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Philip D. Gingerich, Director

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PARTIAL SKELETONS OF *INDOCETUS RAMANI* (MAMMALIA, CETACEA) FROM THE LOWER MIDDLE EOCENE DOMANDA SHALE IN THE SULAIMAN RANGE OF PUNJAB (PAKISTAN)

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Abstract—Indocetus ramani is an early middle Eocene archaeocete described by Sahni and Mishra from Kutch in western India. The type and only specimen known previously is a partial skull. New specimens from the marine lower middle Eocene Domanda Shale of the Sulaiman Range in Pakistan show that *Indocetus* retained a long neck; a robust, solidly-fused sacrum composed of a minimum of four vertebrae; a pelvis with a large, deep acetabulum; a robust femur (incompletely preserved); and a tibia of normal mammalian proportions, including distal articular facets for a broad astragalus. The pelvis from the *Indocetus ramani* type locality that Sahni and Mishra described as *Protosiren fraasi* and the solidly fused sacrum from the type locality that they described as cf. Moeritheriid almost certainly belong to *Indocetus ramani* as well. *Indocetus*, placed in the new subfamily Indocetinae, is an important intermediate stage in the early evolution of Cetacea. It combines an advanced *Protocetus*-like archaeocete skull with a more primitive postcranial skeleton retaining the long neck and well developed hind limbs of a land mammal.

INTRODUCTION

Protocetus atavus from the middle Eocene of Egypt was, for a long time, the oldest and most primitive cetacean known in the fossil record. *Protocetus* is represented by a skull with teeth, and by several isolated vertebrae. Primitive features include retention of a full dental formula of 3.1.4.3, retention of protocones on upper molars, and retention of a distinct sacrum with iliosacral articulations at the ends of the transverse processes (Fraas, 1904). Advanced features include broad flat frontals and an elongated, anteriorly-protruded palate and dentition, giving the skull the characteristic shape of an archaeocete. *Protocetus* is found in the Lower Building Stone Member of the marine Mokattam Formation, which is middle Lutetian in age

[1]Geological Survey of Pakistan, 84 H-8/1, Islamabad

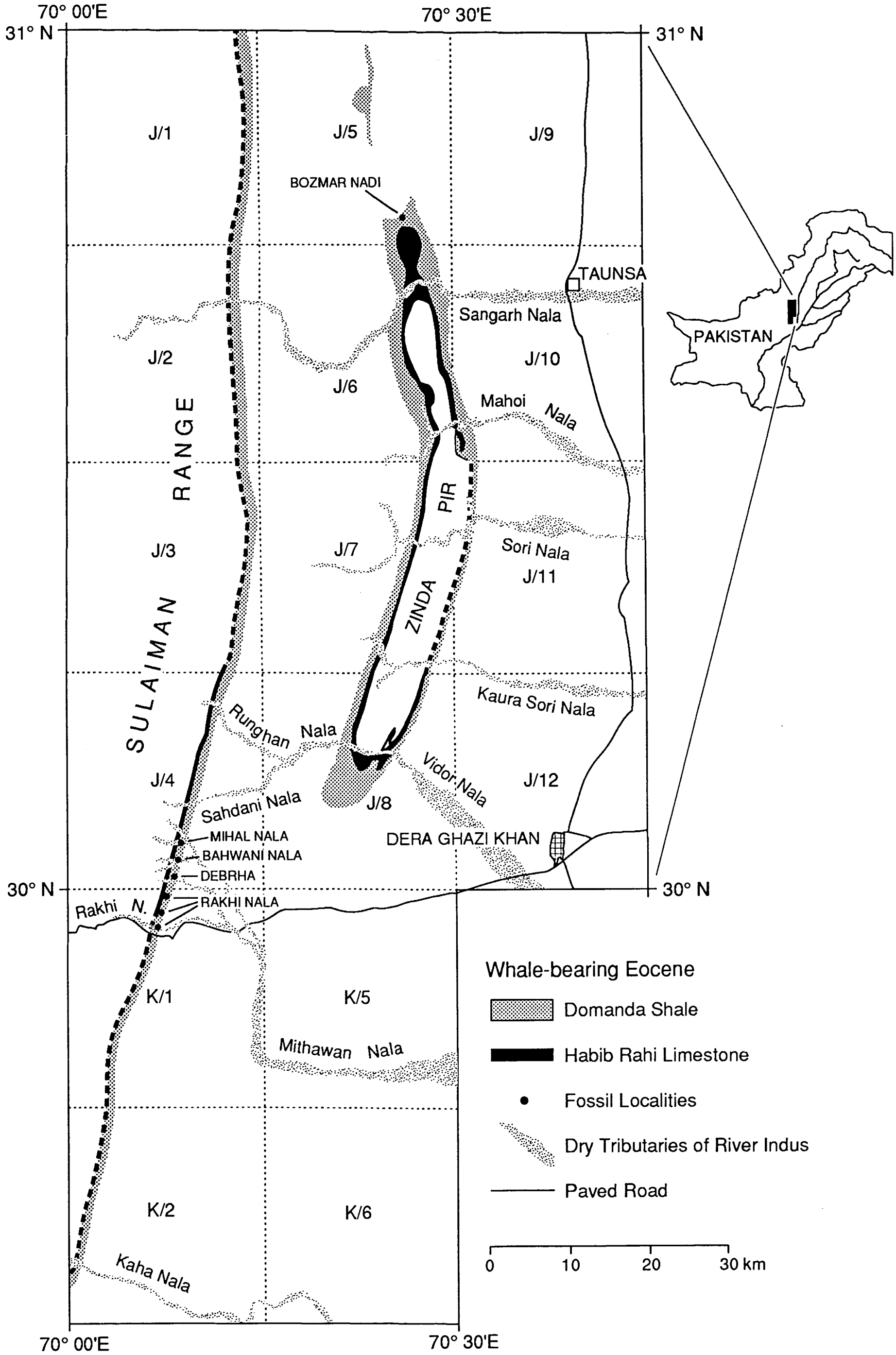

FIG. 1—Map showing outcrop pattern of Domanda Shale and early middle Eocene fossil localities discussed in the text. Prospecting in 1977 and 1981 was concentrated on exposures on the eastern flank of the Sulaiman Range in the vicinity of Rakhi Nala. Our 1992 expedition investigated exposures in Bozmar Nadi near the northern end of the Zinda Pir anticlinorium. Both areas are richly fossiliferous, and much intervening outcrop remains to be explored.

(probably planktonic foraminiferal zone P11, ca. 46 million years before present [Ma]), deposited in a marine shallow shelf environment of the ancient Tethys Sea (Gingerich, 1992).

In recent years, new protocetid and other primitive cetaceans have been described from eastern Tethys in India (Sahni and Mishra, 1972, 1975; Kumar and Sahni, 1986) and in Pakistan (Dehm and Oettingen-Spielberg, 1958; West, 1980; Gingerich and Russell, 1981, 1990; Gingerich et al., 1983; Thewissen and Hussain, 1993), but none of these specimens includes significant postcranial remains. Experience in Egypt shows that many of the most interesting evolutionary changes in early whale evolution involved the postcranial skeleton (Gingerich et al., 1990).

Indocetus ramani is the most *Protocetus*-like of all of the eastern Tethyan cetaceans. This was described by Sahni and Mishra (1975) from the marine lower middle Eocene Chocolate or Shell Limestone near Harudi in Kutch in western India. A correlative Pakistan formation is the marine lower middle Eocene "lower chocolate clays" of Eames (1952b,c), Domanda Shale Member of the Khirthar Formation (Hemphill and Kidwai, 1973; Wells, 1984; Geological Survey of Pakistan, 1986; Qureshi et al., 1987), or Sirki Member of the Khirthar Formation (Cheema, Raza, and Ahmad, *in* Shah, 1977). The "lower chocolate clays" are a unit on the order of 300 m thick, mappable over a large area, that Gingerich et al. (1979) treated as a full formation: the Domanda Formation (erroneously attributing the rise to formational status to Cheema et al.). Here we will refer to the "lower chocolate clays" simply as Domanda Shale, leaving aside the question of formational status. The Domanda Shale is extensively and well exposed on the eastern flank of the Sulaiman Range and in the parallel Zinda Pir anticlinorium farther to the east (Fig. 1).

The Domanda Shale in Pakistan has now yielded isolated cranial and postcranial elements of mammals from five localities of interest here (Table 1). Most of the isolated elements found in 1977 and 1981 could not be identified when they were found, but the cranium from Debrha, GSP-UM 1853, was referred to *Indocetus* on the basis of size when it was first studied. More careful comparison with a cast of the holotype and comparison of associated postcranial elements confirm this identification (see below).

During our 1992 expedition, one of us (M. Arif) found two fragmentary partial skeletons, GSP-UM 3009 and 3015, each including associated cranial and postcranial remains of an archaeocete cetacean. These were found 20 m apart at the same stratigraphic level in brown clays of the upper Domanda Shale near the mouth of Bozmar Nadi (valley) just south of Bor or Sohr Nala (Dhodak quadrangle, 39 J/5; Geological Survey of Pakistan, 1986) in the foothills of the Sulaiman Range northwest of Taunsa in Punjab Province. Both have *Indocetus*-like vomers and both preserve identical axis vertebrae, showing that two conspecific skeletons are represented (a third vomer-like bone may indicate that fragmentary parts of two skulls are represented in GSP-UM 3015). The new specimens are sufficient in themselves to document several distinctive skeletal characteristics of the archaeocete represented, and they permit one skull and several vertebrae and other postcranial elements collected in previous years to be referred to *Indocetus ramani*, revealing much more about this important genus and species than was known before.

ABBREVIATIONS

Institutional abbreviations used in this paper are as follows:

GSP-UM — Geological Survey of Pakistan-University of Michigan collection, Islamabad
LUVP — Lucknow University vertebrate paleontology collection, Lucknow
SMN — Staatliches Museum für Naturkunde, Stuttgart
YPM-PU — Princeton University collection at Yale Peabody Museum, New Haven

TABLE 1—Localities in Pakistan yielding cranial and postcranial remains of *Indocetus ramani*. All localities are in the eastern foothills of the Sulaiman Range, southwestern Punjab Province (Fig. 1).

Field no.	Specimen	Description
1. RN-2, south side of Rakhi Nala (29°56'N latitude, 70°7'E longitude) on D. G. Khan series map 39K/1		
77-015	GSP-UM 9	Proximal caudal vertebrae in articulation (2)
77-020	GSP-UM 15	Maxilla fragment
Larger specimens questionably referred to *I. ramani*:		
77-016	GSP-UM 11	Sacrum
77-017	GSP-UM 12	Vertebral fragments (possibly part of GSP-UM 11)
77-019	GSP-UM 14	Atlas (2 pieces)
2. RN-3, north and south sides of Mihal Nala (30°3'N latitude, 70°9'E longitude) on map 39J/4 (Gulu Sheikh)		
77-030	GSP-UM 19	Cervical vertebra (C5 or C6, centrum w. transverse processes)
77-031	GSP-UM 77	Sacrum
77-032	GSP-UM 20	Lumbar vertebra (ant. part of centrum)
Larger specimen questionably referred to *I. ramani*:		
77-029	GSP-UM 18	Acetabulum of pelvis
3. RN-4, 1.6 km north of Rakhi Nala (29°58'N latitude, 70°7'E longitude) on map 39K/1		
Larger specimen questionably referred to *I. ramani*:		
77-050	GSP-UM 24	Thoracic vertebra (centrum)
4. RN-5, Debrha (30°1'N latitude, 70°8'E longitude) on map 39J/4 (Gulu Sheikh)		
81-262	GSP-UM 1853	Cranium
81-276	GSP-UM 1854	Lumbar vertebra (centrum)
5. BN-1, near mouth of Bozmar Nadi (30°47'N latitude, 70°27'E longitude) on map 39J/5 (Dhodak)		
92-013	GSP-UM 3009	Cranial fragments, vertebrae, sacrum, acetabulum of pelvis
92-015	GSP-UM 3015	Cranial fragments, vertebrae, proximal femur, tibia

CRANIUM

The type specimen of *Indocetus ramani*, LUVP 11034, is a partial cranium from the Chocolate or Shell Limestone near Harudi in Kutch, western India. This was described by Sahni and Mishra (1975) and illustrated in their plate IV, figures 1-3. The type is a skull in two pieces, one including the frontal shield and the other including the right occiput and right auditory bulla. Sahni and Mishra mentioned cranial elongation, a lateral profile with the frontal meeting the sagittal crest at an obtuse angle, a postorbital process of moderate size, a massive typically whale-like bulla, and retention of a well developed protocone on upper molars as characteristics of the genus.

The new skull found in 1981, GSP-UM 1853, is in several pieces, of which the most important is the neurocranium with the occiput and right auditory bulla (Figs. 2 and 3). The right frontal is attached, but large parts of the sagittal and nuchal crests are missing. A second piece includes the left frontal and much of the rostrum and palate, extending as far forward as the alveoli for left and right P^1. A third piece includes the anterior parts of both premaxillae, with alveoli for all three incisors. Measurements of the new skull are compared with those of the holotype in Table 2.

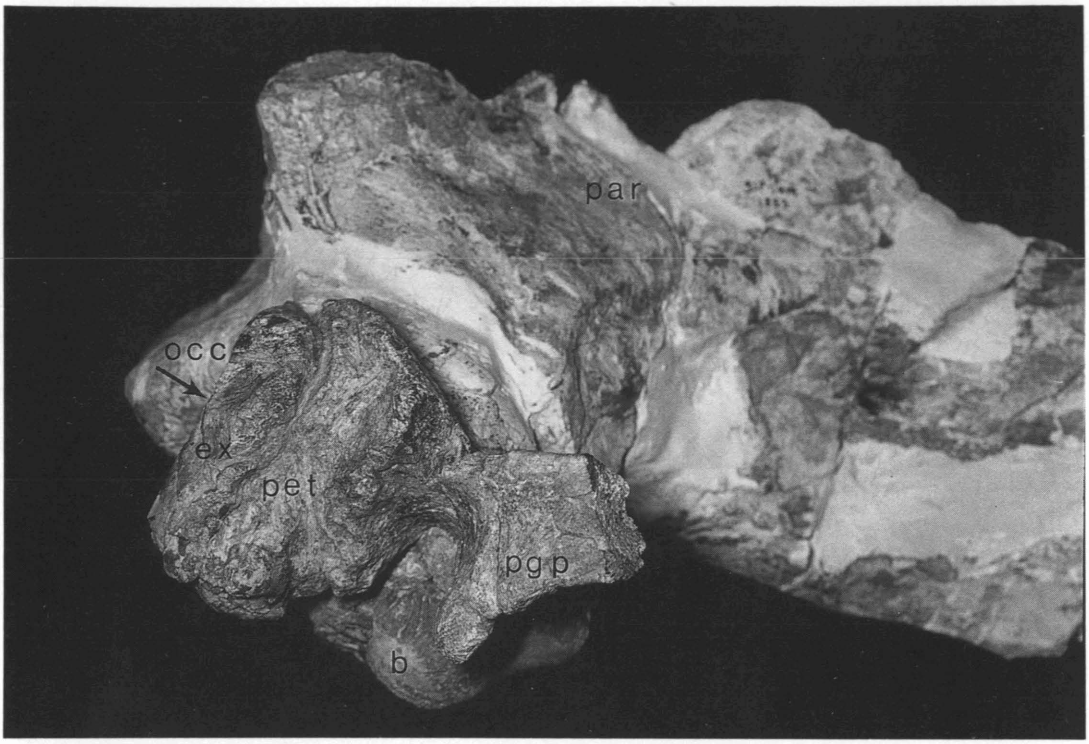

FIG. 2—Right exoccipital and squamosal of skull of *Indocetus ramani*, GSP-UM 1853, from Debrha. Note flat posterior surface of exoccipital (arrow) similar to that in the type of *Indocetus ramani*. Specimen is shown in right lateral view. See Figure 3 for orientation and scale. Abbreviations: *b*, auditory bulla; *ex*, exoccipital; *occ*, occipital condyle; *par*, parietal; *pet*, petrosal; *pgp*, postglenoid process.

The occiput and auditory bulla of GSP-UM 1853 resembles that of LUVP 11034 very closely. These are distinctive among known protocetids in having a relatively flat posterior surface of the exoccipital (Fig. 2). The foramen magnum opens more posteriorly than ventrally. Another important feature of the new skull is retention of stone endocasts of the left and right narial passages, showing that the external nares opened above the canine alveoli, anterior to the front of preserved P^1 alveoli and posterior to preserved alveoli for I^3 in the premaxillae. These stone endocasts envelope the vomer, which is a large, long, sharply keeled bone that is now exposed ventrally in the midline of the skull. The narial passages and vomer are normally covered ventrally by palatines, but these are broken away in GSP-UM 1853. Isolated vomers of GSP-UM 3009 and 3015 are illustrated in Figure 4.

The right auditory bulla in GSP-UM 1853 measures 62 mm in length anteroposteriorly and 45 mm in breadth transversely. Sahni and Mishra (1975, p. 19) gave these measurements as 70 mm and 45 mm, respectively, in the holotype. The new bulla is not well preserved, but it does confirm that *Indocetus* had large, dense, typically whale-like tympanic bullae.

Alveoli show the upper incisors and P^1 to have been single-rooted. P^2 was double-rooted. P^3 was double-rooted, with a broad posterior root. P^4 appears to have been three-rooted, and M^1 and M^2 were clearly three-rooted. M^3 was double-rooted, or possibly single-rooted (it is not possible to determine whether the roots for M^3 diverged). The presence of an alveolus for M^3 is important because it is not possible to determine from the type skull whether this tooth

TABLE 2—Measurements of the new cranium of *Indocetus ramani*, GSP-UM 1853, from Debrha in Pakistan, compared to the holotype of *Indocetus ramani*, LUVP 11034, from Harudi in Kutch, western India (measurements of holotype from Sahni and Mishra, 1975, p. 20), and to the holotype of *Protocetus atavus*, SMN 11084, from Gebel Mokattam in Egypt (measurements from Fraas, 1904, p. 203).

	Indocetus ramani		*Protocetus atavus*
	GSP-UM 1853	LUVP 11034 (holotype)	SMN 11084 (holotype)
Condylobasal length:	62 cm*	---	58 cm
Length of the P^3-M^2 series	11.2 cm	10 cm	---
Width of skull at level of anterior root of P^3	8.6 cm	8 cm	---
Width across supraorbital processes of frontal shield:	21 cm	20 cm	16.7 cm
Width across exoccipitals:	22 cm	22 cm	---
Width across zygomatic arches:	26 cm*	---	24 cm

*Estimate

was retained or not, and the new skull shows clearly that M^3 was still present in *Indocetus* (M^3 is lost in some later archaeocetes). Measurements of roots and alveoli of upper teeth in the new skull are compared to measurements of alveoli of upper teeth in the holotype in Table 3. These are generally similar, and differences may be attributable to the difficulty of measuring alveoli consistently. Judging from alveoli, the dentition of *Indocetus* was much like that of *Protocetus*. The only tooth of *Indocetus* known to date is the partial crown of M^1 illustrated by Sahni and Mishra (1975) in their plate IV, fig. 3. This is distinctive in having a lingual cingulum surrounding a broad and flatly worn protocone.

DENTARY

Dentaries were not found with the type specimen of *Indocetus ramani*, and no recognizable dentaries have been found in subsequent collections either. However, there is one Indian specimen, LUVP 11003, that is too large to belong to any of the taxa to which it has been referred. This dentary measures 60 to 63 mm deep beneath alveoli for P_4 and M_1, respectively (Sahni and Mishra, 1972, p. 493).

LUVP 11003 was first described and illustrated by Sahni and Mishra (1972, p. 493, plate 97, figs. 6-7), who identified it as *Protocetus sloani* (type specimen LUVP 11002). Sahni and Mishra (1972, p. 492) implied that LUVP 11002 and 11003 were part of a collection of cetacean remains from the gypsiferous clays 3 km southeast of Baranda in Kutch. Later, Sahni and Mishra (1975, p. 21) listed LUVP 11002 and 11003 as part of a collection from the Shell Limestone and from ossiferous gypseous shales at Harudi (which is 3 km southeast of Baranda). Finally, Kumar and Sahni (1986, p. 341) indicated that LUVP 11002 came from the Chocolate Limestone at the Harudi fossil locality. Kumar and Sahni did not mention LUVP 11003, but this shares the same good preservation with bones from the Chocolate Limestone, and it is reasonable to suspect that LUVP 11003, like LUVP 11002, came from the Chocolate Limestone at Harudi. If so, then LUVP 11003 is from the same locality and horizon as the

FIG. 3—Cranium of *Indocetus ramani*, GSP-UM 1853, from Debrha. A and B, dorsal and right lateral views. Note elongated rostrum and braincase, broad frontal shield (*f*) above orbits, and cast of nares (*n*) extending forward to open above canine (missing region of rostrum). Supraoccipital nuchal crest, zygomatic arches, and all teeth are also missing. Scales are in cm. Measurements are given in Tables 2 and 3.

type specimen of *Indocetus ramani*, with which it agrees much more closely in size and form than it does with other dentaries of *Protocetus* (now *Remingtonocetus*) *sloani* (see Kumar and Sahni, 1986, p. 341).

The importance of LUVP 11003 is in showing that the mandibular symphysis in *Indocetus ramani* was not fused back as far as P_4. This specimen has the potential, with further cleaning, to show the size of the mandibular foramen or canal in *Indocetus*, which might indicate the degree of development of underwater hearing in the genus. Thewissen and Hussain (1993) stated that *Pakicetus* is the only cetacean with a small mandibular foramen. A good cast of LUVP 11003 provided by Kumar and Sahni gives no indication of enlargement of the mandibular canal, but this needs to be checked on the original specimen.

VERTEBRAL COLUMN

GSP-UM 3009 and 3015 are important because they preserve, respectively, nine and fifteen vertebral centra from all parts of the vertebral column. These are not as informative as more or better preserved vertebrae would be, but they do reveal a number of distinctive features of *Indocetus ramani* that were not known previously.

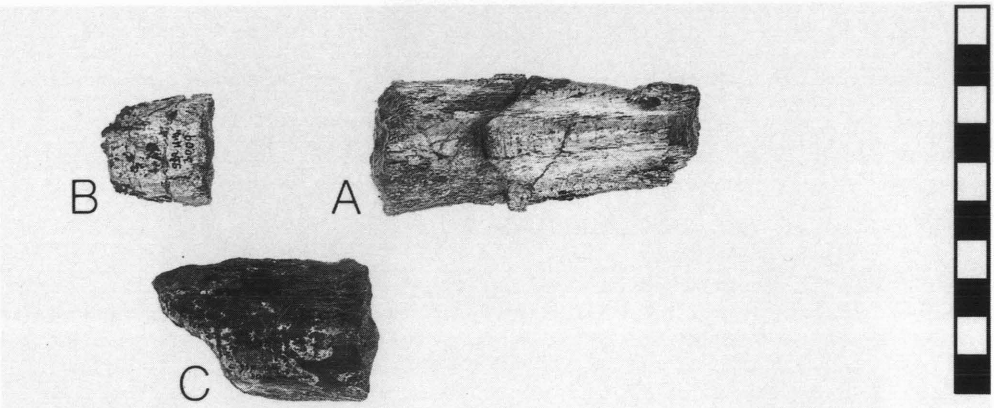

FIG. 4—Elongated vomers of *Indocetus ramani* from Bozmar Nadi. A, central portion of GSP-UM 3009. B, posterior tip of GSP-UM 3009. C, posterior portion of GSP-UM 3015. All are shown in ventral view. Overlap in preserved parts shows that two specimens are represented. Scale is in cm.

TABLE 3—Comparison of measurements (mm) of the roots or alveoli (in parentheses) of cranial teeth in *Indocetus ramani*, GSP-UM 1853, from Debrha in Pakistan, with alveoli (in parentheses) in the holotype LUVP 11034 from Harudi in India.

Tooth position	GSP-UM 1853		LUVP 11034 (holotype)	
	Length	Width	Length	Width
I^1	(23.8)	(15.9)	---	---
I^2	(27.7)	(16.4)	---	---
I^3	(20.0)	(13.3)	---	---
C^1	---	---	---	---
P^1	21.2	12.6	---	---
P^2	(37.2)	(15.9)	---	---
P^3	33.4	20.0	(30.0)	(20.0)
P^4	27.9	21.9	(28.5)	(24.5)
M^1	---	---	(17.0)	(22.0)
M^2	24.0	18.7	(17.0)	(19.0)
M^3	12.0	18.8	---	---

Cervical vertebrae—GSP-UM 14 is the only atlas vertebra known from the upper Domanda Shale (Fig. 5A). It articulates reasonably well with GSP-UM 1853, but seems large and surprisingly advanced in morphology (with flat axis facets like those of Egyptian *Prozeuglodon*), and it is here questionably referred to *I. ramani*. GSP-UM 14 is broken, with only the left side preserved. The anterior articulation for the left occipital condyle spirals obliquely forward and upward. The posterior articulation is kidney-shaped, measuring 45 mm in maximum length and about 31 mm in maximum breadth; it is distinctive in being almost perfectly flat, and it is not clear how this could have articulated with an axis vertebra like that

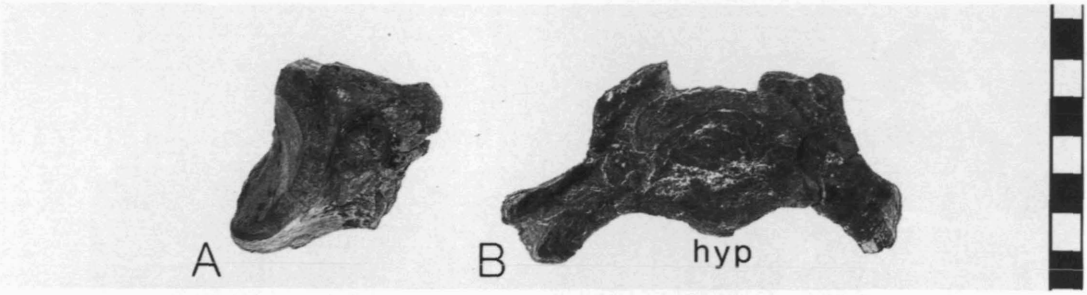

FIG. 5—Cervical vertebrae from Rakhi Nala and Mihal Nala referred to *Indocetus ramani*. A, portion of left half of atlas vertebra, GSP-UM 14 from RN-2, in cranial view. Note curved anterior articular surface for left occipital condyle of skull. Posterior articular surface is kidney-shaped and almost flat. B, centrum of C5 or C6, GSP-UM 19 from RN-3, in cranial view. Note weak hypapophysis (*hyp*) and downwardly-angled transverse processes. Scale is in cm.

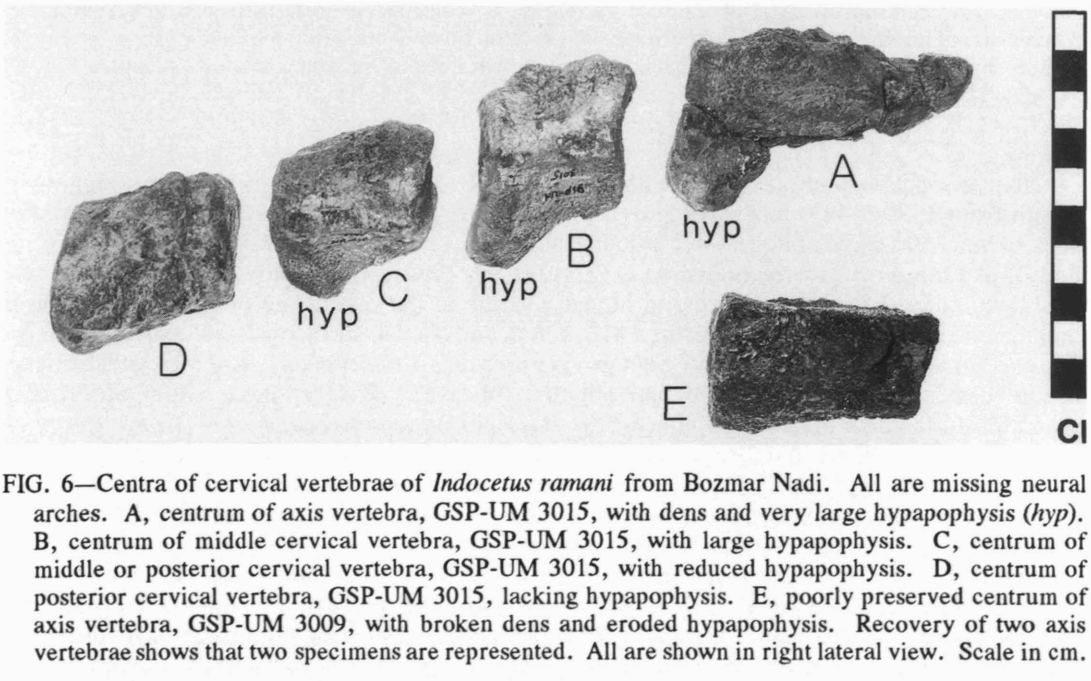

FIG. 6—Centra of cervical vertebrae of *Indocetus ramani* from Bozmar Nadi. All are missing neural arches. A, centrum of axis vertebra, GSP-UM 3015, with dens and very large hypapophysis (*hyp*). B, centrum of middle cervical vertebra, GSP-UM 3015, with large hypapophysis. C, centrum of middle or posterior cervical vertebra, GSP-UM 3015, with reduced hypapophysis. D, centrum of posterior cervical vertebra, GSP-UM 3015, lacking hypapophysis. E, poorly preserved centrum of axis vertebra, GSP-UM 3009, with broken dens and eroded hypapophysis. Recovery of two axis vertebrae shows that two specimens are represented. All are shown in right lateral view. Scale in cm.

associated with GSP-UM 3015, which appears to have had a more oblique articulation. This specimen indicates either that the axis of *I. ramani* had broad flat anterior articular surfaces or, alternatively, the presence of a larger, more advanced cetacean in the upper Domanda Shale. GSP-UM 14 has a large arterial foramen 7.5 mm in diameter perforating the transverse process. The functional length of the atlas is 15.5 mm, which is the closest possibly approximation of the occipital condyles of the skull to the anterior articular surface of the axis vertebra (other vertebral measurements are given in Table 4).

There are two axis vertebrae, one preserved with GSP-UM 3009 (Fig. 6E) and the other with GSP-UM 3015 (Fig. 6A). The former is badly eroded, and adds nothing beyond what can be seen in GSP-3015. The latter is distinctive in having a relatively large projecting odontoid process, a long centrum, and an extraordinarily large hypapophysis.

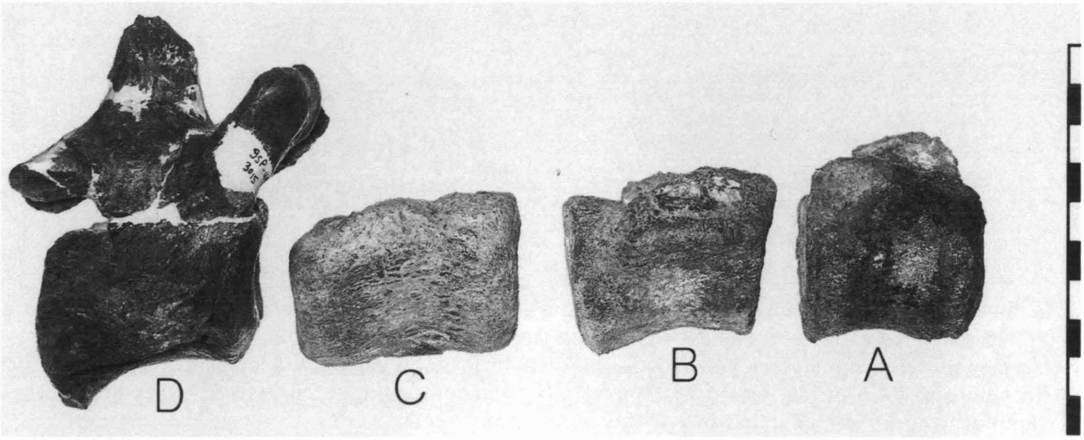

FIG. 7—Thoracic, lumbar, and caudal vertebrae of *Indocetus ramani*, GSP-UM 3015, from Bozmar Nadi. A, centrum of anterior thoracic vertebra. B, centrum of posterior thoracic vertebra. C, centrum of lumbar vertebra. D, anterior caudal vertebra with neural arch, pre- and postzygapophyses, and short transverse processes. Specimens are shown here in right lateral view (compare Fig. 8). Scale is in cm.

Other cervical vertebrae found with GSP-UM 3015 (Fig. 6B-D) have centra ranging in length from 36.0 to 42.6 mm, averaging about 40 mm, which is long for an archaeocete of this size. The centra have obliquely-set articular surfaces (relative to the cranial-caudal axis of the body), like those of *Pachyaena ossifraga* (Zhou et al., 1992), which indicates that the head was habitually carried farther forward and higher relative to the rest of the body than was true in more advanced archaeocetes. As in *Pachyaena*, the cranial surface of the centrum is more flattened in anterior view, with a distinct groove crossing it transversely, and the caudal surface of the centrum is more rounded and slightly concave. Finally, these show progressive reduction in the size of the hypapophysis in more posterior vertebrae.

One specimen, GSP-UM 19, is a cervical with large, downward-turned transverse processes indicating that it is probably C5 or C6 (Fig. 5B). This has large pedicles for a strong neural arch dorsally, and a broad hypapophysis ventrally. The arterial canals perforating the base of each transverse process measure about 6 mm in diameter.

Thoracic vertebrae—Thoracic vertebrae are difficult to position in the vertebral column unless pedicles, neural spines, and rib articulations are well preserved. None of the vertebrae available here preserve neural arches or rib articulations. Anterior thoracics are identified on the basis of their short and deep centrum (Fig. 7A), which tapers laterally toward the rib articulations and neural arches (Fig. 8A). Posterior thoracics have longer centra, and retain some evidence of articulating ribs. Measurements of thoracic centra are listed in Table 4, which shows that anterior thoracics of *I. ramani* averaged about 40 mm in length, while posterior thoracics averaged about 47 mm in length.

Lumbar vertebrae—Lumbar vertebrae of *Indocetus* have relatively long centra that are oval to symmetrically kidney-shaped in cross-section (Figs. 7B,C and 8B,C). These average about 54 mm in centrum length (Table 4).

Sacrum—One of the most interesting bones found with GSP-UM 3009 is a partial sacrum in two pieces. The larger piece has the centra of the second and third sacral vertebrae (S2 and S3) solidly fused, with co-ossified transverse processes (pleurapophyses) forming a broad marginal shelf for muscle attachment (Figs. 9B, 10A). This shelf encloses left and right dorsal and ventral sacral foramina that carried spinal nerves. The sacrum retains a stone endocast of the neural canal, which is roughly triangular in cross-section, measuring about 17.5 mm high

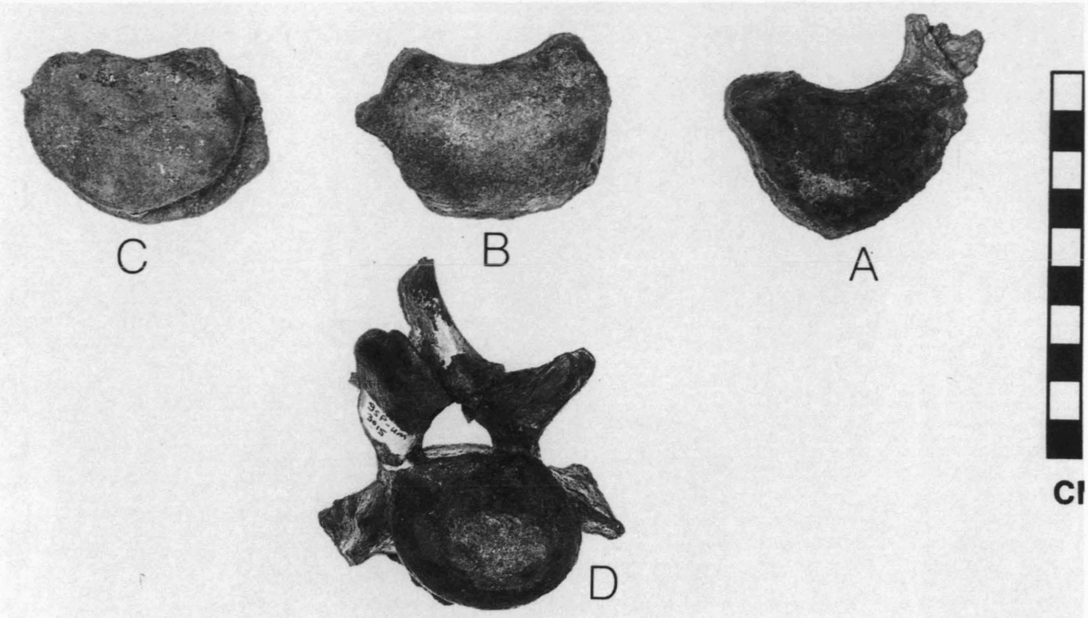

FIG. 8—Thoracic, lumbar, and caudal vertebrae of *Indocetus ramani*, GSP-UM 3015, from Bozmar Nadi. A, centrum of anterior thoracic vertebra. B, centrum of posterior thoracic vertebra. C, centrum of lumbar vertebra. D, anterior caudal vertebra with neural arch, pre- and postzygapophyses, and short transverse processes. Specimens are shown here in anterior view (compare Fig. 7). Scale is in cm.

and 22.5 mm wide at the base. This stone endocast shows clearly how left and right spinal nerves angled backward from the spinal cord and then branched to send off dorsal and ventral rami through the sacral foramina.

The second sacral vertebra preserves the posterior part of the right auricular surface for articulation with the pelvis, which is how it can be identified with certainty as S2. The smaller piece of sacrum in GSP-UM 3009 includes a large part of the auricular surface of the left side (Fig. 9A), which was originally part of both S1 and S2. The auricular surface of the sacrum is large relative to the rest of the sacrum, indicating the substantial articulation with the pelvis characteristic of land mammals.

There is a sharp break at the posterior end of S3 (Fig. 9B), which appears not to have been firmly co-ossified with S4, but the broad marginal shelf formed by sacral pleurapophyses extends to the back of S3, with a roughened surface showing where the pleurapophysis of S3 articulated with the pleurapophysis of S4, meaning that the full sacrum included a minimum of four sacral vertebrae. Finally, the neural arch in GSP-UM 3009 is partially preserved on S3 but not on S2.

Recovery of a fused sacrum with GSP-UM 3009 indicates that sacra found in the Domanda Shale in 1977 are probably cetacean as well. The best preserved of these is GSP-UM 77 from Mihal Nala (RN-3), mentioned by Gingerich et al. (1979, p. 109) and illustrated here in Figures 9C and 10B. This is virtually identical to GSP-UM 3009 in size (Table 4) and in the form of comparable parts, which include parts of the left auricular surface and the body of S2. GSP-UM 77 preserves the first and second sacral centra (S1 and S2) solidly co-ossified. Parts of both left and right auricular surfaces are preserved (and the sacrum is about 95 mm in width across what remains of these), but neither is as well preserved as the left auricular surface of

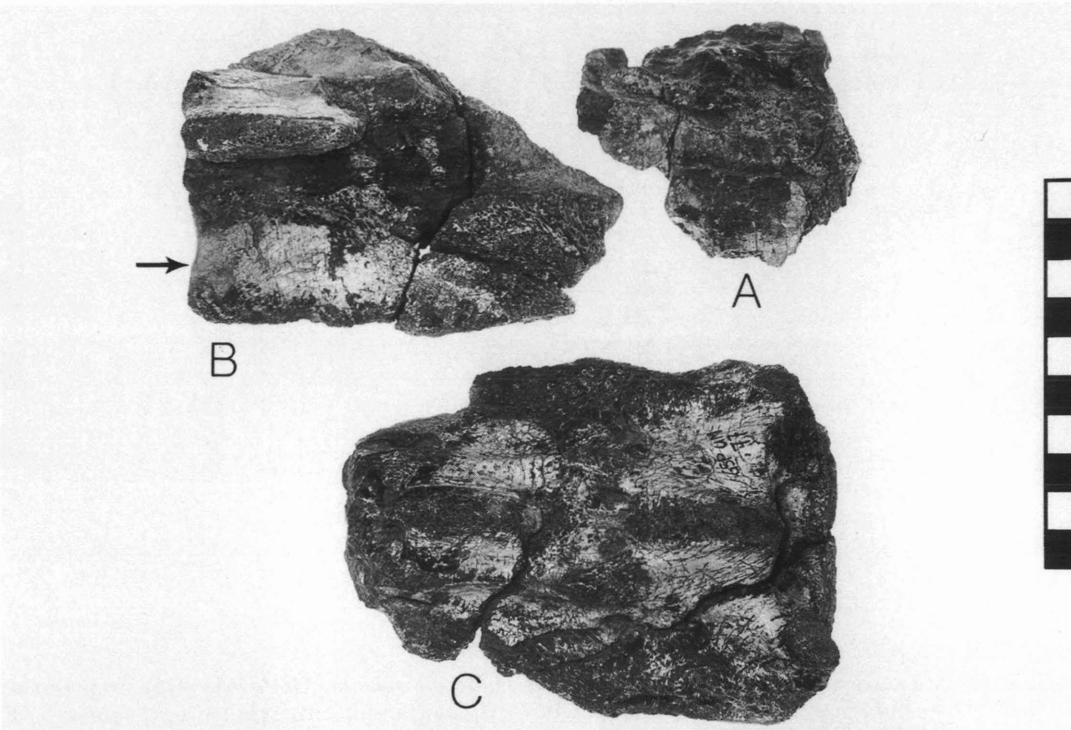

FIG. 9—Sacra of *Indocetus ramani* from Bozmar Nadi and Mihal Nala. A, left auricular surface of the transverse process of the sacrum in GSP-UM 3009. This auricular surface indicates a large area of articulation with the pelvis. B, fused sacral vertebrae S2 and S3 in GSP-UM 3009. Auricular surface of transverse process is partially preserved, and the broad marginal shelf formed by fusion of pleurapophyses of both vertebrae is well preserved on the right side of this sacrum. S3 preserves part of neural arch, and an endocast of the neural canal. The marginal shelf ends abruptly at the posterior end of S3 (arrow), showing that this sacrum had a fourth vertebra with well-formed pleurapophyses that was less solidly fused to the others. C, fused sacral vertebrae S1, S2, and part of S3 in GSP-UM 77. Left and right auricular surfaces of the transverse processes of S1 and S2 are partially preserved. Pre- and postzygapophyses, pleurapophyses, and vertebral centra are all solidly fused. Specimens are shown in dorsal view; anterior is to the right (compare Fig. 10). Scale is in cm.

GSP-UM 3009. Each auricular articulation runs the length of S1 and most of S2, where these merge smoothly into the broad marginal shelf formed by co-ossified pleurapophyses. Dorsal and ventral sacral foramina are well preserved perforating this shelf where S1 joins S2 and where S2 joins S3. Prezygapophyses and postzygapophyses joining S1 to S2 and joining S2 to S3 are solidly co-ossified, and each set of zygapophyses surrounds deep paired pits for tendinous muscle origination. Neural spines are present, but these are not well preserved.

In cranial view, the anterior articular surface of the centrum of S1 is oval in outline and compressed dorsoventrally, with a height-to-width ratio of 0.61 or 1.65, depending on how this is expressed (based on measurements in Table 4). The lateral margins of the anterior articular surface of S1 are defined by grooves for spinal nerves, which separate this articular surface from the impinging transverse processes. The neural canal is well preserved. As in GSP-UM 3009, this is triangular in cross-section. The canal measures 27 mm wide at the base, and it is 15.5 mm high in the midline.

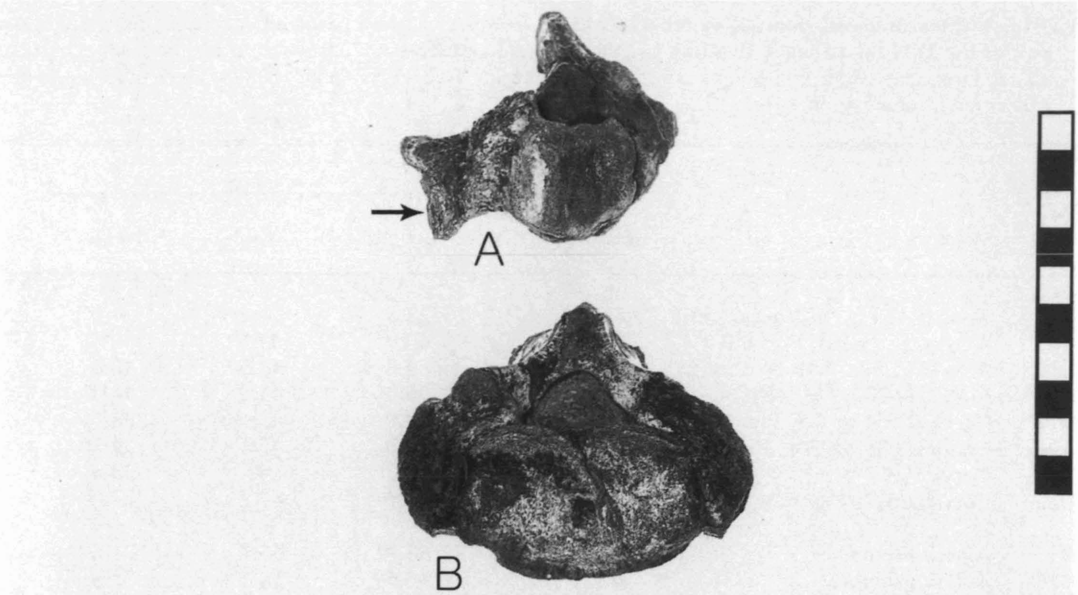

FIG. 10—Sacra of *Indocetus ramani* from Bozmar Nadi and Mihal Nala. A, fused sacral vertebrae S2 and S3 in GSP-UM 3009, with part of auricular surface (arrow) and the broad marginal shelf formed by fusion of pleurapophyses showing on the right side. B, fused sacral vertebrae S1, S2, and part of S3 in GSP-UM 77. Left and right auricular surfaces of the transverse processes are partially preserved. Specimens are shown in anterior view (compare Fig. 9). Scale is in cm.

Taken together, GSP-UM 77 and GSP-UM 3009 indicate that the sacrum of *Indocetus ramani* was long (ca. 210 to 220 mm long), relatively narrow (estimated at ca. 115 mm wide), and massive, with large auricular processes for firm articulation with the pelvis.

A third partial sacrum, GSP-UM 11 from Rakhi Nala locality RN-2, preserves S1 and part of S2. This may represent *Indocetus ramani*, but it is even larger than GSP-UM 77 and GSP-UM 3009. It differs somewhat in shape (a difference possibly exaggerated by a different pattern of breakage), and GSP-UM 11 may represent a different and slightly larger archaeocete.

Caudal vertebrae—The best preserved caudal vertebrae are GSP-UM 3015 (Figs. 7D and 8D) from Bozmar Nadi and GSP-UM 9 (two caudals preserved in articulation) from Rakhi Nala locality RN-2. GSP-UM 3015 has a well preserved centrum and the neural arch intact. The centrum is distinctive in having very short, robust, transverse processes, indicating that this is one of the anteriormost caudals, and in having a pair of well developed chevron (hemal arch) articulations on the posteroventral margin of the centrum. The dorsal part of the neural arch arises from pedicles extending along the anterior two-thirds of the dorsal surface of the centrum, and this bears large flat prezygapophyses facing inward and oriented at an angle of about 45° to the sagittal plane. These extend well forward of the anterior surface of the centrum. Large flat postzygapophyses face outward and these too are oriented at an angle of about 45°. These extend just past the posterior surface of the centrum. By comparison, the neural spine appears small and weak (some of the dorsal part of this is missing). The neural canal is triangular in cross-section like that of the sacrum; this measures about 18 mm wide at the base and 13 mm high in the midline.

The more anterior of the two anterior caudal vertebrae in articulation in GSP-UM 9 is very similar to the anterior caudal of GSP-UM 3015 described above, differing in having a smaller neural canal and thinner transverse processes. The more posterior caudal vertebra of GSP-

TABLE 4—Measurements (mm) of vertebral centra of *Indocetus ramani* based on specimens from the upper part of the Domanda Shale. Centrum lengths of sacral vertebrae are measured to and/or from centers of sacral foramina; width and height are given for anterior face of S1 only. Dittos mark separate centra preserved in articulation.

GSP-UM	Vertebra	Locality	Centrum Length	Centrum Width	Centrum Height
14	Atlas (C1; Fig. 5A, quest. ref.)	RN-2	38.5	---	---
3009	Axis (C2, eroded; Fig. 6E)	BN-1	60.0*	43.5*	---
3015	Axis (C2; Fig. 6A)	BN-1	69.8	43.5	42.8
3015	Cervical (C3?; Fig. 6B)	BN-1	36.0	45.3	44.0
3015	Cervical (C4 or C5; Fig. 6C)	BN-1	39.8	43.6	38.7
19	Cervical (C5 or C6)	RN-3	39.0	47.1	39.8
3009	Cervical (C7?)	BN-1	40.7	---	33.4
3015	Cervical (C7; Fig. 6D)	BN-1	42.6	45.2	37.0
3015	Anterior thoracic	BN-1	38.9	53.4	31.6
3015	Anterior thoracic	BN-1	40.5	54.3	35.4
24	Ant. thoracic (quest. ref.)	RN-4	39.0	58.1	42.3
3015	Anterior thoracic	BN-1	42.0	54.9	31.5
3015	Ant. thoracic (Fig. 7A, 8A)	BN-1	42.6	58.6	37.4
3009	Anterior thoracic	BN-1	38.4	---	---
3009	Anterior thoracic	BN-1	39.7	---	---
3015	Posterior thoracic	BN-1	45.8	---	31.2
3009	Posterior thoracic	BN-1	47.4	---	---
3015	Posterior thoracic(?)	BN-1	48.7	---	38.0
3015	Lumbar (Figs. 7B, 8B)	BN-1	48.7	53.6	40.4
3015	Lumbar (Figs. 7C, 8C)	BN-1	53.3	60.0	36.8
3015	Lumbar	BN-1	55.1	57.3	36.7
1854	Lumbar	RN-5	60.2	57.5	39.7
3009	Sacral (S2; Fig. 9B, 10A)	BN-1	51.7	---	---
"	Sacral (S3; Fig. 9B, 10A)	"	55.7	---	---
77	Sacral (S1; Fig. 9C, 10B)	RN-3	56.5	65.1	39.5
"	Sacral (S2; Fig. 9C, 10B)	"	51.5	---	---
11	Sacral (S1, questionably ref.)	RN-2	65.8	---	45.3
3009	Proximal caudal	BN-1	55.6	---	---
3009	Proximal caudal	BN-1	48.3	58.9	38.8
3015	Prox. caudal (Figs 7D, 8D)	BN-1	48.2	49.0	40.3
3015	Prox. caudal (dorsovent. flat.)	BN-1	49.2	---	---
9	Proximal caudal	RN-2	48.6	---	---
"	Proximal caudal	"	44.5	---	---

*Estimate

UM 9 is similar to the vertebra in front of it, but the neural spine slopes forward as if to articulate with the preceding postzygapophyses, and the postzygapophyses on this vertebra are much reduced in size.

The remaining caudal vertebrae are centra that add little to our understanding of tail structure in *Indocetus*.

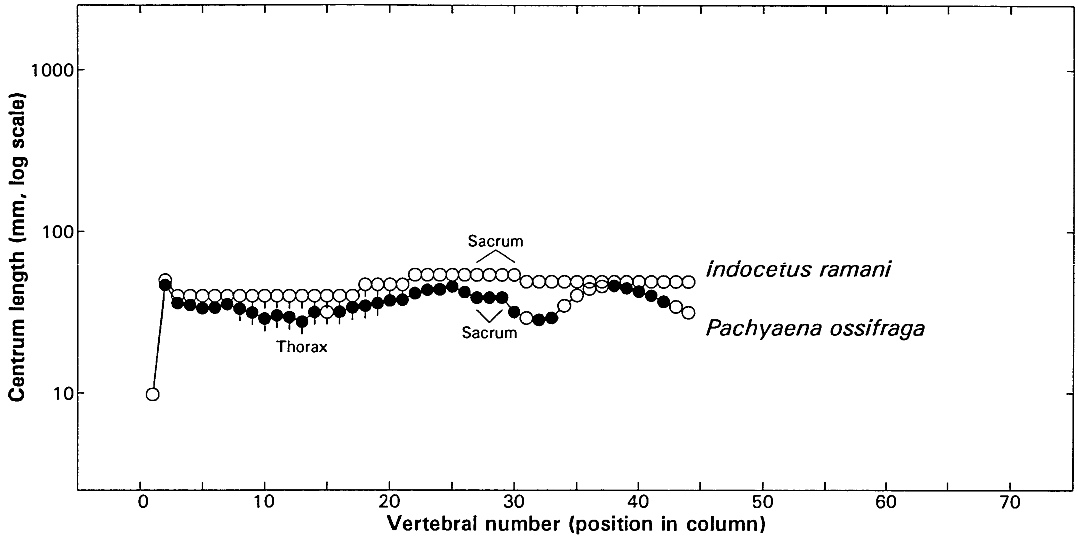

FIG. 11—Averaged length-of-vertebrae profile of partially marine middle Eocene *Indocetus ramani* (open circles) compared to length-of-vertebrae profile of the terrestrial North American early Eocene mesonychid *Pachyaena ossifraga* (closed-and-open circles; from Zhou et al., 1992). This shows *I. ramani* to have been a little larger than *P. ossifraga*. Cervical vertebrae of *Indocetus* are proportionally as long as those of terrestrial *Pachyaena*, not shorter like those of later archaeocetes and other cetaceans. *Indocetus* had a sacrum with at least four sacral centra, while *Pachyaena* had a sacrum with three sacral centra. The greatest difference in vertebral columns of the two genera appears to be the relatively longer (and heavier) sacrum and proximal caudal vertebrae of *Indocetus*, suggesting that aquatic locomotion in *Indocetus* may have been driven by a tail powered by strong dorsal and ventral sacrococcygeal muscles originating from the lumbars, sacrum, and anterior caudal vertebrae. The number of cervical, thoracic, lumbar, and caudal vertebrae in *Indocetus* is not yet known; values plotted here are averaged from Table 4.

Vertebral size and proportions—It is not possible to say very much about the length or structure of the vertebral column in *Indocetus ramani* without more complete specimens. However, assuming that this taxon had 7 cervical vertebrae, 14 thoracics, 5 lumbars, 4 sacrals, and a tail of moderate length, we can construct a length-of-vertebrae profile based on the average length of vertebrae at each position documented in Table 4. This length-of-vertebrae profile is compared with that of the mesonychid land mammal *Pachyaena ossifraga* in Figure 11. The plot shows that *I. ramani* was uniformly a little larger than *P. ossifraga*, and it shows that the neck of *Indocetus* had the length typical of a land mammal of its size. Later and more advanced aquatic archaeocetes and other cetaceans have much shorter cervical vertebrae for their size than those described here for *Indocetus*. The largest consistent discrepancy between *Indocetus* and *Pachyaena* in this vertebral length profile is in the sacral region, where *Indocetus* has a much longer sacrum than *Pachyaena*, with longer sacral centra and a minimum of four sacral vertebrae instead of three, and in the proximal caudal region, where *Indocetus* has longer vertebrae (both absolutely and relatively) than *Pachyaena*.

HIND LIMB

Pelvis—GSP-UM 3015 includes much of a right pelvis (Fig. 12B). The acetabulum is large and deep, with a diameter of 40 mm around the margin of the lunate surface and a depth of

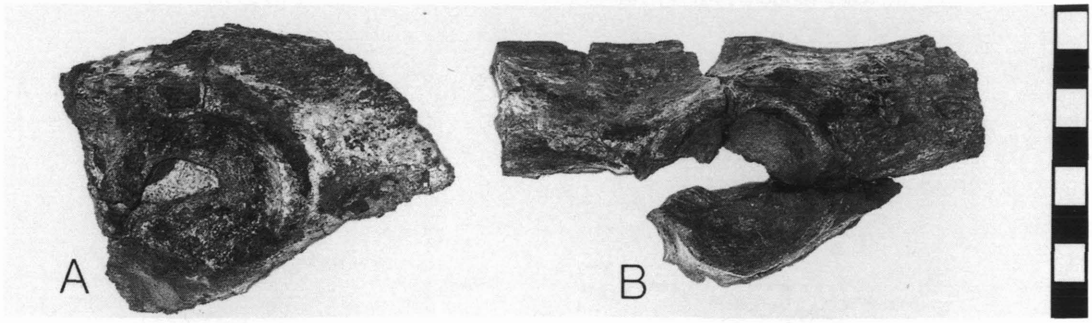

FIG. 12—Partial right pelves of archaeocete cetaceans from the Domanda Shale of Pakistan. A, Acetabulum questionably referred to *Indocetus*, GSP-UM 18 from Mihal Nala, in right lateral view. B, right pelvis of *Indocetus ramani*, GSP-UM 3015 from Bozmar Nadi, in right lateral view. Scale is in cm.

about 17 mm (measured to the deepest part of the lunate surface, not into the acetabular fossa). The acetabular fossa opens posteroventrally, directly opposite the ilium. The dorsal surface of the pelvis above the acetabulum is widest transversely above the anterior edge of the acetabulum, where it measures 35 mm. A short section of the body of the ilium is preserved; this is oval in cross-section, with the longest diameter of the oval being 36.5 mm and the shortest diameter of the oval being 20.5. The rest of the body of the ilium is missing, including all of the sacral articular surface. A short section of the body of the ischium is also preserved, which is D-shaped in cross-section, with the longest axis of the D being the medial surface running from the dorsal surface to the obturator foramen. This measures 36.5 mm. A shorter axis of the D, perpendicular to the longest axis, measures 16.2 mm. The broken base of the pubic ramus is present, but nothing is preserved of the ramus itself. The obturator foramen was clearly large, but this is not sufficiently preserved to permit measurement. There is a raised ridge of bone running anteriorly from the dorsal margin of the acetabulum on the lateral side of the ilium (corresponding to an iliopectineal tubercle?), and this is separated from the anterior margin of the acetabulum by a distinct shallow fossa measuring about 2.4 mm in length and 1.2 mm in width.

The acetabular region of another right pelvis, GSP-UM 18 (Fig. 12A), was found at Mihal Nala (RN-3) in 1977. This is less well preserved than GSP-UM 3015, and its shallow acetabulum makes reference to *Indocetus* questionable. The acetabulum is about 40 mm in diameter measured around the margin of the lunate surface, but this is only about 10 mm deep (measured as before).

Femur—The proximal end of the right femur is preserved with GSP-UM 3015 (Fig. 13A). This is large and heavily built, with a massive greater trochanter, a deep trochanteric fossa, and a strongly developed intertrochanteric crest. The femoral head and neck are broken away and missing, as is the lesser trochanter. To judge from the size of the acetabulum of GSP-UM 3015 described above, the femoral head must have been about 40 mm in diameter. The femoral shaft where it is broken 10 cm below the top of the greater trochanter, probably somewhat above midshaft, measures 34.7 × 27.7 mm in diameter. The full length of the femur cannot be measured, of course, but if it was as long as the tibia then it was probably something on the order of 25 cm in length.

Tibia—Both proximal and distal ends of the right tibia are preserved with GSP-UM 3015 (Fig. 13B). These were originally found in separate concentrations of bone some 10 m apart in the field and regarded as parts of two different individuals, but later a piece of midshaft

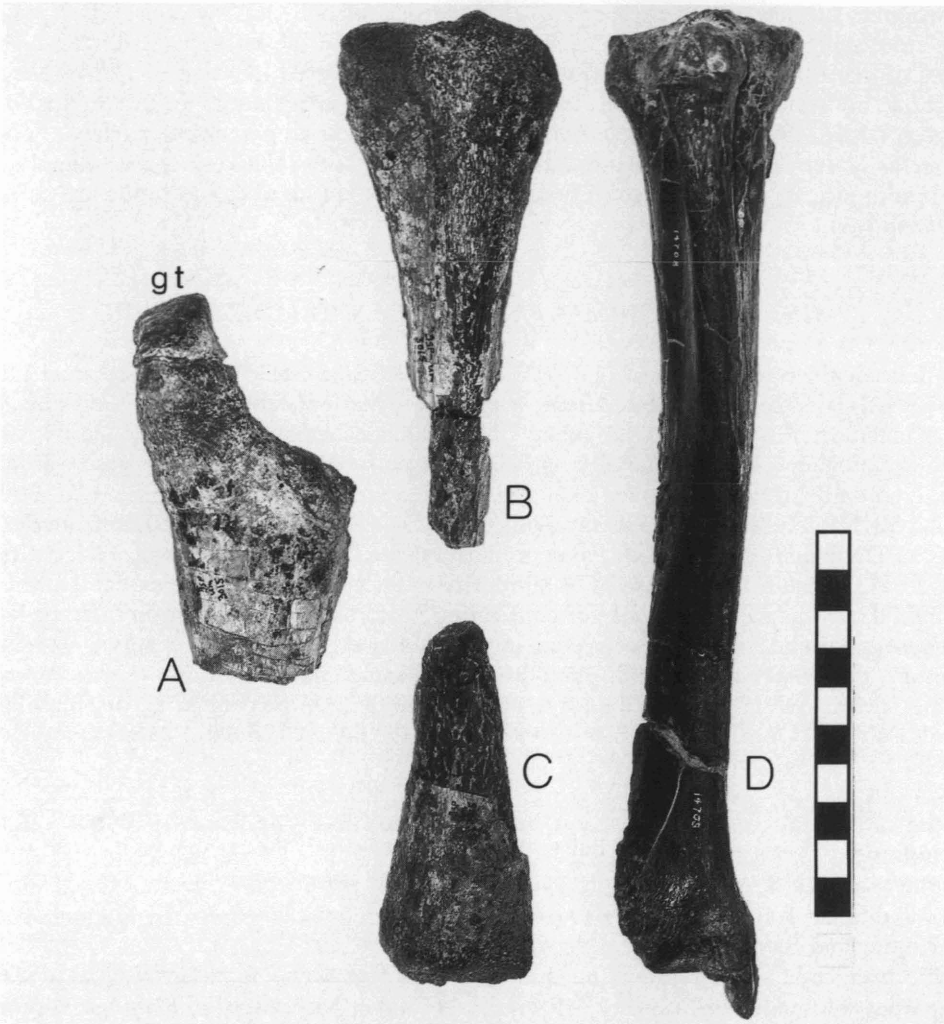

FIG. 13—Hind limb elements of *Indocetus ramani*, GSP-UM 3015, from Bozmar Nadi. A, proximal end of right femur with large greater trochanter (*gt*), in anterior view (head is missing). B and C, proximal and distal ends of right tibia, in anterior view. D, right tibia of *Pachyaena ossifraga*, YPM-PU 14708, in anterior view for comparison. Scale is in cm.

discovered with the distal end was found to fit onto the proximal end, demonstrating that both concentrations of bone belong to a single individual animal.

The tibia of *Indocetus ramani* compares closely in size and form to the tibia of *Pachyaena ossifraga* (Fig. 13C). The proximal end is slightly eroded, but medial and lateral condylar surfaces (plateaus) are well defined and these appear to have been about equal in height, like those of *Pachyaena*. The tibial tuberosity for insertion of the patellar ligament appears to have been less strongly developed than in *Pachyaena*, but the tibial or cnemial crest curves medially and downward as in *Pachyaena* making the upper shaft triangular in cross-section. The proximal end measures 57 mm in breadth across the condylar surfaces and approximately 44 mm anteroposteriorly across the tibial tuberosity. The distal end of the tibia is missing much of its surface bone, but it flares to a width of approximately 43 mm distally, and the distal articular surface is well preserved. This consists of two shallow concavities positioned side-by-side, separated by a low rise of bone, indicating that the proximal articular surface of the body of the astragalus (not found) was shallowly trochleated like that of *Pachyaena*. This articulation is very different than the tibio-astragalar articulation in later *Basilosaurus* (Gingerich et al., 1990) where these two bones join along a single simple surface. The tibia of *Indocetus* is very different in being larger and longer, both relatively and absolutely, and it is different in lacking any evidence of fusion with the fibula (the tibia and fibula are co-ossified in *Basilosaurus*).

SAHNI AND MISHRA'S *PROTOSIREN* AND MOERITHERIID

The most distinctive features of GSP-UM 3009 and GSP-UM 3015 are postcranial: a fused sacrum, a pelvis with a deep acetabulum, a massive proximal femur, and a long tibia with a distal articulation for a broad astragalus. Most archaeocetes have similar skulls, and the cranium of archaeocetes is generally not as informative of evolutionary grade as are the vertebral column and appendicular skeleton. Thus, once we referred GSP-UM 3009 and GSP-UM 3015 to the same taxon as the skull GSP-UM 1853, because all come from the upper part of the Domanda Shale and all have similarly shaped vomers, and once we identified the skull as *Indocetus ramani*, because of its similarity to the type skull (to the extent that these can be compared), it was natural to look for confirming postcranial evidence from the type locality. If *Indocetus* in Pakistan is distinctive in having a fused sacrum and a pelvis with a deep acetabulum, then *Indocetus* in India should have the same characteristics.

Sahni and Mishra (1975) described five mammalian taxa, three cetaceans, one sirenian, and one proboscidean, from the chocolate-colored Shell (or later Chocolate) Limestone at Harudi in Kutch:

(1) the protocetid cetacean *Indocetus ramani*, based on a partial skull (LUVP 11034, holotype)
(2) the protocetid (now remingtonocetid) cetacean *Protocetus sloani*, based on a mandibular fragment (LUVP 11002, holotype, now placed in *Remingtonocetus*; Kumar and Sahni, 1986)
(3) the protocetid (now remingtonocetid) cetacean *Protocetus harudiensis*, based on a partial skull with dentaries (LUVP 11037, holotype, now placed in *Remingtonocetus*; Kumar and Sahni, 1986)
(4) the protosirenid sirenian *Protosiren fraasi*, based on the acetabular region of a pelvis (LUVP 11038), with another bone possibly representing part of the ilium (LUVP 11039)
(5) a possible moeritheriid proboscidean, based on a sacrum with two and a one-half vertebral centra fused together (LUVP 11069).

As noted above, the partial dentary LUVP 11003 may be from this stratigraphic interval and locality as well.

The acetabular region of the Harudi pelvic fragment, LUVP 11038 (see Sahni and Mishra, 1975, fig. 4 and plate VI fig. 1), is similar in form, in pattern of breakage, and in size to GSP-UM 3015. Sahni and Mishra (1975, p. 28) gave two measurements of the diameter of the acetabulum: a diameter of 46 mm measured anteroposteriorly, and a diameter of 35 mm measured in some other direction. The average of these two measurements (for a structure that must accommodate a spherical femoral head, being the same diameter in all directions) is 40.5 mm, which compares very closely with the acetabulum diameter of 40 mm in GSP-UM 3015 reported above. Sahni and Mishra stated that the acetabular region of the pelvis is broad, with a width of 52 mm, which compares well with a depth (in life position) of 54 mm in

GSP-UM 3015. After comparison with GSP-UM 3015, there is little doubt that LUVP 10038 is the acetabular region of a pelvis of *Indocetus ramani*. The bone that suggested sirenian affinity is the isolated element, LUVP 10039, found within a meter of LUVP 10038 and interpreted as a narrow and slender ilium. This does not contact 10039 and it could be a fragment of any of the as yet poorly known long bones of *Indocetus*.

The Harudi sacrum, LUVP 11069 (see Sahni and Mishra, 1975, fig. 5 and plate VI fig. 2), is similar in form, in pattern of breakage, and in size to both GSP-UM 77 and GSP-UM 3009. LUVP 11069 is said to include three fused vertebrae (S1-S3), which Sahni and Mishra (1975, p. 30) measured as 122 mm in total length (lengths of individual centra are not given). The total length of S1-S3 in GSP-UM 77 and in GSP-UM 3009 is on the order of 168 mm (Table 4). S3 in the Harudi sacrum appears to be much shorter than S1 or S2 in the photograph in Sahni and Mishra's plate VI, fig. 2a, which shows the spacing of sacral foramina, and we suspect that the Harudi sacrum is broken through the middle of S3 (as GSP-UM 77 is broken through the middle of S3). Measurements of the width and height of the centrum of S1 in the Harudi sacrum, measured anteriorly, are slightly smaller than those of known Pakistan specimens, but the height-to-width ratio is similar. Measurements of the height and width of the neural canal are similar. All have similarly developed auricular processes for articulation with the pelvis, similarly developed pleurapophyses, similar-sized sacral foramina, similarly developed neural spines, and similarly developed zygapophyseal pits.

Sahni and Mishra (1975, p. 30) wrote in discussing the Harudi sacrum:

> With the possible exception of *Indocetus ramani* gen. et sp. nov., no other Kutch marine mammal known at present would have possessed such a well-developed sacrum.

New specimens from Pakistan show that whales very similar or identical to *Indocetus ramani* had both (1) a pelvis with a large, deep acetabulum like that from Harudi, and (2) a sacrum composed of multiple fused vertebrae like that from Harudi. Since the type specimen of *Indocetus ramani* is itself from Harudi, this association is documented there as well. Consequently, there is little doubt that our Pakistan specimens belong to *Indocetus ramani*, and it seems clear that this genus retained many characteristics of hind limb structure more typical of land mammals, as Sahni and Mishra hinted.

DISCUSSION

The age, living environment, and functional morphology of *Indocetus* are all important for interpretation of its evolutionary grade.

Age—Many authors have studied the age of lower and middle Khirthar strata in Pakistan, which includes the Domanda Shale yielding *Indocetus ramani*. Nuttall (1926) regarded this as Lutetian middle Eocene. Biostratigraphic and systematic examination of Eocene mollusks at Rakhi Nala and Zinda Pir (Eames, 1951, 1952a), studied in the context of their distribution elsewhere, convinced Eames (1952b,c) that correlation of the Khirthar Formation or Series of Pakistan with the middle Eocene elsewhere is justified. Since his "lower chocolate clays" or Domanda Shale are in the lower part of the Khirthar Formation or Series, this means that whales from the upper part of the Domanda Shale, like those described here, must be early or middle Lutetian in age.

Nagappa (1959) reviewed all of the foraminiferal evidence and corroborated Eames' placement of the "lower chocolate clays" in the early middle Eocene. Latif (1962) carried out a detailed investigation of pelagic forams at Rakhi Nala. While it is difficult to relate Latif's published stratigraphic section to that of Eames (or to strata in the field), it is clear that Latif placed the lower-to-middle Eocene boundary higher than Eames did (see Latif, 1962, p. 37). The discrepancy may not be meaningful because it concerns a 900 foot thickness of sediments that yielded no planktonic forams (the Domanda Shale?), but the effect, if any, for correlation to the global time scale would be to make the Domanda Shale older than Eames thought. Hemphill and Kidwai (1973) regarded the Domanda Shale as lower middle Eocene.

Our best estimate at present is that the Domanda Shale is early Lutetian in age (planktonic foraminiferal zone P10, ca. 48 Ma), an estimate that should become much more precise in the future as this problem is studied using cetacean and foraminiferal biostratigraphy with paleomagnetic reversal stratigraphy in the context of sea level change and sequence stratigraphy. If *Indocetus* lived 48 million years before present, then it was about 2 m.y. older than Egyptian *Protocetus*.

Depositional environment and taphonomy—Investigations of the Domanda Shale have almost all concentrated on its age. Nuttall (1926, p. 496) interpreted the lower and middle Khirthar series, from the Sulaiman Range in the north, yielding the *Indocetus* studied here, to Kutch in the south, yielding the *Indocetus* studied by Sahni and Mishra, to have been deposited in a uniformly "tranquil sea of moderate depth." This is the Sindhu Sea of Sahni and Kumar (1974).

The lower part of the Domanda Shale in the Sulaiman Range is predominantly green in color and composed of clay shales. The upper part of the Domanda Shale yielding the *Indocetus* remains described here includes more-oxidized red and brown clay shales and minor siltstones and sandstones. The unit as a whole has yielded a large marine molluscan fauna (Eames, 1951, 1952a), and remains of other marine organisms including echinoids, small corals, and crustaceans (Gingerich et al., 1979). The only faunal element described from the Domanda Shale and said to be nonmarine is an edentulous maxilla of a "mesonychid" mammal from Safed Tobah south of Rakhi Nala (Pilgrim, 1940). Gingerich et al. (1979) concluded that the maxilla could possibly represent an archaeocete rather than a land mammal, and we are now almost certain of this. There is no evidence that any of the Domanda Shale is nonmarine.

The two partial skeletons that form the basis of this report, GSP-UM 3009 and 3015, include bones encrusted on one surface with bivalve spat, which indicates that the skeletons were defleshed and disarticulated, and scattered on the sea bottom for a significant period of time before burial. This may explain why the skeletons are not more complete, and why isolated elements of each were found scattered over an area with a radius of 5-10 meters.

Functional morphology—The skull of *Indocetus* has the characteristic features of an archaeocete, including an elongated rostrum with an anteriorly-protruded palate and dentition; broad flat frontals; large, dense auditory bullae; and a foramen magnum opening more posteriorly than ventrally. The dentition is poorly known, but it is clear from alveoli that the anterior teeth were well spaced in the skull and that the premolars were the largest teeth. Upper molars retained a distinct protocone (Sahni and Mishra, 1975).

The postcranial skeleton of *Indocetus* is still poorly known, but it is clear that *Indocetus* retained a number of features that are primitive for a cetacean but commonly found in land mammals. The neck is as long as expected for a land mammal like *Pachyaena* (Fig. 11), and it is not short like that of Egyptian *Protocetus* (Fig. 14) or later archaeocetes (Kellogg, 1936). The relatively long neck of *Indocetus* compared to more advanced archaeocetes may represent nothing more than retention of an ancestral condition, but it may also have been advantageous for catching fish or whatever *Indocetus* fed on. Large hypapophyses on anterior cervical vertebrae of *Indocetus* indicate the presence of a strong anterior ventral longitudinal ligament in the cervical region, which may have been required to stabilize its long neck while swimming and diving.

As noted above, *Indocetus* has a much longer sacrum than *Pachyaena*, with longer sacral centra and a minimum of four sacral vertebrae instead of three, and it has a longer proximal caudal region, with longer vertebrae (both absolutely and relatively) than *Pachyaena*. We interpret these differences as evidence that *Indocetus* was specialized to some degree as a caudally-driven swimming mammal, which is consistent with recovery from shallow marine shelf paleoenvironments and with modifications of the skull, including enlarged and dense

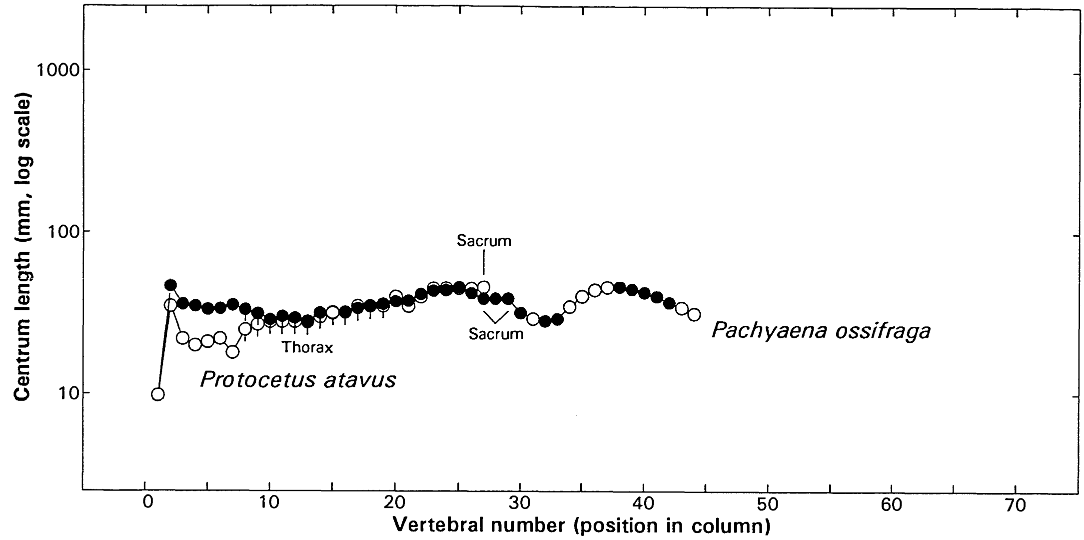

FIG. 14—Length-of-vertebrae profile of the Egyptian marine middle Eocene archaeocete *Protocetus atavus* (open circles) compared to length-of-vertebrae profile of the terrestrial North American early Eocene mesonychid *Pachyaena ossifraga* (closed-and-open circles; from Zhou et al., 1992). This shows *P. atavus* to have been very similar in size to *P. ossifraga*. Cervical vertebrae of *Protocetus* are both absolutely and relatively shorter than those of terrestrial *Pachyaena*, unlike those of *Indocetus ramani* (Fig. 11). *Indocetus* had a sacrum with at least four sacral centra and *Pachyaena* had a sacrum with three sacral centra, while *Protocetus* had a sacrum with a single sacral centrum. The number of cervical, thoracic, lumbar, and caudal vertebrae in *Protocetus* is not known with certainty, and no measurable caudals have been found; identifications of vertebrae and measurements plotted here are from Fraas (1904).

auditory bullae. *Protocetus* has a single sacral centrum, indicating that it had a more flexible lower back and suggesting that much more of the thorax and lumbus, in addition to the tail, was involved in swimming.

Finally, *Indocetus* is distinctive in having large auricular surfaces on the transverse processes of the sacrum, indicating broad articulation of the sacrum with the pelvis. The pelvis has a large and deep acetabulum, the proximal femur is robust, the tibia is long, and there is evidence of a broad tibioastragalar articulation, although the foot of *Indocetus* has not yet been found. All of these features, taken together, indicate that *Indocetus* was probably able to support its weight on land, and it was almost certainly amphibious, as early Eocene *Pakicetus* is interpreted to have been (based on different evidence; Gingerich et al., 1983). We speculate that *Indocetus*, like *Pakicetus*, entered the sea to feed on fish, but returned to land to rest and to birth and raise its young. The basicranium of *Indocetus*, with its large *Protocetus*-like auditory bullae, shows that *Indocetus* was more aquatic than *Pakicetus*, but retention of a sacrum consisting of at least four co-ossified vertebral centra that articulated with a pelvis and long hind limb shows that *Indocetus* was more terrestrial than *Protocetus*.

Classification—If there was any doubt before that *Indocetus* is distinct from *Protocetus*, this now appears settled: *Indocetus* is clearly different in retaining a much longer neck, and *Indocetus* is clearly different in the size and structure of its sacrum and, by inference, its hind limb and tail. These differences have important functional and life history implications, and *Indocetus*, in addition to being older geologically, appears to have been a more primitive cetacean as well. *Indocetus* was classified as a protocetid because of cranial resemblances to

Protocetus (Sahni and Mishra, 1975). We do not disagree, but for determining grade of evolution of archaeocetes, skulls are proving to be less informative than the postcranial skeleton.

In recognition of its differences, we propose that *Indocetus* be classified within Protocetidae in a new subfamily **Indocetinae.** Indocetine protocetids differ from remingtonocetids, dorudontids, and basilosaurids in having *Protocetus*-like skulls, while retaining long necks, multiple-vertebral sacra, and substantial hind limbs not seen in protocetines. Indocetines were more aquatic than *Pakicetus* and other pakicetines (Gingerich and Russell, 1990), but at the same time amphibious tail-swimmers less advanced than *Protocetus*. Protocetines evidently supported very little body weight on their hind limbs, and they were able to use more of their dorsal and ventral musculature to power swimming that involved increased flexion of the lower back and tail. *Indocetus* represents an important intermediate stage in the early evolution of Cetacea.

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