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NEW SPECIES OF *PROTOSIREN* (MAMMALIA, SIRENIA) FROM THE EARLY MIDDLE EOCENE OF BALOCHISTAN (PAKISTAN)

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IYAD S. ZALMOUT¹, MUNIR UL-HAQ², AND PHILIP D. GINGERICH¹

Abstract — *Protosiren eothena* is a new species of early Lutetian (early middle Eocene) sirenian collected from sediments deposited in a coastal marine setting in eastern Tethys. It was found in the upper part of the Habib Rahi Formation in the vicinity of Kunvit, near Rakhni, in eastern Balochistan Province, Pakistan. The new sirenian is represented by distinctive thoracic vertebrae and ribs of a mature adult. Features of *Protosiren* that are generally diagnostic include the presence of large keyhole-shaped neural canals perforating thoracic vertebrae, presence of cartilaginous rather than synovial articulations of rib heads, and a lack of rib pachyostosis. *Protosiren eothena* is the oldest and smallest species of *Protosiren* known to date. It retains synovial articulations on rib heads, and it is about 10-12% smaller in linear dimensions than *P. fraasi* from the early middle Eocene of Egypt.

INTRODUCTION

Sirenians are relatively large herbivorous mammals that inhabit warm, near-shore, marine waters today. They made their first appearance in the early middle Eocene some 50 million years ago. The oldest sirenians known to date come from the early middle Eocene of Jamaica. These belong to two genera and species: *Prorastomus sirenoides* (Owen, 1855; Savage et al., 1994) and *Pezosiren portelli* (Domning, 2001). The fossil record documents a gradual transition from amphibious ancestral forms like these, with well developed hind limbs attached to a multivertebral sacrum (Domning, 2001), to living representatives such as *Trichechus manatus* and *Dugong dugon* that are fully aquatic and have hind limbs reduced to internal vestiges.

Eocene sirenians have a reasonably well documented evolutionary history, and are known from all continents except Australia and Antarctica. *Protosiren*, classified in the monotypic family Protosirenidae, represents one of the more widely distributed Eocene genera, ranging across the southern part of the eastern Tethys Sea from North Africa (Egypt) to South Asia (Indo-Pakistan). *Protosiren* is known from skulls and partial skeletons (Abel, 1907; Domning and Gingerich, 1994; Gingerich et al., 1994, 1995). It is distinctive and easily recognized from postcranial elements because thoracic vertebrae have a large oval to keyhole-shaped neural canal, articular surfaces of rib heads are generally roughened rather than smooth (indicating that they were connected exclusively by ligaments or flexible cartilage rather than synovial joints), and ribs lack pachyostosis.

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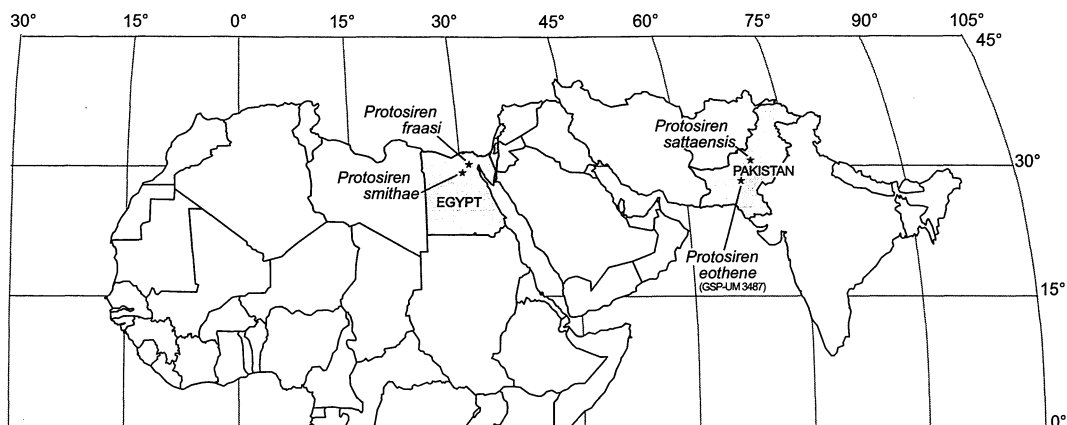


FIG. 1 — Map showing the geographic distribution of *Protosiren* species in Tethyan regions of Egypt and Pakistan.

Protosiren is represented by three species described previously (see Figure 1 for geographic distribution). The first, *Protosiren fraasi*, was named by Abel (1907) on the basis of a well preserved skull and some postcranial remains (first described by Andrews, 1906). These came from the Lower Building Stone Member of the Mokattam Limestone of Cairo (Egypt), which is middle Lutetian in age (early middle Eocene, ca. 45–46 Ma; Gingerich, 1992). The second species, *P. smithae*, was described and named by Domning and Gingerich (1994). This is a larger species, and it is more derived than *P. fraasi* morphologically in details of the skull. All known specimens of *P. smithae* were collected from the Gehannam and Birket Qarun formations in Wadi Hitan (Whales Valley or Zeuglodon Valley), located on the western margin of the Fayum Depression in Egypt. *P. smithae* is latest Bartonian to earliest Priabonian in age (latest middle to earliest late Eocene, ca. 36–37 Ma; Gingerich, 1992). The third species of this genus, *P. sattaensis*, was described by Gingerich et al. (1995). This is a large species that is slightly more primitive than *P. smithae* in having a larger obturator foramen and longer femur (Gingerich et al., 1995, 1997). *P. sattaensis* comes from western Punjab Province, in central Pakistan, from green shales in the middle part of the Drazinda Formation of middle Bartonian age (late middle Eocene, 39–40 Ma; Gingerich et al., 1997, 2001b).

Here we report the smallest and oldest Tethyan *Protosiren*, based on an association of diagnostic vertebrae and ribs collected from the upper part of the Habib Rahi Formation, in the transition to the overlying Domanda Formation, on the eastern flank of the Sulaiman Range in central Pakistan (this discovery was previously noted by Zalmout et al., 2001). The age is early Lutetian (early middle Eocene, ca. 47–48 Ma; Gingerich et al., 2001b). Now the oldest and one of the youngest species of *Protosiren* are known from Pakistan, and the genus has a temporal range of approximately 8 million years.

ABBREVIATIONS

- | | |
|--------|---|
| CGM | — Cairo Geological Museum, Cairo (Egypt) |
| GSP-UM | — Geological Survey of Pakistan-University, Islamabad (Pakistan) |
| SMNS | — Staatliches Museum für Naturkunde, Stuttgart (Germany) |
| UM | — Museum of Paleontology, University of Michigan, Ann Arbor (USA) |
| UMMZ | — Museum of Zoology, University of Michigan, Ann Arbor (USA) |

SYSTEMATIC PALEONTOLOGY

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

***Protosiren eothene*, new species**
Figs. 2a-b; 3c,f

Holotype.— GSP-UM 3487, partial thorax including parts of ten thoracic vertebrae, some with neural arches and spines, and partial to complete ribs. All were found as parts of a weathered associated skeleton. The best of these are illustrated in Figures 2a-b and 3c,f.

Type locality.— Kunvit Basin at 30° 05' 21" N and 69° 47' 40"E, north and west of the town of Rakhni in eastern Balochistan Province, central Pakistan (Fig. 1). The type specimen of *Protosiren eothene* was found within tens of meters geographically, and from the same narrow stratigraphic interval, as the type specimen of the early archaeocete *Rodhocetus balochistanensis* (Gingerich et al., 2001a).

Age and distribution.— GSP-UM 3487 was found in the alternation of thin marly limestones and thicker clay shales marking the transition from platy marl and limestone of the Habib Rahi Formation into the lowermost light green shale of the overlying Domanda Formation. Köthe et al. (1988) identified calcareous nanofossils from this transition as representing nannoplankton zones NP14-15, indicating an early Lutetian age for the new sirenian (see correlation chart in Gingerich et al., 2001b: fig. 11). *Protosiren eothene* is known only from the type locality on the east side of the Sulaiman Range, Balochistan Province, in central Pakistan. This was in the eastern Tethys (Neotethys) Sea paleogeographically.

Diagnosis.— *Protosiren* is distinctive among sirenians in having large keyhole-shaped neural canals perforating thoracic vertebrae, generally having cartilaginous rather than synovial articulations of rib heads, and lacking rib pachyostosis. *Protosiren eothene* differs from other species of *Protosiren* in being smaller (anterior thoracic centra are about 10-12% shorter than those of *P. fraasi*), in having at least partially synovial rib head articulations with vertebrae, and in having well formed but distinctly small rib tubercula relative to the size of the rib heads.

Etymology.— *eothene*, Gr., early, eastern; this species is both early in time and eastern in geographic distribution relative to other known *Protosiren*.

Description.— Vertebrae of *Protosiren eothene*, probably belonging to thoracics T1-T8, T12?, and T14?, are assigned to position in the vertebral column based on the pattern of increase in centrum length, on direct comparison to vertebrae of *P. fraasi*, and on comparison to good vertebral series of *P. smithae* and *P. sattaensis*. Measurements are listed in Table 1.

Thoracic vertebrae T1 and T2 are represented by centra only. These are weathered, but otherwise undeformed. The centrum of T1 is hemicylindrical and more nearly the length of T2 than would be expected by comparison with anterior thoracics in later *Protosiren*. This may imply that the neck and cervical vertebrae of *P. eothene* were longer than those of later *Protosiren*. The centrum of T2 has the circular to ellipsoidal anterior articular surface, and broad, vaguely pentagonal posterior articular surface seen in other *Protosiren*. Neural arches for these vertebrae were not recovered. Demifacets for rib articulations are poorly preserved but still present on both centra (showing that these cannot be cervicals as they were first interpreted to be).

Thoracic vertebrae T3 (Fig. 2a), T4, and T5 (Fig. 2b) are almost complete, although the neural arch is deformed and the neural spine deformed or broken in each. Centra here are longer and higher than those of T1 and T2, with centrum height being approximately equal to centrum width. These differ from centra of later *Protosiren* in being more cardiform than elliptical in cross section. Pedicles of the neural arches rise high above the centra. Neural canals are well preserved and have



FIG. 2 — Thoracic vertebrae of *Protosiren* spp. (Protosirenidae), *Eosiren* sp. (Dugongidae), and *Trichechus manatus* (Trichechidae). A-B, T3 and T5 of *Protosiren eothene* from the early middle Eocene of Pakistan (GSP-UM 3487, holotype). C, T12 of *Protosiren sattaensis* (GSP-UM 3001) from the late middle Eocene of Pakistan. D, T8 of *Protosiren smithae* (UM 101224) from the latest middle Eocene of Egypt. E, T5 of *Eotheroides* sp. (UM uncat.) from the latest middle Eocene of Egypt. F, T3 of *Trichechus manatus* from the Recent of Florida (UMMZ 106206). Note the large vertebral canal with a keyhole-shaped cross section in *Protosiren* vertebrae. Scale is in cm.



FIG. 3 — Anterior ribs of Eocene sirenians from Pakistan and Egypt. A-B, second and first ribs of *Eotheroides* sp. (UM uncat.) from the latest middle Eocene of Egypt. C, first right rib of *Protosiren eoethene* (GSP-UM 3487; holotype) from the early middle Eocene of Pakistan. D, first right rib of the Egyptian *Protosiren smithae* (UM 101224) from the latest middle Eocene of Egypt. E, first right rib of *Protosiren sattaensis* (GSP-UM 3001) from the late middle Eocene of Pakistan. F-G, enlarged views of the proximal ends of the head of the first rib of *Protosiren eoethene* (GSP-UM 3487, holotype) from the Eocene of Pakistan and *Protosiren smithae* (UM 101224) from the latest middle Eocene of Egypt. Note the lack of well-formed joint surfaces on articular processes of both ribs. Scales are in cm.

the large oval to keyhole-shaped cross section typical of *Protosiren*. Zygapophyses are developed high on the neural arch, and metapophyses are prominent. Neural spines are gracile and not nearly so robust as those in some later *Protosiren*. Demifacets for rib articulations are again poorly

TABLE 1 — Measurements (mm) of thoracic vertebrae of GSP-UM 3487, holotype of *Protosiren eothene*. Abbreviations: L, length; W, cranial width; H, height; NAH, neural arch height; NCW, neural canal width; NCH, neural canal height. Measurements marked with asterisks are estimated.

Vertebra	Centrum			Neural arch	
	L	W	H	NCW	NCH
Th1	22.3	41.0	21.0	--	--
Th2	22.5	40.0	25.0	--	--
Th3	25.0	42.0	31.0	35.0	37.8
Th4	27.0	43.6	32.0	33.0	31.6
Th5	28.0	39.5	31.0	36.0	37.0
Th6	29.4	51.0	32.0	--	--
Th7	29.8	28.5	25.0*	--	--
Th8	31.3	37.0	25.0	--	--
Th12?	35.1	29.0	32.0	--	--
Th14?	35.8	37.0	25.0	--	--

preserved but clearly evident on the centra. Anterolateral surfaces of metapophyses generally have small surfaces for articulation with, or ligamentous connection to, rib tubercula.

Thoracic vertebra T6 is represented by a simple, massive, isolated centrum with weakly convex cranial and caudal articular surfaces. This is broader than high, but not as broad as those of later *Protosiren*. Demifacets for rib articulations are shallow but evident. T7-T8, T12?, and T14? are represented by deformed centra lacking neural arches. Pedicles of neural arches are longer anteroposteriorly than those of T4 and T5. Again, as expected for thoracics, these centra retain small demifacets for rib articulations.

The best preserved rib is a complete right R1 (Fig. 3c,f). This is gracile, curved, and anteroposteriorly flattened like those of later *Protosiren*. It lacks pachyostosis but is dense and osteosclerotic. The head (caput costae) of this rib is weathered slightly, but it has a concavoconvex articular surface (Fig. 3f) that looks like it may have retained a synovial or partially synovial articulation with the centrum of T1. It is not so conspicuously concave and ligamentous as the head of R1 in *P. smithae* (Fig. 3g). The tubercle (tuberculum costae) of R1 is much smaller in comparison to that of *P. smithae*, and here again it appears possibly to have been synovial or partially synovial.

One proximal piece of a rib, probably from the middle of the rib series, is circular in cross section, indicating that some ribs were more robust than others. Cortical bone here is thick and dense, but it also appears that bone in the center of the rib was cancellous. This rib piece has a distinctively spherical tuberculum. The head of this rib is missing, but enough remains of the base to see that the head was flattened transversely like those in *Eosiren* and unlike any in later *Protosiren*.

DISCUSSION

Vertebrae and ribs of *Protosiren* are sometimes confused with those of archaeocetes because they lack the pachyostosis and osteosclerosis characteristic of contemporary sirenians in the families Prorastomidae and Dugongidae. Such an example is shown in Figure 4, a specimen of *Protosiren fraasi* from the Mokattam middle Eocene of Egypt that lacks associated cranial material and has long been identified, questionably, as *Protocetus*. Skulls of early sirenians and cetaceans are distinctive of course, but so are their vertebrae and ribs. Thoracics of *Protosiren* have large, deep



FIG. 4 — Vertebrae and ribs of *Protosiren fraasi* (SMNS 11090) from the lower Mokattam stage, early middle Eocene of Egypt. Note the rugose articular surface of the capitulum and the reduced tuberculum on the ribs, and the large oval to keyhole-shaped neural canals perforating thoracic vertebrae (bottom row). Scale is in cm.

neural canals that are oval to keyhole-shaped in cross section (seen in anterior or posterior view). Late species of *Protosiren* have demifacets on the lateral surfaces of the vertebrae for articulation with rib capitula that are deeply excavated and rugose, indicating the presence of a ligamentous or cartilagenous rather than smooth synovial articulation. Similarly, articular facets on rib capitula are relatively flat to concave, with a rugose surface again indicating the presence of a ligamentous or cartilagenous connection rather than development of a smooth bony surface to support a synovial articulation. Sickenberg (1934: p. 88) interpreted these unusual rib articulations in *P. fraasi* to indicate distinctive respiratory mechanics. *P. eoethene* described here is more generalized in retaining a synovial component of at least some rib head articulations, and it is probably primitive compared to later *Protosiren* in this respect. Tubercula on ribs of *P. fraasi* and *P. eoethene* are much smaller than those of later *Protosiren* and this too is probably primitive. The principal characteristic that all species share is the presence of unusually large neural canals.

Discovery of a species of *Protosiren* in the early Lutetian (early middle Eocene) of eastern Tethys enhances the possibility that the Ypresian (early Eocene) vertebra referred to *Ischatherium subathuensis* by Sahni and Kumar (1980) and Sahni et al. (1980) might be a sirenian, although, if so, it would be a prorastomid or dugongid rather than a protosirenid. If the vertebra referred to *Ischatherium* is a sirenian it would be the oldest known anywhere (it could also be an anthracobunid or moeritheriid proboscidean). *Protosiren eoethene* is the oldest protosirenid, and it is virtually the same age as the prorastomids *Prorastomus sirenoides* (Owen, 1855; Savage et al., 1994) and *Pezosiren portelli* (Domning, 2001) from the early middle Eocene of Jamaica. Substantial morphological diversity and such a broad geographic distribution so early in the middle Eocene suggests that Sirenia diversified in the early Eocene, paralleling the diversification of archaeocete Cetacea in Tethys (Bajpai and Gingerich, 1998; Gingerich et al., 2001a), and diversification of other orders of mammals on land.

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