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Reports

Origin of Whales in Epicontinental Remnant Seas: New Evidence from the Early Eocene of Pakistan

Abstract. *Pakicetus inachus* from the early Eocene of Pakistan is the oldest and most primitive cetacean known. The dentition of *Pakicetus* resembles that of carnivorous mesonychid land mammals as well as middle Eocene cetaceans. The otic region of the cranium lacks characteristic specializations of whales necessary for efficient directional hearing under water. *Pakicetus* occurs with a land-mammal fauna in fluvial sediments bordering epicontinental Eocene remnants of the eastern Tethys seaway. Discovery of *Pakicetus* strengthens earlier inferences that whales originated from terrestrial carnivorous mammals and suggests that whales made a gradual transition from land to sea in the early Eocene, spending progressively more time feeding on planktivorous fishes in shallow, highly productive seas and embayments associated with tectonic closure of eastern Tethys.

The origin of whales and their transition from land to sea is one of the most interesting problems of mammalian evolution. Middle Eocene whales have been known from marine sediments in Egypt (1), Nigeria (2, 3), and Texas (4) for many years, and similar finds have recently been made in India (5), but fossil whales have not been reported from older marine rocks (6). We report diagnostic cranial remains of whales of early Eocene age. The specimens were recovered from fluvial red sediments of the lower Kuldana Formation (7) at Chorlakki in the Kohat District of Pakistan, where they were found in association with a terrestrial mammalian fauna. The postcranial skeleton of early Eocene whales is not known, but a comparative study of cranial anatomy suggests that whales were probably not yet fully aquatic in the early Eocene.

Three genera of primitive cetaceans are known from the Kuldana Formation of Pakistan: *Gandakasia*, *Ichthyolestes*, and *Pakicetus* (8). *Gandakasia* and *Ichthyolestes*, known only from teeth, were originally described as mesonychid *Condylarthra* (9), the group of terrestrial mammals from which whales are thought to have evolved (10, 11). Fossil remains of *Gandakasia* occur in marginal marine sediments of the upper Kuldana Formation, and *Gandakasia* was recently recognized as a possible cetacean rather than mesonychid because of this association with marine facies (12). The basicranium of *Pakicetus* is unequivocally that of a primitive cetacean. *Ichthyolestes* is included in Cetacea because of dental resemblances to *Pakicetus*. Anatomically, *Pakicetus* is the best known

genus, being represented by the posterior portion of an exceptionally well preserved cranium, two dentaries, and isolated upper and lower cheek teeth (8, 13).

The cranium of *Pakicetus* (Fig. 1), estimated to have been about 30 to 35 cm in length and 14 to 15 cm in breadth, is distinctive in that it has a high, narrow sagittal crest bordered posteriorly by prominent lambdoidal crests. Dimensions of the outer surface of the braincase indicate that the relative size of the brain was small. Upper molars of *Pakicetus* are simple tritubercular teeth with a large central protocone, large pointed paracone, reduced metacone, and no accessory cusps. Lower premolars are high crowned, with a single protoconid cusp bordered anteriorly and posteriorly by crests that are smooth or slightly serrated. Lower molars have a massive triangular protoconid cusp and a simple keeled talonid. Teeth of *Pakicetus* resemble those of terrestrial mesonychid *Condylarthra* and are similar to teeth of middle Eocene archeocete Cetacea such as *Protocetus* and *Indocetus* (1, 5). Mesonychids and protocetids are thought to have been carnivorous or piscivorous, or both (14).

The basicranium of early Eocene archeocetes is known only in *Pakicetus*. In the holotype of *P. inachus* (GSP-UM 084) (Fig. 1D), the auditory bulla (tympanic) is preserved intact on the right side. It is relatively small by comparison with that of *Protocetus* (1) and other archeocetes but appears to be composed of dense bone. The bulla differs from that in other archeocetes in that it has a much more distinct notch for the eustachian

tube and a flatter involucrum. The left auditory bulla is missing in GSP-UM 084, and the middle ear is exposed (Fig. 2). The petrosal (periotic) is a long narrow bone wedged between the sphenoid, occipital, and squamosal, and partly underlain ventrally by the pterygoid. The ventral surface of the promontorium of the petrosal is broad and flat. The anterior process of the petrosal is small, but the posterior process is expanded distally, underlying an enlarged exoccipital process. The auditory bulla articulated with the basicranium in four places: a large bullar process of the squamosal, a smaller bullar process of the posterior part of the petrosal, and two small processes of the occipital (stippled areas, Fig. 2A). These articulations were not solidly fused in our specimen. Bullar processes present on the squamosal and occipital of *Pakicetus* have been lost in *Protocetus* and all later cetaceans for which the skull is known (4). The auditory bulla in *Protocetus* and later cetaceans is attached to the petrosal by the posterior pedicle or bullar process (present in *Pakicetus*) and by an anterior pedicle or fibrous connection possibly equivalent to the bullar process of the squamosal in *Pakicetus*, suggesting that this latter connection shifted from the squamosal to the petrosal as the tympanic and petrosal became isolated from surrounding bones of the skull early in cetacean evolution. There are no fossae for accessory air sinuses associated with the middle ear in *Pakicetus*. These fossae are absent or poorly developed in *Protocetus* as well, but a peribullar sinus is conspicuously developed in later archeocetes and in other cetaceans (4).

There is a distinct fossa for the tensor tympani muscle in *Pakicetus*. This fossa (TTF, Fig. 2B) measures about 1.5 by 2.0 mm in diameter and 3.5 mm in length. In land mammals the tensor tympani muscle inserts on the manubrium of the malleus, keeping the tympanic membrane taut. Pinnipeds adapted for hearing in water by bone resonance and conduction rather than stapedial impulse lack this tensor fossa and have a reduced tensor tympani muscle (15). The presence of a well developed fossa for the tensor tympani indicates that *Pakicetus* almost certainly retained a functional tympanic membrane.

Hearing in mammals requires selective matching of the density and impedance of some ear elements (for example, air in the middle ear cavity of land mammals) with the surrounding medium, while other elements have contrasting densities. In land mammals, there are air-filled chambers in the left and right middle ears

Table 1. Early Eocene mammalian fauna from red beds of the lower Kuldana Formation, in the eastern end of Panoba Dome, 4 km north northwest of Chorlakk Village, Kohat District, northwest Frontier Province, Pakistan. Coordinates of the fossil locality are 33°37'20" north latitude, 71°55'20" east longitude.

Order Proteutheria (Family <i>incertae sedis</i>) <i>Pakilestes lathrius</i> Russell and Gingerich, 1981 (28)	Order Tillodontia (Esthonychidae) <i>Basalina basalensis</i> Dehm and Oettingen-Spielberg, 1958 (9)
Order Lipotyphla (Family <i>incertae sedis</i>) <i>Seia shahi</i> Russell and Gingerich, 1981 (28)	Order Creodonta (Hyaenodontidae) <i>Paratriemnodon indicus</i> Ranga Rao, 1973 (33)
Order Chiroptera Chiropteran indet. A (28) Chiropteran indet. B (28)	Order Cetacea (Protocetidae) <i>Pakicetus inachus</i> Gingerich and Russell, 1981 (8)
Order Primates (Omomyidae) <i>Kohatius coppensi</i> Russell and Gingerich, 1980 (29)	Order Artiodactyla (Dichobunidae and Raoellidae) <i>Chorlakkia hassani</i> Gingerich <i>et al.</i> , 1979 (34) <i>Dulcidon gandaiensis</i> (Dehm and Oettingen-Spielberg), 1958 (9) <i>Diacodexis pakistanensis</i> Thewissen <i>et al.</i> , 1983 (37) <i>Indohyus cf. indirae</i> Ranga Rao, 1971 (35) <i>Khirtharia dayi</i> Pilgrim, 1940 (36)
Order Rodentia (Ctenodactylidae) <i>Birbalomys ijlsti</i> (Hussain <i>et al.</i>), 1978 (30, 32) <i>Birbalomys sondaari</i> (Hussain <i>et al.</i>), 1978 (30, 32) <i>Birbalomys vandermeuleni</i> (?) (Hussain <i>et al.</i>), 1978 (30, 32) <i>Birbalomys woodi</i> (?) Sahn and Khare, 1973 (31, 32) <i>Chapattimys wilsoni</i> Hussain <i>et al.</i> , 1978 (30, 32) <i>Chapattimys debruijini</i> Hartenberger, 1982 (32) Cf. <i>Petrokoslavia</i> sp. (32) <i>Gumbatamys asifi</i> Hartenberger, 1982 (32)	Order Perissodactyla (Brontotheriidae) <i>Eotitanops? dayi</i> Dehm and Oettingen-Spielberg, 1958 (9)
	Order Proboscidea (Moeritheriidae) <i>Lammidhanja wardi</i> (Pilgrim, 1940) (36) <i>Pilgrimella pilgrimi</i> Dehm and Oettingen-Spielberg, 1958 (9)

that are separated and isolated by bone and soft tissues that have densities greater than air, preventing one ear from hearing exactly what the other does and making directional hearing possible. Directional hearing in water requires functional modification because an aqueous medium is similar in density to most

mammalian tissues. Modern cetaceans (16) achieve a perceptible impedance contrast with surrounding tissues in water by having unusually dense tympanic bullae. The tympanic and petrosal bones in each ear are connected by anterior pedicles, posterior pedicles, or both, to form a petrotympanic unit on each side

of the skull. These left and right petrotympanic units are isolated from each other and from the rest of the cranium by highly vascularized, foam-filled sinuses that have the same density as the surrounding medium. Density differences between the tympanic bone on the one hand and surrounding tissues and water on the other provide the contrast necessary for signal detection. Isolation of left and right petrotympanic units from each other in separate foam-filled sinuses facilitates directional hearing. Vascularization of these sinuses permits engorgement of cavernous tissue with blood to maintain pressure during diving. The auditory ossicles of modern cetaceans are massive. The malleus is fused directly to the tympanic bulla instead of being connected to a taut tympanic membrane, and the tensor tympani muscle is greatly reduced. The malleus, incus, and stapes transmit differential vibration that is induced between the dense tympanic and corresponding petrosal of each isolated petrotympanic unit to the cochlea of the inner ear within each petrosal.

The tensor tympani fossa in *Pakicetus* is slightly smaller than one might expect in a land mammal of its size (17), the tympanic bulla appears to be composed of relatively dense bone, and there is a distinct sigmoid process of the tympanic that may indicate partial fusion of the tympanic and malleus. These characteristics suggest that the tympanic bulla may have been used to some limited extent in *Pakicetus* in the reception of water-borne sound. However, the petrosal is firmly attached to surrounding bones of the skull, the tympanic articulates with the squamosal and occipital as well as the petrosal, and there are no fenestrae or sinuses isolating the left and right auditory regions from each other.

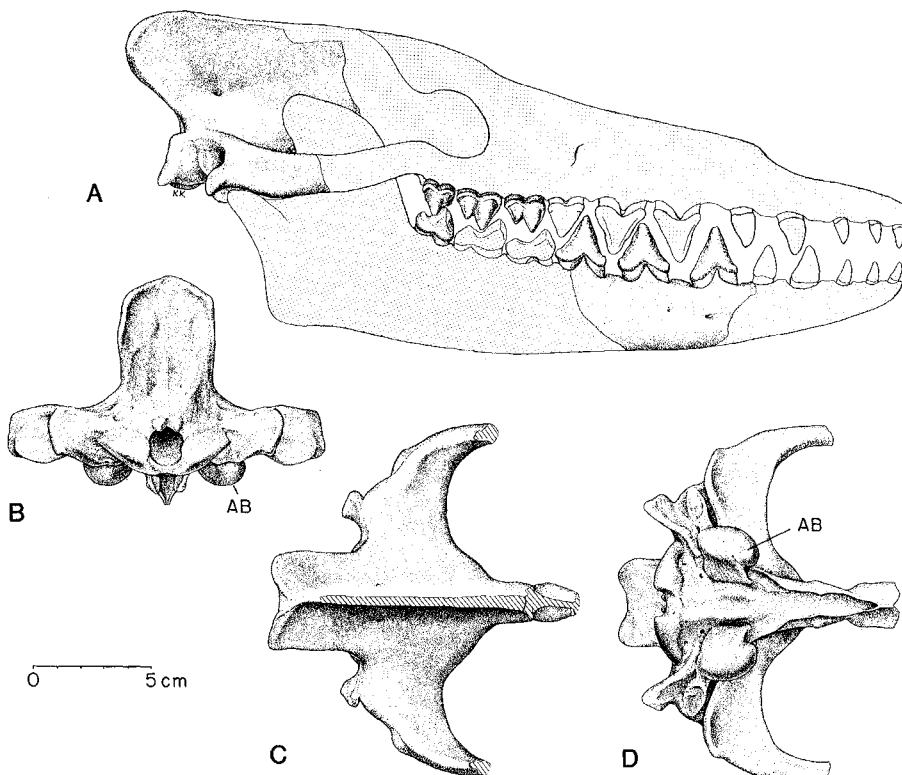


Fig. 1. Cranium of *Pakicetus inachus*. (A) Reconstruction of skull in lateral view from University of Michigan—Geological Survey of Pakistan [UM-GSP] specimens 081 (dentary with P_{2-4}), 082 (M_3), 083 (M^1), 084 (posterior cranium), 085 (M^3), and 134 (M^2). Actual specimens of *P. inachus* are shaded, reconstructed areas are shown in even stippling. Outline of lower jaw is derived from dentary of holotype of closely related *Pakicetus attockii* described by West (13), and length of cranium is reconstructed on this basis. Posterior portion of cranium UM-GSP 084 is also shown in (B) posterior view, (C) dorsal view, and (D) ventral view. Note large pointed cheek teeth with simple crowns, high sagittal and lambdaoidal crests arising from small braincase, posteriorly and downwardly directed occipital condyles, flaring zygomatic arches, and small auditory bullae (AB). Left auditory bulla is reconstructed from right side.

Consequently there is no evidence that *Pakicetus* could hear directionally under water. There is no indication of vascularization of the middle ear to maintain pressure during diving, and early Eocene whales were probably incapable of diving to any significant depth. In terms of function, the auditory mechanism of *Pakicetus* appears more similar to that of land mammals than it is to any group of extant marine mammals.

The fauna associated with *Pakicetus* at Chorlakkhi is dominated by land mammals (Table 1). Nonmammalian remains include poorly preserved *Planorbis*-like snails, fishes (particularly catfish), turtles, and crocodylians. All of these are found together in several closely spaced 10- to 40-cm beds of coarse calcareous granule stone within a 50-m red shale sequence of the lower Kuldana Formation. The calcareous granules are interpreted as reworked soil nodules because they have a fabric with irregular concentric growth, episodic formation of irregular rings of hematitic stain, and septarian nodule-like radial and concentric cracks.

The granules also have stable isotope values indicative of formation and diagenesis in soil water (18). Altogether this evidence indicates a fluvial and continental rather than marine environment for *Pakicetus* during at least part of its daily or annual life cycle. At Chorlakkhi, deciduous teeth of *Pakicetus* are found with approximately the same frequency as permanent teeth, supporting Fordyce's suggestion that breeding and parturition in primitive archeocetes may have taken place in freshwater or on land (19).

At the beginning of the Eocene, the Pakistan side of eastern Tethys became confined to a series of shallow linear basins parallel to the eventual suture between Indo-Pakistan and Eurasia (20). This change was caused by Indo-Pakistan and central Asia converging and trapping microplates between them (21). During the early Eocene, the Kohat depositional basin became an enclosed saline epicontinental remnant sea of restricted circulation with marginal coastal sebkha environments producing dolomite and gypsum grading into halite. Continental red beds of the lower Kuldana Formation, of latest early Eocene age, are underlain and partly overlain by coastal and marine evaporites. These red beds represent progradation of basin-margin alluvial plains into the basin during a low-stand of the sea (22).

Saline lakes and embayments, such as those whose deposits interfinger laterally with the lower Kuldana Formation, are typically high in primary plankton and

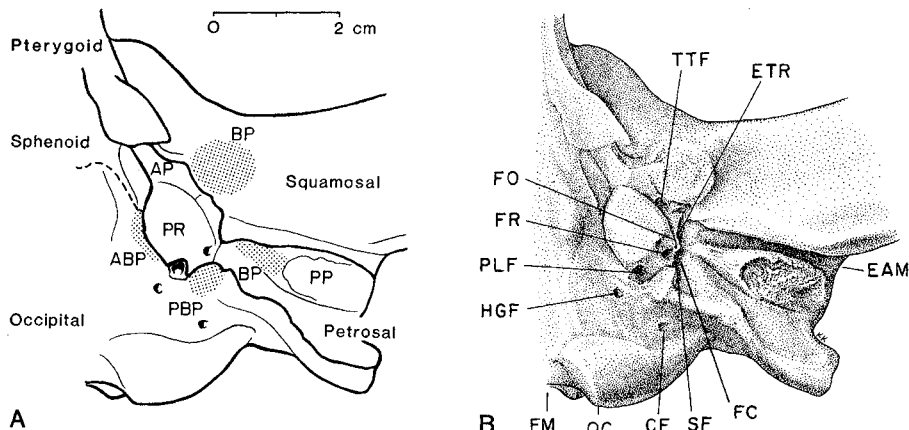


Fig. 2. Detail of left auditory region of cranium of *Pakicetus inachus* (GSP-UM 084) in ventral view with tympanic bulla removed. (A) Relationships of petrosal to surrounding squamosal, basioccipital, sphenoid, and pterygoid bones. Stippled areas are processes or surfaces for articulation with the tympanic bulla. The bulla is not shown. (B) Shaded drawing of the same area as in (A) to show the positions of foramina, cochlear fenestrae, and muscular fossae. Note the presence of a distinct fossa for the tensor tympani muscle. *ABP*, anterior bullar process of basioccipital; *AP*, anterior process of petrosal; *BP*, bullar process of petrosal and squamosal; *CF*, condylar foramen; *EAM*, external auditory meatus; *ETR*, epitympanic recess; *FC*, facial canal; *FM*, foramen magnum; *FO*, fenestra ovale (hidden); *FR*, fenestra rotunda; *HGF*, hypoglossal foramen; *OC*, occipital condyle; *PBP*, posterior bullar process of basioccipital; *PLF*, posterior lacerate foramen; *PP*, posterior process of petrosal; *PR*, promontorium of petrosal (overlies cochlea in this view); *SF*, stapedia fossa; *TTF*, tensor tympani fossa.

secondary fish productivity (23). Clupeid fishes (herrings and their allies) have occupied such habitats since the late Cretaceous (24) and were present in saline waters of the Kohat Basin during the Eocene (25). We speculate that ancestral whales first entered shallow epicontinental remnants of Tethys in the early Eocene to feed on abundant planktivorous clupeids, or larger fishes higher in the food chain. Lipps and Mitchell (26) suggested that successful invasion of the sea by archeocetes was made possible by an increase in the intensity of oceanic upwelling during the late Paleocene and Eocene, with concomitant increase in available nutrients and biotic productivity. Our proposal is similar, but we suggest that the initial marine invasion occurred in shallow saline epicontinental remnants of Tethys like those marginal to the lower Kuldana Formation in our study area. Subsequently whales probably colonized nearshore and then offshore areas of upwelling. Microplate congregation along the western edge of Indo-Pakistan and adjacent portions of Tethys in the early Cenozoic (21) would have increased both the length of shoreline and the areal distribution of highly productive saline epicontinental and marginal seas (27). It is unlikely that protocetaceans invaded areas of oceanic upwelling without going through a nearshore, shallow water stage, although subsequent colonization of areas of upwelling may have led to major adaptive radiations of Cetacea in the Eocene, Oligocene, and Miocene.

The dentition and cranial anatomy of *Pakicetus* indicate that it was well equipped to feed on fishes in the surface waters of shallow seas, but it lacked auditory adaptations necessary for a fully marine existence. We do not yet know anything about the postcranial anatomy of early Eocene whales. The fact that *Pakicetus* is preserved in fluvial red sediments in association with land mammals indicates that early Eocene whales may still have spent a significant amount of time on land. Evidence suggests that *Pakicetus* and other early Eocene cetaceans represent an amphibious stage in the gradual evolutionary transition of primitive whales from land to sea.

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Interstellar Carbon in Meteorites

Abstract. *The Murchison and Allende chondrites contain up to 5 parts per million carbon that is enriched in carbon-13 by up to +1100 per mil (the ratio of carbon-12 to carbon-13 is approximately 42, compared to 88 to 93 for terrestrial carbon). This "heavy" carbon is associated with neon-22 and with anomalous krypton and xenon showing the signature of the s-process (neutron capture on a slow time scale). It apparently represents interstellar grains ejected from late-type stars. A second anomalous xenon component ("CCFXe") is associated with a distinctive, light carbon (depleted in carbon-13 by 38 per mil), which, however, falls within the terrestrial range and hence may be of either local or exotic origin.*

Primitive meteorites contain several noble gas components of anomalous isotopic composition, at least some of which seem to be of exotic, presolar origin (1-6). These noble gas components are trapped in solid, mainly carbonaceous, carrier phases constituting less than 1 percent of the meteorite, and differ from each other in isotopic ratio, release temperature on stepped heating, and grain size of the carrier phase (Table 1). Together with their noble gas components, these carriers contain a rich record of stellar nucleosynthesis and interstellar chemistry that is waiting to be deciphered.

The $^{12}\text{C}/^{13}\text{C}$ ratio varies greatly in stars, as production and survival of carbon isotopes depend sensitively on stellar mass, temperature, and hydrogen abundance (7, 8). This ratio ranges from 4 to > 100 in late-type stars, and even the mean interstellar ratio, 60 ± 8 or 67 ± 10 (9), differs appreciably from the terrestrial ratio of 89. Thus exotic carbon in meteorites should be easily recognizable by its anomalous isotopic ratio.

Previous studies of meteoritic carbon revealed only modest isotopic variations, with $\delta^{13}\text{C}$ (10) ranging from +65 per mil for carbonates to -30 per mil for organic matter (11). This variation, though exceeding the normal terrestrial range of +10 to -45 per mil (10), is consistent with kinetic isotope fractionation in the hydrogenation of CO at 350 to 500 K (12) and hence does not require nuclear processes. Recently, however, Kerridge (13) found traces of distinctly heavier carbon (+110 per mil) in the 1050°C fraction from stepped combustion of organic matter from the Murray C2 chondrite and suggested that it reflected nucleosynthesis rather than mass fractionation. Comparable enrichments in ^{14}N have been found for nitrogen and have likewise been attributed to nuclear processes (14).

Table 1. Anomalous noble gas components with carbonaceous carrier phases.

Property	Ne-E (L)*	s-Xe	CCFXe
Characteristic ratio	$\frac{^{20}\text{Ne}}{^{22}\text{Ne}}$	$\frac{^{130}\text{Xe}}{^{132}\text{Xe}}$	$\frac{^{136}\text{Xe}}{^{132}\text{Xe}}$
Component	< 0.01	0.48	0.64
Atmosphere	9.8	0.15	0.32
Release T, °C	600	1400	1000
Carrier	C α	C γ	C δ
Grain size, μm	1-10	0.1-3	0.01-1

*There is a second type of Ne-E that is located in an inorganic carrier [spinel and/or apatite (6)] and has a much higher gas release temperature (1200°C). On the basis of release temperature, these two components are designated L (low) and H (high).