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ANN ARBOR**

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Philip D. Gingerich, Director

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A NEW EARLY OLIGOCENE DUGONGID (MAMMALIA, SIRENIA) FROM FAYUM PROVINCE, EGYPT

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AND FRIDERUN A. ANKEL-SIMONS³

Abstract—*Eosiren imenti*, new species, is described on the basis of a cranium from the early Oligocene Gebel Qatrani Formation in Fayum Province, Egypt. The new species is similar to, but more derived than, late Eocene species *Eosiren libyca* and "*Prototherium*" *intermedium*, and it is closer cladistically to its still more derived contemporary *Halitherium schinzii*. Occurrence in predominantly fluviatile Gebel Qatrani deposits suggests that this primitive dugongid may have had a wide salinity tolerance in the manner of modern Florida manatees. Alternatively, it may have been washed inland during a storm.

INTRODUCTION

Fossil Sirenia of the Fayum Province of Egypt have been studied since the beginning of this century, when Andrews (1902) first described *Eosiren libyca* from the late Eocene (Priabonian) Qasr el-Sagha Formation. Subsequent workers, chiefly Abel and Sickenberg, added much to our knowledge of this species and other Fayum sirenians. Recently, Gingerich and colleagues have extended the Fayum sirenian record back into the middle Eocene (Bartonian; Gingerich, 1992) in Wadi Hitan (Zeuglodon Valley) in western Fayum Province (see e.g., Domning and Gingerich, 1994). The youngest sirenians previously described from Fayum come from the Qasr el-Sagha Formation. However, in 1978 the sirenian remains described here were discovered, unexpectedly, in the overlying fluvial Gebel Qatrani Formation of early Oligocene age. At this writing the new specimen, a cranium with associated ribs, is the only sirenian known from the Oligocene of Egypt. It represents a new species of *Eosiren*.

The Gebel Qatrani sirenian has been mentioned in the literature in support of an early Oligocene age for the Gebel Qatrani Formation (Fleagle et al., 1986a). That age estimate, derived from the specimen's stage of evolution, was preliminary and based on examination of photographs of the skull early in 1986 (by D.P.D.). Our first opportunity to study the new

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skull first-hand in comparison to others from Fayum and elsewhere came in 1993. The result of this examination, together with subsequent research on the stratigraphy and age of Fayum deposits, has been slight modification of preliminary assessment of the specimen as evolutionarily intermediate between Eocene *Eosiren libyca* from Fayum and Oligocene *Halitherium schinzii* (Kaup, 1838) from Europe. It now appears that the Gebel Qatrani sirenian probably was derived from *E. libyca* as previously proposed, but independent evidence shows that it lived roughly coeval with *H. schinzii*. The Gebel Qatrani sirenian has at least one derived character state (separation of the nasals by an incisure) not seen in *Halitherium*.

ABBREVIATIONS

Institutional abbreviations used in this paper are as follows:

- CGM — Cairo Geological Museum, Cairo (Egypt)
 UM — Museum of Paleontology, University of Michigan, Ann Arbor (U.S.A.)

Standard measurements abbreviated in Table 1 follow Domning (1988). For ease of reference, the following text makes explicit reference to the sirenian characteristics and character states described and numbered in the phylogenetic analysis of Domning (1994; see also Table 2). Character numbers, often enclosed in square brackets, are prefaced with a fraktur C, followed by a colon and character state number, if any; e.g., [C 3:0] refers to character number three and associated character state zero.

SYSTEMATIC PALEONTOLOGY

- Class MAMMALIA Linnaeus, 1758
 Order SIRENIA Illiger, 1811
 Family DUGONGIDAE Gray, 1821
 Subfamily HALITHERIINAE (Carus, 1868) Abel, 1913
Eosiren Andrews, 1902

Eosiren imenti, new species
 Figs. 1-7

Eotheroides sp., Bown et al., 1982, p. 618.

Sirenian [gen. et sp. indet.], Fleagle et al., 1986a, p. 9.

Holotype.—CGM 40210 (Duke University field number 78-194), a well-preserved and relatively complete adult skull (lacking the basicranial region, the crowns of all but one of the teeth, and the mandible), and four associated right ribs. Casts of the skull and the one complete rib are deposited at the University of Michigan (UM 101947).

Type locality.—Level of Duke University fossil vertebrate Quarry O and about 200 m southeast of Quarry O itself (UTM grid zone 36R at coordinates 36265315 m E and 3281736 m N). This is about 2 km east of Quarry I, and about 6 meters below it stratigraphically (at about the 240-245 m level) in the Upper Fossil Wood Zone of the Gebel Qatrani Formation, Fayum Province, Egypt.

Age.—Early Oligocene (Rupelian; Bown and Kraus, 1988; Gingerich, 1992, 1993). The Gebel Qatrani Formation is a 340 m thick continental unit of brightly colored fluvial sediments that (para)conformably overlies the nearshore marine and fluvial Qasr el-Sagha Formation. The invertebrate fauna of the upper Qasr el-Sagha Formation is traditionally considered latest Eo-

TABLE 1. Measurements (mm) of skull of *Eosiren imenti* (holotype, CGM 40210). Letters in parentheses denote measurements used by Domning (1988). * = estimate, + = minimum estimate based on broken specimen.

Measurement	CGM 40210
Condylobasal length (AB)	400*
Height of jugal below orbit (ab)	44
Length of premaxillary symphysis (AH)	107+
Zygomatic breadth (CC')	184
Length of frontals, level of tips of supraorbital processes to rear of interfrontal suture (F)	133
Breadth across supraorbital processes (FF')	144*
Breadth of cranium at frontoparietal suture (GG')	69
Length of mesorostral fossa (HI)	144 (max.)
Width of mesorostral fossa (JJ')	55
Maximum height of rostrum (KL)	51
Posterior breadth of rostral masticating surface (MM')	62
Anteroposterior length of zygomatic-orbital bridge of maxilla (no)	61
Length of zygomatic process of squamosal (OP)	110
Length of parietals, frontoparietal suture to rear of external occipital protuberance (P)	97
Length of right row of tooth alveoli (P ² -M ³)	108
Anteroposterior length of root of zygomatic process of squamosal (QR)	43
Maximum width between labial edges of left and right alveoli (rr')	76
Dorsoventral thickness of zygomatic-orbital bridge (T)	16
Anterior breadth of rostral masticating surface (tt')	33
Dorsoventral breadth of zygomatic process (WX)	42
Length of jugal (YZ)	160*
Length of frontals in midline (LFr)	83+
Height of supraoccipital (HSo)	55+
Width of supraoccipital (WSo)	90

cene (Priabonian) in age, and the contact between the two units is dated to approximately the Eocene-Oligocene boundary (Bown and Kraus, 1988; Gingerich, 1992). The Gebel Qatrani Formation is capped by a pronounced erosional unconformity filled by Widan el-Faras Basalt, the base of which has been dated at 31.0 ± 1.0 Ma (Fleagle et al., 1986b) and more recently at 23.64 ± 0.035 Ma (Kappelman et al., 1992). Van Couvering and Harris (1991) proposed that the Gebel Qatrani Formation is all Eocene in age, but their interpretation of sea-level stratigraphy in Fayum is inconsistent with field observations (Gingerich, 1992, 1993). In spite of some continuing disagreement about exact placement of the Eocene-Oligocene boundary in Fayum, there is long-standing and broad current consensus that the upper part of the Gebel Qatrani Formation of interest here is Rupelian early Oligocene in age (Fleagle et al., 1986a,b; Bown and Kraus, 1988; Gingerich, 1992, 1993; Rasmussen et al., 1992; Kappelman et al., 1992). This is consistent with the stage of evolution of the new sirenian (see below) and other taxa in the mammalian fauna (Fleagle et al., 1986a,b).

Diagnosis.—*Eosiren* differing from *E. libyca* in having the following more derived character states: more overlap of premaxilla and frontal [C 5:1], narrower palate [C 17:1], nasals apparently separated in the midline by an incisure [C 31:1], no distinct crista intratemporalis [C 41:1], sharp and upraised temporal crests separated by a broadly concave parietal roof [C 59:3], more anteriorly located ventral process of jugal [C 85:1], and loss of I²⁻³ [C 143:1]. Shares all these states except C 31:1 with *Halitherium schinzii*; is more primitive than the latter in retaining canines [C 144:1] and DP or P¹ [C 145:0] (for differentiation from other taxa, see Table 3).



FIG. 1—Photographs of holotype cranium of *Eosiren imenti*, CGM 40210. A, lateral view. B, anterior view. Scale is in cm. See Fig. 2 (opposite) for explanation.

Etymology.—Conjectural vocalization of Old and Middle Egyptian *imnti*, Westerner, i.e., one of the dead (noun in apposition, treated as indeclinable), in allusion to the species' fossil occurrence in the Western Desert of Egypt.

Description

Premaxilla.—The premaxillary symphysis is somewhat enlarged relative to the cranium; the ratio of symphyseal length to estimated condylobasal length is close to and possibly exceeds 0.27 [© 3:1?]. The dorsal keel is rather thick anteriorly, and becomes broad and flat posteriorly. Its dorsal outline turns downward rather abruptly near the tip. The anterior end of the incisive foramen is undefined. The masticating surface of the rostrum is trapezoidal. A rather small terminal alveolus (measuring about 9×8 mm) contained a first incisor tusk; just ventral to this alveolus is a slightly smaller pit representing the premaxillary canal. The depth of the tusk alveolus seems to have been much less than half the length of the premaxillary

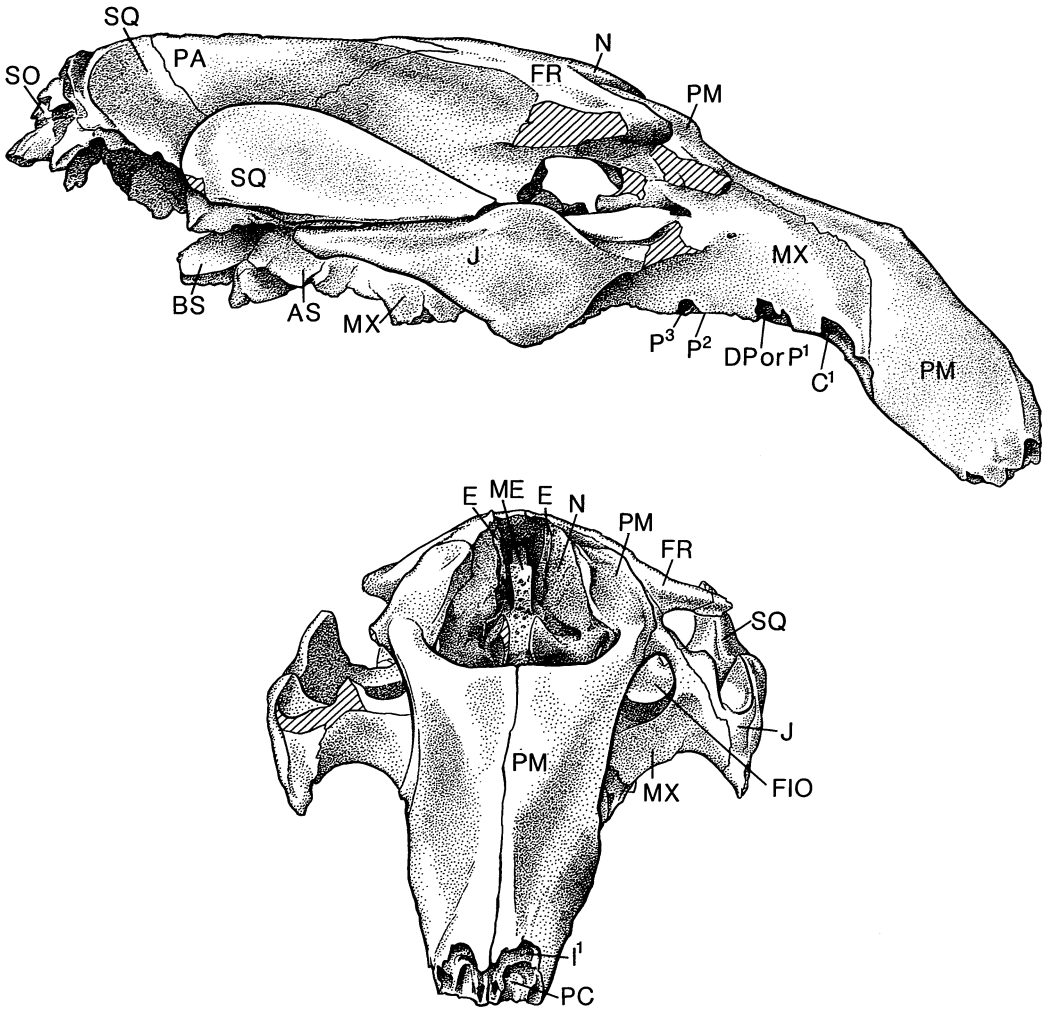


FIG. 2.—Outline drawings of holotype cranium of *Eosiren imenti*, CGM 40210, shown in photographs of Figure 1. A, lateral view. B, anterior view. Abbreviations: AS, alisphenoid; BS, basisphenoid; C¹, upper canine alveolus; DP, deciduous premolar alveolus; E, ethmoid (lamina papyracea); FIO, infraorbital canal; FR, frontal; I¹ etc., upper incisor alveoli; J, jugal; ME, mesethmoid; MX, maxilla; N, nasal; P¹ etc., upper premolar alveolus or alveoli; PA, parietal; PC, premaxillary canal; PM, premaxilla; SO, supraoccipital; SQ, squamosal.

symphysis [C 140:0]. A series of small pits, each about 2-3 mm in diameter (one on the left, three on the right), is located on each lateral edge of the palatal surface up to about 2 cm behind where the rostrum is broken off, but these seem to lie too far anterior to be vestiges of alveoli for the second and third incisors. The external nares are enlarged and retracted, as in all sirenians [C 8:1]. The nasal processes are long [C 7:0]; the portions in contact with the lacrimal and frontal are flattened and tapering and overlap more than half of the anteroposterior length of the supraorbital process [C 5:1, C 6:0, C 9:1]. This posterior portion of the nasal process has a distinctly upturned medial edge. The maxillary-premaxillary suture terminates anteriorly at about the level of the rear end of the premaxillary symphysis. Rostral deflection is about 45°.



FIG. 3—Photographs of holotype cranium of *Eosiren imenti*, CGM 40210. A, dorsal view. B, ventral view. Scale is in cm. See Fig. 4 (opposite) for explanation.

Nasal.—The nasals are large bones underlying the entire lateral walls of the dorsal part of the nasal cavity, but they have only limited dorsal exposure. Each nasal extends forward medial to, and is broadly overlapped anterolaterally by, the premaxilla. The posterolateral outline (frontonasal suture) is rounded. The medial edge of each nasal is thin, smooth, upraised, and apparently undamaged. There is no indication of dorsomedial extensions of the nasals to form a high arched roof over the nasal cavity, as in many Eocene dugongids (e.g., the Fayum specimen UM 94809, in which these portions of the nasals are as much as 7 mm thick where they meet in an interdigitated median suture). The nasals are instead separated in the midline to form a posterior extension of the mesorostral fossa about 2 cm wide [© 31:1, © 32:1]; no part of the frontal seems to have lain between them. Some damage to this area

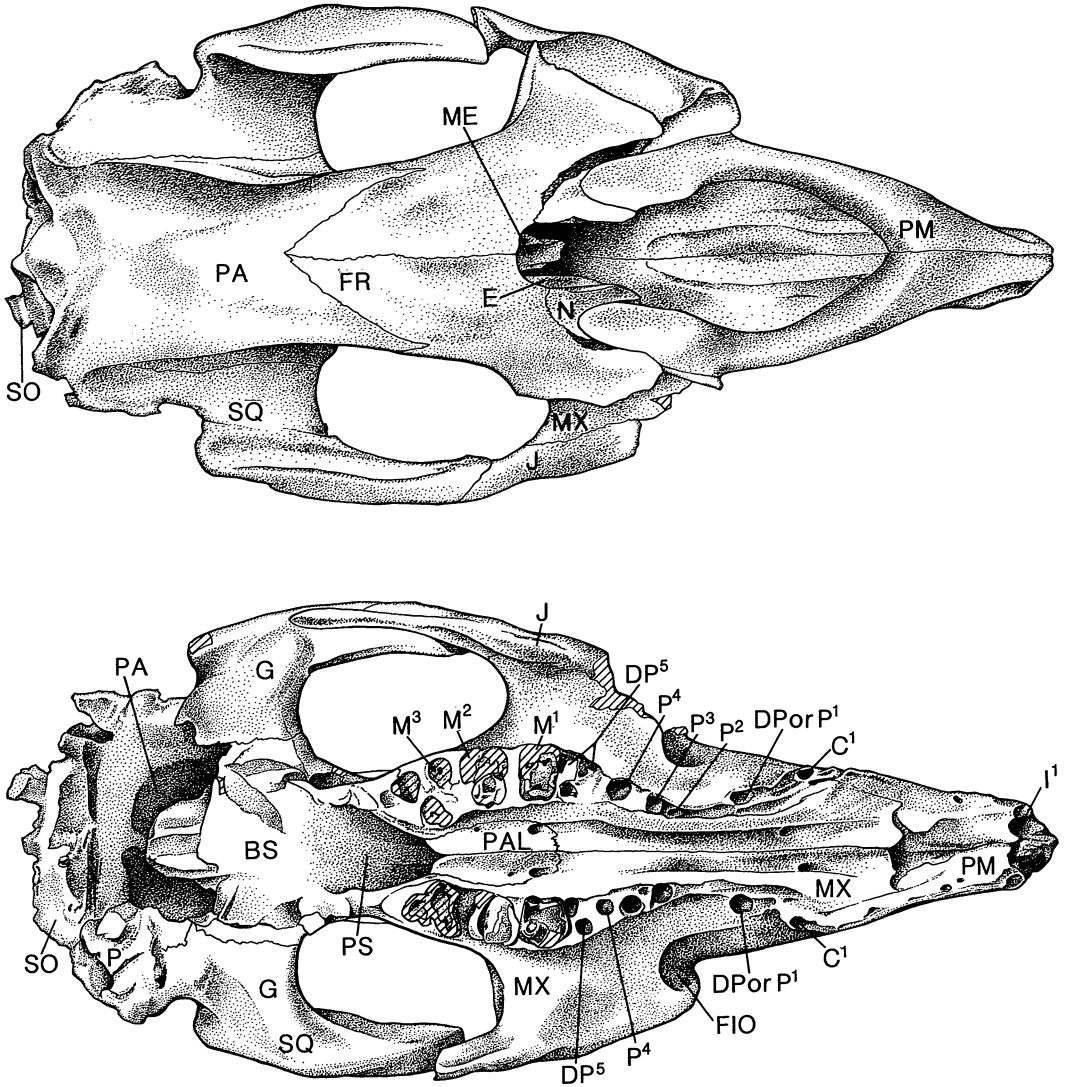


FIG. 4—Outline drawings of holotype cranium of *Eosiren imenti*, CGM 40210, shown in photographs of Figure 3. A, dorsal view. B, ventral view. Abbreviations: BS, basisphenoid; C¹, upper canine alveolus; DP, deciduous premolar alveolus or alveoli; E, ethmoid (lamina papyracea); FIO, infraorbital canal; FR, frontal; G, glenoid articulation (temporal condyle); I¹ etc., upper incisor alveoli; J, jugal; M¹ etc., upper molar or alveoli; ME, mesethmoid; MX, maxilla; N, nasal; P, periotic; P¹ etc., upper premolar alveolus or alveoli; PA, parietal; PAL, palatine; PM, premaxilla; PS, presphenoid; SO, supraoccipital; SQ, squamosal.

cannot be altogether excluded (see below), but natural sandblasting (which might remove considerable bone yet be hard to detect) is unlikely because the nasals are on the dorsal surface of the skull, which is not the surface that was exposed and weathered.

Ethmoidal region.—The mesethmoid forms a prominent perpendicular plate about 8 mm thick, which at its anterior end extends about 2.5 cm below the roof of the narial passages.

TABLE 2. Some characters used in cladistic analysis. 0, primitive state; 1, 2, 3, successive derived states in a transformation series. For some characters, none of the species analyzed here shows the most primitive state(s). Asterisks (*) indicate characters used by Domning (1994).

-
-
- 5. Nasal process of premaxilla: (0) overlaps one-third or less of anteroposterior length of supraorbital process of frontal; (1) overlaps more than one-third of length of process.
 - 11.* Ventral side of zygomatic-orbital bridge of maxilla: (0) nearly level with palate; (1) elevated above palate, with its ventral surface lying > 1 cm above alveolar margin.
 - 17. Width of palate between M²s: (0) greater than M²⁻³ length; (1) less than or equal to M²⁻³ length.
 - 31.* Nasals: (0) meet in midline; (1) separated in midline by frontals or an incisure, or absent.
 - 41. Crista intratemporalis of frontal: (0) present; (1) absent.
 - 54. Length of parietals in midline (including external occipital protuberance): (0) greater than width of parietal roof; (1) less than or equal to width of parietal roof.
 - 59. Temporal crests: (2) broad and flat, with distinct medial and lateral edges, and closely approximated in midline; (3) more or less sharp and upraised, best defined on lateral edges, and concave laterad (unordered character).
 - 85.* Ventral extremity of jugal: (0) lies posterior to orbit and to postorbital process of jugal; (1) lies below posterior edge of orbit, slightly anterior to postorbital process.
 - 97.* Posterior border of palate: (0) not incised, merely shallowly concave; (1) incised or deeply indented.
 - 140.* Depth of I¹ alveolus: (0) much less than half the length of the premaxillary symphysis; (1) about half the length of the symphysis.
 - 143.* Second and third upper incisors: (0) present, at least in part; (1) all absent.
 - 144.* Canines: (1) present, single-rooted; (2) absent.
 - 145. Premolars 1-4: (0) all present; (1) P2-4 present, DP or P1 lost.
 - 147. Crown length of M³: (0) greater than or equal to that of M²; (1) less than that of M².
-

The front surface of the plate is recessed at its dorsal end. No turbinals are preserved, but large portions of the thin laminae papyraceae remain on the medial surfaces of the nasals. These form the walls of the nasal cavity dorsally; these walls are concave above, where they are separated by 20 mm, and convex below, where the cavity narrows to about 14 mm above the roof of the nasal passages. The crista galli is well developed, but the cribriform plates are not visible.

Vomer.—Not preserved.

Lacrimonal.—Not preserved; was large, filling a space 3.5 cm long and 1.5 cm high on the dorsolateral surface of the jugal and maxilla anterior to the tip of the supraorbital process of the frontal [C 91:0 or 1].

Frontal.—The supraorbital process is well developed, with a strong, pointed posterolateral corner that juts outward almost perpendicularly from the temporal crest [C 36:0]. This process is dorsoventrally rather thin, and slopes downward and laterally [C 43:0]. Its lateral edge is somewhat rugose, and its anterior end is bluntly but acutely pointed. The anterior margin of the frontals is broadly concave, being in its present state shallowly incised for a distance of about 1 cm posterior to the rear edges of the dorsal exposures of the nasals, rather than extending forward between the nasals [C 37:0]. This thin internasal margin is somewhat chipped, but is only about 4 mm thick at its present anterior edge, so it seems unlikely that the bone extended even as much as 1 cm farther forward, or that it ever separated the exposed parts of the nasals. The dorsal surface of the frontals is strongly and smoothly convex [C 42:0], with only minor irregularities and with overhanging edges that diverge somewhat anteriorly. Orbicular apophyses are absent, as is a distinct crista intratemporalis [C 41:1]; the lower part of the temporal wall is only slightly recessed, and the lamina orbitalis was thin or absent [C 38:0].

Parietal.—The cranial vault is square in cross section with a smoothly concave roof and sharp edges [C 51:1]. The temporal crests are strong, sharp backward continuations of the straight edges of the frontals; they never approach each other in the midline, but come closest

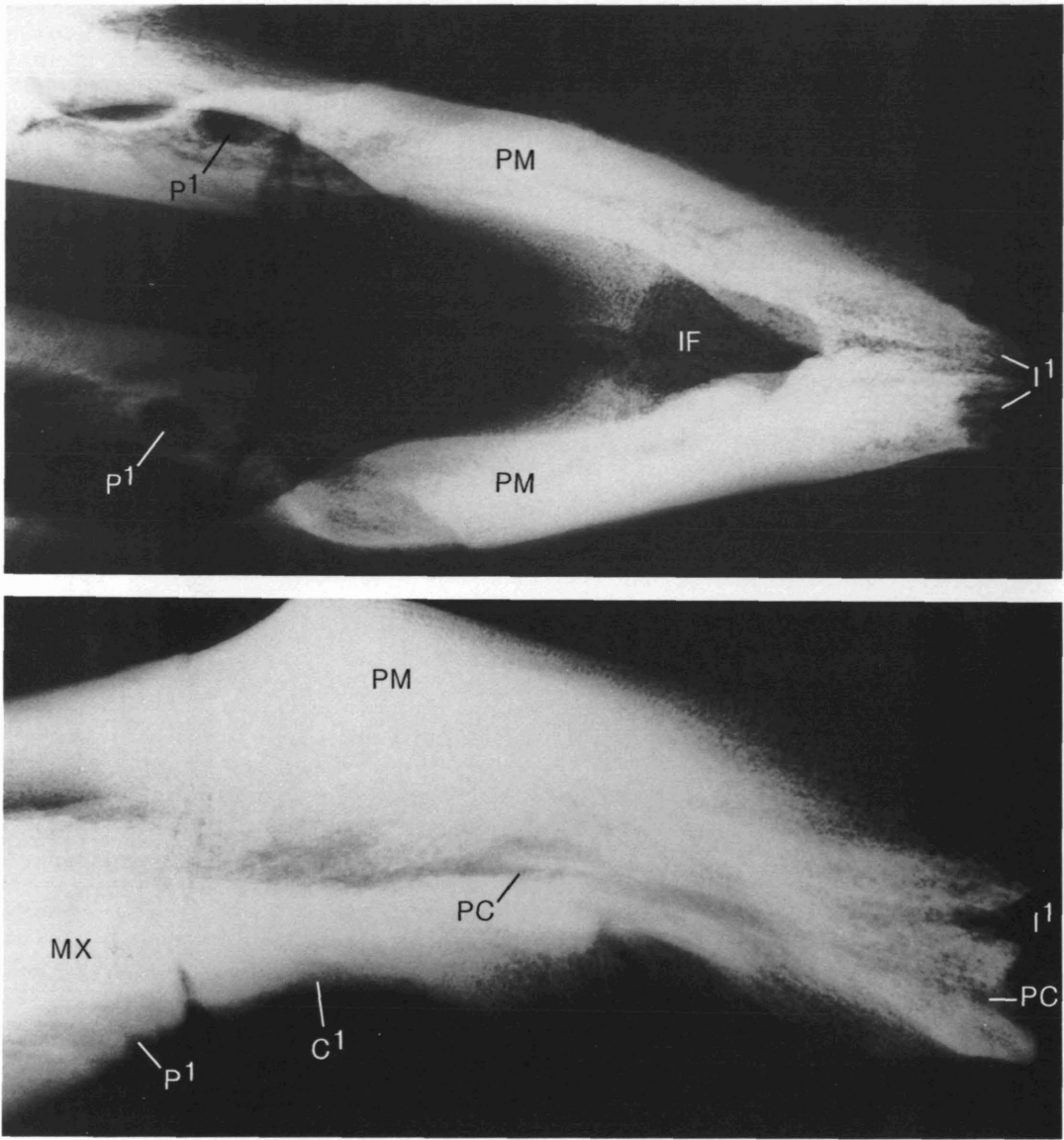


FIG. 5—Radiograph of rostrum of holotype cranium of *Eosiren imenti*, CGM 40210. A, dorsal view. B, lateral view (with anterior part of rostrum raised relative to its position in A). Both reproduced natural size. Abbreviations: C^1 , alveolus for upper canine; I^1 , alveolus for upper incisor; *IF*, incisive foramen (anterior palatine foramen); *MX*, maxilla; P^1 , alveolus for upper first premolar; *PC*, premaxillary canal; *PM*, premaxilla. Note shallowness of alveolus for I^1 , indicating very small size of any upper incisor tusk.

to the midline about halfway along the length of the parietals. Abaft this, they diverge slightly anterior to the nuchal crest. Internally, the tentorium osseum, transverse sulcus, internal occipital protuberance, and bony falx cerebri are prominent. The latter, however, is short and appears to have flattened out well before reaching the frontoparietal suture.

TABLE 3. Some character states of dugongid species analyzed in this study. Characters 5 to 147 and their states are defined in Table 2. Numbers in parentheses show the sizes of samples in which each character was observed; when characters varied intraspecifically, these numbers show the number of individuals exhibiting each state. EA, *Eotheroides aegyptiacum*; PV, *Prototherium veronense*; EL, *Eosiren libyca*; ES, *Eosiren stromeri*; PI, "*Prototherium*" *intermedium*; EI, *Eosiren inenti*, n. sp.; HS, *Halitherium schinzii*; HC, *Halitherium christolii*.

Character	EA	PV	EL	ES	PI	EI	HS	HC
5.	0 (1)	0 (2)	0 (5)	0 (1)	1 (1)	1 (1)	1 (2)	? —
11.	0 (1)	1 (3)	0 (5)	0 (1)	0 (1)	0? (1)	0 (12)	0 (1)
17.	0? (1)	0/1? (2,2)	0/1 (3,1)	1 (1)	1 (1)	1 (1)	1 (5)	1? (1)
31.	0 (2)	0 (2)	0/1? (7,2)	0? (1)	0 (1)	1 (1)	0 (13)	? —
41.	0 (1)	0 (2)	0 (2)	0 (1)	0 (1)	1 (1)	1 (20)	0? (1)
54.	0 (5)	0 (2)	0 (11)	1 (1)	? —	0 (1)	0 (21)	0 (5)
59.	2 (4)	2 (2)	2/3 (5,1)	2 (1)	? —	3 (1)	3 (20)	3 (5)
85.	? —	0 (2)	0 (3)	? —	0 (1)	1 (1)	1 (3)	? —
97.	0 (1)	1? (1)	? —	1? (1)	? —	1 (1)	1 (1)	? —
140.	? —	0? (1)	0 (8)	0? (1)	1? (1)	0 (1)	1 (2)	? —
143.	0 (1)	0? (2)	0/1 (4,2)	0? (1)	0? (1)	1 (1)	1 (2)	1 (2)
144.	1 (1)	1 (2)	1 (4)	1? (1)	1? (1)	1 (1)	1? ¹ / ₂ (1,2)	2 ¹ (2)
145.	0 (1)	0? (2)	0 (3)	0? (1)	0? (1)	0 (1)	1 (3)	1? ¹ (2)
147.	0 (1)	0 (3)	0 (4)	1 (1)	0 (2)	0 (1)	0 (10)	0 (1)

¹Known only for lower dentition.

Supraoccipital.—Badly damaged ventrally, but apparently narrower at the bottom than at the top. Forms angle of 135° with the posterior part of the parietal roof. The external occipital protuberance is a broad, prominent triangular boss flanked by deep concavities for the semispinalis muscle insertions. The top of the protuberance is flush with the parietal roof; it extends ventrally as a strong median ridge. The upper borders of the semispinalis insertions are sharp projecting ridges that form the lateral parts of the nuchal crest.

Exoccipital, basioccipital.—Not preserved.



FIG. 6.—Detail of left orbit and surrounding bones in holotype cranium of *Eosiren imenti*, CGM 40210, in oblique lateral view. Scale is in cm. Abbreviations: *E*, ethmoid (lamina papyracea); *FR*, frontal; *J*, jugal; *MX*, maxilla; *N*, nasal; *PA*, parietal; *PM*, premaxilla; *SQ*, squamosal. Solid ink line outlines opening of mesorostral fossa. Dashed lines clarify courses of some sutures between bones. Lacrimal, now lost, contacted rugose surface of jugal and maxilla in space anterior to supraorbital process of frontal.

Basisphenoid, presphenoid, orbitosphenoid, alisphenoid.—Poorly preserved; not seen to differ from those of other dugongids. The foramen ovale appears to have been opened to form a notch or incisure [© 103:1].

Pterygoid.—Not preserved.

Palatine.—The portions extending forward from the pterygoid process are convex medially and at first approach each other gradually; then, when level with the middle of the third molar, their edges abruptly turn toward the midline and meet to form a broad palatal incisure, trapezoidal in outline [© 97:1]. The palatines extend forward, joined by a median suture, to the level of the anterior side of M^1 —hence well forward of the after edge of the zygomatic-orbital bridge [© 99:0]. Two foramina on each side asymmetrically mark the maxillopalatine sutures.

Maxilla.—The dental capsule has atrophied following the eruption of M^3 . The zygomatic-orbital bridge is long anteroposteriorly [© 14:0], thick posteriorly, and thin anteriorly where it forms the lower edge of the large infraorbital foramen; the anterior opening of the latter measures 22×17 mm [© 13:1]. The bridge is elevated about 11 mm above the alveolar border [© 11:0 or 1]. The palate is thin, only about 5 mm thick at the level of M^2 [© 16:0]. The lyrifform edges of the palatal surface are closest together about 2 cm forward of the bridge. A broad, deep median gutter with thick, rounded edges occupies the palate in front of the molars; anteriorly, this bears a thin median crest flanked asymmetrically by a pair of foramina.

Squamosal.—Dorsally in contact with the squared posterior part of the parietal roof [© 76:1]. The sigmoid ridge is prominent and rounded near its upper end [© 74:0]; the lower end is

missing. The postglenoid process and postarticular fossa are distinctly developed. The processus retroversus (posterior end of the zygomatic process), though only slightly inflected, is also well developed, forming a broad notch at the rear edge of the zygomatic root [C 77:1]. The rear edge of the zygomatic root is continued by a sharp ridge running a short distance posteriorly and somewhat dorsally; ventral to this is a distinct concavity. In lateral view, the zygomatic process shows a straight or slightly convex posterodorsal and a straight anterodorsal outline; the posterodorsal edge is slightly convex laterad. Both lateral and medial sides of the process are relatively flat [C 84:0].

Jugal.—The preorbital process is flattened against the maxilla; it measures 21 mm in posteromedial-anterolateral breadth and 11 mm in anteromedial-posterolateral thickness [C 88:0]. The jugal is separated from the premaxilla by a 5 mm-wide portion of the maxilla exposed in the floor of the space occupied by the lacrimal [C 87:0]. Ventral to this space, a rounded longitudinal ridge protrudes laterally, forming part of the orbital rim. The ventralmost point of the jugal lies below the rear edge of the orbit and slightly forward of the broad, blunt summit of the postorbital process [C 85:1]. The zygomatic process is longer than the anteroposterior diameter of the orbit [C 89:0] and extends back to the level of the temporal condyle. The jugals noticeably converge anteriorly in dorsal view.

Periotic.—Present on left side but poorly preserved; set as usual into a socket in the squamosal [C 115:1].

Dentition.—The upper dental formula in this adult is 1.1.5?3 [C 150:0, C 151:0, C 155:1]. Except for the molars, all the teeth are represented only by their empty alveoli. These lie along the lyriform edges of the anterior palate; posterior to the palatal constriction the toothrows are strongly convex laterad, with the greatest breadth of the palate being reached at the level of M^1 . The first incisor alveolus is little enlarged (Fig. 6), and the tusk must have been very small, with the alveolus extending much less than half the length of the premaxillary symphysis (partly broken away); the remaining portion is about 9×8 mm in diameter [C 139:0, C 140:0]. As noted above, the second and third incisors seem to have been absent [C 143:1]; what appear to be vestigial alveoli are located too far forward in comparison with the locations of these teeth in other *Eosiren*. Even smaller pits that lie farther aft are probably nutrient foramina; at most, vestigial incisors may have been present in the animal's youth but were lost before adulthood.

The canine alveolus, 5 mm in diameter, marks the corner of the widest part of the rostrum and lies 1.5 cm behind the maxillopremaxillary suture [C 144:1]. A larger alveolus (7 mm in diameter) for P^1 (or DP^1) follows at a distance of 15-18 mm. A small (5 mm diameter) socket for P^2 lies 19 mm farther aft on the right side; on the left it is larger (6 mm) and farther (24 mm) behind P^1 . Immediately adjacent to P^2 on the right and larger (7 mm diameter) is the P^3 alveolus, separated by 7 mm from that of P^4 (8 mm diameter). On the left side the P^{3-4} alveoli are respectively 7 and 5 mm in diameter and separated from the preceding alveoli by 6 and 3 mm; hence the left P^{2-4} are shifted aft relative to those on the right. All these appear to have been single-rooted teeth [C 157:1]. P^4 is immediately followed on each side by the alveoli for a 3-rooted DP^5 ; evidently no replacement occurred at the P^5 locus [C 146:1].

Of the three 3-rooted molars, whose roots all remain in place, only the left M^1 has an intact crown. It is heavily worn, with a single lake of dentine bordered by a rim of smooth enamel [C 156:0]. Its crown length is 17.7 mm; anterior width, 17.6 mm; posterior width, 16.8 mm. All the molars were of normal size [C 158:0]; M^2 had a crown length of about 20 mm, while that of M^3 was 25 mm or more.

Ribs (Fig. 7).—The only complete rib measures 42 cm from capitulum to distal end, 5.8 cm from capitulum to tuberculum, about 13 cm from tuberculum to angle, and 4.6×3.1 cm in midshaft diameters. The other three ribs are slightly larger, the largest measuring 6.6 cm from capitulum to tuberculum, about 8 cm from tuberculum to angle, and 4.8×3.2 cm in midshaft diameters. All have distal ends that taper abruptly in the last 6 cm, ending in narrow, tapered tips with areas about 1 cm long for cartilage attachment. The distal end of the complete rib



FIG. 7—Photograph of four ribs found with holotype cranium of *Eosiren imenti*, CGM 40210. All ribs are from the right side. A and B are shown in anterior view. C and D are shown in posterior view. Reproduced ca. 0.25 × natural size. Scale is in cm.

is more abruptly swept back in the last 13 cm, and a slight shoulder marks its posterior edge 11 cm from the tip.

COMPARISONS

The enlarged rostrum [C 3:1], enlarged infraorbital foramen [C 13:1], incised palate [C 97:1], extension of the squamosal to the temporal crest [C 76:1], and well-developed processus retroversus of the squamosal [C 77:1] clearly mark this specimen as a dugongid rather than a prorastomid or protosirenid. Its dental formula and lack of any hydrodamaline or dugongine derived characters place it within the basal dugongid subfamily Halitheriinae (although some possible tendencies in the direction of the Dugonginae will be remarked on below). Indeed, the only dugongid genera which are both adequately known and sufficiently primitive to warrant detailed comparison with it are *Eotheroides* Palmer, 1899 (middle Eocene of Egypt); *Eosiren* Andrews, 1902 (middle to late Eocene of Egypt); *Prototherium* de Zigno, 1887 (late Eocene of Italy); and *Halitherium* Kaup, 1838 (Oligocene of Europe and possibly North America, the Caribbean, India, and elsewhere).

In comparing these taxa with our new species, we consider both the characters used by Domning (1994) and some additional ones which may or may not prove to be of diagnostic value. Of the latter, those which seem most likely to be phylogenetically informative have been assigned numbers and are listed in Tables 2 and 3 together with selected characters from Domning's (1994) set.

The Eocene Dugongidae are seriously in need of taxonomic revision. The existing nominal taxa and their distribution were briefly summarized by Domning et al. (1982). *Eosiren* was long considered a synonym of *Eotheroides* (e.g., by Simpson, 1945; Reinhart, 1951, 1959; Domning, 1978; Domning et al., 1982). However, cladistic analysis (Domning, 1994) now suggests that *Eotheroides aegyptiacum* (Owen, 1875) is distinctly more primitive than, and cladistically separated from, all the species of *Eosiren*, and in particular the type species *E. libyca*. *E. aegyptiacum* also appears to be the sister group of all other dugongids. Therefore, it seems prudent to retain the two species in separate genera (the species are type species of *Eotheroides* and *Eosiren*, respectively), pending thorough revision. Moreover, Bizzotto (1983) has proposed synonymization of "*Eotheroides*" *sensu lato* with *Prototherium*. For the purposes of this discussion, however, all three generic names will be provisionally retained.

Eotheroides (sensu stricto) contains a single species, *E. aegyptiacum*. It is known from several skulls from the lower Mokattam beds (lower Building Stone Member, Lutetian) near Cairo (Abel, 1913).

Eotheroides aegyptiacum differs from our specimen in that the nasals are in contact anteriorly [C 31:0] though separated by the frontals posteriorly; a distinct crista intratemporalis is present [C 41:0]; the parietal roof is bilaterally convex [C 59:2]; the nasal processes of the premaxilla overlap less than one-third of the anteroposterior length of the supraorbital process [C 5:0]; the palate is broader [C 17:0?]; the posterior border of the palate, formed by the palatines, lies abaft the rear of the toothrow [C 97:0]; the jugal is excluded from the anterior margin of the orbit, which is formed only by the maxilla; the fissura ovalis was in at least some cases closed posteriorly by a bony bridge to form a true foramen ovale [C 103:0]; and the overall size of the skull of *E. aegyptiacum* is about 25% smaller.

Eosiren includes three species. *E. libyca*, the type, is represented by a number of skulls from the Qasr-el-Sagha Formation in the Fayum. Sickenberg (1934) used *Eosiren* as a subgenus and named two additional species from Egypt: "*Eotherium (Eosiren) abeli*" and "*Eotherium stromeri*", both of which he felt also pertained to *Eosiren* (Sickenberg, 1934: 131). (The preoccupied name *Eotherium* Owen, 1875 was replaced by *Eotheroides* Palmer, 1899.) *Eosiren abeli* was based on a small amount of material from the lower Mokattam beds, including a skull at Munich that was destroyed in World War II. *Eosiren stromeri* (Sickenberg) Kordos, 1977 is based on a skull and skeleton from the upper Qasr el-Sagha Formation found in the Fayum west of Dimeh.

Eosiren libyca, the best-known Eocene dugongid, differs from our specimen in that the nasals are joined anteriorly in the midline in most if not all cases [C 31:0 or ?1]; see discussion below) and separated posteriorly by the frontals; the supraorbital processes have less pronounced posterolateral corners in most cases ("St. XVIII" and "St. XIX" of Sickenberg, 1934, are apparent exceptions); the nasal process of the premaxilla overlaps less than one-third of the anteroposterior length of the supraorbital process [C 5:0]; a distinct crista intratemporalis is present [C 41:0]; the parietal roof is usually bilaterally convex [C 59:2]; "St. XXXIV" of Sickenberg, 1934, is an exception); the palate is usually wider [C 17:0 or 1]; and the ventral process of the jugal is positioned slightly abaft the dorsal process [C 85:0]. Alveoli for I² frequently (and I³ sometimes) are absent, but were present in at least some individuals, as demonstrated by the holotype [C 143:0 or 1].

The skull of *Eosiren abeli* was described and illustrated (as "*Eotherium aegyptiacum*, Ind. VI") by Abel (1913). It differed from our specimen in that its temporal crests apparently approached each other closely on the parietal roof, which was bilaterally convex [C 59:2].

Eosiren stromeri differs from our new specimen in several ways. The skull roof has a pronounced constriction near the frontoparietal suture; there is a distinct crista intratemporalis [C 41:0]; the parietal roof is bilaterally convex [C 59:2]; the width of the parietals is about as great as their length in the midline [C 54:1]; the supraorbital processes are blunter and dorsoventrally thicker than in our specimen and their lateral edges are more parallel to the midline; the nasal process of the premaxilla overlaps less than one-third of the anteroposterior length of the supraorbital process [C 5:0]; the frontals are much longer than the parietals in the midline, and extend forward a short distance between the nasals, which Sickenberg (1934: fig. 22) reconstructs as meeting in the midline [C 31:0?]; and M^3 is smaller than M^2 [C 147:1].

Prototherium nominally contains two species from the late Eocene of Italy: *P. veronense* (de Zigno, 1875) and *P. intermedium* Bizzotto, 1983. Both are represented by skulls. Pilleri et al. (1989) have recently named two additional Bartonian species from Spain, *P. solei* and *P. montserratense*, but these seem similar if not identical to the Priabonian *P. intermedium* and we have not personally examined the Spanish material in any case.

Prototherium veronense, best described by Sickenberg (1934), differs most dramatically from our specimen in its unusually large nasals joined in a long median suture [C 31:0, C 32:0] and its very narrow skull roof. Other differences include: a convex rather than flattened dorsal surface of the posterior part of the premaxillary symphysis; apparently an evenly convex dorsal outline of the symphysis; a nasal process of the premaxilla that overlaps less than one-third of the anteroposterior length of the supraorbital process [C 5:0]; a distinct crista intratemporalis [C 41:0]; bilaterally convex temporal crests [C 59:2]; a zygomatic-orbital bridge elevated quite high above the palate [C 11:1]; probably a wider palate [C 17:0 or ?1]; a posteriorly-positioned ventral process of the jugal [C 85:0]; and a less developed processus retroversus (though this process is not completely absent, *pace* Sickenberg; hence scored 77:1).

"*Prototherium*" *intermedium* differs from our specimen in having the nasals joined in the midline [C 31:0] and separated posteriorly by the frontals, in having the ventral process of the jugal posterior to the dorsal process [C 85:0], in apparently having deeper tusk alveoli [C 140:1], in apparently having at least one pair of posterior incisors [C 143:0], and in having an evenly convex dorsal outline of the rostrum and a distinct crista intratemporalis [C 41:0]. The holotype was restored and illustrated (Bizzotto, 1983: fig. 3; pl. 1a; Pilleri et al., 1989: figs. 5b, 6b) with closely approximated temporal crests, and these crests do converge posteriorly on the frontal roof, which is narrower and more concave than in our specimen; but in fact no real bone is visible on the parietal roof, and the accuracy of this largely plaster restoration is very doubtful. This taxon has been shown by cladistic analysis (Domning, 1994) to be well removed from *P. veronense* and is probably not congeneric with it.

Halitherium includes two European Oligocene species: *H. schinzii* (Rupelian of Germany, Hungary, Switzerland, Belgium, and France) and *H. christolii* Fitzinger, 1842 (late Oligocene [Egerian] of Austria). Cranial material is available for both and is abundant for *H. schinzii*. *H. pergense* (Toula, 1899) and *H. abeli* Spillmann, 1959 from Austria are here considered synonyms of *H. christolii*. "*H.*" *bellunense* de Zigno, 1875 from Italy is inadequately known and of uncertain generic affinity, but is probably distinct from *Halitherium* and may be a dugongine (Domning, 1989a). Named species from outside Europe are inadequately known. They include *H. alleni* Simpson, 1932, from the eastern United States, which is similar to *H. christolii*, and ?*H. antillense* Matthew, 1916, from Puerto Rico.

Halitherium schinzii differs from our specimen in that its nasals are in contact anteriorly [C 31:0] and separated posteriorly by the frontals; the temporal crests approach each other more closely on the parietal roof; the dorsal outline of the rostrum is relatively straight and not markedly downturned anteriorly; the tusk alveolus is deeper [C 140:1]; the canine is lost [C 144:1 or 2], as is DP or P¹ [C 145:1]; and the posterodorsal outline of the zygomatic process of the squamosal is concave in most specimens.

Halitherium christolii differs from our specimen in that its frontal roof is slightly concave; a crista intratemporalis appears to be present [C 41:0?]; the temporal crests are more

pronounced and closer together on the parietal roof; the supraorbital processes have longer, narrower bases, extend farther laterally, and are hooked posteriorly; and the posterodorsal outline of the zygomatic process of the squamosal is concave. The upper anterior dentition is unknown, but judging from the mandible, canines and DP or P1 were probably absent [C 144:2, C 145:1?].

We may conclude from the above that the Gebel Qatrani sirenian is phenetically most similar to *Eosiren* and *Halitherium* but distinct from any previously described species. To clarify its phyletic relationships, it was analyzed cladistically in conjunction with the other Paleogene and some Neogene sirenians, using Hennig86 and the characters and data of Domning (1994), supplemented by additional characters shown in Table 2. Several experimental runs with different suites of taxa (including some not analyzed by Domning, 1994), using Hennig86's successive-weighting option and the 1994 character set only, consistently and unambiguously placed *Eosiren imenti* as the sister group to *Halitherium schinzii* plus other Oligocene and later taxa; the next outgroup to these comprised the unresolved grouping *E. libyca*-*E. stromeri*-"*Prototherium*" *intermedium*. When the additional characters [C 5, 17, 41, 54, 59, and 145] were added, *E. imenti* remained the sister group to *H. schinzii* plus the other Oligocene and later taxa; however, "*P.*" *intermedium* became the sister group to all these, with the unresolved grouping *E. libyca* + *E. stromeri* as the next outgroup.

Leaving aside *E. stromeri* as too specialized to have given rise to the later forms, the characters that support these arrangements among *E. libyca*, "*P.*" *intermedium*, *E. imenti*, and *H. schinzii* are the following. The latter three species share C 5:1 (increased overlap of premaxilla and frontal) and C 17:1 (narrowed palate). *E. imenti* and *H. schinzii* share C 41:1 (loss of crista intratemporalis), C 59(3) (form of temporal crests), C 85:1 (position of ventral process of jugal), and C 143:1 (loss of I²⁻³). In contrast to the other three species, *H. schinzii* displays C 144:2 (loss of canines) and C 145:1 (loss of DP or P¹). It possibly shares (incongruently) with "*P.*" *intermedium* C 140:1 (enlargement of tusks).

Finally, *E. imenti* displays the apparent autapomorphy C 31:1 (separation of nasals); this is paralleled in some other sirenians but is not definitely known to occur in *E. libyca*, "*P.*" *intermedium*, or *H. schinzii*. Andrews (1906) described two specimens of *E. libyca*, including the type, as having separated nasals, but this is probably the result of damage in the anterior midline of the internasal suture; better-preserved specimens consistently show the nasals joined anteriorly. The same is true of *H. schinzii*, despite Sickenberg's (1934: 222) statement to the contrary, which does not agree with our observations of Mainz Basin specimens.

DISCUSSION

Eosiren imenti is plausibly regarded as a direct descendant of *E. libyca*, because the latter is cladistically one of its possible sister species (or the next outgroup thereof), shows no autapomorphies, and is stratigraphically earlier. ("*Prototherium*" *intermedium* is also a possible ancestor of *E. imenti*, but appears less likely because its tusk alveolus seems to be deeper and hence more derived.) This leaves the question of whether *E. imenti* gave rise to any other species. Of the known Oligocene and post-Oligocene Sirenia, the most likely candidates are *Halitherium* spp. and the dugongines.

The type and other classic material of *Halitherium schinzii* from the Mainz Basin of Germany has been collected from two successive stratigraphic units: the Rupelton and (especially) the overlying Unterer Meeressand. These are both regarded as lower Rupelian in age and correlative with the Suevoian land-mammal age (Tobien, 1980). They are also correlated with nannoplankton zones 23 and 24 and with the MP 22 and MP 23 zones (Tobien, 1988). The Unterer Meeressand has also produced the hyaenodontid creodont *Apterodon*

flonheimensis (Andreae, 1887), which Andrews (1906, p. 226) described as "strikingly similar to" the Gebel Qatrani species *A. macrogathus* (Andrews, 1904).

Although these Mainz Basin units have generally been spoken of as middle Oligocene, they in fact correspond to the lower Oligocene in the sense used here. What Tobien (1980) considers lower Oligocene (i.e., Lattorfian or Headonian) correlates with the Priabonian, here considered upper Eocene. Therefore, the Mainz Basin sample of *Halitherium schinzii* is approximately coeval with, and not demonstrably younger than, the Gebel Qatrani specimen. Since, therefore, *H. schinzii* is distinct from and coeval with *Eosiren imenti*, it apparently represents a lineage that branched off from *Eosiren* around the end of the Eocene.

The exact relationship of the nasals and frontals is unknown in *Halitherium christolii*, but later halitheriines generally have nasals separated by the frontals (Domning and Thomas, 1987), not generally by an incisure as seems to have been true in *E. imenti*. Thus there is no special reason to derive them from the latter species.

We may also consider the possibility that *Eosiren imenti* gave rise to the Dugonginae. The latter first appear in the late Oligocene of the southeastern United States, where they were already differentiated into at least two and probably more lineages (Domning, 1989b). The most primitive known form is *Crenatosiren olseni* (Reinhart, 1976). Dugongine synapomorphies include a distinct nasal incisure extending into the frontal margin [C 37:1], a downturned supraorbital process [C 43:1 (absent in some *C. olseni*, Domning, in prep.)], and a thickened preorbital process of the jugal [C 88:1]. Of these, only the incisure in the frontals may be present in the Gebel Qatrani sirenian, and this is doubtful, though it may be foreshadowed by the wide separation of the nasals [C 31:1]. The evidence for dugongine affinities is therefore weak or nonexistent. The apparent nasal incisure in *E. imenti* is perhaps best regarded as an anomaly, perhaps an individual variant; a similar feature in *Metaxytherium arctodites* Aranda-Manteca, Domning and Barnes, 1994 also appears to be cladistically incongruent and probably uninformative (Aranda-Manteca et al., 1994).

A final possibility is involvement of *Eosiren imenti* in the origins of the Trichechidae. This family was expanded by Domning (1994) to include not only the manatees (Trichechinae) but also the Miosireninae, a northern European clade comprising two genera. The earlier of these is *Anomotherium* Siegfried, 1965, from the late Oligocene of Germany, and the trichechid clade as a whole seems from the 1994 analysis to have been derived from late Eocene or early Oligocene dugongids—hence the potential relevance of *E. imenti* in this connection. Trichechids in this broader sense appear to be characterized by a secondarily reduced rostrum [C 3:0] and processus retroversus [C 77:0], while miosirenines evidently revert to large, conjoined nasals [C 31:0, C 32:0] and develop a greatly thickened lamina orbitalis of the frontal [C 38:1]. Future analyses may show that these supposed reversals are in fact merely primitive retentions and that Trichechidae are rooted closer to the base of the sirenian tree than they are presently conceived to be; but in any case *E. imenti* shows none of these features, and therefore no potential as a trichechid ancestor or close relative.

PALEOECOLOGY

Quarry I and other nearby sites in the Gebel Qatrani Formation are point-bar deposits in a major coastal river or rivers. There is evidence of freshwater lakes, and a flora and fauna (Bown et al., 1982: tab. 3) which suggest that the sea must have been at least several km away to the north or northwest. Olson and Rasmussen (1986) concluded that "the paleoenvironment of the Fayum during the Oligocene closely resembled modern Ugandan swamps bordered by forest and open woodland or grassland."

Fossil and living dugongid sirenians, in contrast to manatees (Trichechinae), are known only from marine environments. The occurrence of a dugongid together with brackish-water mollusks, sharks, and rays in the fluvial Gebel Qatrani deposits suggests that "storms and/or

tidal incursions increased the salinity of the streams for several kilometers inland" (Bown et al., 1982: 628; see also Fleagle et al., 1986a,b). In 1984, a cyclone washed dugongs (*Dugong dugon*) as far as 9 km inland in the McArthur River delta, northern Australia (Marsh, 1989).

However, an alternative possibility is also worth considering. The avifauna of the Gebel Qatrani Formation is particularly rich in families of birds (such as Jacanidae and Balaenicipitidae) that today are characteristic of swamps with dense mats of floating vegetation (Olson and Rasmussen, 1986). Jacanas, the most frequently encountered birds in the fauna, are anatomically specialized for walking on lily pads and other floating plants. Moreover, fossils of lily pads (*Nelumbo*) have actually been reported from the Gebel Qatrani Formation together with other aquatic plants (*Salvinia*, *Typha*, mangroves; Bown et al., 1982). It is generally assumed that sirenians first entered the water in freshwater or estuarine environments such as those still inhabited by manatees today; the marine adaptation of dugongids is seen as a later development. *Eosiren* is one of the most primitive dugongid genera; therefore it would not be surprising if it were more euryhaline than its descendants. However, its rostral deflection of 45-55° is greater than that of modern West African and Amazonian manatees (*Trichechus senegalensis* and *T. inunguis*), which feed mainly on floating mats of vegetation, including Nymphaeaceae (Best, 1981), and is more comparable to that of Florida manatees (*T. manatus latirostris*), which feed extensively on marine seagrasses in addition to freshwater plants (Domning, 1982; Domning and Hayek, 1986). Thus it may be that this isolated occurrence of *Eosiren* in the Gebel Qatrani Formation is not the chance result of a storm, but rather the first fossil evidence that dugongids once frequented fresh as well as salt water, in the manner of Florida manatees today. This would be consistent with the suggestion of Savage (1971: 219), who attributed the apparently high diversity of Eocene sirenians to fluvial rather than truly marine habits. The discovery of additional specimens in the same deposits would strengthen this interpretation.

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