CHAPTER 15

# Paleobiological Perspectives on Mesonychia, Archaeoceti, and the Origin of Whales

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## 1. Introduction

Organisms living today are grouped together taxonomically because they are similar to each other and different from others. How similar organisms are within a group and how different the group is from other groups depends on the broader context of similarities and differences uniting and distinguishing groups. The rank to which a group is assigned depends in part on similarities and differences, but also on what we know about evolutionary history. Extant whales (order Cetacea) have long been known to be mammals because they share with other mammals such basic distinguishing characteristics as endothermy, lactation, large brains, and a high level of activity. Living cetaceans share, in addition, a suite of special characteristics related to life in water that distinguish them from land mammals: These include large body size, a reduced and simplified dentition, an audition-dominated sensory and communication system, a hydrodynamically streamlined body form with a muscular propulsive tail, and of course many ancillary anatomical, behavioral, and physiological differences.

Extant Mysticeti (baleen whales) and Odontoceti (toothed whales) are usually considered suborders of Cetacea, but they are sufficiently different from each other that some whale specialists in the past have regarded them as distinct orders. This illustrates the role context plays in determining how broadly taxonomic groups are drawn, and it also reflects the interdependence of morphology, classification, and evolutionary history: When mammals as different as mysticetes and odontocetes were classified in different orders, this was interpreted to reflect a long history of evolutionary independence (the history had to be long because of a general belief that evolution is so slow that differences take a long time to accumulate). We now know, thanks to the fossil record, that the modern suborders Mysticeti and Odontoceti have a fossil record extending back to the Oligocene epoch of the geological time scale, and they are thought to have diverged from each other sometime in the late

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Eocene or early Oligocene, no more than about 40 m.y. ago (Fordyce and Barnes, 1994). Whales that are known from the earth's Eocene rivers and oceans all belong to a third suborder, Archaeoceti, which is a group with much more generalized morphology. Archaeoceti includes the earliest aquatic whales.

No whales of any kind are known before the Eocene, and thus the evolutionary history of Cetacea is similar in length to that of other modern orders of mammals. And, like other modern orders (e.g., ungulate Artiodactyla), there are Paleocene land mammals, condylarthran Mesonychia in this case, that resemble Archaeoceti closely enough to suggest ancestor–descent relationship. Such a relationship is by no means proven as yet, but Mesonychia are clearly the best candidates for archaeocete ancestry by virtue of their morphological similarity and their overlapping temporal and geographic distributions. Mesonychia and Archaeoceti jointly are the subject of this topical perspective.

## 1.1. Study of Whale Origins

Most mammals live on land, and the aquatic specializations of Cetacea have long been viewed as derived characteristics acquired by whales when they made the transition from land to sea. This idea is reinforced by the long geological record of mammals on land (beginning in the late Triassic some 200 m.y. before present) and the relatively short geological record of cetaceans in the sea (beginning much later, in the early Eocene, some 50 m.y. before present). However, few would consider such inferential evidence of evolution from land mammals a satisfying solution to the problem of whale origins. I use *origins* advisedly here, not because whales had multiple or independent origins, but because their common origin had many equally important threshold stages—no single change made land mammals into whales.

What group of land mammals gave rise to whales? Where did it happen? When did it happen? How did it happen? What was the context? What were the consequences? These are all questions in the past tense, about a transformation we think happened in the past. All are paleobiological questions that group naturally into what might be considered the three broad objectives of study of fossil whales (or any group known from the fossil record):

1. Identification of the morphologically, geographically, and temporally intermediate stages of change (here the stages by which whales made the transition from land to sea). These intermediates, when known, are direct evidence (and the only direct evidence we have) telling us what happened in evolution.
2. Association of the times of acquisition of distinctive morphological specializations with other changes in morphology within the group of interest (here Cetacea) and with biotic- and physical-environmental changes outside the group of interest. These associations provide a context critical for understanding how any evolutionary transition took place.
3. Evaluation of consequences. What was the effect of any change on the group under study? This can be measured in terms of morphological disparity, taxonomic diversity, or taxon longevity.

It is difficult to appreciate that study of a group like Archaeoceti is still in its infancy. The first archaeocete to be studied and named, *Basilosaurus*, was collected in 1832, a year

before Charles Lyell named the Eocene. *Basilosaurus* was recognized as a cetacean in 1841, the year that Richard Owen named Dinosauria. When the first archaeocete skeleton was mounted for exhibition at the U.S. National Museum in 1913 (again *Basilosaurus*), it was a composite and the number of vertebrae was unknown, the hands were reconstructed like flippers of a sea lion because they were not known (Lucas, 1900), the pelvis was mounted incorrectly, and the animal was assumed to have had no feet (Gidley, 1913). Remington Kellogg summarized all that was known at the time in his classic *Review of the Archaeoceti* (Kellogg, 1936), but there were still only three genera and species with reasonably complete skeletons (*Basilosaurus cetoides* and *Zygorhiza kochii* from the late Eocene, and *Protocetus atavus* from the middle Eocene; "Dorudon" *osiris* of Kellogg and others is a confusing composite including specimens of *Dorudon atrox*), and none of these had complete vertebral columns, hands, or feet.

*Protocetus* interested Kellogg largely because Fraas (1904) and Andrews (1906) regarded it as having the skull of an archaeocete and the dentition of a creodont (Fraas went so far as to remove archaeocetes from Cetacea, placing them in Creodonta). Kellogg retained Archaeoceti in Cetacea but concluded:

> In summation, it would appear that the evidence seems to point toward the concept that the archaeocetes are related to if not descended from some primitive insectivore-creodont stock, but that they branched off from that stock before the several orders of mammals that reached the flood tide of their evolutionary advance during the Cenozoic era were sufficiently differentiated to be recognized as such. Morphologically the archaeocetes seem to stand relatively near to the typical Mysticeti and Odontoceti, although all three suborders were separated from each other during a long interval of geologic time. It is not necessary to assume that any known archaeocete is ancestral to some particular kind of whale, for the archaeocete skull in its general structure appears to be divergent from rather than antecedent to the line of development that led to the telescoped condition of the braincase seen in skulls of typical cetaceans. On the contrary it is more probable that the archaeocetes are collateral derivatives of the same blood-related stock from which the Mysticeti and the Odontoceti sprang. (Kellogg, 1936, p. 343)

George Gaylord Simpson echoed these conclusions in his midcentury *Classification of Mammals:*

> 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. (Simpson, 1945, p. 213)

> 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. . . . Thus the Archaeoceti . . . are definitely the most primitive of cetaceans, but they can hardly have given rise to the other suborders [Mysticeti and Odontoceti]. (Simpson, 1945, p. 214)

The first quotation from Simpson inspired Alan Boyden and Douglas Gemeroy to attack the problem of whale relationships serologically. Boyden and Gemeroy (1950) compared immunological cross-reactions of serum proteins of Cetacea with those of all other orders using precipitin tests. This was one of the first attempts to infer phylogenetic relationships from immunology. Boyden and Gemeroy found that interordinal reactions were generally weak, averaging about 2%, with the exception that the artiodactyl–cetacean comparisons were distinctly higher, averaging about 9–11%. This greater immunological reac-

tivity Boyden and Gemeroy interpreted as indicating a close blood and genetic relationship of Cetacea to Artiodactyla.

Modern molecular gene sequencing has largely confirmed this Cetacea–Artiodactyla sister-group relationship. However, conflicting claims that (1) sperm whales are mysticetes (e.g., Milinkovitch *et al.*, 1993, 1995; Milinkovitch, 1995; but see Ohland *et al.*, 1995); (2) Cetacea originated *within* Artiodactyla as the sister group of extant camels, of extant hippopotami, or extant ruminants (Goodman *et al.*, 1985; Sarich, 1993; Irwin and Arnason, 1994; Graur and Higgins, 1994; Arnason and Gullberg, 1996; Gatesy, this volume); or (3) whales are the sister group of perissodactyls (McKenna, 1987), taken together, cast doubt on our ability to reconstruct past evolutionary history from living animals.

Van Valen (1966) approached the problem of cetacean relationships paleontologically:

> 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. . . . Diverse and apparently equally valid objections exist for the various groups of Paleocene insectivores, one common to all being their small size. All marine mammals are large or rather large mammals. (Van Valen, 1966, p. 90)

Van Valen (1966, p. 92) drew attention to the late Eocene *Andrewsarchus* as a mesonychid having "a skull remarkably similar in shape to that of *Protocetus*, even to a largely longitudinal series of incisors" (the claim about remarkable similarity of skull shape is debatable). He reasoned (p. 93) that whales took to the sea in middle or late Paleocene times. And finally, he noted (p. 93) that Boyden and Gemeroy's serological argument for a special relationship between Cetacea and Artiodactyla is made more plausible by the evidence of an ancestral–descendant mesonychian-to-archaeocete relationship.

Although Boyden and Gemeroy's conclusions are consistent with those of Van Valen, it should be emphasized that a sister-group relationship between extant Artiodactyla and Cetacea like that hypothesized by Boyden and Gemeroy is different than a "mother-group"or ancestral–descendant relationship between Mesonychia and Archaeoceti like that hypothesized by Van Valen. The postulated divergence of proto-Artiodactyla from proto-Cetacea is not the same event as the transition from Mesonychia to Archaeoceti, nor is the time of divergence associated with the former likely to be equivalent to the time of transition of the latter. We shall return to this point later, and it is sufficient to note here that most authors now accept as a working hypothesis Van Valen's idea that Mesonychia gave rise to Archaeoceti.

## 1.2. Diversity and Morphology of Mesonychia

There are about 20–28 known genera of Mesonychia (depending on how these are counted), grouped in two, three, or four families: Hapalodectidae, Mesonychidae, and, questionably, Andrewsarchidae and Wyolestidae (Fig. 1). *Andrewsarchus* was included in Mesonychidae by Osborn (1924) and placed in a separate family-level group Andrewsarchinae by Szalay and Gould (1966). Van Valen (1978) considered andrewsarchines

| MESONYCHIA | PALEOCENE | | | EOCENE | | | OLIG. |
|---|---|---|---|---|---|---|---|
| | Early | Middle | Late | Early | Middle | Late | Early |
| **HAPALODECTIDAE** | | | | | | | |
| *Hapalodectes* | | | | A,N | A | | |
| *Hapalodectes?* | | | A | | | | |
| *Hapalorestes* | | | | | N | | |
| **MESONYCHIDAE** | | | | | | | |
| *Ankalagon* | | N | N | | | | |
| *Dissacus* | | A,N | A,E,N | E,N | E | | |
| *Dissacusium* | | A | | | | | |
| *Harpagolestes* | | | | | A,N | A,N | A |
| *Hessolestes* | | | | | N | N | |
| *Honanodon* | | | | | A | | |
| *Honanodon?* | | | | A | | | |
| *Hukoutherium* | A? | A | | | | | |
| *Jiangxia* | | | A | | | | |
| *Lohoodon* | | | | | A | A | |
| *Mesonyx* | | | A? | | A,N | | |
| *Metahapalodectes* | | | | | A | | |
| *Mongolestes* | | | | | | | A |
| *Mongolonyx* | | | | | A | | |
| *Olsenia* | | | | | | A | |
| *Pachyaena* | | | A | E,N | | | |
| *Pachyaena?* | | | | | A | | |
| *Plagiocristodon* | | | A? | A? | | | |
| *Sinonyx* | | | A | | | | |
| *Synoplotherium* | | | | | N | | |
| **?ANDREWSARCHIDAE** | | | | | | | |
| *Andrewsarchus* | | | | | A | | |
| *Paratriisodon* | | | | | A | | |
| **?WYOLESTIDAE** | | | | | | | |
| *Wyolestes* | | | | N | | | |
| *?Mongoloryctes* | | | | | A | | |
| *?Yantanglestes* | | A | A | | | | |
| **Key and total genera** | | | | | | | |
| N = N. Am.: | 0 | 2 | 2 | 4 | 5 | 2 | 0 |
| E = Europe: | 0 | 0 | 1 | 2 | 1 | 0 | 0 |
| A = Asia: | ? | 4 | 6-8 | 2-3 | 11 | 3 | 2 |
| World total: | ? | 5 | 7-9 | 5-6 | 15 | 4 | 2 |

**FIGURE 1.** Temporal and geographic distribution of Mesonychia based on published literature compiled by Zhou (1995) and by the author. Taxa preceded by a query are questionably included in the higher taxon in which they are listed. Generic names followed by a query probably represent additional diversity. Note that the first appearance of mesonychians is recorded as being in the early Paleocene of Asia, although the triisodontid arctocyonians that early mesonychians resemble closely are best known from the early and middle Paleocene of North America. Mesonychian generic richness is highest in Asia during all subepochs except the early Eocene (which is not yet as well sampled in Asia).

to be Arctocyonidae, and he may be right. Wang (1976) proposed that Didymoconidae are closely related to Mesonychidae. When describing *Wyolestes* (Gingerich, 1981), I was impressed by dental resemblances to *Yantanglestes* and *Mongoloryctes*, the former a mesonychian and the latter then classified as a didymoconid. Meng *et al.* (1994) have since shown that *Wyolestes* is unlikely to be a didymoconid and didymoconids are very different from mesonychians. However, dental resemblances of *Wyolestes* to *Yantanglestes* and *Mongoloryctes* still stand and I have grouped all here in Wyolestidae (with question marks re-

Mesonychidae       *Pachyaena ossifraga*       53-54 Mɛ

**A**

Skull len.: 40 cm

UM 95074
Predicted body mass: 160 kg ( 110 – 220 kg)
Body mass ~65 kg (pred. from long bones), brain mass ~40 g
Encephalization: $EQ_{TC} \approx 0.18$   $ER_{TC} \approx -2.50$

Zhou et al. (1992)

Measurements norm. to ant. thoracic centr. hgt. (orders of magnitude, meas. in mm)

1.5   1.0   0.5   0.0   -0.5   -1.0

Cerv.   Thorax   Lumb.   S.   Cauda

TCNDSFB   0   5   10   15   20   25   30   35   40   45   50   55   60   65   SHRC   IFTT
Skull     Position in vertebral column (centrum length and height)     Forel.   Hind l.

Canidae       *Canis lupus*       Extanᵗ

**B**

Skull len.: 23 cm

UMMZ 38960 (Wolf)
Predicted body mass: 90 kg ( 30 – 260 kg)
Actual body mass ~30 kg, brain mass ~140 g
Encephalization: $EQ_{TC} \approx 1.10$   $ER_{TC} \approx 0.14$

Measurements norm. to ant. thoracic centr. hgt. (orders of magnitude, meas. in mm)

1.5   1.0   0.5   0.0   -0.5   -1.0

Cerv.   Thorax   Lumb.   S.   Cauda

TCNDSFB   0   5   10   15   20   25   30   35   40   45   50   55   60   65   SHRC   IFTT
Skull     Position in vertebral column (centrum length and height)     Forel.   Hind l.

**FIGURE 2.** Diagrams of skeletal proportion comparing skull lengths, vertebral lengths and heights, forelimb long bone lengths, and hind limb long bone lengths of the early Eocene mesonychid *Pachyaena ossifraga* (A) to those of the skeletally similar extant wolf *Canis lupus* (B). All measurements are represented as a profile of bars, normalized to the mean height of the centrum of the six anterior thoracic vertebrae (dotted baseline). Two profiles are superimposed for vertebral measurements, representing centrum length and centrum height, and the bar shown is the *difference* between these (the position of the bar represents vertebral size and the length of each bar reflects measurement difference or shape): This is solidly filled when length exceeds height (as for most vertebrae here), and open when height exceeds length (as in the first cervical, vertebra 1, of *C. lupus*). Values for which reliable estimates can be interpolated or extrapolated are shown with hatching.

Note that *Pachyaena* has a slightly longer skull compared with the rest of its skeleton; *Canis* has a longer longest-cheek-tooth (T). Condylobasal skull length (C), external narial position (N), dentary length (D), and mandibular symphyseal position (S) decrease progressively in size; the greatest diameter of the mandibular foramen (F) is small in both; and the auditory bulla (B) is substantially longer than the mandibular foramen.

flecting uncertainty). Andrewsarchidae and Wyolestidae are regarded as families rather than subfamilies, paralleling Hapalodectidae, which was raised to family status by Ting and Li (1987).

Mesonychia range in age from early or middle Paleocene (ca. 63 Ma) through early Oligocene (ca. 33 Ma), and are found on all three of the northern continents. The number of mesonychian genera known from Asia exceeds that known from North America or Europe in every subepoch of the Paleocene through early Oligocene, save the early Eocene, which is not yet well sampled in Asia. Thus, Asia was possibly the center of origin of Mesonychia and Asia was certainly an important center of their evolutionary diversification.

Four genera of Mesonychidae are well known osteologically in being represented by complete or virtually complete postcranial skeletons: middle Paleocene *Hukoutherium* (Xue *et al.*, 1996; Xue, in preparation), late Paleocene *Sinonyx* (Zhou *et al.*, 1995; Gingerich *et al.*, in preparation), early Eocene *Pachyaena* (Matthew, 1915; Zhou *et al.*, 1992; O'Leary and Rose, 1995; Rose and O'Leary, 1995), and middle Eocene *Mesonyx* (Scott, 1886; Matthew, 1909). In contrast, very little is known about the postcranial osteology of hapalodectids, andrewsarchids, or wyolestids. It is perhaps possible that whales originated from one of these other families, but mesonychids are much better known and make a good model for cetacean ancestry.

## Skeleton of Early Eocene *Pachyaena*

The skeleton of early Eocene *Pachyaena ossifraga* is represented in a *diagram of skeletal proportion* in Fig. 2, where it is compared with a skeleton of the extant wolf *Canis lupus*. Diagrams of skeletal proportion facilitate comparisons of functionally related cranial measurements, vertebral sizes and shapes, forelimb measurements, and hind limb measurements, all in terms of proportion. The common reference scale, average height of the six anteriormost thoracic vertebral centra (horizontal dashed line), is somewhat arbitrary. This reference scale was chosen to avoid any area of obvious functional specialization in the skeletons of mesonychians and cetaceans (skulls, necks, thoracolumbar vertebrae, tails, forelimbs, and hind limbs all have a range of different dimensions and proportions in the animals being compared). Because all diagrams of skeletal proportion are scaled in the same

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Vertebral centrum length and height form three graphical vertebral arches, an anterior cervical arch rising from the anterior thorax where the forelimb originates (shaded box), a central thoracic and lumbar arch connecting this to the sacrum where the hind limb originates (second shaded box), and a posterior caudal arch. Size of each vertebral rectangle represents its proportions when viewed laterally (high solid rectangles represent vertebrae that are long and low, high open rectangles represent vertebrae that are short and high). Anterior thorax and sacrum (shaded boxes) are stable inflexible regions of the vertebral column characteristic of quadrupedal mammals.

Forelimbs (scapula S, humerus H, radius R, and longest metacarpal C) and hind limbs (innominate I, femur F, tibia T, and longest metatarsal T) of *Canis* are longer relative to the rest of the skeleton than those of *Pachyaena*, and the third segments (radius R and tibia T) are longer relative to other elements of the same limb. Compare these profiles with those of more aquatic mammals in Figs. 4–6.

Body masses predicted here are based on comparison with vertebrae of marine mammals (see text) to show that vertebral size of marine mammals overestimates the mass of terrestrial mammals by a factor of 2 to 3 (compare 160 kg with 65 kg, and 90 kg with 30 kg).

way, proportions can be compared between skeletons of different animals, even when these differ in absolute size as is true in the comparison of *Pachyaena* and *Canis*. All measurements are represented as a profile of bars, except for vertebral measurements where two profiles are plotted (centrum length and height) and the bar shown is the *difference* between these (the position of the bar represents vertebral size and the length of each bar reflects vertebral shape).

The skull of *Pachyaena* resembles that of *Canis* in relative size, with both being about an order of magnitude greater than the anterior-thoracic-height baseline. Anterior–posterior length of the longest cheek tooth (T in Fig. 2) is less in *Pachyaena* because it does not have the carnassial specialization of *Canis*. The relationships of cranial condylobasal length (C) to nasal position (N), dentary length (D), and mandibular symphysis position (S) are very similar in the two. The size of the mandibular foramen (F) is less than the baseline and less than auditory bulla length (B) in both.

The vertebral column of *Pachyaena* resembles that of *Canis* in relative size, and it has a pattern typical of cursorial land mammals. Postatlas cervical vertebrae (positions 2 through 7) show decreasing centrum length coupled with increasing and then decreasing centrum height in both *Pachyaena* and *Canis* (the atlas itself is difficult to measure in any functionally meaningful way). The important point is that cervicals are relatively long in *Pachyaena* and *Canis* (both have long necks compared with what we will see in archaeocetes), and the cervical series together with anterior thoracics forms an *anterior arch* supporting the skull anterior to and above the shoulder (shaded box) where the axial skeleton is connected to the forelimb. Note that when centrum height exceeds length, the normalized height and length measurements are connected by an open bar representing shape difference (the higher the open bar, the more height exceeds length). When centrum length exceeds height, the normalized length and height measurements are connected by a solid bar that again represents shape difference (but this time the higher the open bar, the more length exceeds height). A run of open bars represents a sequence of vertebrae with centra shorter than they are high, and a run of solid bars like the cervicals shown in Fig. 2 represents a sequence of vertebrae with centra longer than they are high.

Posterior thoracic, lumbar, and sacral centra in *Pachyaena* and *Canis* form a second arch or *central arch*, again similar in both, of increasing and then sharply decreasing length and slightly increasing and then decreasing height between the shoulder (first shaded box) and sacrum where the axial skeleton is connected to the hind limb (second shaded box). This is followed in both by a *posterior arch* of increasing and then slightly decreasing caudal centrum length, and slightly increasing and then sharply decreasing caudal centrum height in the tail. Bar segments of similar size represent vertebral centra of similar shape, whereas the position of the bar segment on the diagram is a measure of centrum size. Thus, the posterior caudal centra in both *Pachyaena* and *Canis* are similar in shape but decrease progressively in size. The anterior, central, and posterior arches shown here correspond to those in classic representation of the skeleton of a land mammal as a "bridge that walks" (e.g., Gregory, 1937).

The forelimbs of *Pachyaena* and *Canis* are similar in relative length of the scapula (S), humerus (H), radius (R), and longest metacarpal (C), and the hind limbs are similar in relative length of the pelvis or innominate (I), femur (F), tibia (T), and longest metatarsal (T). Fore- and hind limbs are similar in size relative to each other, and in size relative to the skull

and vertebral column. However, fore- and hind limbs of *Pachyaena* differ in two important ways from those of *Canis*. The radius is shorter than the humerus in the forelimb and the tibia is shorter than the femur in the hind limb in *Pachyaena*, and the metacarpals and metatarsals of *Pachyaena* are shorter than those of *Canis*, indicating a slightly heavier build (*Pachyaena* is a larger and heavier animal) and somewhat less fully cursorial locomotor adaptation.

Important anatomical details of the teeth, vertebrae, and hands and feet of mesonychids cannot be represented on a diagram of skeletal proportion. Central cheek teeth of *Pachyaena* are not enlarged like those of many carnivorous mammals (including later archaeocetes) and they do not have the sharpness or the carnassial shearing specialization expected of predatory meat eaters. Lumbar vertebrae of *Pachyaena* and other mesonychids are unusual in having revolute zygapophyses like those of arctocyonid condylarths (Russell, 1964) and later artiodactyls (Slijper, 1947), making them stiff-backed runners (Zhou *et al.*, 1992). Terminal phalanges of *Pachyaena* are fissured ungules or hooves, which is consistent with nonpredatory behavior and with cursoriality. The overall skeletal similarity of early Eocene *Pachyaena* to extant *Canis* shown in Fig. 2 is interpreted as indicating similar behavior in life, recognizing that *Pachyaena*, with a metatarsal/femur ratio of just 0.31, cannot have been an active pursuit predator like a wolf (Janis and Wilhelm, 1993). Mesonychians are usually interpreted as solitary carrion feeders and scavengers that spent many of their waking hours trotting in search of dead animals and were best able to chew flesh after it was partially decomposed (Boule, 1903; Osborn, 1910; Scott, 1913; Zhou *et al.*, 1992). This is plausibly the kind of animal from which archaeocetes evolved.

## 1.3. Diversity and Morphology of Archaeoceti

There are about 25 known genera of Archaeoceti, grouped in six families: Ambulocetidae, Basilosauridae, Dorudontidae, Pakicetidae, Protocetidae, and Remingtonocetidae (Fig. 3). These range in age from latest early Eocene (ca. 49.5 Ma) through late Eocene (ca. 36 Ma), and are found on the margins of most of the world's oceans. The number of mesonychian genera known from Tethys exceeds that known elsewhere in every subepoch of the Eocene, save the late Eocene, which is not yet well sampled in Tethys. Thus, it appears that Tethys was possibly the center of origin of Cetacea and, more certainly, a center of their evolutionary diversification.

Six genera of Archaeoceti are well enough known osteologically to make meaningful comparisons using a diagram of skeletal proportion: Lutetian (early middle Eocene) *Rodhocetus* (Gingerich *et al.*, 1994; Gingerich, in preparation), *Dalanistes* (Gingerich *et al.*, 1995), and *Protocetus* (Fraas, 1904); late Bartonian latest middle Eocene *Dorudon* (Uhen, 1996); late Bartonian to Priabonian late middle to late Eocene *Basilosaurus* (Kellogg, 1936; Gingerich, in preparation); and Priabonian late Eocene *Saghacetus* (Gingerich, in preparation). These include four of the six archaeocete families: Protocetidae, Remingtonocetidae, Dorudontidae, and Basilosauridae. Ambulocetidae and Pakicetidae are known from important limb bones (*Ambulocetus*; Thewissen *et al.*, 1996) and cranial material (*Ambulocetus, Pakicetus*; Gingerich *et al.*, 1983; Thewissen *et al.*, 1996), but little is yet known of the vertebral skeleton, which is central to analyses of the kind presented here.

| ARCHAEOCETI | PALEOCENE | | | EOCENE | | | | OLIG. |
|---|---|---|---|---|---|---|---|---|
| | Early | Middle | Late | Ypresian | Lutetian | Barton. | Priabon. | Early |
| **AMBULOCETIDAE** | | | | | | | | |
| *Ambulocetus* | | | | | T | | | |
| *Gandakasia* | | | | T | | | | |
| **BASILOSAURIDAE** | | | | | | | | |
| *Basilosaurus* | | | | | | M,T | W,A? | |
| *Basiloterus* | | | | | | T | M? | |
| **DORUDONTIDAE** | | | | | | | | |
| *Ancalecetus* | | | | | | M | | |
| *Dorudon* | | | | | | W,M | | |
| *Pontogeneus* | | | | | | M | W | |
| *Saghacetus* | | | | | | | M | |
| *Zygorhiza* | | | | | | E? | W | |
| **PAKICETIDAE** | | | | | | | | |
| *Ichthyolestes* | | | | T | | | | |
| *Nalacetus* | | | | T | | | | |
| *Pakicetus* | | | | T | | | | |
| **PROTOCETIDAE** | | | | | | | | |
| *Babiacetus* | | | | | | T | | |
| Cross whale | | | | | | W | | |
| *Eocetus* | | | | | | M | | |
| *Gaviacetus* | | | | | E?,T | | | |
| *Georgiacetus* | | | | | | W | | |
| *Indocetus* | | | | | | T | | |
| *Pappocetus* | | | | | E | | | |
| *Protocetus* | | | | | W?,E?,M | | | |
| *Rodhocetus* | | | | | T | | | |
| *Takracetus* | | | | | T | | | |
| **REMINGTONOCETIDAE** | | | | | | | | |
| *Andrewsiphius* | | | | | | T | | |
| *Dalanistes* | | | | | T | | | |
| *Remingtonocetus* | | | | | T | T | | |
| **Key and total genera** | | | | | | | | |
| W = W. Atlantic: | 0 | 0 | 0 | 0 | ? | 3 | 3 | 0 |
| E = E. Atlantic: | 0 | 0 | 0 | 0 | 1-3 | 0-1 | 0 | 0 |
| M = Med. Tethys: | 0 | 0 | 0 | 0 | 1 | 5 | 1-2 | 0 |
| T = E. Tethys: | 0 | 0 | 0 | 4 | 6 | 6 | 0 | 0 |
| A = Austral seas: | 0 | 0 | 0 | 0 | 0 | 0 | 0-1 | 0 |
| World total: | 0 | 0 | 0 | 4 | 8 | 13 | 5 | 0 |

**FIGURE 3.** Temporal and geographic distribution of Archaeoceti based on a survey of the published literature. Note that the first appearance of archaeocetes, as Pakicetidae and Ambulocetidae, is in the latest Ypresian and earliest Lutetian, early middle Eocene, of eastern Tethys (Indo-Pakistan). Protocetidae and Remingtonocetidae predominate in the Lutetian early middle Eocene and are best known from eastern Tethys. Basilosauridae and Dorudontidae predominate in the Bartonian late middle Eocene and Priabonian late Eocene and are best known from the western Atlantic and mediterranean Tethys.

## 1.3.1. Skeletons of Early Middle Eocene *Rodhocetus* and *Dalanistes*

The skeleton of early middle Eocene *Rodhocetus* (Protocetidae) is represented in a diagram of skeletal proportion in Fig. 4, where it is compared to the skeleton of early middle Eocene *Dalanistes* (Remingtonocetidae). Skulls of both differ from those of *Pachyaena* (Fig. 2) in having the external nares (N) open at a position behind the front of the dentary,

and both differ in having a much larger mandibular foramen (F)—this opening is now as high as the auditory bulla (B) is long. A mandibular foramen this large is typical of archaeocetes and later whales with a well-developed acoustic window and wave guide (Norris, 1968), indicating an auditory system specialized for hearing in water.

Vertebral centrum length tends to be more similar to centrum height in *Rodhocetus* and *Dalanistes* compared with what was seen in *Pachyaena*, and cervical vertebrae are relatively shorter compared with those of *Pachyaena*. Cervicals of *Rodhocetus* are particularly noteworthy in having centra that are even shorter than they are high, which is a characteristic of all later archaeocetes, mysticetes, and odontocetes. Shortening the neck is one component of hydrodynamic streamlining characteristic of living whales.

The thoracic, lumbar, and sacral centra of *Rodhocetus* increase progressively in both length and height, retaining just a hint of the central arch seen in land mammals that support their weight on land. There is a central arch in *Dalanistes*, but even here it is less conspicuously developed than in *Pachyaena* (Fig. 2A) because the sacral centra are higher. *Rodhocetus* and *Dalanistes* both have long neural spines on thoracic vertebrae, supporting the idea that they were able to use their forelimbs to lift much of their body weight on land. *Rodhocetus* retains a four-centrum sacrum, although the centra are not fused to each other (open box in Fig. 4A), whereas *Dalanistes* has a four-centrum sacrum with centra solidly fused (shaded box in Fig. 4B). The tail is poorly known in both, but proximal caudals in *Dalantistes* are longer than they are high, suggesting that it had a tail more like that of *Pachyaena*.

Forelimbs have not yet been found for either *Rodhocetus* or *Dalanistes*, but the presence of large pelves (I) and robust femora (F) is consistent with support and movement on land. *Rodhocetus* and *Dalanistes* differ from each other in relative length of the skull. The rostrum of *Rodhocetus* is normally proportioned for an archaeocete, whereas that of *Dalanistes* is unusually long and narrow. There is little doubt that these animals fed differently, and a shorter rostrum and more mobile vertebral column with unfused sacral centra means *Rodhocetus* was a better swimmer and probably an aquatic pursuit predator like later whales, whereas the long rostrum and fused sacrum of *Dalanistes* means it was a slower swimmer and probably an aquatic ambush predator like earlier *Ambulocetus* (Thewissen *et al.*, 1996). These behavioral differences are consistent with differences in cervical centrum lengths and differences in caudal centrum sizes and proportions.

## 1.3.2. Skeletons of Middle to Late Eocene *Dorudon* and *Basilosaurus*

The skeleton of late middle Eocene *Dorudon* (Dorudontidae) is represented in a diagram of skeletal proportion in Fig. 5, where it is compared with the skeleton of late Eocene *Basilosaurus* (Basilosauridae). Skulls of *Dorudon* and *Basilosaurus* differ from those of *Pachyaena* (Fig. 2) and from *Rodhocetus* and *Dalanistes* (Fig. 4) in having the external nares (N) opening farther back on the rostrum. In the vertebral column, cervical centra are much shorter, there is no sacrum, and the thoracolumbar or central and caudal or posterior vertebral arches together form a single long vertebral arch. These are different in detail but similar in overall functional conformation to vertebral arches of extant odontocetes and mysticetes (compare with profiles in Fig. 6). Forelimbs are now well known in *Dorudon* (Uhen, 1996) and *Basilosaurus* (Kellogg, 1936; Gingerich and Smith, 1990) and the humerus (H) is always much longer than forearm bones like the radius (R). The elbow joint
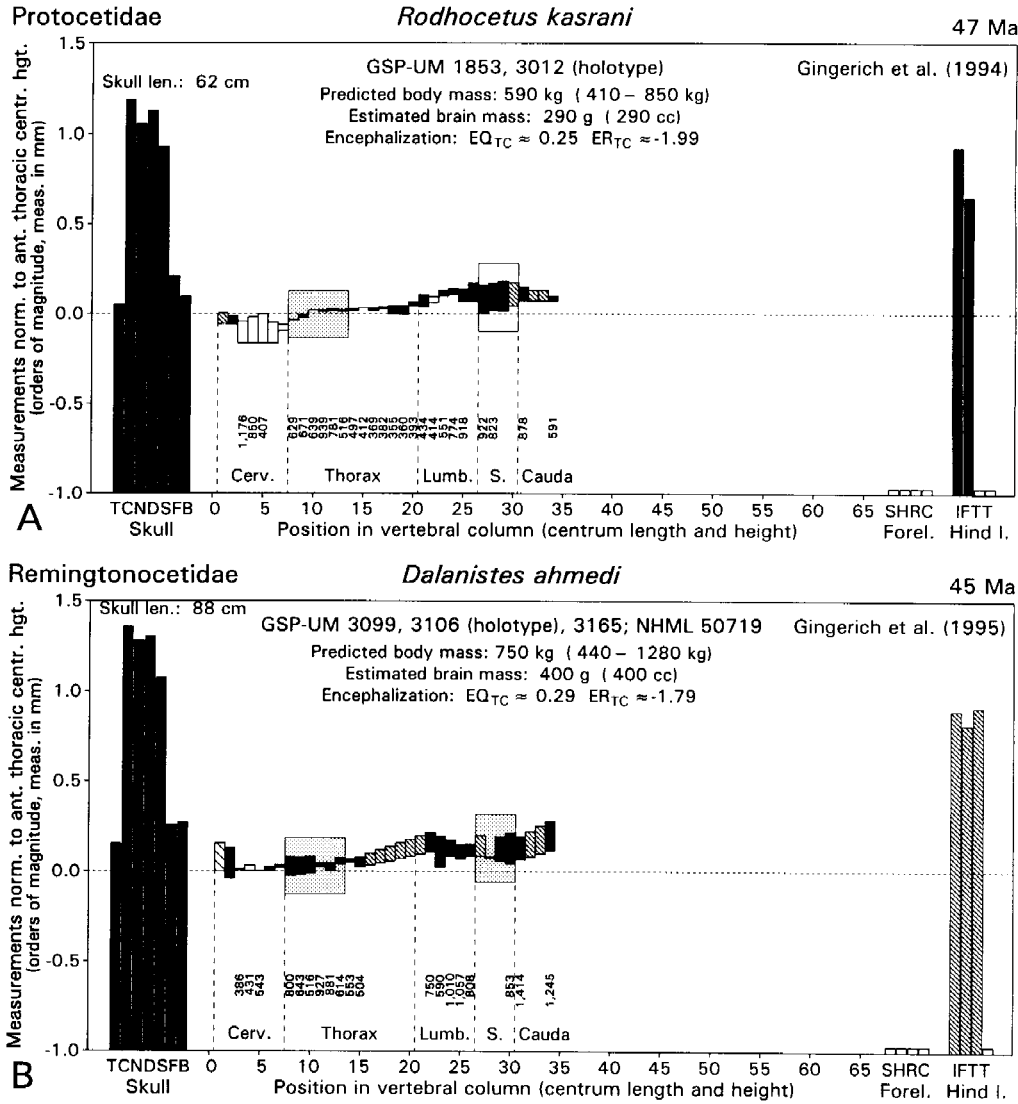
**FIGURE 4.** Diagrams of skeletal proportion comparing skull, vertebral, forelimb, and hind limb lengths and proportions of the early middle Eocene protocetid archaeocete *Rodhocetus kasrani* (A) with those of the contemporary and slightly later remingtonocetid archaeocete *Dalanistes ahmedi* (B). All measurements are those described in Fig. 2. Note that *Dalanistes* has a longer skull compared with the rest of its skeleton, but proportions within the skull are similar. Skulls of *Rodhocetus* and *Dalanistes* differ from those of *Pachyaena* and *Canis* (Fig. 2) in having the external nares and mandibular symphysis located more posteriorly. *Dalanistes* has shorter cervicals for its size than *Pachyaena*, and those of *Rodhocetus* are shorter still. *Dalanistes* has a central vertebral arch connecting stable anterior thoracics to a stable sacrum that is similar to those of *Pachyaena* and *Canis* but flatter, and the posterior arch appears to be *Pachyaena*-like as well. *Rodhocetus* has an even flatter thoracolumbar vertebral column and no indication of the caudal arch. There is a four-centrum sacrum in *Rodhocetus* but these vertebrae are not fused and hence they were not stable like those of land mammals (shown diagrammatically as an open box). Forelimbs of *Rodhocetus* and *Dalanistes* are not yet known. Both genera have substantial innominates and femora that are similar in size relative to the rest of the skeleton, although the femur of *Rodhocetus* is shorter than that of

is still mobile in both. Hind limbs are present in both *Dorudon* and *Basilosaurus* though these are reduced in size both relative to the forelimbs and relative to hind limbs in earlier archaeocetes. Because there is no trace of a sacrum and the pelvis floated in muscle in the ventral body wall, it was impossible for either *Dorudon* or *Basilosaurus* to support its weight on land and both were clearly fully aquatic.

The principal differences between skeletons of *Dorudon* and *Basilosaurus* are the relative sizes and shapes of posterior thoracic, lumbar, and anterior caudal vertebrae. This shows clearly in the diagrams of skeletal proportion of Fig. 5. In *Basilosaurus* the ninth thoracic is notably longer than the eighth and it is notably longer than either is high. This increase in size affects both length and height separately and affects the two together as well, hence the marked change in shape. Elongation of thoracic through caudal centra gives *Basilosaurus* its anguilliform body shape, but the increase in centrum height (and width) over the proportion seen in *Dorudon* suggests more is happening than simple elongation, which must have affected swimming in important ways. Vertebrae of *Basilosaurus* are sometimes densely mineralized and heavy when found as fossils, but when these are not secondarily permineralized they are fragilely cancellous and light. In life they were marrow-filled, and surface-to-volume allometry means enlargement would have made them more buoyant. Large buoyant vertebrae suggest that *Basilosaurus* lived predominantly at the sea surface rather than being a three-dimensional diving swimmer like *Dorudon*, which is consistent with Slijper's (1946) interpretation, from vertebral metapophyses and neural spines, that *Basilosaurus* moved partly by lateral undulation.

## 1.4. Body Mass of Mesonychids and Archaeocetes

Mesonychians are typical land mammals for which body mass can be estimated in the usual ways, from long bone lengths and diameters (e.g., Gingerich, 1990) and tooth size (e.g., Legendre and Roth, 1988). Zhou (1995) found that body masses estimated from long bone lengths and diameters were closely collinear with log $M_2$ lengths and diameters for the 14 mesonychid specimens (representing six genera and ten species) having both, scaling like mass to carnassial size in felid Carnivora. From this he derived a regression equation for predicting body mass in kilograms from $M_2$ crown area in square millimeters: log $Y = 1.327 \log X - 1.457$. Zhou found that mesonychids ranged from about 7 to 194 kg in body mass. Gunnell and Gingerich (1996) extended this to Hapalodectidae and found body masses ranging from about 1 to 8 kg. Thus, Hapalodectidae all fall in the 0.5 to 10 kg range that is considered medium-sized in mammals, whereas most Mesonychidae fall in the 10 to 250 kg range of large mammals.

Archaeocetes may have been similar to mesonychids when they originated, but archaeocetes are not typical land mammals. Skulls, necks, tails, forelimbs, and hind limbs are

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*Dalanistes. Dalanistes* and *Rodhocetus* are intermediate in skeletal proportions and vertebral profile between land mammals like early Eocene *Pachyaena* and later fully aquatic archaeocetes like *Dorudon* (Fig. 5). Body mass predictions here are based on comparison with vertebrae of marine mammals (see text), and brain masses are estimated from endocranial casts associated with skulls. Calculation of encephalization quotients (EQ) and residuals (ER) is explained in the text.
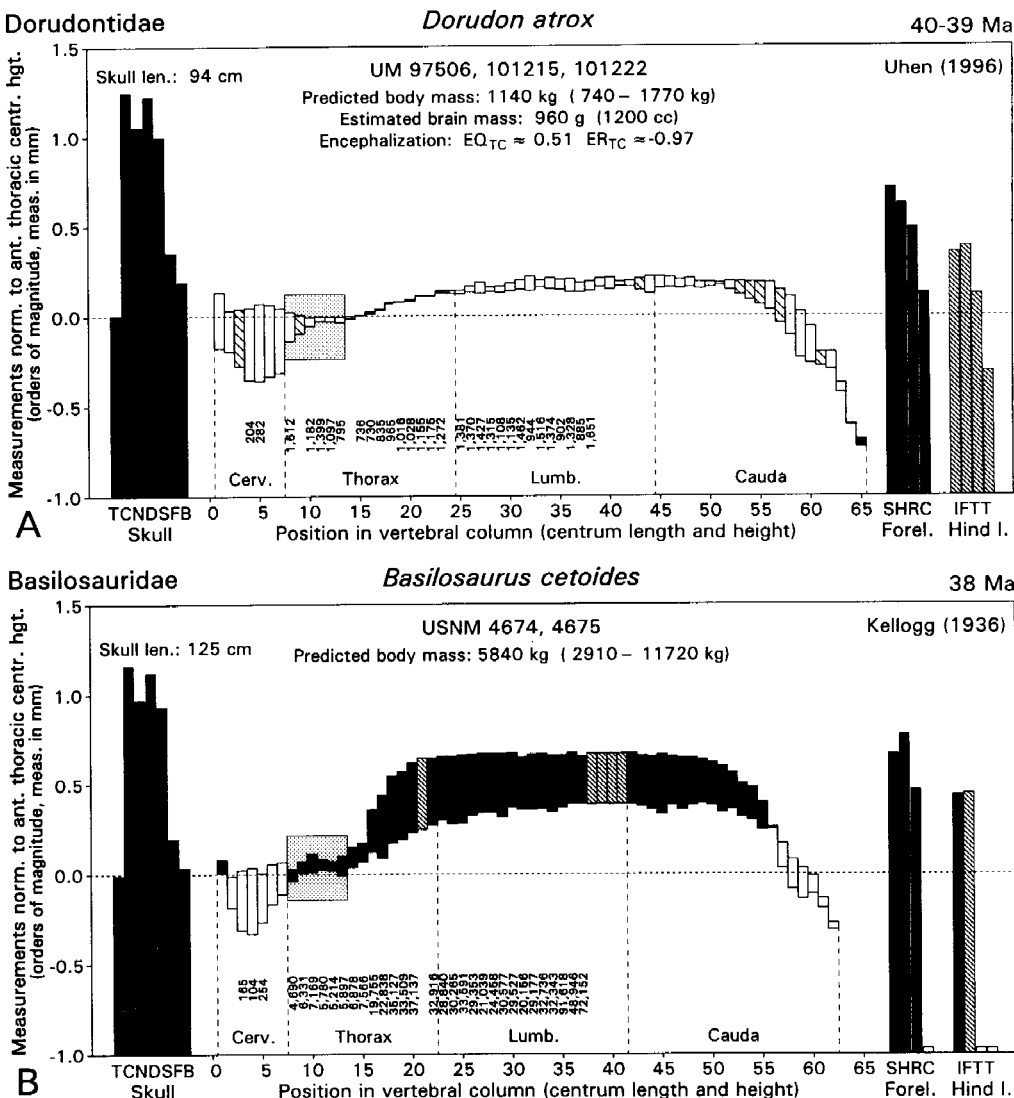
**FIGURE 5.** Diagrams of skeletal proportion comparing skull, vertebral, forelimb, and hind limb lengths and proportions of the late middle Eocene dorudontid archaeocete *Dorudon atrox* (A) with those of the slightly later basilosaurid archaeocete *Basilosaurus cetoides* (B). All measurements are those described in Fig. 2. Note that skulls of *Dorudon* and *Basilosaurus* are similar in relative size and proportions to that of *Rodhocetus*, though the external nares are positioned more posteriorly, closer to the position of the mandibular symphysis. Both have shorter cervicals for their size than *Rodhocetus*. The remaining vertebrae of *Dorudon* are almost all shorter than they are high (open rectangles), whereas most of the remaining vertebrae of *Basilosaurus* are much longer than they are high (solid rectangles). There is no real arch to the central vertebrae and although the anterior thoracics are a stable interval of the column anchoring the forelimbs (shaded box), there is no real sacrum and the rest of the vertebral column is flexible like that of later whales (Fig. 6). *Dorudon* and *Basilosaurus* both have vertebral centra that shorten rapidly after about vertebral position 55 (posterior caudals). Both probably had a caudal fluke of some kind. Forelimbs are large in *Dorudon* and *Basilosaurus,* and the humerus is long (the humerus is even longer than the scapula in *Basilosaurus*). Both genera had reduced innominates and femora. Lengths of hind limb elements

commonly enlarged or reduced relative to the rest of the skeleton in archaeocetes (as shown in the diagrams of skeletal proportion here), and for this reason a method for estimating body mass has been developed that is based on selected vertebrae. The reference sample includes eight cetaceans ranging in size from 150 to 23,500 kg and five pinnipeds ranging in size from 85 to 1210 kg. Body mass was regressed successively on vertebral centrum length, width, and height (simultaneously) at each vertebral position from vertebra 2 to vertebra 40, yielding a body mass estimate for each vertebra. These analyses showed that vertebrae 2–3, 6–7, and 38–40 have multiple regression coefficients of determination $(r_2)$ less than 0.5 and estimates based on these were not used. Estimates based on the remaining vertebrae are written vertically at the appropriate position in Figs. 2, 4, 5, and 6. The predicted body mass (and its 95% confidence interval) for an archaeocete species, written near the top of each chart, is the median of all of the separate estimates. Use of the median rather than a mean ensures that outliers attributable to unusual vertebral sizes or proportions have no effect on the final estimate. Predicted body masses for Basilosauridae are based on the median of the first 12 estimates.

## 1.5. Brain Mass and Relative Brain Size of Mesonychids and Archaeocetes

Brain mass is now known for two mesonychids, middle Eocene *Mesonyx obtusidens* (Radinsky, 1976) and early Eocene *Pachyaena ossifraga* (Gingerich, in preparation) and these can be combined with estimated body weights to yield a measure of relative brain size.

As background, analysis of an extensive data base of $\log_{10}$ values of brain and body mass for 778 terrestrial mammalian species yielded a regression slope of 0.740 and a corresponding intercept of $-1.205$ (Gingerich, in preparation). Exponentiating, the brain mass $E_p$ predicted for a given body mass $P$ is $E_p = 0.062\,P^{0.740}$. Analysis order by order yields a weighted mean slope of 0.668 and intercept of 0.104 that are very close to the familiar values of 2/3 and 0.12 used by Jerison (1973) to calculate encephalization quotients (EQ). I interpret Jerison's scaling to be that expected for *terrestrial mammals analyzed at an ordinal scale*. Here (and in general) we are concerned with mammals as a class, comparing individual species or groups of species in relation to the whole. The corresponding EQ is $EQ_{TC}$ (where T refers to *terrestrial* and C refers to a *class*-level taxonomic scale). Volant and marine mammals scale differently, but $EQ_{TC}$ is appropriate as an initial baseline, even when volant or marine mammals are considered, because both evolved from terrestrial ancestors. EQ is calculated as the ratio of observed brain mass $E$ (in grams) to brain size $E_p$ predicted for a given body mass $P$ (also in grams). Finally, EQs assume the asymmetrical and unequally scaled range of values typical of ratios, ranging from infinitesimally small to unity (when observation = prediction) to infinitely large. There are both practical and

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for *Dorudon atrox* are scaled down from those of *Basilosaurus isis*, which they resemble closely in preserved parts (proximal half of femur, patella, and astragalus). Comparable hind limb elements of these genera are substantially shorter than those of *Rodhocetus* or *Dalanistes* (Fig. 4). *Dorudon* is intermediate in skeletal proportions and vertebral profile between earlier archaeocetes like *Dalanistes* and *Rodhocetus* (Fig. 4) and later odontocetes and mysticetes (Fig. 6). Body mass predictions here are based on comparison with vertebrae of marine mammals (see text), and brain mass of *Dorudon* is estimated from endocranial casts associated with skulls. Calculation of encephalization quotients (EQ) and residuals (ER) is explained in the text.
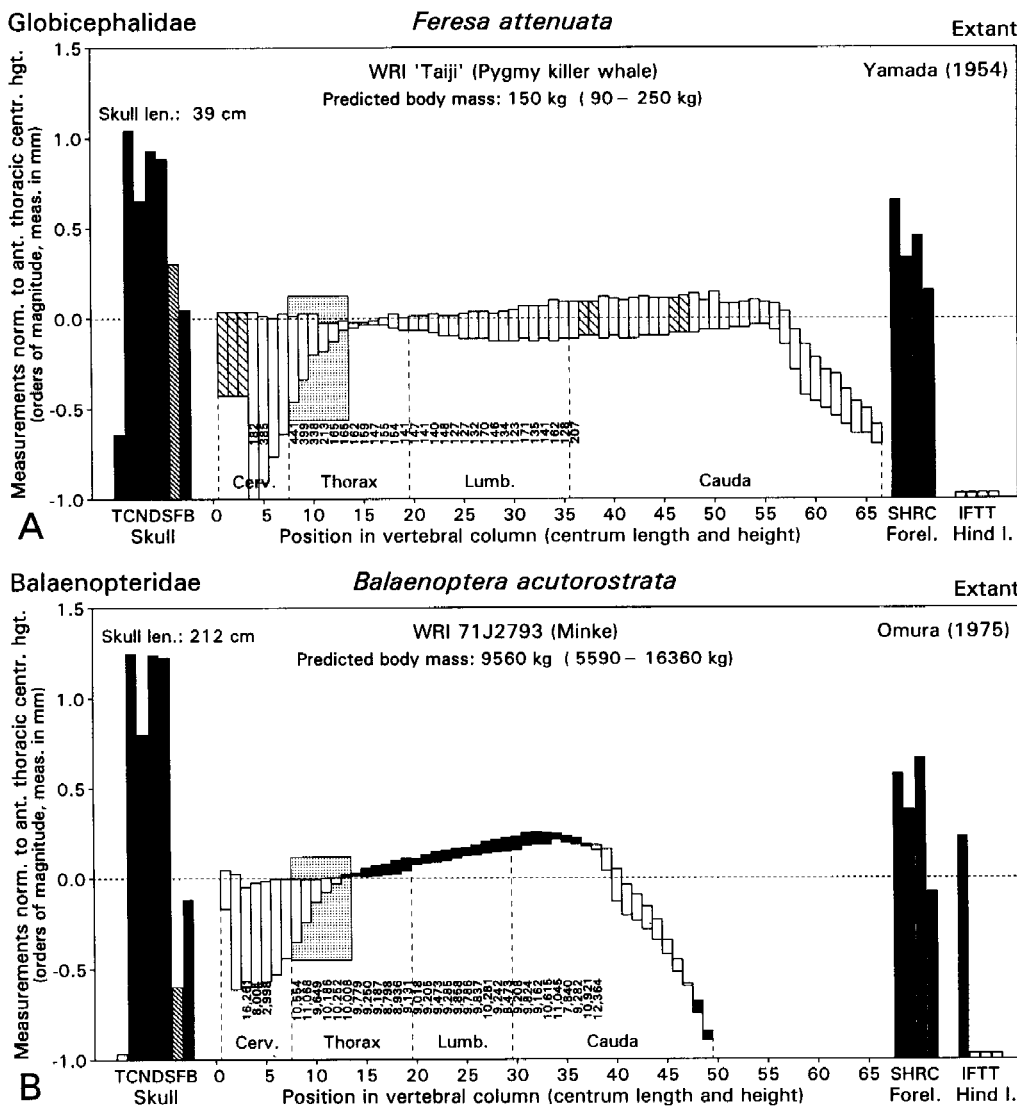
**FIGURE 6.** Diagrams of skeletal proportion comparing skull, vertebral, forelimb, and hind limb lengths and proportions of the extant globicephalid odontocete *Feresa attenuata* (A) with those of the extant balaenopterid mysticete *Balaenoptera acutorostrata* (B). All measurements are those described in Fig. 2. Note that *Balaenoptera* has a longer skull, compared with the rest of its skeleton, whereas *Feresa* has a larger mandibular canal and larger auditory bulla. *Feresa* has smaller teeth than those of archaeocetes, relative to other measures of size (and *Balaenoptera* of course has lost its teeth). Both have external nares positioned farther back on the skull than do archaeocetes. *Feresa* and *Balaenoptera* both have short cervical vertebrae. Thoracic, lumbar, and caudal vertebrae of *Feresa* are more numerous and more uniform in size than those of *Balaenoptera*. There is a single flattened vertebral arch behind the anterior thorax and there is no sacrum. Posterior caudal vertebrae decrease rapidly in size, as in *Dorudon* and *Basilosaurus*, and the tail is of course fluked. Forelimbs of *Feresa* and *Balaenoptera* are similar to those of advanced archaeocetes, but the humerus is shorter. Both have innominates as remnants of the hind limb (not plotted here), and *Balaenoptera* often retains a femur as well (again, not plotted here). *Feresa* and *Bal-*

theoretical advantages to comparing relative brain size in terms of ER, an encephalization residual on a doubling scale, where ER can be calculated from EQ as $ER = \log_2 (EQ)$. ERs have a symmetrical and equally scaled range from negative infinity to zero (when observation = prediction) to positive infinity. Familiar EQ and corresponding ER values are both reported here.

Radinsky (1976) estimated the endocranial volume of *Mesonyx obtusidens* to be 80 cm² representing a brain of about 80 g. He estimated the body mass of *M. obtusidens* from skull length and body length, and calculated body masses of about 40 and 55 kg. The corresponding $EQ_{TC}$s are 0.51 and 0.40, respectively ($ER_{TC}$s are $-0.98$ and $-1.32$). The endocranial volume of *Pachyaena ossifraga* is 40 cm³, corresponding to a brain of about 40 g (one-half the size estimated for *M. obtusidens*). The body mass of *P. ossifraga* is abut 65 kg (Zhou *et al.*, 1992). These numbers yield an $EQ_{TC}$ for *Pachyaena* of 0.18 ($ER_{TC} = -2.50$), which is less than one-half that of *Mesonyx* (the genera differ by more than one unit on a proportional halving-doubling or $\log_2$ scale).

Jerison (1973, 1978), following Dart (1923), reported that the endocranial volume (and corresponding brain mass) of *"Dorudon" osiris* was about 480 cm³ (g); that of *"Dorudon intermedius"* was about 780 cm³ (g); and that of *"Prozeuglodon atrox"* was about 800 cm³ (g). Jerison estimated body masses of the three species as 350, 530, and 20,000 kg. $EQ_{TC}$s calculated from these numbers would be 0.61, 0.73, and 0.05, respectively ($ER_{TC} = -0.71$, $-0.45$, and $-4.29$), which seem seriously discrepant in archaeocetes that are sometimes classified in the same family and are the same or almost the same age geologically. Three problems are confounded here. The first is systematic, Dart's endocranial casts represent two species, not three. These are now identified (Gingerich, 1992) as *Saghacetus osiris*, for which Dart (1923) published endocranial volumes of 310 cm³ (for a subadult) and 480 and 490 cm³ for adults; and as *Dorudon atrox*, for which Dart (1923) published endocranial volumes of 785 and 800+ cm³ for subadults. Jerison, following the literature (e.g., Barnes and Mitchell, 1978), associated the latter with postcranial remains now known to be *Basilosaurus isis* (Gingerich *et al.*, 1990), for which no brain casts or endocranial volumes were known at the time Jerison was writing. University of Michigan field parties working in Egypt have recovered new endocasts of all three species associated with identifiable skulls and postcranial skeletons: These average 485 cm³ for *S. osiris*, 1200 cm³ for *D. atrox*, and 2800 cm³ for *B. isis*.

The second problem with Jerison's interpretation of brain size in archaeocetes is in conversion of endocranial volume to brain mass. Marples (1949) and Breathnach (1955) showed that much of what Dart (1923) interpreted as a massive cerebellum in Egyptian archaeocetes is really a large intracranial vascular rete mirabile. Uhen (1996) has recently estimated that this comprises some 20% of endocranial volume in *Dorudon atrox*. *Saghacetus, Dorudon*, and *Basilosaurus* are at a similar grade of brain expansion, with similar retia, and their endocranial volumes of 485, 1200, and 2800 cc are thus thought to correspond, respectively, to 388, 960, and 2520 g brain masses.

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*aenoptera* illustrate the skeletal proportions of modern fully aquatic cetaceans, which are not very different from those of *Dorudon atrox* (Fig. 5A). Body mass predictions here are based on comparison with vertebrae of marine mammals (see text), and these agree closely with published body masses for each species (150 and 9000 kg, respectively; Watson and Ritchie, 1981).

The third problem with interpretation of brain size in Egyptian archaeocetes has to do with estimation of body mass for the three species. The method described here yields predicted body masses of 350 kg (identical to Jerison's estimate) for *Saghacetus osiris*, 1140 kg for *Dorudon atrox* (Fig. 5A; more than double Jerison's estimate), and 6480 kg for *Basilosaurus isis* (slightly heavier than the estimate of *B. cetoides* in Fig. 5B, but much less than Jerison's estimate of 20 metric tons). Combining these new estimates of brain mass with new estimates of body mass yield reasonably consistent $EQ_{TC}$ estimates of 0.49, 0.51, and 0.37 ($ER_{TC}$ = $-1.02$, $-0.97$, and $-1.43$). Middle-to-late Eocene archaeocetes have $EQ_{TC}$ values averaging about 0.46, meaning that they have brains about 46% as large as those of an average terrestrial mammal of the same body mass living today. Stating the same result in terms of residuals, middle-to-late Eocene archaeocetes have $ER_{TC}$ values averaging about $-1.13$, meaning that they have brains a little more than one unit smaller on a proportional $\log_2$ scale than expected for a terrestrial mammal of the same body mass living today.

For comparison, endocranial volumes of early middle Eocene *Rodhocetus kasrani* and *Dalanistes ahmedi* are given in Figure 4, along with body mass estimates. From the morphology of the endocasts it is clear that there was no substantial intracranial vascular rete in either of these genera, as there was none in *Indocetus* (Bajpai et al., 1996), and brain mass is thus essentially the same as endocranial volume. $EQ_{TC}$s calculated for *R. kasrani* and *D. ahmedi* are 0.25 and 0.29, respectively ($ER_{TC}$ = $-1.99$ and $-1.79$). Early middle Eocene archaeocetes have $EQ_{TC}$ values averaging about 0.27, meaning that they have brains about 27% as large as those of an average terrestrial mammal of the same body mass living today. Stating the same result in terms of residuals, middle-to-late Eocene archaeocetes have ER values averaging about $-1.89$, meaning that they have brains almost two units smaller on a proportional $\log_2$ scale than expected for a terrestrial mammal of the same body mass living today. This is 0.76 of a unit less than the encephalization of middle-to-late Eocene archaeocetes.

## 2. Trends in the Morphology and Adaptation in Archaeoceti

Eocene Archaeoceti are important for understanding the land-mammal ancestry of whales because they are intermediate in time, space, and form between slightly earlier Paleocene and early Eocene Mesonychidae and slightly later Oligocene Mysticeti and Odontoceti. Mesonychids are found in early Eocene sediments on the Central Asian and Indo-Pakistan continental masses bordering eastern Tethys to the north and south. Eastern Tethys is where we have the best record of early archaeocetes.

The morphological intermediacy of archaeocetes can be seen by comparing profiles of archaeocete skeletal proportions in Figs. 4A and 5A with those of *Pachaena* in Fig. 2A and extant cetaceans in Fig. 6A,B. Tooth size (T) was large throughout archaeocete evolution before teeth were reduced in odontocetes and lost in mysticetes. Nasals moved back on the skull through time, as reflected by the depth of the notch in the profiles over N compared with flanking skull length (C) and dentary length (D). Similarly, the height of the mandibular foramen (F) expanded to equal and exceed auditory bulla length (B, before receding again in mysticetes).

Three trends are clear in the vertebral column. The length of cervicals decreased at

each stage relative to overall size while the cervical height remained almost constant, meaning that cervical shape changed greatly as well. Second, the central vertebral arch involving posterior thoracic, lumbar, and sacral vertebrae, and the posterior vertebral arch involving caudal vertebrae merged into a single relatively straight-sided arch with reduction and finally elimination of the sacrum as an intermediate point of support. Inflection of this single arch is effectively where it was in the posterior of the original arches. In addition, vertebrae composing the new arch assumed a more equidimensional shape as their functions became more uniform and more uniformly shared. Trends in the fore- and hind limbs are less clear in the diagrams of skeletal proportion, although the former were modified into flippers and the latter lost all external exposure.

I have quantified several other changes in the transition from mesonychids to cetaceans in Figs. 7 and 8. These involve body size, trophic specialization as indicated by size of the largest tooth, auditory specialization as indicated by bulla length (reflected too in size of the mandibular canal), hydrodynamic streamlining and limb reduction as indicated by femur length (reflected too in shortened cervical vertebrae).

## 2.1. Body Size

A graph of body masses for archaeocetes of different ages is shown in Fig. 7A, where these are compared with the body mass ranges of Mesonychidae and modern Cetacea. Archaeocetes for which body mass can be estimated reliably have masses similar to but larger than those estimated for most mesonychians. Thewissen *et al.* (1996) estimated that *Ambulocetus* weighed 141–235 kg from cross sections of long bones but I have used my own estimate of 720 kg based on vertebral size. Archaeocetes fall comfortably within the range of body masses of extant cetaceans (cf. Downhower and Blumer, 1988). There is a trend toward larger body mass through the course of the middle and late Eocene but archaeocetes of relatively small mass are known from the late Eocene (e.g., *Saghacetus*) and the trend involves an expansion of the range of body masses upward through time.

## 2.2. Trophic Specialization

Figure 7B shows a trend toward larger tooth size through time in archaeocetes, but this trend follows the trend toward larger body mass very closely and it can be explained largely as a consequence of the increasing range of body sizes (see Fig. 8B). The length of the largest cheek tooth in archaeocetes is no larger than that of mesonychids, but interestingly the largest cheek tooth in mesonychids is usually $M_2$ where as that in archaeocetes is usually $P^3$ or $P_3$. Furthermore, incisors of *Pakicetus* are delicate and pointed (Gingerich and Russell, 1990), unlike those of any known mesonychid. Both of these differences from mesonychids imply that the change to a characteristically archaeocete dentition and trophic specialization was achieved very early in archaeocete evolution. There was some experimentation with cranial and dental specialization in ambulocetids and remingtonocetids early in archaeocete evolution, presumably related to feeding. Later archaeocetes are remarkably uniform cranially and dentally, and trophic specializations, to the extent these were important, involved differences in swimming to catch prey.
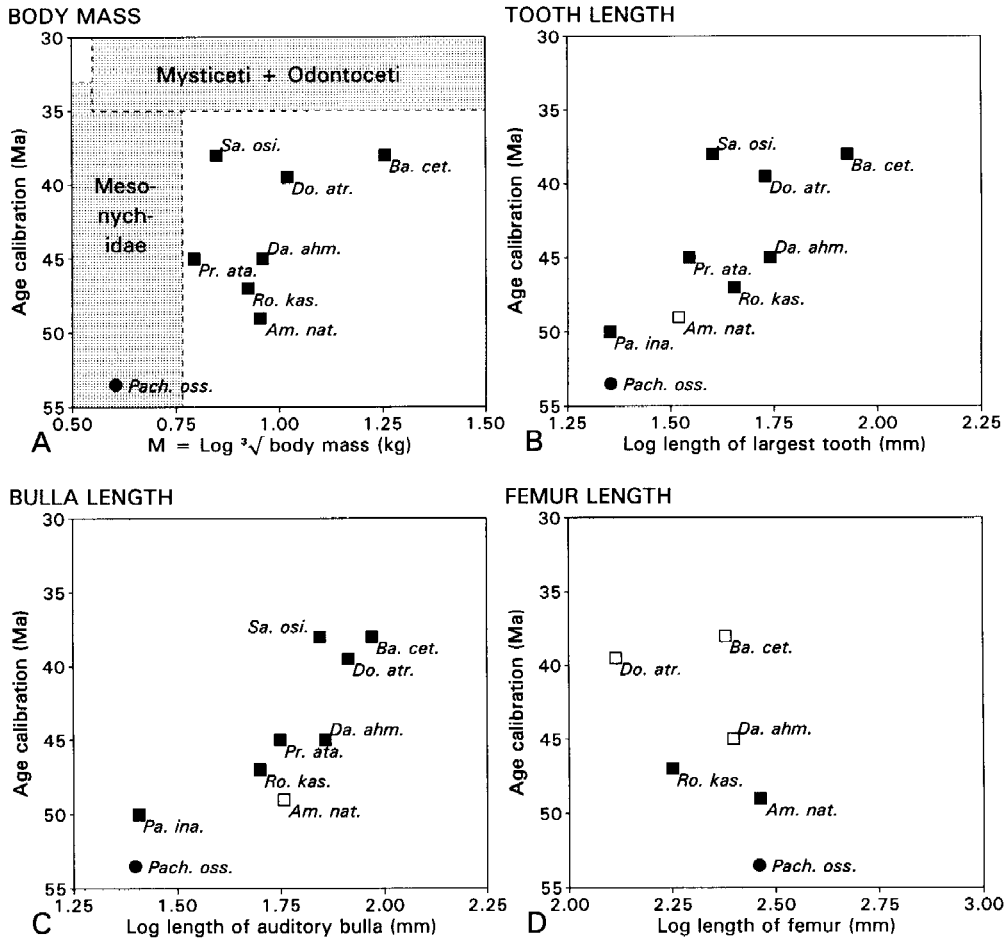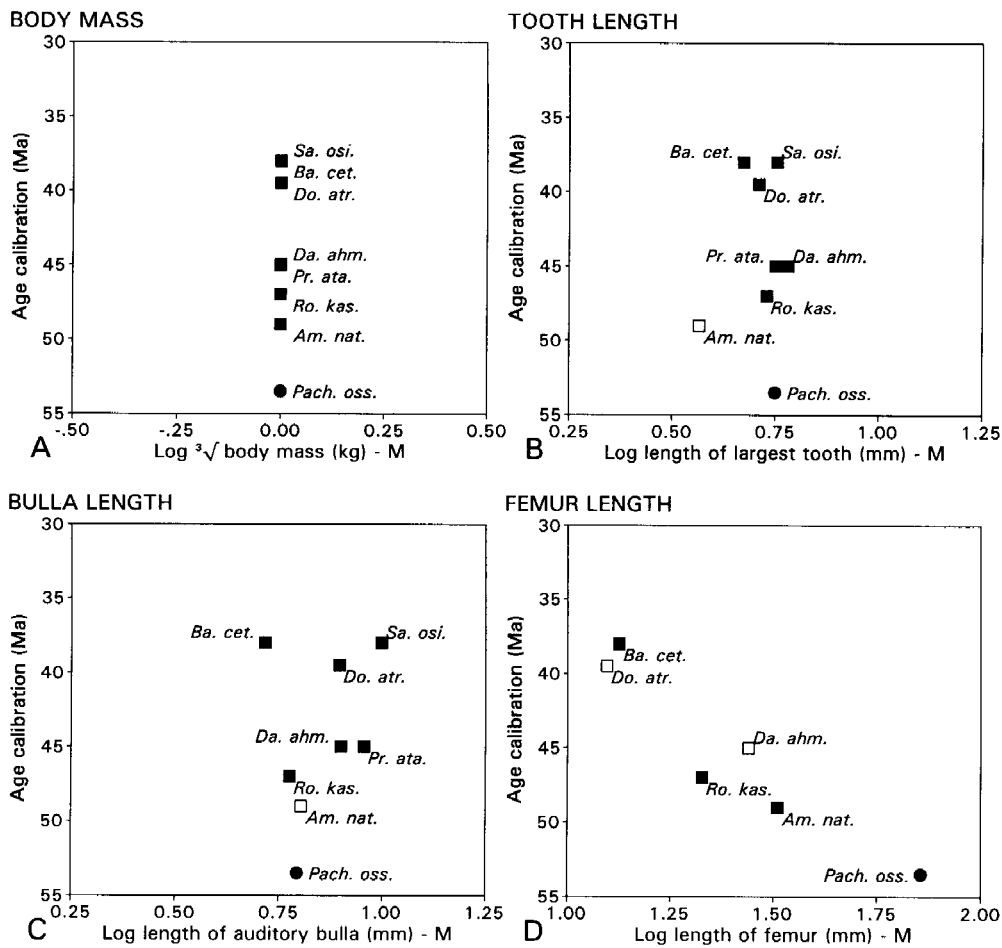
**FIGURE 7.** Trends of changing body mass (A), tooth length (B), auditory bulla length (C), and femur length (D) in the evolution of Archaeoceti. The same trends are normalized in Fig. 8 by subtracting body mass. Note that archaeocetes are generally larger than Mesonychidae, and hence much larger than Hapalodectidae and Wyolestidae, but lie within the broad range of body masses of extant cetaceans. Body masses of archaeocetes increased through time largely as a result of an expansion of their range of variation. Increase in tooth sizes largely reflects the increase in body masses. Bulla length increased in size through time, but this appears to have happened more rapidly early, e.g., between *Pakicetus* and *Ambulocetus*, and less rapidly later. Femur length decreased in size through time. Solid circle is mesonychid *Pachyaena ossifraga*. Solid and open squares are archaeocetes (*Am. nat.*, *Ambulocetus natans; Ba. cet.*, *Basilosaurus cetoides; Da. ahm.*, *Dalanistes ahmedi; Do. atr.*, *Dorudon atrox; Pa. ina.*, *Pakicetus inachus; Pr. ata.*, *Protocetus atavus; Ro. kas.*, *Rodhocetus kasrani; Sa. osi.*, *Saghacetus osiris*; symbol is open when values are estimated or, in the case of tooth length in *Ambulocetus*, when the tooth measured may not have been the longest).

**FIGURE 8.** Size-normalized trends of body mass (A), tooth length (B), auditory bulla length (C), and femur length (D) in the evolution of Archaeoceti (compare with Fig. 7). A tightly clustered vertical distribution like that for tooth length means most observed variation can be explained by differences in body mass. Bulla size is only partially explained by increasing body mass, and the presence of relatively large bullae in small *Saghacetus osiris* and small bullae in large *Basilosaurus cetoides* suggests that there is some intermediate optimum size. Femur length decreased in size through time and this trend is stronger when body mass is taken into account. Symbols as in Fig. 7.

## 2.3. Auditory Specialization

Figure 7C shows the size of the auditory bulla in archaeocetes of different ages for which bulla size is known. This pattern too appears at first to be similar to that for tooth length, but there is more separation between *Pakicetus* and other archaeocetes. When *Pakicetus* is set aside, auditory bullae appear to increase slightly in size through time, but this change is not so great as would be expected from the expansion in range of known body masses. When the effect of body mass on bulla size (Fig. 8C) is subtracted as it was for tooth

size, the remaining variance is larger than that for tooth size, the largest late archaeocete (*Basilosaurus*) has the smallest bullae, and the smallest late archaeocete (*Saghacetus*) has much larger bullae for its body size. This suggests that bulla size in archaeocetes is determined by a common factor like the density or some related acoustic characteristic of sea water in addition to archaeocete body size. The relatively small auditory bullae of mysticetes (Fig. 6B) support this idea.

## 2.4. Hydrodynamic Streamlining and Hind Limb Reduction

One of the most interesting changes in archaeocete evolution is reduction of the hind limb from a limb size typical of land mammals to the small limb of *Basilosaurus* and *Dorudon*. Reduced limbs in late archaeocetes probably retained a functional role in reproduction, but these are clearly too small to support the body on land (Gingerich *et al.*, 1990). Disarticulation of innominate bones of the pelvis from the sacrum is part of the same trend. Reduction of the hind limb can be represented by femur length, which shows a trend toward smaller absolute size through time while overall body mass is increasing (Fig. 7D). Subtracting the effect of changing body mass shows this to be an even stronger trend. Reduction of the hind limb coincides with shortening of cervical vertebrae, and both are part of the hydrodynamic streamlining necessary for efficient swimming. The greatest reduction relative to body size is seen in middle to late Eocene dorudontids and basilosaurids, which lack any articulation of innominate bones with the vertebral column and also have short cervical vertebrae. There is little doubt that *Dorudon* and *Basilosaurus* were fully aquatic, with all of the life history changes (e.g., precocial birth) that this implies. *Dorudon* appears to have been an efficient tail-powered swimmer like modern whales (Uhen, 1996), whereas *Basilosaurus*, though fully aquatic, was divergently specialized (possibly as more of a floating than diving mammal—see above).

## 2.5. Encephalization

The encephalization quotients ($EQ_{TC}$) and residuals ($ER_{TC}$) calculated above to represent relative brain size are most meaningful when interpreted in the context of similar values for mesonychids and for extant cetaceans. These comparisons are shown graphically in Fig. 9. Early archaeocetes appear to have had the encephalization of mesonychids, with $ER_{TC}$ in the range of $-1.5$ to $-2.5$ indicating brains about one-quarter (two halvings) the size of those expected for a terrestrial mammal of the same size living today. Later archaeocetes had larger brains, but these were still smaller than expected for a mammal of the same size living today.

When we compare the relative brain size of extant whales, they span virtually the full range of sizes seen in terrestrial mammals living today. Mysticetes tend to have brains smaller than expected for their body mass, which can be explained in part by their unusually large body masses made possible by hydrostatic support in an aquatic medium. However, odontocetes tend to have brains larger than expected for their body mass, while their body mass tends to be large in comparison with terrestrial mammals. If a correction were to be made to brain-size-in-relation-to-body-size to account for increased body mass re-
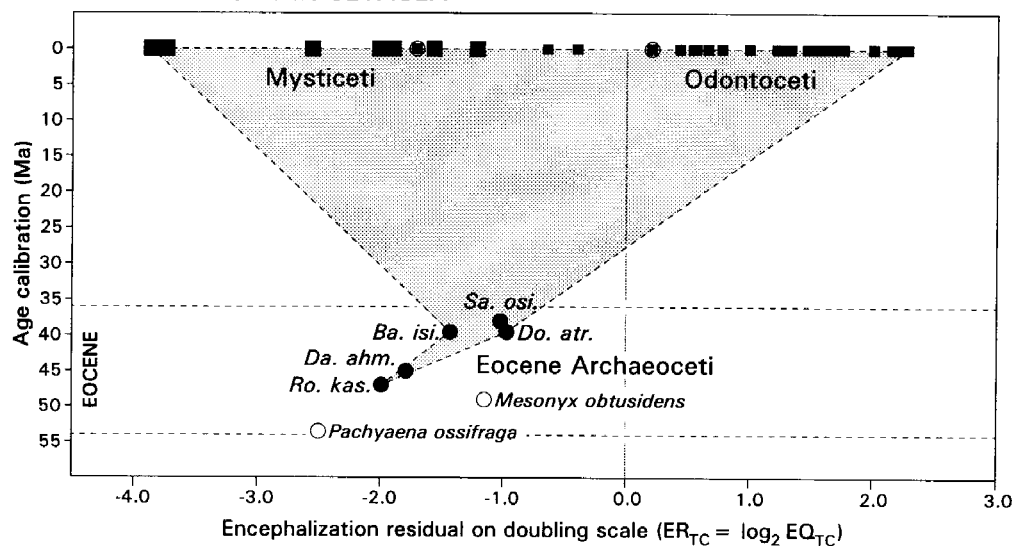
RELATIVE BRAIN SIZE IN CETACEA



**FIGURE 9.** Pattern of change of relative brain size through geological time in Eocene Archaeoceti compared with relative brain sizes of Mysticeti and Odontoceti living today. Relative brain size is plotted as an encephalization residual (ER) on a $\log_2$ doubling scale, where the reference group is terrestrial mammals analyzed as a class. An encephalization residual has the advantage that zero is the null expectation and equivalent proportional differences are represented by equal arithmetic distances. Mysticetes are represented by larger solid squares, odontocetes by smaller solid squares, and physeterids (sperm whales) by small squares within circles. Note that all mysticetes have brains smaller than expected for an average terrestrial mammal living today and most odontocetes have brains larger than expected for an average terrestrial mammal living today (*Physeter*, with ER in the mysticete range, is a conspicuous exception). Archaeocete encephalization residuals (solid circles) lying between about $-2.00$ in *Rodhocetus* (Fig. 4A) and about $-1.00$ in *Dorudon* (Fig. 5A) span approximately the range of overlap of extant mysticetes and odontocetes. Taxonomic abbreviations are the same as in Fig. 7. Mesonychid encephalization residuals, where known (open circles), are shown for comparison.

sulting from an aquatic medium, odontocetes as a group would undoubtedly prove to have the largest brains of all mammals.

## 3. Summary and Conclusions

The most important thing that can be said about Eocene Archaeoceti is that they are beginning to fill the temporal, geographic, and morphological gap between Paleocene land mammals and Oligocene and later whales. The temporal and geographic distributions of Mesonychia and Archaeoceti in Figs. 1 and 3 support this. Size-adjusted comparisons of morphological characteristics of the skull, vertebral column, forelimb, and hind limb in Figs. 2, 4–6 show the general pattern of change from a wolflike mesonychid model ancestor through primitive remingtonocetid and protocetid archaeocetes to more advanced dorudontid and basilosaurid archaeocetes, to modern mysticetes and odontocetes. Charac-

teristics of archaeocetes such as body mass, tooth size, auditory bulla size, femur length, and relative brain size are documented in Figs. 7–9, which are related to progressive trophic, auditory, locomotor, cognitive, and life history adaptation to life in the sea.

The fossil record does not support, indeed it positively refutes, Kellogg's (1936) idea that Archaeoceti, Mysticeti, and Odontoceti were separated during a "long interval" of geological time. We no longer view the archaeocete skull as divergent from the line of development that led to the telescoped condition seen later. Similarly, I do not think anyone working on archaic whales would now argue with Simpson (1945) that Cetacea arose very early from a relatively undifferentiated eutherian ancestral stock (i.e., Mesonychia—"very early" would still be during the Paleocene or early Eocene; Gingerich and Uhen, 1998). Boyden and Gemeroy's early serological association of Cetacea with Artiodactyla and Van Valen's linking of mesonychids to the ancestry of archaeocetes and later cetaceans are now widely accepted. Primitive archaeocetes are much better known than they were when Van Valen studied mesonychid ancestry of archaeocetes, and we can now cite much broader morphological trends in support of his general hypothesis.

Of the three broad objectives I list for study of fossil whales, we are beginning to have enough intermediates to say with confidence what happened in the transition of whales from land to sea. We can see that important changes took place at different times, with trophic dental changes happening at the beginning of the archaeocete radiation (Gingerich *et al.*, 1983), auditory changes happening next (Thewissen and Hussain, 1993; Luo and Gingerich, in press), and locomotor adaptation to a fully aquatic life happening later (Gingerich *et al.*, 1994), but there is still much to be learned about the context of the transition from land to sea. Finally, it is still too early to say very much about the consequences of change in archaeocetes for their morphological disparity, taxonomic diversity, or taxon longevity.

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