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# A new middle Eocene sirenian (Mammalia, Protosirenidae) from India

Sunil Bajpai, Roorkee, Daryl P. Domning, Washington DC, Debi P. Das, Kolkata and Vijay P. Mishra, Lucknow

With 5 figures and 1 table

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**Abstract:** *Ashokia antiqua* is a new genus and species of protosirenid sirenian based on a subadult skull from the early middle Eocene (Lutetian) Harudi Formation of Kutch district, Gujarat State, western India. While more derived than prorastomids, and more primitive than trichechids or dugongids, in comparison with other protosirenids it displays a mosaic of primitive and derived character states that places it at the evolutionary grade of a relatively primitive protosirenid. Cladistically, its sister group may be an unnamed genus and species of protosirenid from the Lutetian of Libya, which shares with it several synapomorphies of the zygomatic arch and ear region. This relationship with the unpublished Libyan form reinforces a pattern in Eocene paleobiogeography previously noted by SAGNE (2001): generically-distinct and endemic sirenian faunas on the north and south shores, respectively, of the former Tethys Seaway. The Kutch sirenian fauna, with *Eotheroides, Eosiren, Protosiren*, and now a relative of the Libyan protosirenid, resembles the fauna from North Africa, while the European genera *Halitherium, Prototherium*, and *Sirenavus* are absent – as predicted by SAGNE's (2001) hypothesis.

Key words: Sirenia, Protosirenidae, Eocene, India, Tethys, palaeobiogeography.

# 1. Introduction

The Order Sirenia (sea cows; dugongs and manatees) comprises large herbivorous marine mammals and has a 50-million-year-long fossil record extended throughout much of the world. Sirenian evolution is especially well documented in Europe, the Mediterranean-North African region, the West Atlantic-Caribbean region, and both American and Asian (Japanese) shores of the North Pacific Ocean (DOM-NING 2001 a). However, the margins of the Indian Ocean have barely begun to be sampled for fossils of these animals. Apart from isolated and fragmentary finds in Madagascar, Java, Pakistan, and Sri Lanka,

nearly all the known sirenian fossils from this region are from India, and those are entirely from the district of Kutch (also spelled Kachchh) in Gujarat State, western India (reviewed by BAJPAI & DOMNING 1997).

The Order Sirenia is divided into four families (DOMNING 2001 a): two that are extinct and known only from the Eocene epoch (Prorastomidae and Protosirenidae), and two with living members: the manatees of the Atlantic basin (Trichechidae), and the dugongs (Dugongidae), with a worldwide Eocene-Pliocene distribution, but represented today only by *Dugong dugon* which occurs throughout the tropical Indian and southwest Pacific oceans. Two of these



**Fig. 1.** *Ashokia antiqua* n. sp. (holotype, K60/448): skull, photograph (A) and sketch (B) in dorsal view. Scale = 5 cm. Abbreviations for Figs. 1-5: ACA, anterior opening of alisphenoid canal; ACP, posterior opening of alisphenoid canal; AS, alisphenoid; BO, basioccipital; BS, basisphenoid; EAM, external auditory meatus; EO, exoccipital; FO, foramen ovale; FR, frontal; HF, hypoglossal foramen; IOC, natural cast of left infraorbital canal; IOF, infraorbital foramen; J, jugal; L, lacrimal; M2, remnants of second upper molar; M3, remnants of incompletely erupted third upper molar; MF, mastoid foramen; MX, maxilla; N, nasal; OC, occipital condyle; PA, parietal; PAL, palatine; PE, pars petrosa of periotic; PM, premaxilla; PP, paroccipital process (broken); PT, pterygoid process (broken); SF, supracondylar fossa; SO, supraoccipital; SQ, squamosal; SR, sigmoid ridge of squamosal; T, tympanic; TT, tegmen tympani. Dashed lines indicate interpretations of sutures or other features; pattern of diagonal lines indicates broken bone surface; stippling indicates matrix.

families are represented among the fossils so far known from two different time intervals in Kutch: middle Eocene protosirenids, middle Eocene dugongids, and late Oligocene to early Miocene dugongids. Here we describe a new middle Eocene protosirenid from Kutch, previously mentioned by BASU et al. (1991), and possibly the most primitive member of that family yet known. Abbreviations: GSI, Palaeontology Division - I, Geological Survey of India, Kolkata, India; IITR-SB, Paleontology Laboratory, Department of Earth Sciences, Indian Institute of Technology, Roorkee, Uttarakhand, India; c, character state as defined and numbered by DOMNING (1994) or BAJPAI & DOMNING (1997): e.g., c. 140(1) refers to character number 140 and associated character state one. Note that for character 74, the hypothesized polarities of the states 0 and 1 have been reversed from their earlier definitions. (A thorough revision of DOMNING's 1994 phylogenetic analysis of sirenians is in progress, and will be published at a later date together with an updated list of characters and character states.)

### 2. Systematic paleontology

Class Mammalia LINNAEUS, 1758 Mirorder Tethytheria MCKENNA, 1975 Order Sirenia ILLIGER, 1811 Family Protosirenidae SICKENBERG, 1934 Genus *Ashokia*, new

### Ashokia antiqua n. sp. Figs. 1-5, Table 1

Holotype: K 60/448, subadult skull lacking the rostrum, left zygomatic arch, left exoccipital, left pterygoid process, left maxillary alveolar process, and the crowns of the right cheek teeth.

Etymology: The genus is named for Dr. ASHOK SAHNI, in honor of his numerous contributions to Indian paleontology. Its gender is feminine. The species epithet (Latin: ancient) refers to its standing as one of the oldest known sirenians, and one of the most plesiomorphic other than members of the Prorastomidae.

Type locality: About 1 km E of Waghapadar, district of Kutch, Gujarat State, India; lat. 23° 28' 50" N, long. 68° 45' 00" E (BASU et al. 1991; see map, BAJPAI et al. 2006: fig. 1).

Type horizon and age: Gypsified clay of the Harudi Formation, near its contact with the underlying, lower Eocene Naredi Formation (formerly the horizon of the specimen was referred to the Naredi Formation; BASU et al. 1991). Early middle Eocene (Lutetian).

Diagnosis: A protosirenid sirenian sharing with its apparent sister group, the unnamed Libyan protosirenid described by HEAL (1973), the following synapomorphies: premaxilla-frontal contact lost due to intrusion of the lacrimal between them; jugal with elongate midsection; squamosal zygomatic process posteriorly broad but abruptly tapering anteriorly; ventral side of mastoid foramen extended backward; and tegmen tympani with ventral protuberance related to (but not fused with) the alisphenoid. It is more primitive than the Libyan form in its narrower frontal roof and lack of a processus retroversus on the squamosal, but more derived than the Libyan genus in displaying elevation of the zygomatic-orbital bridge of the maxilla, a prominent sigmoid ridge on the squamosal, a horizontal ridge along the ventral side of the mastoid foramen, and a wider external auditory meatus.

Description: This description emphasizes characters considered to be of phylogenetic value and defined by DOMNING (1994) and/or BAJPAI & DOMNING (1997). The unique holotype skull is gypsified and presents problems of preparation; some details are not clearly visualized. It has also been obliquely deformed tectonically, with destruction of the left cheek tooth row and pterygoid process. The last molar seems to have been incompletely erupted, and the basioccipital-basisphenoid suture may be unfused, suggesting that this individual was subadult.

Premaxilla: The posterior end of the mesorostral fossa is preserved, bordered as usual by the nasal processes of the premaxillae (Fig. 1). The external nares are retracted just to the level of the anterior margins of the orbits [c. 8(1)]. The nasal process is long [c. 7(0)], thin and tapering at its posterior end [c. 6(0)], and contacts the nasal and the frontal [c. 9(1)]. It slopes steeply upward (Fig. 2) as in the primitive dugongid *Eotheroides aegyptiacum*.

Nasal: The nasals are large [c. 32(0)] and meet in the midline [c. 31(0)]. Their posterior border is notched by a small anterior extension of the frontals. They are rather strongly arched, as in *Eotheroides*. Although their anterior border is slightly damaged, it appears nearly complete; there is no nasal incisure [c. 37(0)].

Ethmoid: Covered by matrix; details not visible.

Vomer: Partially preserved in the posterior portion of the mesorostral fossa. As in other sirenians, it forms a trough on the floor of the fossa that supported the cartilage of the nasal septum.

Lacrimal: Large, occupying an area of  $2 \ge 2$  cm on the anteromedial wall of the orbit, with a rounded border that prominently protrudes anterolaterad. It is adequately exposed to determine that no foramen or nasolacrimal canal is present [c. 91(1)]. The lacrimal is wedged a short distance in between the lateral portions of the premaxilla and the frontal, as in other Eocene sirenians (this is discernible on the undistorted right side, but on the left, the tectonic distortion of the skull has produced a transverse right-lateral fault through the orbital region and pushed medially the bones anterior to the supraorbital process, obscuring the anatomical relationships).

Frontal: The supraorbital process is thin (circa 1 cm) and flattened dorsoventrally in a nearly horizontal plane, and its lateral margin is not indented [c. 36(0), 43(0), 44(0)]. The frontal roof is slightly convex [c. 42(0)]. The frontoparietal suture lies about 65 mm behind the nasal-frontal suture in the midline, and 130 mm anterior to the rear surface of the nuchal crest (= external occipital protuberance), making the frontal roof short relative to the parietal.

Parietal: Although the parietal roof is somewhat damaged, it seems clear that it is rounded with a slight median furrow posteriorly, as in other protosirenids; a sagittal crest



**Fig. 2.** Ashokia antiqua n. sp. (holotype, K 60/448): skull, photograph (A) and sketch (B) in right lateral view. Abbreviations as in Fig. 1.

is evidently absent [c. 51(1)]. The temporal crests lie close to the midline (about 1 cm apart just anterior to the nuchal crest) and are concave laterad. The nuchal crest is thick and concave posteriorly as in *Protosiren*.

Supraoccipital: Its surface forms an angle of about 115° with the plane of the parietal roof. The ends of the nuchal crest slightly overhang the lateral margins of the bone, making the supraoccipital wider dorsally than ventrally. Only a slight convexity occupies the position of an external occipital protuberance.

Exoccipital: The dorsolateral border is rounded and smooth, and less than 1 cm thick [c. 70(0)]. The exoccipitals meet in a suture above the foramen magnum [c. 66(0)]. There is a deep supracondylar fossa above the occipital condyle [c. 67(2)]. The paroccipital process is broken, but it would

have extended below the condyle, since even its broken edge extends as far ventrally as the condyle (Fig. 5). There is a single large hypoglossal foramen.

Basioccipital: Bears rugose convexity for longus capitis muscle insertions as in other sirenians.

Basisphenoid, Presphenoid, Orbitosphenoid: Poorly preserved or not exposed.

Alisphenoid: A large alisphenoid canal is present [c. 101(0)]. Its posterior opening, about 5 mm in diameter, is on the posterolateral side of the alisphenoid; its anterior opening is about 18 mm farther forward. A bifurcate canal with a dual opening, as reported for the Libyan protosirenid (HEAL 1973), is not apparent. The foramen ovale, some 7 mm in diameter, is mostly if not entirely encircled by bone [c. 103(1?)]; the posterad opening of this apparent notch





**Fig. 3.** Ashokia antiqua n. sp. (holotype, K60/448): detail of right basicranial region, photograph (A) and sketch (B) in ventrolateral view. Abbreviations as in Fig. 1.

is blocked by a projection of the tegmen tympani (see below).

Pterygoid: The pterygoid region is short anteroposteriorly, as in all sirenians except prorastomids. The pterygoid process is elongated ventrally and robust, about 18 mm thick. A pterygoid fossa was probably absent [c. 102(0?)].

Palatine: Poorly preserved; the palatal portion is evidently thin [c. 16(0)], but other aspects of its form and extent are not discernible [c. 97(?), 99(?)].

Maxilla: The zygomatic-orbital bridge is long anteroposteriorly [c. 14(0)], with a thick posterior edge and probably a thin anterior edge; it is elevated above the palate and 2 cm or more above the alveolar margin [c. 11(1)]. This degree of elevation of the bridge is unique among the Sirenia. The infraorbital foramen is small, with diameters of about 10 x 12 mm where preserved on the left side as a natural cast [c. 13(0)]. The palatal gutter anterior to the molars is 1 cm deep and a maximum of 1.5 cm wide.



Fig. 4. Ashokia antiqua n. sp. (holotype, K 60/448): skull, photograph (A) and sketch (B) in ventral view. Abbreviations as in Fig. 1.

Squamosal: The cranial portion does not extend as far up as where the temporal crest would normally be, ending about 1 cm below the level of the parietal roof [c. 76(0)]. The glenoid area is a broad transverse convexity. The postglenoid process is small. The posttympanic process has no distinct anteriorly-projecting facet for insertion of the sternomastoid muscle [c.73(0)]; its anterior side descends straight vertically from the top of the auditory meatus, as in Anomotherium langewieschei (SIEGFRIED, 1965: fig. 4) and Miosiren kocki (SICKENBERG, 1934: pl. 10, fig. 2). The sigmoid ridge is prominent [c. 74(0)]. Perpendicular to its midsection, just below the level of the zygomatic root, another ridge extends backward to the posterior edge of the squamosal at the ventral end of the mastoid foramen. The external auditory meatus is slightly more than 1 cm long mediolaterally [c. 75(0)], and is slightly wider anteroposteriorly than high  $(13 \times 8 \text{ mm})$  [c. 82(1), tending toward 82(2)].

A processus retroversus is absent [c. 77(0)]; a sharp ridge runs straight posterodorsally from the posterior end of the zygomatic process. The medial side of the zygomatic process is not swollen [c. 84(0)]. The zygomatic process is very broad posteriorly, but rapidly tapers anteriorly.

Jugal: The ventral extremity lies far posterior to the orbit [c. 85(0)]. The preorbital process is flat and thin [c. 88(0)] and does not contact the premaxilla [c. 87(0)]. The posterior (zygomatic) process is much longer than the diameter of the orbit [c. 89(0)], reaching the posterior edge of the temporal condyle (and displaced medially to overlie the condyle). The overall form of the jugal is highly unusual, in that it is very long and the postorbital process is widely separated horizontally from both the ventral extremity and the front of the squamosal zygomatic process. There is no dorsal process immediately in front of the tip of the squamosal zygomatic process.



Fig. 5. Ashokia antiqua (holotype, K 60/448): skull, photograph (A) and sketch (B) in posterior view. Abbreviations as in Fig. 1.

Ear region: The pars mastoidea of the periotic is partly visible through the mastoid foramen. The ventral part of the juncture between pars mastoidea and tegmen tympani is visible through the external auditory meatus (evidently because the periotic has slipped downward and medially a short distance out of its socket on the inner side of the squamosal); the notch marking this juncture is narrow, almost V-shaped. The tympanic ring is of the typical sirenian teardrop form, with its point directed anteroventrad. Between its anteroventral tip (displaced downward and medially along with the periotic) and the basioccipital is a mass of bone that evidently represents the anteromedial extremity of the tegmen tympani. Along the anteroventral edge of this bone, a transverse ridge extends laterad between the tympanic and the alisphenoid, and then turns sharply anterad, ending in (and blocking) the constricted posterior opening of the incisure that forms the foramen ovale. This ridge may correspond to a protuberance of the tegmen tympani in the Libyan protosirenid illustrated by HEAL (1973: figs. 11, 16), and to the part of the tegmen tympani that is fused to the alisphenoid in *Prorastomus sirenoides*; but no such synostosis exists in the Libyan protosirenid, nor can we demonstrate one in Ashokia [c. 115(1?)]. In P. sirenoides and the Libyan protosirenid, however, the protuberance of the tegmen tympani is a longitudinal ridge lying in a parasagittal plane and well lateral to the foramen ovale, and therefore it seemingly differs from the condition in Ashokia. Furthermore, in the Libyan protosirenid this protuberance seems to have served as the anterior point of attachment of the tympanic ring (as is the case in later sirenians including Trichechus and Dugong), whereas the protuberance in Ashokia is well separated from the tympanic attachments as in Prorastomus. Therefore the anatomy of this region in Ashokia remains to be clarified. No auditory ossicles are visible.

Dentition: Remnants of the right cheektooth row are present [c. 151(0), 158(0)], including fragments of smooth enamel [c. 156(0)], but badly damaged and difficult to distinguish. The crown length of the partly erupted, broken right M3 is estimated at 23 mm. Anterior to it are broken roots of five teeth which collectively have a length of 87 mm; the front of this series of five teeth lies at the level of the infraorbital foramen. The third and fourth in the series appear to have been triangular, 3-rooted teeth (M1-2). The second tooth from the front also appears not to have been circular; hence it was probably DP5 rather than P5. Whether it would have been replaced at maturity is unknown [c. 146(?)]. The root of the anteromost tooth is about 17 mm in mesiodistal diameter and 14 mm in labiolingual diameter. Broken off just below the crown, it does not reveal whether this tooth was 3-rooted (hence DP4) or single-rooted (P4). Separated from this tooth by a 1-cm diastema is the remnant of an alveolus for a single-rooted tooth (P3), which has a counterpart on the left side. Preceding these at a distance of 1 cm (right) or 0.5 cm (left) is a similar pair of alveoli (P2). Immediately in front of the right P2 (but with no visible counterpart on the left) is what may be the broken root of a ?DP or ?P1, 8 mm in diameter. The rostrum is broken off 1 cm anterior to this. Judging from other protosirenids and Eocene sirenians in general, the dental formula is inferred to have been I 3, C 1, P 5, M 3.

#### 3. Comparisons

*Ashokia* is distinguished from prorastomids, the most primitive family of sirenians, by the following characters: a shortened pterygoid region; evident lack of the sagittal crest seen in *Pezosiren* [c. 51(1)]; a prominent sigmoid ridge on the squamosal [c. 74(0)]; a wider

| Dimension |   | E/GSI/Pal-I |
|-----------|---|-------------|
| BI        | Rear of occipital condyles to anterior end of interfrontal suture                     | 233         |
| ~~.       | Rear of occipital condyles to anterior end of internasal suture                       | 285         |
| CC'       | Zygomatic breadth   | 196e        |
| cc'       | Breadth across exoccipitals   | 134e        |
| de        | Top of supraoccipital to ventral sides of occipital condyles                          | 112e        |
| F         | Length, level of tips of supraorbital processes to frontoparietal suture in midline   | 115e        |
| FF'       | Breadth across supraorbital processes   | 114         |
| ff'       | Breadth across occipital condyles   | 126e        |
| GG'       | Breadth of cranium at frontoparietal suture   | 58 e        |
| gg'       | Width of foramen magnum   | 48 e        |
| hi        | Height of foramen magnum  | 33 e        |
| JJ'       | Width of mesorostral fossa  | 35          |
| no        | Anteroposterior length of zygomatic-orbital bridge of maxilla                         | 73 e        |
| OP        | Length of zygomatic process of squamosal  | 101         |
| OT        | Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen     | 137e        |
| Р         | Length of parietals, frontoparietal suture to rear of external occipital protuberance | 130e        |
| pq        | Length of row of tooth alveoli (DP5-M3)   | 72 e        |
| OR .      | Anteroposterior length of root of zygomatic process of squamosal                      | 50e         |
| ss'       | Breadth across sigmoid ridges of squamosals   | 170e        |
| ST        | Length of cranial portion of squamosal  | 104e        |
| Т         | Dorsoventral thickness of zygomatic-orbital bridge                                    | 16          |
| UV        | Height of posterior part of cranial portion of squamosal                              | 105         |
| WX        | Dorsoventral breadth of zygomatic process   | 42          |
| YZ        | Length of jugal   | 186e        |
| LFr       | Length of frontals in midline   | 65 e        |
|           | Length of nasals in midline   | 60e         |
| HSo       | Height of supraoccipital  | 52 e        |
| WSo       | Width of supraoccipital   | 78e         |

**Table 1.** Measurements (in mm) of skull of *Ashokia antiqua* (holotype, K 60/448). Dimensions are designated by letters as in DOMNING (1988) and earlier works; e = estimated, N/A = not applicable, + = measurement on incomplete element.

external auditory meatus [c. 82(1)] and a periotic not fused to the alisphenoid [c. 115(1)], both in contrast to *Prorastomus* though in agreement with *Pezosiren*; and a foramen ovale opened into a notch [c. 103(1)]. All of these are also synapomorphies found in sirenians other than prorastomids.

Ashokia is more derived than other protosirenids (including the unnamed Libyan form) in having the prominent sigmoid ridge [c. 74(0) of DOMNING (1994); polarity now altered], the wider external auditory meatus [c. 82(1)], and an elevated zygomatic-orbital bridge of the maxilla [c. 11(1)].

Ashokia is more primitive than other known protosirenids in having a thinner exoccipital border [c. 70(0)] and an anteriorly-tapering zygomatic process of the squamosal. It is more primitive than *Protosiren fraasi* and *P. smithae* in its larger nasals [c. 32(0] and narrower anterior palatal gutter. It is also more primitive than P. smithae in its shorter nasal process of the premaxilla and its contact between the exoccipitals [c. 66(0)]. It is more primitive than the undescribed Libyan protosirenid in its lack of a processus retroversus on the squamosal [c. 77(0)]; its retention of temporal crests; its retention of contact between the premaxilla and frontal, rather than separation of these by the lacrimal; its narrower anterior palatal gutter (1.5 cm wide, vs. 2.6-3.3 cm in the Libyan form); and possibly its separation between the ventral protuberance of the tegmen tympani and the anterior attachment of the tympanic. Also, the skull roof of the Libyan protosirenid widens noticeably from the parietals to the frontals, but in Ashokia the parietal roof and the posterior part of the frontal roof are about equal in width.

Ashokia is more primitive than trichechids (including miosirenines) and primitive dugongids in having a thinner exoccipital border [c. 70(0)], a longer external auditory meatus [c. 75(0)], an alisphenoid canal [c. 101(0)], and no pterygoid fossa [c. 102(0)]. It is additionally more primitive than trichechids (including miosirenines) in its squamosal that does not reach the level of the temporal crest [c. 76(0)] and an external auditory meatus that is not broadened [c. 82(1)]. Finally, it is more plesiomorphic than primitive dugongids in its lack of a processus retroversus [c. 77(0)].

Therefore, by being more derived than prorastomids and more primitive than trichechids or dugongids, *Ashokia* represents the evolutionary grade of the (possibly paraphyletic) Protosirenidae. Among known protosirenids, it shows some character states that are more plesiomorphic or more apomorphic than others; no clear overall phyletic pattern within this family is yet apparent.

However, Ashokia does have several features that seem to ally it uniquely with the unnamed genus and species of protosirenid from the Lutetian of Libya (HEAL 1973). In both forms, the jugal has an elongate midsection, with the postorbital process well separated horizontally from the squamosal, and no separate dorsal process immediately in front of the squamosal. (The ventral process of the jugal, as in other primitive sirenians, lies well behind the orbit.) The zygomatic process of the squamosal is dorsoventrally broad in its posterior portion, but abruptly tapers toward its anterior tip. The posterior border of the squamosal is (as usual) deeply notched by the mastoid foramen, but the ventral side of this notch extends farther posterad than usual (uniquely in Ashokia, the notch is also bordered beneath by a horizontal ridge connected to the sigmoid ridge). There is a ventral protuberance from the tip of the tegmen tympani that is closely related to the alisphenoid (but not fused to it as in Prorastomus sirenoides, and not connected to the tympanic ring as in the Libyan protosirenid). The ratio of midsagittal lengths of frontal roof to parietal roof (0.50) is smaller than that of more typical sirenians (e.g., Protosiren fraasi: 0.63-0.98), apparently a modification in the direction of the more extreme Libyan protosirenid (0.38-0.40).

Finally, the form of the posttympanic process in *Ashokia* resembles that of the miosirenines *Anomo-therium* and *Miosiren*. This tends to support the relationship between protosirenids and miosirenines (and other trichechids) hypothesized by SAGNE (2001).

The above-cited resemblances clearly place this new sirenian in the same clade as the Libyan protosirenid. However, since *Ashokia* also displays characters more derived than the Libyan taxon – elevation of zygomatic-orbital bridge, c.11(1); more prominent sigmoid ridge, c.74(0); wider external auditory meatus, c.82(1) – it cannot be considered a structural ancestor of the latter, but rather a nearly-contemporary sister taxon.

On the whole, *Ashokia* is about as primitive as any protosirenid; and given its Lutetian date, it comes close to being as old as any presently-recognized sirenian (only *Prorastomus sirenoides* may be as old as late early Eocene). Thus *Ashokia antiqua* has a fair claim to its name.

Also reported from the Harudi Formation along with Ashokia, and therefore likely to have lived sympatrically with it in the middle Eocene of Kutch, is material of Protosiren sp. (BAJPAI et al. 2006). Characters observed to distinguish the latter from Ashokia include its narrow external auditory meatus [c. 82(0)], very long lateral border of the supraorbital process, and shallower and wider anterior palatal gutter (2 cm wide in the Kutch Protosiren sp. vs. 1.5 cm in A. antiqua). The former condition is considered by SAGNE (2001: c. 5) to be a synapomorphy uniting protosirenids and trichechids. Interestingly, one of these Kutch specimens (IITR-SB 2865; BAJPAI et al. 2006: fig. 2B) has an overall size and skull roof proportions resembling those of the Libyan protosirenid or Ashokia (nasofrontal contact damaged; minimum likely midsagittal length of dorsal exposure of nasals = 58e mm, maximum possible LFr = 49e mm, P = 98emm; LFr/P ratio = 0.50), though in other characters, including its narrow external auditory meatus [c. 82(0)], it agrees with other *Protosiren*. Collection of more and better specimens from the Kutch deposits will be necessary to resolve the questions about diversity and identity of these animals.

## 4. Discussion

The first recorded Eocene sirenians from India that were referable to known genera were reported by BAJPAI et al. (2006). These comprised several skull fragments and other specimens referred to *Protosiren* sp.; the new species *Eotheroides babiae*, based on a mandible and other bones; and two other mandibles and a scapula referred to *Eosiren* sp. indet. All are from the early middle Eocene (Lutetian) Harudi Formation. This fauna has the same generic composition as the Lutetian sirenian fauna of Egypt (DOMNING et al. in press). This is not surprising, since Egypt and India were then connected by the continuous Tethys Seaway (CLEMENTZ et al. 2006: fig. 5).

SAGNE (2001) was the first to call attention to an apparent faunal differentiation at the generic level between Eocene and Oligocene sirenians on the north shore (Europe) and south shore (North Africa), respectively, of the former Tethys Seaway. Within the Old World, *Sirenavus, Prototherium*, and *Halitherium* seemed to be confined to Europe, while *Eotheroides, Eosiren*, and an unpublished genus of protosirenid from Libya appeared to be endemic to North Africa. Only *Protosiren* was reported from both continents, and its single supposed European occurrence (*Protosiren minima* in southwestern France) is questionable (see SICKENBERG 1934: 186-191, "*Protosiren* (*?*) *dubia*").

Subsequent discoveries farther east have followed the same pattern: new material from Madagascar appears referable to Eotheroides and cf. Eosiren (SAMONDS et al. 2007), and the only identifiable specimens from Pakistan are referred to Protosiren (ZALMOUT et al. 2003). A specimen from Kutch formerly referred to Protosiren by SAHNI & MISHRA (1975) has since been reidentified as a cetacean by GINGERICH et al. (1993). Along with Africa, both of these landmasses lay south of Tethys. The Kutch fauna reported by BAJPAI et al. (2006) likewise matches the North African fauna, supporting SAGNE's hypothesis of north/south Tethyan endemism. The new protosirenid Ashokia antiqua continues this pattern, as it appears most closely related to the Libyan protosirenid described by HEAL (1973) in his unpublished dissertation. If further study of this new Libyan genus (SORBI & DOMNING, in preparation) confirms that it and Ashokia form a distinctive clade within the Protosirenidae, then this will add still more weight to the conclusion that the northern and southern Tethys shores were, for perhaps 20 million years, separate zoogeographic provinces, at least for sirenians.

During the Quaternary and down to the present, no two genera of sirenians are known to have occurred sympatrically anywhere in the world. In recent years, however, multi-genus sirenian paleocommunities have been discovered to be the rule for the Tertiary, not only in Tethys but also in the Caribbean-western Atlantic and the eastern North Pacific. This poses interesting problems of functional anatomy, coevolution with marine plant resources, and feeding-niche partitioning (DOMNING 2001B; DOMNING & BEATTY 2007). As the known diversity of fossil sirenians continues its current rapid growth (in contrast to the order's depauperate state today), these problems will become more challenging.

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#### Addresses of the authors:

SUNIL BAJPAI, Department of Earth Sciences, Indian Institute of Technology, Roorkee 247667, India; e-mail: sunilfes@iitr.ernet.in

DARYL P. DOMNING, Department of Anatomy, Howard University, Washington, DC 20059, USA; e-mail: ddomning@howard.edu

D. P. DAS, Geological Survey of India, Palaeontology Division – I, Kolkata 700016, India;

V. P. MISHRA, Palaeontology Division, Geological Survey of India, Lucknow 226024, India.