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LATE MIDDLE EOCENE OF WADI HITAN, EGYPT**

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**PROTOSIREN SMITHAE, NEW SPECIES (MAMMALIA, SIRENIA), FROM THE  
LATE MIDDLE EOCENE OF WADI HITAN, EGYPT**

By

DARYL P. DOMNING<sup>1</sup> AND PHILIP D. GINGERICH<sup>2</sup>

*Abstract*—*Protosiren smithae* is a new protosirenid sirenian described on the basis of associated cranial and postcranial material from the late middle Eocene (latest Bartonian) Gehannam Formation of Wadi Hitan (Zeuglodon Valley), Fayum Province, Egypt. The new species is similar to *Protosiren fraasi* Abel, 1907, from the earlier middle Eocene (Lutetian) of Egypt, but it is younger geologically and more derived morphologically. *P. smithae* is probably a direct descendant of *P. fraasi*. The postcranial skeleton of *P. smithae* includes well-developed hindlimbs, which suggest some lingering amphibious tendencies in this otherwise aquatically-adapted primitive sea cow.

INTRODUCTION

Fossil sirenians from Eocene deposits of Egypt have been collected and studied for almost a century, but many aspects of their anatomy remain to be clarified. The numbers of species in successive faunas and the identification of some of these species are still unclear. As noted by Domning et al. (1982), this is because most of the specimens hitherto described have been incomplete: skulls without jaws; skeletons without heads; and teeth, mandibles, other bones, and even endocranial casts found separated from more diagnostic elements and then referred to established taxa only conjecturally if at all.

This unsatisfactory situation has now begun to improve, owing to several seasons of fieldwork in Wadi Hitan (Zeuglodon Valley) in the far western part of Fayum Province, Egypt. In addition to numerous cetacean skeletons, a smaller number of sirenian skeletons has been recovered here from middle to late Eocene (Bartonian to Priabonian) rocks of the Gehannam and Birket Qarun Formations (Fig. 1). These specimens are intermediate in age between the

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<sup>1</sup>Laboratory of Paleobiology, Department of Anatomy, Howard University, 520 W Street, N.W., Washington, D.C. 20059

<sup>2</sup>Museum of Paleontology and Department of Geological Sciences, The University of Michigan, Ann Arbor, Michigan 48109-1079

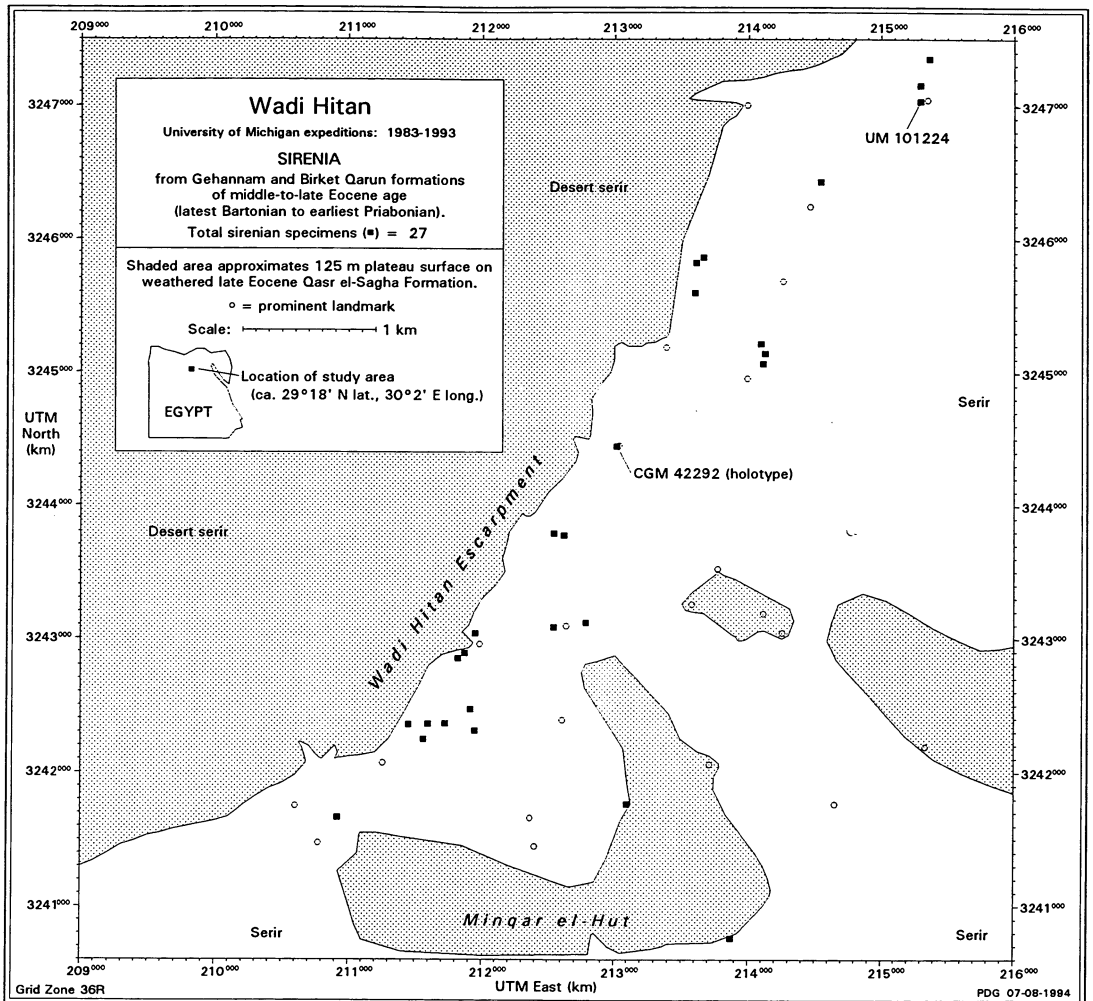


FIG. 1—Map of Wadi Hitan (Zeuglodon Valley), Egypt, showing locality of holotype partial skeleton of *Protosiren smithae* new species, CGM 42292, and referred partial skeleton UM 101224, in the context of other sirenian remains (closed squares) found in Wadi Hitan by University of Michigan expeditions. Sirenians mapped here come from the latest Bartonian through earliest Priabonian Gehannam and Birket Qarun formations of late middle and early late Eocene age. Strata strike NE-SW and dip gently to northwest. Shaded areas are tablelands rising above sirenian-bearing strata and capped by indurated and erosion-resistant beds of the Umm Rigl Member, late Eocene Qasr el-Sagha Formation. Map is 7 km × 7 km, with specimens located by reference to their positions on a triangulated field map, fit to Universal Transverse Mercator coordinates (grid zone 36R) of prominent landmarks.

classic Egyptian sirenian fossils from the early middle Eocene (Lutetian) lower Mokattam beds near Cairo, and those from the late Eocene (Priabonian) Qasr el-Sagha Formation of the Fayum (Gingerich, 1992). They are also more complete than most previously-collected specimens, and in some cases include associated skull, mandible, and appendicular as well as axial elements. As a result the new specimens serve as veritable "Rosetta stones" in revealing the true associations among the disparate bones described by earlier workers. Thanks to their

intermediate age, they also, potentially, can shed light on phyletic connections between previously known middle and late Eocene taxa.

The aim of this paper is to describe a new taxon from these intermediate beds, based on two of the best Fayum specimens recovered to date. It is a new species of *Protosiren*, likely descended from the lower Mokattam species *P. fraasi* Abel, 1907. Notwithstanding detailed study of the latter by Sickenberg (1934), the new material has revealed errors in what we thought we knew about it, and has given us a much fuller picture of the anatomy and probable lifestyle of this very early seacow.

#### ABBREVIATIONS

Institutional abbreviations used here are as follows:

- CGM — Cairo Geological Museum, Cairo (Egypt)
- SMNS — Staatliches Museum für Naturkunde, Stuttgart (Germany)
- UM — Museum of Paleontology, University of Michigan, Ann Arbor (U.S.A.)
- USNM — U. S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (U.S.A.)
- YPM — Yale Peabody Museum, Yale University, New Haven, Connecticut (U.S.A.)

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). Character numbers are enclosed in square brackets, prefaced with a fraktur C and followed by a colon and the character state number; e.g., [C 3:0] refers to character number three and associated character state zero.

#### STRATIGRAPHY AND AGE

Wadi Hitán is an uninhabited broad, flat, dry desert valley in a remote part of western Fayum Province in north central Egypt (Fig. 1). Bedrock strata, where exposed, are eroded continuously by wind and blowing sand. Three marine Eocene formations are exposed in Wadi Hitán. The lowest, the Gehannam Formation, is predominantly brown shale with gypsum and fine white and yellow sandstones deposited on a shallow shelf. This is Bartonian late middle Eocene to Priabonian late Eocene in age. The middle formation, the Birket Qarun Formation, is a massive yellow sandstone that is lenticular in cross-section and interpreted as an offshore barrier sandbar complex buried by a rapidly rising sea during earliest Priabonian marine transgression. The highest formation, the Qasr el-Sagha Formation, is a lagunal complex including abundant oysters and other bivalves that is Priabonian late Eocene in age.

The floor of Wadi Hitán is soft shale of the Gehannam Formation. Induration of bivalve-rich hard beds in the lowest Umm Rigl member of the Qasr el-Sagha Formation makes these resistant to erosion, and the Qasr el-Sagha Formation generally stands exposed as a tableland (stippled in Fig. 1) separated from eroded valleys by 20-50 m escarpments. Where the Birket Qarun Formation is thickest, as on the southern face of Minqar el-Hut, it is eroded into spectacular sandstone cliffs standing more than 100 m above the valley floor. Much of the surface of valley floors and high tablelands is covered with a desert pavement or serir of siliceous gravel.

The age of Wadi Hitán strata is constrained by the succession of microfossil, invertebrate, and vertebrate fossils studied in Fayum and elsewhere in northern Egypt, and by evidence of a low sea stand in Wadi Hitán itself. This low sea stand corresponds to a major marine regression bringing sea level low enough to accommodate mangrove at the end of Bartonian time



FIG. 2.—Photograph of holotype cranium and mandible of *Protosiren smithae*, CGM 42292, in lateral view. Most teeth are missing. Upper molars remaining in the cranium and occluding lower molar remaining in the mandible are hidden by zygomatic arch. Specimen, found in sandstone, is exceptionally complete and virtually undistorted. Reproduced ca.  $0.4 \times$  natural size. Casts of skull and mandible shown here are catalogued as UM 94810. Scale in cm.

(end of the middle Eocene), and the Birket Qarun barrier bar complex was evidently buried by rapid sea level rise just after the low stand. These events refine correlation based on other evidence, and mean that most of the Gehannam Formation is late Bartonian, while the uppermost Gehannam, laterally equivalent Birket Qarun, and overlying Qasr el-Sagha formations are Priabonian (Gingerich, 1992, 1993). Wadi Hitán is best known paleontologically for its abundant fossil cetaceans and sirenians. Cetaceans and sirenians in Wadi Hitán come from both latest Bartonian and earliest Priabonian strata. There is no indication of significant faunal change in the Wadi Hitán stratigraphic section, and it is not possible to tell the late Bartonian and early Priabonian apart locally using macroinvertebrates or vertebrate fossils.

The type specimen of *Protosiren smithae* described here, CGM 42292, is considered to be latest Bartonian in age because it comes from the Gehannam Formation 18 m above the base of the Wadi Hitán ZV-54 measured stratigraphic section (fig. 35 in Gingerich, 1992), which places it just below the base of the Birket Qarun barrier bar complex and just below the beginning of Priabonian transgression (see fig. 43 in Gingerich, 1992). The referred specimen, UM 101224, comes from a white layer in the Gehannam Formation that appears correlative with the base of the ZV-54 measured stratigraphic section. Thus UM 101224 too is latest Bartonian in age (late middle Eocene).

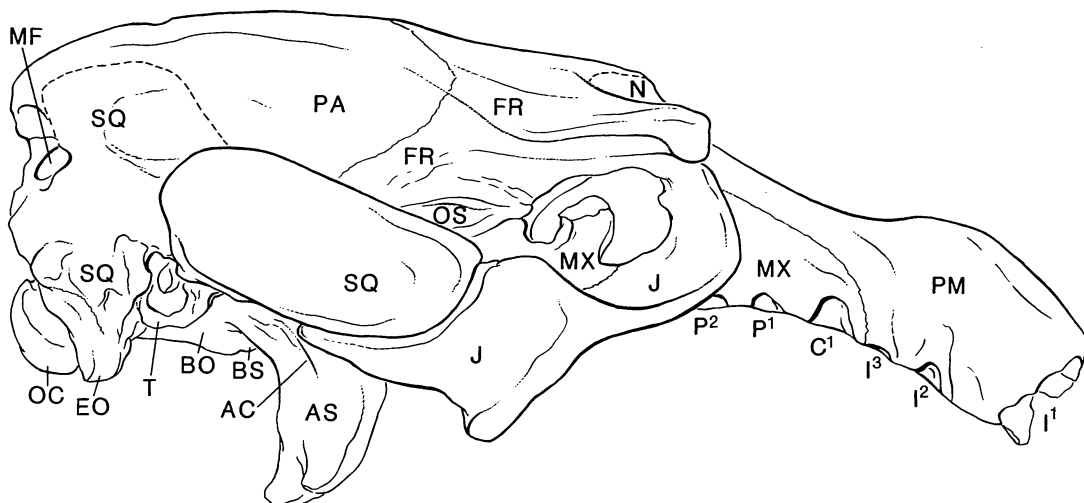


FIG. 3—Outline drawing of *Protosiren smithae* cranium shown in Figure 2, CGM 42292 (holotype), lateral view, with principal bones and landmarks identified. Abbreviations: *AC*, alisphenoid canal; *AS*, alisphenoid; *BO*, basioccipital; *BS*, basisphenoid; *C*<sup>1</sup>, upper canine alveoli; *EO*, exoccipital; *FR*, frontal; *I*<sup>1</sup> etc., upper incisor alveoli; *J*, jugal; *MF*, mastoid foramen; *MX*, maxilla; *N*, nasal; *OS*, orbitosphenoid; *OC*, occipital condyle; *P*<sup>1</sup> etc., upper premolar alveoli; *PA*, parietal; *PM*, premaxilla; *SQ*, squamosal; *T*, tympanic.

SYSTEMATIC PALEONTOLOGY

Order SIRENIA Illiger, 1811

Family PROTOSIRENIDAE Sickenberg, 1934

*Protosiren* Abel, 1907

*Protosiren smithae*, new species

Figs. 2-11

*Holotype*.— CGM 42292, partial skeleton of a dentally-mature adult, including skull, both mandibles, left and right M<sup>2-3</sup>, right M<sub>3</sub>, two hyoid elements, centra of 20 or more vertebrae, one complete rib and fragments of others, one complete sternebra and parts of two others, both scapulae, both humeri, parts of both radii and ulnae, several metacarpals and phalanges, both innominates, parts of both femora, one tibia, and one fibula. Type specimen was found by B. H. Smith in 1987, weathering out of the face of an isolated erosional remnant. This was collected by persistent effort in 1987, 1989, 1991, and 1993. The skull and forelimbs were found by P.D.G. in 1991 in a sandstone block lying at the base of the exposure. All bones from this site, with the exception of a few weathered cetacean fragments, clearly represent one associated sirenian skeleton dispersed somewhat at the time of burial and then further scattered by erosion.

*Type locality*.— Wadi Hitan locality ZV-54 (see map in Fig. 1). Stratigraphic position of type locality in Gehannam Formation is shown in measured section in Gingerich (1992, figs. 35 and 43; see discussion above).



FIG. 4—Photograph of cranial roof of referred specimen of *Protosiren smithae*, UM 101224, in dorsal view, showing dorsal cranial sutures and broad frontal separation of nasals. Reproduced ca.  $0.5 \times$  natural size. Scale is in cm. Abbreviations: *FR*, frontal; *N*, nasal; *PA*, parietal; *PM*, premaxilla.

*Referred specimens.*— UM 101224, including a partial skull and mandible, nearly complete axial skeleton lacking tail, partial fore and hind limbs (locality ZV-227, Gehannam Fm., latest Bartonian (see above). This was found by W. J. Sanders in 1993.

In addition, UM 101229, a large, thick, partial frontal, a right premaxilla, and associated bone fragments from the early Bartonian Midawara Formation at Dur el-Milaha in Wadi Rayan, Egypt, appear to represent this species. This was found by W. C. Clyde in 1993.

*Age and distribution.*— Bartonian, late middle Eocene.

*Diagnosis.*— *Protosiren* differing from *P. fraasi* in having much larger upper incisor tusks, a more trapezoidal masticating surface of the rostrum, slightly greater rostral deflection, nasals separated in the midline by the frontals, and wide separation of exoccipitals in the dorsal midline.

*Etymology.*— Named for Dr. B. Holly Smith, who discovered the type specimen, in recognition of her many contributions to the success of Wadi Hiton expeditions.

### Description

Among previously described sirenians, this species is most similar to (although more derived than) *Protosiren fraasi* Abel, 1907, whose cranial osteology was first described by Andrews (1906) under the name "*Eotherium aegyptiacum* (?)." Sickenberg (1934) described additional specimens of *P. fraasi*, and Gingerich et al. (1994) recently restudied Andrews' specimen, the type, using CT imaging. Description of *P. smithae* here is abbreviated, emphasizing the skull, mandible, and dentition in comparison to those of *P. fraasi*, and largely restricted to diagnostic characteristics tabulated by Domning (1994). Statements apply to the holotype except where otherwise indicated. Measurements of the cranium of *P. smithae* are listed in Table 1. A more complete description, including the postcranial skeleton, will appear in a forthcoming study.



TABLE 1— Measurements of holotype and referred crania of *Protosiren smithae*.  
All measurements in mm (\* = estimate).

Abbr.	Measurement	CGM 42292	UM 101224
AB	Condylobasal length	350*	—
ab	Height of jugal below orbit	55	—
AH	Length of premaxillary symphysis	70*	—
BI	Rear of occipital condyles to anterior end of interfrontal suture	224	—
CC'	Zygomatic breadth	185	—
cc'	Breadth across exoccipitals	136	—
de	Top of supraoccipital to ventral sides of occipital condyles	114	—
F	Length of frontals, level of tips of supraorbital processes to frontoparietal suture	106	132
FF'	Breadth across supraorbital processes	139	148
ff'	Breadth across occipital condyles	80	—
GG'	Breadth of cranium at frontoparietal suture	92*	76*
gg'	Width of foramen magnum	39*	—
HI	Length of mesorostral fossa	112	107*
hi	Height of foramen magnum	44	—
JJ'	Width of mesorostral fossa	52	52
KL	Maximum height of rostrum	53	58*
MM'	Posterior breadth of rostral masticating surface	77	—
no	Anteroposterior length of zygomatic-orbital bridge of maxilla	55	59
OP	Length of zygomatic process of squamosal	98	—
OT	Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen	132	—
P	Length of parietals, frontoparietal suture to rear of external occipital protuberance	100	86
QR	Anteroposterior length of root of zygomatic process of squamosal	40	46
rr'	Maximum width between labial edges of left and right alveoli	81	—
ST	Length of cranial portion of squamosal	76	87
ss'	Breadth across sigmoid ridges of squamosals	136*	—
T	Dorsoventral thickness of zygomatic-orbital bridge	14	16
tt'	Anterior breadth of rostral masticating surface	38	—
UV	Height of posterior part of cranial portion of squamosal	85*	79+
WX	Dorsoventral breadth of zygomatic process	43	33+
yy'	Maximum width between pterygoid processes	21	—
YZ	Length of jugal	140*	—
LFr	Length of frontals in midline <sup>1</sup>	87*	116
HSo	Height of supraoccipital	57*	62
WSo	Width of supraoccipital	94	115
HIf	Height of infraorbital foramen	15*	—
WIf	Width of infraorbital foramen	10*	—
RD	Deflection of masticating surface of rostrum from occlusal plane (degrees)	54*	—

<sup>1</sup>The frontals in CGM 42292 are interpreted as extending all the way to the mesorostral fossa.

*Premaxilla*.— The premaxillary symphysis is shorter relative to the cranium than it appeared to be in the holotype of *P. fraasi*. However, the symphysis in the latter specimen (CGM 10171) was incorrectly restored (see Gingerich et al., 1994). In life it was probably similar to that of *P. smithae* [C 3:0, rather than C 3:1 as provisionally indicated by Domning (1994)]. The dorsal surface of the symphysis is strongly convex transversely, and there is no trace of

TABLE 2— Measurements of holotype and referred mandibles of *Protosiren smithae*.  
All measurements in mm (\* = estimate).

Abbr.	Measurement	CGM 42292	UM 101224
AB	Total length	222	--
AG	Anterior tip to front of ascending ramus	154	--
AP	Anterior tip to rear of mental foramen	70	--
AQ	Anterior tip to front of mandibular foramen	160	--
AS	Length of symphysis	65	--
BG	Posterior extremity to front of ascending ramus	74	--
BQ	Posterior extremity to front of mandibular foramen	65	--
CD	Height at coronoid process	154	--
DF	Distance between anterior and posterior ventral extremities	113	--
DK	Height at mandibular notch	114	--
DL	Height at condyle	131	--
EF	Height at deflection point of horizontal ramus	66	84*
EU	Deflection point to rear of alveolar row	86	112*
GH	Minimum anteroposterior breadth of ascending ramus	63	60
GP	Front of ascending ramus to rear of mental foramen	76	--
IJ	Maximum anteroposterior breadth of dorsal part of ascending ramus	76	--
MN	Top of ventral curvature of horizontal ramus to line connecting ventral extremities	26	--
MO	Minimum dorsoventral breadth of horizontal ramus	37	54
RR'	Maximum breadth of masticating surface	51	--
SQ	Rear of symphysis to front of mandibular foramen	99	76*
VV'	Maximum width between labial edges of left and right alveoli	59*	--
WW'	Minimum width between angles	70*	--
XX'	Minimum width between condyles	100*	--
MD	Deflection of symphyseal surface from occlusal plane (degrees)	58	--

the rostral lacuna found in CGM 10171 (Gingerich et al., 1994). The premaxillae bear alveoli for a pair of tusks much larger than those of *P. fraasi*. External nares are enlarged and retracted, as in all sirenians [C 8:1]. Nasal processes are long [C 7:0]. Their posterior ends are rounded, little expanded mediolaterally, flattened dorsoventrally [C 6:0], and set into deep sockets in the anterior margins of the frontals [C 9:1]. The rostral deflection is about 54°, in contrast to *P. fraasi* (about 40°-50° as newly restored by Gingerich et al., 1994).

*Nasal.*— The anterior nasal border is strongly arched, and not incised [C 37:0]. The frontonasal sutures are not clearly discernible in the holotype. In UM 101224, the nasals are clearly visible and lie lateral and dorsomedial to the nasal cavity; their dorsomedial edges are 20 mm apart, separated by thin anterior projections of the frontals, and their dorsal exposures end only 2-3 mm behind the nasal processes of the premaxillae [C 31:1, C 32:1].

*Frontal.*— The supraorbital process is well developed, with a prominent, dorsoventrally-flattened posterolateral corner [C 36:0] that is gently inclined ventrolaterad [C 43:0], with a thicker, blunt anterior tip. The entire frontal roof is smoothly convex [C 42:0]. The lateral margins of the roof (temporal crests) are very prominent, strongly overhanging, and these converge backward from the posterolateral corners of the supraorbital processes in almost straight lines extending to the parietal; there is no narrowed "waist" at the frontoparietal suture as in the holotype of *P. fraasi* (Andrews, 1906: fig. 66d). The lower part of the temporal wall is slightly depressed to form a fossa supraoptica. The lamina orbitalis that forms the floor of this fossa is apparently thin [C 38:0] but substantial; in UM 101224 it is up to 6 mm thick.

*Parietal.*— The frontoparietal suture divides the skull roof into roughly equal nasal-frontal and parietal portions. The parietal roof continues the dorsal convexity of the frontal roof, with only a slight median furrow (deeper in UM 101224) about 20 mm wide; there is no suggestion of a sagittal crest [C 51:1]. The parietal roof is extended posterolaterally on each side by a massive bony protuberance more than 20 mm thick that supports the lateral wings of the nuchal crest. The endocranial surface is smoothly concave, with no bony falx cerebri, internal occipital protuberance, or tentorium; in UM 101224 the falx and tentorium are very faintly marked.

*Supraoccipital.*— The nuchal crest is massive, slightly overhanging, and strongly concave posteriorly, as in the holotype of *P. fraasi*.

*Exoccipital.*— Exoccipitals are separated in the midline by 12 mm, so that the foramen magnum reaches the supraoccipital [C 66:1]. Sickenberg (1934: 52) stated that this occurred in only one of his specimens of *P. fraasi* ("Stück V" = SMNS 10576); however, examination of SMNS 10576 (by D. P. D.) suggested this might not be the case. In CGM 42292, and to a lesser extent in UM 101224, the dorsomedial corners of the exoccipitals are posteriorly convex and protrude strongly backward; these accentuate what appear to be otherwise shallow supracondylar fossae [C 67:1]. The lateral borders of the exoccipitals are strongly convex and angular in outline (in posterior view), with jutting corners level with the tops of the condyles. The dorsolateral borders are slightly roughened but not thickened or overhanging in the holotype; in UM 101224 a more irregular and overhanging flange is developed [C 70:0 or 1].

*Basioccipital.*— Fused with exoccipitals and basisphenoid, indicating adulthood.

*Alisphenoid.*— Forms the lateral side of the pterygoid process. A large alisphenoid canal is present [C 101:0]. The foramen ovale is converted into a broadly open notch, confluent with the large opening surrounding the periotic [C 103:1].

*Pterygoid.*— Fused with surrounding bones; forms the posteromedial part of the remarkably long pterygoid process. This ends posteriorly in a single smooth edge, which is hooked backward slightly at its tip; there is no real pterygoid fossa [C 102:0]. However, 10-20 mm from the tip of the process there begins a low ridge on the lateral side that marks the anterior edge of a rudimentary fossa, at the ventral end of which is a surprisingly well-developed hamular trochlea. Hence it appears that, despite the absence of a well-developed fossa, a functional tensor veli palatini muscle was present.

*Palatine.*— The anterior sutures are not clear, but the anterior ends of the palatines may lie at the level of M<sup>1</sup>, hence well forward of the posterior end of the zygomatic-orbital bridge [C 99:0]. The posterior border is not incised, merely shallowly concave [C 97:0], and lies well behind M<sup>3</sup>.

*Maxilla.*— The anterior part of the palate is broad, giving a more trapezoidal shape to the palatal surface of the rostrum than is seen in *P. fraasi*. Behind this, the palate narrows and bears a flat-bottomed median gutter. More posteriorly, the palate again broadens, and is relatively thin (9 mm thick at the level of M<sup>2</sup> in UM 101224 [C 16:0]). The anterior part of the maxilla is distinctly deflected as in *P. fraasi*, and forms a gentle curve transitional between the palatal planes of the maxillae and premaxillae. The zygomatic-orbital bridges are nearly level with the palate [C 11:0], are long anteroposteriorly [C 14:0], and are thick posteriorly. The infraorbital foramen is small for a sirenian, measuring about 15 x 10 mm in diameter [C 13:0].

*Squamosal.*— The dorsal end lies about 1 cm below the level of the posterior parietal roof and temporal crest [C 76:0]. The posterior edge is indented by a rather small mastoid fenestra that is only about 1 cm in diameter. A sigmoid ridge, although damaged, was present but weak; as in *P. fraasi*, it was not prominent in posterior view [C 74:0]. This condition should probably be regarded as distinct from, and more primitive than, the more prominent ridge seen in most other sirenians. The external auditory meatus is slightly narrower anteroposteriorly (7 mm) than high dorsoventrally (10 mm) [C 82:0], though not so narrow as in *P. fraasi*. Mediolaterally the meatus is more than 1 cm long [C 75:0]. There is no distinct posttympanic

TABLE 3— Linear dimensions of cheek teeth of *Protosiren smithae* holotype (CGM 42292).  
All measurements in mm (\* = estimate, w = dimension reduced by wear).

Measurement	Left	Right
<i>Upper dentition</i>		
M <sup>2</sup> length	19.4w	19.7w
M <sup>2</sup> anterior width	18.0	18.0
M <sup>2</sup> posterior width	17.2	17.0
M <sup>3</sup> length	22.2*	21.8
M <sup>3</sup> anterior width	19.2	19.0
M <sup>3</sup> posterior width	15.8	15.6
<i>Lower dentition</i>		
M <sub>3</sub> length	--	25.0
M <sub>3</sub> anterior width	--	16.0
M <sub>3</sub> posterior width	--	15.6

process with a projecting facet for insertion of the sternomastoid muscle [C 73:0]. The rear edge of the zygomatic root is very shallowly notched, but a distinct processus retroversus like that of dugongids is not present [C 77:0]. In lateral outline, the zygomatic process is irregularly elliptical with a bluntly rounded anterior end like that of *P. fraasi* or *Trichechus*; it does not taper anteriorly as in typical dugongids. In UM 101224 the outline is concave ventrally. The lateral surface of the process is concave; the medial side is nearly flat [C 84:0].

*Jugal.*— The preorbital process is a thin plate [C 88:0] forming the anteromedial wall and anterior border of the orbit; it is separated from the premaxilla by the maxilla [C 87:0]. A broad, blunt postorbital process lies against the tip of the zygomatic process of the squamosal. The ventral process is smooth-surfaced and mediolaterally compressed, with a rounded tip; it lies directly beneath the rear edge of the postorbital process, hence well behind the orbit [C 85:0]. Both zygomatic processes, which are slender and oval in cross section, are broken at their tips, but they were longer than the anteroposterior diameter of the orbit [C 89:0] and probably reached the anterior edge of the temporal condyle.

*Mandible.*— The mandible of CGM 42292 (Fig. 2, measurements in Table 2) resembles specimens referred to *Eotheroides aegyptiacum* by Andrews (1906: fig. 67) and by Abel (1913: fig. 5; pl. 32, fig. 1) in size and morphology. In contrast to the specimen referred to *Protosiren fraasi* by Priem (1908; "Stück L" of Sickenberg, 1934), the masticating surface of the symphysis in CGM 42292 is broad [C 121:1], bearing two rows of large alveoli separated by a deep groove 1-1.5 cm wide (this groove is about 0.5 cm wide in UM 101224); the lateral borders of the alveoli are overhanging. The symphyseal surface is deflected about 58° from the occlusal plane. The horizontal ramus is narrow dorsoventrally where it joins the symphysis [C 128:0], but rapidly becomes broader posteriorly. The ventral arch of the ramus is asymmetrical, its anterior limb (forming the posterior side of the symphysis) being turned down abruptly and almost vertically [C 122:1]. The posterior limb of the arch is not tangent to the mandibular angle [C 129:1]. In contrast to *P. fraasi*, a single large mental foramen is present on each side in the holotype; on the left, where it is better preserved, the posterior part of this foramen is very narrow and opens more dorsally than laterally, due in part to the slope of the bone's lateral surface at this point. In UM 101224, however, this narrow region appears pinched off to form a separate foramen, so this character probably varied in the species [C 123:0 or 1]. The coronoid process is high, very narrow and recurved, and extends some-

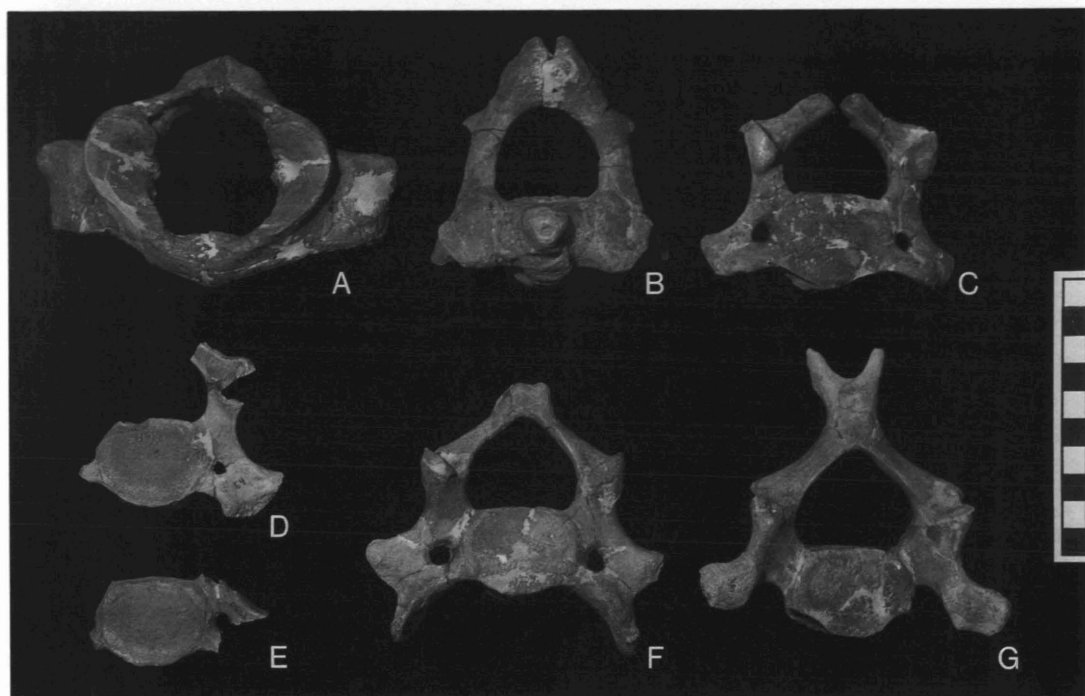


FIG. 5.—Postcranial elements of *Protosiren smithae*, CGM 42292 (holotype). A, atlas C1. B, axis C2. C, cervical vertebra C3. D, cervical vertebra C4 with broken neural arch. E, cervical vertebra C5 with broken neural arch. F, cervical vertebra C6. G, cervical vertebra C7. Note bifurcated neural spine on C7 like that on T1 (Fig. 6). All specimens are shown in anterior view. Scale is in cm. Casts of cervical vertebrae shown here are catalogued as UM 94810.

what forward of its base [C 126:1]. The posterior edge of the ascending ramus is interrupted by a prominent right-angled step in its outline (processus angularis superior [C 125:1]). The large mandibular canal, which exposes the dental capsule [C 127:1], forms a single, unbridged opening with the posterior opening of the small coronoid canal, as in most other sirenians.

*Upper dentition.*— The dental formula was apparently 3.1.5.3 in both upper and lower jaws [C 150:0, C 151:0, C 155:1].  $M^2$  is heavily worn in the holotype;  $M^3$  and  $M_3$  are moderately worn. Measurements of upper and lower molars in the holotype are listed in Table 3.

The upper first incisors formed very large tusks [C 139:0]; their alveoli are elliptical [C 141:0] and about 30 x 18 mm in diameter, compared with the 14 x 11 mm diameters of the broken tusks in the holotype of *P. fraasi*. The alveoli are filled with matrix but surely extend more than half the length of the short premaxillary symphysis [C 140:2].

Following a diastema of 20-30 mm, round alveoli for two more incisors, each about 1 cm in diameter and separated by about 0.5 cm [C 143:0], are present along the edges of the premaxillae. They are so close to the edge, in fact, that they cause prominent bulges on the lateral sides of the rostrum. The same is true of the alveolus for the single-rooted canine [C 144:1], likewise 1 cm in diameter and located about 0.5 cm behind  $I^3$  (1.5 cm in UM 101224).

Similar-sized alveoli for single-rooted  $P^{1-2}$  follow at intervals of 8 and 9 mm, respectively (10 and 17 mm in UM 101224). A slightly smaller socket almost confluent with that of  $P^2$  probably represents  $P^3$ . A stronger septum, 3 mm thick, separates the latter from the 6 mm



FIG. 6—Postcranial elements of *Protosiren smithae*, CGM 42292 (holotype). A, thoracic vertebra T1. B, thoracic vertebra T2. Note bifurcated neural spine on T1 like that on C7 (Fig. 5). Both specimens are shown in anterior view. Scale is in cm. Casts of thoracic vertebrae shown here are catalogued as UM 94810.

diameter  $P^4$ , which is followed at the same interval by that of  $P^5$ , a mere 5 mm in diameter. Thus all five premolars appear to have been single-rooted [C 146:0, 157:1]. In the incomplete and rather poorly preserved maxilla of UM 101224, the dental formula is less clear, but only two single alveoli for premolars are visible behind  $P^2$ . These follow the latter at intervals of 12 and 6 mm on the right side and 14 and 7 mm on the left, having diameters slightly less than 1 cm. They are immediately succeeded by the alveoli for a three-rooted tooth. It is conceivable that this represents  $DP^5$  and that  $P^5$  has not yet developed; however, the specimen is adult. In both specimens the canine alveolus lies at the widest point of the rostrum and the  $P^2$  alveolus lies just in front of the zygomatic-orbital bridge.

Immediately behind the  $P^5$  alveolus in the holotype, there are three sets of sockets for the three-rooted molars. The left and right  $M^{2-3}$  are preserved. They are robust teeth with smooth enamel [C 156:0, C 158:0] that is 1-2 mm thick. The crown pattern of  $M^2$  is almost obliterated; that of  $M^3$  is identical to that of *P. fraasi*, with a strong anterior cingulum, a tricusate and obliquely oriented protoloph, a smaller metaloph with three cusps in a nearly straight but even more oblique line, and a weak ridge descending the posterior side of the hypocone, not quite enclosing a basin. In each loph the lingual cusp is the largest and the labial the smallest.

The only upper tooth preserved in UM 101224 is an incomplete, heavily worn right ? $M^2$  measuring 17.2 mm in anterior width. The metaconule contacts the base of the protoloph; a low spur of the metacone blocks the labial end of the transverse valley.

**Lower dentition.**—The most anterior pair of lower incisor alveoli visible in the holotype is damaged; it is uncertain whether a still more anterior pair existed. Succeeding alveoli are progressively more prominent, reaching maximum size (up to 1 cm in diameter) at the fourth position (as now preserved) from the front. The next socket (for either  $P_1$  or  $P_2$ ) is slightly smaller, and is succeeded without any diastemata by indistinct sockets for three smaller single-

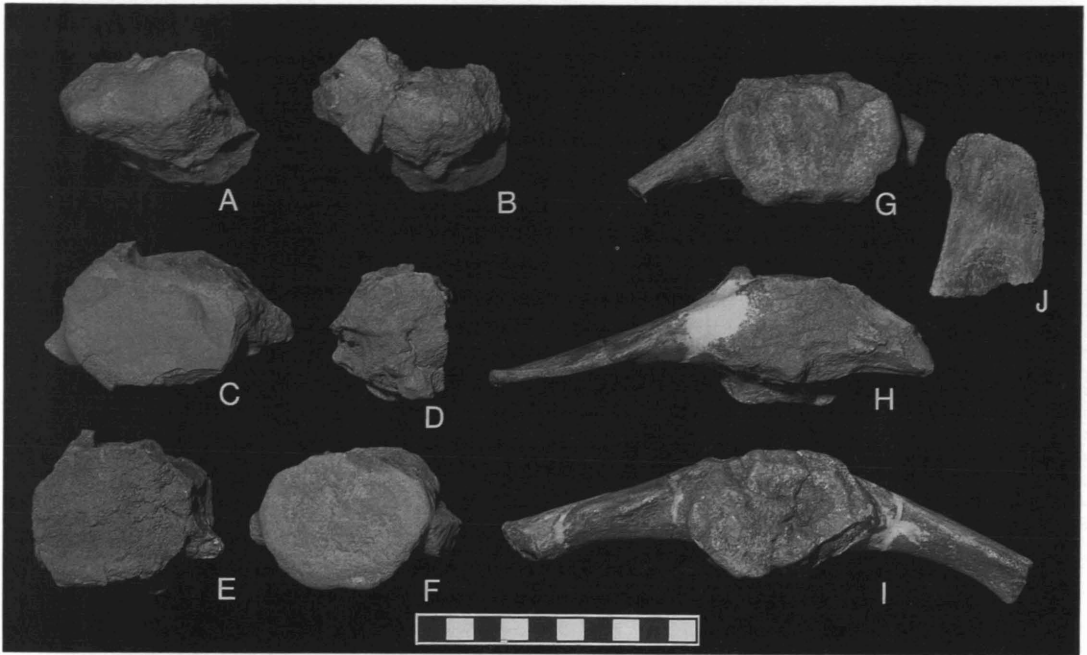


FIG. 7—Postcranial elements of *Protosiren smithae*, CGM 42292 (holotype). A-D, centra of unidentifiable lumbar and/or caudal vertebrae. E, centrum of anterior caudal vertebra, anterior view. F, centrum of unidentified lumbar or caudal vertebra. G, centrum and left transverse process of lumbar vertebra, posterior view. H, centrum and right transverse process of lumbar vertebra, anterior view. I, sacral vertebra S1 with both transverse processes ending as flat rugose surfaces, anterior view. J, neural spine of lumbar vertebra, right lateral view. Scale is in cm. Casts of some vertebrae shown here (E, G-J) are catalogued as UM 94810.

rooted premolars (these are easier to distinguish on the left side than on the right, where the sockets for  $P_{3-4}$  are more closely appressed and obliquely aligned). Next comes a pair of transversely-elongated alveoli, measuring about 11 and 12 mm across, respectively, and together measuring about 11 mm anteroposteriorly, apparently for a two-rooted  $M_1$ . The pair of large sockets for  $M_2$  measures 21 mm front to back and 14 mm across.  $M_3$ , still present on both sides, occupies a pair of alveoli 25 mm long and 14 mm wide.

Only three sets of alveoli attributable to two-rooted, molariform teeth are present; hence the last premolar was single-rooted and part of the permanent series, as in the skull. Given that all adequately known Eocene sirenians had five premolar loci (Domning et al., 1982), and that the mandible described by Andrews (1906: fig. 67; CGM 42297, formerly numbered CGM 10171) can be similarly interpreted, we conclude that the mandible of CGM 42292 likewise possessed a full 3.1.5.3 dentition but has lost its first pair of incisor alveoli to postmortem damage.

In UM 101224,  $M_{2-3}$  are present and are preceded by the alveoli for  $M_1$ . In front of this is a poorly preserved series of three closely appressed alveoli, together occupying a space of 26 mm. They are preceded by a 9 mm diastema and then by four more alveoli, of which the anteriormost is incomplete. These apparently represent  $I_3$ - $P_5$ . If so, then in both specimens  $P_2$  occupied the first alveolus behind the point of deflection of the anterior masticating surface.

The crown of  $M_3$  is preserved only on the right side in the holotype; it measures 25.0 mm in length, 16.0 mm in anterior width, and 15.6 mm in posterior width. The protolophid and

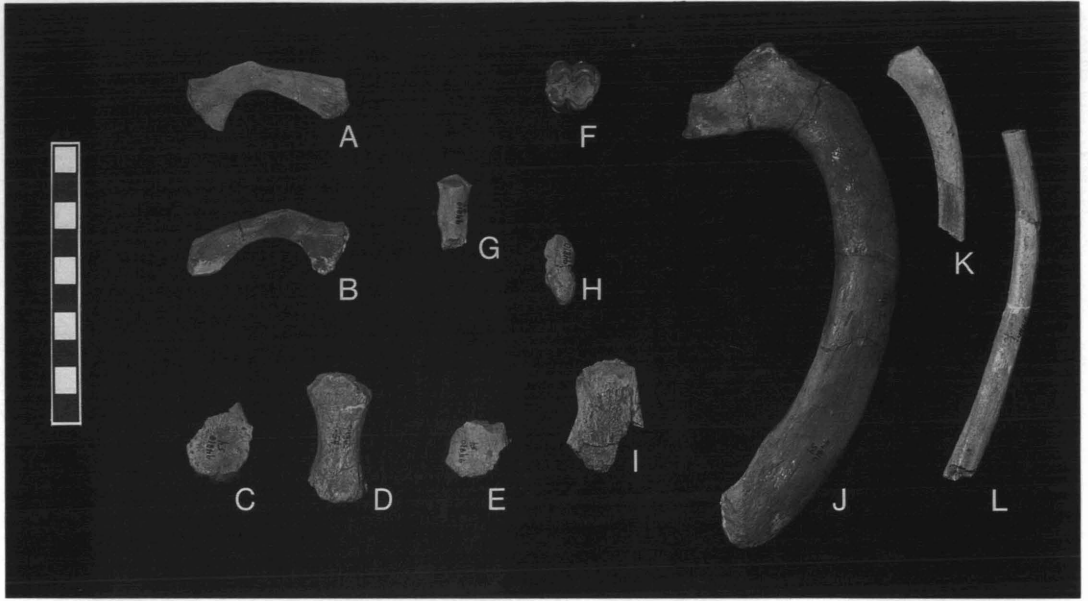


FIG. 8—Postcranial elements of *Protosiren smithae*, CGM 42292 (holotype). A-B, left and right thyrohyals. C, half-sternebra. D, complete sternebra. E, half-sternebra. F, right  $M^2$  found isolated, occlusal view. G, unidentified bone fragment, possibly part of neural arch of cervical vertebra. H, unidentified bone fragment. I, unidentified bone fragment, possibly part of sternal element or part of transverse process of thoracic vertebra. J, left first rib, anterior view. K-L, unidentified rib fragments of immature cetacean found in pieces with CGM 42292. Scale is in cm. Casts of most elements shown here are catalogued as UM 94810.

metalophid are each reduced by wear to a single lake of dentine, and the two lakes are almost confluent. The large hypoconulid lophule has not quite had its enamel breached, but its relief has been reduced to a broad, smoothly concave basin, revealing little or nothing of its original cusp pattern. The posterior root is larger than the anterior, and is elongated anteroposteriorly.

In UM 101224,  $M_{2-3}$  are both heavily worn and damaged. The former has a crown length of about 20 mm (estimated) and an anterior width of 15.0 mm; the crown of the latter was at most 23 mm long.

*Postcranial skeleton.*— The most striking features of the postcranial skeleton of *Protosiren smithae* are described here, based on CGM 42292 (Figs. 5-11) and, to a lesser extent, UM 101224. These complement known postcranial remains of *P. fraasi* (Sickenberg, 1934), and reveal details of the axial skeleton, forelimbs and hind limbs for the first time. A detailed description, with measurements, is in preparation.

*Protosiren smithae* has seven cervical vertebrae. The atlas and axis are massive. C3-C7 have very short centra and delicate neural arches (Fig. 5). Neural spines are high on anterior thoracic vertebrae (Fig. 6). Lumbar and caudal vertebrae have massive centra with broad transverse processes (Fig. 7). There is a single sacral vertebra having stout but elongate transverse processes with dorsoventrally expanded ends (Fig. 7i), suggesting flexible ligamentary or cartilaginous connection to the pelvis.

The sternum is unlike that of any sirenian yet described, with sternebrae (e.g., Fig. 8D) resembling instead those of land mammals whose sterna consist of a chain of similar, short, blocklike bones alternating with costal cartilages. Sternal elements seem not to resemble the more conventionally sirenian-like elements described, but not illustrated, by Sickenberg (1934:



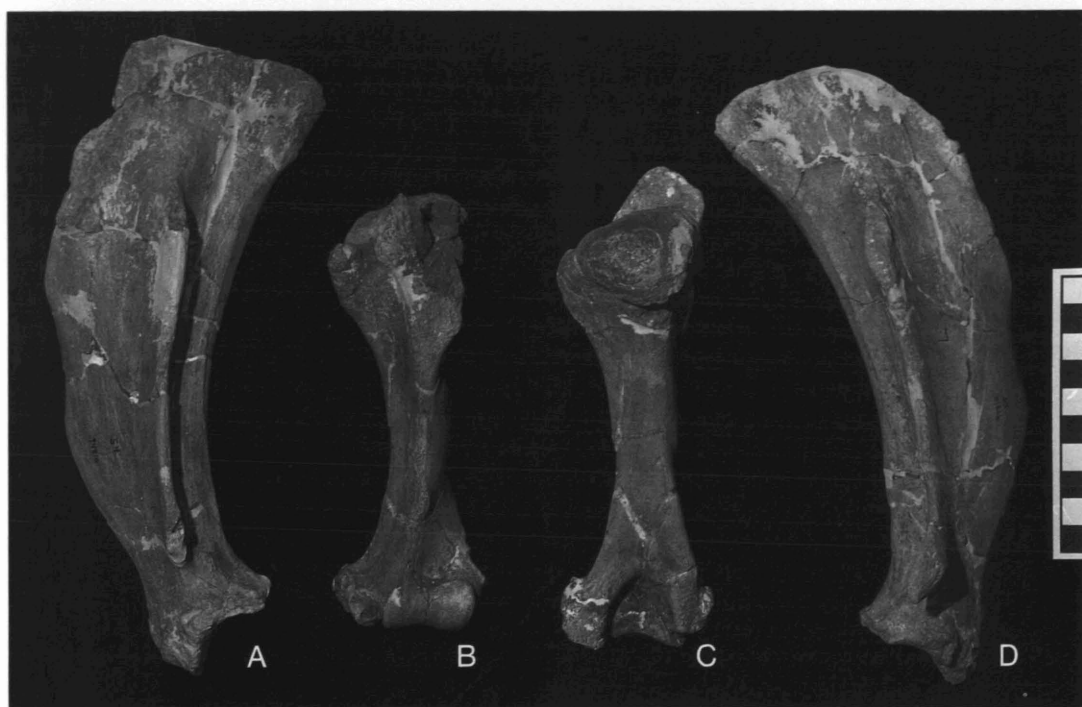


FIG. 9—Postcranial remains of *Protosiren smithae*, CGM 42292 (holotype). A, left scapula, lateral view. B, left humerus, anterior view. C, right humerus, posterior view. D, right scapula, lateral view. Scale is in cm. Casts of elements shown here are catalogued as UM 94810.

88-89), which he referred, questionably, to *P. fraasi*. The only complete rib in CGM 42292 is the first (Fig. 8J), but UM 101224 preserves much of the rib cage. Ribs in *Protosiren* are osteosclerotic (dense) but not as pachyostotic (swollen) as those of *Prorastomus*, *Eotheroides*, or *Eosiren*. Rib heads seem to have been largely cartilaginous, in contrast to those of other sirenians (as Sickenberg, 1934, recognized).

The scapula of *Protosiren smithae* (Fig. 9A,D) resembles the very sickle-shaped scapula of *P. fraasi* illustrated by Sickenberg (1934: pl. 3, fig. 2), but the suprascapular fossa is broader. The radius is completely separate from the ulna (Fig. 10A-B, I-J), although attached to it by flat, rugose surfaces that precluded any pronation or supination in life. Several metacarpals (Fig. 10C-E) and phalanges (Fig. 10F-H) are preserved in CGM 42292. The former are relatively short and heavy, with distal epiphyses fused (indicating maturity). There is still some uncertainty about the homology of metacarpal elements in CGM 42292 and UM 101224, but these resemble metacarpals of condylarths in terms of proportion and mode of articulation. Manual phalanges are flattened and more suggestive of sirenian phalanges.

Innominate of *Protosiren smithae* (Fig. 11A,B) are larger, but otherwise resemble innominates described by Abel (1904: pl. 7, fig. 1; see also Andrews, 1906: fig. 68C), which were originally referred to *Eotherium aegyptiacum* but later identified as *Protosiren fraasi* (by Sickenberg, 1934, p. 94). The innominates have a rodlike ilium, a broad and flattened ischium, a well-developed pubis, and a large acetabulum. The obturator foramen is large, but smaller in comparison to the size of the innominate as a whole than that of *P. fraasi*. The femur (Fig. 11C-E) is 14 cm long, with a distinct greater and lesser trochanter, but no third trochanter. A shallow trochanteric fossa is present, and there is a clearly marked intertrochan-

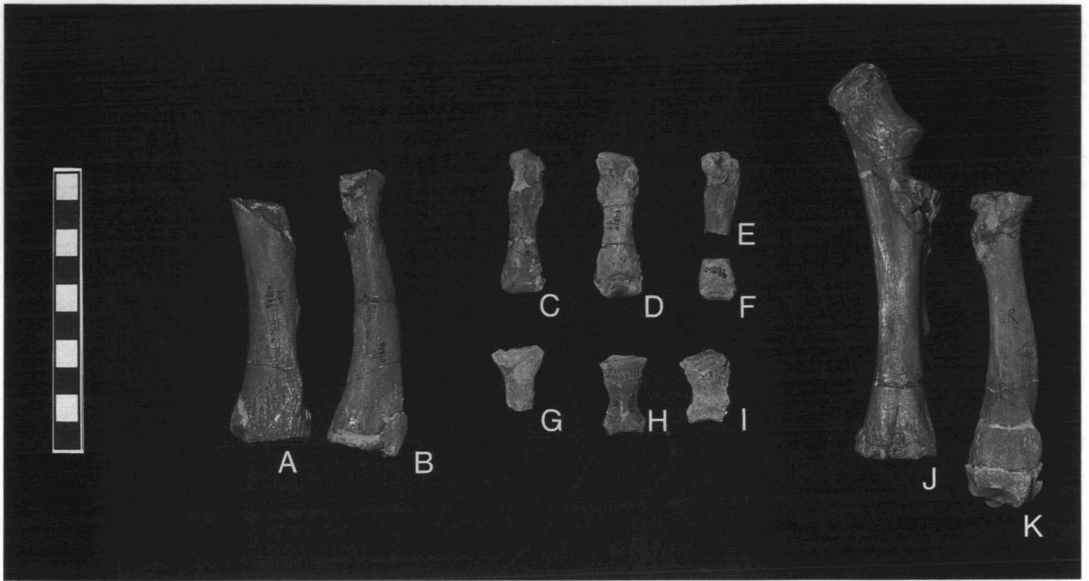


FIG. 10—Postcranial elements of *Protosiren smithae*, CGM 42292 (holotype). A, left distal ulna lacking distal epiphysis, posterior view. B, left radius with proximal articular surface but no distal epiphysis, medial view. C, right metacarpal II or III with distal epiphysis solidly co-ossified, dorsal view. D, right metacarpal III or IV with distal epiphysis solidly co-ossified, dorsal view. E, proximal half of left metacarpal V, dorsal view. F, distal part of unidentified metacarpal with distal epiphysis solidly fused, dorsal view. G, unidentified manual phalanx with proximal epiphysis fused, dorsal view. H, unidentified manual phalanx with proximal epiphysis fused, ventral view. I, unidentified manual phalanx with proximal epiphysis fused, ventral view. J, right ulna lacking distal epiphysis, anterolateral view. K, right radius with proximal articular surface and distal epiphysis, posterolateral view. Scale is in cm. Casts of elements shown here are catalogued as UM 94810.

teric crest. The shaft is flattened anteroposteriorly. The patellar surface and condyles are well developed. The patella (Fig. 11F) is large, as are the tibia (about 13 cm long) and the fibula (Fig. 11G). Nothing is known at present of the foot, but retention of functional hip and knee articulations and a well formed tibia and fibula indicate that *Protosiren* almost certainly retained a mobile foot (greatly reduced or lost in later sirenians).

#### DISCUSSION

Phenetically, *P. smithae* is closest to *P. fraasi* among known sirenians. However, this resemblance is due largely to absence in these two taxa of many derived character states seen in other sirenians. Of the characters used in the analysis by Domning (1994), only the absence of a pterygoid fossa [C 102:0], interpreted as a reversal in *Protosiren*, unites the two species, and its polarity is uncertain. Other synapomorphies of *P. fraasi* and *P. smithae* probably exist, but require further study. For example, the lack of a bony falx cerebri in these two species may prove to be a derived condition, if the presence of this structure in *Prorastomus* can be established.

Also, the discovery of *P. smithae* has led us to conclude that the mandibles from the lower Mokattam Formation formerly referred (e.g., by Domning et al., 1982) to *P. fraasi* and *Eo-*

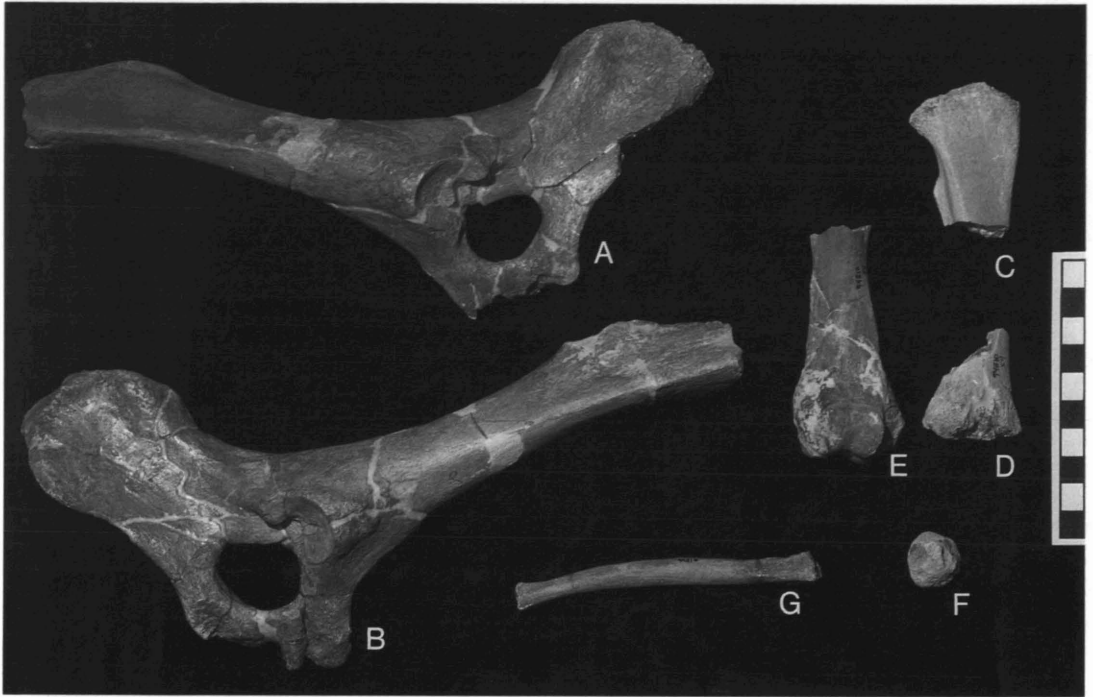


FIG. 11—Postcranial elements of *Protosiren smithae*, CGM 42292 (holotype). A, left pelvis with well developed ilium, ischium, acetabulum, obturator foramen, and broken pubis, lateral view. B, right pelvis, lateral view. C, left proximal femur lacking proximal epiphyses, anterior view. D, left distal femur lacking distal epiphysis, anterior view. E, right distal femur with prominent patellar groove and distal epiphysis bearing condyles for articulation with tibia, anterior view. F, patella, anterior view. G, fibula lacking proximal and distal epiphyses. Scale is in cm. Casts of elements shown here are catalogued as UM 94810. Remainder of right femur, right tibia lacking distal epiphysis, and proximal epiphysis of left tibia of this specimen (not illustrated) were found in 1993.

*theroides aegyptiacum* were incorrectly assigned. The striking breadth of the mandibular masticating surface in CGM 42292 [C 121] is more similar to the form of the mandibles described by Andrews (1906: fig. 67) and Abel (1913: pl. 32, fig. 1) than to that of the specimen described by Priem (1908) and Sickenberg (1934: "Stück L"). This conclusion is supported by evidence from other new Fayum specimens (Domning and Gingerich, in preparation). Accordingly, we now think that the latter (narrow) morph more likely pertains to *Eotheroides* and/or early *Eosiren*, and the former (broad) morph to *Protosiren*. Since the narrow morph is clearly primitive, based on its occurrence in *Prorastomus* (Savage et al., 1994), this particular kind of broad morph (with well-developed alveolar rows widely separated by a more or less deep median concavity) is probably an additional synapomorphy of *Protosiren* spp. It follows that character 121 needs to be redefined, and this broad state distinguished from the more moderately broadened condition seen, for example, in later *Eosiren* and in *Halitherium*, as well as from the broad condition lacking lower incisors and canines that is seen in still more derived forms like *Metaxytherium*.

This conclusion also implies that the narrow-jawed sirenian from the Eocene of North Carolina referred to *Protosiren* sp. by Domning et al. (1982) does not belong to that genus, but is more likely a primitive dugongid, as in the case of the Lower Mokattam specimens. This is also supported by comparisons of its ribs and other elements with our new Fayum material,

as will be reported elsewhere. The skullcap (USNM 307609) from North Carolina, however, does resemble *Protosiren* in its lack of a bony falx cerebri.

Since *P. fraasi* displays no autapomorphies, and is older than *P. smithae* (Lutetian as compared with Bartonian), it is plausibly viewed as the direct ancestor of the latter. At this time, cladistic analysis does not support the derivation of any other known sirenians from *Protosiren*, so this genus appears to have died out without issue before the end of the Eocene.

*Protosiren smithae* was evidently still an amphibious animal, as shown by its well-developed fore- and hindlimbs, and by the high anterior thoracic neural spines that probably served to support the head by way of a nuchal ligament. Thus it seems safe to assume that still more primitive sirenians (*Protosiren fraasi*, *Prorastomus sirenoideus*) were at least equally capable of terrestrial locomotion. This has recently been confirmed by postcranial remains of *Prorastomus* discovered in Jamaica (Domning, in preparation). However, the legs of *P. smithae* were very short relative to its body, and it seems questionable whether the animal could have lifted its body off the ground; it may have merely slid or rested on its belly when out of the water, in a manner analogous to that of modern pinnipeds.

The emerging picture of *Protosiren*, then, is of an animal divergently specialized from other early sirenians, and less fully aquatic than contemporary primitive dugongids. Its ribs were less swollen, and had a unique form of articulation with the vertebrae that led Sickenberg (1934: 88) to conclude that its respiratory mechanics were distinctive. Its pelvis and hindlimbs were much less reduced than those of the Gehannam Formation dugongids (Domning and Gingerich, in preparation). Its broadened rostral masticating surfaces, furthermore, hint at different dietary preferences. Although the broadened masticating surfaces by themselves foreshadow developments in much later sirenians, the retention of large incisors and canines along the margins of these broadened surfaces is unique and may indicate a style of feeding like that of no other sirenian. The increase in the breadth of masticating surfaces from *P. fraasi* to *P. smithae*, together with increases in tusk size and rostral deflection, and separation of the nasals and exoccipitals, parallel trends in other sirenian lineages. Nonetheless, *Protosiren* seems to illustrate yet again the profound extent to which the life of each past age differed from that of all others.

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