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Philip D. Gingerich, Director

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**PROTOSIREN AND BABIACETUS (MAMMALIA, SIRENIA AND CETACEA)
FROM THE MIDDLE EOCENE DRAZINDA FORMATION,
SULAIMAN RANGE, PUNJAB (PAKISTAN)**

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Abstract—*Protosiren sattaensis* is a new late Lutetian protosirenid based on a partial skeleton found in the Drazinda Formation of the Sulaiman Range, Punjab Province, Pakistan. The new species is similar to *Protosiren fraasi* and *P. smithae* from the middle Eocene of Egypt in having thoracic vertebrae with large, keyhole-shaped neural canals that lack ossified epiphyses and synovial rib articulations. Ribs are densely ossified, but lack the pachyostotic expansion and osteosclerotic isotropy seen in contemporary dugongids. *P. sattaensis* differs from other species of *Protosiren* in having a large pelvis with a large obturator foramen. *P. sattaensis* is important in confirming that the geographic range of *Protosiren* extended into eastern Tethys, and it is important as a temporal and morphological intermediate linking the two previously known species.

Babiacetus indicus recently described from Kutch in India is now known from a skull and lower jaws from the Drazinda Formation in Pakistan. It is distinctive as the largest protocetid archaeocete known to date from Indo-Pakistan, and it is also distinctive among protocetids in having a fused mandibular symphysis joining left and right dentaries and in having double-rooted upper and lower first premolars. Similar microfaunas suggest correlation of the Harudi Formation of India and the Drazinda Formation of Pakistan, and the presence of Sirenia and *Babiacetus indicus* in both supports this correlation.

INTRODUCTION

Sirenians have been reported from the Eocene of eastern Tethys in India or Pakistan for many years (Grant, 1840; Sahni and Mishra, 1975; Sahni and Kumar, 1980; Sahni et al., 1980;

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Bajpai et al., 1989; Thewissen, 1993). Grant's original specimens turned out to be Miocene (Sahni and Mishra, 1975), and other specimens described to date are fragmentary and difficult to identify. The new species described here is important as the first sirenian from eastern Tethys that can be identified to genus on the basis of much of the postcranial skeleton. The skull and lower jaws of *Babiacetus indicus* reported here are important in augmenting our knowledge of its cranial and dental anatomy, and they extend the range of this distinctive species 600 km to the north from Kutch in India where it was previously reported. *Protosiren* and *Babiacetus* are the first fossil mammals to have been found in the Drazinda Formation of Pakistan, which holds great promise for improving our understanding of the diversity and evolution of late Lutetian Sirenia and Cetacea.

Hemphill and Kidwai (1973, p. 16) named the Drazinda Shale Member of the Khirthar Formation to replace the descriptive term "Upper Chocolate Clays" of Eames (1952a,b). Shah (1991, p. 68) recognized the Drazinda Shale as a distinct formation. Previous authors have interpreted Drazinda shales as being middle to late Eocene in age, as discussed in the next section of this report. The only previous investigation of vertebrate remains from the Drazinda Formation was a 1978 survey by West et al. (1991), which yielded an extensive suite of cartilaginous and bony fishes based on teeth (Case and West, 1991) and otoliths (Nolf, 1991).

The type specimen of *Protosiren sattaensis* was collected after being reported to the Geological Survey of Pakistan by a German-Pakistan research team. It was said to be in the Sanghar Lahar (Sanghar Nala) drainage west of Taunsa Sharif in southwestern Punjab. When relocated in the field, the site was found to lie across a drainage divide to the north of Sanghar Lahar, in the drainage of Bari Nadi about 2 km south of Satta Post (a Punjab tribal Border Military Police post). The skull of *Babiacetus indicus* was found by prospecting while the *Protosiren* skeleton was being collected. The geographic locations of the *P. sattaensis* type locality and the *B. indicus* skull locality are shown on the map of Figure 1, which shows the sites of discovery of other important fossil vertebrate remains from the Domanda and Drazinda formations on the eastern and northern flanks of Rodho Anticline.

STRATIGRAPHY

The type locality of *Protosiren sattaensis* is shown in the photograph of Figure 2, which was taken during excavation of the skeleton. The view is toward the north and east. The stratigraphic position of the type specimen in the local stratigraphic section is shown in the sketch of Figure 3, drawn looking northward along the strike of the strata, which here dip steeply toward the east. The Drazinda section conformably overlies steeply-dipping middle Eocene Pir Koh Limestone, but its upper contact with the overlying lower Miocene Chitarwata Formation (Hemphill and Kidwai, 1973; Downing et al., 1993) is a disconformity and much or all of late Eocene and Oligocene time is lost in this hiatus.

Within the Drazinda Formation, the lower part of the section is a softly-weathering green clay shale, the "passage beds" of Eames (1952a, pp. 163-164), lightened on the surface by precipitation of alkali. The middle part of the Drazinda section, the "Upper Chocolate Clays (lower part)" of Eames, is green shales dominated by four to six ridge-forming beds packed with foraminifera, with the most conspicuous being large saddle-shaped forams ca. 5 cm in diameter identified as *Discocyclus sowerbyi* by Nuttall (1926, p. 149) and Eames (1952b, p. 181). These are found in Eames' local zones 11-12 in Rakhi Nala (mainly in 12) and at Zinda Pir (Eames, 1952b, pp. 177, 181). Eames (1952a, p. 164) described the beds from which these came as "brown, impure limestone bands." The skull of *Babiacetus* described here came from brown shales between these limestone bands, and both specimens of *Protosiren* came from a thin interval of green shale overlying the *Discocyclus* limestones (in the "unexposed gap" of Eames). The upper part of the Drazinda section, the "Upper Chocolate Clays (upper part)" of Eames, is brown and reddish-brown shale through most of the section.

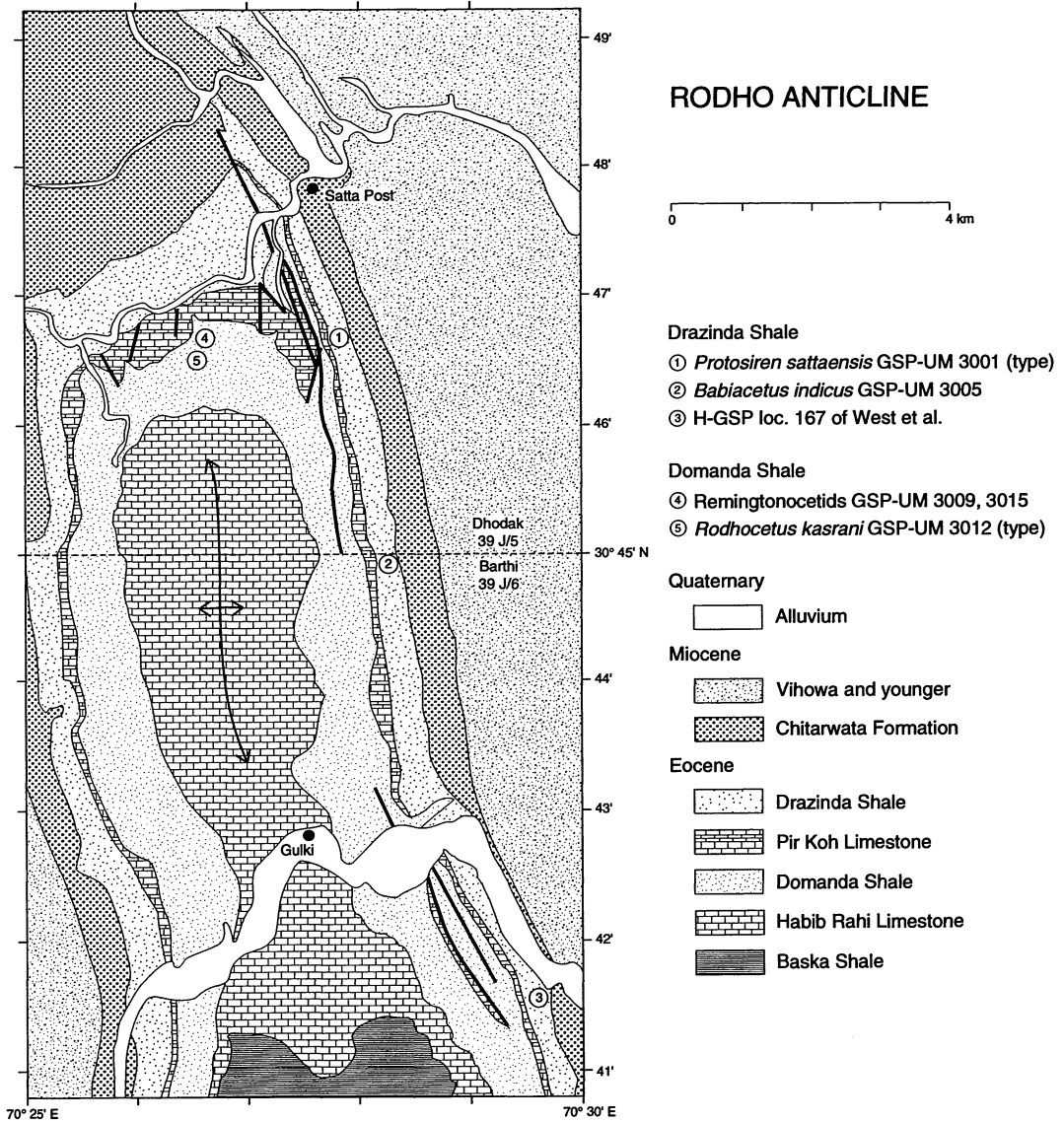


FIG. 1—Geological map of Rodho anticline in the Zinda Pir anticlinorium bordering the Sulaiman Range west of Taunsa Sharif in southwestern Punjab, Pakistan. Locality numbered 1 here is site where the type specimen of *Protosiren sattaensis* was found. Locality 2 is where the skull and lower jaws of *Babiacetus indicus* were found. Locality 3 on map is locality H-GSP 167 from 1978 survey of West et al. (1991). Locality 4 is source of two partial skeletons of *Remingtonocetus* cf. *R. harudiensis* described by Gingerich et al. (1993, 1995). Locality 5 on map is type locality of *Rodhocetus kasrani* described by Gingerich et al. (1994). Localities 4 and 5 are in Bozmar Nadi. Settlement of Gulki shown here is on the northern edge of Sanghar Lahar (Sanghar Nala).

The uppermost part of the Eocene section includes the "Tapti series" or "*Pellatispira* beds" of Eames. We did not study the Drazinda section south of Satta in any detail beyond that necessary to gain a general understanding of lithological change and locate fossil localities



FIG. 2—Photograph of *Protosiren sattaensis* type locality 1.9 km south of Satta Post. View is looking along strike to the NNW from the top of a ridge of *Discocyclus* limestone south of the fossil locality. Left arrow shows locality, and right arrow points to a person for scale. See Figure 3 for stratigraphic interpretation.

accurately relative to conspicuous marker beds, and these beds have not yet been prospected thoroughly for fossil vertebrates.

The Pir Koh and Drazinda formations, taken together, appear to represent a single shallowing-upward regressive marine sequence. Deeper-water white limestone and marl at the base have little clastic content and must have been deposited at some distance from shore. Green clay shales contain fine-grained clastics, but exhibit little oxidation, suggesting that they too were deposited offshore at some depth. Upper beds are clayey but also more silty and (rarely) sandy. These are often oxidized to some extent, and are brown or red-brown in color. The origin of the ridge-forming *Discocyclus* beds was not studied in detail, but these may represent reef-like shoals resulting from higher organic productivity in a relatively shallow sea. The Pir Koh and Drazinda formations can be traced for hundreds of kilometers along the eastern flank of the Zinda Pir anticlinorium, and their lithologies are notably uniform along strike except that the number of *Discocyclus* limestone beds seems to decrease toward the north and increase toward the south and east. The apparent absence of any coarser-clastic deltaic deposits suggests that the environmental setting was a long, uninterrupted, shallow shelf in Tethys on the passively-subsiding northwestern margin of the Indo-Pakistan subcontinent, offshore from a continental mass of low topographic relief.

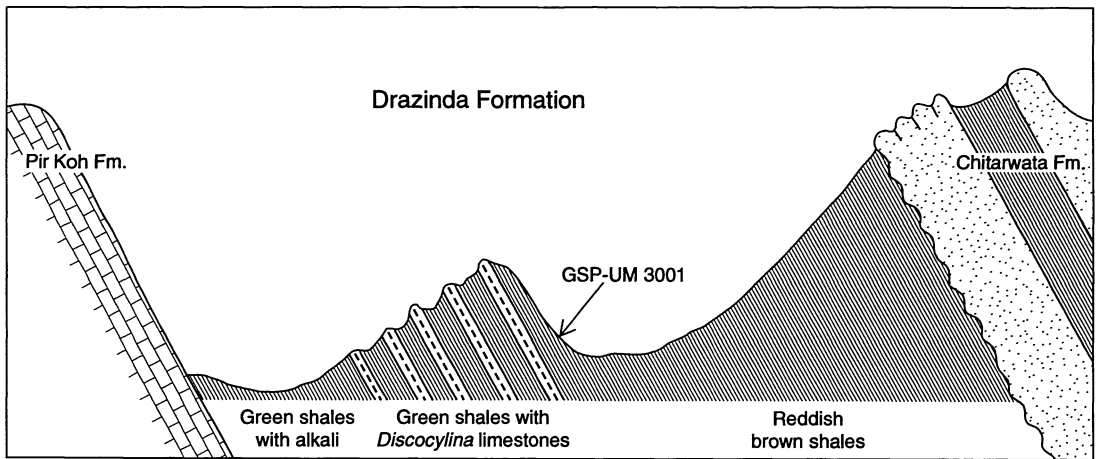


FIG. 3—Field sketch of Drazinda Formation stratigraphic section at the *Protosiren sattaensis* type locality, drawn looking NNW from the top-most ridge of *Discocyclina* limestone on the next hill to the south. Drawing is not to scale (compare with photograph in Figure 2). Steep wall of limestone at left is Pir Koh Formation. Valley of shales with ridge of *Discocyclina* limestones in the middle is Drazinda Formation. Ridge at right is Miocene Chitarwata Formation continental molasse separated from the Drazinda Formation by a disconformity representing a hiatus spanning much of late Eocene and Oligocene time. *Protosiren sattaensis* type locality is just above the ridges of *Discocyclina* limestone in the middle part of the formation. Note the regressive sequence from deeper-water Pir Koh limestone interpreted as representing the high sea stand in sea level cycle TA3.3 of Haq et al. (1987), shallowing upward through green shales, and then overlain by brown and red-brown Drazinda shelf-margin clastics possibly as young as cycle TA3.5. In this interpretation, the *Discocyclina* limestones are considered to have been deposited during the high sea stand in sea level cycle TA3.4 (see Figure 4).

AGE OF THE DRAZINDA FORMATION

In the preceding study (Gingerich et al., 1995), we combined sea level sequence stratigraphy (Haq et al., 1987) with micropaleontological evidence (Latif, 1961; Haq, 1972; Köthe et al., 1988) to infer that the Habib Rahi Formation of the Sulaiman Range was deposited in early Lutetian planktonic foraminiferal zone P10 and nannoplankton zones NP14-15; that the Domanda Formation was deposited during early Lutetian planktonic foraminiferal zone P10 and nannoplankton zone NP15; and that the Pir Koh Formation was deposited during middle Lutetian planktonic foraminiferal zone P11 and nannoplankton zone NP15.

Haq et al. (1987) correlated the TA3.3-TA3.4 regressive sequence with P12 (late Lutetian) and NP15-16 (middle to late Lutetian). This is consistent with Haq's (1972) identification of nanofossils from upper Drazinda shales as NP16 (late Lutetian), with Samanta's (1972, 1973) identification of planktonic foraminifera from the lower Drazinda as P12-13 (late Lutetian-early Bartonian), and with Köthe et al.'s (1988) identification of nanofossils from the lower Drazinda as NP16 (late Lutetian-early Bartonian). Samanta's (1972, 1973) study placed the middle Drazinda, evidently including the *Discocyclina* limestones, in P14 (Bartonian), and Köthe et al.'s (1988) study placed their "*Discocyclina* marl" in NP16-17 (Bartonian). Given

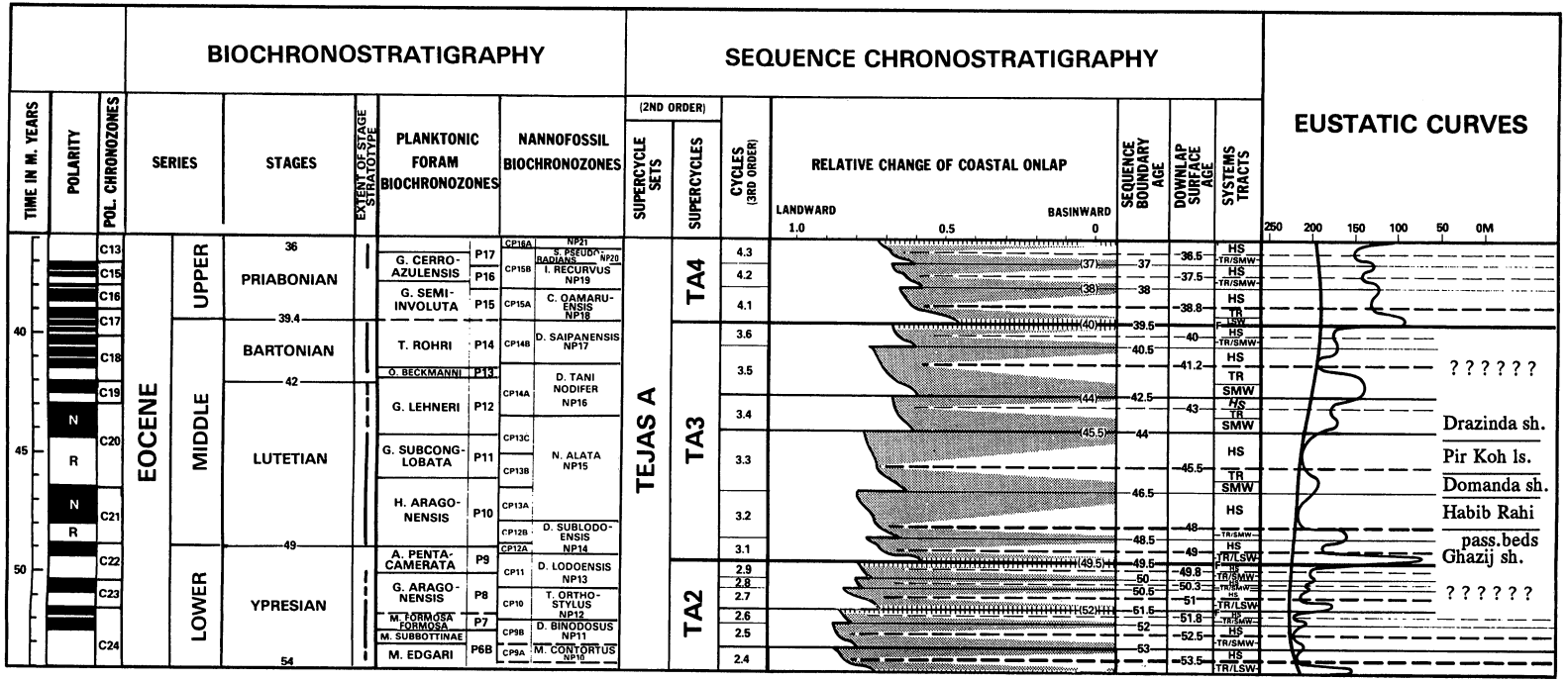


FIG. 4—Correlation chart showing inferred ages of Ghazij, Habib Rahi, Domanda, Pir Koh, and Drazinda formations, listed at far right, in relation to sea level sequence stratigraphy of Haq et al. (1987). Thicknesses of formations composed of different lithologies are not always proportional to temporal duration of deposition. Habib Rahi and Pir Koh limestones are relatively thin in the field but represent a considerable duration of time because they were deposited offshore with relatively little clastic influx, while Ghazij, Domanda, and Drazinda shales are relatively thick in the field but represent much less time than their thickness would suggest because they were deposited closer to shore and are predominantly clastic in composition.

the evident continuity of sedimentation within the Drazinda Formation, we would expect the "Tapti" or "*Pellatispira*" high-stand, comprising the very top of the Drazinda Formation, to be correlative with P12 and NP16 (late Lutetian). This is consistent with Haq's (1972) identification of nannofossils from upper Drazinda shales as NP16, but not with Samanta's (1972, 1973) identification of planktonic foraminifera from the upper Drazinda as belonging to P15-17 (Priabonian) nor with Köthe et al.'s identification of nannofossils from this interval as NP18-20 (Priabonian). Paleontological control on the upper part of the Eocene sequence is limited in the Sulaiman Range by the late Eocene and Oligocene depositional and/or erosional hiatus, and this contributes to uncertainty of the age range of the higher strata.

We interpret the age of the *Discocyclus* limestones and shales in the middle part of the Drazinda Formation, yielding the fossils described here, to be late Lutetian in age, or about 43-44 Ma on the Haq et al. (1987) time scale. This is based on the pattern of inferred sea level change locally, on correlation with late Lutetian strata of Kutch (Biswas, 1965; Mohan and Soodan, 1970; Singh and Singh, 1991) using Drazinda *Discocyclus sowerbyi* and *Babiacetus indicus* (both first described from Kutch), and on part of the nannofossil evidence of Haq (1972) and Köthe (1988; with other foraminiferal and nannofossil evidence suggesting that the upper part of the Drazinda Formation may possibly be Bartonian in age). A tentative correlation of Sulaiman Range formations with biochronostratigraphy and sea level sequence stratigraphy is shown graphically in Figure 4.

ABBREVIATIONS

- CGM — Cairo Geological Museum, Cairo (Egypt)
 GSP-UM — Geological Survey of Pakistan—University of Michigan collection, Islamabad (Pakistan)
 H-GSP — Howard University—Geological Survey of Pakistan project, Islamabad (Pakistan)
 SMNS — Staatliches Museum für Naturkunde, Stuttgart (Germany)
 UCMP — University of California Museum of Paleontology, Berkeley (U.S.A.)
 UM — Museum of Paleontology, University of Michigan, Ann Arbor (U.S.A.)
 UMMZ — Museum of Zoology, University of Michigan, Ann Arbor (U.S.A.)

SYSTEMATIC PALEONTOLOGY

- Class MAMMALIA Linnaeus, 1758
 Order SIRENIA Illiger, 1811
 Family PROTOSIRENIDAE Sickenberg, 1934
Protosiren Abel, 1907

Protosiren sattaensis, new species
 Figs. 6-9, 10B, 11C

Holotype.—GSP-UM 3001, a good series of posterior cervical, thoracic, lumbar, sacral, and caudal vertebrae, most with the centrum complete but lacking the neural arch and accessory processes. The type also includes several complete or nearly complete ribs, many rib fragments, and both innominate pelvic bones.

Type locality.—1.9 km up a tributary of Bari Nadi (stream) to the south of Satta Post of the Border Military Police, at 30°46'45" north latitude, 70°27'50" east longitude (Fig. 2; Survey

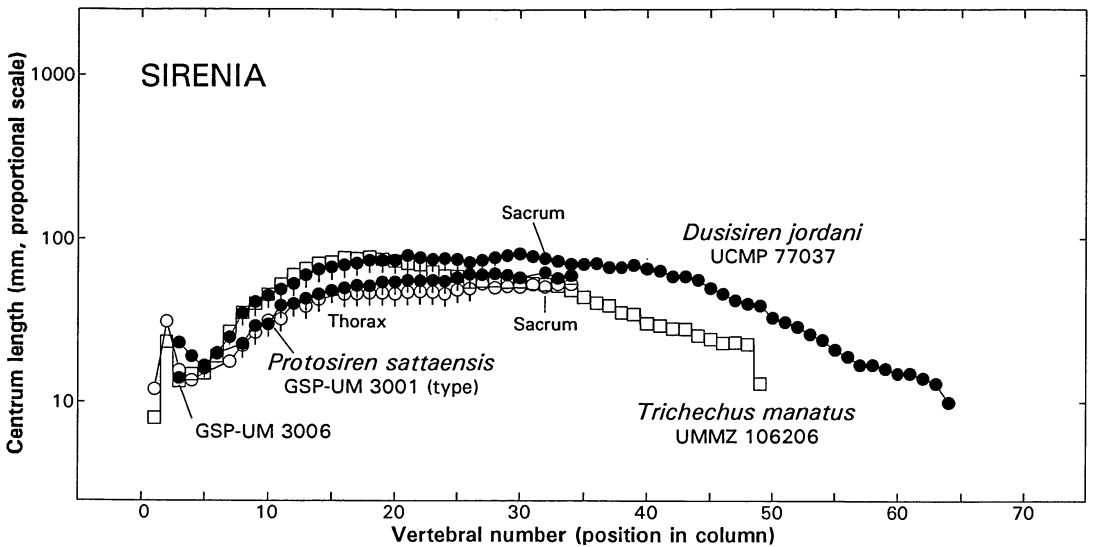


FIG. 5—Length-of-vertebrae profile of protosirenid *Protosiren sattaensis* (GSP-UM 3001, type (Table 1), and GSP-UM 3006) shown with solid circles, compared to those of dugongid *Dusisiren jordani* (UCMP 77037; upper profile of solid circles) and trichechid *Trichechus manatus* (UMMZ 106206; open squares). Profile of *Protosiren smithae* (UM 101224), shown with open circles, overlaps and is partly hidden by GSP-UM 3001 because the latter is similar in proportion but slightly larger. Thoracic vertebrae are shown with symbolic vertical ribs. Note that profiles of both species of *Protosiren* shown here parallel the profile of *Dusisiren* in having thoracic centra that become longer posteriorly, with the longest centra located in the posterior thorax and lumbus. Profile of *Trichechus*, in contrast, is longest in the mid-thorax, and has fewer and shorter lumbar and caudal vertebrae compared to *Dusisiren*. Measurements of *Protosiren sattaensis* are from Table 1 and those of *Dusisiren jordani* are from Domning (1978).

of Pakistan topographic quadrangle 39 J/5; Dhodak quadrangle of the Geological Survey of Pakistan, 1986).

Referred specimen.—GSP-UM 3006, two substantial pieces of the centrum of cervical vertebra C3, with bases of transverse processes on both sides, found in association with vertebral and rib fragments. The referred specimen was found east of Gulki village and 4 km north of Sangarh Lahar (Sangarh Nala). It was found 50 m east of the *Babiacetus* skull found at 30°44'50" north latitude, 70°28'15" east longitude (Survey of Pakistan topographic quadrangle 39 J/6; Barthi quadrangle of the Geological Survey of Pakistan, 1986; locality 2 in Fig. 1 here). This is approximately 2.9 km along strike to the south of the type locality of *Protosiren sattaensis*, at about the same level in the Drazinda Formation.

Age and distribution.—*Protosiren sattaensis* is presently known only from the Drazinda Formation, late Lutetian, in the vicinity of the type locality in southwestern Punjab Province, Pakistan. Pelvis from Kutch attributed to *Protosiren fraasi* by Sahni and Mishra (1975) is archaeocete (Gingerich et al., 1993). Sirenian remains are known from the late Lutetian of Kutch (Bajpai et al., 1989), and some or all of these may prove to be *P. sattaensis*.

Diagnosis.—*Protosiren* differing from *P. fraasi* in being about 1/3 larger in comparable lengths of vertebral centra (Sickenberg, 1934, p. 95, gives the length of the thorax as 679 mm in *P. fraasi*, whereas the sum of vertebral centra lengths in Table 1 here is 902 mm (making no allowance for intervertebral connective tissue); linear measures of other comparable features differ by 8 to 45%). Differs from *P. smithae* in being slightly smaller (Fig. 5), and in having a pelvis with a larger *P. fraasi*-like obturator foramen of the pelvis. These are minor differ-

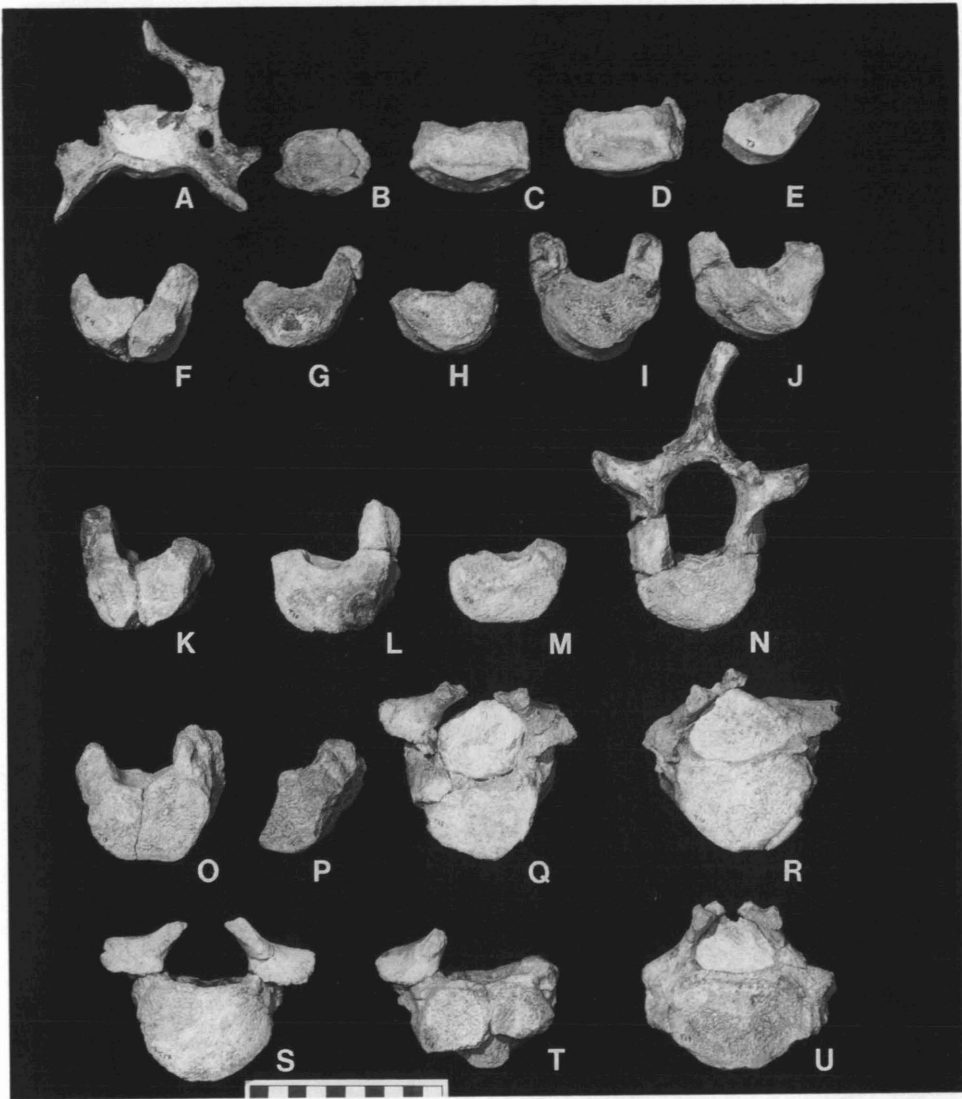


FIG. 6—Cervical and thoracic vertebrae of *Protosiren sattaensis*, GSP-UM 3001 (holotype). A, cervical C6. B, C5. C, thoracic T1. D, T2. E, T3. F, T4. G, T5. H, T6. I, T7. J, T8. K, T9. L, T10. M, T11. N, T12. O, T13. P, T14. Q, T15. R, T16. S, T17. T, T18. U, T19. All vertebrae shown in anterior view except C5, which is shown in posterior view. Vertebrae were identified to position by comparison with those of *Protosiren smithae*, principally the CGM 42292 cervical series and the UM 101224 axial skeleton. Note large keyhole-shaped cross-section of neural canal of T12, which is typical of mid-thoracic vertebrae of *Protosiren* and very different from neural canal cross-section of other contemporary sirenians. Scale is in cm (vertebrae shown approximately 0.25× natural size).

ences, but they are differences in features of little inherent variability: known specimens of *P. fraasi* from the Mokattam Limestone and *P. smithae* from Wadi Hitan in Egypt show that vertebral size, overall body size, and relative size of the obturator foramen of the pelvis are not highly variable in larger samples.

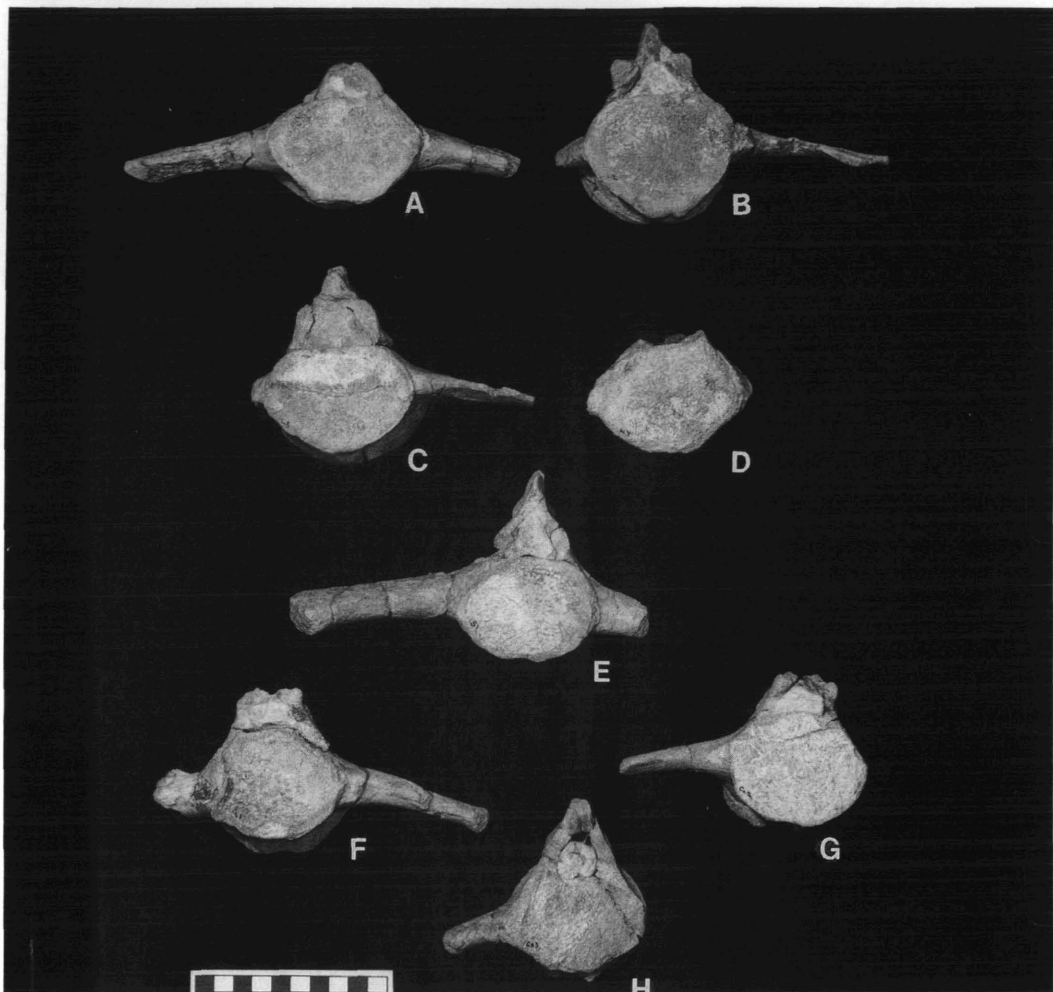


FIG. 7.—Lumbar, sacral, and caudal vertebrae of *Protosiren sattaensis*, GSP-UM 3001 (holotype). A, lumbar L1. B, L2. C, L3. D, L4. E, sacrum S1. F, caudal Ca1?. G, Ca2?. H, Ca3?. All vertebrae shown in anterior view. Vertebrae were identified to position by comparison with those of *Protosiren smüthae*, principally the UM 101224 axial skeleton. Scale is in cm (vertebrae shown approximately $0.25\times$ natural size).

Etymology.—Named for Satta Post, the only named geographic feature near the type locality.

Description

The type specimen of *Protosiren sattaensis*, GSP-UM 3001, is a partial skeleton including two cervical vertebrae, much of the thorax and lumbus, sacrum and innominate bones comprising the pelvis, and parts of three caudal vertebrae. With exception of one cervical vertebra described here, C3, which belongs to referred specimen GSP-UM 3006, all of the following description pertains to GSP-UM 3001. Vertebrae, ribs, and pelvic bones described here are distinctive among early sirenians and diagnostic of *Protosiren*.

Cervical vertebrae retain some indication of thin epiphyses fused to the vertebral bodies, but remaining vertebrae have rough intervertebral articular surfaces, suggesting that epiphyses failed to ossify. Sickenberg (1934, p. 193) lists this reduction of vertebral epiphyses as a distinctive characteristic of *Protosiren* distinguishing it from contemporary sirenians (see also Gingerich, Domning, et al., 1994, table 1). Loss of epiphyses is seen in extant sirenians, and must be related in some way to change in the pattern of movement or alteration of stress in the vertebral column associated with sirenian activity patterns (loss of epiphyses is not seen in extant cetaceans). Vertebral zygapophyses in *Protosiren* have smooth articular surfaces, and these intervertebral articulations were evidently normal synovial joints.

Measurements of vertebrae of the *Protosiren sattaensis* are listed in Table 1 and vertebral lengths are plotted in Figure 5.

Cervical vertebrae.—Three cervical vertebrae are known in *Protosiren sattaensis*, out of a total of seven expected in more complete specimens of *Protosiren* (Domning and Gingerich, 1994, fig. 5). The first of the known cervicals of *P. sattaensis*, among fragmentary bones of the referred specimen GSP-UM 3006, includes left and right sides of a single centrum, each with the bases of the transverse processes. This centrum is clearly sirenian because of its shortness (measurements in Table 1) and because of its flat anterior and posterior articular surfaces (cervical centra of archaeocetes have distinct sulci crossing anterior and posterior articular surfaces transversely). The centrum, fragmentary as it is, is identifiable as C3 by comparison with C3 in the type specimen of *Protosiren smithae*, CGM 42292 (Domning and Gingerich, 1994, fig. 5C; cast UM 94810): both have a Λ -shaped ventral keel pointing anteriorly, with a depression between legs of the Λ . This is also found on C4 in CGM 42292, but it is not as prominent.

In GSP-UM 3001, the fifth cervical, C5, has a simple centrum (Fig. 6B) with flat anterior and posterior articular surfaces. It is identified as C5 by its size, and by comparison with C5 in CGM 42292 and C6 in GSP-UM 3001. The centrum of C6 is well preserved (Fig. 6A), with flat anterior and posterior articular surfaces and much of the neural arch and transverse process present on the left side. The transverse process is perforated by a 7 mm wide and 9 mm high foramen for the vertebral artery, and it then divides into a strong but simple lateral process and a large anteroposteriorly-elongated, ventrolaterally-directed process extending some 4.5 cm from the vertebral body. This is very similar to the transverse process of C6 in CGM 42292 (Domning and Gingerich, 1994, fig. 5F). Elongated ventrolaterally-directed transverse processes are a characteristic landmark of C6 found in many mammals.

Thoracic vertebrae.—Thoracic vertebrae were identified to position on the basis of centrum measurements (Table 1) and by comparison with a good series of thoracic vertebrae in *Protosiren smithae* (UM 101224). The highest-numbered thoracic Sickenberg (1934, p. 46) identified in *Protosiren fraasi* was a 17th thoracic, but *P. sattaensis* and *P. smithae* both appear to have had nineteen thoracic vertebrae (and *P. fraasi* may have had 19 as well).

The first thoracic vertebra, T1 (Fig. 6C), has a simple centrum that is relatively short anteroposteriorly and broad transversely, being almost rectangular in anterior or posterior view, with rib facets clearly depressed into the ventrolateral corners of its posterior surface. The centrum of T2 (Fig. 6D) is similar to that of T1, but longer. T3 (Fig. 6E) is badly broken, but clearly differs from T1 and T2 and resembles more-posterior thoracic centra in being more curved ventrally. T4 through T11 (Figs. 6F-M) are represented by centra only: these are dorsoventrally compressed, with concave dorsal surfaces and convexly curved ventral surfaces typical of anterior thoracics in *Protosiren* (Sickenberg, 1934). All have the unusual angular, rough-surfaced, anterior and posterior demifacets where pedicles of the neural arch join the centrum. These indicate that articulations with rib heads were not ossified and synovial but cartilaginous and ligamentous, which is a distinctive characteristic of *Protosiren* (Sickenberg, 1934, p. 193).

Thoracic vertebra T12 (Fig. 6N) is the best preserved of all of the known vertebrae of *Protosiren sattaensis*. Sickenberg (1934, p. 81, fig. 16) illustrated T12 of *P. fraasi*, and T12



FIG. 8—Ribs of *Protosiren sattaensis*, GSP-UM 3001 (holotype). A, mid-thoracic rib. B, mid-thoracic rib. C, anteriormost rib (R1). R1 is complete, but two mid-thoracic ribs lack distal ends. Note lack of pachyostosis, which distinguishes ribs of *Protosiren* from those of contemporary middle Eocene sirenians. Ribs were identified to position by comparison with nearly complete rib cage of *Protosiren smithae*, UM 101224. Scale is in cm (ribs shown approximately 0.5 \times natural size).

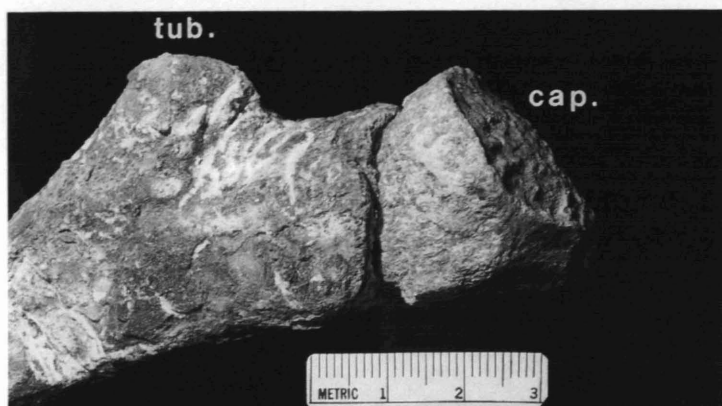


FIG. 9—Detail of distinctive rugose surface of rib capitulum (*cap.*) and reduced rib tuberculum (*tub.*) in GSP-UM 3001 (*Protosiren sattaensis* holotype). Note rugose surface of capitulum indicating the presence of an unossified cartilaginous head. Note also the small nonarticulating tuberculum for ligamentous attachment to vertebrae. Both features are characteristic of rib articulations in *Protosiren* (Sickenberg, 1934). Scale is in cm (rib head shown is approximately natural size).

in *P. sattaensis* is very similar to this. The centrum is dorsoventrally compressed, with a concave dorsal surface, convex ventral surface, and flat anterior and posterior articular surfaces. The neural canal is unusually high, narrow compared to its height, and shaped like a keyhole, with the upper part of the canal being wider than the lower part (see measurements in Table 1). Pedicles of the neural arch are sharply keeled anteriorly, broader and more rounded posteriorly, smooth on their medial surfaces, and excavated on their lateral surfaces (for attachment of costal musculature). Transverse processes are confluent with laminae of the neural arch and bear lateral foveae indicating some connection with rib tubercula, but this was evidently ligamentous rather than a normal synovial joint. The maximum breadth of T12 measured across the transverse processes is 111 mm. Prezygapophyses are relatively small and simple, face dorsally, and extend anteriorly about 5 mm beyond the cranial surface of the centrum. There is a conspicuous groove in the anterior edge of left and right laminae that crosses the anterior surface of the neural spine and connects left and right prezygapophyses. Postzygapophyses are gracile, face downward and outward, and extend posteriorly less than a centimeter beyond the caudal surface of the centrum. The neural spine appears to be complete, and it is relatively small and gracile, measuring 35 mm in length (anteroposteriorly) at the base, 11.5 mm in width at the middle, and rising 65 mm above the top of the neural canal. Neural arches of thoracic vertebrae in *Protosiren* show none of the pachyostosis seen in other contemporary sirenians. Angular, rough-surfaced, anterior and posterior demifacets for rib attachment are well preserved on this vertebra.

Thoracics T13 and T14 (Figs. 6O,P) are represented by fragmentary centra that are not very informative, but T15 through T19 are more complete (Figs. 6Q-U). These posterior thoracics differ from anterior thoracics in having greater centrum height (measured dorsoventrally) that increases progressively posteriorly from centrum to centrum, and in having more circular neural canals, with transverse processes moving downward from the neural laminae to the vertebral body in a similar posterior progression from centrum to centrum. Foveae for attachment of rib capitula and rib tubercula are distinct on T15, ambiguously confluent on T16, and confluent, forming a single obliquely-elongated depression on each side, on T17 and T18. The last thoracic, T19, has very short (ca. 1 cm long) and thick transverse processes that appear as little more than lateral swellings of the vertebral body. Each swelling has a large,

TABLE 1—Measurements of vertebrae of *Protosiren sattaensis*, based on GSP-UM 3001 (holotype) and GSP-UM 3006 (C3 only). Length-of vertebrae profile is shown in Figure 5. Centrum widths in parentheses are measured over rib facets. Abbreviations: *H*, height; *L*, length; *W*, width. *DW* and *VW* are dorsal and ventral widths of keyhole-shaped neural canal. Asterisk indicates estimate. Measurements are in mm.

| Vertebra | Centrum | | | Neural canal | | |
|----------|---------|-------------|------|--------------|------|------|
| | L | W | H | DW | VW | H |
| C3 | 14.0 | -- | -- | -- | -- | -- |
| C5 | 16.8 | 47.0 | 34.4 | -- | -- | -- |
| C6 | 19.8 | 51.8 | 34.3 | -- | 51.6 | 25.8 |
| T1 | 22.8 | 50.1 (60.3) | 34.6 | -- | -- | -- |
| T2 | 29.3 | 45.0 (62.0) | 32.0 | -- | -- | -- |
| T3 | 30.0 | -- | 31.9 | -- | -- | -- |
| T4 | 39.0 | 52.0 | 30.6 | -- | 41.1 | -- |
| T5 | 40.0 | 51.4 | 30.9 | -- | -- | -- |
| T6 | 43.2 | 52.1 | 30.2 | -- | -- | -- |
| T7 | 45.9 | 61.1 | 33.9 | -- | 36.8 | -- |
| T8 | 48.3 | 67.9 | 33.0 | -- | 33.8 | -- |
| T9 | 50.1 | 66.8 | 33.2 | -- | 30.2 | -- |
| T10 | 51.9 | 61.5 | 35.7 | -- | 30.2 | -- |
| T11 | 51.6 | 60.6 | 34.9 | -- | -- | -- |
| T12 | 54.4 | 61.3 | 37.6 | 36.6 | 33.2 | 52.9 |
| T13 | 54.5 | 63.3 | 41.2 | -- | 34.7 | -- |
| T14 | 55.8 | -- | -- | -- | -- | -- |
| T15 | 55.6 | 64.9 | 44.1 | 40.7 | 44.7 | 44.5 |
| T16 | 55.9 | 69.8 | 47.6 | -- | 48.6 | 37.4 |
| T17 | 55.2 | 68.0 | 49.4 | -- | 41.9 | -- |
| T18 | 57.8 | 65.2 | 46.2 | -- | 43.0 | -- |
| T19 | 60.7 | 76.2 | 49.7 | -- | 37.3 | 35.7 |
| L1 | 60.6 | 76.5 | 51.3 | -- | 35.5 | 22.7 |
| L2 | 61.2 | 76.0 | 52.4 | -- | 32.7 | 24.5 |
| L3 | 60.2 | 76.1 | 55.3 | -- | 34.7 | 27.4 |
| L4 | 57.8* | 75.2 | -- | -- | -- | -- |
| L5 | -- | -- | -- | -- | -- | -- |
| S1 | 62.5 | 75.3 | 55.0 | -- | 26.5 | 24.8 |
| Ca1? | 57.5 | 70.1 | 60.8 | -- | 29.9 | 19.7 |
| Ca2? | 59.7 | 71.3 | 59.7 | -- | 28.2 | 24.2 |
| Ca3? | -- | -- | 59.3 | -- | 19.7 | 24.0 |

rugose, almost circular central depression for rib attachment. T19 has a broader, more lumbar-like centrum than other thoracics.

Lumbar vertebrae.—The number of lumbar vertebrae in *Protosiren* is not known with certainty. Lumbar interpreted as L1-L3 (Figs. 7A-C) are well preserved here, L4 is a centrum only (Fig. 7D; with the posterior surface badly weathered), and there may have been an L5 (but nothing of this was found). L1-L4 all have centra that are dorsoventrally high and transversely broad. The anterior articular surface of the centrum is slightly but distinctly convex transversely (but not dorsoventrally; i.e., this curvature is visible in dorsal or ventral view, but not in lateral view). The posterior articular surface is similar in being slightly but distinctly concave transversely (again, this is only visible in dorsal or ventral view). Transverse processes are preserved on L1-L3, arising from the body of the centrum. The bases of both transverse process of L1 are long anteroposteriorly and relatively deep dorsoventrally;

the transverse process on the right side extends laterally at least 8 cm from the centrum (the end is broken); the anterior edge is thinner than the posterior edge, and the anterior edge is slightly but distinctly angled, with the apex of the angle about 5 cm from the centrum. The bases of transverse process are similarly long anteroposteriorly, but they are not as deep dorsoventrally on L2 and L3. On L2 the transverse process of the left side is complete and extends laterally 8.2 cm from the centrum; the anterior edge is again thinner than the posterior edge, and the anterior edge has a distinct 70-80° angulation about 6 cm from the centrum, where it angles back to a relatively pointed posterodistal end of the transverse process. Neural arches are preserved on L2 and L3, enclosing sediment-filled neural canals. These show that pre- and postzygapophyses were gracile, and that both extended little beyond the anterior or posterior articular surfaces of the centra.

Sacrum.—There is a single sacral vertebra, S1 (Fig. 7E), in *Protosiren sattaensis*, as there is in *P. fraasi* (Sickenberg, 1934, p. 86) and *P. smithae* (Domning and Gingerich, 1994, fig. 7I). This is similar to the lumbar vertebrae just described but differs in having flatter anterior and posterior articular surfaces of the centrum, and in having more robust transverse processes with more thickly rounded anterior and posterior edges. The right transverse process is nearly complete. This expands distally, both anteroposteriorly and dorsoventrally. The transverse process ends in a planar, rugose, oval surface that is distinctly angled (inward toward the front). Rugosity of the planar distal surface indicates cartilaginous and/or ligamentous connection to pelvic bones (see below).

Caudal vertebrae.—Anterior caudal vertebrae, probably Ca1-Ca3 (Fig. 7F-H), are similar to the sacrum in having more robust transverse processes than those seen on lumbar vertebrae. Caudals differ in having smaller neural canals and shorter transverse processes than the sacrum, and the distal ends are not expanded like those of the sacrum.

Ribs.—Three ribs of GSP-UM 3001 are complete or nearly so. These include one complete first rib, R1 (Fig. 8C), and two nearly complete mid-thoracic ribs (Fig. 8A,B; both lack distal ends). Ribs were identified to position by comparison with a nearly complete rib cage of *Protosiren smithae*, UM 101224. There are, in addition, many associated rib heads and partial ribs or rib pieces collected with the type specimen of *P. sattaensis* that cannot be identified to position.

Ribs of *P. sattaensis*, like those of other *Protosiren* species (Sickenberg, 1934; Domning and Gingerich, 1994), are distinctive in two ways. They differ from ribs of contemporary *Eotheroides* and *Eosiren* in lacking well formed joint surfaces (Fig. 9), and they differ in *not* being pachyostotic. The first characteristic was discussed by Sickenberg (1934, p. 89-91, 193). Rib capitular epiphyses, like vertebral epiphyses, failed to ossify, and rib heads were connected to vertebral bodies by cartilaginous or ligamentous connective tissue rather than synovial articulations. Rib tubercula are also poorly formed and linked to vertebrae by connective tissue rather than a synovial joint. The second characteristic, rib pachyostosis, was dismissed by Sickenberg (1934, p. 91) as negligible compared to pachyostosis observed in *Eotheroides*. Ribs of *Protosiren* are densely ossified, but they are neither pachyostotic nor osteosclerotic.

Pelvis.—Abel (1904, p. 187) was the first to describe and illustrate innominate bones of *Protosiren*, which, with the sacrum (described above), constitute the pelvis. The innominates described by Abel were first identified as "*Eotherium*", but later recognized as belonging to *Protosiren fraasi*. The two most distinctive features of the innominates of *P. fraasi* (Fig. 10B), compared to those of other sirenians, are retention of a large, well-formed acetabulum and retention of a relatively large obturator foramen. Abel interpreted the former as indicating the presence of a functional femur. Domning and Gingerich (1994) described innominates associated with the type specimen of *P. smithae* that are larger than those of *P. fraasi* but have a relatively smaller obturator foramen (Fig. 10A, 11A). Pelvic bones of *P. sattaensis* resemble those of both species, but differ in combining large size with retention of a large obturator foramen (Figs. 10C, 11B). The right innominate of *P. sattaensis* is 28 cm in total length,

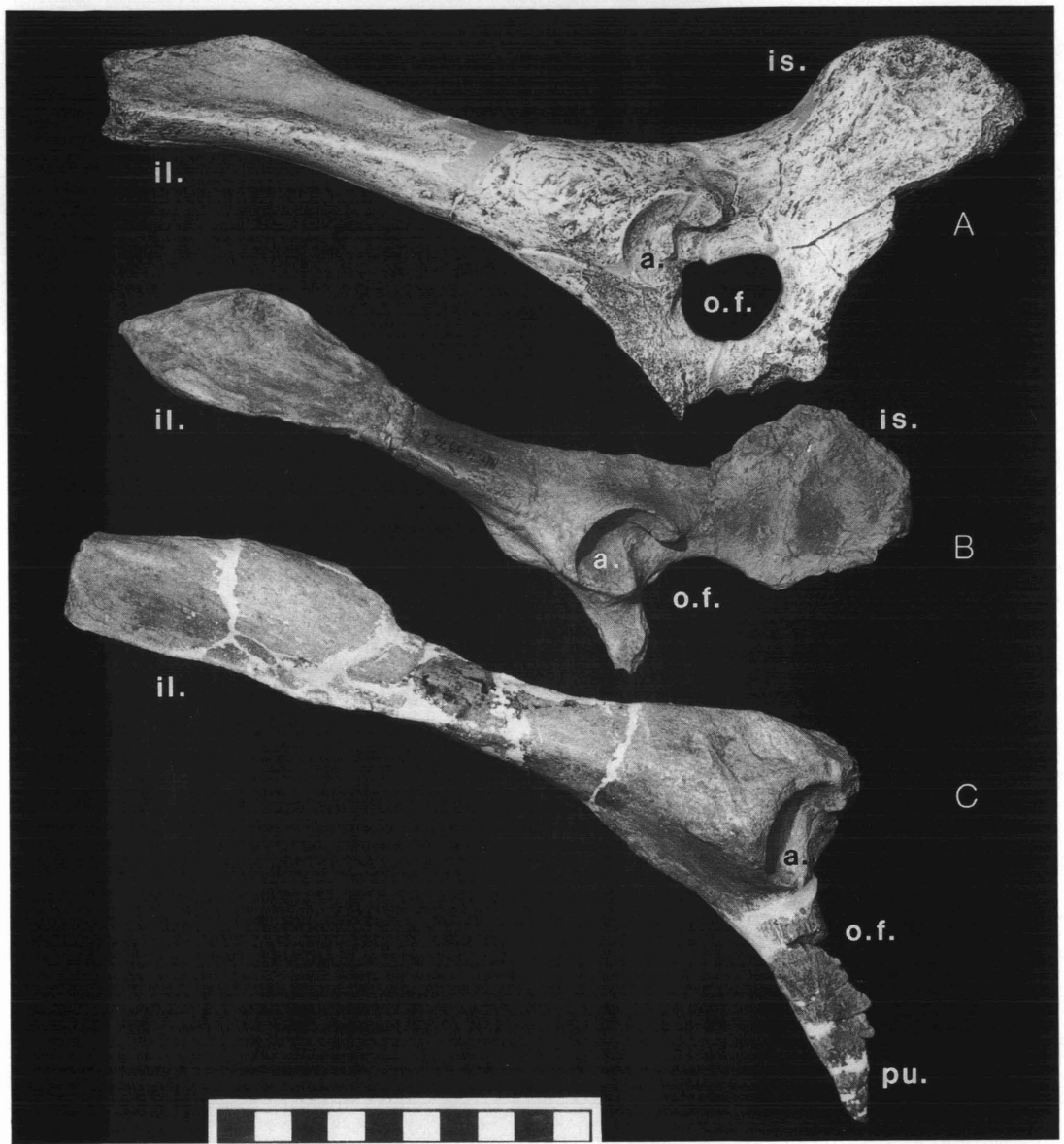


FIG. 10—Comparison of left innominate pelvic bones of *Protosiren smithae* (A, CGM 42292 holotype [cast]), *Protosiren fraasi* (B, SMNS 43976b [cast]), and *Protosiren sattaensis* (C, GSP-UM 3001, holotype). Note longer ilium in *P. sattaensis*, large obturator foramen in *P. fraasi* and *P. sattaensis*, and retention of well-formed acetabulum in all three. All pelves are shown in lateral view. Scale is in cm (pelves shown approximately 0.5× natural size).

measured from the anterior end of the ilium to the posterior end of the ischium, with the obturator foramen measuring about 4.6 cm anteroposteriorly and 3.9 cm dorsoventrally.

The ilium in *P. sattaensis* is long; it measures 20 cm from the center of the acetabulum to the most distant point on the iliac crest. The body of the ilium is triangular in cross-section for two-thirds of its length, but the anterior or proximal third, comprising the ala or wing, is



FIG. 11—Comparison of right innominate pelvic bones of *P. smithae* (A, CGM 42292 holotype [cast]) and *Protosiren sattaensis* (B, GSP-UM 3001 holotype). Note longer ilium and larger obturator foramen in *P. sattaensis*, and retention of well-formed acetabulum in both taxa. Both pelves are shown in lateral view. Scale is in cm (pelves shown approximately 0.5× natural size).

more flattened. There is a distinct dorsal iliac spine on the dorsal surface of the ala. There is no auricular surface for articulation with the sacrum, but the anterior surface of the ala is rugose. In life this almost certainly was linked to the rugose distal surface of the transverse process of the sacrum by ligamentous connective tissue. Thus *P. sattaensis* probably had a functional hind limb, but the limb could not have been used in terrestrial locomotion because it was too small and because there was no sacroiliac articulation. Lack of a sacroiliac joint

means that there was no way to lift the body and tail, and no way to stabilize movement if these could be lifted.

The pubis of *P. sattaensis* extends medioventrally 8.5 cm from the center of the acetabulum, and the pubic ramus anterior to the obturator foramen measures 19.9×14.6 mm in diameter. Left and right pubes both end ventrally and medially in a well-formed point of bone (Fig. 10C, 11B), showing that there was no pubic symphysis. Left and right pubes were probably linked with connective tissue, but they did not make bony contact. Lack of a bony pubic symphysis together with absence of any sacroiliac articulation means that pelvic bones on the left and right sides could move independently of each other, which constrains possible interpretations of the functions of the hind limb of *P. sattaensis*.

The ischium in *P. sattaensis* extends posteriorly 9 cm from the center of the acetabulum. The body or ramus of the ischium dorsal to the obturator foramen measures 24.7×13.2 mm, and this flares distally into a broad bone with a distinct ischiatic tuberosity. The bony connection between the ischium and pubis is very narrow and thin, measuring only 5.8×4.8 mm in diameter, but this is sufficient to enclose the obturator foramen posteriorly.

The acetabulum is shallow on each innominate, with a broad lunate surface and a very shallow acetabular notch or incisure. The superior part of the lunate surface barely overhangs this incisure posteriorly. This feature may vary in development in different individuals, but the incisure is deeper and the overhang greater in the acetabulum of *P. fraasi*.

Order CETACEA Brisson, 1762
Suborder ARCHAEOCETI Flower, 1883
Family PROTOCETIDAE Stromer, 1908

Babiacetus indicus Trivedy and Satsangi, 1984
Figs. 12, 14-15

Holotype.—GSI 19647, left and right dentaries with cheek teeth (Fig. 12).

Type locality.—Babia Hills, $23^{\circ}00'42''$ N latitude, $68^{\circ}46'30''$ E longitude, Kutch District, Gujarat, India.

Referred specimen.—GSP-UM 3005, much of skull and lower jaws. The referred specimen was found just east of Gulki village and 4 km north of Sangarh Lahar at $30^{\circ}44'50''$ north latitude, $70^{\circ}28'15''$ east longitude (Fig. 13; Survey of Pakistan topographic quadrangle 39 J/6; Barthi quadrangle of the Geological Survey of Pakistan, 1986). This is approximately 2.9 km along strike to the south of the *Protosiren sattaensis* type locality, at a slightly lower level, from brown shales between the upper *Discocyclus* limestones of the Drazinda Formation (Fig. 3).

Age and distribution.—*Babiacetus indicus* is presently known only from the type locality in gypsaceous shale of the Babia stage, late Lutetian middle Eocene, in Kutch in India (Mohan and Soodan, 1970; Trivedy and Satsangi, 1984; Singh and Singh, 1991), and from the Drazinda Formation, late Lutetian, in the Sulaiman Range of Punjab (Fig. 13; specimen described here).

Diagnosis.—*Babiacetus* is distinctive among protocetids in combining relatively large size, large anterior premolars (P^1 and P_1 are double-rooted), and a fused mandibular symphysis, with fusion extending posteriorly to the back of P_2 .

Description

The type specimen of *Babiacetus indicus*, GSI 19647, is a somewhat gypsum-encrusted mandible with left and right dentaries and many of the lower cheek teeth in place (Fig. 12; note

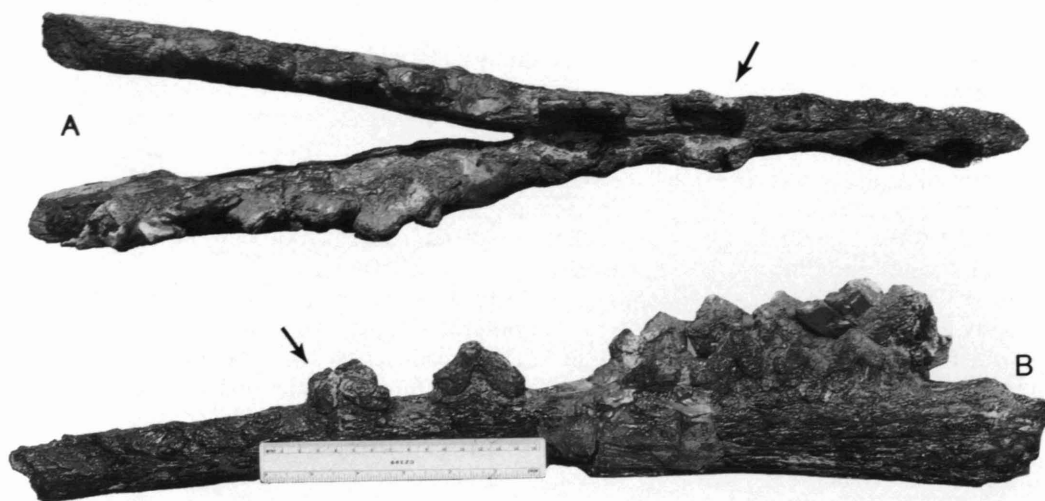


FIG. 12—Type specimen of *Babiacetus indicus* Trivedy and Satsangi, GSI 19647, as photographed at the Geological Survey of India in Calcutta in 1979. A, left and right dentaries in left lateral view; anterior is at left. B, left and right dentaries in occlusal view; anterior is at right. Dentaries, as preserved, are 58 cm long. Note large, double-rooted P_1 (arrows) separated by a diastema from the long massive crown of P_2 ; diastema separating P_2 from closely-spaced P_3 - M_3 ; and solidly-fused mandibular symphysis extending posteriorly to the diastema between P_2 and P_3 . Scale is in cm.

that none of the teeth in the type are well preserved). Trivedy and Satsangi (1984) described the mandible as being 580 mm long, as preserved (lacking both the anterior and posterior parts of both dentaries). They described the mandible as being nearly circular (in cross-section) with a flat dorsal surface in the symphyseal region. Trivedy and Satsangi described the mandibular symphysis as extending to the posterior root of P_3 , but after comparison with new material we interpret their P_3 as being P_2 ; hence the symphysis extends to the posterior root of P_2 . Further, this symphysis is not the usual open symphysis or syndesmosis of protocetid and basilosaurid archaeocetes, but instead left and right rami are solidly fused in a true synostosis. Trivedy and Satsangi described P_3 [P_2] as the longest tooth in the lower dentition, measured anteroposteriorly, with P_4 [P_3] being smaller than P_2 [P_1]. They further noted that lower molars are continuous, with no spaces between them, and much smaller than the premolars. The size and spacing of lower cheek teeth in the type is very similar to those of teeth in the referred specimen described here, where P_1 is double-rooted and P_{1-4} increase progressively in size (anteroposterior length).

Dentary.—The new specimen of *Babiacetus indicus* from Pakistan includes a mandible with left and right dentaries, GSP-UM 3005 (Fig. 14), that is very similar in size and preservational completeness to the holotype (measurements are given in Table 2). GSP-UM 3005 has the same symphyseal synostosis and the same double-rooted P_1 seen in the holotype, and the anteroposterior length of lower premolars increases progressively from P_1 to P_4 . The most anterior tooth in GSP-UM 3005 is I_3 , which has a robust but simple, pointed, caniniform crown. Enamel on the lingual side of the crown has faint vertical crenulations, while that on the labial side is smooth. C_1 is larger, but has a crown of similar shape. Enamel is weathered, making any pattern of crenulation obscure. P_1 and all of the remaining cheek teeth are double-rooted. P_{1-4} have similar mediolaterally-compressed crowns, with a single prominent central cusp. Lower premolars, like I_3 , have faint vertical crenulations in enamel on the lingual side



FIG. 13—*Babiacetus indicus* locality in the middle Drazinda Formation in a tributary of Sangarh Nala northeast of Gulki and south of Satta Post. Referred skull and dentaries, GSP-UM 3005, were found in situ near the folding shovel and stack of white collecting bags in the foreground. Ridge in center of photograph is capped by an east-dipping bed of *Discocyclina*-rich limestone. Slope in distance shows light 'Tapti' or *Pellatispira* beds of Eames in the upper part of the upper Drazinda Formation, capped by fluvial sandstones of the Miocene Chitarwata Formation.

of the crown, while enamel on the labial side is smooth. Molars have a higher trigonid than talonid, but this is not as high, relative to the length of the crown, where it can be measured (Table 2), as that of *Rodhocetus kasrani* (Gingerich, Raza, et al., 1994). The crown of M_3 , for example, is longer than it is high in *Babiacetus*, while it is higher than it is long in *Rodhocetus*. The crown of M_3 in *Babiacetus* further differs from that of *Rodhocetus* in having a lateral as well as a medial beaded ridge of enamel running up the front of the crown. Molar enamel is faintly textured on both sides of the crown. Both dentaries have large mandibular canals and there is a large mandibular foramen on the medial surface of the posterior part of each dentary.

Cranium.—GSP-UM 3005 includes much of the cranium of *Babiacetus indicus* (Fig. 15), which is the first to be known for this genus and species. Measurements are given in Table 2. The skull was found with the mandible and lower teeth tightly occluded against the palate and upper cheek teeth (which served to protect both from damage when exposed subaerially). The back of the skull was partly missing due to weathering when found, and much of the braincase, including both occipital condyles, is missing. The specimen has also suffered some postmortem deformation that involved simultaneous bending and twisting of the long axis of the skull. The rostrum is massive and is the least deformed. Alveoli are present for I^{2-3} and C^1 . The alveolus for C^1 indicates that the root was incipiently divided. P^1 is present on both sides, and it is double-rooted like P_1 . P^2 is represented by an isolated double-rooted tooth found in exca-



FIG. 14—Dentaries of the referred specimen of *Babiacetus indicus*, GSP-UM 3005, from the Drazinda Formation of Rodho anticline, for comparison with the type shown in Figure 13. A, occlusal view. B, right lateral view. Note large, double-rooted P_1 (arrows) separated by a diastema from the long massive crown of P_2 ; diastema separating P_2 from closely-spaced P_3 - M_3 ; and solidly-fused mandibular symphysis joining left and right dentaries as far posteriorly as the back of P_2 . Scale is in cm.

vating the skull. It has no trace of a medial third root, and the crown is less strongly arched than that of lower premolars. P^3 and P^4 are both three-rooted, with the paracone being the dominant cusp. Each has a smaller metacone directly posterior to the paracone. There is a prominent surface on the medial side of the tooth sloping toward the medial root in the position where a protocone would be expected. This is more prominent on P^4 than it is on P^3 , but neither has any trace of an actual protocone cusp.

Upper molars are preserved on the left side only. The most prominent cusp on M^{1-3} is the paracone. The crown of M^1 is damaged, but there is a small metacone on M^2 and M^3 . There is no protocone cusp on upper molars, and only a very weak lingual cingulum surrounding the area above the medial root where a protocone would be if it were present. All of the upper molars are worn to some degree, with flat apical wear on the paracone of M^1 and M^3 (and probably M^2 , where the apex is broken). M^2 has a deep wear facet on the anteromedial surface of the tooth. Unworn enamel surfaces are faintly textured. There are no accessory cusps or cuspules suggesting serration on any of the upper or lower cheek teeth.

Cranial characteristics of note in *Babiacetus indicus* include external nares opening above P^1 , an infraorbital foramen opening above the anterior root of P^3 , the broad frontal shield typical of protocetids and later basilosaurids, and the densely ossified tympanic bulla with a prominent sigmoid process typical of archaeocetes (not visible in Fig. 15 because of postmortem torsion of the skull). The bulla is attached to the skull at several places: there is a broad contact anteriorly with the squamosal and second contact with the posterior process of the periotic. In addition, the bulla may contact the basioccipital and the paroccipital process of the exoccipital but this cannot be determined with certainty at present. There is no indica-

TABLE 2—Selected measurements of upper and lower teeth, alveoli, diastemata, cranium, and dentary of *Babiacetus indicus* based on GSP-UM 3005. Abbreviations: D, diastema following tooth; H, height; L, length; W, width. Asterisk marks estimated measurement; superscript *a* indicates estimate is of the length or width of an alveolus (alveoli in the case of teeth with multiple roots). Upper molar widths are marked as estimates because the widths of these teeth are so difficult to deline.

| Cranium | | | | | | | | |
|---|---|-------------------|---|-------|---|-------|-------|----|
| I ¹ | L:W:H:D: | -- | : | -- | : | -- | mm | |
| I ² | L:W:H:D: | -- | : | -- | : | -- | | |
| I ³ | L:W:H:D (single-rooted alveolus): | 31.5 ^a | : | -- | : | -- | 30.0 | |
| C ¹ | L:W:H:D (incipiently double-rooted alveolus): | 37.0 ^a | : | -- | : | -- | 58.9 | |
| P ¹ | L:W:H:D (double-rooted): | 36.7 | : | 17.0 | : | 22.1 | 28.0 | |
| P ² | L:W:H:D (double-rooted): | 41.7 | : | 15.9* | : | 30.0* | 27.8 | |
| P ³ | L:W:H:D (triple-rooted): | 43.8 | : | 23.0 | : | 25.6 | 30.0 | |
| P ⁴ | L:W:H:D (triple-rooted): | 36.8 | : | 25.6 | : | 25.6 | 4.0 | |
| M ¹ | L:W:H:D (triple-rooted): | 21.7 | : | 20.0* | : | -- | 0.0 | |
| M ² | L:W:H:D (triple-rooted): | 21.6 | : | 18.3* | : | -- | 0.0 | |
| M ³ | L:W:H (triple-rooted): | 20.5 | : | 15.5* | : | -- | -- | |
| Skull length (condylobasal): | | | | | | | 85* | cm |
| Diameter of orbit: | | | | | | | -- | |
| Diameter of infraorbital foramen: | | | | | | | 1.3 | |
| Breadth of frontal shield at postorbital process (maximum): | | | | | | | 29.9 | |
| Breadth across nasals on frontal shield (maximum): | | | | | | | 8.7 | |
| Breadth of rostrum at C ¹ : | | | | | | | 7.4 | |
| Breadth of rostrum at P ² : | | | | | | | check | |
| Breadth of palate at M ³ : | | | | | | | -- | |
| Height of skull above palate at M ²⁻³ : | | | | | | | -- | |
| Breadth of skull across zygomatic arches (maximum): | | | | | | | -- | |
| Breadth of skull across squamosals: | | | | | | | -- | |
| Breadth of skull across exoccipitals: | | | | | | | -- | |
| Foramen magnum W:H: | | | | | | | -- | : |
| Height of nuchal crest above foramen magnum (maximum): | | | | | | | -- | |
| Tympanic bulla L:W:H (width measured across sigmoid process): | | 6.45 | : | 4.60 | : | -- | | |
| Mandible | | | | | | | | |
| I ₁ | L:W:H:D: | -- | : | -- | : | -- | mm | |
| I ₂ | L:W:H:D: | -- | : | -- | : | -- | | |
| I ₃ | L:W:H:D (single-rooted): | 21.8 | : | 14.5 | : | -- | 29.0 | |
| C ₁ | L:W:H:D (single-rooted): | 28.1 | : | 18.3 | : | 40.0* | 58.0 | |
| P ₁ | L:W:H:D (double-rooted): | 35.7 | : | 15.0 | : | 26.2* | 35.0 | |
| P ₂ | L:W:H:D (double-rooted): | 40.1 | : | 17.5 | : | 27.0 | 24.5 | |
| P ₃ | L:W:H:D (double-rooted): | 44.0 | : | 19.3 | : | -- | 14.5 | |
| P ₄ | L:W:H:D (double-rooted): | 49.5 | : | 18.2 | : | -- | 0.0 | |
| M ₁ | L:W:H:D (double-rooted): | 25.2 | : | 13.2 | : | -- | 0.0 | |
| M ₂ | L:W:H:D (double-rooted): | 31.5 | : | 15.5* | : | 28.5* | 0.0 | |
| M ₃ | L:W:H:D (double-rooted): | 35.4 | : | 16.7 | : | 28.9 | 0.0 | |
| Length of right dentary as preserved: | | | | | | | | |
| Depth of dentary below C ₁ : | | | | | | | 6.0 | cm |
| Depth of dentary below P ₃₋₄ : | | | | | | | 8.4 | |
| Depth of dentary below M ₁ : | | | | | | | 11.6 | |
| Depth of dentary below M ₃ : | | | | | | | 12.2 | |
| Posterior opening of mandibular canal W:H: | | | | | | | 3.2 | : |



FIG. 15—Cranium of the referred specimen of *Babiacetus indicus*, GSP-UM 3005, from the Drazinda Formation of Rodho anticline. Photograph shows the left side of the cranium, in lateral view, as reconstructed from casts of the principal cranial elements. The skull as a whole was bent and twisted to some degree during burial. Note opening of external nares above double-rooted P¹ (arrows) and broad frontal shield typical of Protocetidae (orbit is partially reconstructed, but supraorbital process of frontal is original). Auditory bulla on left side is present but hidden by the squamosal. Scale is in cm.

tion of development of the pterygoid sinus that helps to isolate the bulla in basilosaurids and later whales.

DISCUSSION

Extant Sirenia or sea cows are distinctively specialized aquatic herbivorous mammals. The order includes three species of trichechids or manatees living in Atlantic and Caribbean coastal waters in North and Central America, in the Amazon River drainage of South America, and in Atlantic coastal waters of West Africa (all in genus *Trichechus*), and one species of dugongid or dugongs living in Red Sea and Indo-Pacific coastal waters ranging from Egypt to Australia (genus *Dugong*). A second dugongid, Steller's sea cow (*Hydrodamalis*), survived until historical times in the North Pacific. Manatees have broad, rounded, paddle-like tails and are generally found in coastal rivers and estuaries, while dugongs have more cetacean-like crescentic tails and are truly marine. As might be expected, the more sessile manatees are the more speciose of sirenians, with geographically smaller species ranges, and the wider-ranging dugongs are less speciose with a broad geographic range.

Sirenia first appear in the fossil record in the Eocene. They are widely distributed geographically in middle and late Eocene deposits, especially marginal marine deposits of the ancient Tethys Sea separating Europe and North Africa, and in Caribbean and Atlantic coastal deposits of North America (Domning et al., 1982; Savage et al., 1994). The earliest fossil sirenians show many specializations characteristic of modern Sirenia, and tracing their origin to an inferred land-mammal ancestry remains a challenge. Middle Eocene *Protosiren*, in spite of its relatively large pelvis and hind limb, is already highly specialized as a sirenian and it contributes little to understanding the origin of Sirenia.

The type specimen of *Protosiren sattaensis* was found as a jumble of associated vertebrae, ribs, and pelves weathering from a steeply-dipping green shale bed. This was excavated in the field as deeply as bone could be traced down-dip into the earth. Fragmentation of bones appears to have been caused by erosion and weathering, because we were able to reassemble many of the pieces to make more complete bones. However, in the end all that was found of the skeleton was the lower part of the neck, almost all of the thorax and lumbus, the sacrum

and proximal tail, and both pelves. No trace of the skull was found (no cranial bones, no dentaries, and no teeth). No fragments of forelimb elements were found, nor were any bones of a hind limb or tail found in the excavation. It seems certain that the specimen had lost its head and anterior cervicals, all of its limbs, and much of its tail before being buried. If the skeleton was disarticulated randomly, we would expect to have found teeth, cranial bones, forelimb, or hind limb elements in our excavation. Thus it seems likely that the missing body parts were removed by scavengers. Alternatively, they may have fallen from a floating carcass before it reached its final resting place.

Pelvic bones of *P. sattaensis* described here resemble those of *P. fraasi* in relative proportions of the ilium, ischium, pubis, acetabulum, and obturator foramen, but resemble those of *P. smithae* in overall size, which is, of course, consistent with the large size of vertebrae and the rest of the skeleton of *P. sattaensis*. The inferior border of the obturator foramen, where the pubis and ischium join, is very thin and delicate in *P. sattaensis* and *P. fraasi* and much more robust in *P. smithae*. If pelves of the three species are aligned in a simple morphocline and assumed to represent a single evolutionary lineage, it appears that the transition from *P. fraasi* to *P. sattaensis* and then to *P. smithae* involved first increasing overall size and then a decrease in the relative size of the obturator foramen.

The unusual intervertebral articulations of *Protosiren*, with most vertebrae lacking epiphyses or end plates, suggest that it was already somewhat specialized as a swimmer. This interpretation is supported by loss of the sacroiliac articulations required for hind-limb support of the lumbus and tail, and it is supported by the *Protosiren* vertebral length profiles shown in Figure 5. Profiles of *P. sattaensis* and *P. smithae* parallel that of the dugongid *Dusisiren* in that thoracic centra become longer posteriorly, with the longest centra located in the posterior thorax and lumbus. The profile of *Trichechus*, in contrast, is longest in the mid-thorax, and it has fewer and shorter lumbar and caudal vertebrae than *Dusisiren* and probably *Protosiren*. This suggests that *Protosiren* was in the middle Eocene already a capable marine swimmer similar to modern wide-ranging dugongids rather than more-sessile trichechids.

There are now three species of *Protosiren* known: (1) *P. fraasi*, described by Abel (1907; see also Gingerich, Domning, et al., 1994) came from the top of the Lower Building Stone of the Mokattam Formation of Egypt; this is middle Lutetian in age, probably corresponding to Paleogene planktonic foraminiferal zone P11 and nannoplankton zone NP15, in the high sea stand of sea level cycle TA3.3 calibrated at 45.5 Ma (Haq et al., 1987; Gingerich, 1992); (2) *P. sattaensis* described here came from the middle part of the Drazinda Formation; this is late Lutetian in age, probably corresponding to zones P12 and NP16, and just above the high sea stand in sea level cycle TA3.4, calibrated at 43.5 Ma (Haq et al., 1987); (3) *P. smithae*, described by Domning and Gingerich (1994) came from the Gehannam Formation in Egypt; this is latest Bartonian in age, probably corresponding to zones P14 and NP17, and at the top of the high sea stand of sea level cycle TA3.6 calibrated at 39.5 Ma (Haq et al., 1987). Thus the known duration of *Protosiren* is about six million years.

Protosiren sattaensis is important in being intermediate in age between the two species known previously, and it combines morphological features of both: *P. sattaensis* retains the pelvis with large obturator foramen of *P. fraasi*, but it has the large size of *P. smithae*. *Protosiren sattaensis* is also important in extending the geographic range of *Protosiren* from the southern margin of Tethys in Egypt eastward to the southern margin of Tethys in Indo-Pakistan. If our present understanding of paleogeography is correct, this connection crossed substantial open ocean separating Africa or Afro-Arabia from Indo-Pakistan. However *Protosiren* appears to have had an axial skeleton with dugong-like rather than manatee-like proportions and a broad geographic distribution is thus not surprising.

Babiacetus indicus was named in an abstract, and Figure 12 here is, to our knowledge, the first published illustration of the type specimen. Fortunately, brief description of the holotype by Trivedy and Satsangi (1984) has been followed by recovery of the more complete specimen

described here, which shows that symphyseal fusion and a double-rooted P_1 are characteristic of this genus and species. *Babiacetus* has the hydrodynamic skull shape and pointed, anteroposteriorly-aligned incisors typical of archaeocetes, and it has the densely ossified auditory bulla and the large mandibular canal that indicate specialization for hearing in water. We infer from its large size and robust teeth that *Babiacetus* probably fed on relatively large fish or other aquatic vertebrates. Unfortunately, nothing is known of the postcranial skeleton of *Babiacetus*, and thus nothing is known about its mode of swimming nor the completeness of its adaptation to water.

The only previous study of vertebrate faunas from the Drazinda Formation involved screen washing for microvertebrate remains in this area (West et al., 1991), which yielded teeth of selachians and teleosts (Case and West, 1991) and otoliths of teleosts (Nolf, 1991). The principal locality yielding vertebrates, H-GSP locality 167, was published as being on the west side of the Zinda Pir anticlinorium (West et al., 1991, text-fig. 2) or, alternatively, in Sanghar Lahar 16 km (Nolf, 1991) or 20 km (Case and West, 1991) west of Taunsa. We were able to relocate the site shown in the photograph of West et al.'s (1991) Plate 1, which is on the east side of the Zinda Pir anticlinorium at 30°41'40" north latitude and 70°29'30" east longitude.

West et al. (1991) called the Drazinda shale middle to late Eocene in age, Case and West (1991) identified cartilaginous and bony fishes from the Drazinda shale as being late Eocene (Priabonian), and Nolf (1991) called it simply middle Eocene. H-GSP locality 167 is at a somewhat higher stratigraphic level than the sirenian specimens described here, judging from West et al.'s (1991) measured section. It is possible that the upper part of the Drazinda Formation is Priabonian late Eocene in age (as Samanta, 1972, 1973, and Köthe et al., 1988, suggested too), but this would mean that two high sea stands in the Bartonian are missing in what otherwise seems to be a continuous sequence of marine deposition. As outlined above, we interpret the lower and middle parts of the Drazinda Formation in Pakistan as being late Lutetian in age. This conclusion is based on (1) planktonic foraminifera and nannoplankton; (2) sea level stratigraphy; (3) the intermediate morphology of preserved remains of Tethyan *Protosiren sattaensis* of Pakistan compared to remains of Tethyan middle Lutetian *P. fraasi* and Bartonian *P. smithae* of Egypt; and (4) the presence of *Discocyclus sowerbyi*, Sirenia, and *Babiacetus* in late Lutetian strata of Kutch. The age of the upper Drazinda Formation, including the "Tapti" or *Pellatispira* beds of Eames, may be significantly younger and this deserves further study.

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LITERATURE CITED

- ABEL, O. 1904. Die Sirenen der mediterranen Tertiärbildungen Oesterreichs. *Abhandlungen der Geologischen Reichsanstalt, Wien*, 19(2): 1-223.
- . 1907. Die Stammesgeschichte der Meeressäugetiere. *Meereskunde, Institut für Meereskunde, Berlin Universität*, 1(4): 1-36. [English translation in Annual Report of the Smithsonian Institution, 1907, 473-496.]
- BAJPAI, S., S. SRIVASTAVA, and A. JOLLY. 1989. Sirenian-moeritherid dichotomy: some evidence from the middle Eocene of Kachchh, western India. *Current Science*, 58: 304-306.
- BISWAS, S. K. 1965. A new classification of the Tertiary rocks of Kutch, western India. *Bulletin of the Geological, Mining, and Metallurgical Society of India*, 35: 1-6, chart.
- CASE, G. R., and R. M. WEST. 1991. Geology and paleontology of the Eocene Drazinda Shale Member of the Khirthar Formation, central Western Pakistan. Part II. Late Eocene fishes. *Tertiary Research, Leiden*, 12: 105-120.
- DOMNING, D. P. 1978. Sirenian evolution in the North Pacific Ocean. *University of California Publications in Geological Sciences*, 118: 1-176.
- and P. D. GINGERICH. 1994. *Protosiren smithae*, new species (Mammalia, Sirenia), from the late middle Eocene of Wadi Hitán, Egypt. *Contributions from the Museum of Paleontology, University of Michigan*, 29: 69-87.
- , G. S. MORGAN, and C. E. RAY. 1982. North American Eocene sea cows (Mammalia: Sirenia). *Smithsonian Contributions to Paleobiology*, 52: 1-69.
- DOWNING, K. F., E.H. LINDSAY, W. R. DOWNS, and S. E. SPEYER. 1993. Lithostratigraphy and vertebrate biostratigraphy of the early Miocene Himalayan foreland, Zinda Pir Dome, Pakistan. *Sedimentary Geology*, 87, 25-37.
- EAMES, F. E. 1952a. A contribution to the study of the Eocene in western Pakistan and western India: A. The geology of standard sections in the western Punjab and in the Kohat District. *Quarterly Journal of the Geological Society of London*, 107: 159-171.
- . 1952b. A contribution to the study of the Eocene in western Pakistan and western India: D. Discussion of the faunas of certain standard sections, and their bearing on the classification and correlation of the Eocene in western Pakistan and western India. *Quarterly Journal of the Geological Society of London*, 107: 173-196.
- GEOLOGICAL SURVEY OF PAKISTAN. 1986. Geological map of Dhodak. *Geological Survey of Pakistan Map Series*, 4: 157 (1 sheet).
- GINGERICH, P. D. 1992. Marine mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: stratigraphy, age, and paleoenvironments. *University of Michigan Papers on Paleontology*, 30: 1-84.
- , M. ARIF, and W. C. CLYDE. 1995. New archaeocetes (Mammalia, Cetacea) from the middle Eocene Domanda Formation of the Sulaiman Range, Punjab (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan*, 29: in press.
- , D. P. DOMNING, C. E. BLANE, and M. D. UHEN. 1994. Cranial morphology of *Protosiren fraasi* (Mammalia, Sirenia) from the middle Eocene of Egypt: a new study using computed tomography. *Contributions from the Museum of Paleontology, University of Michigan*, 29: 41-67.

- , S. M. RAZA, M. ARIF, M. ANWAR, and X. ZHOU. 1993. Partial skeletons of *Indocetus ramani* (Mammalia, Cetacea) from the lower middle Eocene Domanda Shale in the Sulaiman Range of Pakistan. Contributions from the Museum of Paleontology, University of Michigan, 28: 393-416.
- , S. M. RAZA, M. ARIF, M. ANWAR, and X. ZHOU. 1994. New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature*, 368: 844-847.
- GRANT, C. W. 1840. Memoir to illustrate a geological map of Cutch. Transactions of the Geological Society of London, Second Series, 5: 289-329.
- HAQ, B. U. 1972. Paleogene calcareous nannoflora. I. The Paleocene of west-central Persia and the upper Paleocene-Eocene of West Pakistan. *Stockholm Contributions in Geology*, 25: 1-56.
- , J. HARDENBOL, and P. R. VAIL. 1987. Chronology of fluctuating sea levels since the Triassic. *Science*, 235: 1156-1167.
- HEMPHILL, W. R., and A. H. KIDWAI. 1973. Stratigraphy of the Bannu and Dera Ismail Khan areas, Pakistan. Geological Survey of Pakistan, Professional Papers, 716-B: 1-36.
- KÖTHE, A., A. M. KHAN, and M. ASHRAF. 1988. Biostratigraphy of the Surghar Range, Salt Range, Sulaiman Range and the Kohat area, Pakistan, according to Jurassic through Paleogene calcareous nannofossils and Paleogene dinoflagellates. *Geologisches Jahrbuch, Hannover, Reihe B*, 71: 1-87.
- LATIF, M. A. 1961. The use of pelagic foraminifera in the subdivision of the Paleocene-Eocene of the Rakhi Nala, West Pakistan. *Geological Bulletin of Punjab University, Lahore*, 1: 31-46.
- MOHAN, M., and K. S. SOODAN. 1970. Middle Eocene planktonic foraminiferal zonation of Kutch, India. *Micropaleontology*, 16: 37-46.
- NOLF, D. 1991. Geology and paleontology of the Eocene Drazinda Shale Member of the Khirthar Formation, central Western Pakistan. Part III. Otoliths. *Tertiary Research, Leiden*, 12: 121-126.
- NUTTALL, W. L. F. 1926. The zonal distribution and description of the larger Foraminifera of the middle and lower Khirthar Series (Middle Eocene) of parts of western India. *Records of the Geological Survey of India*, 59: 115-164.
- SAHNI, A., and K. KUMAR. 1980. Lower Eocene Sirenia, *Ischatherium subathuensis*, gen. et. sp. nov. from the type area, Subathu Formation, Subathu, Simla Himalayas, H. P. *Journal of the Palaeontological Society of India*, 23-24: 132-135.
- , ——— and B. N. TIWARI. 1980. Lower Eocene marine mammal (Sirenia) from Dharampur, Simla Himalayas, H. P. *Current Science*, 49: 270-271.
- SAHNI, A., and V. P. MISHRA. 1975. Lower Tertiary vertebrates from western India. *Monograph of the Paleontological Society of India*, 3: 1-48.
- SAMANTA, B. K. 1972. Planktonic foraminiferal biostratigraphy of the early Tertiary of the Rakhi Nala section, Sulaiman Range, West Pakistan. *Journal of the Geological Society of India*, 13: 317-328.
- . 1973. Planktonic foraminifera from the Paleocene-Eocene succession in the Rakhi Nala, Sulaiman Range, Pakistan. *Bulletin of the British Museum (Natural History), Geology*, 22: 421-482.
- SAVAGE, R. J. G., D. P. DOMNING, and J. G. M. THEWISSEN. 1994. Fossil Sirenia of the West Atlantic and Caribbean region. V. The most primitive known sirenian, *Prorastomus sirenoides* Owen, 1855. *Journal of Vertebrate Paleontology*, 14: 427-449.
- SHAH, S. M. I. 1991. Lithostratigraphic units of the Sulaiman and Kirthar Provinces, lower Indus Basin, Pakistan. *Geological Survey of Pakistan Information Release*, 519: 1-82.
- SICKENBERG, O. 1934. Beiträge zur Kenntnis tertiärer Sirenen. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 63: 1-352.
- SINGH, P., and M. P. SINGH. 1991. Nannofloral biostratigraphy of the late middle Eocene strata of Kachchh region, Gujarat State, India. *Geoscience Journal*, 12: 17-51.
- THEWISSEN, J. G. M. 1993. Eocene marine mammals from the Himalayan foothills. *National Geographic Research and Exploration*, 9: 125-127, 487.
- TRIVEDY, A. N., and P. P. SATSANGI. 1984. A new archaeocete (whale) from the Eocene of India. *In: N. A. Bogdanov (ed.), Abstracts of 27th International Geological Congress, Moscow*, 1: 322-323.
- WEST, R. M., J. R. LUKACS, S. T. HUSSAIN, and M. ARIF. 1991. Geology and palaeontology of the Eocene Drazinda Shale Member of the Kirthar Formation, central Western Pakistan. Part I: Introduction. *Tertiary Research, Leiden*, 12: 97-103.

