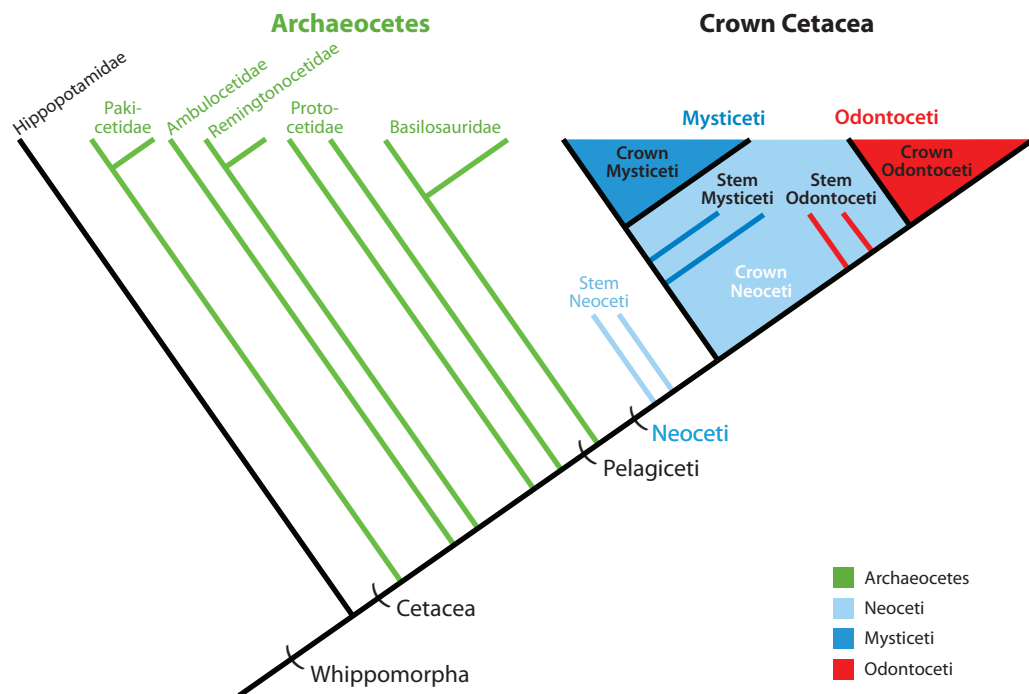
Figure 1

Cetacean phylogeny schematic. Note that the molecular origin dates for Cetacea are all dates for the clade identified as crown Cetacea (also known as crown Neoceti). Paleontological dates for the time of origin of Cetacea apply to the base of the paraphyletic archaeocetes. The family Hippopotamidae is shown as the living sister taxon of cetaceans, although additional fossil taxa may also be involved in the origin of Cetacea. Relationships among families of archaeocetes are represented as currently understood, many of which are likely to be paraphyletic.

crown group Cetacea, so they have also been referred to as stem Cetacea (Fordyce 2008). A great deal of evidence discovered in recent decades demonstrates that Odontoceti and Mysticeti are derived from the archaeocete family Basilosauridae (Fordyce 2008, Uhen 2004). The erection of the taxon Pelagiceti formally recognized this relationship, and it includes the last common ancestor of Basilosauridae and Neoceti along with all its descendants (Uhen 2008d). Herein the term archaeocete is used to identify members of Cetacea that are not part of Neoceti; Cetacea is used in the broader sense, to include archaeocetes and Neoceti (see Archaeocetes and Dentition sidebar).

This brings up one final important point about the use of higher taxon names in Cetacea. Originally, the term Cetacea was coined for living cetaceans (Brisson 1762). Later, the concept was expanded to include fossil forms such as *Basilosaurus* and other archaeocetes because of their close relationship to modern cetaceans (Fordyce 2008). In a similar fashion, the term Neoceti may be justifiably expanded to include forms that have the characteristics shared by both subclades of modern Cetacea. Thus, although they have yet to be described as such, there almost certainly exist fossil forms that could be included in the Neoceti that are neither Mysticeti nor Odontoceti. Readers should consult the Paleobiology Database (Uhen 2005) for a full current list of all taxa included in Cetacea, as well as a current taxonomy for the group.

The characteristics that delimit the base of the cetacean clade are all found in the head, whereas the dramatic transformation of the body and limbs comes at various later stages of the cetacean

Pelagiceti: the clade of cetaceans that are fully aquatic; includes Neoceti plus Basilosauridae

Archaeocete: a member of a paraphyletic group of basal whales that retain heterodont dentitions, diphyodonty, and skulls that lack the cranial specializations of either Mysticeti or Odontoceti

ARCHAEOCETES AND DENTITION

An archaeocete is a member of a paraphyletic group of basal whales that retain heterodont dentitions, diphyodonty, and skulls that lack the cranial specializations of either Mysticeti or Odontoceti. Heterodonty is the condition of having teeth differentiated into functional groups. Mammals primitively have four sets of teeth, from anterior to posterior: incisors, canines, premolars, and molars. Homodonty, on the other hand, is the condition of having undifferentiated teeth that are all similar to one another. Diphyodonty is the condition of erupting two sets of teeth: one deciduous and one permanent.

phylogeny (see Phylogenetic Terms sidebar). The earliest cetaceans display the following synapomorphies (evolutionary innovations) with other, later cetaceans (**Figure 2**): a pachyosteosclerotic bulla with a large involucrum and sigmoid process (Geisler & Luo 1998, Luo & Gingerich 1999, Thewissen et al. 2001); incisors and canines that are in line with the cheek teeth (Uhen 2007a); lower molars that lack trigonid and talonid basins, and a small or absent trigon basin of the upper molars (Thewissen et al. 2007); cheek teeth modified for shearing with reentrant grooves on the anterior margins of the molars (O'Leary & Uhen 1999); and a long, narrow postorbital/temporal region of the skull (Thewissen et al. 2007). Thewissen et al. (2007) also point out that the raoellid artiodactyl *Indohyus* possesses an enlarged tympanic bulla with an involucrum, which indicates an origin of this feature within a traditional artiodactyl rather than at the base of Cetacea. The origin of Cetacea in the broad sense as well as the origin of modern cetaceans (Neoceti) constitute important morphological and ecological transitions in the history of modern cetaceans, so both are covered here.

WHEN IS A WHALE?

The earliest whale known is *Himalayacetus*, dating back approximately 52.5 Mya from the Ypresian Subathu Formation of Kuthar Nala, India (Bajpai & Gingerich 1998). Fossils such as this provide a minimum age constraint on the time of origin of a group of organisms. This constraint does not, however, preclude estimation of the time or origin for such groups (Donoghue & Benton 2007). One way to make such an estimate is to use the genetic differences among living members of the group and to use a reasonable model of evolution of the genes under study. However, there are several problems with such an approach. First, constraining the estimated parameters of the evolution model is difficult because the genes may not evolve at a constant rate along all the branches (Pulquério & Nichols 2006), although this problem can be overcome with more complex models of molecular evolution (see Steeman et al. 2009 for an example with Cetacea).

PHYLOGENETIC TERMS

Synapomorphy is a shared, derived characteristic, whereas symplesiomorphy is a shared, primitive characteristic. Taxonomic groups are said to be paraphyletic if they exclude some of their descendants, and monophyletic if they include all of their descendants.

A crown group is a monophyletic group containing all living members of a clade and all the descendants of its common ancestor. A stem group, on the other hand, is a paraphyletic group that includes some or all of the synapomorphies of a clade but falls outside the crown group.
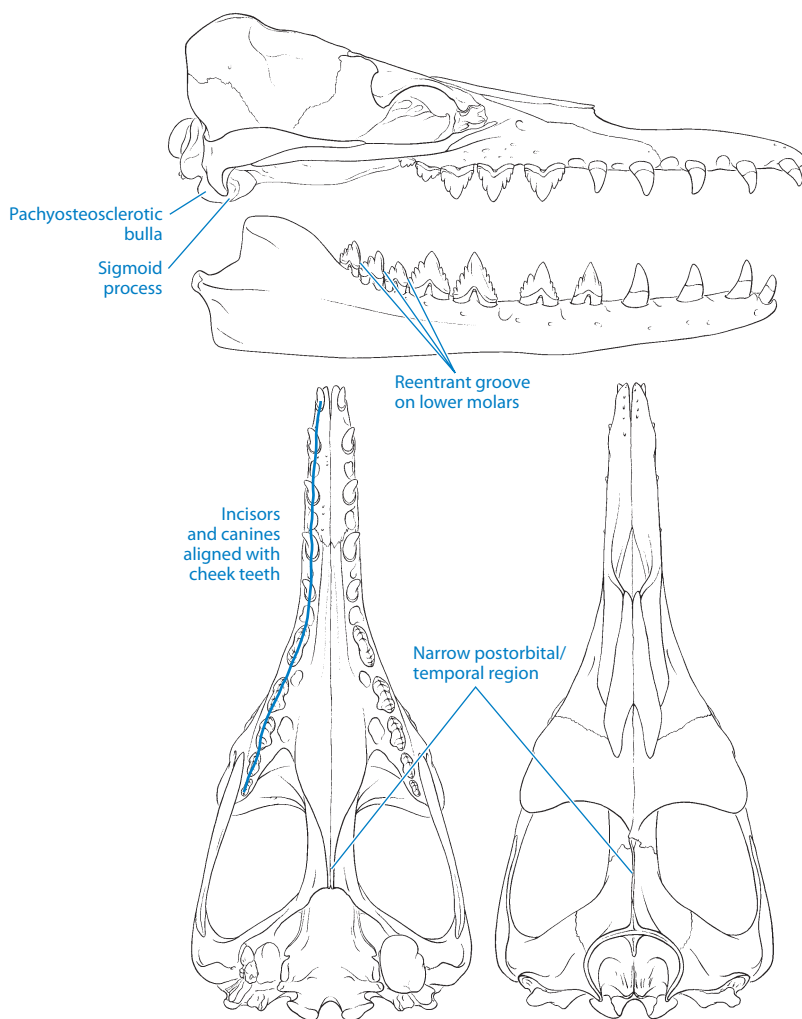
Figure 2

Cetacean synapomorphies (evolutionary innovations), shown on the skull and lower jaw of *Dorudon atrox* (Basilosauridae, 37 Mya) in lateral, dorsal, and ventral views. The earliest cetaceans display the following synapomorphies: a pachyosteosclerotic bulla with a large involucrum and sigmoid process (Geisler & Luo 1998, Luo & Gingerich 1999, Thewissen et al. 2001); incisors and canines in line with the cheek teeth (Uhen 2007a); cheek teeth modified for shearing with reentrant grooves on the anterior margins of the molars (Thewissen et al. 2007); and a long, narrow postorbital/temporal region of the skull (Thewissen et al. 2007). Some of these synapomorphies are lost in more derived cetaceans.

Second, one or more divergence times for branches in the tree must be known from the fossil record (Marshall 2008). The quality of these known divergence times is often poor, owing to poor choice of calibration nodes or poor research into the ages of the fossils at those nodes (Donoghue & Benton 2007). Third, molecular dating of divergence times will date the origin of crown clades only, excluding stem taxa known only as fossils.

Another approach to determining the time or origin of a group of organisms represented by fossils is to understand that the distribution of fossils over time has statistical properties that can be
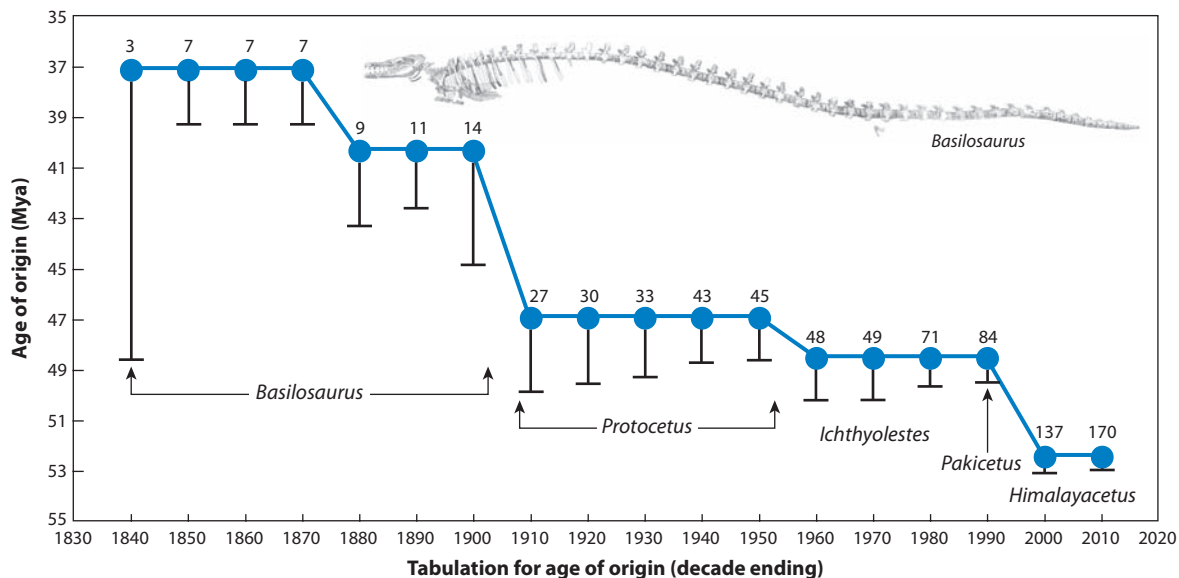
Figure 3

The age of the oldest Cetacean fossil, along with a measure of how much the oldest fossil age might underestimate the actual origin of whales over historical time. Blue circles represent the oldest fossil whales known at the time in the historical past. Ages for the fossils are based on modern interpretations of the stratigraphic record, not historical interpretations. The names of each of the genera that have marked the first occurrence of Cetacea in the fossil record are below each estimate. Jumps down in the blue age line indicate discoveries of older fossil whales. The black bars represent a 95% confidence interval on the time of origin of archaeocetes. Numbers above the circles indicate the number of fossil horizons used in each calculation. Note that the confidence interval is huge on the first decade (1840), and in most segments of the graph the confidence interval shrinks toward the next jump in the age line. 1900 is an exception to that pattern: The confidence interval expanded because a much younger fossil than the previously youngest archaeocete was discovered. Also note that the confidence interval gets very short toward the present. The 2010 figures are incomplete because the calculations were performed in May 2009.

understood and used to construct a confidence interval on the time of origin for the group (Marshall 1990, Strauss & Sadler 1989). In all cases, the single best point estimate for the group's time of origin is the date of the earliest fossil. Then, a confidence interval can be calculated based on the available fossil record for the group. These methods also make several assumptions about the fossil record (Marshall 1997), but in cases where the fossil record is good, they are relatively insensitive to these assumptions. Gingerich & Uhen (1998) calculated the time or origin for Archaeoceti (and thus Cetacea) to be 49.5 Mya with a 95% confidence interval added, yielding an estimate of 51.64 Mya. This is not quite as old as the soon thereafter described *Himalayacetus* at 52.5 Ma old (Bajpai & Gingerich 1998). This earlier age mostly arises from a new age estimate of the Subathu Formation (which had been included by Gingerich & Uhen), rather than any fault of the method. Calculating a new classic confidence interval (Strauss & Sadler 1989) for archaeocetes using 160 collections that include archaeocete fossils in the Paleobiology Database (Uhen 2005) gives a 95% confidence interval on the time of origin of the first cetaceans of 54 Mya. **Figure 3** shows how our understanding of the time of origin of Cetacea has evolved over time. The extension of the time of origin farther and farther into the past results from the discovery of new fossils as well as improved dating of the beds containing the oldest fossils. The contraction of the confidence interval results from the increased sampling of archaeocete whales, which decreases our uncertainty in the actual time of origin of the group. Recent molecular clock estimates on the time of the split between Hippopotamidae and Cetacea are at approximately 54.9 Mya (Bininda-Emonds et al. 2007).

ORIGIN OF CETACEA

Geography and Environment

The earliest cetacean fossils are known from the Indo-Pakistan region. This area represents the ancient Tethys Sea, which lay between Asia and India during the early stages of the collision between these two continental masses (Ali & Aitchison 2008). Although there is some debate about the precise age of *Pakicetus* and *Himalayacetus*, several other fossils of early Eocene (Ypresian) age have been noted. A dentary with a lower molar fragment from the Subathu Formation of Babbian Gala was originally described as *Ichthyolestes* (Kumar & Sahni 1985) and was later transferred to *Pakicetus* (Thewissen & Hussain 1998). Another tooth was described by Bajpai & Thewissen (2002) as a canine of Cetacea (*Kutchicetus minimus*?) from the Ypresian Panandhro lignite of Kachchh, India. All of these Ypresian specimens are extremely incomplete, but they do provide evidence of the presence of cetaceans in Indo-Pakistan in the late early Eocene.

The environments of deposition that produce Ypresian and early Lutetian whale fossils are quite varied. *Pakicetus*, long considered the oldest whale, was originally described from fluvial red beds of the Kuldana Formation, associated with other freshwater vertebrate and invertebrate fossils (Gingerich et al. 1983). This presented a neat evolutionary story of early whales evolving in freshwater continental habitats, and only later invading coastal marine followed by open marine environments. The story became more complicated with the discovery of *Himalayacetus* from the marine Subathu Formation (Bajpai & Gingerich 1998), which is earlier than the Kuldana Formation (Gingerich 2003b). The equally old whale specimen from the Panandhro lignite is said to be from "backswamp deposits," which are clearly freshwater in origin (Bajpai & Thewissen 2002). Other Lutetian deposits producing whales in Indo-Pakistan range from freshwater fluvial deposits to coastal and more open marine deposits.

Analysis of oxygen isotopes in dental enamel has shown that the earliest cetaceans, *Himalayacetus* and *Pakicetus*, inhabited freshwater environments, despite the fact that *Himalayacetus* was found in marine deposits (Clementz et al. 2006). This discovery indicates either that *Himalayacetus* lived in freshwater environments with only occasional forays into the marine environment, or that it lived in freshwater and its remains were transported into the marine environment after death. Other, later Lutetian whales such as *Babiacetus*, *Dalanistes*, and *Remingtonocetus* have dental oxygen isotope values that fall in the range of modern semiaquatic pinnipeds, indicating a similar way of life.

Early Hypotheses of Whale Origin

The position of the order Cetacea within Eutheria has been a matter of great debate for many years. Remington Kellogg (1936) explored a range of hypotheses on the origin of whales put forth by previous authors, from origins among the marine Reptilia (Steinmann 1907, among others) to origins among early mammals of various sorts (Albrecht 1886, Stromer 1903), including marsupials (Ameghino 1905), insectivores (Gregory 1910), and creodonts (Fraas 1904, Gregory 1910). Kellogg rejected all these affinities for whales because the hypotheses were based on convergences and/or symplesiomorphies (shared primitive characteristics). Other, earlier authors hypothesized that the Cetacea were related to various living groups of mammals such as the Pinnipedia (Thompson 1890), Edentata (Blainville 1816), Artiodactyla (Flower 1883a,b), Perissodactyla (Anthony 1926), and Sirenia (Gill 1873), all of which Kellogg rejected because they were also based on convergence or symplesiomorphies. In the end, Kellogg determined the following:

> The true place of origin and the ancestry of the Archaeoceti can not be demonstrated conclusively from the available evidence. The arguments advanced, however, for some insectivore-creodont like

Artiodactyla: the order of mammals that includes the even-toed ungulates (such as cows and hippos) and cetaceans (such as sperm whales and right whales)

precursor seem to have a more adequate basis than those adduced for an ungulate ancestry or for any other theory of descent.

He made this determination despite the fact that, earlier in the text, he dismissed the idea of an insectivore-creodont ancestry because it was based on shared primitive characteristics, and despite the fact that he failed to reject the evidence of a relationship with artiodactyls. The lack of enthusiasm for the artiodactyl hypothesis may have been because it was based on soft-tissue characters in modern artiodactyls and whales, rather than any osteological evidence that could be observed in archaeocetes.

Whales Are Artiodactyls

In 1883, William H. Flower delivered an insightful lecture at the Royal Institution titled "On Whales, Past and Present, and Their Probable Origin" (Flower 1883a,b). At the time of this lecture, not much was known of the fossil record of whales beyond the cranial and axial skeleton of *Zeuglodon* (now *Basilosaurus*). Despite this lack of fossil data, Flower listed several soft-tissue structures found in modern whales that were shared with artiodactyls. Among "[t]hese are the complex stomach, simple liver, respiratory organs, and especially the reproductive organs and structures relating to the development of the young." This idea did not find much purchase in the scientific community, and for many decades mammalogists had basically no idea how cetaceans fit in the phylogeny of mammals.

For instance, Simpson, in his 1945 comprehensive *Classification of Mammals*, describes a single cohort (Mutica) with only one order within it: the Cetacea. He stated:

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 is open to question and is indeed quite impossible to determine in any purely objective way.

This statement of abject uncertainty prompted Boyden & Gemeroy (1950) to undertake a series of immune reactivity tests in an attempt to determine which among the living orders of mammals are most closely related to Cetacea. They showed that Artiodactyla sera were the most reactive with sera of Cetacea, indicating a close relationship between the two orders and thus reviving Flower's earlier hypothesis.

Following this work, between 1950 and 1990, immunological techniques and amino acid comparisons were used in several additional studies, summarized by Gatesy (1998). Most of these studies (but certainly not all) suggested a relationship between Cetacea and Artiodactyla. After about 1990, most molecular studies were based directly on DNA sequences, and almost all the studies show a relationship between Cetacea and Artiodactyla. Some of them even indicate that the Cetacea were derived from within Artiodactyla, and as these studies became more refined, many began to show that Cetacea are most closely related to Hippopotamidae, nested well within Artiodactyla (Gatesy 1998, Gatesy et al. 1999, Milinkovitch et al. 1998, Montgelard et al. 2007). This led to the naming of the clade that includes Hippopotamidae + Cetacea: Whippomorpha (Waddell et al. 1999).

While molecular biologists were accumulating evidence for the artiodactyl origin hypothesis, paleontologists came up with a whale origin hypothesis of their own. Van Valen (1966) suggested that whales originated from the carnivorous condylarth family Mesonychidae based on shared characteristics of the teeth. This idea was supported by additional evidence from the dentitions
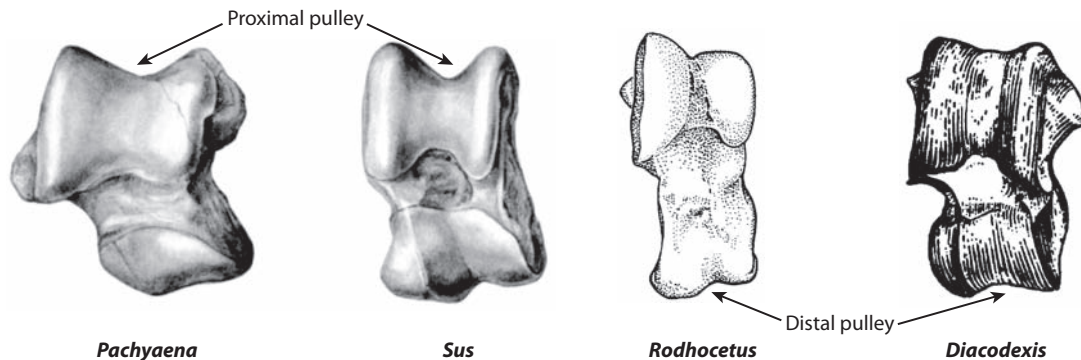
Figure 4

Ankle bones (astragali) of early ungulates, including whales and other artiodactyls: *Pachyaena*, a mesonychian (an extinct carnivorous ungulate); *Sus*, a modern pig; *Rodhocetus*, a middle Eocene protocetid whale; and *Diacodexis*, an Eocene artiodactyl. The double-pulleyed astragalus of *Rodhocetus* is very similar to that of *Diacodexis* and *Sus*, and significantly different from that of *Pachyaena* and other plesiomorphic Eocene mammals. This shared derived suite of characteristics indicates a close relationship among these species. *Pachyaena* after O'Leary & Rose (1995), copyright 1995 The Society of Vertebrate Paleontology, reprinted and distributed with permission from the Society of Vertebrate Paleontology. *Rodhocetus* after Gingerich et al. 2001a, reprinted with permission from AAAS. *Diacodexis* after Schaeffer (1947).

and skeletons of additional mesonychids and archaeocetes for many years (Gingerich et al. 1995, O'Leary & Uhen 1999, Zhou & Gingerich 1991).

Morphological and fossil evidence was neither supportive nor dismissive of the artiodactyl origin hypothesis for a long time because most of the morphological evidence for the monophyly of Artiodactyla is in the ankle region, which is completely missing in modern cetaceans and greatly reduced or absent in many fossil whales. All modern and fossil artiodactyls are characterized by the presence of a double-pulleyed astragalus (one of the ankle bones), along with a suite of other morphological features associated with the astragalus and the bones that surround the astragalus (**Figure 4**). No other mammal has anything like this suite of morphological features, and it delimits a monophyletic group that could be named either Artiodactyla (sensu lato, i.e., inclusive of Cetacea) or Cetartiodactyla (Waddell et al. 1999). The latter name has been applied to this group to distinguish it from the more traditionally delimited Artiodactyla. For many years the most distal element of the hind limb of any Eocene cetacean had been the femur of *Basilosaurus cetoides* (Lucas 1900), until a virtually complete hind limb of *Basilosaurus isis* from Egypt was described (Gingerich et al. 1990). Unfortunately, the astragalus was much too degenerated to derive any phylogenetically useful characteristics because the limbs were greatly reduced and no longer functional for locomotion.

In 2001, two publications provided dramatic evidence of the morphology of the hind limbs, including the astragali. Thewissen et al. (2001) reported on skeletons of basal cetaceans *Pakicetus* and *Ichthyolestes*, whose entire ankle complexes showed all the hallmarks of artiodactyls (**Figure 4**). That said, both were composite skeletons, assembled based on size and geochemical evidence from scattered bones within a bone bed, creating some doubt about the validity of the association of the hind limb material with the diagnostic cetacean cranial and dental material. At the same time, Gingerich et al. (2001a) published data on two slightly younger archaeocete whale skeletons, *Rodhocetus* and *Artiocetus*, that were found in complete articulation. These animals also had the artiodactyl ankle complex, along with large forefeet and hind feet. These and other similar animals are found exclusively in marine deposits and are thought to have lived like modern sea lions. The artiodactyl ankle morphology has been interpreted to be adaptive for running, so it is highly

unlikely that the morphology's presence in an aquatic mammal arose from convergence. Thus, with these new discoveries, the paleontological and molecular evidence came into alignment.

Thewissen et al. (2001) included a phylogenetic analysis of their new data on *Pakicetus* and other early whales, along with other artiodactyls, mesonychians, and condylarths. The analysis showed Cetacea as the basal sister taxon to all other Artiodactyla. This hypothesis of relationships allows for a monophyletic Cetartiodactyla, along with monophyletic Cetacea and Artiodactyla, but it is not consistent with molecular studies showing a relationship between Cetacea and Hippopotamidae. Geisler & Uhen (2003) showed that a combined analysis of morphological and molecular data supports the relationship between Cetacea and Hippopotamidae, placing whales well within Artiodactyla. Geisler & Uhen (2005) again supported the Whippomorpha hypothesis with an expanded set of morphological, molecular, and stratigraphic data.

Thewissen et al. (2007) described new fossils of the raoellid artiodactyl *Indohyus*, which have a direct bearing on the origin of whales. They note that *Indohyus* has a large tympanic bulla with a large involucrum, just like cetaceans. These authors modified the data matrix of Geisler & Uhen (2005) by adding new codings for *Indohyus*, *Khirtharia*, and several anthracotheres (possible hippo relatives), while dropping the codings for several modern animals along with the entire molecular data partition. Their result (**Figure 5b**) showed a clade that includes Cetacea + Raoellidae, which
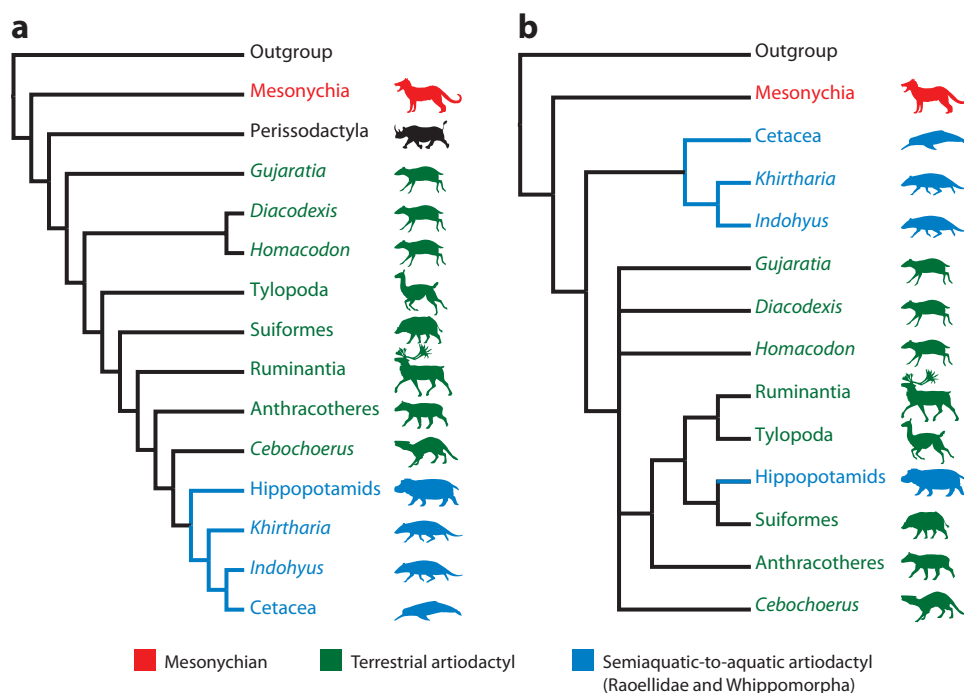

Figure 5

Comparison of recent phylogenetic analyses of whale origins. (*a*) Simplified tree from Geisler & Theodor (2009) when homoplastic characters (features that conflict with the favored topology) are down-weighted. (*b*) Simplified tree from Thewissen et al. (2007). Branches are colored (*blue*) to show when aquatic adaptations, such as bottom walking, are known to have evolved, although they may have evolved earlier. Note that in (*b*), molecular data was excluded from the analysis, with the result that hippopotamids show no close relationship with cetaceans. The tree in (*a*) is supported here. Reprinted by permission from Macmillan Publishers Ltd: *Nature* (Geisler & Theodor 2009), copyright 2009.

comprises the sister taxon to all other artiodactyls, including a suiform clade (pigs and hippos) (Thewissen et al. 2007). Geisler & Theodor (2009) demonstrated that inclusion of all the data from Geisler & Uhen (2005), along with the new character codings from Thewissen et al. (2007), shows a coherent grouping of Raoellidae + Hippopotamidae + Cetacea (**Figure 5a**). This hypothesis of relationships is accepted here because it is based on the most comprehensive data set (both molecular and morphologic data) and because it is consistent with Geisler & Uhen (2005), who also included stratigraphic data.

In contrast to the Whippomorpha hypothesis, O'Leary & Gatesy (2008) published a combined analysis of molecular and morphological data that places Mesonychia as the sister taxon to Cetacea; the next nearest sister taxon is a clade including hippopotamids, anthracotheres, raoellids, and other several other artiodactyls. The unusual feature of this hypothesis is that it requires a complete reversal of the double-pulleyed astragalus character complex at the origin of mesonychians, after it was acquired at a more basal node. This hypothesis is not supported here because it relies heavily on overly parsed dental characters and does not include stratigraphic information. In addition, this group recently published a new phylogenetic analysis that included additional data from *Indohyus* that also supports inclusion of Cetacea within Artiodactyla to the exclusion of Mesonychia (Spaulding et al. 2009).

THE EARLIEST WHALES

The earliest whales (Pakicetidae, Ambulocetidae, and Remingtonocetidae) are all known from the early and middle Eocene of Indo-Pakistan. None of these families has been found outside this area (**Figure 6**). Early cetaceans retain a heterodont dentition with a dental formula of 3.1.4.3/3.1.4.3 (Geisler et al. 2005, Gingerich & Russell 1990). All these families are thought to have been semiaquatic to some extent, able to move around on land as well as in the water. All these groups, plus a wide range of animals in the family Protocetidae, were present in the middle Eocene, indicating a rapid diversification in form and species numbers during the transition from terrestrial to aquatic environments.
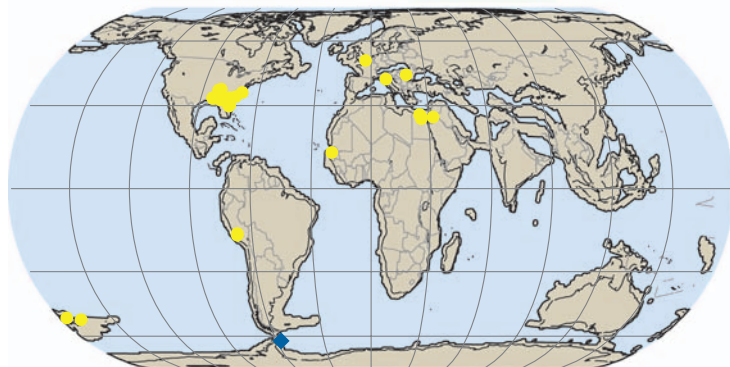
Pakicetidae

The earliest whales are in the family Pakicetidae. This family includes the genera *Pakicetus*, *Ichthyolestes*, and *Nalacetus*. Pakicetids are known from the latest early to early middle Eocene of Indo-Pakistan. They retain many apomorphic features found in terrestrial artiodactyls (**Figure 7**), including a small mandibular foramen and mandibular canal (Bajpai & Gingerich 1998); long cervical vertebrae; long, gracile limbs with a double-pulleyed astragalus in the ankle; long metapodials (Thewissen et al. 2001); and four solidly fused sacral vertebrae (Thewissen et al. 2001).

The cetacean features of pakicetids include a pachyosteosclerotic bulla bearing an involucrum and sigmoid process (Gingerich & Russell 1981); cheek teeth modified for shearing with reentrant grooves on the anterior margins of the molars (O'Leary & Uhen 1999); lower molars that lack trigonid and talonid basins and upper molars that have a very small trigon basin (Thewissen et al. 2007); an anterior dentition (composed of incisors and canines) that is in line with the cheek teeth (Uhen 2007a); and a long, narrow postorbital/temporal region of the skull (Thewissen et al. 2007).

The postcranial features of pakicetids were interpreted by the original authors to indicate that pakicetids were highly terrestrial animals, "no more amphibious than a tapir" (Thewissen et al. 2001). Gingerich (2003a) disagreed, suggesting that the similarities between the postcrania of *Pakicetus* and the later *Rodhocetus* indicate that *Pakicetus* was much more aquatic than a tapir. Madar (2007), looking at both the morphology of the postcrania and the microstructural anatomy

**Early
Oligocene
31 Mya**

**Late
Eocene
36 Mya**
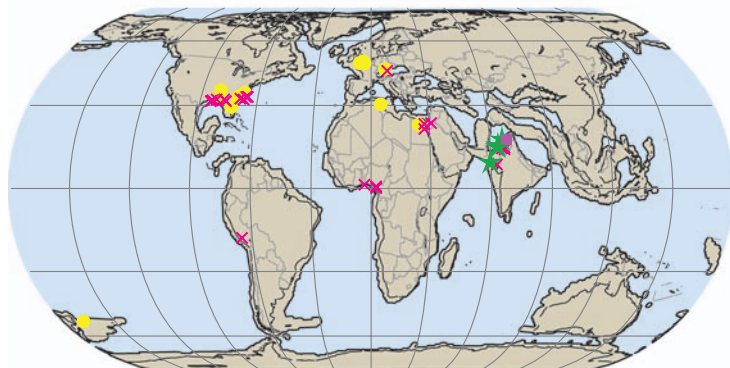
**Middle
Eocene
42 Mya**

**Early
Eocene
52 Mya**

◆ Odontoceti
◆ Mysticeti
● Basilosauridae
✕ Protocetidae
★ Remingtonocetidae
■ Ambulocetidae
▲ Pakicetidae

Plotting software © 2002-2006 J. Alroy
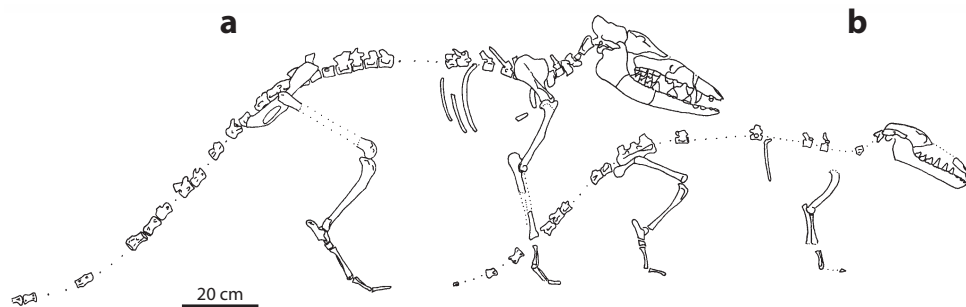
a

b

20 cm

Figure 7

Postcranial osteology of pakicetids. Skeletons of the pakicetid cetaceans *Pakicetus* (*a*) and *Ichthyolestes* (*b*). Reconstructions are based on fossils from H-GSP Locality 62 in Pakistan and are of Eocene age. Reprinted by permission from Macmillan Publishers Ltd: *Nature* (Thewissen et al. 2001), copyright 2001.

of the bones, concluded that pakicetids were undoubtedly tied to an aquatic lifestyle that included bottom walking, paddling, and undulatory swimming. Madar concluded that sustained running was an unlikely locomotor mode largely because of the increased density of the skeleton compared with terrestrial relatives.

Interpretations of pakicetid feeding are equally broad. *Pakicetus* was originally interpreted to have fed on fish found in highly productive epicontinental seas (Gingerich & Russell 1990, Gingerich et al. 1983), despite the observations that the remains of pakicetids described at that time were all known from freshwater deposits (Gingerich et al. 1983). Isotopic evidence later showed that pakicetids spent a great deal of their time in freshwater, most likely drinking freshwater and eating freshwater prey (Clementz et al. 2006, Roe et al. 1998).

Ambulocetidae

The family Ambulocetidae, known from the early middle Eocene of Indo-Pakistan, includes three genera: *Ambulocetus*, *Gandakasia*, and *Himalayacetus*. Whereas *Gandakasia* and *Himalayace-tus* are known only from teeth and mandibular fragments (Bajpai & Gingerich 1998, Dehm & Oettingen-Spielberg 1958, Gingerich & Russell 1990, Williams 1998), the holotype of *Ambulocetus* (**Figure 8a**) includes the skull, teeth, and much of the skeleton (Thewissen et al. 1994, 1996).

Ambulocetus was found in marginal marine deposits and determined to be larger than earlier pakicetids (Thewissen et al. 1994). *Ambulocetus* presents a somewhat enlarged mandibular foramen and canal, but not as large as those seen in protocetids. *Ambulocetus* has a sacrum (where the hip joins the backbone) consisting of four fused vertebrae, like that of *Pakicetus* (Madar et al. 2002). The morphology of the axial and appendicular skeleton indicates that *Ambulocetus* walked on land

←——————————————————————————————————————

Figure 6

Cetacean fossils from the early Eocene to the early Oligocene. Maps were generated from the Paleobiology Database (Uhen 2005). Note that cetaceans (family Pakicetidae) originate during the late early Eocene in Indo-Pakistan. Very soon afterward, in the middle Eocene, whales diversify and become represented by five families: Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae. By the end of the middle Eocene, whales spread across Africa, Europe, North America, and even South America and New Zealand. By the late Eocene all families have gone extinct, except the Basilosauridae. Whereas there are no basilosaurid fossils reported from the early Oligocene, there are some known from the late Oligocene of New Zealand. The earliest mysticete, *Llanocetus*, is known from the latest Eocene of Seymour Island, Antarctica.
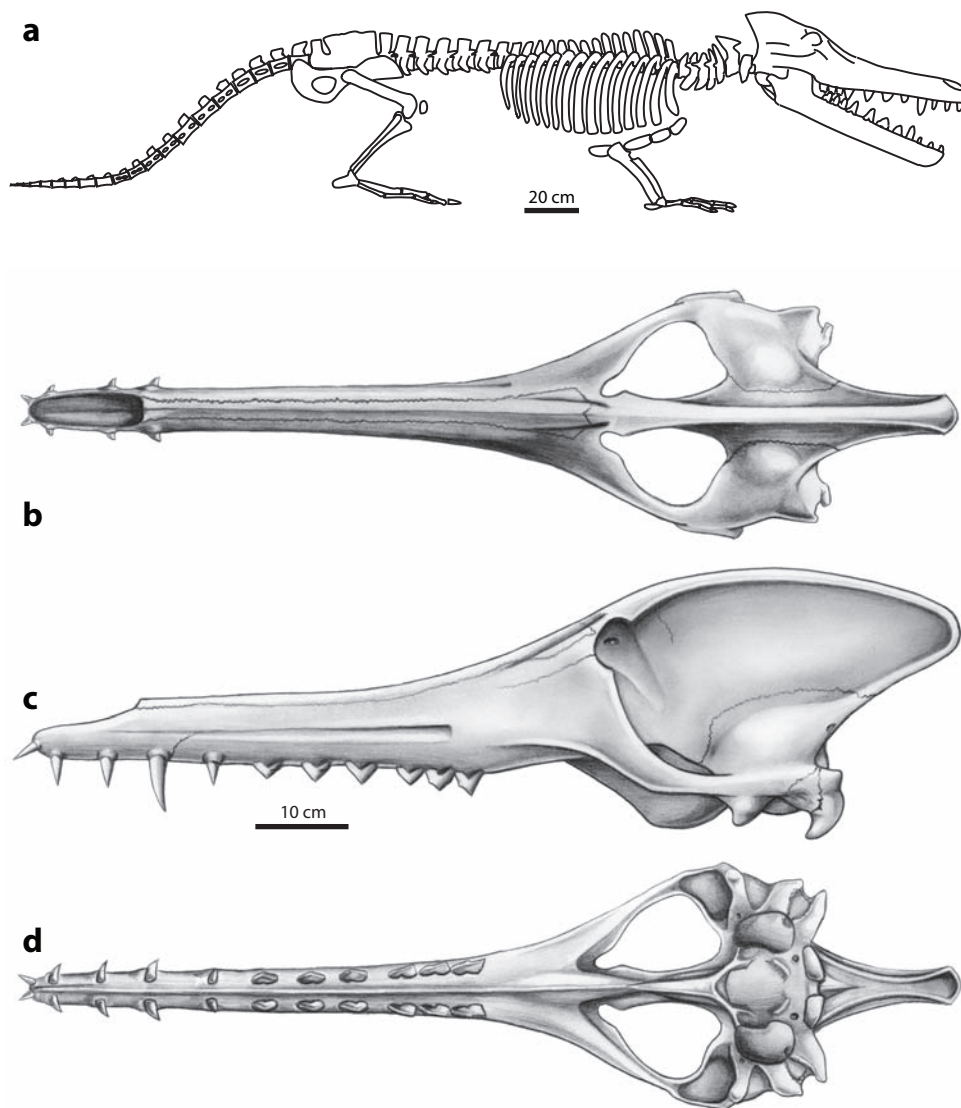
Figure 8

Ambulocetidae and Remingtonocetidae. *Ambulocetus* skeleton in lateral view (*a*). *Andrewsiphius kutchensis* skull in dorsal (*b*), lateral (*c*), and ventral (*d*) views. Note the great elongation of the skull, particularly the rostrum. (*a*) reprinted from the Thewissen Lab Web site (**http://www.neoucom.edu/DEPTS/ANAT/Thewissen/ whale_origins/index.html**); (*b*)–(*d*) used with permission from the *Journal of Paleontology*.

and also swam using pelvic paddling and undulation (Madar et al. 2002, Thewissen et al. 1996). Isotopic evidence suggests that both *Ambulocetus* and *Gandakasia* ate primarily terrestrial prey (Roe et al. 1998). *Himalayacetus* has a combination of low Δ^{18}O and high Δ^{13}C values, indicating that it consumed freshwater but that it had a marine diet, which suggests that *Himalayacetus* foraged in a marine environment but returned to freshwater to drink (Clementz et al. 2006). This finding, along with the placement of the orbits high on the skull, has suggested that *Ambulocetus* may have lain in

wait in shallow water, perhaps at the mouths of rivers, lunging out at terrestrial prey—analogous to the hunting process of crocodilians (Thewissen et al. 1996).

Remingtonocetidae

The family Remingtonocetidae is known from the middle Eocene of Indo-Pakistan. These early whales are characterized by long bodies with relatively short limbs, and long skulls with long mandibles fused as far back as the cheek teeth. The name of this family is derived from the genus *Remingtonocetus*, which was named after the renowned paleocetologist Remington Kellogg. The family includes five genera: *Andrewsiphius*, *Attockicetus*, *Dalanistes*, *Kutchicetus*, and *Remingtonocetus*.

Their long, low bodies and elongate rostra and mandibles make remingtonocetids even more like mammalian crocodiles than *Ambulocetus* (**Figure 8b**) (Thewissen & Bajpai 2009). Like pakicetids and ambulocetids, remingtonocetids have four fused sacral vertebrae (Gingerich et al. 1995). Their limbs, pelvic girdles, and axial skeleton indicate that they could walk on land as well as swim in the water (Bajpai & Thewissen 2000, Gingerich et al. 1995, Thewissen & Hussain 2000). Both sedimentological (Gingerich et al. 1995) and isotopic evidence (Clementz et al. 2006) support an amphibious but fully marine nearshore habitat for remingtonocetids. Isotopic evidence also supports a marine diet, at least for *Dalanistes* (Clementz et al. 2006), but other remingtonocetids need to be tested to see if this is consistent for the entire family. However, this testing is difficult because well-preserved teeth have proven to be rare for remingtonocetids (Thewissen & Bajpai 2001).

DERIVED SEMIAQUATIC WHALES

Protocetidae

The family Protocetidae currently includes 16 genera grouped into 3 subfamilies: Protocetinae, Makaracetinae, and Georgiacetinae (Gingerich et al. 2005). Protocetidae originated in Indo-Pakistan during the early middle Eocene, where they rapidly diversified and spread across North Africa (Andrews 1920, Fraas 1904), Europe (Uhen & Berndt 2008), North America (Geisler et al. 2005; Hulbert et al. 1998; Uhen 1998b, 1999), and western South America (Uhen et al. 2008). Protocetids retain a heterodont dentition with a dental formula of 3.1.4.3/3.1.4.3, and their cheek teeth generally lack accessory denticles (**Figure 9**). *Georgiacetus* is an exception to this generalization in that it presents incipient accessory denticles on the cheek teeth (Hulbert et al. 1998). Protocetids also have greatly enlarged mandibular foramina and mandibular canals when compared with pakicetids and typical terrestrial mammals (Bajpai & Gingerich 1998, Gingerich et al. 1994).

All protocetids have been found in coastal marine deposits. Also, all protocetids for which hind limbs are known have large innominata (pelvic bones) and femora, indicating that they could walk on land as well as swim in the water, except perhaps *Eocetus* and *Georgiacetus*. No protocetids are known to have had posterior caudal (tail) vertebrae that bear any evidence of flukes, although posterior caudal vertebrae are rare.

Protocetids display a broad spectrum of morphologies in the sacrum (hip region). Some protocetids retain sacra that include four vertebrae. In *Maiacetus*, the first three vertebrae are fused and the fourth is free (Gingerich et al. 2009). In *Rodhocetus*, all four vertebrae are unfused (Gingerich et al. 1994). *Qaisracetus* retains four sacral vertebrae: the first two are solidly fused, the third is joined to the second by the pleurapophyses, and the fourth is free (Gingerich et al. 2001b). The sacrum of *Gaviacetus* consists of two unfused sacral vertebrae (Gingerich et al. 1995). *Natchitochia*
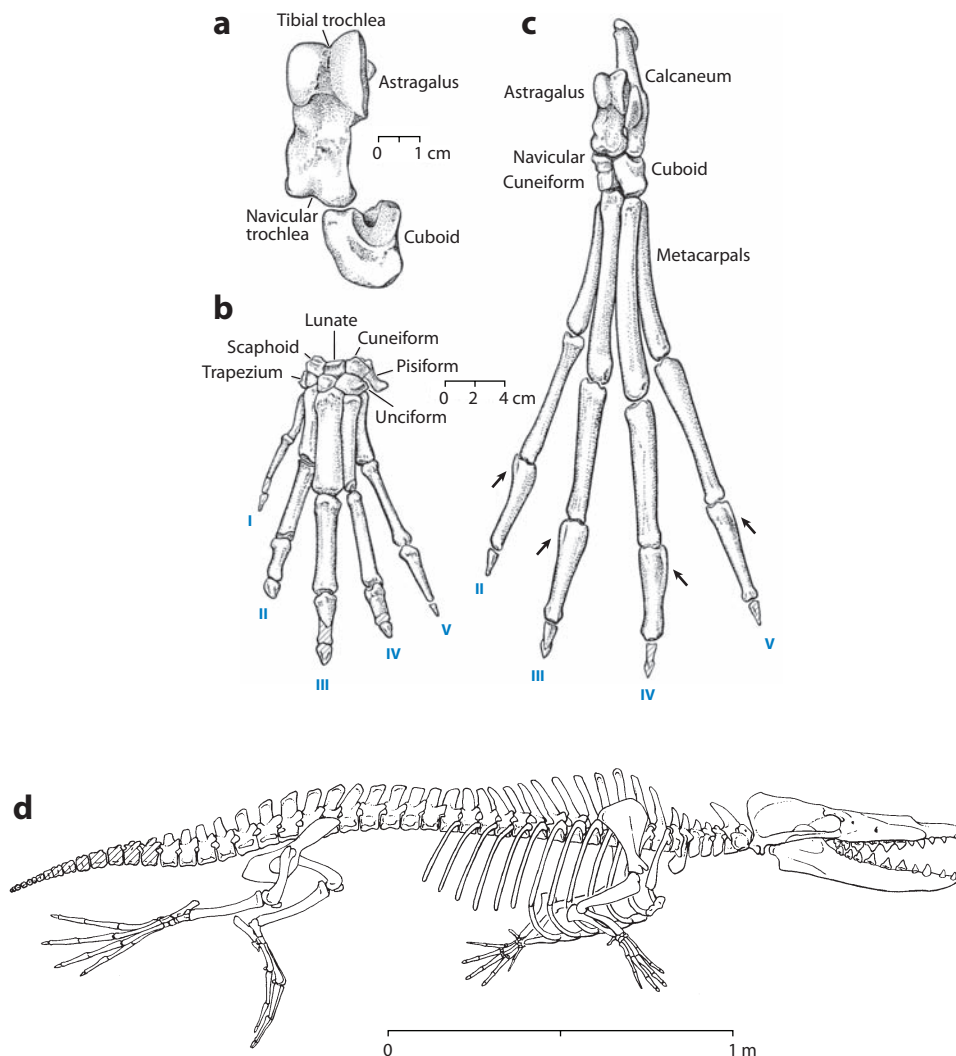
a Tibial trochlea / Astragalus / 0 1 cm / Navicular trochlea / Cuboid

c Astragalus / Calcaneum / Navicular / Cuboid / Cuneiform / Metacarpals / 0 2 4 cm / II III IV V

b Lunate / Scaphoid / Cuneiform / Trapezium / Pisiform / Unciform / I II III IV V

d 0 1 m

Figure 9

Protocetidae: *Rodhocetus*. Right astragalus and cuboid (ankle bones) (*a*) of *Artiocetus clavis*, GSP-UM 3458. Left manus (hand) (*b*) and left pes (foot) (*c*) of *Rodhocetus balochistanensis*, GSP-UM 3485 (pes reversed from right side), in anterior view. Elements with oblique hatching were not recovered. Note the well-developed navicular trochlea on the head of the astragalus, characteristic of artiodactyls. The manus bore nail-like hooves on digits II and IV, flanked by more gracile lateral toes that lacked hooves. The pes bears four long toes, flanges of bone on the medial or lateral bases of the middle phalanges (*arrows*) providing leverage for opening the feet to maximum breadth during extension, and narrowly pointed ungules (distal phalanges preserved on digits II and III). Illustration: Bonnie Miljour. (*d*) Composite restoration of the skeleton of a paddling *R. kasrani* with the limbs scaled up from *R. balochistanensis*, the scapula restored from *A. clavis*, and the proximal humerus restored from other protocetids. Terminal vertebrae of the tail (*hatched*) are conjectural. Illustration: Doug Boyer. Caption after Gingerich et al. (2001a). Figures from Gingerich et al. (2001a). Reprinted with permission from AAAS.

(Uhen 1998b) and *Protocetus* (Fraas 1904) each bear a single sacral vertebra. *Georgiacetus* has large innominata that apparently lacked a bony connection to the axial skeleton (Hulbert 1998). Despite this lack of a bony connection to the innominata or to one another, the four vertebrae of *Georgiacetus* were described as sacral by Hulbert (1998). Whereas these are homologous with sacral vertebrae of earlier whales, they functioned as part of the anterior region of the tail.

Forelimb material for protocetids is somewhat rare. The type specimen of *Artiocetus clavis* includes a rudimentary clavicle and scapula, along with a distal radius and ulna (Gingerich et al. 2001a); the two known specimens of *Maiacetus* include virtually complete forelimb material (Gingerich et al. 2009); a scapula is known from *Eocetus* (Uhen 2001); and parts of forelimb including distal humerus, radius, and ulna, along with virtually complete carpus and manus, are known for *Rodhocetus* (Gingerich et al. 2001a). The scapulae from *Artiocetus* and *Maiacetus* are narrower than those of *Eocetus* and later basilosaurids and modern whales, with supra- and infra-spinous fossae of subequal size (Gingerich et al. 2001a, Gingerich et al. 2009). Taken together, these specimens indicate that early protocetids such as *Artiocetus* and *Maiacetus* could use their forelimbs both for weight-bearing locomotion on land and for paddling or steering while swimming. Whereas the scapula of the more derived protocetid *Eocetus* is very similar to that of later basilosaurids, not much more can be inferred about forelimb use until more material is discovered.

Hind limb material is known for several protocetids. The type specimen of *Artiocetus clavis* includes parts of a pelvic girdle, a distal femur, and a patella, along with a complete astragalus and calcaneum; the type specimen of *Rodhocetus balochistanensis* includes a virtually complete hind limb (Gingerich et al. 2001a); the type specimen of *Eocetus wardii* includes a partial pelvis (Uhen 1999); the type specimen of *Georgiacetus vogtlensis* includes a virtually complete pelvis (Hulbert 1998); and the known specimens of *Maiacetus* include virtually complete hind limbs (Gingerich et al. 2009). Taken together, these specimens indicate that protocetids were able to use their hind limbs both for walking on land and for pelvic paddling and undulation in the water. *Georgiacetus* may be an exception in that it has a large pelvis (suggesting the presence of a large hind limb) that did not have a bony connection to the vertebral column. This indicates that the large hind limbs could not have been used for walking on land. Furthermore, *Georgiacetus* has posterior caudal vertebrae that are not shaped like those of basilosaurids and later cetaceans, which indicates that it also lacked tail flukes and perhaps used the large hind limbs during undulation as hydrofoils (Uhen 2008d). *Eocetus* may also be an exception because it has a moderately reduced pelvis (Uhen 1999). The only other protocetid found with posterior caudal vertebrae preserved is *Maiacetus* (Gingerich et al. 2009), and it too lacks any evidence of tail flukes.

Gingerich et al. (2009) described a specimen of *Maiacetus* that included a partial skeleton of a fetus in the posterior thoracic region. They concluded that this was a late-term fetus and, based on the position of the fetus relative to the mother, that *Maiacetus* (and by inference, other protocetids) gave birth on land. This supports earlier hypotheses that protocetids exhibited habits like those of modern pinnipeds, living and feeding in the water while mating and giving birth on land.

BASAL PELAGICETI

For many years, the families Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae were grouped into the suborder Archaeoceti—an admittedly paraphyletic group—with Basilosauridae being ancestral to Neoceti. Uhen (2008d) recognized a host of synapomorphies and subsequently diagnosed a new clade named Pelagiceti, which includes Basilosauridae + Neoceti. These synapomorphies include multiple accessory denticles on the cheek teeth; greatly reduced size of the pelvis and the pes (Gingerich et al. 1990, Uhen & Gingerich 2001); rotation of the pelvis (Gingerich et al. 1990); a high number of lumbar vertebrae (>10); and rectangular, short,

and dorsoventrally compressed posterior caudal vertebrae (Uhen 1998a, 2004). This grouping still recognizes the paraphyletic nature of Basilosauridae, but eliminates the taxon Archaeoceti.

Basilosauridae

Basilosauridae are known from the late middle Eocene to the late Oligocene and are found throughout the world. The earliest purported basilosaurids, *Basilosaurus drazindai* and *Basiloterus hussaini* (Gingerich et al. 1997), probably represent protocetids with elongate vertebrae akin to *Eocetus*, but this is difficult to determine with certainty because they are known from one and two vertebrae, respectively. After its initial description as a protocetid, *Gaviacetus* has also been suggested to be a basilosaurid based on the lack of room for an M^3 and the association of an elongate caudal vertebra with this taxon (Bajpai & Thewissen 1998). This assignment is not followed here, and *Gaviacetus* is retained in the Protocetidae. By the late Eocene, all protocetids were extinct, and only basilosaurids remained.

In addition to the lack of an M^3, Basilosaurids are characterized by accessory denticles on the cheek teeth, an elongate trunk consisting of additional thoracic and lumbar vertebrae, a much-reduced hind limb that is not connected to the vertebral column, posterior caudal vertebrae that are dorsoventrally flattened, a forelimb with relatively flat long bones, and carpal articular surfaces that are relatively flat (**Figure 10**). Some of these characteristics are also shared with basal Neoceti, as described below.
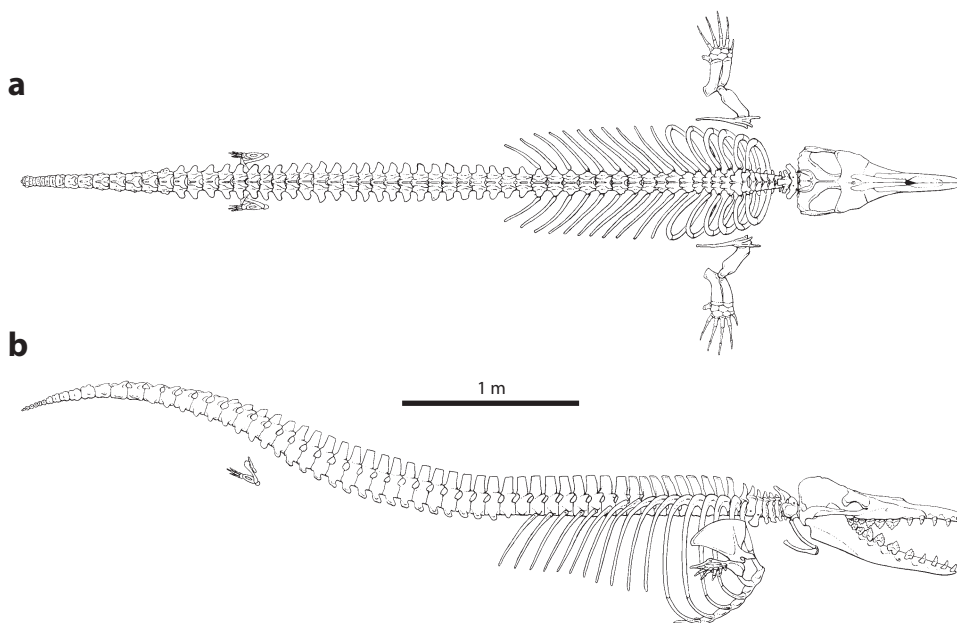

a

b

1 m

Figure 10

Basilosauridae: *Dorudon atrox*. Skeletal reconstruction of *Dorudon atrox* (Gingerich et al. 2009), in (*a*) dorsal view and (*b*) lateral view. The skull of *Dorudon atrox* is also shown in **Figure 2**. Note that the much-reduced hind limb is not connected to the vertebral column when compared with that of *Rodhocetus* in **Figure 9**. Also note the lengthening of the trunk region (posterior thoracic and lumbar region) as compared with *Rodhocetus*. Basilosaurids such as *Dorudon* are also characterized by loss of M^3 and the presence of accessory denticles on the cheek teeth shown in **Figure 2**.

Basilosauridae includes 11 genera divided into three subfamilies: Dorudontinae, Basilosaurinae, and Kekenodontinae. Dorudontines have all the characteristics of Basilosauridae, with no particular additional synapomorphies. Dorudontinae is likely to be paraphyletic, giving rise to Neoceti (Uhen 2004). Members of Basilosaurinae have elongate trunk vertebrae (posterior thoracic, lumbar, and anterior caudal vertebrae) that lack elongate neural arches, neural spines, and transverse processes. Kekenodontinae includes only the genus *Kekenodon*, an enigmatic taxon from the late Oligocene (Duntroonian) of New Zealand. Not much is known of *Kekenodon* other than some cranial fragments and teeth. The Kekenodontinae has been placed within Basilosauridae or in the Mysticeti, somewhat arbitrarily in the past. Until more material of kekenodontines is found, the placement of this subfamily will be subject to question.

Basilosaurids were formerly thought be restricted to the late middle Eocene and late Eocene (Uhen 1998a), when they gave rise to Mysticeti and Odontoceti. But newly discovered fossils, including virtually complete crania, demonstrate the presence of basilosaurids in the late Oligocene of New Zealand (Fordyce 2002a). Basilosaurids were first discovered in North America (Harlan 1834), where they were relatively abundant in the Pachuta Marl Member of the Yazoo Formation of the late Eocene, and somewhat more rare in other latest middle Eocene and late Eocene formations (Uhen 2008c). Basilosaurids are also well known from Fayum (Wadi Al-Hitan), Egypt (Dames 1894, Gingerich 1992). Recently, basilosaurids have also been described from Peru (de Muizon 2009).

Basilosaurids show a host of anatomical features indicating that they were fully aquatic (Uhen 1998a). In the skull, basilosaurids have well-developed pterygoid sinuses around the ear (Uhen 2004). In modern cetaceans, these sinuses are used to help with pressure adjustment during diving and to help acoustically isolate each ear. The neck is shorter in basilosaurids than in protocetids, although none of the cervical vertebrae are fused as in some modern cetaceans. Basilosaurids have a broad, thick, and dense sternum compared with protocetids. The forelimbs of basilosaurids are not capable of supporting the weight of the body on land, as they lack saddle-shaped articular surfaces on the carpals, preventing the positioning of the manus under the body. Also, the scapula is broad and fan shaped for the origins of large muscles to move the humerus. The distal humerus, radius, and ulna are flattened, suggesting that they were all encased in a flipper. As noted above, basilosaurids have an elongate trunk with additional posterior thoracic and lumbar vertebrae compared with protocetids. This may in part be for additional origins of muscles that insert on more posterior vertebrae to help drive the fluke during locomotion. The hind limbs of basilosaurids—known mainly from *Basilosaurus* (Gingerich et al. 1990), *Chrysocetus* (Uhen & Gingerich 2001), and *Dorudon* (Uhen 2004)—are extremely reduced, and could neither bear weight on land nor function in locomotion. Finally, the posterior caudal vertebrae of basilosaurids are dorsoventrally flattened, indicating the presence of soft-tissue tail flukes that were used for propulsion as in modern cetaceans (Uhen 2004).

ORIGIN OF NEOCETI

Although the origin of Cetacea has received a great deal of attention in recent years, the origin of Neoceti (neocetes) from archaeocetes has not received nearly as much. This lack of attention is partly due to a paucity of fossils from the Eocene/Oligocene transition, which is in turn due to a large drop in sea level that either prevented deposition of fossil whales or destroyed ones that had been deposited via erosion (Fordyce 2003a, Uhen & Pyenson 2007). That said, we can discuss what is known about the transition from basilosaurids to Neoceti.

Each suborder of Neoceti—i.e., Mysticeti and Odontoceti—is thought to be strictly monophyletic, based on morphological (Geisler & Sanders 2003) and molecular grounds (Xiong et al.

2009). Also, all recent authors have agreed that Neoceti are derived from the Basilosauridae (Geisler & Sanders 2003, Uhen 2004). Current evidence indicates that Neoceti is monophyletic. One basilosaurid, *Chrysocetus*, has been suggested to have one of the features shared by Mysticeti and Odontoceti: monophyodonty (Uhen & Gingerich 2001). The hypothesis that *Chrysocetus* is monophyodont is based on an interpretation that the type specimen is a juvenile with adult teeth, either having quickly shed the deciduous teeth or never having erupted deciduous teeth. This hypothesis also implies that the teeth found in early Mysticeti and Odontoceti are homologous with the adult teeth of archaeocetes, which has not been confirmed embryologically. That said, additional specimens of latest Eocene and Oligocene basilosaurids need to be compared with the earliest Mysticeti and Odontoceti to test the monophyly of Neoceti.

The following are some characteristics that unite Mysticeti and Odontoceti in Neoceti: The posterior maxilla is at least slightly concave, as opposed to smoothly convex, and bears multiple infraorbital foramina that open dorsally; an open mesorostral groove opens anteriorly such that the premaxillae have no contact along the midline; posteriormost teeth lie anterior to the orbit and antorbital notch; the zygomatic process of the squamosal is more robust than that in archaeocetes; the posterior process of the periotic (mastoid process) is not exposed laterally on the skull wall (amastoid); monophyodonty (one generation of teeth) is presumed but not confirmed for fossil taxa; and polydonty is present in most basal taxa (Fordyce 2008).

Mysticeti

The earliest member of the Mysticeti is *Llanocetus* from the latest Eocene La Meseta Formation of Seymour Island, Antarctica (Mitchell 1989). *Llanocetus* is a large animal that presents a very basilosaurid-like skull, except that the rostrum is broad, flat, and dorsoventrally thin. The teeth are heterodont, and cheek teeth are two rooted and palmate with multiple accessory denticles. Teeth are separated by wide diastemata, and fine grooves around the alveoli indicate the presence of a rich blood supply to the palate. *Llanocetus* has been interpreted as a filter feeder, structurally intermediate between basilosaurids and later mysticetes (Fordyce 2003b).

In addition to *Llanocetus*, other large-toothed forms from the Oligocene of South Carolina have been described as mysticetes (**Figure 11**). These "archaeomysticetes" have large, archaeocete-like teeth and skulls. In addition, they are polydont, displaying one extra cheek tooth in each quadrant, apparently because of terminal addition at the back of the tooth row. Characteristics that archaeomysticetes share with Mysticeti include a laterally directed antorbital process of the maxilla; a temporal crest along the posterior border of the flat and nearly horizontal supraorbital process of the frontal; short and inflated zygomatic processes; and an enlarged peribullary sinus without a pterygoid sinus (Barnes & Sanders 1996a,b). Barnes & Sanders (1996a,b) noted that these animals had a "loose mandibular symphysis," but Geisler & Sanders (2003) noted that the dentaries were joined by a sutural connection rather than a ligamentous one as in other mysticetes. Because these animals have not yet been fully described, more work needs to be done, but for now their placement as basal Mysticeti by Geisler & Sanders (2003) is followed here.

Another group of toothed mysticetes includes the family Mammalodontidae. Mammalodontidae is represented by the genera *Mammalodon* and *Janjucetus* from the late Oligocene of Australia (Fitzgerald 2004, 2006, 2010; Pritchard 1939). Both of these animals are very small, with short rostra. Both retain the basilosaurid dental formula of 3.1.4.3/3.1.4.3. The cheek teeth of *Mammalodon* are worn flat on their occlusal surfaces, whereas those of *Janjucetus* are not. Plus, *Mammalodon* cheek teeth are roughly triangular in outline with strong surface ornamentation and accessory denticles.
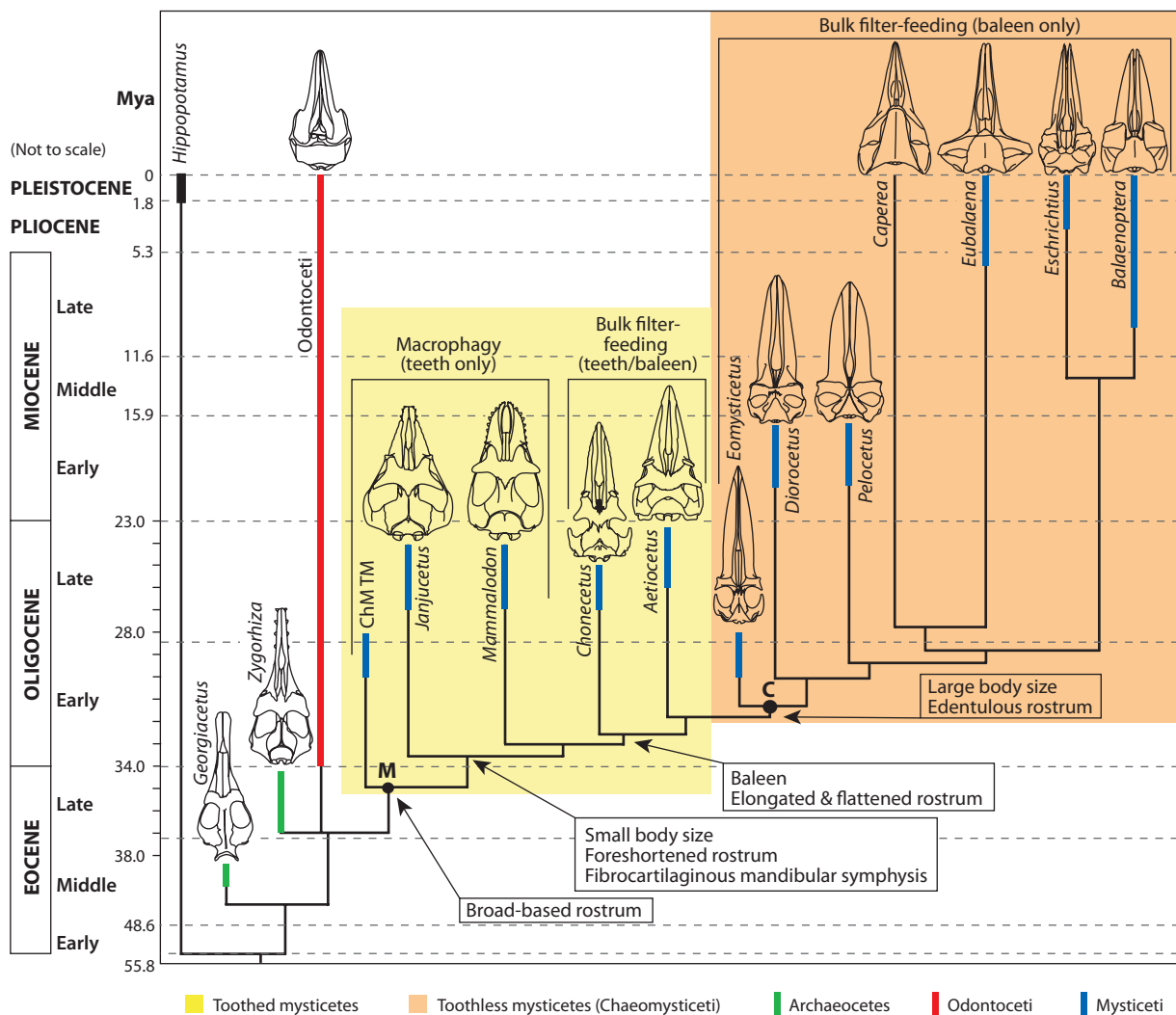

Monophyodonty: the condition of erupting a single set of teeth

Polydonty: the condition of having a greater number of teeth than the ancestral condition; may be a synapomorphy of Neoceti

Figure 11

Phylogeny, stratigraphic record, and feeding ecology of Mysticeti. Skull reconstructions are shown in dorsal view. Morphological characters related to feeding in mysticetes are optimized onto the tree at nodes where they appear. Solid-colored bars represent stratigraphic ranges colored by group. Solid circles denote named clades. Ages are in millions of years, with the timescale being linear only for late Eocene through Oligocene. Abbreviations: ChM TM, Charleston Museum toothed mysticetes (archaeomysticetes); C, Chaeomysticeti; M, Mysticeti (after Fitzgerald 2006). Original figure used by permission. E. M. G. Fitzgerald, *Proceedings of the Royal Society B*, 273, figure 3, p. 2959, 2006, The Royal Society.

Fitzgerald (2006) hypothesizes that *Janjucetus* was a macrophagous predator based on the conformation of the teeth, the wear facets on the teeth, the shape of the rostrum, and the relative size of the orbits.

The most derived group of toothed mysticetes is the family Aetiocetidae (Emlong 1966), represented by five genera: *Aetiocetus*, *Ashorocetus*, *Morawanocetus*, *Chonecetus*, and *Willungacetus*. All of these genera are known from the late Oligocene of the North Pacific (Barnes et al. 1995), except

Willungacetus, which is known from the early Oligocene of Australia (Pledge 2005). Aetiocetids have broad, flat rostra and small, widely spaced triangular cheek teeth with tiny accessory denticles. All aetiocetids for which the teeth are known are at least slightly polydont, with at least 11 teeth in the upper jaw—which is one more cheek tooth than in basilosaurids (Barnes et al. 1995). At least one specimen of an aetiocetid, *Aetiocetus weltoni*, preserves tiny lateral palatal foramina and associated sulci that appear to be homologous with similar but larger structures found in modern mysticetes that carry blood vessels to epithelia from which baleen develops (Deméré & Berta 2008). This represents strong indirect evidence of proto-baleen in addition to the small teeth in aetiocetids, although the earliest specimen of baleen itself preserved in the fossil record is from the late Miocene (Esperante et al. 2008).

The earliest toothless mysticetes that have been described thus far are in the family Eomysticetidae, from the late Oligocene of South Carolina (Sanders & Barnes 2002). Other possible eomysticetids are known from the late Oligocene of New Zealand (Fordyce 2009) and the early Oligocene of Oregon (Uhen 2007b). Eomysticetids have long, flat rostra lacking teeth, with the nares midway from the anterior tip of the snout; an elongate and narrow intertemporal region (shared with more plesiomorphic mysticetes); and "secondary squamosal fossae" (Sanders & Barnes 2002). These animals are presumed to have had baleen for use in filter feeding, but the palate is not well preserved in either of the described specimens.

Odontoceti

The earliest named odontocetes are from the late early Oligocene of North America, although earlier odontocetes have been discovered but not yet described. They are from three or more different families (Agorophiidae, Simocetidae, Xenorophidae, and perhaps others) that are quite different from one another (see **Figure 12** for an example). Unlike the earliest mysticetes, the earliest odontocetes are quite different from their basilosaurid ancestors and appear to have many— if not all—odontocete diagnostic features (synapomorphies) when they are first found in the fossil record. These include a large supraorbital process that overlaps the maxilla; a large facial fossa that houses dorsal infraorbital foramina; premaxillary sac fossae anterior to the nares; premaxillary foramina; premaxillary sulci; a periotic that is excluded from the floor of the braincase; and the presence of a middle sinus (Fordyce 2008).

Basal odontocetes have heterodont and polydont dentitions, but many groups evolve homodonty, and other groups greatly reduce the number of teeth (Uhen 2008b). Most modern odontocetes pursue individual prey items using echolocation. Upon capture, they swallow the prey item whole without any mastication. The one exception to this generalization is *Orca*, the modern killer whale. Killer whales use their teeth to grasp prey larger than they can swallow, then rip off smaller pieces that they can then swallow whole. Most fossil odontocetes are thought to have used the standard mode of odontocete feeding, although some may have fed like modern *Orca* (Bianucci 2005).

Echolocation involves both the production of high-frequency sounds and the perception of the echoes from those sounds. All basal odontocetes appear to have the bony correlates of the soft tissues used both to produce high-frequency sounds and to perceive the echoes. Echolocation clicks in modern cetaceans are produced in the nasopharynx and focused by the melon, a fat body that sits anterior to the nares. The facial fossa and premaxillary sac fossa are correlated with the presence of these soft-tissue structures in modern odontocetes, and all known fossil odontocetes have these bony structures as well. Perception of high-frequency sound takes place inside the cochlea, a structure inside the periotic of the middle ear. The cochlea is a spiral space divided in two by a membrane that covers a distance known as the basilar gap. When compared with
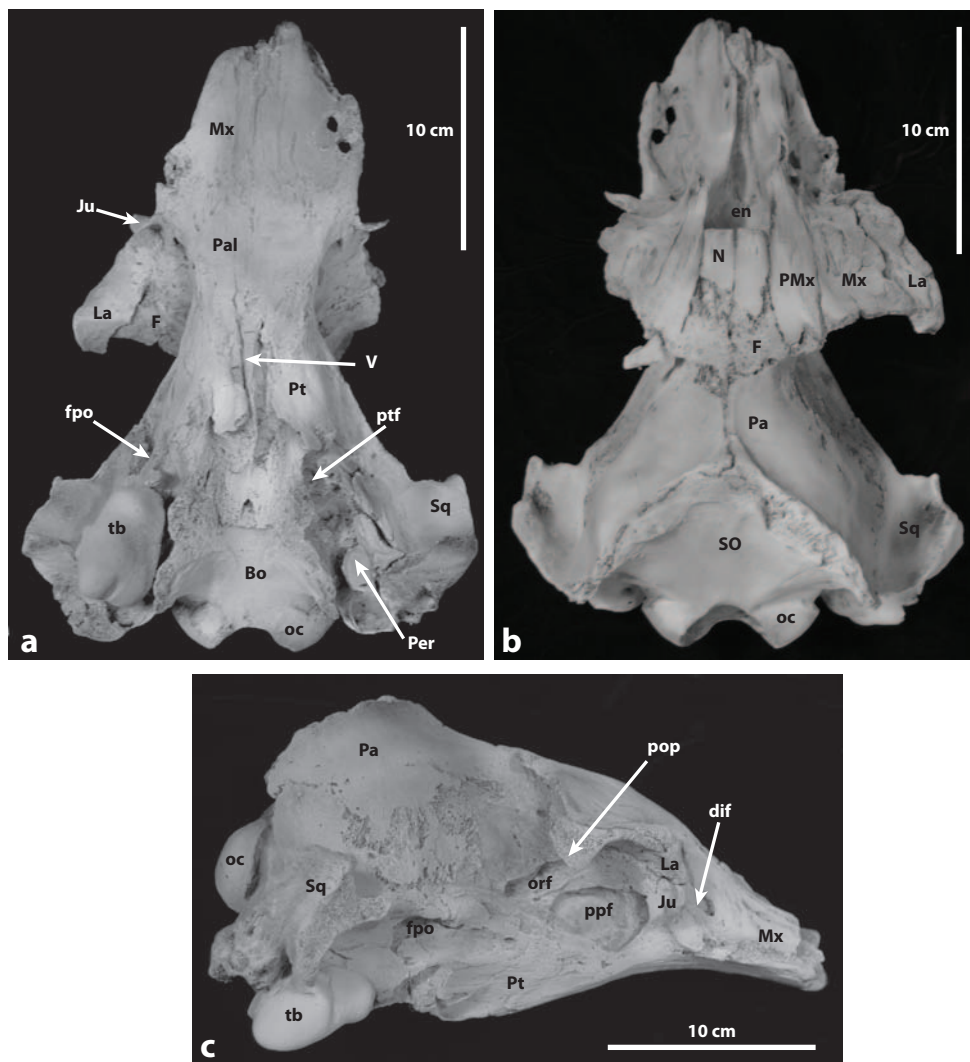
Homodonty: the condition of having undifferentiated teeth that are similar to one another

Diphyodonty: the condition of erupting two sets of teeth—one deciduous, and one permanent

Figure 12

Odontoceti: Xenorophidae, *Albertocetus meffordorum*, USNM 525001 (late Oligocene, North Carolina). Skull in ventral (*a*), dorsal (*b*), and lateral (*c*) views. Abbreviations: Bo, basioccipital; dif, dorsal infraorbital foramen; en, external nares; F, frontal; fpo, foramen pseudovale; Ju, jugal; La, lacrimal; Mx, maxilla; N, nasal; oc, occipital condyle; orf, orbital fissure; Pa, parietal; Pal, palatine; Per, periotic; PMx, premaxilla; pop, postorbital process; ppf, pterygopalatine fossa; Pt, pterygoid; ptf, pterygoid fossa; SO, supraoccipital; Sq, squamosal; tb, tympanic bulla; V, vomer (Uhen 2008a). The skull of this early odontocete is much less telescoped than that of modern odontocetes; that is, the bones of the face and the external nares (the skeletal representation of the blowhole) are much farther forward on the skull.

mysticetes that do not echolocate, odontocetes have a much smaller basilar gap all along the length of the cochlea. All fossil odontocetes that have been examined have a small basilar gap like that of modern odontocetes, suggesting that they too could perceive high-frequency sound (Fleischer 1976). This, combined with the ability to produce high-frequency sound noted above, suggests that all known fossil odontocetes could have echolocated.
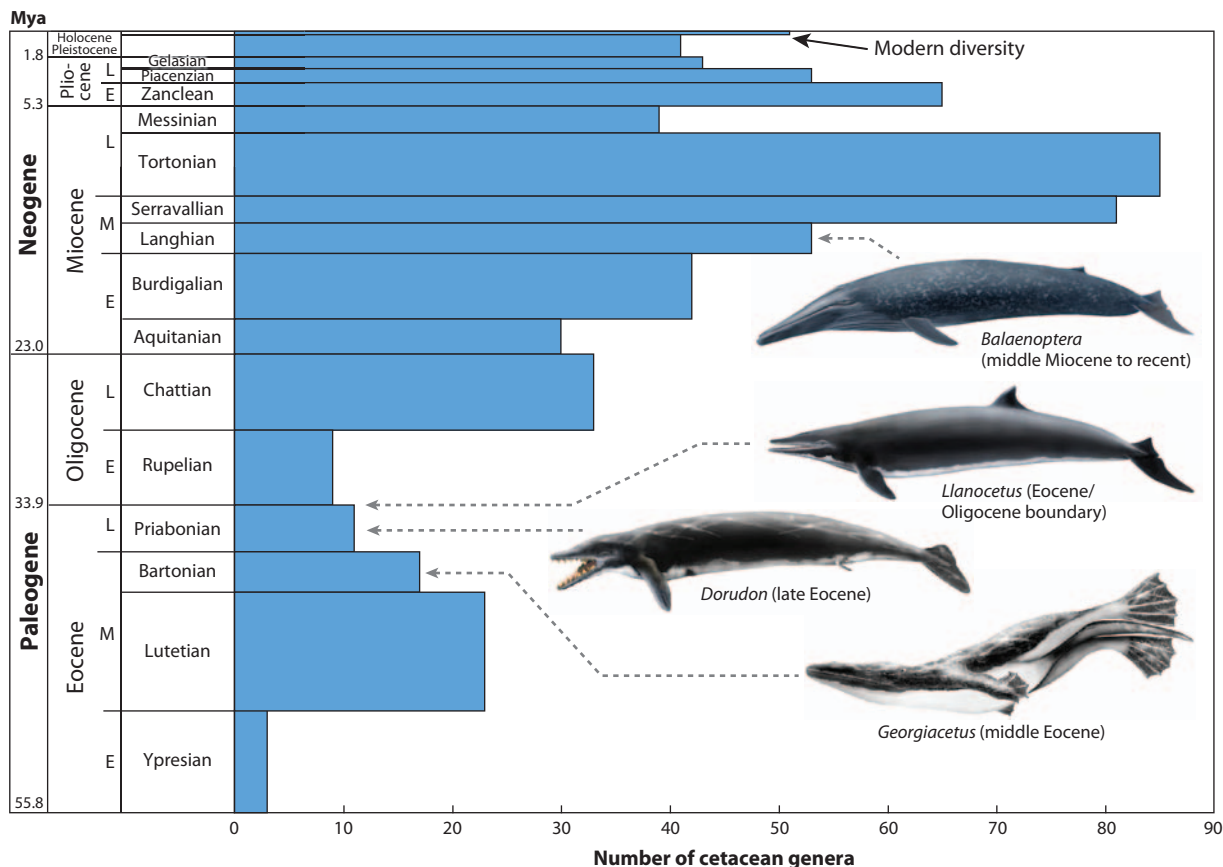
Figure 13

Generic diversity of Cetacea from the late early Eocene to the Holocene. Horizontal bars represent the number of cetacean genera known in each stage, ranged through stages where they are missing, but present earlier and later. Bar height is proportional to stage length, shown on the left. Note the high diversity early in cetacean history and the drop toward the early Oligocene. Diversity then increases to its peak in the late middle Miocene, and finally falls toward the Holocene. Illustrations by Mary Parrish. Timescale after Gradstein et al. (2004).

DIVERSITY PATTERN

Cetaceans diversify both taxonomically and morphologically early in their history. Just after their origin in the early Eocene, several different types of semiaquatic whales appear to have lived simultaneously in Indo-Pakistan. **Figure 13** shows the pattern of generic diversity change in whales over their entire history. This pattern shows a rapid increase from the Ypresian (late early Eocene) until the Priabonian, when diversity falls. This change can be attributed to two factors. First, the middle Eocene (Lutetian plus Bartonian, particularly the Lutetian) is rather long compared with the late Eocene (Priabonian). Thus, a series of whale faunas that lived at separate times may be lumped together, thus artificially increasing the apparent generic diversity during the Lutetian (Uhen & Pyenson 2007). Second, a great deal of early diversity was apparently lost when one lineage, the Basilosauridae, became fully aquatic. Thereafter, no semiaquatic whales are known from the fossil record.

The diversity of whales appears to have remained low across the Eocene/Oligocene boundary until the late Oligocene. This low diversity may also be an artifact of the drop in sea level due to the Oi-1 glaciation event in Antarctica (DeConto & Pollard 2003). This sea-level drop may have caused erosion of rocks containing previously deposited fossils or caused the lack of deposition of fossils (Uhen & Pyenson 2007). By the late Oligocene, a great diversity of archaic groups of both mysticetes and odontocetes had evolved (Fordyce & de Muizon 2001). During the Miocene, a second wave of diversification followed, when most modern families evolved (Fordyce 2008), and cetacean diversity hit its peak during the late middle Miocene (Tortonian) (Uhen & Pyenson 2007). By the Pliocene, most if not all archaic families of cetaceans had gone extinct, and diversity dropped toward modern levels. Pleistocene fossil whale diversity is most likely undersampled owing to flooding of marginal marine deposits at the end of the last ice age (Uhen & Pyenson 2007).

SUMMARY AND CONCLUSIONS

Great strides have been made in the past 25 years regarding the origin(s) of whales. Prior to the discovery of *Pakicetus* and other early and middle Eocene whales in Indo-Pakistan, there were few fossil data to support any particular hypothesis regarding the origin of whales among the various groups of mammals. Van Valen (1966) proposed that whales originated from mesonychians, a group of carnivorous ungulates with teeth similar to those of early whales. This hypothesis is still supported by some (O'Leary & Gatesy 2008), but rejected by most others (Geisler & Theodor 2009, Geisler et al. 2007, Geisler & Uhen 2005, Gingerich et al. 2001a, Thewissen et al. 2007) in support of a relationship of Cetacea from within Artiodactyla.

The hypothesis that Cetacea and Artiodactyla are related was originally proposed by W.H. Flower (1883a,b) and was then revived by molecular biologists, starting with Boyden & Gemeroy (1950). The current consensus among molecular biologists is that cetaceans are most closely related to Hippopotamidae within Artiodactyla. This hypothesis is supported by combined analyses that include all classes of data relevant to the problem: morphological, molecular, and stratigraphic (Geisler & Uhen 2005).

The origin of modern cetaceans from archaeocetes is a more complex, but still tractable problem. New fossils from the late Eocene and Oligocene that are being discovered and described relate both Mysticeti (Fitzgerald 2006, Mitchell 1989) and Odontoceti (Fordyce 2002b, Uhen 2008a) to basilosaurid archaeocetes. Many fossils of the earliest mysticetes and odontocetes remain to be discovered, but many have already been discovered in North America's Pacific Northwest, South Carolina, and New Zealand; these await preparation and description. The addition of these fossils to the our base of knowledge will greatly help clarify the nature of the transition from archaeocetes to neocetes and thus complete the picture of the origin of modern whales.

SUMMARY POINTS

1. Cetacea first appear in the fossil record approximately 52.5 Mya in Indo-Pakistan along the shores of subtropical epicontinental seas.

2. Whales are derived from within the Artiodactyla, and the living sister taxon to whales is the family Hippopotamidae.

3. The earliest whales were primarily terrestrial animals that foraged for food in freshwater.

4. Whales made the transition from land to sea in 10–12 million years and went through a series of stages of increasingly aquatic habits.

5. The earliest fully aquatic whales (basilosaurids) originated approximately 40 Mya and show a host of derived characteristics, largely associated with the limbs, indicating that they could no longer come out of the water.

6. Modern whales (Neoceti) originate from basilosaurids at or near the Eocene/Oligocene boundary, a time of profound change in the global circulation system and climate system.

7. Both mysticetes and odontocetes diversify in number and form throughout the Neogene. Diversity reaches its peak in the late middle Miocene and falls toward the Recent.

FUTURE ISSUES

1. Many fossil whales that have already been collected remain to be prepared, studied, named, and placed into evolutionary context—not to mention those that remain to be discovered in the field.

2. There is a significant northern-hemisphere bias in our understanding of fossil whale evolution. Much more exploration and research needs to be done in South America, sub-Saharan Africa, and Oceania to find and describe fossil whales and to flesh out our understanding of the diversification and distribution of archaeocetes and the origin of Neoceti.

3. Basal odontocetes are as yet unknown or undescribed. The earliest odontocetes that have been described seem to have most if not all synapomorphies of the group. More basal taxa need to be found to fully characterize the evolution of echolocation, which appears to have already been in place in the currently earliest known odontocetes.

4. The latest Eocene and early Oligocene cetacean faunas need to be better characterized so we can understand how the remaining archaeocetes and newly evolved mysticetes and odontocetes interacted with one another and the rest of the marine fauna and environment.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Thewissen et al. name *Ambulocetus natans*, one of the earliest whales for which much of the skeleton is known. *Ambulocetus natans* is the "walking, swimming whale."

Uhen's monograph on *Dorudon atrox* describes virtually every element from the best-known archaeocete whale.

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