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DENTITION OF EARLY EOCENE *PAKICETUS* (MAMMALIA, CETACEA)

By

PHILIP D. GINGERICH and DONALD E. RUSSELL[1]

Abstract.— Thirty deciduous and permanent teeth of *Pakicetus inachus* are described from Chorlakki in Pakistan. Geological sequence stratigraphy indicates that *Pakicetus* is latest early Eocene (latest Ypresian) in age. Incisors of *Pakicetus* are simple high-crowned sharply-pointed teeth. The upper canine may have been double-rooted. Lower canines vary in size and may have been dimorphic. Premolars have simple narrow crowns with coarse serrations on some anterior and posterior crests. Upper molars retain three roots and distinct protocones. Lower molars have simple pyramidal trigonids and narrow trenchant talonids. These teeth are combined in a model based on the type braincase-basicranium showing that all represent a single species. *Pakicetus inachus* may prove to be a junior synonym of *P. attocki* when the latter is better known, but restudy of contemporary *Ichthyolestes* and *Gandakasia* confirms that these genera are distinct. The three early Eocene genera are placed in a new subfamily Pakicetinae of the archaeocete family Protocetidae. Teeth of *Pakicetus* have several distinctively archaeocete characteristics. Upper and lower cheek teeth have wear facets on apices of pointed cusps indicating that the lower jaw was retracted when food was punctured. Buccal phase shearing and lingual phase grinding wear facets are also present. Deciduous teeth at Chorlakki indicate that juveniles and adults were present in approximately equal proportions, suggesting that juveniles, like adults, spent a significant amount of time on land.

INTRODUCTION

Pakicetus is a primitive archaeocete cetacean known from several localities in the Punjab and North-West Frontier provinces of Pakistan. It is one of only three early Eocene archaeocete genera known to date, and it is the best known of the three. *Pakicetus* is interesting and important because it is one of the oldest cetaceans known anywhere, it is found in continental red beds, it is found with a land-mammal fauna, and it has a basicranium and ear region little modified for hearing in water (Gingerich et al., 1983).

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Two closely related species of *Pakicetus* are currently recognized, *P. attocki* (West 1980), and *P. inachus* Gingerich and Russell 1981. The type specimen of the former is a left dentary with several teeth from the Kuldana Formation in the Kala Chitta Range north of Basal, Punjab Province (West, 1980). The type specimen of the latter is a braincase with basicranium from Chorlakki in the Kuldana Formation of Panoba Dome, north of Gumbat, North-West Frontier Province (Gingerich and Russell, 1981). Two additional cetacean genera and species are known from the Kuldana Formation. These are *Gandakasia potens* Dehm and Oettingen-Spielberg 1958, based on a right dentary, and *Ichthyolestes pinfoldi* Dehm and Oettingen-Spielberg 1958, based on a left maxillary fragment. Both come from the Kala Chitta Range north of Basal in Punjab. *Pakicetus inachus* from Chorlakki is the best known of the four species and it is the only species for which the braincase and basicranium are known (Gingerich and Russell, 1981; Gingerich et al., 1983; see also Oelschläger, 1987).

The Chorlakki locality was worked intensively by Geological Survey of Pakistan - University of Michigan / Muséum National d'Histoire Naturelle field parties for several weeks in 1977, 1978, 1979, and again in 1980. The fossiliferous horizon is a calcareous granulestone of reworked soil nodules containing disarticulated and disassociated bones and teeth. This granulestone was deposited on a broad flat floodplain on one flank of the early Eocene Kohat Basin where evaporites accumulated in an epicontinental remnant of the eastern Tethys Sea (Gingerich et al., 1983; Wells, 1983). Larger specimens, including the type of *Pakicetus inachus*, were collected by quarrying, but most specimens were recovered by laboratory processing of granulestone in acid. Preparation is now complete. Approximately 800 vertebrate specimens have been recovered from Chorlakki. Many of these cannot be identified, but 28 are specimens referred to *Pakicetus inachus*. The 28 include isolated teeth and broken teeth, but all add significantly to our understanding of this important species.

The mammalian fauna from Chorlakki is primarily a microfauna, with small rodents being the most common elements. The most common medium-sized mammal is the bunodont artiodactyl *Khirtharia dayi* (Thewissen et al., 1987). *Pakicetus inachus* is the only common large mammal at Chorlakki. Anthracobunid proboscideans of approximately the same tooth size and body size (*Lammidhania* and *Pilgrimella*) are also present, but these are rare and have distinctive teeth easily separable from those of *Pakicetus*. New specimens of *Pakicetus* described here are important in telling us something about mastication and probable diets of early cetaceans, in telling us more about environments inhabited by *Pakicetus*, and in making *Pakicetus inachus* comparable to other contemporary archaeocetes known only from jaw fragments and teeth.

Specimens described here are in collections of the Geological Survey of Pakistan (GSP), Quetta. Specimens collected by University of Michigan expeditions are prefaced UM-GSP, and those collected by Howard University expeditions are prefaced H-GSP. Institutional abbreviations are as follows:

BMNH	Natural History Museum [formerly British Museum (Natural History)], London (UK)
GSP	Geological Survey of Pakistan, Islamabad and Quetta (Pakistan)
IPHG	Institut für Paläontologie und historische Geologie, Munich (FRG)
UM	University of Michigan, Ann Arbor (USA)

AGE OF *PAKICETUS INACHUS*

Eocene mammals from the Kuldana Formation (then lower Chharat series) in the Kala Chitta Range north of Basal were first described by Pilgrim (1940), who regarded them as early Lutetian (middle Eocene) in age based on foraminiferans. This correlation was followed by Dehm and Oettingen-Spielberg (1958) and most subsequent workers. Meissner et al. (1974) recorded early Eocene foraminiferans from the Kuldana Formation (their Mami Khel Clay) in Kohat District, North-West Frontier Province, and Cheema et al. (in Shah, 1977) regarded the Kuldana Formation as early to early middle Eocene in age. We have generally written the age of the Kuldana Formation with a hyphen, as early-middle Eocene (e.g., Gingerich and Russell, 1981), to reflect this ambiguity and uncertainty.

The geological sequence stratigraphy of rock units in Panoba Dome, where Chorlakki is located, provides important evidence for correlation to the worldwide geological time scale. The stratigraphy of Panoba Dome was studied by Wells (1984), who interpreted the Patala Formation, Panoba Shale, Shekhan Formation, and Jatta Gypsum as successive early Eocene formations representing progressive shallowing of a marine environment beginning with euxinic deep-basin limestones and shales (Patala Fm.), overlain by basin slope fine clastics (Panoba Shale), overlain by shallow marine carbonates (Shekhan Fm.), which are overlain in turn by lagoonal evaporites (Jatta Gypsum). This shallowing marine sequence is overlain by continental red beds of the lower Kuldana Formation yielding freshwater snails and land and river vertebrates (including *Pakicetus inachus*). The lower Kuldana Formation is overlain by transitional marine shales and marls of the upper Kuldana Formation, with oysters and both marine and freshwater snails. Finally, the Kuldana Formation is overlain by the fully marine Kohat Formation representing return to a productive shallow sea.

Marine invertebrates of the upper Patala Formation and the Shekhan Formation are uniformly regarded as early Eocene in age (Laki or Ypresian), while marine invertebrates of the Kohat Formation are consistently regarded as middle Eocene in age (Khirthar or Lutetian: Eames, 1952; Nagappa, 1959; Shah, 1977). The eustatic sea level curve of Haq et al. (1987) shows the early Eocene to have been a time of high sea stand. There were relatively minor sea level changes during the early Eocene and a major regression at the end of the early Eocene, followed by transgression across the early to middle Eocene boundary. Haq et al.'s (1987) Tejas A3.1 stratigraphic cycle straddling the early-middle Eocene transition includes a low-stand sediment wedge (here represented by the lower Kuldana Fm.), transgressive deposits (upper Kuldana Fm.), and high-stand deposits (Kohat Formation). Sequence stratigraphy implies that all of the Kuldana Formation is latest early Eocene in age (latest Ypresian), while the overlying Kohat Formation is middle Eocene (Lutetian). Geochronometry is inexact. Berggren et al. (1985) date the latest Ypresian at 53 to 52 million years before present [Ma], while Haq et al. (1987) date this interval at 50 to 49 Ma. Odin and Kreuzer (1988) regard the latest Ypresian as the interval from 46 to 45 Ma.

Eustatic sea level curves like those of Haq et al. (1987) are easily overprinted by sea level changes due to local tectonism, and we here assume (in the absence of evidence) that closure of eastern Tethys was less important than global change in determining sea level in the vicinity of Panoba Dome. It may be that the tectonic closure of Tethys and associated regional uplift caused regression to predominate during most of the early Eocene, but it would be fortuitous indeed if closure reversed near the end of the early Eocene to mimic the marked effect of global change in sea level elsewhere.

Mammalian fossils are consistent with a latest early Eocene age for the Chorlakki fauna, although they do not rule out an early middle Eocene age. *Diacodexis* and *Eotitanops*, in particular, favor an early Eocene rather than middle Eocene age. It should be emphasized that the age of this fauna is tightly constrained in spite of uncertainties discussed here. There is little difference in time between the latest early Eocene and the early middle Eocene. The lower-middle Eocene stratigraphic section in the Kala Chitta Range of Punjab is similar to that discussed here, and it is reasonable to interpret the Kuldana Formation in Punjab as late early Eocene as well. The land-mammal bearing part of the Subathu Formation in Kashmir may also be late early Eocene in age (Wells and Gingerich, 1987), but Kashmir is in a different tectonic setting, lithologies are different, and high-stand deposits equivalent to the Kohat Formation in Tejas cycle A3.1 are lacking.

DENTITION OF *PAKICETUS INACHUS*

Isolated teeth are difficult to identify for taxa with poorly known dentitions. Specimens described here are referred to *Pakicetus inachus* because this is the only archaeocete known

TABLE 1—Measurements of deciduous teeth of *Pakicetus inachus* from Chorlakki, North-West Frontier Province, Pakistan. All measurements in millimeters. Asterisk denotes estimate.

	Tooth position	UM-GSP	Crown Length	Crown Width	Crown Height
Upper dentition	dP^2	108	10.0*	2.5	11.2
		1409	10.0*	2.7	-
	dP^3	1722	15.0*	4.1	10.0*
	dP^4	1509	-	-	-
		1938	15.7	-	9.3
Lower dentition	dP_4	749	14.2	6.0	-
		750	14.5	6.0	-
		1401	-	-	-
		1450	14.8	7.1	-

from Chorlakki, and archaeocetes as a group have teeth distinctively different from those of artiodactyls, perissodactyls, and proboscideans of similar size found at Chorlakki. Dentary BMNH-M 15806 described by Gingerich and Russell (1981) was helpful in identifying deciduous teeth (Figure 1), which are smaller and more delicate, with thinner enamel than their permanent replacements. Dentary H-GSP 1649 described by West (1980) as the holotype of *Protocetus attocki* contains intact crowns of two teeth and the partial crown of another. These were helpful in identifying teeth in UM-GSP 81, illustrated in Figures 2-4. With both specimens available, we concluded that teeth in H-GSP 1649 are $P_{3\text{-}4}$ rather than P_4-M_1. H-GSP 1649 was also helpful in confirming that isolated tooth UM-GSP 82 is an M_3 (Figures 5 and 6A).

Upper cheek teeth in Figure 6 were identified by comparison with those of *Protocetus atavus* described by Fraas (1904). Incisors and lower canines illustrated in Figure 7 were identified by comparison with those of later archaeocetes (Stromer, 1908; Kellogg, 1936). These were assembled into a full-scale model using casts of the holotype braincase-basicranium of *Pakicetus inachus* (UM-GSP 82) and the holotype dentary of *Pakicetus attocki* (H-GSP 1649), and this model is illustrated in Figure 8.

Deciduous Dentition

Nine deciduous teeth of *Pakicetus inachus* are known from Chorlakki, and a composite deciduous dentition based on these is illustrated in Figure 1. All deciduous teeth described here have relatively narrow crowns and thin enamel lighter in color than enamel of permanent teeth. Measurements of deciduous teeth are listed in Table 1.

UM-GSP 108 and 1409 are interpreted as left and right dP^2, respectively. Crowns of each are broken. Roots are thin and divergent. Enamel extends well up the ventral surface of each root. The anterior margin of the crown preserved in UM-GSP 1409 has a smooth raised edge with a single small cuspule just below a distinct wear facet at the base of the crown. The posterior margin of the crown preserved in UM-GSP 108 has two small cuspules near the base, making the crown finely but distinctly notched (Fig. 1A). H-GSP 1974a described by West (1980) as the lower molar of a protocetid (and illustrated in his Pl. 2, fig. 3) is probably dP^2 of *Pakicetus*.

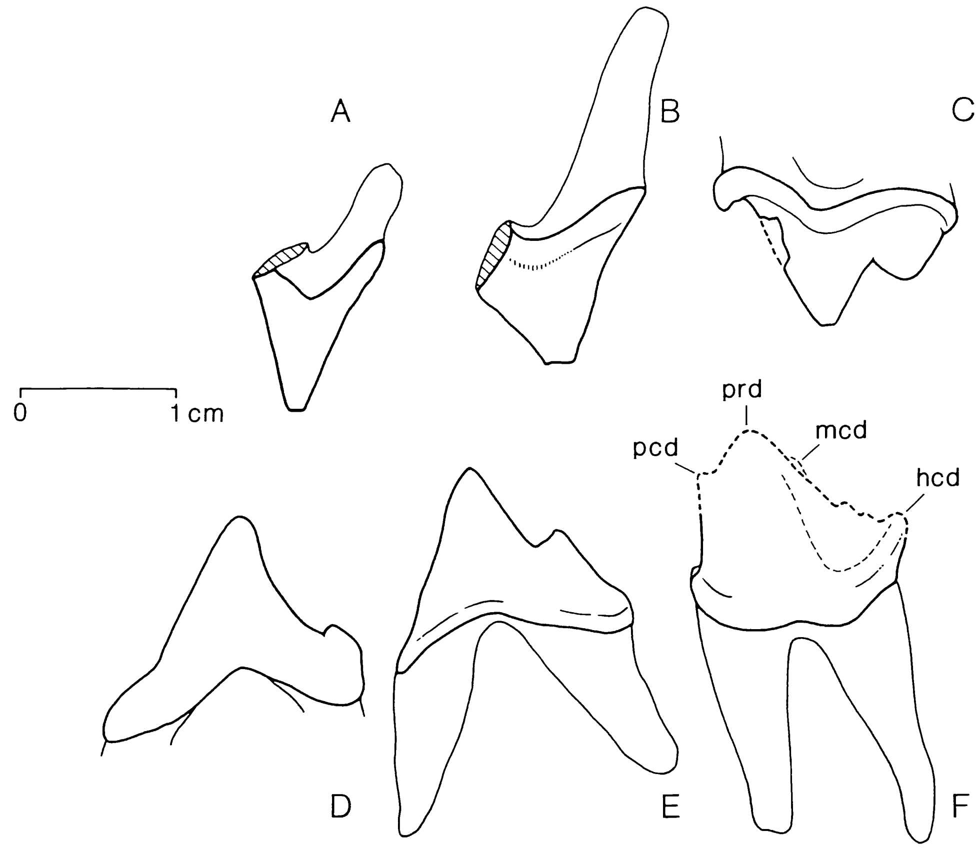

FIG. 1—Deciduous teeth of *Pakicetus*. A, left dP^2, UM-GSP 108 from Chorlakki. B, left dP^3, UM-GSP 1722 from Chorlakki. C, left dP^4, UM-GSP 1938 from Chorlakki. D, right dP_2 or dP_3 (reversed), BMNH-M 15806 from Lammidhan (redrawn from Gingerich and Russell, 1981, fig. 5). E, left dP_3(?), IPHG 1956.II.9 from Dehm locality 24 (redrawn from Dehm and Oettingen-Spielberg, 1956, Pl. 1, fig. 1). F, left dP_4, UM-GSP 749 from Chorlakki (crown reconstructed from cast of H-GSP 536 (illustrated in West, 1980, Pl. 2, fig. 2). Crown of H-GSP 536 retains distinct protoconid (*prd*), paraconid (*pcd*), and metaconid (*mcd*) on trigonid, and distinct hypoconid (*hcd*) on talonid. Note low crowns and divergent roots characteristic of deciduous teeth.

UM-GSP 1722 is the partial crown of a left dP^3 with a single apical cusp and a faint lingual cingulum (Fig. 1B). The crown is slightly convex labially and concave lingually. Enamel is slightly crenulated on the posterior and labial part of the crown.

UM-GSP 1509 and 1938 are parts of two different left dP^4s. The former preserves the lingual part of the crown that flares for a distinct lingual protocone cusp, although the cusp itself is not preserved (wear on the talonid of dP_4 also indicates that dP^4 had a distinct protocone). UM-GSP 1509 has a large wear facet running up the back of the preserved fragment where the protoconid of M_1 was retracted against it. UM-GSP 1938 preserves the complete labial surface of a crown (Fig. 1C), but the lingual part of the tooth is missing. This crown is relatively low compared to those of dP^2 and dP^3. The paracone and metacone are large and well separated. There is a smaller anterior cusp in front of the paracone, and there is a distinct labial cingulum.

Crowns of dP_2 and dP_3 are not preserved in the material available from Chorlakki. Previously described specimens show some variation, and it is not possible at present to identi-

TABLE 2—Measurements of permanent teeth of *Pakicetus inachus* from Chorlakki, North-West Frontier Province, Pakistan. All measurements in millimeters. Asterisk denotes estimate.

	Tooth position	UM-GSP	Crown Length	Crown Width	Crown Height
Upper dentition	$I^?$	1534	6.5	4.5	17.2*
		1546	5.7	5.1	18.5*
	C^1	79	13.1	6.3	23.4
	P^1	1936	16.8	5.4	20.0*
	P^2	136	18.0*	6.8*	16.5*
	P^3	1937	21.5	7.8	18.0*
	P^4	147	-	8.7	-
		751	-	-	-
	M^1	134	17.3	-	14.8
	M^2	83	-	14.3	12.5
		1653	-	-	-
		1672	14.0	13.1	13.1
	M^3	85	13.4	17.6	12.5*
Lower dentition	C_1	1411	10.9	7.7	29.0
		1553	9.6	6.1	24.4
	P_1	110	15.0*	5.0	-
	P_2	81	20.2	7.5	20.6
	P_3	81	22.5	8.0	20.6
	P_4	81	20.5	8.5	23.0
	M_1	113	-	7.9	14.2
	M_2	--	-	-	-
	M_3	82	17.8	8.9	12.0

fy these to position with certainty. Gingerich and Russell (1981) described BMNH-M 15806, a right dentary with one deciduous tooth. This tooth, illustrated here in Figure 1D, was interpreted as dP_3 but it may also be dP_2. Dehm and Oettingen-Spielberg (1958) illustrated a tooth of slightly different morphology as dP_3 of "*Ichthyolestes?*." This tooth may be dP_3 of *Ichthyolestes*, but it could also represent *Pakicetus*.

Four broken specimens of dP_4 are known from Chorlakki: UM-GSP 749, 750, 1401, and 1450. All are from the right side. UM-GSP 749 has the base of the crown well preserved (Fig. 1F). The anterior base of the crown is distinctly notched with two small basal cusps flanking this notch. The trigonid has a prominent preprotocristid curving down to meet the more lingual of these anterior basal cusps. The talonid is trenchant, with a single prominent cusp (hypoconid). Faint labial cingulids border the crown anteriorly and posteriorly. There is a lingual cingulid only on the talonid. The roots differ from those of other deciduous teeth in diverging only slightly. UM-GSP 750 is poorly preserved, but the anterior notch is present and there is a deeply grooved wear facet where the front of the crown occluded against the apical cusp of dP^3. UM-GSP 1401 is a talonid with a worn lingual cingulid. There is a restricted but distinct polished wear facet near the apex of the hypoconid indicating that it occluded with a protocone on dP^4. The labial surface of this talonid has a deeply worn groove where it was retracted against the lingual surface of the paracone of dP^4. UM-GSP 1450 preserves the outline of the base of a right molar crown partially erupted in a dentary fragment. This dentary fragment is so shallow in mandibular depth (17 mm) that the specimen must represent a very young individual.

Permanent Dentition

Nineteen specimens are known from Chorlakki that preserve a total of 21 identifiable permanent teeth. Permanent teeth have thicker enamel than deciduous teeth do, and at Chorlakki permanent teeth are generally more opaque and less translucent than deciduous teeth. Measurements of permanent teeth are listed in Table 2.

Upper incisors.—Two teeth appear to be left upper incisors (but either or both could be right lower incisors). The first of these, UM-GSP 1534 (Fig. 7A), has a relatively straight massive root (often characteristic of upper incisors in generalized mammals). It has a delicate, slightly backwardly-curved, tapering crown that is slightly convex labially and concave lingually. The crown is oval in cross section.

The other incisor, UM-GSP 1546, has none of the root preserved. The crown is similar to that of UM-GSP 1534, but the base of the crown is a little more flattened lingually, and there are more prominent enamel ridges meeting and marking the corners of this lingual flattening. This tooth is an incisor of *Pakicetus*, like UM-GSP 1534, but it represents a different position in the incisor row.

Upper canine.—The only upper canine is UM-GSP 79 (Fig. 6I,J). It appears to have been double-rooted, however the roots are not fully preserved and it is possible that there was a single anteroposteriorly elongated root that was grooved vertically but not really divided. The crown is slightly convex labially and concave lingually, but it is so symmetrical anteroposteriorly that the side, left or right, cannot be determined. The crown is divided at the base, with enamel covering anterior and posterior surfaces well above the level of this division. The enamel is smooth, and there are no cingula. The apex of the crown is blunted by wear, and the anterior and posterior edges of the crown are slightly worn as well.

Upper premolars.—UM-GSP 1936 is a double-rooted P^1 in a fragment of maxillary bone (Fig. 6K,L). The tooth is oriented slightly obliquely relative to the maxillary midline suture, and anterior narrowing indicates that it is from the left side. The maxillary fragment with the tooth is 14 mm wide, indicating that the cranial rostrum was only 28 mm wide at this point. The crown of P^1 has a faint lingual cingulum but no labial cingulum. The posterior edge of the crown is distinctly keeled, with a faint suggestion of fine serrations.

UM-GSP 136 is the labial half of the crown of P^2 with a strong labial cingulum anteriorly, and a faint labial cingulum as well. Enamel is smooth. The crown is convex labially and concave lingually like those of other anterior teeth.

UM-GSP 1937 is a left P^3 (Fig. 6M-O). It has heavy roots and a massive crown by comparison with other cheek teeth. The apex shows blunt wear, but the crown is otherwise little worn (some enamel may have been removed from the posterolabial surface during postmortem transport and burial). The crown is convex labially and convex lingually. There is a faint lingual cingulum. Enamel is smooth except on the posterolingual surface where it is distinctly crenulated.

Two specimens preserve nonoverlapping parts of P^4. UM-GSP 147 is the posterior part of a right premolar with two posterior roots. The posterior edge of the crown is squared, with a faint posterior cingulum bearing an interproximal wear facet where it contacted M^1. The back of the crown has a moderately deep, striated wear facet where the apex of M^1 was retracted

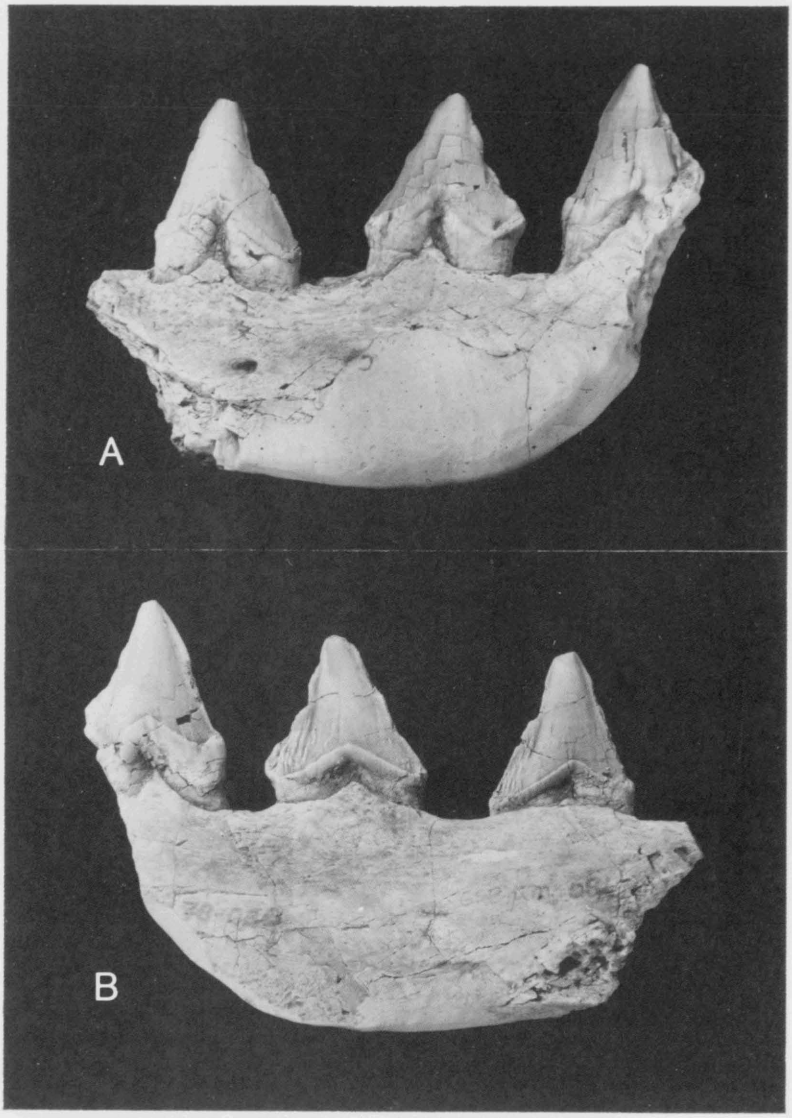

FIG. 2—Left dentary of *Pakicetus inachus*, UM-GSP 81 from Chorlakki. Photographs show crowns of P_{2-4} in lateral (A) and medial view (B). See Fig. 4 for interpretation.

against it. UM-GSP 751 is the anterior half of a premolar with a single long straight root. The crown is massive, with blunt wear on the principal apical cusp. There is a prominent crest running down the anterior edge of the crown to join a small basal anterior cusp and a small but prominent anterolabial cingulum. The labial cingulum is faint on the rest of the crown. The principal apical cusp of P^4 flares lingually, indicating that the posterior part of the tooth was broader than that of P^3. Enamel is smooth, with some polished wear on the lingual surface caused by occlusion with P_4. UM-GSP 751 is a half tooth that could be part of the same individual as UM-GSP 147, but there are no points of contact.

Upper molars.—UM-GSP 134 is the unworn crown of M^1 lacking the protocone. It has a large paracone and a smaller metacone. It resembles other upper molars of *Pakicetus* closely,

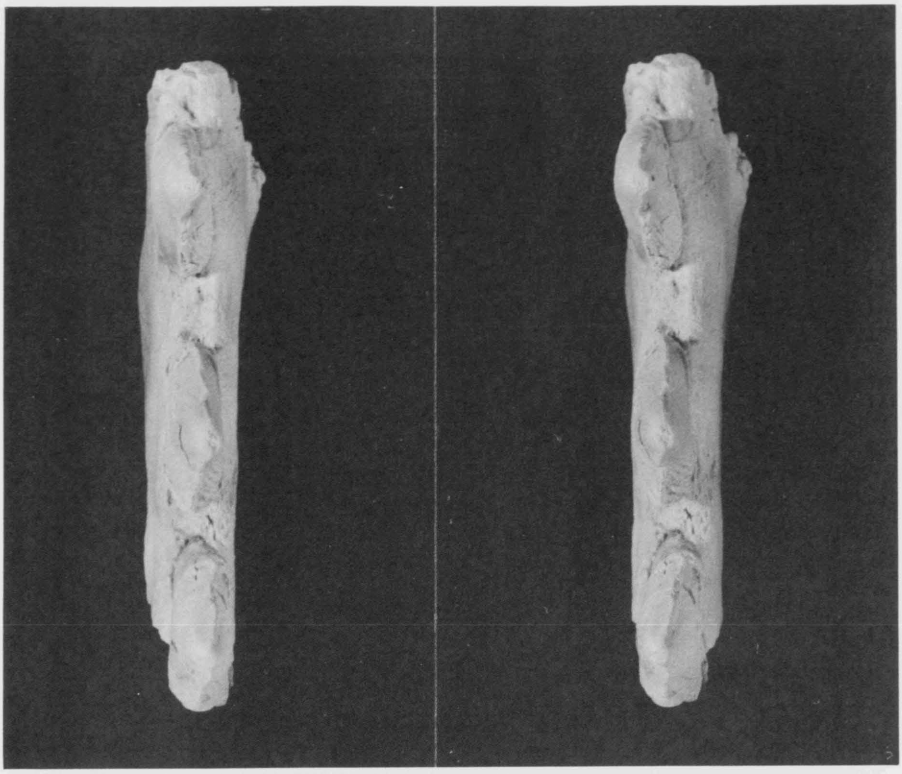

FIG. 3—Left dentary of *Pakicetus inachus*, UM-GSP 81 from Chorlakki. Stereophotograph shows crowns of P_{2-4} in occlusal view. See Fig. 4 for interpretation.

but differs in being larger, in having a prominent labial cingulum, in having the metacone well separated from the paracone, and in having a finely serrated preparacrista, postparacrista, and postmetacrista. These may all be variable characteristics, but they serve to distinguish this tooth of *Pakicetus* from the sample of teeth identified as M^2.

Three upper second molars are known from Chorlakki. UM-GSP 83 is a left M^2 (Fig. 6G,H) lacking the protocone. UM-GSP 1653 is the lingual part of a right M^2. UM-GSP 1672 is a nearly complete left M^2 (Fig. 6E,F). These resemble UM-GSP 134, but differ in being smaller, in having the metacone less well separated from the paracone, in having a faint labial cingulum, and in having smooth prepara- and postmetacristae. Taken together, the specimens show that M^2 is three-rooted. It has a large paracone and smaller metacone near the labial margin of the tooth. There is a prominent protocone that is low, sharply pointed, and bordered lingually by a beaded cingulum. There is a weak posterior cingulum running from the lingual cingulum and wrapping around the labial side of the metacone. The lingual sides of the paracone and metacone bear vertically striated wear facets in all three specimens, but the precise orientation of these is difficult to determine from isolated molars.

UM-GSP 85 is the only M^3 known from Chorlakki (Fig. 6C,D). The crown of M^3 resembles those of preceding molars closely, with the principal distinctions being a shorter crown (anteroposteriorly), and a greatly reduced metacone, represented as a slight swelling on the postparacrista.

Lower incisors.—The only teeth found at Chorlakki that may represent lower incisors are those described above as upper incisors. Lower incisors of *Pakicetus* probably resembled upper incisors very closely in size and form.

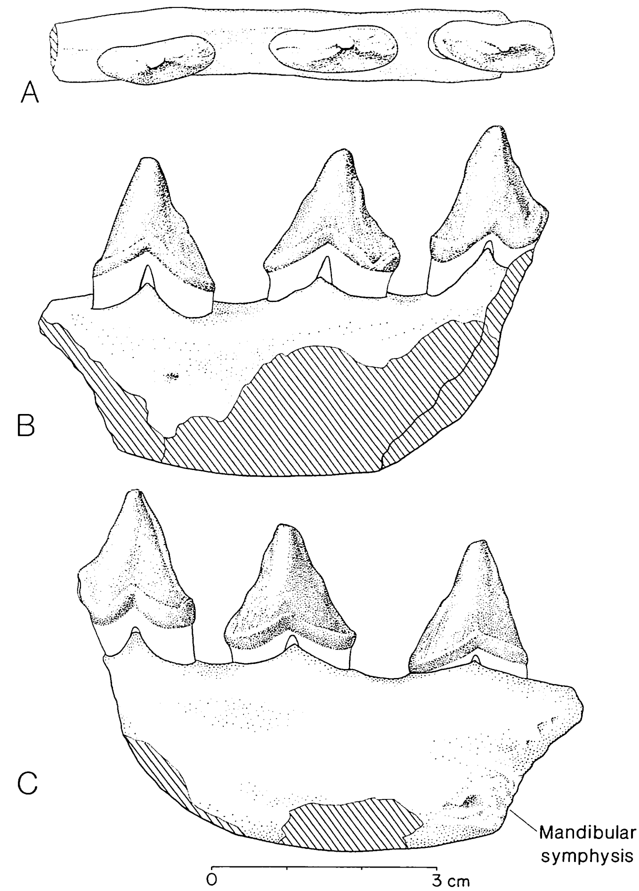

FIG. 4—Drawings of left dentary of *Pakicetus inachus*, UM-GSP 81 from Chorlakki preserving crowns of $P_{2\text{-}4}$, in occlusal (A), lateral (B), and medial view (C). Note mental foramen below P_2 on lateral side of dentary. Depression for a second mental foramen is evident below anterior root of P_3. Note also posterior extension of mandibular symphysis to a point beneath P_2 on medial side of dentary.

Lower canines.—Two lower canines are known. UM-GSP 1411 is a larger left C_1 (Fig. 7C). UM-GSP 1553 is a smaller right C_1 (Fig. 7B). These teeth are very similar. Both have a single massive straight root, and a crown deflected outward and curved backward relative to the root. The crown is oval in cross section, with smooth enamel and a very fine anterior and posterior crest running the length of the crown. These crests are smooth and slightly worn in both specimens. The two specimens are at the upper and lower limits of size expected in a species of normal mammalian variability, and they suggest (but are insufficient to demonstrate) that *Pakicetus* may have been sexually dimorphic in canine size.

Lower premolars.—One example is known of each of the lower premolars. UM-GSP 110 is a broken double-rooted left P_1. It is similar to the upper canine, but flares more at the base, has a labial cingulid, and has the anterior and posterior edges of the crowns more sharply keeled. These edges are somewhat broken, and it is impossible to tell whether they bore the coarse serrations characteristic of $P_{2\text{-}4}$ of this species. Enamel is smooth, and there are vertically-oriented striated wear facets on the labial surface of the crown.

Left dentary UM-GSP 81 has P_2, P_3, and P_4 in position in the jaw (Figs. 2-4), which is fortunate because these teeth are similar to each other and the homology of isolated premolars

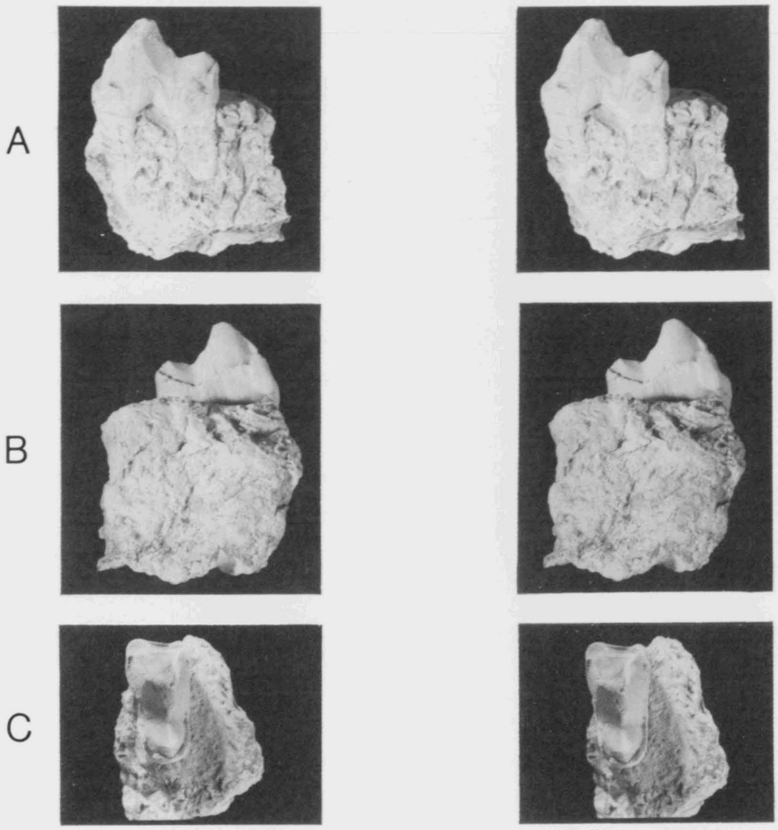

FIG. 5—Stereophotographs of left M_3 of *Pakicetus inachus*, UM-GSP 82 from Chorlakki, in lateral (A), medial (B), and occlusal view (C). Note anterior notch for talonid of M_2, beaded cingulum on medial side of crown, and narrow trenchant talonid. Trigonid retains protoconid and talonid retains hypoconid, but all other major cusps are greatly reduced or lost (see text). Note also wear on anterior lateral surface of trigonid penetrating enamel and exposing dentine, wear on posterior lateral surface of trigonid, and wear on anterior lateral surface of talonid. Medial side of crest connecting trigonid and talonid is also worn from occlusion with upper molar protocone. Patterns of wear indicate orthal retraction of dentary during puncturing phase of occlusion, and retention of some buccal and lingual phase grinding.

would be difficult to determine without reference to associated teeth preserved in a dentary. All three teeth are well preserved. They are double-rooted, similar in form, and similar in size. Each has a single large apical cusp (protoconid). P_2 has the anterior part of the crown and the anterior root shorter anteroposteriorly than the posterior part of the crown and posterior root, respectively. P_3 is most nearly symmetrical. P_4 has the posterior part of the crown and the posterior root shorter anteroposteriorly than the anterior part of the crown and anterior root. P_2 and P_3 have faint labial cingulids, but P_4 has none. All three teeth have distinct lingual cingulids. Crowns of all three teeth have a raised keel of enamel along their anterior and posterior edges. On P_2 the anterior keel is worn but it appears to have been smooth and unserrated, while the posterior keel has one coarse serration. On P_3 the anterior keel has two coarse serrations, while the posterior keel has three coarse serrations. On P_4 the anterior keel appears to have been smooth (there is some slight postmortem damage), while the posterior keel has a single coarse serration. Enamel is generally smooth on all three teeth, but the posterolingual parts of P_2 and P_3 are covered in enamel that is distinctly crenulated. All three

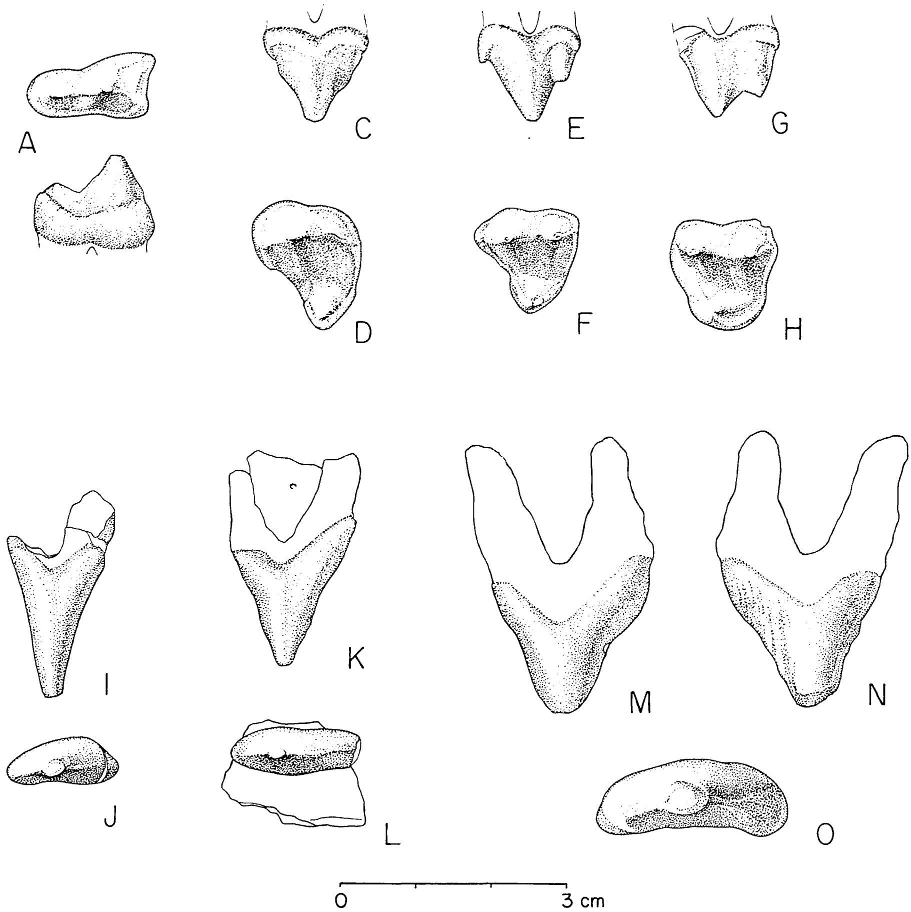

FIG. 6—Molars and premolars of *Pakicetus inachus* from Chorlakki. A and B, left M_3, UM-GSP 82, in occlusal and medial view. C and D, left M^3, UM-GSP 85 in lateral and occlusal view. E and F, left M^2, UM-GSP 1672 in lateral and occlusal view. G and H, left M^2, UM-GSP 83 in lateral and occlusal view. I and J, double-rooted left C^1, UM-GSP 79 in lateral and occlusal view. K and L, maxillary fragment with P^1, UM-GSP 1936 in lateral and occlusal view. Note remnant of midline maxillary-maxillary suture indicating narrow rostrum. M, N, and O, left P^2 or P^3, UM-GSP 1937 in lateral, medial, and occlusal view.

teeth exhibit slight wear on the apex of the principal cusp. P_2 and P_3 in UM-GSP 81 have no wear facets. P_4 has a distinct facet running 5 mm down the anterolabial surface of the crown just below its apex. Curvature of this facet indicates that it was made when the apical cusp was retracted upward and backward past the apex of P^3. P_4 also has a wear facet running 12 mm down from the apex on the posterolabial side of the crown. Curvature on this facet indicates that it was made when the postprotocristid sheared upward and forward against the front of P^4.

Lower molars.—UM-GSP 1450 is a trigonid and anterior root interpreted as representing M_1. Distinctive features are a squared anterior base of the crown, with a strong anterior cingulid that is very slightly notched where it occluded interproximally with the heel of P_4. The squared corners of the anterior cingulid each bear a small cusp. The protoconid is a robust pyramidal cusp worn on its anterolabial and posterolabial sides from occlusion with upper

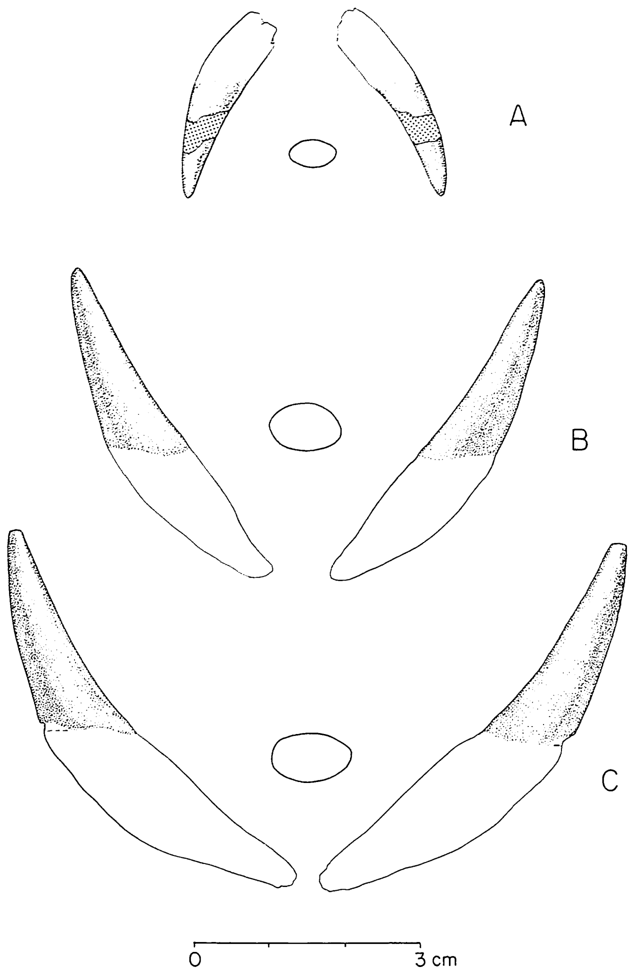

FIG. 7—Incisor and lower canines of *Pakicetus inachus* from Chorlakki. A, left upper incisor, UM-GSP 1534, in lateral (left) and medial view). B, left C_1, UM-GSP 1553 in lateral (left) and medial view. C, right C_1, UM-GSP 1411 in lateral (right) and medial view. Ovals in center of figure show cross sections of teeth at base of crown.

molars. There is a distinct paraconid cusp in front of the protoconid, positioned about half way between the anterior cingulum and the protoconid. A prominent crest of enamel connects the paraconid with the anterolingual cingulid cusp. The anterior cingulid wraps a short distance around the lingual side of the trigonid, but there is no real lingual cingulid and there is no labial cingulid. The talonid of M_1 is broken in such a way that the presence or absence of a metaconid cannot be determined, and the talonid is missing completely.

The only well preserved lower molar is UM-GSP 82, a left M_3 (Figs. 5, 6A,B). This tooth resembles UM-GSP 113 closely, but differs in being more worn, in having a deeper notch for P_4 in the anterior cingulid, having stronger anterior cingulid cusps, having a much weaker paraconid, and in having a lingual cingulid that runs from the anterolingual cingulid cusp and wraps around the talonid. The talonid is narrow and trenchant with a single hypoconid cusp. Trigonid wear surfaces can be oriented parallel to those in UM-GSP 113, and this indicates that the talonid of M_3 was nearly as high as the trigonid in life. This suggests in turn that M_3 was positioned well up on the ascending ramus of the dentary as it is in later archaeocetes.

Model of Skull of *Pakicetus*

One way to test association of teeth from Chorlakki with the holotype braincase and basicranium of *Pakicetus inachus* is to assemble all into one composite model of a complete skull. A full-size model skull of *Pakicetus* based on the holotype and teeth described here is illustrated in Figure 8. The holotype dentary of *Pakicetus attocki* described by West (1980) was used to determine the shape of the posterior part of the dentary in the model and the spacing of teeth in front of the condyle. This three-dimensional model, constructed by William J. Ryan, has a full dental formula of 3.1.4.3 / 3.1.4.3, a condylobasal skull length of 31 cm, and a total skull length of 34 cm. It differs from the graphic model of Gingerich et al. (1983) principally in having more pointed incisors and canines. The new model demonstrates that all cetacean teeth from Chorlakki are the right size to fit into a skull the size of the holotype braincase and basicranium. The composite reconstruction is a reasonable one by comparison with all that is known of later archaeocetes, and thus the Chorlakki cetacean teeth are all appropriately identified as *Pakicetus inachus*.

Several features of the model require comment, and some require slight modification in light of specimens described above. The size and position of the external nares (here located above C^1), the size and position of the infraorbital foramen (here located above P^3), and the confirmation of the frontal shield are all necessarily conjectural. P^4 should be slightly more molariform than it appears in the model, and it should have two posterior roots. Upper molars are now known to have decreased in length from M^1 to M^3, which means that lower molars probably decreased slightly in length from M_1 to M_3 as well. In addition, the spacing of premolars is incorrect: diastemata between P_1-P_2 and between P_2-P_3 should be greater than the diastema between P_3-P_4.

COMPARISON WITH OTHER PROTOCETIDAE

Comparison with *Pakicetus attocki*

Pakicetus attocki is now represented by a total of seven described specimens, all from the Kuldana Formation of the Kala Chitta Range in Punjab. One specimen was described by Dehm and Oettingen-Spielberg (1958) as *Ichthyolestes*?:

(1) left dP_3?, IPHG 1956.II.9.

Another specimen was described by Gingerich (1977) as *Gandakasia potens*:

(2) right M_2, UM 65868.

Four specimens were described by West (1980) under various names:

(3) the holotype dentary, H-GSP 1649;
(4) right permanent M^1, H-GSP 1981b;
(5) left dP_4 H-GSP 536;
(6) right dP^2?, H-GSP 1974a.

One additional specimen was described by Gingerich and Russell:

(7) right dentary with dP_2 or dP_3, BMNH-M 15806.

The holotype of *P. attocki* came from H-GSP locality 62 (West and Lukacs, 1979; West, 1980).

Pakicetus attocki is closely similar in size and general form to *P. inachus*, and the two species may be conspecific. Gingerich and Russell (1981) recognized this but distinguished *P. inachus* because it clearly has serrated lower premolars, whereas *P. attocki* was described as lacking these (West, 1980, p. 515). Other differences include M^1 and dP_4 being larger, and premolars being spaced more closely in *P. attocki*. Samples allocated to the two species clear-

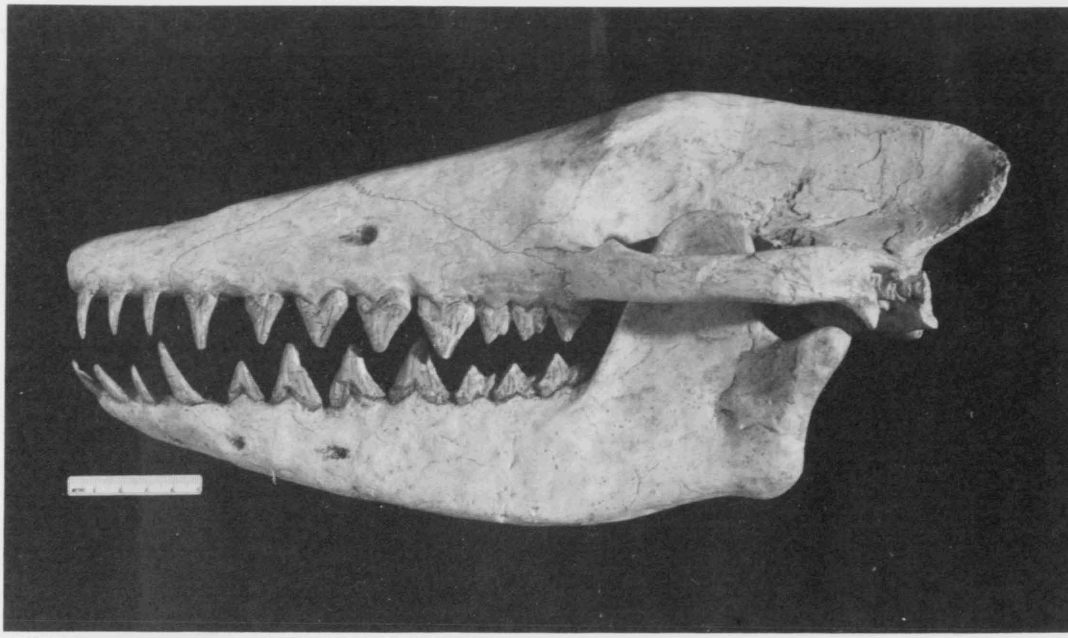

FIG. 8—Composite model of skull of *Pakicetus* reconstructed using specimens from Chorlakki and H-GSP locality 62. This model differs from reconstruction in Gingerich et al. (1983) in having more pointed incisors and in appearing to have a double-rooted upper canine. Large temporal fossa in skull indicates that jaw muscles in *Pakicetus* were temporalis dominated and mastication involved powerful retraction of lower jaw as pointed teeth punctured food. However, retention of a mandibular angle for insertion of masseter-pterygoid musculature is consistent with dental evidence that *Pakicetus* also retained buccal and lingual phases of shearing and grinding mastication lost in most later whales. The size and position of the external nares, the size and position of the infraorbital foramen, and the confirmation of the frontal shield are all necessarily conjectural.

ly differ, but the significance of these differences cannot really be evaluated until *P. attocki* is better known.

Comparison with *Ichthyolestes pinfoldi*

Ichthyolestes pinfoldi is known from a single specimen, the holotype IPHG 1956.II.7 (Fig. 9), from Dehm locality 21 in the Kuldana Formation of the Kala Chitta Range north of Basal (Punjab). This was described by Dehm and Oettingen-Spielberg (1958) as preserving alveoli for M^1 and crowns of M^{2-3}. Comparison with deciduous and permanent teeth of *Pakicetus* described here indicates that alveoli Dehm and Oettingen-Spielberg took to mark the position of M^1 are too greatly separated to represent a permanent molar, and these alveoli instead represent dP^4. This is confirmed by further preparation of the holotype, which now reveals a tooth germ in the crypt above dP^4. Roots of the tooth in place behind dP^4 are close together, indicating that the first crown present in the maxilla belongs to a permanent tooth. Thus the holotype preserves alveoli for dP^4 and crowns of M^{1-2}.

The newly exposed germ of P^4 and revised homologies of molars in the holotype of *Ichthyolestes* further clarify distinctions between *Pakicetus* and *Ichthyolestes*. The germ of P^4 indicates that this tooth had a more sharply conical apical cusp than any on known premolars of *Pakicetus*. The crown of M^1 is more symmetrical anteroposteriorly about a transverse plane than any upper molar of *Pakicetus*. The protocone on M^1 in *Ichthyolestes* is relatively larger and more separated from the paracone and metacone than it is in *Pakicetus*, and M^1 lacks the

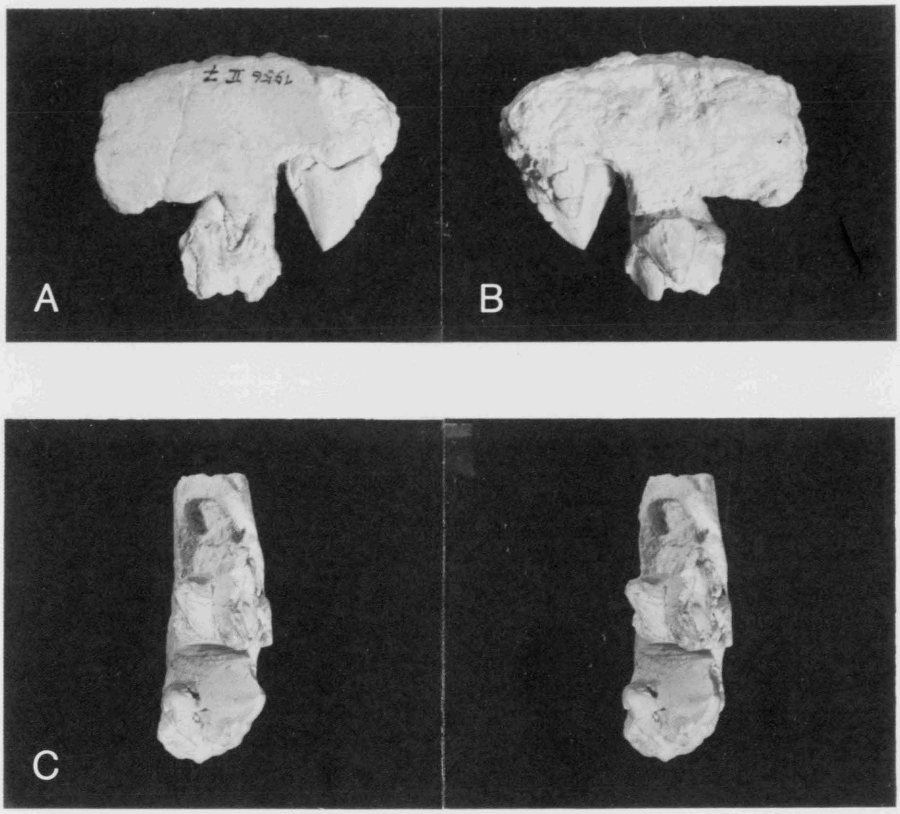

FIG. 9—Left maxilla fragment of *Ichthyolestes pinfoldi*, IPHG 1956.II.7 (holotype), from Dehm locality 21 north of Basal, Punjab Province. Specimen preserves alveoli for dP^4, most of crown of M^1, and erupting crown of M^2. A, lateral view. B, medial view. C, occlusal view (stereophotograph). Apex of crown of P^4 lies in crypt above alveoli for dP^4. *Ichthyolestes* is smaller than *Pakicetus*, upper molars lack lingual cingula, metacones on upper molars are more reduced, and the crown of P^4 is more pointed.

beaded lingual cingulum surrounding the protocone that is characteristic of *Pakicetus*. M^2 in *Ichthyolestes* resembles this tooth in *Pakicetus* but differs in having a much reduced metacone (as noted by Dehm and Oettingen-Spielberg, 1958, p. 15, this tooth may have "nur ein einziger Aussenhügel"), and it also lacks a lingual cingulum surrounding the protocone. Differences in M^1 size suggest that *Ichthyolestes* was only 80-84% as large as *Pakicetus*. These differences indicate that *Ichthyolestes* probably had sharper cusps on all cheek teeth, and suggest that it was even more specialized as a fish eater than *Pakicetus* (lending further justification to its name).

Comparison with *Gandakasia potens*

Gandakasia potens is known from several specimens collected at Dehm locality 18 in the Kuldana Formation of the Kala Chitta Range north of Basal (Punjab) and described by Dehm and Oettingen-Spielberg (1958). The holotype, IPHG 1956.II.4 (Fig. 10A), is a right dentary fragment with the talonid of M_1 and crown of M_2 in place and the associated crown of M_3. Dehm and Oettingen-Spielberg stated (1958, p. 12) that a second specimen, right P_4 IPHG 1956.II.6 (Fig. 10B) was found within a half meter of the holotype, but they regarded it as

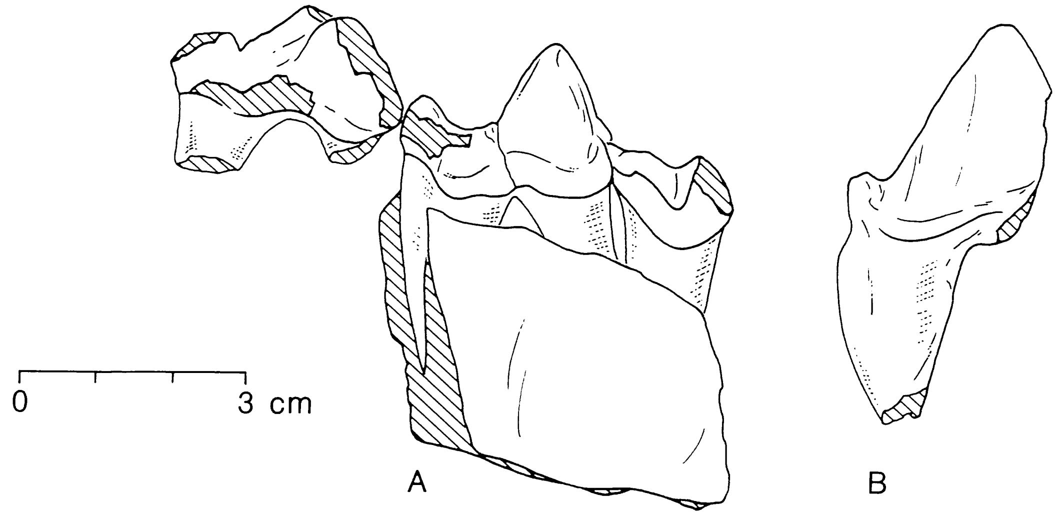

FIG. 10—Right lower cheek teeth of *Gandakasia potens* from Dehm locality 18 north of Basal, Punjab Province. A, right M_1 (broken) through M_3, IPHG 1956.II.4 (holotype). B, right P_4, IPHG 1956.II.5. General form of teeth and pattern of wear are similar to those found in *Pakicetus*. These specimens and IPHG 1956.II.6 were found on the same day at the same locality, and all probably represent a single individual animal.

representing a different individual because it was less worn. These two specimens and a third, IPHG 1956.II.6 with broken P_2 and P_3 and many dentary fragments, were found together on the same day and all have identical preservation. All three are almost certainly parts of the same right dentary. P_2 and P_3 appear to have been longer and lower-crowned than P_4. With careful work it might be possible to reassemble much of this specimen, which would add considerably to our understanding of *Gandakasia potens* and to the morphological diversity of early Eocene cetaceans.

Teeth of *Gandakasia* are similar to comparable teeth of *Pakicetus*. This is most noticeable in the form of lower molars, which are long and narrow, with a squared and notched anterior edge of the trigonid and a simple trenchant talonid. Tooth measurements indicate that *G. potens* was anywhere from 30 - 70% larger than *Pakicetus inachus*. It further differed in having relatively longer and lower-crowned anterior lower cheek teeth.

New Subfamily Pakicetinae

Kumar and Sahni (1986) included a long discussion of protocetid archaeocetes from India and Pakistan in their paper on middle Eocene *Remingtonocetus* and Remingtonocetidae. They emphasized basicranial differences separating *Pakicetus* from *Protocetus* and *Indocetus*, and suggested that *Pakicetus* should be placed in a separate family representing the most primitive and transitional of archaeocete taxa. The early history of whales is still poorly known, but, while there are many features of resemblance shared by *Pakicetus* and *Protocetus*, it does seem clear that *Pakicetus* represents a distinctly more primitive evolutionary grade, both in the basicranium and in the dentition. Consequently we here propose a new subfamily Pakicetinae based on the protocetid archaeocete *Pakicetus*.

Pakicetus and, by inference, other members of the subfamily Pakicetinae differ from other protocetids in retaining four points of contact between the tympanic bulla and the base of the skull, differ in retaining a bulla with no ventral sulcus, differ in lacking peribullar sinuses, and differ in having narrower and more downwardly directed occipital condyles. Pakicetinae differ from other archaeocetes in having higher-crowned cheek teeth and differ in having more sharply conical protocones on upper molar teeth. We include *Pakicetus*, *Ichthyolestes*, and *Gandakasia* in Pakicetinae. Separating these genera in classification is not meant to imply that they are removed from other cetaceans phylogenetically: Pakicetinae are the oldest cetaceans known, and this primitive subfamily appears to be the stem group from which later cetaceans evolved.

Tethyan Archaeoceti include the following species:

Family Protocetidae
- Subfamily Pakicetinae (new)
  - *Gandakasia potens* Dehm and Oettingen-Spielberg 1958
  - *Ichthyolestes pinfoldi* Dehm and Oettingen-Spielberg 1958
  - *Pakicetus attocki* (West 1980)
  - *Pakicetus inachus* Gingerich and Russell 1981
- Subfamily Protocetinae
  - *Protocetus atavus* Fraas 1904
  - *Indocetus ramani* (Sahni and Mishra 1975)

Family Remingtonocetidae Kumar and Sahni 1986
  - *Remingtonocetus sloani* (Sahni and Mishra 1972)
  - *Remingtonocetus harudiensis* (Sahni and Mishra 1975)
  - *Andrewsiphius kutchensis* (Sahni and Mishra 1975)
  - *Andrewsiphius minor* (Sahni and Mishra 1975)

This list is amended from that of Kumar and Sahni (1986), with addition of *Protocetus atavus* (but not *Eocetus schweinfurthi*) and deletion of indeterminate protocetid and basilosaurid records attributed to West (which were based on teeth here reassigned to *Pakicetus* and *Gandakasia*).

DISCUSSION

Nine identifiable teeth of *Pakicetus* from Chorlakki are deciduous teeth and 21 are permanent teeth. Fewer deciduous teeth develop in an individual than do permanent teeth, and a ratio of 9 to 21 suggests, to a first approximation, that juvenile *Pakicetus* were present at Chorlakki in approximately the same number as adults were. The thirty teeth from Chorlakki represent a minimum of four juvenile individuals (minimum number of individuals based on presence of four right dP_4s), and a minimum of two adult individuals (minimum number of individuals based on presence of two lower canines of different sizes and on presence of two left M^2s). This suggests that juveniles may have been twice as common as adults. Most teeth from Chorlakki represent land mammals, and the presence of juvenile as well as adult *Pakicetus* here supports our earlier hypothesis that *Pakicetus* spent a significant amount of time on land (Gingerich et al., 1983). Resting, birthing, and nursing probably took place on land, while some juvenile and all adult feeding took place in water.

Pakicetus inachus has a number of distinctively archaeocete characteristics of the dentition, in addition to archaeocete cranial and basicranial characteristics described previously (Gingerich and Russell, 1981; Gingerich et al., 1983; Oelschläger, 1987). Incisors of *Pakicetus* are simple pointed teeth like those of later archaeocetes. The upper canine is high-crowned and effectively (if not actually) double-rooted. Posterior premolars are the largest teeth in the tooth row. Molars decrease in size from front to back. Upper molars have well developed protocones surrounded by beaded lingual cingula. Lower premolars have coarse serrations on some anterior and posterior edges of the crown presaging development of large accessory denticles. Lower molars have distinct notches to receive talonids of preceding teeth. The mandibular symphysis is archaeocete-like in being shallow and extending back as far as P_2

(Fig. 4). Retention of three molars in the maxillary and mandibular dentition and retention of a paraconid on M_1 are primitive characteristics not seen in some or all later archaeocetes.

Pakicetus inachus has wear facets on some teeth produced by orthal retraction of the mandible, as typically found in temporalis-dominated mammals with sharply pointed teeth, and it also has wear facets on some teeth produced during the buccal and lingual phases of tooth-on-tooth shearing and grinding (Gingerich, 1984). Grinding lingual phase facets are poorly developed, and it is clear that this functional component was much less important than puncturing and shearing. Well developed puncturing cusps and both finely and coarsely serrated shearing crests are consistent with a diet of meat, particularly fish, as proposed earlier (Gingerich et al., 1983).

Oelschläger (1987, p. 681) questioned whether *Pakicetus* spent a significant amount of time on land because animal carcasses are more likely to be preserved in fluvial freshwater sediments than they are to be preserved on land. This explains why terrestrial organisms are preserved in fluvial sediments, but it does not explain why marine organisms are absent at Chorlakki (save ariid fishes, which are marine but enter freshwater fluvial systems) nor why terrestrial elements are such a large component of the fauna. Granulestones containing remains of *Pakicetus* are red because they were deposited and reworked subaerially by meandering streams on broad flat floodplains. Preservation of *Pakicetus* in red sediments with land mammals is most easily explained if it too was a land mammal. *Pakicetus* has a dense auditory bulla showing some (but limited) specialization for hearing in water and it has sharply pointed and serrated teeth specialized for feeding on fishes. In light of present evidence, we interpret *Pakicetus* as an amphibious intermediate stage in the transition of whales from land to sea. Postcranial remains will provide the best test of this hypothesis.

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