

Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls

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Modern members of the mammalian order Cetacea (whales, dolphins and porpoises) are obligate aquatic swimmers that are highly distinctive in morphology, lacking hair and hind limbs, and having flippers, flukes, and a streamlined body. Eocene fossils document much of cetaceans' land-to-water transition, but, until now, the most primitive representative for which a skeleton was known was clearly amphibious and lived in coastal environments. Here we report on the skeletons of two early Eocene pakicetid cetaceans, the fox-sized *Ichthyolestes pinfoldi*, and the wolf-sized *Pakicetus attocki*. Their skeletons also elucidate the relationships of cetaceans to other mammals. Morphological cladistic analyses have shown cetaceans to be most closely related to one or more mesonychians, a group of extinct, archaic ungulates, but molecular analyses have indicated that they are the sister group to hippopotamids. Our cladistic analysis indicates that cetaceans are more closely related to artiodactyls than to any mesonychian. Cetaceans are not the sister group to (any) mesonychians, nor to hippopotamids. Our analysis stops short of identifying any particular artiodactyl family as the cetacean sister group and supports monophyly of artiodactyls.

In contrast to the debate about the cetacean sister group, the relationships among Eocene cetaceans and the content of Cetacea itself are not controversial^{1–5}. All phylogenetic studies indicate that pakicetids are more closely related to living cetaceans than to artiodactyls and mesonychians, and that pakicetids share the cetacean synapomorphies of the ear^{2,3,6}. Pakicetids are followed by ambuloctetids in the cladogram, and modern cetaceans (toothed and baleen whales) are closely related to late Eocene basilosaurids and dorudontids^{1,3–5}. The most archaic cetacean for which the skeleton is known is the amphibious *Ambulocetus natans*^{7,8}. It was a powerful, walrus-sized animal that lived in coastal environments and resembled a crocodile, with the exception of long hind limbs that were used in swimming⁹. Although *Ambulocetus* is unlike modern cetaceans, it also differs strongly from its land mammal relatives, be they artiodactyls or mesonychians. Adaptations for life in water in *Ambulocetus* and later whales complicate determination of their closest relatives among the land mammals. Data from fossil whales that are more basal on the cetacean phylogenetic tree and have fewer aquatic adaptations could presumably yield new phylogenetic insights^{10,11}. Pakicetids are in this position and can be used to test mesonychian and hippopotamid hypotheses.

There are three genera of pakicetid cetaceans: *Pakicetus*, *Nalacetus* and *Ichthyolestes*². *Pakicetus* is the largest, followed by *Nalacetus* (approximately 5% smaller in linear dimensions), and *Ichthyolestes* (approximately 29% smaller). Until now, only teeth, jaws and one braincase have been described for pakicetids^{2,3,12}. We excavated four partial skulls, two of which retain the orbital region, several snout fragments, and approximately 150 isolated postcranial bones of pakicetids from multiple individuals. These were found at a single site in the early Eocene Kuldana Formation of Pakistan. We use these fossils to show (1) that these archaic cetaceans were land mammals; and (2) that cetaceans are more closely related to artiodactyls than to mesonychians.

Pakicetid form and function

Aquatic postcranial adaptations are pronounced in late Eocene basilosaurids and dorudontids, the oldest obligate aquatic cetaceans for which the entire skeleton is known^{13–15}, and therefore can be used to evaluate pakicetid morphology. Aquatic adaptations of basilosaurids and dorudontids include: presence of short neck

vertebrae; thoracic and lumbar vertebrae that are similar in length; unfused sacral vertebrae; lack of a sacro-iliac joint; presence of a short tail with a ball-vertebra (a vertebra at the base of the fluke, with convex articular surfaces); broad fan-shaped scapula with anterior acromion and small supraspinous fossa; an ulna with a large and transversely flat olecranon; a wrist and distal forearm flattened in the plane of the hand; and tiny hind limbs¹⁵.

Pakicetids display none of these features. Pakicetid neck vertebrae are longer than late Eocene whales (Fig. 1a and b), and the trunk vertebrae increase in size from anterior to posterior (Fig. 1c–f), as in land mammals. Lumbar and caudal vertebrae (Fig. 1e–i) are long compared to those of modern fluked cetaceans, but not as long as in extinct cetaceans that swam by undulating their entire spine (for example, the remingtonocetid *Kutchicetus*¹⁶). *Ambulocetus* and *Kutchicetus* have a muscular and flexible lumbar vertebral column, whereas motion in pakicetids is restricted as a result of their revolute zygapophyses (Fig. 1e), a feature in common with stiff-backed runners such as mesonychians¹⁷ and many extinct and modern artiodactyls¹⁸. The pakicetid sacrum consists of four solidly fused vertebrae and there is a strong sacro-iliac joint, as in land mammals and in amphibious whales such as *Ambulocetus*^{8,19} and *Kutchicetus*¹⁶ but unlike later cetaceans¹⁴.

The pakicetid scapula (Fig. 2) has a large supraspinous fossa with a small acromion, unlike any other cetaceans^{13,15}. The humerus is long and slender (Fig. 1j and k), and all but lacks a deltopectoral crest, as in running mammals. This crest is large and reaches distally in modern sirenians and pinnipeds²⁰ as well as in other Eocene cetaceans^{13,15}. Distally, the humerus has a wide, tightly articulating hinge joint for the radius and ulna allowing a great degree of flexion but few other motions. This is unlike other cetaceans, but is common in running mammals²¹. The forearm of pakicetids is not transversely flattened. The olecranon (Fig. 1l and m) makes up less than 12% of the length of the ulna in *Ichthyolestes*, whereas the olecranon is large in *Ambulocetus* (24%). In swimmers, such as basilosaurids¹³ and pinnipeds²⁰, the olecranon is antero-posteriorly and proximo-distally long and provides a strong lever for elbow extension and wrist flexion. Short olecrana occur in runners²¹.

The pakicetid innominate (Fig. 1n) is large and the ischium is longer than the ilium. The tibia is long in pakicetids and has a short tibial crest. Long tibiae are present in fast land mammals²¹ and also

in phocid seals^{20,22}. In phocids, the large ischium, short femur with asymmetrical condyles combined with the long tibia with long tibial crest allow the hamstrings to act as foot adductors (knee flexors with thigh in abducted position) while swimming²⁰. The relative lengths of these bones in pakicetids, their slender appearance, the short tibial crest, high patellar groove, and symmetrical knee make the phocid mode of locomotion unlikely for pakicetids, and their external morphology is more similar to that of running and jumping mammals²¹.

Running features are also found in the ankle where the proximal trochlea of the astragalus is constrained to a tight hinge joint (Fig. 1o–r). Like artiodactyls^{23,24}, pakicetids have a trochleated astragalar head rotating in the dorso-plantar plane. The sustentacular facet is a hinge that also rotates dorso-plantarly, and the ectal facet is small and laterally placed. The calcaneum (Fig. 1s and t) has

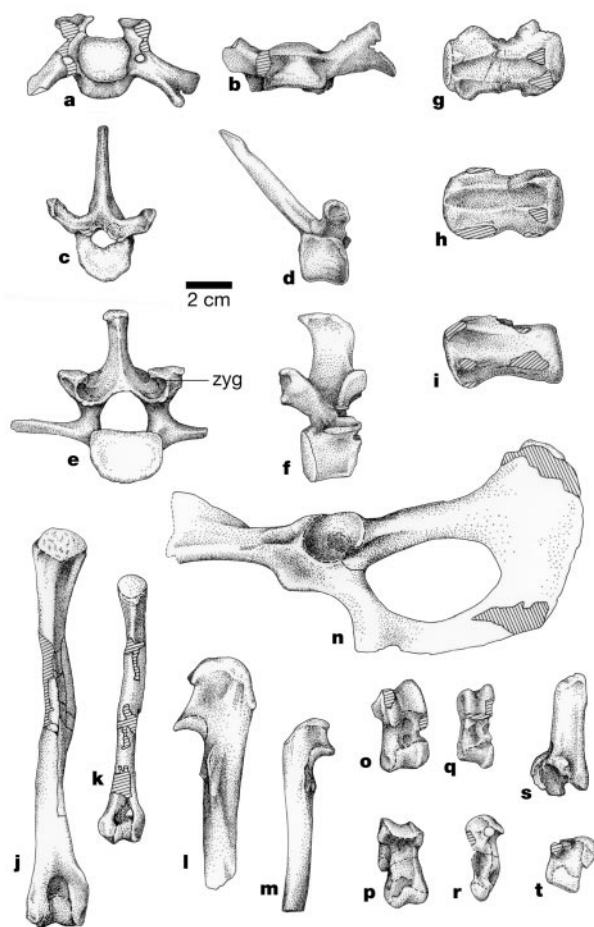


Figure 1 Postcranial osteology of pakicetids. H-GSP 96218, cervical vertebra of *Pakicetus* in anterior (a) and ventral (b) view. H-GSP 96516, thoracic vertebra of *Pakicetus* in anterior (c) and right lateral (d) view. H-GSP 98154, lumbar vertebra of *Pakicetus* in posterior (e) and right lateral (f) view. H-GSP 96564, caudal vertebra of *Pakicetus* in ventral view (g). H-GSP 96305, caudal vertebra of *Pakicetus* in ventral (h) and left lateral view (i). H-GSP 92042, left humerus of *Pakicetus*, subadult, in posterior view (j). H-GSP 30128, left humerus of *Ichthyolestes*, subadult, in posterior view (k). H-GSP 96057, proximal left ulna of *Pakicetus* in medial view (l). H-GSP 30286, proximal right ulna of *Ichthyolestes* in lateral view (m). H-GSP 98134, left innominate of *Pakicetus* in lateral view (n, complete ilium present in H-GSP 30288). H-GSP 98148, left astragalus of *Pakicetus* in dorsal (o) and plantar view (p). H-GSP 98149 left astragalus of *Ichthyolestes* in dorsal (q) and lateral (r) view. H-GSP 96359, right calcaneum of *Pakicetus* in medial view (s, distal part broken). H-GSP 96420, left distal calcaneum of *Pakicetus* in medial view (t). Abbreviation: zyg, zygapophysis of lumbar vertebra, illustrating recurving articular surface.

a long tuber and an obliquely set, narrow cuboid facet. These features are commonly interpreted as adaptations for running^{23–25}, although they are retained in non-running, graviportal artiodactyls.

The hands of *Pakicetus* and *Ambulocetus* are equally robust; the ratio of midshaft width to length of the central metacarpal is 0.17 and 0.18 respectively. On the other hand, the feet of *Ambulocetus* exceed those of *Pakicetus* in robustness by more than 20% (this ratio for metatarsal III is 0.11 and 0.14 respectively). *Ambulocetus* probably swam using its hind limbs as the main propulsor, and its robust feet may be an adaptation for forcefully displacing water during swimming⁹. Pakicetids, on the other hand, had the slender metapodials of running animals.

The cranial morphology of pakicetids is consistent with the evidence from the postcranium. The nasal opening of pakicetids was at the tip of the snout², as in land mammals and other primitive cetaceans²⁶, but unlike late Eocene cetaceans¹³ and other marine mammals²⁷ (sirenians, desmostylians). The lacrimal foramen is present in pakicetids (Fig. 3) and other archaic cetaceans, but is usually absent in aquatic mammals (modern cetaceans²⁷, sirenians²⁷ and pinnipeds²²).

The orbits of pakicetids are close together and are frontated (face dorsally) but are not at the most dorsal point of the head (Fig. 3). This is unlike any other cetacean. Most middle Eocene and all later cetaceans have orbits positioned below the supra-orbital shield and facing laterally^{13,28}, an adaptation for submerged living. The orbits of *Ambulocetus* are not frontated but are positioned dorsally⁸, as in modern amphibious mammals, such as hippopotami. The pakicetid position enhances binocular vision but is not necessarily related to life in water.

Deep, near-vertical gouges constitute most of the dental wear in pakicetids²⁹. Cladistic arguments have been used to link this wear pattern to aquatic predation on fish²⁹, but no functional model or modern analogue is known. Moreover, this kind of dental wear also occurs in raoellid artiodactyls³⁰. Although this dental wear probably represents a distinctive way of food processing, it does not necessarily imply aquatic life.

Unlike any other cetacean, the pakicetid outer ear was unspecialized and similar to that of land mammals⁶. The external auditory meatus opens low on the side of the skull, and the mandible has a small mandibular foramen³¹. In amphibious mammals, the external auditory meatus commonly opens dorsally. The mandibular foramen of late Eocene and Neogene cetaceans is large^{13,15} and transmits underwater sound to the middle ear. Enlargement also occurs in *Ambulocetus*⁸, but the foramen is small in pakicetids^{2,31}.

The pakicetid middle ear was highly specialized and included pachy-osteosclerotic ossicles², an involucrum⁶ and a plate-like sigmoid process⁶. These features have been interpreted as adaptations for underwater hearing³¹, and it has been suggested that the presence of an involucrum facilitates underwater high-frequency transmission in modern odontocetes³² even though the involucrum is also present in low-frequency mysticetes. In the case of pakicetids, the absence of air sinuses insulating the ears¹², the firm fusion of the petrotic to the surrounding bones^{2,12}, and the presence of a flat tympanic membrane^{3,6} suggest that reception of airborne sound is well developed, but are inconsistent with good underwater hearing^{3,12}. It is most likely that the specializations of the pakicetid middle ear are analogous to those of some subterranean mammals³³ and are related to the reception of substrate-borne vibrations or sound when the head is in contact with the ground⁸. Turtles are in close contact with the substrate and gather sensory information using this method³⁴.

Taken together, the features of the skull indicate that pakicetids were terrestrial, and the locomotor skeleton displays running adaptations. Some features of the sense organs of pakicetids are also found in aquatic mammals, but they do not necessarily imply life in water. Pakicetids were terrestrial mammals, no more amphibious than a tapir.

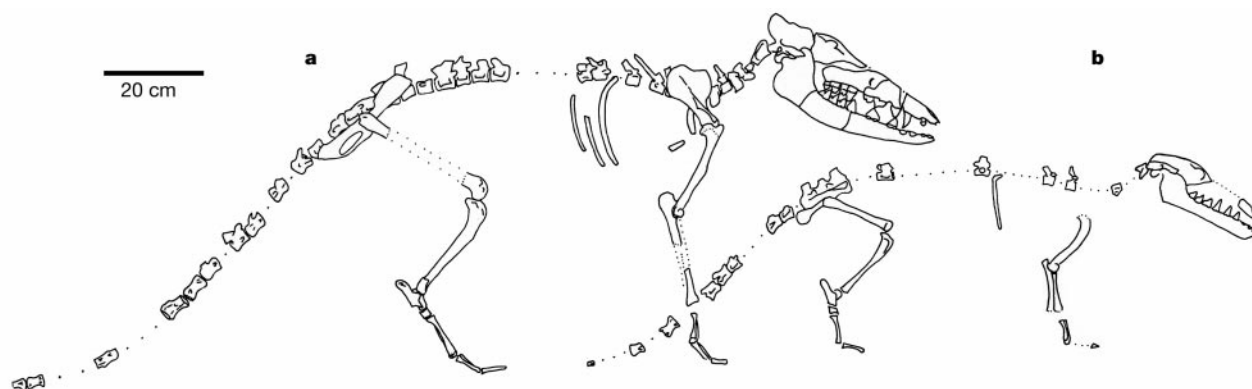


Figure 2 Skeletons of the pakicetid cetaceans *Pakicetus* (a) and *Ichthyolestes* (b). Reconstructions are based on fossils from H-GSP Locality 62 in the Eocene of Pakistan. Unknown elements have not been reconstructed.

Phylogenetic analysis

There are two current hypotheses about the closest relatives of cetaceans, championed by morphological and molecular systematists respectively. Morphological phylogenetic studies^{3,4,35–37} indicate that the sister group to cetaceans is (one of) the mesonychians, an extinct group of flesh-eating ungulates. On the other hand, molecular studies^{38–41} indicate that cetaceans are embedded in paraphyletic artiodactyls and that hippopotamids are their extant sister group.

The hippopotamid hypothesis states that the fossil sister group of cetaceans is an artiodactyl in the lineage of hippopotamids, but not necessarily a species classified in the hippopotamid family. Hippopotamids are known exclusively from the Old World and go back only to the Miocene⁴², whereas cetaceans had already diverged in the Eocene of Asia^{2,12,43}. This implies that the likely cetacean sister group is an Old World artiodactyl of Eocene or older age¹¹. Furthermore, it should be realized that the mesonychian and hippopotamid hypotheses are not mutually exclusive. These hypotheses are in agreement if mesonychians are the cetacean sister group and this entire clade (called Cete) is the sister to the hippopotamid lineage.

In order to test whether the mesonychian hypothesis is robust against the addition of the new morphological data, we analysed a data matrix of dental, cranial and postcranial characters, and included a variety of mesonychians and artiodactyls (Fig. 4). Most importantly, we used our new fossil evidence to score pakicetids and improved our scoring of ambuloctids¹⁹. Our analysis (Fig. 4) supports Cetartiodactyla (the clade that includes Cetacea and Artiodactyla, to the exclusion of mesonychians), but not Cete (monophyletic Cetacea plus Mesonychia). There is strong bootstrap support (77%) for Cetartiodactyla, and we reject the mesonychian hypothesis of cetacean relations. However, our analysis does not support the hippopotamid hypothesis either, because we recovered sister group relations between Cetacea and monophyletic Artiodactyla.

Traditionally, the morphology of the ankle has been used to define artiodactyls (in a character-based definition^{23,25,27,42}). Our new fossils show that these defining characteristics do not only occur in all artiodactyls, but are also present in basal cetaceans. These ankle characters (deeply grooved proximal trochlea, dorso-plantar rotation plane of trochleated head, rectangular and wide sustentacular facet, flat and lateral ectal facet, elongate and oblique calcaneo-cuboid joint) have high consistency indices (1.0). It is now clear that they support the cetartiodactyl node (or the Cetartiodactyla + *Andrewsarchus* node, since no tarsus is known for this genus) in all most-parsimonious trees. Importantly, in none of the most-parsimonious trees was the mesonychian tarsus interpreted as

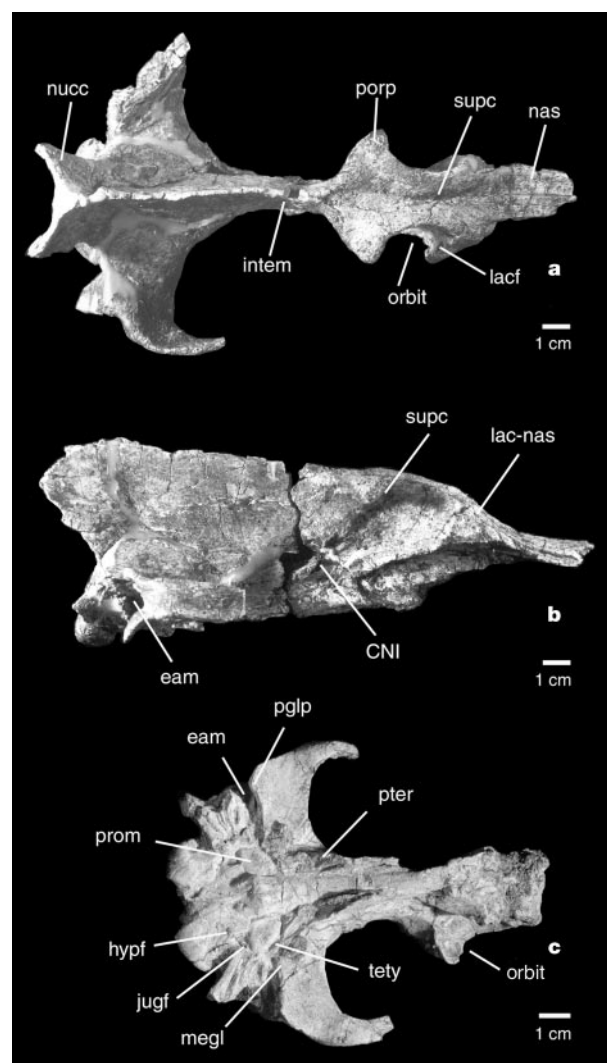


Figure 3 Skulls of the pakicetids *Pakicetus* (H-GSP 96231) in dorsal (a) and lateral (b) view and *Ichthyolestes* (H-GSP 98134) in ventral view (c). Abbreviations: CNI, cranial nerve I, endocast; eam, external auditory meatus; hypf, hypoglossal foramen; intem, intertemporal region; jugf, jugular foramen; megl, medial part of glenoid fossa; nas, nasal bone; nucc, nuchal crest; lacf, lacrimal foramen; lac-nas, lacrimo-nasal suture; porp, postorbital process; pglp, postglenoid process; prom, promontorium; pter, pterygoid process; supc, supraorbital canal; tety, tensor tympani fossa.

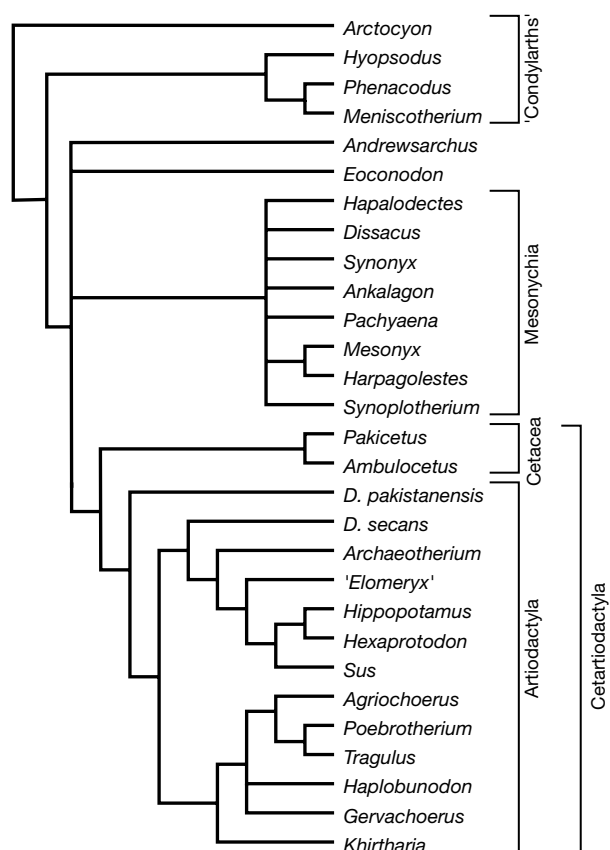


Figure 4 Phylogenetic relations of cetaceans to artiodactyls, mesonychians and primitive ungulates. Strict consensus cladogram of 38 most-parsimonious trees (see Methods for details).

a reversal from an artiodactyl-like morphology (the evolutionary model under which both hippopotamid and mesonychian hypotheses could be true).

The Artiodactyla node in our analysis is inconsistent with the hippopotamid hypothesis for cetacean relations, but is supported by fewer characters and has a lower bootstrap value (48%) than the Cetartiodactyla node. The artiodactyl node does receive support from the unique morphology of the cetacean fourth deciduous premolar (with consistency index, minimum possible number of changes/actual number of changes, of 1)^{37,44}. It is further supported by the reversal of a number of dental apomorphies, such as the large molar metacone and trigon basin, the presence and equal size of paracone and metacone, and a relatively low trigonid. Our analysis implies that the relatively primitive dental morphology of archaic artiodactyls is either a reversal (from a more mesonychian-like morphology) or that mesonychians and cetaceans evolved dental similarities independently. This bears out the prediction that widespread homoplasy occurred in one organ system in the early evolution of the clades in question⁴⁵. Our data suggest that the dentition, not the tarsus, was this organ system. This interpretation is consistent with a previous analysis that concluded that dental data are the primary source for the discrepancy between mesonychian and hippopotamid hypotheses⁴⁶, and that non-dental morphological data are more compatible with the hippopotamid hypothesis.

We suggest that the key to testing the hippopotamid hypothesis lies in the study of the more than ten families of early and middle Eocene artiodactyls from the Old World. Such a study may uncover the Eocene roots of the hippopotamid lineage, and its relation to cetaceans.

Note added in proof: Close cetacean-artiodactyl relations are also implied by protocetid fossils in an upcoming paper⁴⁸. □

Methods

Collection and identification

All pakicetid fossils were found at the early Eocene Howard University/Geological Survey of Pakistan (H-GSP) Locality 62 in the Ganda Kas Area of the Kala Chitta Hills (Punjab, Pakistan)³⁰. This locality outcrops over approximately 20 m² and contains a rich assemblage of isolated specimens with very low diversity. To date, 105 positively identifiable dental specimens have been recovered; 61% of these are pakicetid whales, 11% are anthracobunid proboscideans, 14% are raoellid artiodactyls, and the remainder is made up of small mammals (rodents, insectivores and mouse-sized marsupials³⁰). On the basis of these proportions, cetaceans can be expected to dominate the non-dental remains of this assemblage too. The largest cetaceans (*Pakicetus*, *Nalacetus*) are similar in size to the anthracobunids, but are easily differentiated on the basis of the distinctive postcranial morphology of the latter (which is known from several partial associated skeletons from the Ganda Kas Area). The smallest cetacean (*Ichthyolestes pinfoldi*) is approximately 174% as large (in linear dimensions) as the only known artiodactyl (the raoellid *Khirtharia dayi*) at Locality 62, and bones of these genera are thus not easily confused.

Initial identifications were based on size and anatomical fit between elements, and comparisons to *Ambulocetus*. To test these identifications, we analysed some bones isotopically. This method is destructive, so we limited the number of samples for this test. Isotopically, cetaceans are distinctive; their $\delta^{13}\text{C}$ values of enamel, dentin, and (mandibular) bone range between -11.9 and -13.6 ($n = 11$), whereas the same tissues for raoellid artiodactyls ($n = 5$) and anthracobunids ($n = 4$) range between -8.4 and -11.5 . Thus, among the large mammals at this locality, cetaceans have distinct isotopic values. This method allowed us to isotopically confirm the identity of a cervical vertebra of *Pakicetus* (H-GSP 92082, $\delta^{13}\text{C} = -13.9$), a lumbar vertebra *Pakicetus* (H-GSP 96284, $\delta^{13}\text{C} = -15.0$), a sacrum of *Pakicetus* (H-GSP 30251, $\delta^{13}\text{C} = -13.4$), a caudal vertebra of *Pakicetus* (H-GSP 96422, $\delta^{13}\text{C} = -14.8$), a humerus of *Pakicetus* (H-GSP 92042, $\delta^{13}\text{C} = -14.3$), a humerus of *Ichthyolestes* (H-GSP 96247, $\delta^{13}\text{C} = -13.0$), an innominate of *Pakicetus* (H-GSP 30279, $\delta^{13}\text{C} = -13.7$), an innominate of *Ichthyolestes* (H-GSP 30390, $\delta^{13}\text{C} = -13.0$), a tibia of *Pakicetus* (H-GSP 30315, $\delta^{13}\text{C} = -14.3$), an astragalus of *Ichthyolestes* (H-GSP 97001, $\delta^{13}\text{C} = -13.3$), two astragali of *Ichthyolestes* (H-GSP 98148, $\delta^{13}\text{C} = -13.4$; H-GSP 98149, $\delta^{13}\text{C} = -13.5$), a calcaneum of *Pakicetus* (H-GSP 96420, $\delta^{13}\text{C} = -12.4$), and a metatarsal of *Pakicetus* (H-GSP 30417, $\delta^{13}\text{C} = -14.0$).

There are several distinctive shape differences in the postcranial bones between *Ichthyolestes* and the larger pakicetids. Although *Nalacetus* differs from *Pakicetus* in dental and bullar³ morphology, no shape differences were found in this size cohort in the postcranial skeleton. It is thus likely that some of the bones referred to *Pakicetus* above pertain to *Nalacetus*, but this does not alter any of our conclusions. Our present study also shows that an astragalus attributed to a pakicetid^{24,25} was misattributed.

Cladistic analysis

In order to test the mesonychian and hippopotamid hypotheses, we chose in-group taxa that both sample ungulate diversity and remain pertinent to the question of sister group relations to Cetacea. We chose four archaic ungulates to root the tree in the ungulate radiation with *Arctocyon* as outgroup, a practice followed by many other studies^{4,44,46}. We limited Cetacea to two taxa (pakicetids, *Ambulocetus*) because the identity and basal status of these taxa are generally accepted^{1,45} and the inclusion of more taxa would make the analysis unwieldy. We included a large sample of mesonychians, following a previous study⁴. We also included 13 artiodactyls, sampling across the breadth of the modern suborders (Suina, Tylopoda and Ruminantia), but focusing on hippopotamids, their relatives, and Eocene artiodactyls. Following a previous study⁴² we suspected that the genus *Diacodexis* was paraphyletic. Therefore, we treated its North American *D. secans* and Asian *D. pakistanensis* as separate clades. We also added three families of Eocene Old World artiodactyls: cebochoerids, haplobunodontids, and raoellids. An explicit phylogenetic analysis of artiodactyls⁴² found raoellids near the base of a radiation of bunodont artiodactyls (including hippopotamids), and cebochoerids to be in an unresolved trichotomy with hippopotamids as part of the second clade, and anthracotheriids as the third. Anthracotheriids (represented in this analysis by *Elomeryx*⁴) are commonly considered to be closely related to hippopotamids, and haplobunodontids are traditionally included in the stem group of anthracotheriids. European haplobunodontids are thought to be middle Eocene migrants from Asia, making them possible candidates for the cetacean sister group under the hippopotamid hypothesis. Only three families of artiodactyls are known from Eocene Indo-Pakistan, the probable birthplace of cetaceans. We include all three in our analysis: raoellids, dichobunids (*D. pakistanensis*) and anthracotheriids.

Our matrix contains 29 taxa and 105 characters, 95 of which are parsimony informative and eight of which are ordered. Although gaps and missing characters represent different types of data, they are scored the same. We analysed the matrix using heuristic search algorithms in PAUP 4.0b8 software⁴⁷. ACCTRAN and DELTRAN optimizations were performed to investigate character transformation and estimated bootstrap values were calculated. Our maximum parsimony analysis produced 38 trees with a length of 281, consistency index of 0.39, and retention index of 0.61. A strict consensus cladogram of these trees is provided in Fig. 4. Character descriptions and scores, their sources, our matrix and our analyses are presented as Supplementary Information. Our heuristic search recovered a second island of trees at 282 steps. There are 38 trees with this tree length and both the Cetartiodactyla and Artiodactyla nodes were maintained in all trees.

Our results are robust against addition of *Hyopsodus* as an outgroup, to exclusion of *Menisotherium* and *Phenacodus* (which are dentally derived), and to the exclusion of *Eoconodon* and *Andrewsarchus* (which are in important positions in our cladograms, but are poorly known). The latter two taxa are the primary reason why character support for the Cetartiodactyla node varies with ACCTRAN and DELTRAN optimizations. ACCTRAN optimization shifts several important character changes from the Cetartiodactyla node to the node of Cetartiodactyla + *Andrewsarchus*.

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