CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 25, NO. 11, p. 235–246 (5 text-figs.) December 31, 1981

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

MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

Gerald R. Smith, Editor

This series of contributions from the Museum of Paleontology is a medium for the publication of papers based chiefly upon the collection in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals upon request. A list of the separate papers may also be obtained. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan, 48109.

VOLS. II–XXV. Parts of volumes may be obtained if available. Price lists available upon inquiry.

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

By

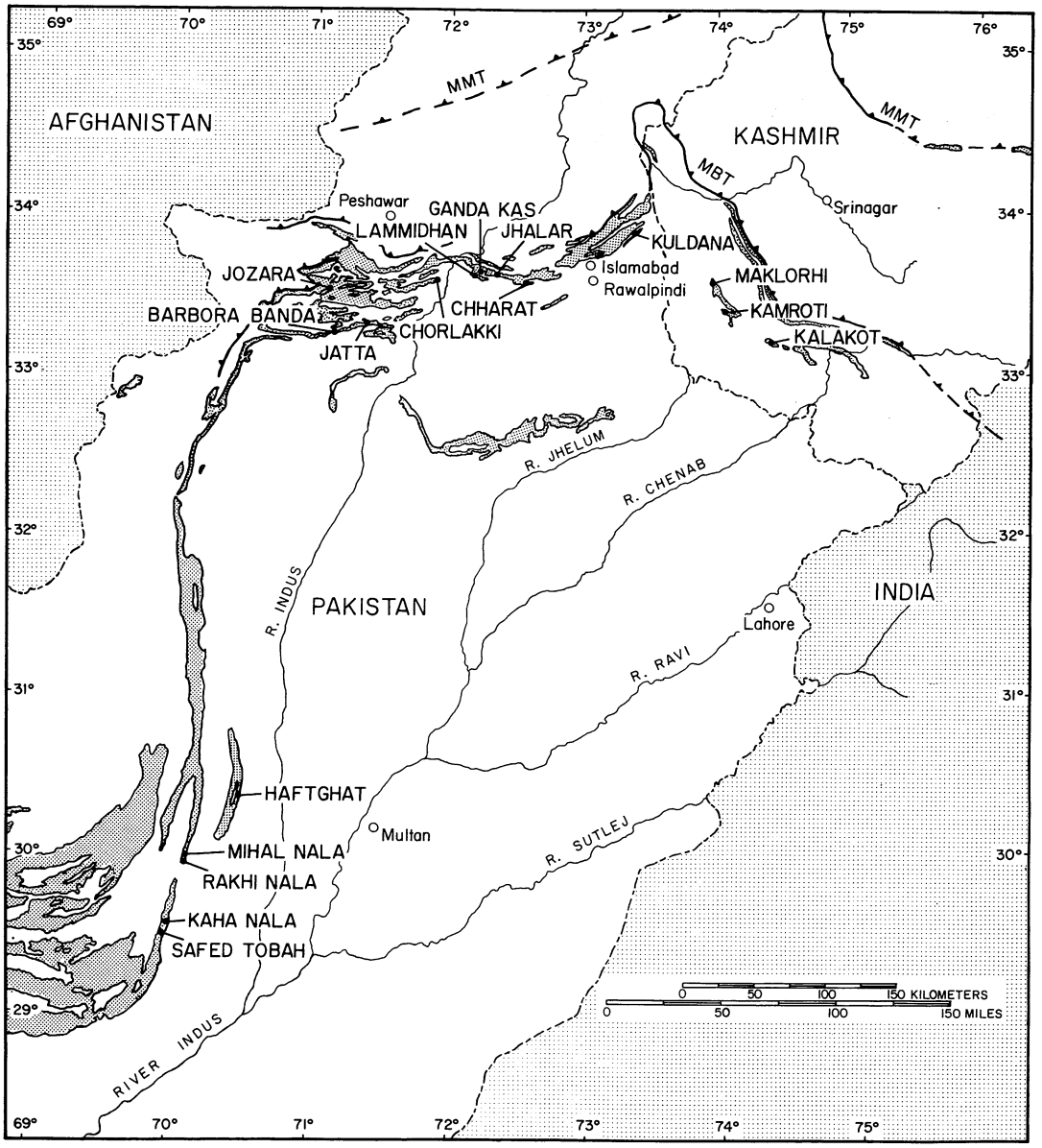
Philip D. Gingerich[1] and Donald E. Russell[2]

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).

[1]Museum of Paleontology, The University of Michigan, Ann Arbor
[2]Institut 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 indirae*. The genus *Dulcidon* appears to be closely related to *Chorlakkia* 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 *Paratritemnodon*. Thus there is no substantiated record of Carnivora in these faunas. Upon further preparation and comparison, the holotype of *Ishatherium subathuensis*, described by Sahni and Kumar (1980) as a sirenian, appears to resemble a partial upper molar of *Pilgrimella*. While it is possible that *Ishatherium* 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 Manning (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

Protocetus (in part), West, 1980, p. 515.
Ichthyolestes (in part), West, 1980, p. 516.
Protocetidae indet., 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 M^3). 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 P_2. 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-*

kasia. 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 P_2-P_4; GSP-UM 082, left M_3; GSP-UM 083, left M^1; GSP-UM 085, left M^3; and GSP-UM 134, crown of left M^2 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.

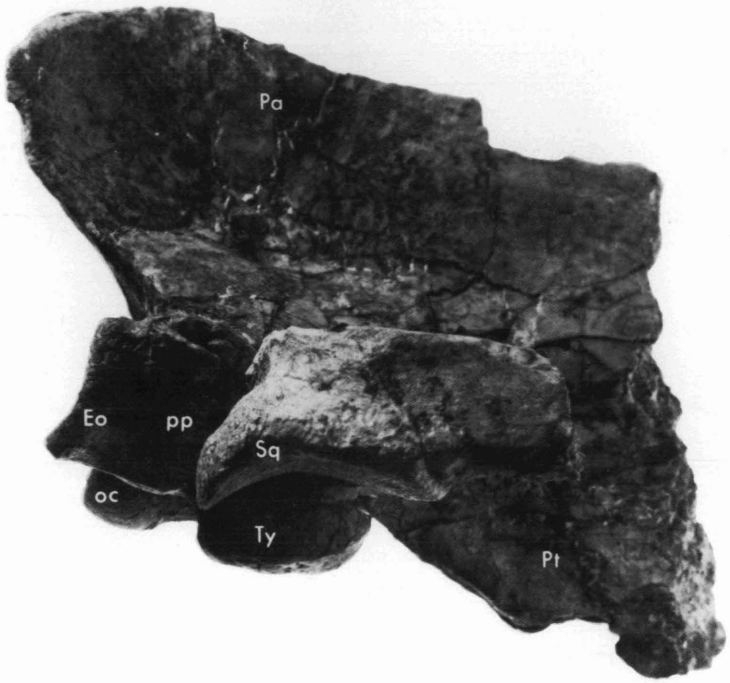
Diagnosis.—Differs from *Pakicetus attocki* (West, 1980) in having serrated anterior and posterior crests on lower premolars (see Text-fig. 4).

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



TEXT-FIG. 2 —Posterior portion of cranium of holotype of *Pakicetus inachus*, GSP-UM 084, in right lateral view, natural size. Abbreviations *Eo*, exoccipital; *oc*, occipital condyle; *Pa*, parietal; *pp*, posterior process of periotic; *Pt*, pterygoid; *Sq*, squamosal; and *Ty*, tympanic bulla.

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.

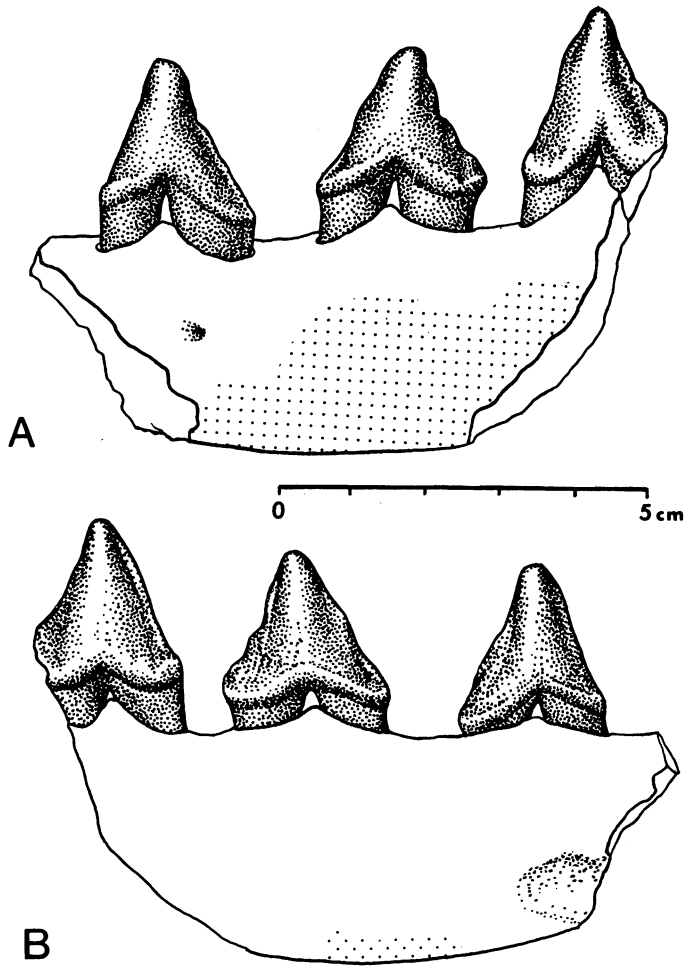
Upper molars referred to *Pakicetus* appear to have been three-rooted. M^1, M^2, and M^3 all have large protocones. These are reduced by comparison with the protocones of *Ichthyolestes*, but they are much more pointed than those of either *Eocetus* or *Indocetus*. A strong beaded cingulum encircles 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 M^1 and M^2, but this cusp is lacking on M^3. M^1 measures approximately 13.5 mm in length and 14.2 mm in breadth. M^2 measures approximately 17.2 mm in length. M^3 measures 13.9 mm in length and 17.9 mm in breadth.

A portion of the mandibular ramus with P_2-P_4 is illustrated in Text-fig. 4. All three of these

TEXT-FIG. 3 —Posterior portion of cranium of holotype of *Pakicetus inachus*, GSP-UM 084, in ventral view, natural size (scale is in mm). Abbreviations: *ap*, anterior process of periotic; *b*, bullar processes of squamosal, paroccipital, and basioccipital, respectively; *Bo*, basioccipital; *Bs*, basisphenoid; *Eo*, exoccipital; *oc*, occipital condyle; *p*, promontorium of periotic; *Po*, paroccipital; *pp*, posterior process of periotic; *Pt*, pterygoid; *s*, fossa for origin of stapedius muscle; *Sq*, squamosal; *tt*, fossa for origin of tensor tympani muscle; and *Ty*, tympanic bulla.

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 P_2-P_4 in lateral view (A) and medial view (B). Note posterior margin of mandibular symphysis below P_2 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 M_2. 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 M_3, but this cingulid is absent on the lateral side of the tooth. M_3 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.
Ichthyolestes pinfoldi (in part), West, 1980, p. 516, Pl. 2, fig. 1.
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 P_3 and P_4, alveoli for I_3, C_1, P_1-P_2, and the broken crown of M_1.

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 attocki*. 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 attocki*.

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

Age and distribution.—*Pakicetus attocki* 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 dP_3, 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 attocki* 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 attocki*, BMNH M-15806, with dP_3 in occlusal view (A) and lateral view (B). Natural size (scale is in mm).

DISCUSSION

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 referrable 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.

ACKNOWLEDGMENTS

We are especially grateful to Dr. R. Ewan Fordyce, U. S. National Museum of Natural History, Washington, for help in identifying basicranial structures in *Pakicetus*. Dr. S. M. Ibrahim Shah, Mr. Mahmoodul Hassan, Mr. Habib Abbas, and Mr. Asif Jah of the Geological Survey of Pakistan all contributed to the success of our field work. J.-L. Hartenberger, Université de Montpellier, found the holotype of *Pakicetus inachus*. We thank Dr. Peter Andrews and Mr. Jeremy Hooker, British Museum (Natural History), London; Prof. R. Dehm and N. Schmidt-Kittler, Institut für Paläontologie, Munich; Prof. H. W. Matthes, Geiseltal-museum, Halle; Dr. A. Ranga Rao. Oil and Natural Gas Commission, Dehra Dun; Dr. A. Sahni, Lucknow University, Lucknow; Drs. M. V. A. Sastry and A. K. Dutta, Geological Survey of India, Calcutta; Dr. Chow Minchen, Institute of Vertebrate Paleontology and Paleoanthropology, Peking; Dr. M. C. McKenna, American Museum of Natural History, New York; and Dr. R. M. West, Milwaukee Public Museum, Milwaukee, for access to type and comparative collections.

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.

LITERATURE CITED

CHOW, M. and B. WANG. 1979. Relationship between the pantodonts and tillodonts and classification of the order Pantodonta. Vert. Palasiatica, 17: 37–48.

COOMBS, W. P. and M. C. COOMBS. 1979. *Pilgrimella*, a primitive Asiatic perissodactyl. Zool. Jour. Linn. Soc., 65: 185–192.

DEHM, R. and T. OETTINGEN-SPIELBERG. 1958. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. Abh. Bayer. Akad. Wiss., Math-Nat. Kl., 91: 1–54.

FRAAS, E. 1904. Neue Zeuglodonten aus dem unteren Mitteleocän vom Mokattam bei Cairo. Geol. Palaeont. Abhandl., Jena, 6: 199–220.

GINGERICH, P. D. 1977. A small collection of fossil vertebrates from the middle Eocene Kuldana and Kohat Formations of Punjab (Pakistan). Contr. Mus. Paleont., Univ. Michigan, 24: 190–203.

———, D. E. RUSSELL, D. SIGOGNEAU-RUSSELL, J.-L. HARTENBERGER, S. M. I. SHAH, M. HASSAN, K. D. ROSE, and R. H. ARDREY. 1979. Reconnaissance survey and vertebrate paleontology of some Paleocene and Eocene formations in Pakistan. Contr. Mus. Paleont., Univ. Michigan, 25: 105–116.

———, D. E. RUSSELL, D. SIGOGNEAU-RUSSELL, AND J.-L. HARTENBERGER. 1979. *Chorlakkia hassani*, a new middle Eocene dichobunid (Mammalia, Artiodactyla) from the Kuldana Formation of Kohat (Pakistan). Contr. Mus. Paleont., Univ. Michigan, 25: 117–124.

HUSSAIN, S. T., H. de BRUIJN, and J. M. LEINDERS. 1978. Middle Eocene rodents from the Kala Chitta Range (Punjab, Pakistan). Proc. Kon. Ned. Akad. Wetenschap., Amsterdam, Ser. B, 81: 74–112.

KELLOGG, R. 1936. A review of the Archaeoceti. Carnegie Inst., Washington, Publ. 482, 366 pp.

KHAN, A. 1973. A new mammalian fossil from the lower Murree of Kalakkot, Jammu and Kashmir State, India. Jour. Geol. Soc. India, 14: 296–301.

McKENNA, M. C., and E. MANNING. 1977. Affinities and palaeobiogeographic significance of the Mongolian Paleogene genus *Phenacolophus*. Géobios, Mém. Spéc, 1: 61–85.

MEISSNER, C. R., J. M. MASTER, M. A. RASHID, and M. HUSSAIN. 1974. Stratigraphy of the Kohat Quadrangle, Pakistan. U. S. Geol. Surv. Prof. Paper, 716D: 1–30.

PILGRIM, G. E. 1940. Middle Eocene mammals from north-west Pakistan. Proc. Zool. Soc., London, Ser. B, 110: 127–152.

RANGA RAO, A. 1971. New mammals from Murree (Kalakot Zone) of the Himalayan foothills near Kalakot, Jammu & Kashmir State, India. Jour. Geol. Soc. India, 12: 125–134.

———. 1972. Further studies on the vertebrate fauna of Kalakot, India. New mammalian genera and species from the Kalakot zone of Himalayan foothills near Kalakot, Jammu & Kashmir State, India. Directorate of Geology, Oil & Natural Gas Commission, Dehra Dun, Spec. Papers, 1: 1–22.

———. 1973. Notices of two new mammals from the upper Eocene Kalakot beds, India. Directorate of Geology, Oil & Natural Gas Commission, Dehra Dun, Spec. Paper, 2: 1–6.

——— and F. A. OBERGFELL. 1973. *Hyrachyus asiaticus*, new species of an upper Eocene tapiroid (Mammalia, Perissodactyla) from Kalakot, India. Directorate of Geology, Oil & Natural Gas Commission, Dehra Dun, Spec. Paper, 3: 1–8.

RUSSELL, D. E. and P. D. GINGERICH. 1980. Un nouveau primate omomyide dans l'Eocène du Pakistan. C. R. Acad. Sci., Paris, 291: 621–624.

——— and P. D. GINGERICH. 1981. Lipotyphla, Proteutheria(?), and Chiroptera (Mammalia) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contr. Mus. Paleont., Univ. Michigan, 25: 277–287.

SAHNI, A. and S. K. KHARE. 1972. Three new Eocene mammals from Rajauri District, Jammu and Kashmir. Jour. Palaeont. Soc. India, 16: 41–53.

——— and S. K. KHARE. 1973. Additional Eocene mammals from the Subathu Formation of Jammu and Kashmir. Jour. Palaeont. Soc. India, 17: 31–49.

——— and K. KUMAR. 1980. Lower Eocene Sirenia, *Ishatherium subathuensis*, gen. et sp. nov. from the type area, Subathu Formation, Subathu, Simla Himalayas, H. P. Jour. Paleont. Soc. India, 23: 132–135.

——— and V. P. MISHRA. 1972. A new species of *Protocetus* (Cetacea) from the middle Eocene of Kutch, western India. Palaeontology, 15: 490–495.

——— and V. P. MISHRA. 1975. Lower Tertiary vertebrates from western India. Monogr. Palaeont. Soc. India, 3: 1–48.

——— and V. C. SRIVASTAVA. 1976. Eocene rodents and associated reptiles from the Subathu Formation of northwestern India. Jour. Paleont., 50: 922–928.

_____ and V. C. SRIVASTAVA. 1977. Eocene rodents of India: their palaeobiogeographic significance. Géobios, Mém. Spéc., 1: 87–95.

SATSANGI, P. P. and P. K. MUKHOPADHYAY. 1975. New marine Eocene vertebrates from Kutch. Jour. Geol. Soc. India, 16: 84–86.

SHAH, S. M. I. 1977. Stratigraphy of Pakistan. Mem. Geol. Surv. Pakistan, 12: 1–138.

TANDON, K. K. 1971. On the discovery of mammalian and reptilian remains from the middle Eocene rocks of S. W. Kutch, India. Curr. Sci., Bangalore, 40: 436–437.

VAN VALEN, L. 1966. Deltatheridia, a new order of mammals. Bull. Amer. Mus. Nat. Hist., 144: 269–318.

_____. 1968. Monophyly or diphyly in the origin of whales. Evolution, 22: 37–41.

_____. 1978. The beginning of the age of mammals. Evol. Theory, 4: 45–80.

WEST, R. M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. Jour. Paleont., 54: 508–533.

_____ and J. R. LUKACS. 1979. Geology and vertebrate-fossil localities, Tertiary continental rocks, Kala Chitta Hills, Attock District, Pakistan. Contr. Biol. Geol., Milw. Publ. Mus., 26: 1–20.

ZHANG, Y. 1978. Two new genera of condylarthran phenacolophids from the Paleocene of Nanxiong Basin, Guangdong. Vert. Palasiatica, 16: 267–274.

_____. 1980. *Minchenella*, new name for *Conolophus* Zhang, 1978. Vert. Palasiatica, 18: 257.