

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 sub-order, 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							
<i>Hapalodectes</i>				A,N	A		
<i>Hapalodectes?</i>			A				
<i>Hapalorestes</i>					N		
MESONYCHIDAE							
<i>Ankalagon</i>		N	N				
<i>Dissacus</i>		A,N	A,E,N	E,N	E		
<i>Dissacusium</i>		A					
<i>Harpagolestes</i>					A,N	A,N	A
<i>Hessolestes</i>					N	N	
<i>Honanodon</i>					A		
<i>Honanodon?</i>				A			
<i>Hukoutherium</i>	A?	A					
<i>Jiangxia</i>			A				
<i>Lohoodon</i>					A	A	
<i>Mesonyx</i>			A?		A,N		
<i>Metahapalodectes</i>					A		
<i>Mongolestes</i>							A
<i>Mongolonyx</i>					A		
<i>Olsenia</i>						A	
<i>Pachyaena</i>			A	E,N			
<i>Pachyaena?</i>					A		
<i>Plagiocristodon</i>			A?	A?			
<i>Sinonyx</i>			A				
<i>Synoplotherium</i>					N		
?ANDREWSARCHIDAE							
<i>Andrewsarchus</i>					A		
<i>Paratriisodon</i>					A		
?WYOLESTIDAE							
<i>Wyolestes</i>				N			
<i>?Mongoloryctes</i>					A		
<i>?Yantanglestes</i>		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-

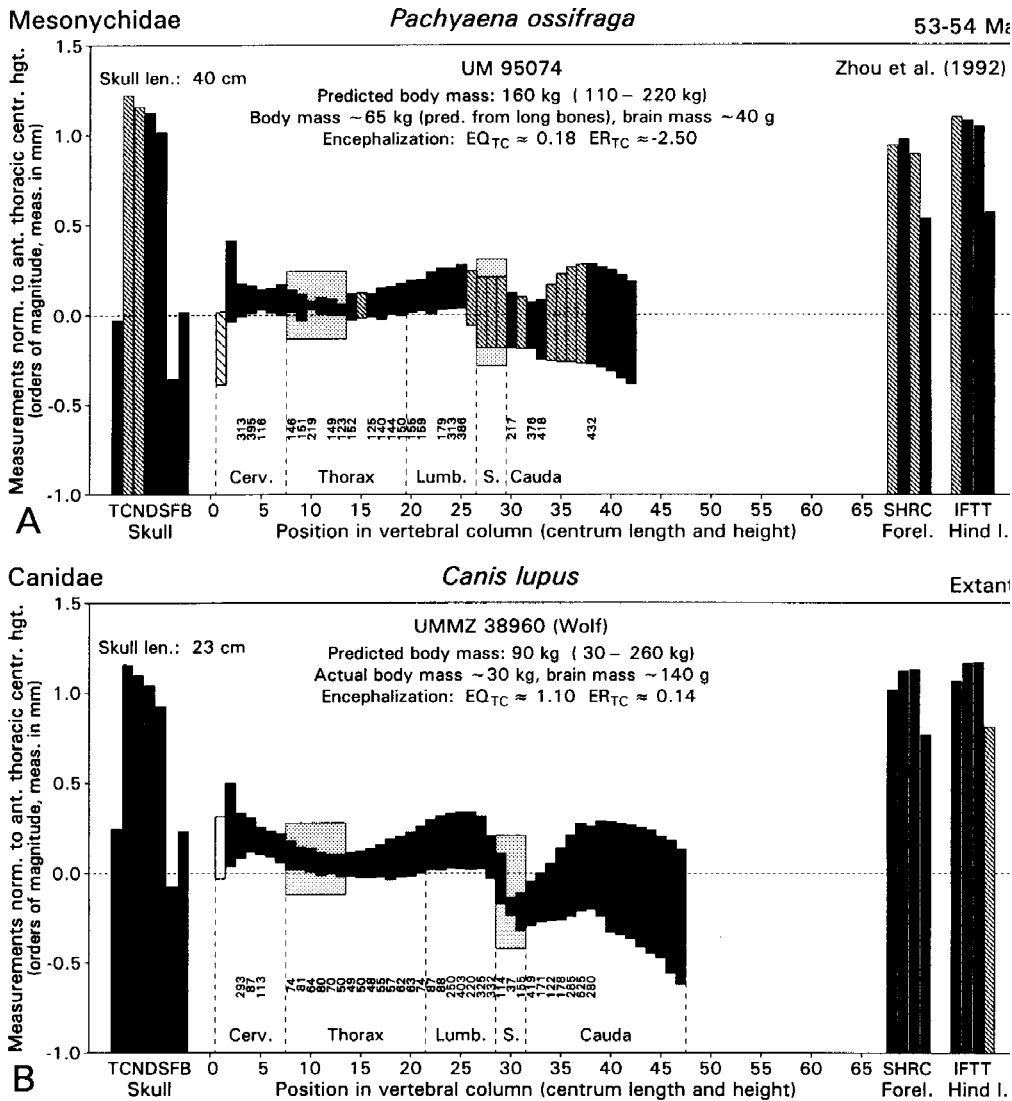


FIGURE 2. Diagrams of skeletal proportion comparing skull lengths, vertebral lengths and heights, forelimb long bone lengths, and hind limb long bone lengths of the early Eocene mesonychid *Pachyaena ossifraga* (A) to those of the skeletally similar extant wolf *Canis lupus* (B). All measurements are 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.