

## Phylogenetic Aspects of Cetacean Origins: A Morphological Perspective

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The evolutionary steps leading up to the origin of cetaceans involved pervasive changes in the masticatory apparatus, the ear, and limb morphology. These changes bear heavily on the phylogenetic relationships of Cetacea, and are investigated here on the basis of two of its earliest members: *Pakicetus* and *Ambulocetus*. A phylogenetic analysis of cetaceans, five groups of mesonychians, and five other groups of ungulates indicates that *Pakicetus* is the sister group to all other cetaceans, and that Cete (mesonychians and Cetacea) is a monophyletic group.

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**KEY WORDS:** Cetacea; Archaeoceti; Condylarthra; Mesonychia; phylogeny.

### INTRODUCTION

Van Valen's (1966) insightful study of cetacean ancestry cleared the way to the realization that the closest relatives of Cetacea are the broadly defined ungulates. This clade includes, among recent mammals, not only artiodactyls and perissodactyls, but also proboscideans, sirenians, and hyracoids (see McKenna, 1975). Cetacean-ungulate relationships are now supported by both morphological (e.g., Barnes et al., 1985; Fordyce, 1980; Novacek, 1994) and molecular (e.g., Milinkovitch, 1992) evidence. Among extant groups, artiodactyls are most commonly proposed to be the sister group of cetaceans. Among fossil taxa, different mesonychians, a taxon that in the past was classified among the paraphyletic Condylarthra, are usually linked to cetaceans. Understanding of the phylogeny of archaic ungulate groups is poor because the morphology of many of these groups is poorly understood, and because extant members of ungulate clades are profoundly different from the earlier members of their orders.

Molecular investigations of the sister group of cetaceans have been hampered by the fact that important extinct groups, such as mesonychians, cannot be studied. This is particularly problematic because fossil groups are known to influence topologies of phylogenetic trees of modern clades (Gauthier *et al.*, 1988; Novacek, 1992; Prothero, 1993). Morphological investigations have been hampered by the fragmentary nature of the fossil record, in particular that of the earliest ungulates and the taxa that are transitional between

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terrestrial quadrupeds and aquatic cetaceans. In addition, comprehensive revisions are available for only a few archaic ungulate (condylarth) families, and there is no stable higher phylogeny for these taxa. A summary outline of archaic ungulate phylogeny, partly based on the work of Prothero *et al.* (1988), is provided by Archibald (in press).

There are several excellent reviews of early cetacean evolution (e.g., Barnes and Mitchell, 1978; Barnes *et al.*, 1985; Fordyce, 1992; Fordyce and Barnes, 1994), but these have become somewhat outdated with the recent recovery of important new archaic cetaceans. At present, research on cetacean origins and sister group relations is advancing at a rapid pace. Molecular data for more relevant taxa are now available and more and more workers study different molecules (e.g., Milinkovitch *et al.*, 1993; Árnason and Gullberg, 1994; Irwin and Árnason, 1994; Milinkovitch *et al.*, 1994). Also, the potential for recovering more fossil material concerning cetacean origins is especially exciting as several researchers are concentrating on the remains of early forms (e.g., Bajpai, 1990; Gingerich *et al.*, 1993, 1994; Hulbert, 1992, 1993, 1994; Thewissen and Hussain, 1993; Thewissen *et al.*, 1994). At least as relevant are new studies of cetacean relatives; new mesonychian material is being described by O'Leary and Rose (in press a and b), Rose and O'Leary (in press), Zhou *et al.* (1992 and in press) and Zhou (1995).

The understanding of cetacean origins is at present in a state of flux and phylogenetic summaries constructed on the basis of material that has only been presented in a summary fashion are prone to become outdated rapidly. Therefore, I will focus here on the position of two ancient cetaceans, *Pakicetus* and *Ambulocetus*, in the phylogenetic scheme of archaic ungulates (Fig. 1). I will analyze a small number of salient morphological changes that play a key role in unravelling cetacean relations. Based on these data and a literature review of additional morphological and molecular results, I find morphological support for two clades proposed previously: Cetacea and Cete, and discuss the potential relatives of the latter. Cetacea and Cete will probably hold up under further scrutiny, but refinement of these phylogenetic hypotheses can only occur when the morphology of early cetaceans and their relatives is better documented. For now, there is sufficient evidence to recognize these clades as part of a working hypothesis. This hypothesis predicts that a number of morphological attributes are present in the cetacean morphotype which can be tested when more material is discovered for the most primitive cetaceans (notably *Pakicetus*).

## MATERIALS AND METHODS

For inclusion in my morphological analysis, I have chosen taxa for which much of the anatomy is known, that are close in time to the original divergence of cetaceans, and that play an important role in archaic ungulate evolution (Fig. 1).

*Pakicetus* (West, 1980; Gingerich and Russell, 1981, 1990; Gingerich *et al.*, 1983; Thewissen and Hussain, 1993) is commonly considered to be the earliest known cetacean. Although only cranial and dental remains have been described, it has played an important role as an ancestral cetacean in reviews of their evolution (Barnes *et al.*, 1985; Fordyce, 1992). The cetacean *Ichthyolestes* Dehm and Oettingen-Spielberg (1958) is found at the same stratigraphic levels as *Pakicetus*. This taxon is at present too poorly known to be significant in analyzing the higher phylogeny of cetaceans. *Ichthyolestes*

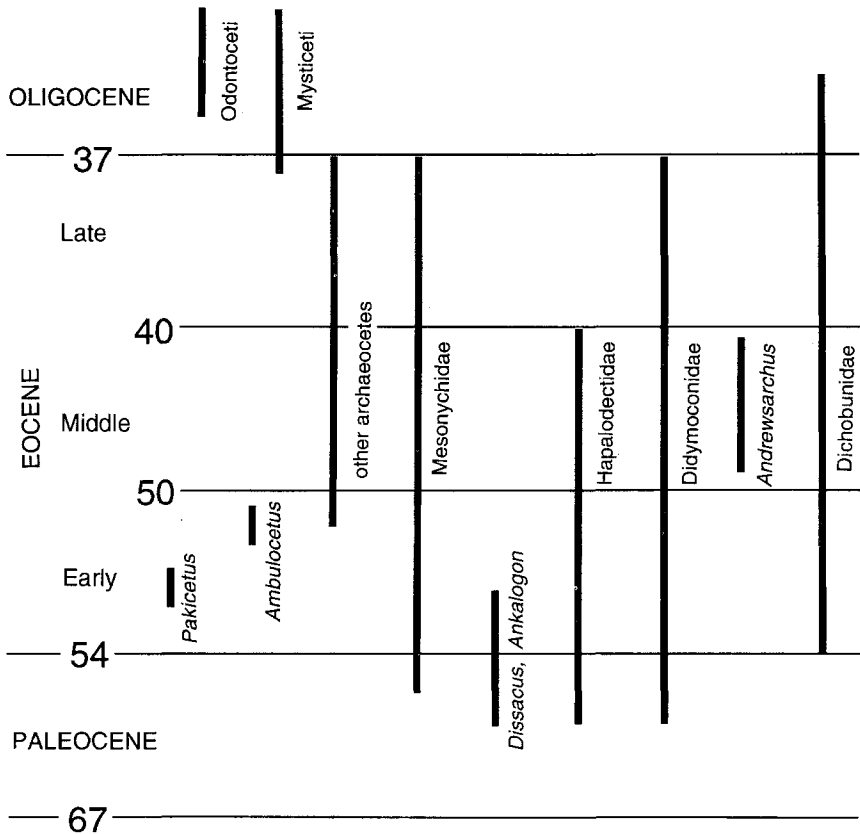


Fig. 1. Approximate chronological ranges for cetaceans and their relatives. Ages are in million years and are approximate. Cetacean ranges are discussed in more detail by Fordyce (1992) and Fordyce and Barnes (1994).

has also been recovered in the redbeds of the Subathu Formation of northern India (Kumar and Sahni, 1985), whereas marine cetaceans are known from beds underlying these redbeds. The Subathu redbeds have been correlated with those of the Kuldana Formation (Wells and Gingerich, 1987), but their associated mammalian fauna suggests that all Subathu cetaceans postdate Kuldana *Pakicetus* and *Ichthyolestes* (Thewissen *et al.*, 1987; Thewissen and McKenna, 1992).

Much of the skeleton is known for the archaeocete *Ambulocetus* (Thewissen *et al.*, 1994). It is known from the same formation as *Pakicetus*, but slightly later in time. *Ambulocetus* is the only primitive archaeocete for which most of the limbs is known. Therefore, it plays a pivotal role in cetacean origins (Novacek, 1994), and its morphology led Berta (1994) to suggest that the definition of Cetacea needs to be re-evaluated.

All other cetaceans are treated here as a single group. Several important primitive archaeocetes included in this presumed clade are not described in detail yet [e.g., *Indocetus* (Sahni and Mishra, 1975; Gingerich *et al.*, 1993); *Rodhocetus* (Gingerich *et al.*, 1994)]. However, based on the present insights, these taxa are more derived than either *Pakicetus* or *Ambulocetus* and therefore would have little effect on the basal nodes.

Hulbert's (1994) parsimony analysis of archaeocete taxa showed that *Pakicetus* is the lowest node within cetaceans. To study interordinal relations, primitive members are of greater interest than derived members (Novacek, 1992; Thewissen and Domning, 1992).

The mesonychians [= Acreodi of some authors, e.g., McKenna (1975)] are probably paraphyletic with respect to cetaceans. In the past, mesonychians were often considered a family of Condylarthra. Here, I only use the term mesonychians to refer to the loose assemblage of five fossil groups, each of which may be monophyletic: Hapalodectidae, Mesonychidae, *Dissacus*, Didymoconidae, and Andrewsarchidae. A comprehensive study of all taxa included in these families is beyond the scope of this study. I follow Archibald (in press, mainly based on Prothero *et al.*, 1988) for the genera included in Mesonychidae. Hapalodectidae here is based on *Hapalodectes* only (Ting and Li, 1987). The position of *Dissacus* and *Ankalogon* is controversial. Prothero *et al.* (1988) and Archibald (in press) consider these genera closely related to *Hapalodectes*, but traditionally they were considered as mesonychids. Zhou *et al.* (in press) considered *Dissacus* to be the sister group of a clade consisting of all other mesonychids. Until this problem is studied in detail, I will not assign *Dissacus* (and closely related *Ankalogon*) to either family. In this analysis, these two genera are treated as a separate clade.

The taxa composing didymoconids were reviewed by Gingerich (1981), but are not always considered to be part of mesonychians (Archibald, in press). The dental structure of the referred didymoconid genera is sufficiently similar to mesonychians that they do need to be considered as possible cetacean relatives. I have not used the morphology of the type genus *Didymoconus* in scoring this family, because it is unlike the referred genera. *Andrewsarchus* is commonly considered to constitute a monotypic clade within mesonychids (Szalay and Gould, 1966; Zhou *et al.*, in press). It is of special importance because Prothero *et al.* (1988) proposed that it was the sister group of cetaceans.

As a whole, mesonychians are in need of revision. New material is currently studied by O'Leary and Rose (in press a and b, and Rose and O'Leary, in rev.), and by X. Zhou and colleagues (e.g., Zhou and Gingerich, 1991; Zhou *et al.* 1992 and in press; Zhou, in prep.). Pending these new studies, my analysis of mesonychian characters is based on published material for a number of genera: mesonychid characters are mainly based on *Mesonyx* (Scott, 1888), *Pachyaena* (Matthew, 1915; Zhou *et al.*, 1992; O'Leary and Rose, in press b), *Sinonyx* (Zhou *et al.*, in press), and *Harpagolestes* (Szalay and Gould, 1966; Szalay, 1969a; West 1981). Scoring for Hapalodectidae is based on *Hapalodectes* (Szalay and Gould, 1966; Ting and Li, 1987). Scores for *Dissacus* and *Ankalogon* are based on descriptions by Osborn and Earle (1895), Szalay (1969a,b), and O'Leary and Rose (in press a). Didymoconid characters are based on *Wyolestes* (Gingerich, 1981), *Archaeoryctes* and *Ardynictis* (Matthew and Granger, 1924). *Andrewsarchus* scores were based on descriptions by Osborn (1924) and Szalay and Gould (1966).

Artiodactyls are represented in this study by dichobunids, their most primitive family (Gentry and Hooker, 1988). *Diacodexis* is one of the most primitive genera and is well known anatomically (Coombs and Coombs, 1982; Thewissen *et al.*, 1983, Rose, 1982, 1985; Russell *et al.*, 1983; Krishtalka *et al.*, 1985; Thewissen and Hussain, 1990).

Archaeocetes, mesonychians, and dichobunids are the focus of this study, but Arc-toeyonidae, Hyopsodontidae, Phenacodonta (Phenacodontidae and Meniscotheriidae) and Pantomesaxonia (Perissodactyla, Hyracoidea, Proboscidea, Sirenia, and Desmostylia) are also important. I have included data for phenacodontids and primitive perissodactyls,

and their discussion is mainly based on the evidence presented by Thewissen and Domning (1992).

## DISCUSSION OF MORPHOLOGICAL CHARACTER SUITES

I will here put some of the changes in early cetacean evolution into a broader functional context. Emphasis is placed on the overall pattern of changes that occurred at various nodes in cetacean phylogeny, suggesting that some of these changes are not independent. A more comprehensive study of taxa will be necessary to test their functional coherence and will eventually form the test for my phylogenetic hypotheses.

My focus is on three morphological character complexes that changed at various steps in the cetacean/ungulate cladogram and that may be functionally linked to some degree. These three complexes are masticatory, auditory, and locomotor morphology.

### Character Complex 1: Masticatory Morphology

*Overall Trends.* Archaeocetes and odontocetes have characteristic specializations of the teeth, jaws, and masticatory muscles, primarily adaptations to catching slippery prey in a dense medium. These changes were not necessarily acquired at the same phylogenetic node and different aspects of this transition may support different clades. Overall, archaeocetes have a narrow snout with long, pointed incisors, a morphology common in piscivores (Massare, 1987). The narrowness of the premaxilla and dentary affects the position of the incisors in the jaw and modifies the morphology of the mandibular symphysis.

Cheek tooth function in primitive mammals involves adduction (closing) as well as mediolateral movements of the jaws (Hiimae and Crompton, 1985), and results in crushing, grinding, and cutting motions. Adduction is the only important masticatory motion in modern cetaceans; they do not chew their food. Mediolateral movements, produced by contraction of masseter and medial pterygoid muscles, are reduced. The region of origin of the masseter, the zygomatic arch, is also reduced. The temporalis of most extant cetaceans is small, but this muscle, as well as the masseter, are large in archaeocetes, including the late Eocene forms (Carpenter and White, 1986).

The talonid basin of *Pakicetus* molars is reduced, suggesting that grinding motions were not important. However, two crushing areas, indicated by heavy wear, occur in its molars: the hypoconid against the trigon basin and the trigonid against cranial and caudal sides of the trigon (Fig. 2). This type of crushing was caused mainly by adduction of the jaws.

*Anatomical Correlates.* Prothero *et al.* (1988) used the antero-posterior alignment of the incisors to characterize Cetacea, and Gingerich *et al.* (1993) suggested that these teeth were not juxtaposed in the early members of the order. Both characters hold for *Pakicetus*, but not for mesonychia (Szalay and Gould, 1966; West, 1981; Ting and Li, 1987). A narrow snout with long, pointed incisors is a synapomorphy for cetaceans (Table I). Prothero *et al.* (1988) observed that  $I^{2-3}$  are aligned with the cheek teeth in *Andrewsarchus*, but the same is also true for *Diacodexis* (Thewissen *et al.*, 1983).

Premolar evolution foreshadows the eventual simplification of cheek tooth morphology of extant cetaceans. Most primitive ungulates (arctocyonids, hyopsodontids, phenacodontids) have semi-molariform premolars:  $P_4$  usually has a metaconid, and  $P^4$

Table I. Character Matrix for Some Primitive Ungulates<sup>a</sup>

Derived character states	Taxa												
	ce	Am	Pk	me	Ds	Ha	dd	An	dc	ar	hp	ph	hy
Incisors not juxtaposed, set rostro-caudally	1	?	1	0	0	0	0	0	0	0	0	0	0
P <sup>4</sup> protocone absent	1	1	1	1	0	0	01	1	0	0	0	0	0
P <sup>4</sup> metacone absent	1	1	1	01	0	0	0	1	1	0	0	0	0
P <sup>4</sup> paracone height twice that of M <sup>1</sup>	01	1	1	0	0	0	0	?	0	0	0	0	0
M <sup>x</sup> trigon basin small	1	1	1	1	1	1	1	?	0	0	0	0	0
P <sub>4</sub> metaconid absent	1	1	1	1	1	1	0	?	1	01	01	0	0
M <sub>1</sub> metaconid absent	1	1	0	01	0	0	0	?	0	0	0	0	0
M <sub>x</sub> talonid basin absent	1	1	1	1	1	1	01	?	0	0	0	0	0
M <sub>3</sub> hypoconulid absent	1	1	1	1	1	1	1	?	0	0	0	0	0
Rostral trigonid of molars concave	1	1	1	0	0	1	0	?	0	0	0	0	0
Three-layered enamel	1	?	1	1	1	?	?	?	1	0	0	1	1
Vascular embrasure pits; high trigonids	1	1	1	0	1	1	1	0	0	0	0	0	0
Bony ventral nasopharynx	1	1	?	01	?	0	?	0	0	0	0	0	0
Preglenoid process present, mandibular fossa elevated	1	?	0	1	?	1	1	1	0	0	0	0	0
Falcate processes on basioccipital	1	1	0	0	?	0	?	?	0	0	0	0	0
Pachyosteosclerotic tympanic	1	1	1	0	?	0	?	?	0	0	0	0	0
Sigmoid process present	1	1	1	0	?	?	?	?	0	?	?	0	0
Pachyostic ossicles	1	?	1	?	?	?	?	?	0	0	?	?	0
Rotated ossicles	1	?	1	?	?	?	?	?	0	?	?	?	0
Crus longum absent	1	?	0	?	?	?	?	?	0	?	?	?	0
Crus longum shorter than crus breve	?	?	1	?	?	?	?	?	1	?	?	?	0
Mandibular foramen large	1	1	0	0	0	0	?	?	0	0	0	0	0

commonly has a metacone. The P<sup>4</sup> of *Pakicetus* and *Ambulocetus* have a large paracone with a lingual bulge, but no protocone or metacone (Fig. 2), whereas in mesonychids a metacone may or may not be present (Zhou *et al.*, in press). P<sub>4</sub> bears a single, large cusp, the protoconid, in *Pakicetus* and *Ambulocetus*. Lower premolars without a metaconid also occur in *Diacodexis* (Krishtalka *et al.*, 1985; Sudre *et al.*, 1983; Thewissen *et al.*, 1983), and mesonychians commonly lack this cusp (Matthew and Granger, 1915; Szalay and Gould, 1966). It is present on the last premolars of didymoconids, most arctocyonids and paenungulates. Reduction of upper and lower premolars forms part of a trend accompanying cetacean origins, but they are not aspects of a single functional modification, because the occlusional relations between P<sub>4</sub> and P<sup>4</sup> are limited to the talonid.

Advanced archaeocetes lack a molar protocone, talonid basin and trigon basin, correlated with reduced grinding movement of their teeth. This was used to characterize cetaceans by Prothero *et al.*, (1988). The molars of *Pakicetus* and *Ambulocetus* retain some traits associated with crushing: the trigon basin is small but still present (Fig. 2) and occludes with the single talonid cusp (hypoconid) as in mesonychids and hapalodectids (Szalay, 1969a). Other ungulates, including artiodactyls, arctocyonids, and

Table I. Continued

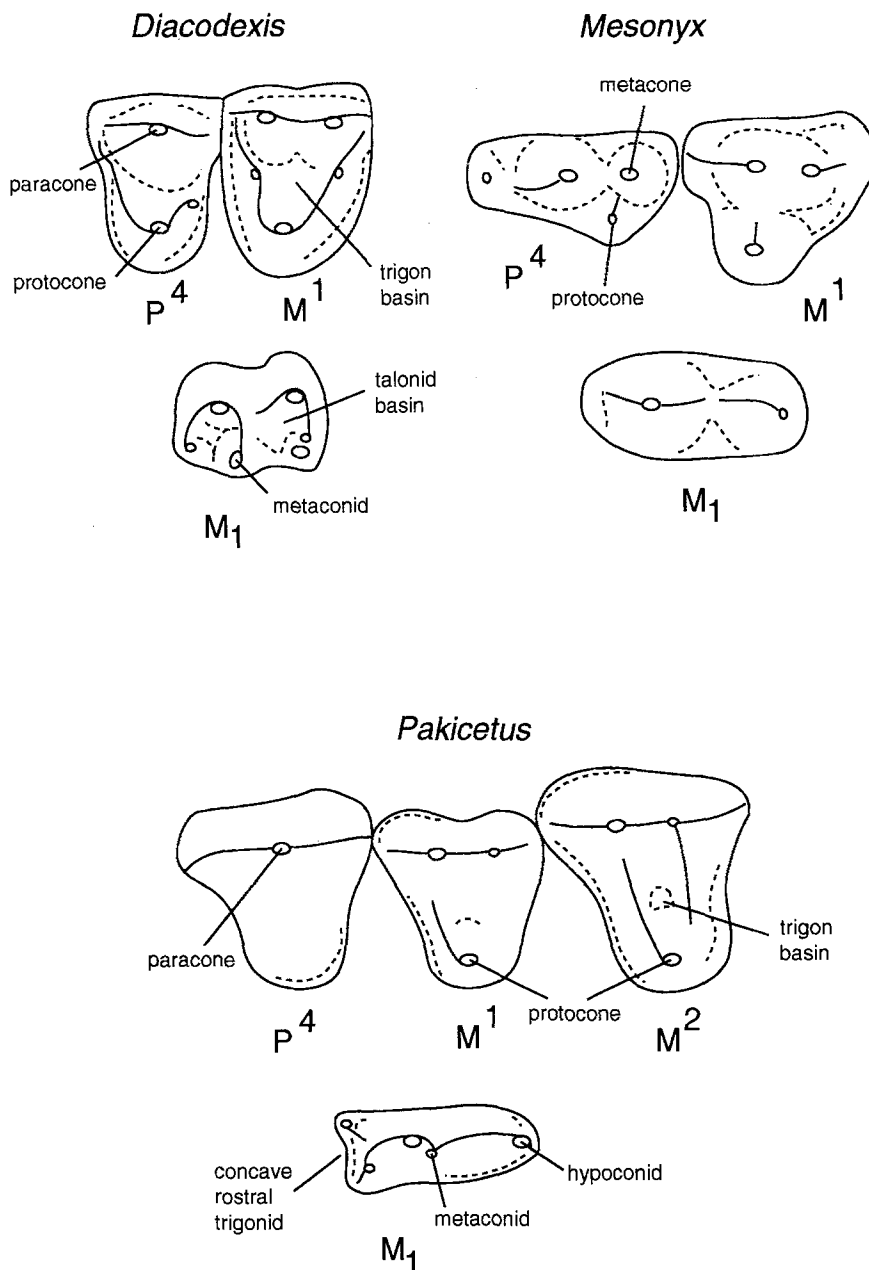
Derived character states	Taxa												
	ce	Am	Pk	me	Ds	Ha	dd	An	dc	ar	hp	ph	Hy
Hypoglossal foramen close to jugular foramen	1	1	1	?	?	0	?	?	0	0	0	0	0
Pterygoid sinus present	1	1	0	0	?	0	?	0	0	0	0	0	0
Clavicle absent	1	?	?	?	?	?	?	?	0	0	0	0	1
Elbow fixed semipronated	1	1	1	1	1	1	?	?	0	01	0	1	1
Centrale absent	0	0	?	0	0	?	?	?	1	01	1	1	1
Astragalar head parasagittal	?	?	?	1	1	?	?	?	1	0	0	0	0
Astragalar trochlea excavated	?	1	?	1	1	?	?	?	1	0	0	1	1
Foot paraxonic	1	1	?	1	?	?	?	?	1	0	0	0	0
Hoof-like unguals	?	1	?	1	1	?	?	?	0	0	0	1	1
Anterior palatine foramina absent	1	?	0	0	?	0	0	0	0	0	0	0	0
Lacrima expanded on face	01	1	?	1	?	0	?	?	1	0	0	0	0
Round foramen separate from sphenorbital fissure	0	0	0	1	?	1	?	?	0	1	0	0	1
Postglenoid foramen absent	1	?	1	1	?	0	?	1	0	0	0	0	0
Large hyoid arch	1	1	?	?	?	?	?	?	0	?	?	0	0
Elongate blastocyst	1	?	?	?	?	?	?	?	1	?	?	?	0
Smooth muscle-based penile erection	1	?	?	?	?	?	?	?	1	?	?	?	0
Three primary bronchi	1	?	?	?	?	?	?	?	1	?	?	?	0

<sup>a</sup>Primitive character states = 0, derived character states = 1, both primitive and derived character states occurring = 01. Taxa: ce, derived archaeocetes; Am, *Ambulocetus*; Pk, *Pakicetus*; me, mesonychids; Ds, *Disaccus* (including *Ankalogon*); Ha, *Hapalodectes*; dd, didymoconids; An, *Andrewsarchus*; dc, dichobunid artiodactyls (*Dicodexis*); ar, arctocyonids; hp, hyopsodontids; ph, phenacodontids; hy, hyracotheres.

hyopsodontids, display the primitive placental morphology: strong protocones, and large trigon and talonid basins. Associated with the reduction of the talonid is the loss of a large hypoconulid on M<sub>3</sub>. Although this cusp is primitively large in ungulates (Matthew, 1937; Van Valen, 1978), it is absent in mesonychians and cetaceans.

The molar trigonid is also remodelled; it loses the triangular shape of primitive mammals by reduction of the paraconid and metaconid. Both cusps are present in many mesonychians and *Pakicetus* (Fig. 2), but the metaconid of *Ambulocetus* is probably absent. This reduction makes the trigonid wedge-shaped and best suited for its main function, crushing between its rostral side and the caudal trigon of the molar rostral to it and between its caudal face and the rostral trigon of the subsequent upper molar. In addition, the rostral side of the lower molars is concave medio-laterally (re-entrant groove of Ting and Li, 1987). Prothero *et al.* (1988) listed addition of accessory cusps on the molars as a cetacean character, but these cusps are absent in *Pakicetus*, *Ambulocetus*, as well as in *Protocetus* (Kellogg, 1936).

The maxilla is excavated between consecutive upper molars and these depressions (embrasure pits) have many vascular foramina in mesonychians (Gingerich, 1981; Szalay, 1969a; Ting and Li, 1987) and cetaceans. Vessels passing through these foramina could perfuse a keratinous pad that might prevent damage from the hard food objects that are forced between upper molars by the high trigonid. These pits are uncommon among other ungulates which have a low trigonid. In conjunction with the formation of



**Fig. 2.** Simplified diagrams of cheektooth morphology explaining some of the terms used in the text. Cusps are indicated as ovals, crests as lines, and grooves as dashed lines. Shown are the early artiodactyl *Diacodexis*, which has a more or less primitive ungulate dentition. The mesonychian *Mesonyx* shows some of the characters that cetaceans and mesonychians have in common, but also has certain autapomorphies. For the cetacean *Pakicetus* three upper teeth are figured because M<sup>1</sup> is damaged; it was probably similar to M<sup>2</sup>. Figured are left upper premolar and molar(s) and right lower first molar in occlusal view. Superposing the figured upper or lower teeth shows the occlusal relations in an X-ray view. *Diacodexis* is based on a specimen described by Thewissen *et al.* (1983) and *Mesonyx* by Scott (1888). *Pakicetus* specimens are undescribed.



embrasure pits and the development of the high trigonid, the paracone of P<sup>4</sup> is also very high in the earliest cetaceans, but not in mesonychians.

O'Leary and Teaford (1992) suggested that mesonychians ate hard and brittle objects, and that they had few shearing planes on their teeth, consistent with the observations of Szalay (1969a). The high forces on mesonychian teeth could be dissipated in part by the presence of decussation planes in the enamel. Mesonychians and early cetaceans have three-layered enamel: decussating enamel is sandwiched between two layers of radial enamel (Sahni, 1981; Maas and Thewissen, in press). The same is true for *Diacodexis*, many arctocyonids, paenungulates, but not hyopsodontids (Koenigswald *et al.*, 1987; Maas and Thewissen, in press).

The bony ventral wall of the nasopharynx (secondary bony palate) of cetaceans extends farther caudal than that of nearly all land mammals (Kellogg, 1928; Barnes and Mitchell, 1978). In cetaceans, this may give the nasopharynx rigid walls that withstand collapse and backflow of water into the nose during swallowing, or protect the nasopharyngeal duct from damage caused by struggling prey. It is present in *Ambulocetus*, and certain mesonychians (Van Valen, 1966), but not in *Mesonyx* (Scott, 1888), *Sinonyx* (Zhou *et al.*, in press), or hapalodectids (Ting and Li, 1987).

The shape of the lambdoid crest of the skull has also been used to diagnose cetaceans (Prothero *et al.*, 1988). From the sagittal plane it bends strongly ventral, extending in a vertical plane. Somewhat above the level of the zygomatic process of the squamosal it flares laterally and extends more or less horizontally. The lambdoid crest thus describes a sigmoid curve in caudal view. The lambdoid crest gives origin to the temporalis muscle and its shape probably affects the lever arm of part of this muscle, the most important jaw muscle in archaeocetes. This arrangement occurs in *Proctocetus* (Kellogg, 1936) and *Pakicetus* (Gingerich *et al.*, 1983). However, this morphology is also found in large bodied archaic ungulates (e.g., *Arctocyon*, Russell, 1964; *Sinonyx*, Zhou *et al.*, in press). It also occurs to a lesser extent in primitive dichobunids (Brunet and Sudre, 1980; Russell *et al.*, 1983), where it is less pronounced as a result of the (proportionally) larger brain. Brainsize scales negatively with bodysize (Eisenberg, 1981), and as a consequence, larger animals have a proportionally smaller braincase than small mammals. This reduces the surface area available for the origin of the temporalis. This reduction may be compensated by enlargement of the sagittal crest. These kinds of allometric differences between brain- and body weight may account for most of the differences in sagittal crest development in mammals of different sizes.

Extensions of the maxillary toothrows on the zygomatic arch is often cited as a synapomorphy for cetaceans, but it does not occur in *Pakicetus* and *Ambulocetus* or the remingtonocetids (Kumar and Sahni, 1986). Kellogg (1928) listed absence of anterior palatine (incisive) foramina as characterizing cetaceans, but these are present in *Pakicetus*.

The position of the mandibular fossa is also systematically important (Kellogg, 1928; Prothero *et al.*, 1988); its surface is somewhat raised (ventrally) over the surface of the root of the squamosal in many cetaceans, partly due to the presence of a preglenoid process. This also occurs in some, but possibly not all (Prothero *et al.*, 1988), mesonychians (Szalay, 1969a). An elevated mandibular joint is not present in *Pakicetus*. The left side of the holotype of *P. inachus* (Gingerich *et al.*, 1981) suggests that a preglenoid

process is present, but this is due to a break in the zygomatic arch. A cast of the specimen shows that the right side was undamaged and lacks a preglenoid process.

The mandibular symphysis of archaeocetes is usually long, extending caudally to the region of the premolars, and this is sometimes suggested to be a cetacean character (Oelschläger, 1987). This is a plesiomorphy: the mandibular symphysis also extends to the premolars in mesonychians [*Harpagolestes*, *Dissacus* (Szalay and Gould, 1966), *Sinonyx*, (Zhou *et al.*, in press)], *Diacodexis* (Thewissen *et al.*, 1983), and many other archaic ungulates (e.g., *Chriacus*, *Hyopsodus*, *Ectocion*, *Hyracotherium*).

### Character Complex 2: Auditory Morphology

*Overall Trends.* The ear of modern cetaceans is very different from that of other mammals (Reysenbach de Haan, 1957; Purves, 1966; Ketten, 1991). In part, these differences are adaptations to accommodate the physical properties of underwater sound, which differ from those of airborne sound (Lancaster, 1990). In addition, modern cetaceans have accumulated other specializations which tune the ear to low frequencies (in mysticetes) or high frequencies (in odontocetes). The morphology of the bony labyrinth reflects the frequency specializations of the suborders (Ketten and Wartzok, 1990; Ketten, 1992; Luo and Eastman, in press), but the middle ear ossicles of mysticetes and odontocetes are remarkably similar to each other and very different from those of land mammals. The function of these specializations is unclear (Ketten, 1991).

The middle ear ossicles of cetaceans (Fig. 3c) are pachyosteosclerotic (Giraud-Sauveur, 1969; terminology of Domning and Buffr enil, 1991). Pachyostosis also occurs in phocids, but is absent in closely related otariids (Repenning, 1972; Wyss, 1987). Moore and Schusterman (1987) noted that the underwater audiograms for these two families of pinnipeds differ; phocid ears are much more sensitive to high frequency sounds. If this difference is functionally related to the difference in middle ear morphology, it forms an interesting parallel to middle ear pachyostosis of cetaceans, and suggests that even archaeocete ears (Pompeckj, 1992; Lancaster, 1990) were adapted for reception of high frequency sounds. The inner ear of few archaeocetes has been studied and what is known about their morphology is consistent with this hypothesis; known forms have a cochlea tuned to high frequencies (Ketten, 1992; but see Fleischer, 1976). Possibly then, archaeocetes display similar auditory specializations as odontocetes, consistent with the inferences of Pilleri *et al.* (1986).

It is commonly claimed that the odontocete middle ear ossicles are enlarged as a result of high frequency specializations (Reysenbach de Haan, 1957; Fleischer, 1978; Oelschläger, 1990) but this appears to be in conflict with the presence of similar morphologies in mysticetes. If, however, the archaeocete ancestors of both mysticetes and odontocetes had ears tuned to high frequencies, then the low frequency adaptations of mysticetes could be autapomorphies acquired at a later time. In this scenario, the mysticete ossicles would display phylogenetic inertia: their morphology did not change to reflect present (low-frequency) function, but instead is a left-over from a (high-frequency) specialization of the past.

Interestingly, this evolutionary scenario is consistent with phylogenetic trees in which Mysticeti are a subclade of odontocetes as originally proposed on the basis of mitochondrial rDNA and myoglobin sequences (Milinkovitch *et al.*, 1993), and later supported by other molecular studies (Douzery, 1993;  rnason and Gullberg, 1994;

Milinkovitch *et al.*, 1994). This phylogenetic model has been unpopular with morphologists (Barnes *et al.*, 1985; Heyning, 1989; Muizon, 1991; Fordyce, 1992), and topologies based on different molecular evidence vary significantly in spite of their agreement on odontocete paraphyly. On the other hand, most morphological characters that have been listed as synapomorphies of odontocetes (e.g., Heyning, 1989) are related to high frequency echolocation (Novacek, 1993a). If the functional analogy between pinniped and cetacean ossicles is correct, then the high frequency specializations may be symple-siomorphies for a clade uniting all modern cetaceans and their ancestors. A structure reminiscent of the melon has been found in mysticetes (Heyning and Mead, 1990), and the melon of odontocetes is involved in production of focussed high frequency echolocating bursts. This could be interpreted as corroborating high frequency hearing in mysticete ancestors.

*Anatomical Correlates.* The bony connections between the petrosal, tympanic, and basicranium are sometimes used to characterize cetaceans (Gingerich *et al.*, 1983; Oelschläger, 1986). The petrosal and tympanic are only loosely attached to the rest of the skull in modern cetaceans, and often lack any bony connection. In modern cetaceans, the petrosal and tympanic are surrounded by airfilled outpouchings of the auditory tube, but this feature cannot be investigated directly for the fossil forms. Barnes (1984) used the presence of falcate processes on the basioccipital as one of the traits that characterize cetaceans, and these processes are probably related to the airfilled sinuses surrounding the ear, by forming their wall. *Pakicetus* lacks such processes, but they are present in *Ambulocetus*. These airfilled spaces insulate the ear acoustically and thus assist in the isolation of hearing organ from the skull. However, these characters are not always correlated, as a loosely attached petrotympanic is common among other ungulate groups (Table I), notably perissodactyls, proboscideans, and phenacodontids (Thewissen and Domning, 1992).

Gingerich *et al.* (1983) noted that the tympanic and petrosal of *Pakicetus* are more strongly attached to the skull than in most modern cetaceans. A loose connection between tympanic and basicranium occurs in many primitive ungulates in which the tympanic has never been found (e.g., most mesonychians, arctocyonids, hyopsodontids). For instance, the tympanic is bulla-shaped in *Diacodexis* and loosely attached to the skull (Russell *et al.*, 1983), just as in primitive cetaceans (e.g., *Pakicetus*), and mesonychids (West, 1981; Zhou *et al.*, in press).

The wall of the tympanic of cetaceans consists of dense bone and is thick (pachyosteosclerotic) and it shows a prominent medial involution. These features have been used as cetacean characteristics (Barnes, 1984). Pachyosteosclerosis occurs in all cetaceans including *Pakicetus* (Gingerich and Russell, 1981) and *Ambulocetus* (Thewissen *et al.*, 1994). It is absent in known primitive ungulates such as *Diacodexis* (Russell *et al.*, 1983). Few tympanics are known for archaic ungulates, including mesonychians. These tympanics are thin-walled where known (e.g., *Hapalodectes*, Ting and Li, 1987; *Sinonyx*, Zhou *et al.*, in press; *Ectocion*, Thewissen, 1990), and the lack of preservation in other taxa is consistent with these structures being delicate.

The sigmoid process is an elongated prominence of the tympanic rostral to the external auditory meatus. It may serve as a buttress for the malleus (Fraser and Purves, 1976), and may assist in the reorientation of the middle ear that cetaceans underwent (Lancaster, 1990). It is present in the earliest protocetids, *Pakicetus*, and *Ambulocetus*.

No auditory ossicles are known for mesonychians, and only a few have been recovered for condylarths in general (e.g., *Arctocyon*, Russell, 1964), but the ossicles of modern artiodactyls and perissodactyls are probably good models for those of dichobunids and hyracotheres. Three specializations occur in the ossicles of cetaceans but not those of most other ungulates. First, they are pachyosteosclerotic (Fig. 3). As suggested above, this may be related to high frequency reception of underwater sounds. The incus of *Pakicetus* is pachyosteosclerotic (Thewissen and Hussain, 1993), but not as strikingly so as that of other archaeocetes and modern cetaceans (Pompeckj, 1922; Lancaster, 1990).

Second, the lever arms of the ossicles are reduced; the malleus loses its manubrium and the incus has a reduced crus longum. Fleischer (1976) suggested that these changes are related to high frequency reception. The crus longum of the incus is longer than the crus breve in all ungulates, except for artiodactyls and cetaceans (Doran, 1878).

Thirdly, the position of the ossicles in the middle ear is rearranged; evolutionarily the ossicles have rotated (Fleischer, 1976; Lancaster, 1990). This rotation is unique to cetaceans (Fig. 3), and only partly expressed in *Pakicetus* (Thewissen and Hussain, 1993). The function of this rotation is not clear, but the orientation might facilitate differential motions of the ossicular chain as a whole with respect to the tympano-periotic as a whole (Thewissen and Hussain, 1993). This could be consistent with the theories of McCormick *et al.* (1970, 1980) for middle ear sound transmission in cetaceans.

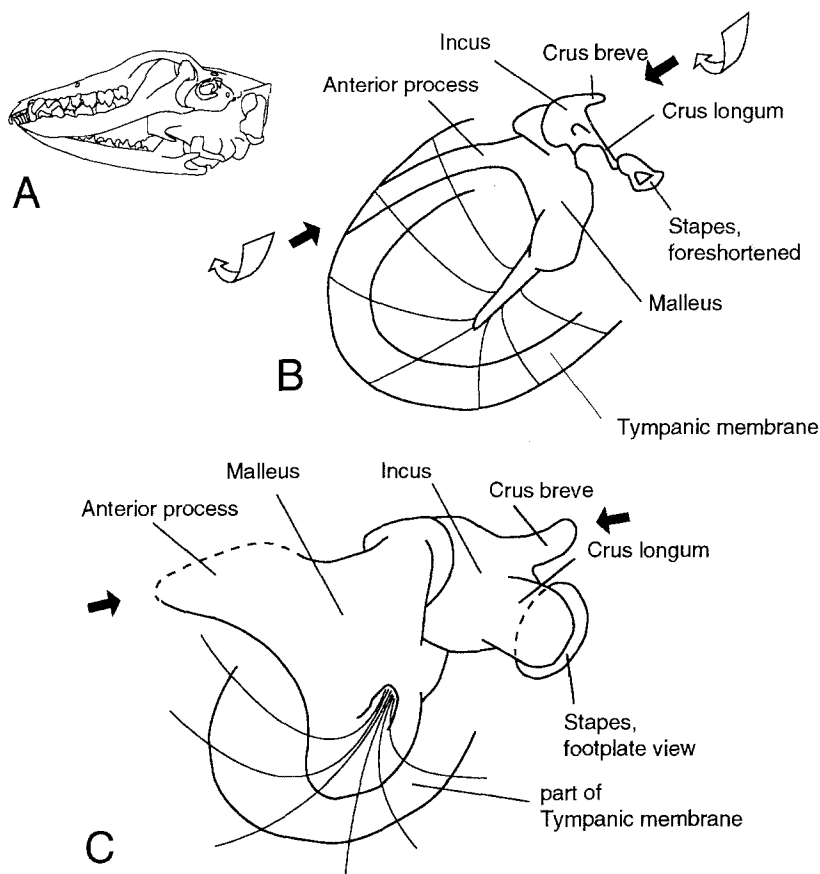
Unrelated to the changes in auditory morphology discussed above, but sometimes incorrectly cited as a synapomorphy of Cetacea (e.g., Barnes and Mitchell, 1978), is the fusion of the anterior process of the malleus to the tympanic wall. This fusion is plesiomorphic for mammals (Fleischer, 1976).

Unlike land mammals, modern odontocetes use their mandible for sound reception (e.g., Norris, 1980). Sounds received by the dentary are transmitted to the tympanic by a fat pad in odontocetes (Bullock *et al.*, 1968). This fat pad extends from the alveolar canal of the mandible through the mandibular foramen to the tympanic. This adaptation is also present in derived archaeocetes (e.g., Kellogg, 1936). The mandibular foramen of *Pakicetus* is similar in size to that of a land mammal (Thewissen and Hussain, 1993). The canal of *Ambulocetus* is enlarged, and encompasses about 50% of the depth of the jaw at M<sub>3</sub>. It is thus smaller than in other cetaceans.

### Character Complex 3: Locomotor Morphology

*Overall Trends.* The locomotor system underwent the most pervasive and best understood change of any organ system in cetacean evolution. Mesonychians displayed a variety of locomotor behaviors, but none that are related to aquatic locomotion; they were fully terrestrial, quadrupedal mammals (Matthew, 1915; Zhou *et al.*, 1992; O'Leary and Rose, in press b). Modern cetaceans swim by undulating their tail in a vertical plane and use their forelimbs in steering (Fish and Hui, 1991). Between these extremes was a transitional locomotor system suited for life on land and in water (Thewissen *et al.*, 1994).

Although the changes in locomotor morphology that accompanied the move to the water are dramatic and can be interpreted directly in a functional context, they do not bear strongly on higher mammalian phylogeny because they are autapomorphies for cetaceans (or one of the derived clades that compose it). Of greater importance is a number



**Fig. 3.** Diagram of the auditory ossicles of a modern cetacean, compared to that of a generalized mammal (*Monodelphis*). (A) *Monodelphis* skull showing at which view Figs. B and C are drawn. (B) *Monodelphis* auditory ossicles (malleus, incus, and stapes) and approximate shape of the tympanic membrane is indicated. Tympanic membrane is suspended from the tympanic ring, but the ectotympanic and other bones of the ear are not indicated. Black arrows indicate the direction of the physiological axis of rotation during ossicular movement and sound transmission. White arrows indicate the direction of evolutionary rotation in the cetacean middle ear around this physiological axis of rotation. (C) cetacean (*Tursiops*) auditory ossicles. Notice the bulky ossicles, and the reduction of the length of the crus longus. Ossicles have rotated around the axis of the black arrows by moving into the plane of the drawing (white arrows in B). This evolutionary rotation dragged the figured part of the tympanic membrane, making the part of it attached to the malleus into a narrow band of tissue (Fleischer, 1978; Lancaster, 1990).

of postcranial specializations that occur in the land-living relatives of cetaceans and that may be retained in part by cetaceans. Some of these changes are well understood because they relate to cursorial locomotion (e.g., Howell, 1944; Gambaryan, 1974). They include such character suites as enhanced parasagittal mobility of the limbs, reduction of medio-lateral mobility, shortening of proximal and lengthening of distal limb elements, reduction of the number of digits, and a shift to digitigrady or even unguligrady. On the other hand, changes relating to cursorial locomotion are found in many ungulate groups

(artiodactyls, perissodactyls, litopterns), and it is likely that several ungulate clades evolved cursoriality independently. Cursoriality was primitive for the paenungulates (e.g., Phenacodonta, Perissodactyla, Hyracoidea, Sirenia, Proboscidea) and was secondarily lost in some of these (Thewissen and Domning, 1992).

If cetaceans had cursorial ancestors, then some traits reminiscent of these specializations might be present in the skeleton of early aquatic cetaceans, whereas others would be overprinted by adaptations for swimming. Limbs are known for Eocene *Ambulocetus*, and these display many aquatic specializations (Thewissen *et al.*, 1994). *Pakicetus* postcranials may be more primitive and may reveal features of interest for higher mammalian phylogeny, but none have been described. When identified, these bones will form a critical test to determine the cursorial abilities of early cetaceans.

*Anatomical Correlates.* Absence of a clavicle is related to reduction of mediolateral mobility of the shoulder (Jenkins, 1974). Prothero *et al.* (1988) used this to support monophyly of paenungulates, mesonychians and cetaceans, but the bone is present in primitive paenungulates [e.g., *Phenacodus* (Thewissen, 1990); the suggestion by Williamson and Lucas (1992, p. 48), that this bone was an incorrectly identified ‘‘fibula or tibia’’ remains unsubstantiated]. No clavicle is known for adult cetaceans, but the bone has been reported in many archaic ungulates (Cifelli, 1983; Prothero *et al.*, 1988; Thewissen, 1990).

The scapular acromion and coracoid, as well as the humeral deltoid crest, are weak in cursorial taxa as a result of the reduction of the deltoid muscle, an abductor of the humerus. This occurs in many ungulates, such as *Diacodexis* (Rose, 1985), the perissodactyl *Heptodon* (Radinsky, 1965), and the phenacodontid *Copecion* (Thewissen, 1990).

No postcranials have been described for *Pakicetus*, but a distal humerus from a locality where *Pakicetus* is by far the most common animal resembles described archaeocete humeri (Kellogg, 1936). This referred distal humerus has a narrow radial capitulum suggesting that the elbow was fixed in a semi-pronated position as in *Ambulocetus* (Thewissen *et al.*, 1994) and later cetaceans (Kellogg, 1936). This is also the case in mesonychids (O’Leary and Rose, in press b), but not in primitive artiodactyls such as *Diacodexis* (Thewissen and Hussain, 1990).

The centrale is present in the carpus of *Ambulocetus*, and its presence was previously inferred in other archaeocetes (Kellogg, 1936; Gingerich 1990) as well as in mesonychids (Matthew, 1915; Osborn and Earle, 1895; Scott, 1888; Rose and O’Leary, in review). This bone is absent in primitive artiodactyls such as *Diacodexis* (Thewissen and Hussain, 1990) and nearly all other ungulates (Matthew, 1937). *Kopidodon* (Koenigswald, 1983) and *Numidothierium* (Court, 1994) are exceptions.

The astragalus of *Ambulocetus* has a deeply excavated trochlea, similar to that of *Diacodexis* (Thewissen and Hussain, 1990). The depth of the trochlea at its most dorsal point is 19% of its width in *Ambulocetus* and 38% in *Diacodexis*. The trochlea of mesonychians is less excavated (11% in *Dissacus*, Thewissen, 1991), whereas it is extremely flat in *Hyopsodus* (1.5%) and the arctocyonid *Neoclaenodon* (1.8%). An excavated trochlea restricts mediolateral motions at the ankle joint and has evolved independently in many cursorial clades. It also occurs in Paenungulata (*Tetraclaenodon*, 8%; *Hyracotherium*, 25%).

The astragalar head of artiodactyls has been modified to form a strong trochlea

(Schaeffer, 1947), and this is often used to diagnose the order. This morphology is unique among mammals, although an enhancement of parasagittal mobility at the expense of mediolateral mobility also occurs in mesonychians (Szalay and Gould, 1966). It does not occur in perissodactyls, proboscideans, arctocyonids and phenacodontids, and the condition in early cetaceans is unclear.

*Ambulocetus*, *Diacodexis* (Rose, 1985; Thewissen and Hussain, 1990), and mesonychians have a paraxonic hindfoot: the third and fourth metatarsals are approximately equal in length, whereas II and V are shorter and more slender. The first toe is reduced to a single bony element that may fuse to the tarsals in *Diacodexis* (Thewissen and Hussain, 1990). The first toe of mesonychids is also reduced (Matthew, 1915; O'Leary and Rose, in press b). Paraxony is less obvious in the forefoot (Osborn and Earle, 1895). Elongation of the central digits was probably originally a cursorial specialization.

The terminal phalanx of *Ambulocetus* is a hoof-like ungual; it is wider (medio-laterally) than deep (dorso-palmarly), has a more or less flat palmar surface, its articular facet was at right angles to the palmar surface, and in life it bore a medio-laterally convex nail. This type of phalanx is also known in mesonychians (Osborn and Earle, 1895; Matthew, 1915), phenacodontids (Rose, 1990), and hyracotheres (Rose, 1990). The terminal phalanges are medio-laterally compressed in *Diacodexis* (Rose, 1985; Thewissen and Hussain, 1990), arctocyonids (Russell, 1964), and hyopsodontids (Gazin, 1968).

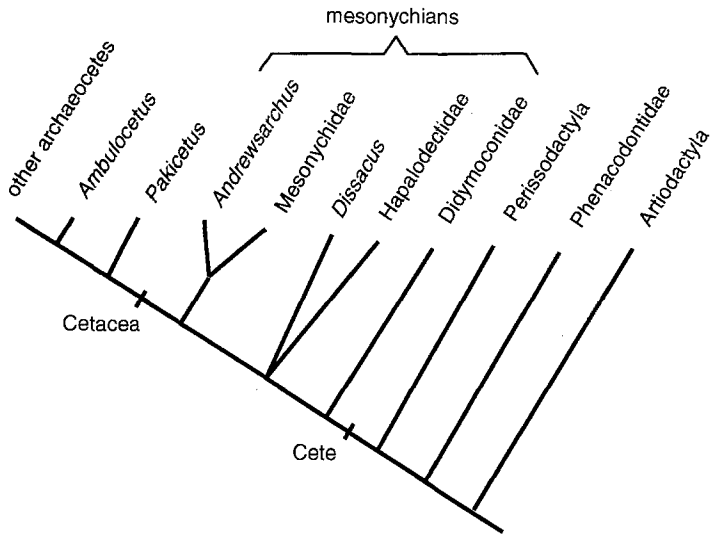
## PHYLOGENETIC ANALYSIS

The 39 morphological features listed in Table I were analyzed using the Branch-and-Bound option of the computer program PAUP, version 3.1.1. (Swofford, 1989). Arctocyonidae and Hyopsodontidae were considered outgroups. There were three equally parsimonious solutions, each 49 steps long (c.i. 0.796). Figure 4 is a consensus cladogram for these three most parsimonious results. Using Arctocyonidae as the only outgroup does not change the topology of the consensus cladogram.

Most nodes of the analysis are relatively unstable. In a consensus cladogram based on all cladograms of 50 or fewer steps, only Cetacea, Cete, and the node linking *Ambulocetus* to the derived archaeocetes are retained. At 51 steps, only the latter two of these remain resolved.

The anatomy of didymoconids and andrewsarchids is poorly known and these taxa were deleted. This search resulted in three most parsimonious cladograms, the consensus of which was totally consistent with that of Figure 4.

These analyses support three clades strongly: *Ambulocetus* with derived archaeocetes, Cetacea, and Cete. It is likely that more resolution will emerge in the cladogram when the morphology of the mesonychians, especially *Andrewsarchus* and didymoconids, becomes better known. Archibald (in press) supports the idea that didymoconids are not closely related to primitive ungulates, and exclusion of this group could also alter the cladogram of Figure 4. In addition, improved understanding about outgroup morphology will enhance resolution. Although these are shortcomings of the character matrix, I feel that the phylogenetic pattern that emerges from the analysis is sufficiently strong to support the phylogeny of the best supported nodes.



**Fig. 4.** Phylogenetic hypothesis for cetaceans and their relatives. Cladogram is based on strict consensus of the three most parsimonious cladograms of the PAUP analysis on the basis of the characters listed in Table I. Outgroups were Arctocyonidae and Hyopsodontidae.

## DISCUSSION OF CLADES

### Clade CETACEA Brisson, 1762

The morphological changes that the terrestrial ancestors of cetaceans underwent are so pervasive that, in the past, it was easy to diagnose the known members of the order Cetacea. With the recovery of more complete material for primitive archaeocetes such as *Pakicetus* (West, 1980; Gingerich and Russell, 1981, 1990; Gingerich *et al.*, 1983; Thewissen and Hussain, 1993), *Ambulocetus* (Thewissen *et al.*, 1994), *Indocetus* (Sahni and Mishra, 1975; Gingerich *et al.*, 1993), *Rhodocetus* (Gingerich *et al.*, 1994) and the remingtonocetids (Sahni and Mishra, 1975; Kumar and Sahni, 1986; Bajpai, 1990), it is becoming clear that these typical cetacean characters were not all acquired at the same node. Therefore, as pointed out by Berta (1994), a decision needs to be made concerning the lowest node on the cladogram that will still be included in Cetacea. Although this decision does not affect the actual cladogram topology, it remains important because the term Cetacea is used in contexts far beyond systematics. Stability is best served by choosing the context of cetaceans in such a way that it coincides with an already existing, common use of the term and a node that is well supported by character evidence and therefore unlikely to change as details are added to our understanding of cetacean morphology and diversity.

Gingerich *et al.* (1983), Barnes *et al.* (1985) and Fordyce (1992) all acknowledged that *Pakicetus* was the oldest or most plesiomorphic cetacean. Enough of the anatomy of *Pakicetus* is known to unambiguously characterize the order at its node. Characterizing Cetacea inclusive of *Pakicetus* coincides also with the first evidence of the specializations that are most characteristic for the order: those for life in the water.



This concept of Cetacea is sufficiently wide to allow inclusion of the ancestors of both mysticetes and odontocetes. It is also consistent with the molecular and cytogenetic data which strongly suggest that extant cetaceans are monophyletic (Czelusniak *et al.*, 1990; Árnason and Ledje, 1993; Milinkovitch *et al.*, 1993). Morphologically, there is no reason to assume that these suborders had an independent origin from land animals. Diphyly was suggested in the past at a time when only extremely derived archaeocetes were well known skeletally, but its morphological support was always scanty as pointed out by Barnes and Mitchell (1978). It is now clear that several derived archaeocetes, such as *Basilosaurus* (Andrews, 1906; Barnes and Mitchell, 1978; Gingerich *et al.*, 1990) did not give rise to modern taxa (Barnes *et al.*, 1985), and that the origins of the latter must be sought in early or middle Eocene protocetids or late Eocene durodontines.

*Synapomorphies for Cetacea.* Many traits of the ear can be recruited to characterize Cetacea, including the presence of a sigmoid process, pachyosteosclerotic ectotympanic and incus, and rotation of the ossicles. These character states are certainly derived (Fleischer, 1976) and are at least partly independent of underwater hearing specializations, given their absence in other marine mammals. They are probably not present in any other ungulates, although fossil evidence for the morphology of the three ear ossicles remains scanty for such important groups as mesonychians and arctocyonids.

Masticatory characters are more widely sampled among ungulates and some can be used to support Cetacea, such as the arrangement of the incisors and the height of the paracone of P<sup>4</sup>. To a large extent, however, mesonychians (or some of its members) are very similar to cetaceans dentally, and the bulk of dental morphology supports lower nodes on the cladogram.

The hypoglossal foramen opens close to the jugular foramen in all cetaceans, and this has been used to characterize the order (Barnes, 1984). The hypoglossal and jugular foramina of *Pakicetus* and *Ambulocetus* are closer than in some mesonychians, but the skulls of other mesonychians are poorly known.

*The Position of Ambulocetus.* The clade including *Ambulocetus* and its sister group is characterized by some features that have been used to diagnose Cetacea in the past. These include the presence of falcate processes of the basioccipital, the enlarged mandibular foramen, and the presence of the pterygoid sinus. *Pakicetus* lacks all three of these synapomorphies.

Several potentially important features cannot yet be evaluated in the context of archaic cetaceans. The shape of the supraorbital process (used in delineating cetaceans by Barnes, 1984) is not known for *Pakicetus*, but in *Ambulocetus* it is narrow, somewhat similar to mesonychians. In other archaeocetes (*Rhodocetus* Gingerich *et al.*, 1994; and *Indocetus* Gingerich *et al.*, 1993) this process is developed as a supraorbital shield and the eyes face laterally. This shape is a synapomorphy for derived archaeocetes. An additional synapomorphy is the extension of the tooththrow onto the zygomatic arch. This character occurs in *Rhodocetus*, but apparently not in remingtonocetids (Kumar and Sahni, 1986).

Absence of the postglenoid foramen was used by Van Valen (1966) to link cetaceans and mesonychians. The foramen is absent in *Protocetus* and also in *Pakicetus* (the zygomatic arches of the specimen described by Gingerich and Russell, 1981, and Gingerich *et al.*, 1983, are now lost in the type of *P. inachus*, but the cross-section of the zygomatic process indicates that it did not carry a venous sinus). The foramen is also

absent in most mesonychids, but not in *Dissacus* (Van Valen, 1966) and *Hapalodectes* (Ting and Li, 1987).

Prothero *et al.* (1988) used the retraction of the nasals to characterize Cetacea. The condition of this character is not clear in *Ambulocetus*, but in *Pakicetus* the nasals extend rostral as far as I<sup>2</sup>.

### Glade CETE Linnaeus, 1758

Several mesonychians have been suggested as possible sister group for cetaceans, including taxa as different as the tiny hapalodectids (Szalay, 1969b) and the enormous *Andrewsarchus* (Prothero *et al.*, 1988). A complete revision of the paraphyletic mesonychians is necessary before it can be determined which of its composing clades is most closely related to cetaceans (Zhou, in prep.). In the modern literature, there are few authors who reject the notion that the fossil sister group of cetaceans must be sought among the mesonychians, and the name Cete is here used to include cetaceans and their terrestrial relatives.

Mesonychians are a diverse group, and some of the younger members display highly derived characters that exclude them from close ties to the (geologically much older) earliest cetaceans. For the study of higher phylogeny, the more primitive clades are the most relevant (Novacek, 1992; Thewissen and Domning, 1992). In addition, the inclusion of didymoconids into mesonychians is tentative, open to further testing when more complete material is discovered for its more primitive members and inclusion into cladistic analysis of taxa outside of ungulates.

*Synapomorphies for Cete.* Dental similarities are the clearest synapomorphies for Cete; they include reduction of the trigon basin, reduction of the talonid basin, and absence of the hypoconulid of M<sub>3</sub>.

Prothero *et al.* (1988) noted that the mandibular fossa of cetaceans and a number of their terrestrial sister groups protrudes below the level of the zygomatic arch. This is mainly due to the presence of a pregenoid process. This process is absent in *Pakicetus* and the fossa is not elevated. Vascularized embrasure pits are present in most (but not all) Cete and could be an additional synapomorphy.

### Comments on the Monophyly of CETE Plus PAENUNGULATA

All three most parsimonious cladograms (Fig. 4) suggest that Cete are closely related to perissodactyls (*Hyracotherium*) and phenacodontids. Support for this hypothesis comes from several characters that are related to cursoriality such as the fixed elbow and the dorso-ventrally flattened unguals. This proposed affinity implies that homoplasy has occurred between artiodactyls and Cete in some characters that are commonly thought to be good estimators of phylogeny, such as paraxonic feet.

Close ties between Cete, perissodactyls, and phenacodontids have been proposed previously by Prothero and co-workers (Prothero *et al.*, 1988; Prothero, 1993). However, some of the characters used to link these groups (Prothero *et al.*, 1988, Fig. 8.1, node 21; Prothero, 1993) are ambiguous. The absence of a clavicle, for instance, does not characterize the group; the bone is present in phenacodontids. The scapular acromion and coracoid and the humeral deltoid tubercle are weakly developed in Cete and paenungulates, but also in artiodactyls. As pointed out by MacPhee (1994), position of an

exposed mastoid on the wall of the skull (lateral or occipital) is problematic. The mastoid is in approximately the same position in *Diacodexis* (Russell *et al.*, 1983) and *Phenacodus* (Thewissen, 1990). There are no apparent differences in the postglenoid foramen of phenacodontids and early artiodactyls, and the foramen is absent in a number of cetans. An inflated tegmen tympani, fused cochlear fissure and posterior lacerate foramen, and absence of the proximal stapedia artery have also been listed in support of a clade that includes Cete and Paenungulata (Prothero *et al.*, 1988). However, the tegmen tympani of *Pakicetus* is small and nearly flat, and this character is poorly defined (MacPhee, 1994). The jugular (posterior lacerate) foramen is always on the boundary of periotic and occipital and will fuse with the cochlear fissure if the size of the bulla increases. The same occurred in *Diacodexis*. The proximal stapedia artery is reduced independently in many ungulate lineages (Wible, 1987). Close ties between paenungulates (phenacodontids and perissodactyls of this analysis) and Cete remain possible, but character support for this union is weak, and most molecular analyses disagree.

### Comments on CETUNGULATA

Molecular studies commonly find evidence for a clade called Cetungulata, which includes perissodactyls, artiodactyls, and cetaceans, but not proboscideans (Czelusniak *et al.*, 1990; Goodman *et al.*, 1982, 1985; Irwin *et al.*, 1991; Irwin and Wilson, 1993; Irwin and Árnason, 1994; Jong, 1985; Miyamoto and Goodman, 1986). This hypothesis is inconsistent with the monophyly of paenungulates [a term used here to include, e.g., phenacodontids, perissodactyls, hyracoids, sirenians, and proboscideans, following Thewissen and Domning (1992) (for a different interpretation of Paenungulata, see Novacek, 1993b)]. Alpha-crystallin data (de Jong *et al.*, 1993) and some immunological data (Shoshani, 1986) dissent with the Cetungulata concept. Cetungulata differs from the broader Ungulata only in the exclusion of proboscideans and tethytheres. Morphologists have commonly found these pantomesaxonian clades plus Perissodactyla to be monophyletic (Fischer, 1986, 1988; Novacek, 1992; Novacek and Wyss, 1986; Shoshani, 1986; Prothero *et al.*, 1988; Thewissen and Domning, 1992; Fischer and Tassy, 1993), although the exact relations are disputed. The aim of this study was not to investigate the question of paenungulate relations, and many clades and characters relevant to that question were omitted. However, the most parsimonious results of this analysis (Fig. 4) failed to support paenungulate monophyly.

Shoshani (1993) constructed a phylogeny of the ungulates based on myological data that showed some morphological support for Cetungulata. He found an unresolved tetrachotomy of artiodactyls, perissodactyls, cetaceans, and paenungulates (tethytheres plus hyracoids in his definition). Shoshani interpreted his data cautiously and left this polychotomy unresolved, but one character appears to support the cetungulate concept: absence of palmaris longus. However, this muscle is present, and large, in both horses and ruminants; it is called flexor digitorum superficialis in the veterinarian literature because its distal tendons are perforated. It is, however, not homologous to the human muscle of that name, but instead to palmaris longus. Primitively, there are three digital flexors in the mammalian forearm and hand (a situation still found in, e.g., humans and dogs): palmaris longus, flexor digitorum superficialis, and flexor digitorum profundus of human terminology. Commonly, two of these are large and attach to, respectively, the perforating and perforated tendons of the fingers. These receive the names of flexor

digitorum superficialis and profundus, but their position (superficial, intermediate, or deep) with respect to the third muscle and the palmar carpal ligament varies. Homology is best inferred from their relations to each other and the palmar carpal ligament (Spoor and Badoux, 1986), in which case they are easily homologized to similar muscles in reptiles. One muscle passes superficial to the ligament (palmaris longus) and the remaining two pass deep (superficial and deep digital flexors). In different mammals, different sets of two forearm muscle bellies have connected to different sets of palmar tendons.

In summary, there is molecular but no morphological support for Cetungulata. This discrepancy hinges essentially on the relations among perissodactyls, hyracoids, and the tethytheres. As such it is only peripherally related to cetacean relations.

### Comments on Paraxonia

Mesonychians or Artiodactyla are most commonly cited as the sister group of Cetacea, and the union of all three groups is sometimes called Paraxonia, a term used by Simpson (1945) to include artiodactyls only. The most parsimonious cladograms of the present analyses do not support paraxonian monophyly. Overall, cladograms based on molecular data suggest that cetaceans are more closely related to artiodactyls than to perissodactyls [pancreatic ribonucleases (Beintema and Lenstra, 1982), and mitochondrial DNA (Milinkovitch *et al.*, 1993; Honeycutt and Adkins, 1993)]. Other molecular evidence leaves an unresolved trichotomy of artiodactyls, perissodactyls, and cetaceans based on analyses of myoglobin amino acid sequences (Milinkovitch *et al.*, 1993) and on cytochrome *b* gene sequences (Irwin and Arnason, 1994). If artiodactyls and Cete are sister groups, it is possible that they diverged soon after the paenungulate-paraxonian dichotomy, and that little molecular and morphological evolution occurred in the lineage segment between the two nodes.

Some molecular studies, however, go well beyond the paraxonian concept and consider cetaceans a subclade of paraphyletic artiodactyls (Graur and Higgins, 1994). This hypothesis is based on little molecular evidence and analyses of few clades. It is poorly supported and other molecular evidence dissents with it, showing that both Cetacea and Artiodactyla are monophyletic, e.g., the mitochondrial DNA sequence studies of Arnason *et al.* (1991) and Milinkovitch *et al.* (1994). Morphologists do not doubt the monophyly of artiodactyls (excluding cetaceans), although the derived morphology of cetaceans poses some problems. Prothero (1993) listed a number of autapomorphies of Artiodactyla. Several of these cannot be evaluated for cetaceans (double-pulleyed astragalus), or are present in several other clades (paraxonic feet). However, there are no derived characters shared by artiodactyls and cetaceans that are not also present in some or all mesonychians. Mesonychian postcranial morphology is well known, and this group lacks such important characters as the well-developed double-pulleyed astragalus (Szalay and Gould, 1966). If Cete is held up, cetaceans are not a subclade of Artiodactyla.

Cetacea, mesonychians, and Artiodactyla are different in dental and cranial traits, which could be due in part to the large differences in size and diet among their early members. A potential strong synapomorphy for Paraxonia is the relative length of the crura of the incus (Doran, 1878), but no incus is known for mesonychians and arctocyonids and the condition in artiodactyls is based on that of modern forms. Similarities in the locomotor skeleton among the paraxonians are important because they exist in spite of the pervasive locomotor changes that cetaceans underwent in becoming aquatic.

The most significant of these is the paraxonic foot, interpreted as a homoplasy in Figure 4. No astragalar head is known for protocetids, and thus the implications of its shape cannot be assessed.

There is also soft-anatomy support for a union of artiodactyls and cetaceans. Although these types of analyses cannot investigate mesonychians or primitive ungulate morphology, they support the artiodactyl-cetacean clade to the exclusion of perissodactyls, proboscideans and their relatives. These characters include the presence of three primary bronchi of the lung, a condition highly unusual in mammals (Slijper, 1958). The mechanism of penile erection in cetaceans and artiodactyls also differs from that of other mammals (Struthers, 1893; Daudt, 1898; Getty, 1975). The penis has little cavernous tissue and erection is mainly effectuated by relaxation of the retractor penis muscle. Moreover, in both cetaceans and artiodactyls, the flaccid penis is kept in a sigmoid curve or loop inside the body wall. These characters do not occur in perissodactyls (Getty, 1975) or other paenungulates.

Slijper (1962) and Mossman (1987) commented on phylogenetic implications of the similarities between the fetal membranes of artiodactyls and cetaceans, but Luckett (1993) considered most of these to be symplesiomorphies. An exception is the greatly elongated shape of the blastocyst and early somite embryo, discussed by Mossman (1987). Luckett (pers. comm., 1994) notes that this is certainly a derived character that is shared only by cetaceans and artiodactyls.

In summary, most molecular studies support paraxonian monophyly, and there is potentially strong morphologic support for the group from characters unknown in many fossil groups. The morphological analysis of Figure 4 does not support Paraxonia, and this could be due to large amounts of missing data in the character matrix.

## CONCLUSIONS

Our understanding of early cetacean evolution is improving rapidly with the recovery of important new early cetacean fossils, and the analysis of more and more molecular data of extant cetaceans and their relatives.

Following most previous authors, I suggest that the order Cetacea is best characterized with *Pakicetus* as its lowest node. Cranial and dental data can be recruited to support this node. Some aquatic adaptations probably originated with the cetacean clade, but in the absence of postcranials for the earliest members, the extent of these adaptations is poorly documented. Auditory morphology also gives support, but interpretation of these characters is hampered by our limited knowledge of the ear of mesonychians and other archaic ungulates. *Pakicetus* and other archaeocetes may have been specialized for high frequency sound reception, and this was probably part of the cetacean morphotype. This is consistent with an evolutionary scenario proposed on the basis of molecular data (Milinkovitch *et al.*, 1993). Mysticetes may have lost high frequency reception secondarily. *Ambulocetus* is the next node on the cetacean cladogram and shares several primitive features with *Pakicetus* that are lost in other cetaceans.

The Cete concept (mesonychians plus Cetacea) is uncontroversial, and supported by several strong dental specializations relating to diet. Many mesonychians may have specialized in food with a hard and brittle component (O'Leary and Teaford, 1992),

such as vertebrate bone or mollusc shells. Early cetaceans may have had a similar diet. Whatever their sister group, the diet of Cete is very different from that of other ungulates.

Mesonychians are extremely diverse, and the position of individual clades along the segment leading to cetaceans is not well understood. They represent a paraphyletic stem taxon for cetaceans and the proposed phylogeny (Fig. 4) is consistent with the results of Zhou *et al.* (in press). Understanding the phylogeny of Cete allows inferring the morphology of the cetacean morphotype and that of its terrestrial sister group. These can be tested when more fossil material for these clades is discovered. This phylogeny predicts that *Pakicetus* had a paraxonic foot and an astragalar head that was restricted to parasagittal motions, but lacked a trochlea. Phylogenetic inference helps us to understand the functional changes that took place in the transition from land to the water in early cetaceans.

It is unclear what the sister group of Cete is. Molecular evidence commonly suggest artiodactyls, consistent with a number of morphological characters that are not known in some of the fossil groups. Other morphological analyses, including that of Fig. 4, dissent. Early artiodactyls were probably unselective herbivores that may have accidentally or deliberately ingested a small amount of animal food also (Richter, 1987). Their diet differed strongly from that of Cete, and so did their dental morphology.

The cladogram of Fig. 4 can also be interpreted in a biogeographical context. The most plesiomorphic cetacean genus (*Pakicetus*) and the most plesiomorphic artiodactyl genus (*Diacodexis*), as well as several primitive paenungulates (anthracobunids, perisodactyls) all occur in the same early Eocene formation: the Kuldana Formation of northern Pakistan. The origin of cetaceans and artiodactyls may have occurred in the early Eocene of Indo-Pakistan, but the modern artiodactyl suborders (such as ruminants and suinans) did not evolve until the late Eocene. Only one likely mesonychian has been reported from Eocene Indo-Pakistan, cf. *Honanodon* (Ranga Rao, 1973), although they were diverse on the Asian mainland (Russell and Zhai, 1987). This evidence is consistent with the origin of many modern mammalian orders on Indo-Pakistan (Krause and Maas, 1990).

The greatest future advance in our understanding of the lower nodes on the ungulate cladogram, including the paraxonian and paenungulate groups, may come from a better understanding of arctocyonid morphology and the ungulate morphotype.

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