PAKICETUS INACHUS, A NEW ARCHAEOCETE
(MAMMALIA, CETACEA) FROM THE EARLY-MIDDLE EOCENE
KULDANA FORMATION OF KOHAT (PAKISTAN)

BY

PHILIP D. GINGERICH and DONALD E. RUSSELL
CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

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PAKICETUS INACHUS, A NEW ARCHAEOCETE (MAMMALIA, CETACEA) FROM THE EARLY-MIDDLE EOCENE KULDANA FORMATION OF KOHAT (PAKISTAN)

By

Philip D. Gingerich¹ and Donald E. Russell²

Abstract.—A new genus and species of primitive protocetid whale, Pakicetus inachus, is described from the early-middle Eocene Kuldana Formation at Chorlakki, Kohat District, North-West Frontier Province, Pakistan. The holotype is a nearly perfectly preserved posterior portion of a cranium. Pakicetus is distinctive among whales in retaining an extremely primitive auditory region. The auditory bulla articulates with the squamosal, basioccipital, and paroccipital in addition to a normal cetacean articulation with the posterior process of the periotic. The cochlear part of the periotic articulates with both the squamosal and the basioccipital. Three genera of early-middle Eocene whales are now known from Pakistan. Pakicetus is intermediate in size between Ichthyolestes and Gandakasia, and it resembles both to some degree in dental morphology. "Protocetus" attocki from Ganda Kas is here referred to Pakicetus.

INTRODUCTION

The early Cenozoic mammalian fauna of Pakistan and India is poorly known. This region is critical for understanding the biogeographic history of mammals and, consequently, in 1975 we began a cooperative program to study Paleocene and Eocene faunas and sediments with the Geological Survey of Pakistan. The initial descriptions of Eocene mammals from Pakistan by Pilgrim (1940) and Dehm and Oettingen-Spielberg (1958) have been supplemented in recent years by descriptions of new mammals from the Subathu Formation in the vicinity of Kalakot in Jammu-Kashmir (Ranga Rao, 1971, 1972, 1973; Ranga Rao and Obergfell, 1973; Sahni and Khare, 1972, 1973; Sahni and Srivastava, 1976, 1977; Kahn, 1973), the Subathu Formation in the Simla Hills (Sahni and Kumar, 1980), the Berwali Series in the vicinity of Baranda in Kutch (Tandon, 1971; Sahni and Mishra, 1972, 1975; Satsangi and Mukhopadhyay, 1975), the Kuldana Formation in the vicinity of Ganda Kas in northwestern Punjab (Gingerich, 1977; Hussain et al., 1978; West and Lukacs, 1979; West, 1980), and the Kuldana Formation between Panoba and Chorlakki in Kohat District (Gingerich et al., 1979a, 1979b; Russell and Gingerich, 1980). Our work in 1978 and 1979 was concentrated at the Chorlakki locality in the extreme eastern end of Panoba Dome, Kohat District. In 1980 we made good collections of Eocene mammals at new localities in the Subathu Formation near Kamroti in Kashmir, and at Jozara Rest House and Barbora Banda in Kohat District (Text-fig. 1).

¹Museum of Paleontology, The University of Michigan, Ann Arbor
²Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris
TEXT-FIG. 1 —Eocene fossil vertebrate localities in the Indus Basin of Pakistan. Heavy stippling shows the outcrop pattern of Eocene sedimentary rocks. MBT and MMT are the Main Boundary Thrust and Main Mantle Thrust, respectively, representing the suture between Indo-Pakistan and Eurasian lithospheric plates. Specimens described in this paper were collected at Chorlakki in Kohat District, North-West Frontier Province, and at Lammidhan and Ganda Kas in Attock District, Punjab Province. New Eocene mammal-bearing localities have recently been discovered by Geological Survey of Pakistan-University of Michigan field parties at Maklorhi and Kamroti in Kashmir, and at Jozara Rest House and Barbora Banda in Kohat District.

Ten orders of mammals are represented in the early-middle Eocene collections described from India and Pakistan to date: Primates, Condylarthra(?), Creodonta, Cetacea, Sirenia(?), Rodentia, Tillodontia, Artiodactyla, Perissodactyla, and Proboscidea. The only record of Condylarthra at present is a possible mesonychid tooth described by Ranga Rao (1973) as cf.
Honanodon. The specimen referred to Mesonychidae by West (1980) is a left lower premolar of the artiodactyl Indohyus indira. The genus Dulcidon appears to be closely related to Chorlakkaia and we now refer Dulcidon to the Artiodactyla rather than the Condylarthra. West (1980), citing an unpublished report by Gingerich, listed “Miacidae indet.” from the Chorlakki locality. This record was originally listed with a query in an unpublished report, and the specimen on which it was based is probably a partial upper molar of Parastriptemnodon. Thus there is no substantiated record of Carnivora in these faunas. Upon further preparation and comparison, the holotype of Isthatherium subathuesis, described by Sahni and Kumar (1980) as a sirenian, appears to resemble a partial upper molar of Pilgrimella. While it is possible that Isthatherium is a sirenian, the evidence available at present is insufficient to document this.

Coombs and Coombs (1979) referred Pilgrimella to the order Perissodactyla, while West (1980) discussed this genus as a junior synonym of Anthracobune, which he placed in Moeritheriidae (Proboscidea). West (1980) followed most authors in listing Lammidhania as an anthracothere (Artiodactyla). We maintain the validity of both Pilgrimella and Anthracobune, and group these with Lammidhania in Moeritheriidae. Based on their resemblance to Minchenella Zhang (1980) from the late Paleocene of China, Anthracobune, Lammidhania, and Pilgrimella could also possibly be included in the family Phenacolophidae (Zhang, 1978). This would not necessarily preclude a relationship to Moeritherium, a more advanced form known from the late Eocene and Oligocene of Egypt. Ordinal placement of Phenacolophidae is problematical. Zhang (1978) placed this family in Condylarthra, Van Valen (1978), following McKenna and Mannig (1977), placed it in Embrithopoda, and Chow and Wang (1979) placed it in Pantodonta. We suggest that it might also be related to the ancestry of Proboscidea.

In this paper we describe a new genus and species of archaeocete cetacean, Pakicetus inachus, based on a partial cranium and dental remains found in the bone bed at Chorlakki. The locality and fauna known to date are discussed in Gingerich et al. (1979a,b) and Russell and Gingerich (1980). In a following report we describe the first insectivores and bats from Chorlakki (Russell and Gingerich, 1981).

The first suggestion that whales were present in early-middle Eocene mammalian faunas of Pakistan was the discovery of a fragmentary specimen of Gandakasia, previously regarded as a mesonychid condylarth, in transitional marine beds at the top of the Kuldana Formation or bottom of the Kohat Formation (depending on how this formational boundary is defined) near Lammidhan in Punjab (Gingerich, 1977). Discovery in 1978 and 1979 of the specimens described here indicated that Ichthyolestes, also initially regarded as a mesonychid, is probably a cetacean as well. On this basis, West (1980) included Ichthyolestes in the family Protocetidae, order Cetacea. Gandakasia and Ichthyolestes are known only from fragmentary dental specimens. The new cetacean specimens described here include a remarkably complete posterior portion of a cranium that demonstrates beyond question the presence of whales in the early-middle Eocene Kuldana Formation of Pakistan. No dental remains were found with the cranium, but upper and lower teeth from the same bed are the correct size to belong to it. They have the morphology of Eocetus, Indocetus, and other undescribed cetacean remains from Kutch, and we refer them to the new form without question. The new teeth also resemble those of Gandakasia and Ichthyolestes, further substantiating their classification in Protocetidae.

AGE OF THE KULDANA FORMATION

Pilgrim (1940) first identified mammals from the Kuldana Formation at Lammidhan and Ganda Kas as middle Eocene in age, based on foraminiferal correlations of the Lower Chharat series (now Kuldana Formation) with the lower Khirthar series of Sind and the lower Lutetian
stage in Europe. This assignment has been followed by most subsequent authors discussing the age of mammalian fossils from the Kuldana Formation. Meissner et al. (1974) recorded early Eocene Foraminifera from the Kuldana Formation (= Mami Khel Clay) in Kohat. Cheema, Raza, and Ahmad (in Shah, 1977) regarded the Kuldana Formation as early to early middle Eocene in age. Our work also appears to indicate that the Kuldana Formation as a whole straddles the early to middle Eocene boundary (Wells, pers. comm.). The cetacean basicranium described here is more primitive than that of the related genus and species Protocetus atavus from the early or middle Lutetian of Egypt. It could be either latest early Eocene or earliest middle Eocene in age, judging from its evolutionary grade. Apart from West's (1980) identification of Gobiohyus in the fauna from Ganda Kas, there is nothing in the remaining mammalian fauna from either Chorlakki or Ganda Kas to preclude a latest early Eocene age for the principal mammal-bearing horizons. It is possible that the mammal-bearing portion of the Kuldana Formation is early Eocene in age in Kohat, and early middle Eocene in age in Punjab, with the equivalent part of the Subathu Formation being middle or late Eocene in Jammu-Kashmir. However, the general similarity of mammalian faunas from all three areas argues against any marked time transgression. Given the present state of uncertainty, we have hyphenated early-middle Eocene in this paper to indicate that the age of the mammal-bearing bed in the Kuldana Formation at Chorlakki may be either early or middle Eocene; the age of this bed is, in any case, close to the transition between the early and middle Eocene.

SYSTEMATIC PALEONTOLOGY

Order CETACEA
Suborder ARCHAEOCETI
Family PROTOCETIDAE

Pakicetus, new genus

Ichthyolestes (in part), West, 1980, p. 516.

Type species.—Pakicetus inachus, new species.

Included species.—Type species and “Protocetus” attocki West, 1980.

Diagnosis.—Small protocetid with exceptionally high narrow sagittal and nuchal crests, narrow pterygoid rostrum, and small braincase. Distinct conical nuchal tubercles over foramen magnum. Upper molars three-rooted, with a distinct protocone, paracone, and reduced metacone (lost on M3). Lower premolars with simple high narrow crowns; anterior and posterior crests may be smooth (P. attocki) to faintly serrated (P. inachus). Lower molars with a single large trigonid cusp (protoconid) and a smaller talonid cusp (hypoconid). Mandibular symphysis may extend as far posteriorly as Pz. Differs from Protocetus in retaining distinct protocones on upper molars and in having a flat promontorium filling the middle ear and contacting the basioccipital. Differs from Eocetus and Indocetus in being much smaller and in having sharper protocones on upper molars. Differs from Pappocetus in lacking complete cingula and ornamented enamel on lower molars. Intermediate in size between Ichthyolestes and Ganda-
Parasitica. Differs from the former in having smaller, narrower protocones on upper molars, with a strong beaded cingulum extending around the lingual half of each tooth. Differs from Gandakasia in having more sectorial lower molars and in having more gracile premolars without cusped talonids.

Etymology.—Pak, abbreviation for Pakistan derived from the initial letters of Punjab, Afghan Frontier (NWFP), and Kashmir provinces, each of which now produces Eocene mammals; and cetus, L. (masc.), whale.

Pakicetus inachus, new species

Text-figs. 2-5

Holotype.—Geological Survey of Pakistan—University of Michigan [GSP-UM] specimen 084, posterior portion of a cranium with the right auditory bulla intact (Text-figs. 2 and 3).

Referred specimens.—GSP-UM 081, left mandibular ramus with P2-P4; GSP-UM 082, left M1; GSP-UM 083, left M2; GSP-UM 085, left M3; and GSP-UM 134, crown of left M4 with protocone broken off.

Type locality.—4 km NNW of Chorlakki village, Kohat District, North-West Frontier Province, Pakistan. Coordinates of the Chorlakki locality are 33°37'20" N latitude, 71°55'20" E longitude.

Age and distribution.—Late early Eocene or early middle Eocene Kuldana Formation, Kohat District Pakistan.

Diagnosis.—Differs from Pakicetus attocki (West, 1980) in having serrated anterior and posterior crests on lower premolars (see Text-fig. 4).

Etymology.—Named for Inachus, mythical river god, son of Tethys and father of Io, in allusion to the riverine habitus of this species, its close relationship to Tethyan biogeography, and a possible relationship to ungulates as well.

Description.—Pakicetus inachus has a cranium 14.5 cm in breadth across the zygomatic arches. We estimate its original length to have been about 30 to 35 cm. The sagittal crest rises 3 cm above the top of the braincase. The nuchal crest is high and narrow, projecting 7 cm above and 2 cm behind the occipital condyles. There are moderately large parietosquamosal foramina opening into the temporal fossa above the braincase on each side of the skull. The temporal fossa itself is large, indicating that the temporalis musculature was extremely well developed in Pakicetus. The foramen magnum measures 16 mm in height and 15 mm in width, and there are two distinctive conical nuchal tubercles just above the foramen magnum. Sutures separating individual bones are not well preserved, making it difficult or impossible to estimate the relative size of most bones contributing to the braincase. Judging from the external size of the braincase, the brain itself was very small in Pakicetus by comparison with other Eocene mammals (Text-fig. 2).

The basicranium of the holotype of Pakicetus inachus is extremely well preserved (Text-fig. 3). It has the auditory bulla preserved in articulation with the rest of the skull on the right side. The bulla is conveniently missing on the left side, exposing the internal morphology of the middle ear. The bulla itself is entirely ectotympanic in origin. It is relatively small for an archaeocete, measuring 25.5 mm in maximum anteroposterior length and 22.5 mm in maximum breadth. There is a distinct notch visible for the eustachian tube, and the ventral surface of the involucrum is furrowed and flat, sloping at about 45° to the sagittal plane. The sigmoid process of the tympanic is present on the lateral surface of the bulla where it joins the posterior process of the periotic.

Within the middle ear, the cochlear part of the periotic has a broad, flat ventral surface. The
anterior process of the periotic is moderately developed, while the posterior process is well developed, fitting between the squamosal and paroccipital-exoccipital as is characteristic of archaeocetes. There is a distinct fossa measuring about 1.5 mm by 3.5 mm just lateral to the cochlea for origin of the tensor tympani muscle. The external auditory meatus has the form of a deep groove about 3 mm wide and nearly 30 mm long extending from the tympanic recess to the lateral margin of the skull. It is confined anteriorly by the postglenoid process of the squamosal and posteriorly by the posterior process of the periotic.

The tympanic bulla articulates with the posterior process of the periotic and there may be some connection with the anterior process as well. In addition, it has a large oval articulation with a bullar process of the squamosal, a moderately large articulation with a bullar process of the paroccipital, and a smaller but significant articulation with the lateral margin of the ventral muscular tubercles or crests of the basioccipital. Each of these bullar articulations is labelled b in Text-fig. 3. The periotic itself is attached firmly to the squamosal and to the basioccipital.

Upper molars referred to Pakicetus appear to have been three-rooted. M¹, M², and M³ all have large protocones. These are reduced by comparison with the protocones of Ichthyolestes, but they are much more pointed than those of either Eocetus or Indocetus. A strong beaded cingulum encircles the protocone as in Indocetus. The paracone is a large pointed cusp projecting much farther than the protocone. A distinct metacone, slightly smaller than the paracone, is present on M¹ and M², but this cusp is lacking on M³. M¹ measures approximately 13.5 mm in length and 14.2 mm in breadth. M² measures approximately 17.2 mm in length. M³ measures 13.9 mm in length and 17.9 mm in breadth.

A portion of the mandibular ramus with P₂-P₄ is illustrated in Text-fig. 4. All three of these
premolars are similar in shape, having a large central cusp and no accessory cusps. The crowns are compressed laterally, and there is a sharp crest anterior and posterior to the central cusp. This crest is distinctly serrated, although the serrations themselves are not deeply incised. The posterior part of the mandibular symphysis is preserved on the medial side of this ramus, and it extends posteriorly as far as \( P_2 \). \( P_2 \) measures 20.2 mm in length and 7.5 mm in breadth. \( P_3 \) measures 22.5 mm in length and 8.0 mm in breadth. \( P_4 \) measures approximately 20.5 mm in length and it is 8.5 mm in breadth. The mandibular ramus is 28.5 mm in depth below \( P_2 \).

The only lower molar known at present is GSP-UM 082, a left \( M_3 \). The trigonid consists of a
TEXT-FIG. 4 — Left mandibular ramus of *Pakicetus inachus*, UM-GSP 081, with P₂–P₄ in lateral view (A) and medial view (B). Note posterior margin of mandibular symphysis below P₂ in medial view. Natural size.

single large centrally placed cusp (protoconid) with a large flat wear facet sloping anterolaterally away from the protoconid and preprotocristid. The anterior margin of the tooth is square, with a distinct groove or notch for articulation with M₂. This keying of adjacent cheek teeth is similar to that found in *Gandakasia*. The talonid consists of a single cusp (hypoconid) connected to the protoconid by a high sharp crest. There is a distinct beaded cingulid extending along the medial side of M₃, but this cingulid is absent on the lateral side of the tooth. M₃ measures 17.8 mm in length and 8.9 mm in breadth.

No postcranial remains can be referred to *Pakicetus inachus* at present.

*Pakicetus attocki* (West, 1980)

Text-fig. 5

*Protocetus attocki* West, 1980, p. 515, Pl. 1, fig. 5.


*Protocetidae*, indet., West, 1980, p. 516, Pl. 2, fig. 3.
HOLOTYPE.—Hussain-Geological Survey of Pakistan [H-GSP] specimen 1694, a left dentary with crowns of P₃ and P₄, alveoli for I₃, C₁, P₁-P₄, and the broken crown of M₁.

REFERRED SPECIMENS.—H-GSP 1981b is probably an upper second molar of this species. It is too large to belong to *Ichthyolestes pinfoldi* and it has the flatter protocone surrounded by a beaded cingulum characteristic of *Pakicetus*. H-GSP 1974a is probably a deciduous lower molar of *Pakicetus attaoki*. Both of these specimens were described and illustrated by West (1980). British Museum (Natural History) [BMNH] specimen M-15806, described below, is probably the mandibular ramus of a juvenile *Pakicetus attaoki*.

TYPE LOCALITY.—H-GSP locality 62, Kuldana Formation at Ganda Kas, Attock District, Punjab, Pakistan.

AGE AND DISTRIBUTION.—*Pakicetus attaoki* is known only from the early-middle Eocene at Ganda Kas and Lammidhan, Attock District, Pakistan.

DIAGNOSIS.—Differs from *Pakicetus inachus* in lacking serrations on the anterior and posterior crests of the lower premolars.

DESCRIPTION OF NEW MATERIAL.—An unusual dentary from Lammidhan, near Ganda Kas in Pakistan, is preserved in the British Museum (Natural History) collection. This specimen, BMNH M-15806 (Text-fig. 5), was previously interpreted as the mandible of a juvenile artiodactyl (Gingerich, 1977). However, further study of the specimen indicates that it is almost certainly the mandibular ramus of a juvenile archaeocete. The crown of one tooth, probably dP₃, is preserved intact. This resembles an adult premolar of *Pakicetus* (Text-fig. 4) in general form, although it is much more gracile and the roots are more divergent. The mandibular bone of BMNH M-15806 is porous in texture, which is another indication that it represents a young individual. The specimen is the right size and morphology to belong to *Pakicetus*, and it is referred to *Pakicetus attaoki* rather than *P. inachus* because it was found near the type locality of the former. Comparison with H-GSP 1974a described by West (1980) suggests that this tooth is also a deciduous premolar of *Pakicetus*.

TEXT-FIG. 5 —Right mandibular ramus of juvenile *Pakicetus attaoki*, BMNH M-15806, with dP₃ in occlusal view (A) and lateral view (B). Natural size (scale is in mm).
The holotype *Pakicetus inachus* described here includes the best preserved basicranium of any protocetid known. It is generally similar to *Protocetus atavus* described by Fraas (1904) and Kellogg (1936), but differs in having both the cochlear part of the periotic and the auditory bulla much more firmly attached to the bones surrounding the middle ear. *Pakicetus* has the large posterior process of the periotic characteristic of archaeocetes, and it appears to have the thick, dense auditory bulla characteristic of all cetaceans, but *Pakicetus* exhibits few of the other specializations of this group required for hearing under water. *Pakicetus* is one of the oldest whales known anywhere, and with further study it should contribute to our understanding of both the origin of whales and the functional evolution of hearing in cetaceans.

Three archaeocete genera are now known from the early-middle Eocene of Pakistan. These are, in order of increasing tooth size and presumably body size, *Ichthyolestes*, *Pakicetus*, and *Gandakasia*. In our present state of knowledge, the three genera are differentiated only on dental characteristics. The cranium is known only for *Pakicetus*, and no postcranial remains referable to any of these genera have yet been described. *Ichthyolestes* and *Gandakasia* were both originally described as mesonychid condylarths, and a mesonychid origin of Cetacea is plausible (Van Valen, 1966, 1968). The primitive nature of the dentition in *Ichthyolestes*, *Pakicetus*, and *Gandakasia*, the fact that all three genera are found in association with land mammals, and the primitive nature of the basicranium in *Pakicetus* combine to suggest that whales may have made the transition from land to sea as late as the early or early-middle Eocene.

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The holotype of *Pakicetus inachus* was prepared by Mr. Gerald Paulson. Ms. Karen Payne drew the map and illustrations in Text-figs. 1 and 4. Mr. George Junne took the photographs in Text-figs. 2, 3, and 5. Field research in 1977, 1978, 1979, and 1980 was sponsored by the Geological Survey of Pakistan and the Smithsonian Foreign Currency Program.
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P. D. GINGERICH and D. E. RUSSELL


