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# CRANIAL MORPHOLOGY OF *PROTOSIREN FRAASI* (MAMMALIA, SIRENIA) FROM THE MIDDLE EOCENE OF EGYPT: A NEW STUDY USING COMPUTED TOMOGRAPHY

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PHILIP D. GINGERICH[1], DARYL P. DOMNING[2], CAROLINE E. BLANE[3]
AND MARK D. UHEN[1]

*Abstract*—The type skull of *Protosiren fraasi* Abel is restudied using computed tomography to reveal details of the cranium and endocranial cavity that are otherwise inaccessible for study. The dorsal surface of the endocranium is smooth, with no suggestion of the bony falx cerebri characteristic of contemporary *Eotheroides aegyptiacum* (Owen). This reaffirms validity of *Protosiren fraasi* as a valid genus and species distinct from *Eotheroides aegyptiacum*. The brain of *P. fraasi* has a volume estimated at 185 cc, which is about 23% larger than that of *E. aegyptiacum*. The end of the rostrum of the type specimen of *P. fraasi* is now broken, showing that it was incorrectly reconstructed when described by Andrews. *Protosiren* has complex ethmoturbinal scrolls, frontals as much as 3 cm thick, well developed alisphenoid canals, large teeth, and a broad mandibular symphysis connecting robust left and right dentaries. In addition, the type cranium of *P. fraasi* is distinctive among known sirenians in having a well developed rostral lacuna (median depression atop the premaxillary symphysis); its interpretation is problematical.

## INTRODUCTION

Sirenia is the order of aquatic mammals that includes living manatees and dugongs. The earliest evidence of Sirenia comes from fossils of late early Eocene age (ca. 50 million years before present [Ma]). Eocene sirenians have been known since the nineteenth century (Domning et al., 1982), but the evolution and systematic relationships of early sirenians are

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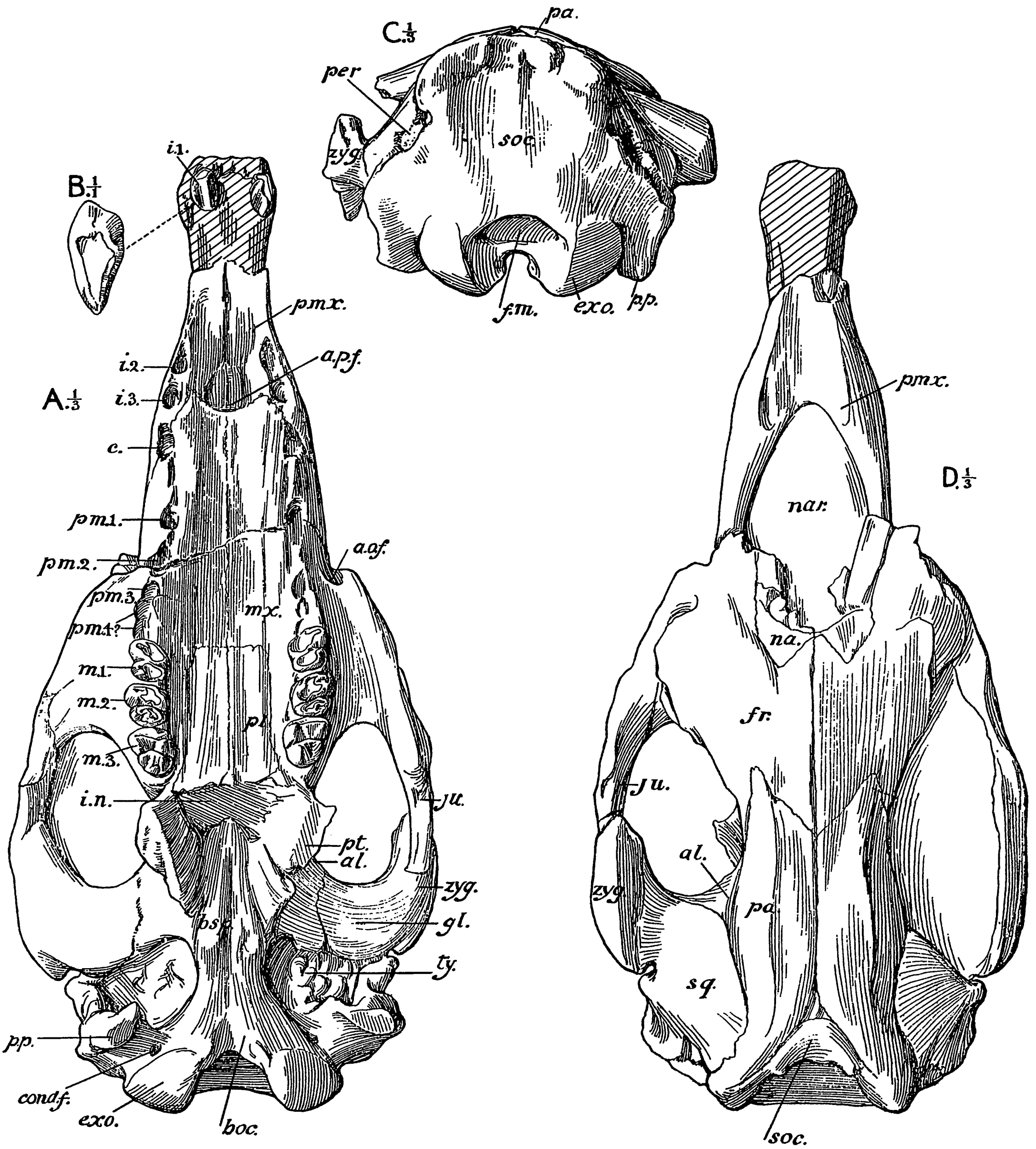

FIG. 1—Type specimen of *Protosiren fraasi* Abel as illustrated, 1/3 natural size, by Andrews (1906) [CGM 10171]. Type is a nearly complete cranium shown here in A, ventral view; C, posterior view; and D, dorsal view. B shows worn surface of right $I^1$ tusk (crowns of left and right $I^1$ tusks are preserved as casts in NHML and UM replicas of the type made at the turn of the century, but they are no longer preserved in the original type). Reconstruction of premaxillary rostrum shown here is too long and straight (plaster reconstruction, now missing in original type, is shown with cross-hatching). Andrews (1906) and Abel (1928) interpreted $P^4$ or $dP^4$ as having multiple roots, but *Protosiren* is now known to have retained both $P^4$ and $P^5$ as single-rooted teeth. Temporal fossa on right side remains filled with sedimentary matrix. Note rostral lacuna and suggestion of semicircular line on left side only (both labeled in Fig. 7). Abbreviations: *al.*, alisphenoid; *a.o.f.*, antorbital (infraorbital) foramen; *a.p.f.*, anterior palatine (incisive) foramen; *boc.*, basioccipital; *bsp.*, basisphenoid; *c.*, canine; *cond.f.*, condyloid (hypoglossal) foramen; *exo.*, exoccipital; *f.m.*, fora- ⇒

poorly understood because morphological and taxonomic diversity was high early in sirenian history and because most known specimens are fragmentary or poorly studied. For example, Richard Owen's (1855) type specimen of *Prorastomus sirenoides* from the late early Eocene of Jamaica is a skull, but this has only recently been cleaned and fully studied (Savage et al., 1994). Owen's (1875) type specimen of *Eotherium* [now *Eotheroides*] *aegyptiacum* from the middle Eocene of Egypt is a natural stone endocast of a braincase, with an associated rib fragment but no other bone useful for comparison.

The specimen of primary interest here, CGM 10171, is a well preserved skull (Fig. 1) from the same general locality and stratigraphic interval as Owen's type of *Eotheroides aegyptiacum*. All specimens described here are from the Lower Building Stone Member of the Mokattam Limestone of Cairo (Egypt), which is early-to-middle Lutetian in age (Gingerich, 1992; ca. 46 Ma). CGM 10171 was first described by Charles Andrews (1906), who tentatively referred the skull to Owen's genus and species. Following Andrews' publication, Othenio Abel (1907) published a review of marine mammals in which he mentioned *Eotherium*, indicated that "with this appears a second, more highly developed genus, *Protosiren*" (Abel, 1907, p. 29), and cited his own reproduction of Andrews' illustration (Abel, 1907, fig. 22).

The illustration of CGM 10171 in Abel (1907) is labelled "Skull of a sea-cow, *Protosiren fraasi* Abel, from the lower middle Eocene of Egypt." Abel had previously mentioned *Protosiren fraasi* as a new genus and species in 1904 (Abel, 1904, p. 214) and again in 1906 (Abel, 1906, p. 51), without indicating in either publication any particular specimen to which this name might refer. As a result, Abel's (1907) labelling of his figure 22 is taken as the first indication that Abel's name is based on evidence; CGM 10171 is the type specimen of *P. fraasi*; and valid publication of the name *Protosiren fraasi* dates from Abel (1907) (see Sickenberg, 1934, pp. 43-44; Domning et al., 1982, p. 36). Abel (1913) described skulls of *Eotherium* [*Eotheroides*] *aegyptiacum* in detail, but never published more than a cursory characterization of *Protosiren fraasi*. Details were left for Sickenberg (1934), who described the cranial morphology of *Protosiren* and much of the postcranial skeleton of both *Protosiren* and *Eotheroides*.

When CGM 10171 was first described, Andrews (1906) conservatively considered it to be a skull of Owen's *Eotheroides aegyptiacum*. Abel (1907) placed CGM 10171 in a new genus and species, *Protosiren fraasi*, but published no diagnosis stating why he thought it was different. Abel (1928) mentioned differences in the skull roof indicating that the cerebral hemispheres of the brain were broader and not separated by a deep median cleft, differences in development of pachyostosis, and differences in the pelvis, but Sickenberg (1934) was the first to describe these in detail. Sickenberg's list of the seventeen most important differences between skulls and skeletons of *Protosiren* and *Eotheroides*, translated, is listed in Table 1. According to Sickenberg, the presence of a ventrally-raised bony falx cerebri on the midline of the ventral surface of the parietals (corresponding to Abel's median cleft separating cerebral hemispheres) is a common characteristic distinguishing both skulls and endocasts of the brain of *Eotheroides* from those of *Protosiren*, but this has never been studied in the type specimen CGM 10171. Ongoing confusion about allocation of specimens to *Protosiren* prompted us to borrow CGM 10171 for comparison with newly-collected specimens and for detailed examination of the braincase using noninvasive computed tomography.

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men magnum; *fr.*, frontal; *gl.*, glenoid articulation; *i.1-3*, incisors; *i.n.*, internal nares; *ju.*, jugal; *m.1-3*, molars; *mx.*, maxilla; *na.*, nasal; *nar.*, external nares; *pa.*, parietal; *per.*, periotic; *pl.*, palatine; *pm.1-4*, premolars; *pmx.*, premaxilla; *p.p.*, paroccipital process; *pt.*, pterygoid; *soc.*, supraoccipital; *sq.*, squamosal; *ty.*, tympanic; *zyg.*, zygomatic process of squamosal. Illustration and abbreviations reproduced from Andrews (1906).

TABLE 1— Differences between skulls and postcranial skeletons of *Protosiren* and *Eotheroides*, as listed by Sickenberg (1934, p. 192-193; our observations in brackets).

| | *Protosiren fraasi* | *Eotheroides aegyptiacum* |
|---|---|---|
| 1. | Premaxilla straight | Premaxilla deflected |
| 2. | Maxilla deflected | Maxilla straight [Taken together, characteristics 1 and 2 mean that the rostrum is deflected more anteriorly in *Eotheroides*—this is not evident in our restoration in Fig. 8] |
| 3. | Premaxillary-maxillary suture much farther back than premaxillary symphysis [anteriormost part of suture is just behind posteriormost part of symphysis in CGM 10171] | Premaxillary-maxillary suture below premaxillary symphysis |
| 4. | Alisphenoid canal present | Alisphenoid canal absent |
| 5. | Squamosal does not contribute to back of skull | Squamosal contributes to back of skull [meaning more of squamosal is visible in posterior view] |
| 6. | Squamosal and supraoccipital completely separated by a process of the parietal | Squamosal and supraoccipital joined [this is ambiguous in most specimens] |
| 7. | Posttympanic process of squamosal absent | Posttympanic process of squamosal present [meaning a distinct attachment for the sternomastoid muscle is present] |
| 8. | Supra-auditory region thickened, outer ear passage somewhat elongated | Supra-auditory region not thickened, ear passage not elongated |
| 9. | Lamina orbitalis of the frontal contributes substantially to separation of the orbits and nasal cavity | Lamina lateralis of the ethmoid contributes substantially to separation of the orbits and nasal cavity, whereas there is no lamina orbitalis of the frontal [this is often broken and indeterminate] |
| 10. | Bony falx, bony tentorium, and internal occipital protuberence absent | Bony falx, bony tentorium, and internal occipital protuberence present |
| 11. | Numerous ethmoturbinalia | Few ethmoturbinalia [numerous or not, these are seldom preserved] |
| 12. | Periotic with processus fonticulus of mastoid portion | Periotic without processus fonticulus of mastoid portion [processus fonticulus inserts in and is visible through the mastoid foramen] |
| 13. | Temporal part of periotic larger than mastoid part | Temporal part of periotic smaller than mastoid part |
| 14. | No facial canal | Facial canal present |
| 15. | Dental formula 3.1.5.3 / 3.1.5.3 | Dental formula 2-3.1.4.d.3 / 3.1.4.d.3 [dP5 is not replaced] |
| 16. | Connection between ribs and transverse processes lost on middle thoracic vertebrae | Articular connection between ribs and transverse processes present on all thoracic vertebrae |
| 17. | Epiphyses on vertebral bodies reduced | Epiphyses on vertebral bodies not reduced |

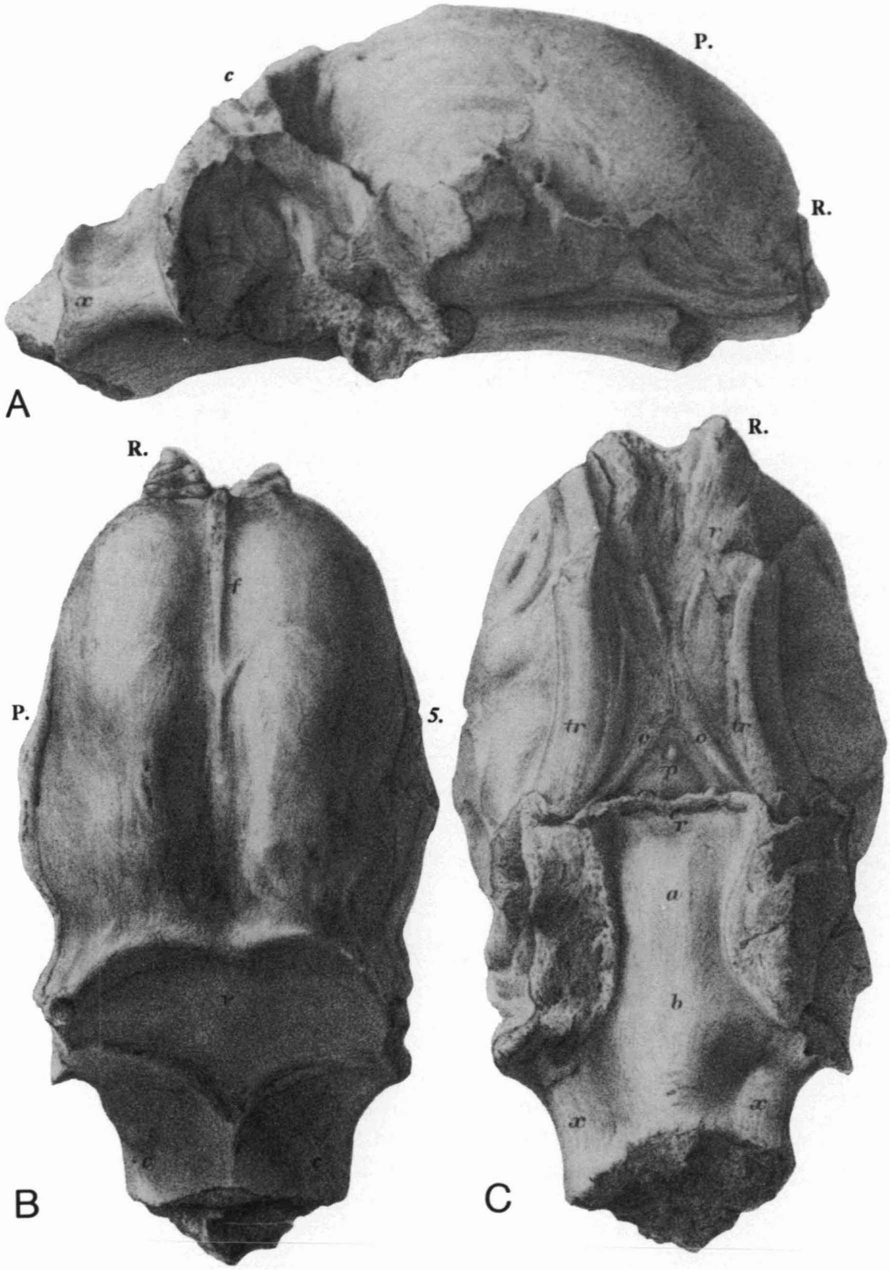

FIG. 2—Type specimen of *Eotheroides aegyptiacum* (Owen) as illustrated, natural size, by Owen (1875) [specimen is now catalogued as NHML 46722]. Type is a natural stone endocast shown here in A, right lateral view; B, dorsal view; and C, ventral view. Abbreviations are as follows: *a*, "pons Varolii"; *b*, anterior myelonal columns; *c*, limit of posterior myelonal columns; *f*, falx cerebri; *o*, optic nerve; *r*, transverse ridge separating impressions of basisphenoid and basioccipital; *p*, pedicle of pituitary body; *R*, rhinencephalon (olfactory bulb); *tr*, trigeminal nerves; *v*, upper vermiform process; *x*, lateral myelonal columns; *5*, prominence anterior to sylvian fissure. Illustration and abbreviations reproduced from Owen (1875).

TABLE 2— Measurements of brain endocasts or endocranial vaults of *Eotheroides aegyptiacum* and *Protosiren fraasi* (lengths and widths in mm, volumes in cc). Measurements are from Edinger (1933) unless otherwise indicated. Bold typeface highlights new measurements of type specimens first reported here. Measurements marked with asterisks are minimum estimates based on incomplete or compressed specimens.

| Specimen | Total length | Cerebrum length | Cerebrum width (front. lobe) | Cerebrum width (temp. lobe) | Endocranial volume |
|---|---|---|---|---|---|
| *Eotheroides aegyptiacum* (Owen) | | | | | |
| NHML 46722 (holotype) | 94 | 63.5[1] | 50.8[1] | 59.3[1] | **150** |
| = *Masrisiren abeli* Kretzoi | | | | | |
| Prague (syntype; Abel II) | 86 | – | – | – | – |
| SMNS 43990 (syntype; Abel IX) | ~75 | – | **45*** | **45*** | – |
| ? *Eosiren abeli* (Sickenberg) | | | | | |
| BSPM 1905.XIII.e.6 (Abel VI) | 75 | 52[2] | – | – | – |
| *Protosiren fraasi* Abel | | | | | |
| CGM 10171 (holotype) | **97.5** | **75** | **50** | **64** | **185*** |
| BSPM 1905.XIII.e.2 (Abel V) | 94 | 72 | 52 | 68 | – |
| BSPM 1905.XIII.e.3 (Abel VI) | 102 | 73 | – | 68 | – |
| SMNS 43969 (Sickenberg X) | – | 75 | – | 59 | – |
| SMNS 43972 (Sickenberg XI) | 98 | 76 | – | 62 | – |
| SMNS 43968 (Sickenberg XII) | 99 | 73 | – | 58 | – |
| SMNS 43971 (Sickenberg XIII) | – | – | – | 68 | – |
| Cairo University | 98[3] | 83[3] | 47[3] | 60[3] | – |

[1] Owen (1875)
[2] Sickenberg (1934)
[3] Edinger (1939)

## INSTITUTIONAL ABBREVIATIONS

Institutional abbreviations used here are as follows:

BSPM — Bayerische Staatssammlung für Paläontologie, Munich (Germany)
CGM — Cairo Geological Museum, Cairo (Egypt)
NHML — Natural History Museum, London (United Kingdom)
SMNS — Staatliches Museum für Naturkunde, Stuttgart (Germany)
UM — University of Michigan Museum of Paleontology, Ann Arbor (U.S.A.)

## ENDOCAST OF *EOTHEROIDES AEGYPTIACUM*

Owen's endocast and type specimen of *Eotheroides aegyptiacum*, NHML 46722, provides a logical basis for comparison with the type skull of *Protosiren fraasi*. Owen's illustration of this is reproduced in Figure 2. Salient features of the endocast are its small linear dimensions, small endocranial volume, and conspicuous midline sulcus representing a bony falx cerebri.

According to Owen (1875, p. 101), the type endocast of *Eotheroides aegyptiacum* measures 50.8 mm in breadth across the frontal lobes of the cerebrum and 59.3 in maximum breadth (our own measurements of these are 49.5 and 57.0 mm, respectively), and the type endocast measures 63.5 in cerebral length (our measurement). Sickenberg (1934, p. 36) gives the latter length as 61.5 mm, which he contrasts with 52 mm measured along the midline in *Eosiren abeli* (on Abel's *E. aegyptiacum* Stück VI). We estimate the endocranial volume of *E. aegyptiacum* to be about 150 cc (Table 2), based on measurement of the endocranial volume of an excellent copy of the type endocast using water displacement in a graduated beaker.

The falx cerebri, strictly speaking, is a strong falciform or sickle-shaped membrane attached to the ventral surface of the parietals along the midline and occupying the longitudinal fissure separating left and right cerebral hemispheres of the brain. The presence of a membranous falx cerebri in *Eotheroides aegyptiacum* was noted by Owen (1875, p. 101), and the broader ossified base of the falx, referred to as a 'bony falx' (e.g., *knöcherne Falx cerebri* of Edinger, 1933, p. 9; Sickenberg, 1934, p. 62), is conspicuous as a corresponding longitudinal sulcus on the dorsal midline of the parietal part of all endocasts of *E. aegyptiacum*. According to Edinger (1933, p. 10), extant sirenians have no true tentorium cerebelli, but there is evidence of a raised bony tentorium in skulls of *Eotheroides*, where this appears on endocasts as a distinct transverse groove passing through the deep median pit for the internal occipital protuberance. This trace lies immediately anterior to the transverse sulcus, which is represented on endocasts by a prominent, posteriorly-convex, transverse ridge.

## COMPUTED TOMOGRAPHY OF *PROTOSIREN FRAASI* CRANIUM

The type specimen of *Protosiren fraasi*, cranium CGM 10171, represents a young adult individual with all permanent teeth erupted, significant wear on first molar teeth, but little wear on third molars. The cranium, as preserved, is 330 mm long and 175 mm in maximum breadth across the zygomatic arches. It is shown in dorsal and ventral views in Figure 1, where illustrations from Andrews (1906) are reproduced. Computerized tomography [CT] has been used to study vertebrate fossil skulls by Conroy and Vannier (1984, 1987), Conroy et al. (1990), and others, allowing a specimen to be sectioned radiographically at closely and equally-spaced intervals. Tomography here was carried out using a General Electric HiLight Advantage system at 140kV and 170 mA. The skull was scanned axially with 3 mm collimation at successive 2.5 mm intervals. A total of 136 transverse sections were computed (136 × 2.5 mm = 340 mm ≈ length of skull; several sections at front or back did not intersect skull). The locations of 43 images, representing sections 7.5 mm apart beginning at the front of the skull and ending at the back are shown in Figure 3, and the images themselves are shown in the composite multipage illustration of Figure 4 (43 × 7.5 mm = 322.5 mm ≈ length of skull; blank sections were omitted). Individual images in this composite are referred to as Figure 4.005, Figure 4.008, ... Figure 4.131, where the mantissa is the CT image number. Abbreviations for labels are given in the caption for Figure 4.

The first three images in Figure 4 (4.005, 4.008, and 4.011) preserve roots of the tusks, left and right $I^1$, set in premaxillae, with dense dentine of the tusks being relatively opaque to radiation and thus white in the CT sections. A small open pulp cavity is visible in the center of each tusk root. Crowns of left and right $I^1$, originally part of the type specimen, are now lost. These were already separated and set in a plaster extension of the rostrum when the specimen was illustrated by Andrews (see Fig. 1 here). A vertical midline symphysis [*Symph.*] joining left and right premaxillae, now slightly open and matrix-filled, is evident in images 4.005 through 4.020. Dorsomedial surfaces of left and right premaxillae in images 4.011 through 4.029 are conspicuously excavated, producing a median rostral lacuna [*rost. lac.*] (see below).

Matrix-filled alveoli for left and right $I^2$ are visible in images 4.014 and 4.017, alveoli for left and right $I^3$ are visible in images 4.020 and 4.023. Image 4.023 shows the incisive or anterior palatine foramina [*FAP*] in the ventral midline of the premaxillae. Alveoli for left and right $C^1$ are visible in the suture separating premaxillae [*PM*] from maxillae [*MX*] in images

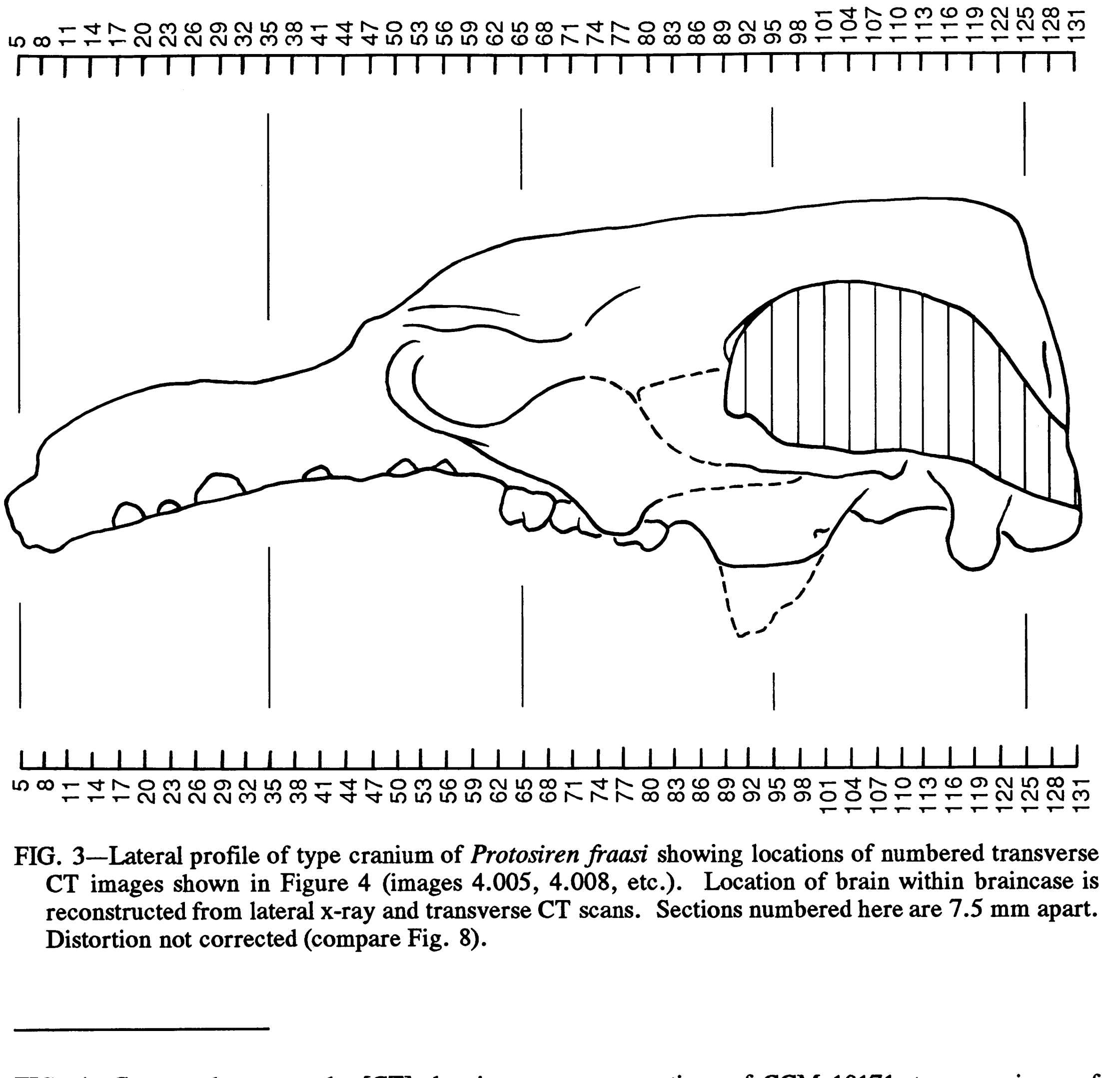

FIG. 3—Lateral profile of type cranium of *Protosiren fraasi* showing locations of numbered transverse CT images shown in Figure 4 (images 4.005, 4.008, etc.). Location of brain within braincase is reconstructed from lateral x-ray and transverse CT scans. Sections numbered here are 7.5 mm apart. Distortion not corrected (compare Fig. 8).

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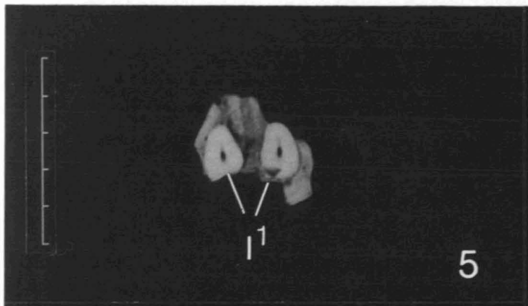
FIG. 4—Computed tomography [CT] showing transverse sections of CGM 10171, type specimen of *Protosiren fraasi* (figure includes images 4.005 through 4.131 on following eight pages). Sections are illustrated one-half natural size (scale in cm), and images run anterior-to-posterior, with successive sections spaced at 7.5 mm intervals. View is from posterior, meaning that the left and right sides of each image show the left and right sides of the skull. Note that narial passages, temporal opening on right side, and braincase all retain original calcareous sedimentary matrix in which specimen was found. Ventral parts of pterygoids and paroccipital processes were sawed off in a plane before Andrews (1906) described the specimen. Bright white highlights in some images are radio-opaque mineral deposits. Scale is in cm. Abbreviations (after Domning, 1978, with additions): *AC*, alisphenoid canal; *alv.*, alveolus; *BS*, basisphenoid; *cond. for.*, condyloid foramen; *cr. gal.*, crista galli; *crib. pl.*, cribriform plate of exethmoid; *EO*, exoccipital; *ET*, ethmoturbinal scrolls; *FAP*, anterior palatine (incisive) foramen; *FIO*, infraorbital foramen; *font.*, processus fonticulus; *FR*, frontal; *max. n.*, course of maxillary nerve; *ME*, mesethmoid; *MX*, maxilla; *N*, nasal; *OC*, occipital condyle; *olf. b.*, location of olfactory bulb; *opt. tr.*, location of optic tract; *P*, periotic; *PA*, parietal; *PAL*, palatine; *PM*, premaxilla; *rost. lac.*, rostral lacuna; *SQ*, squamosal; *symph.*, maxillary symphysis; *T*, tympanic; *V*, vomer.



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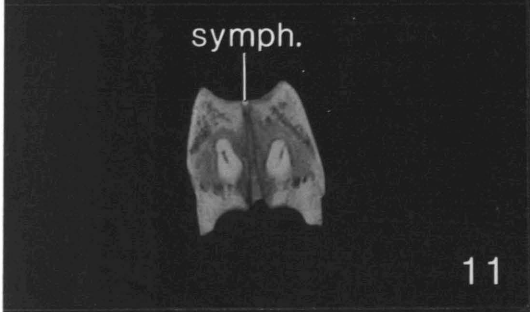

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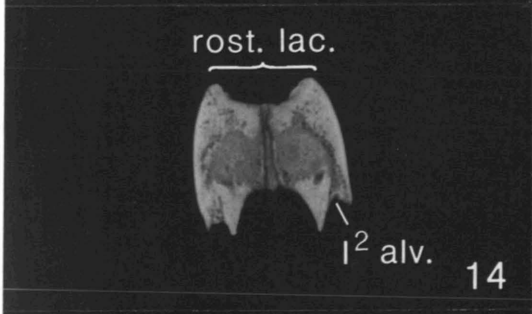

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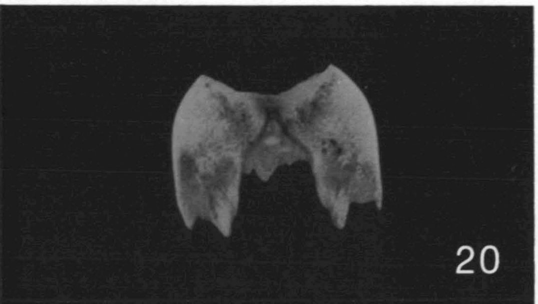
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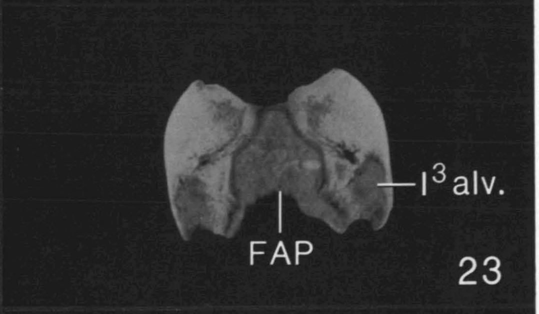

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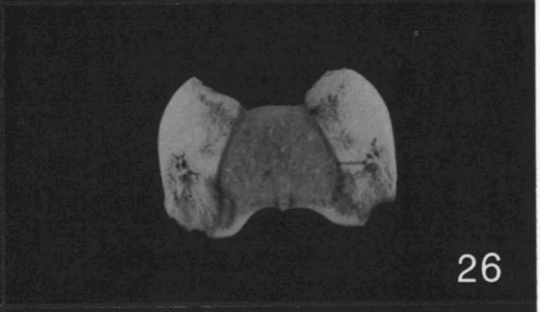
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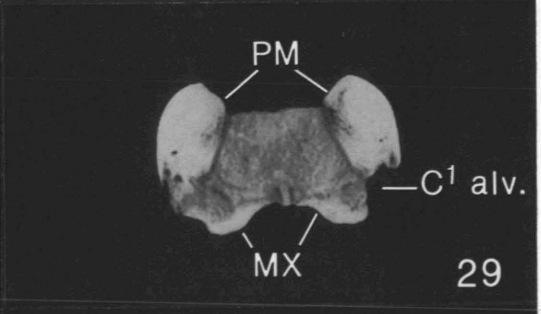

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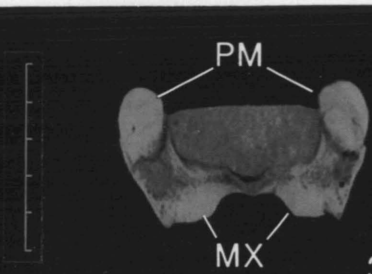

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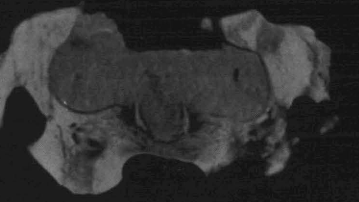

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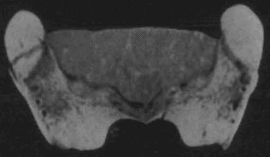

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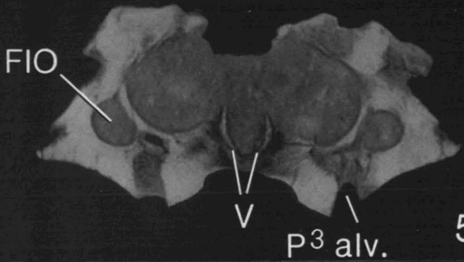

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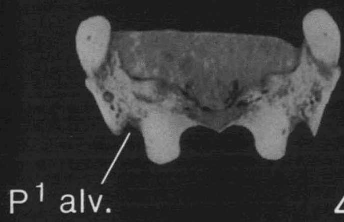

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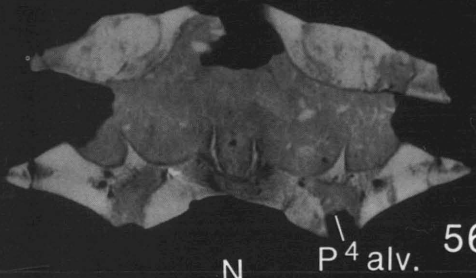

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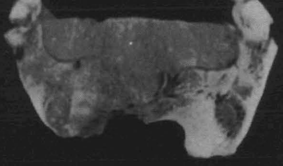

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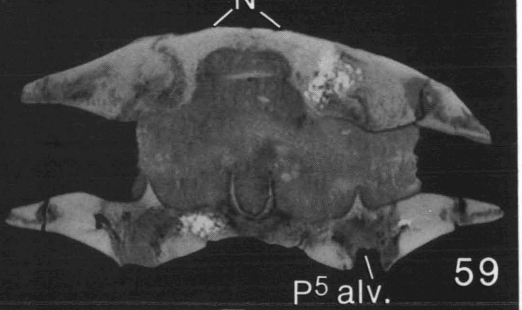

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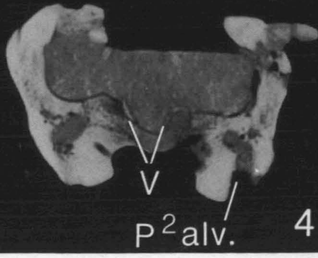

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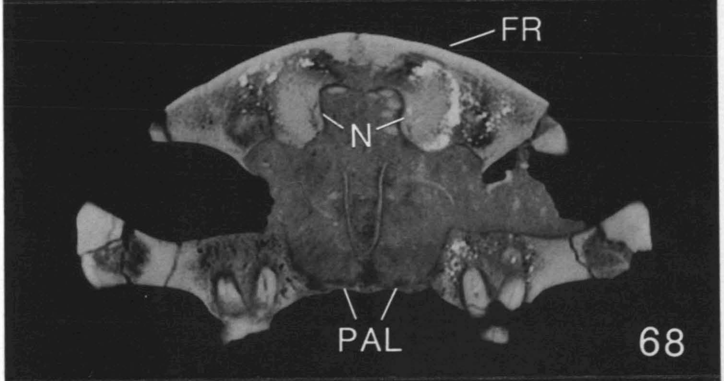

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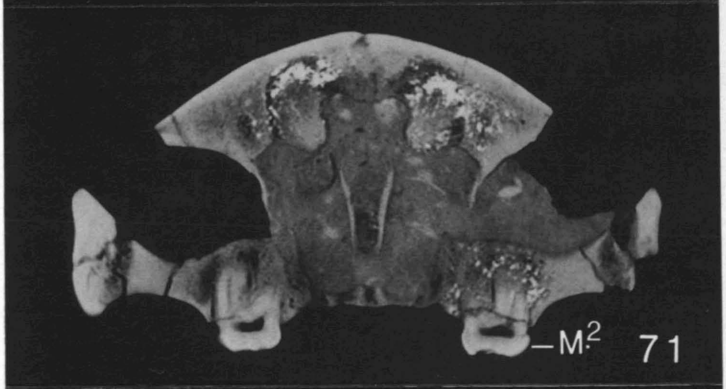

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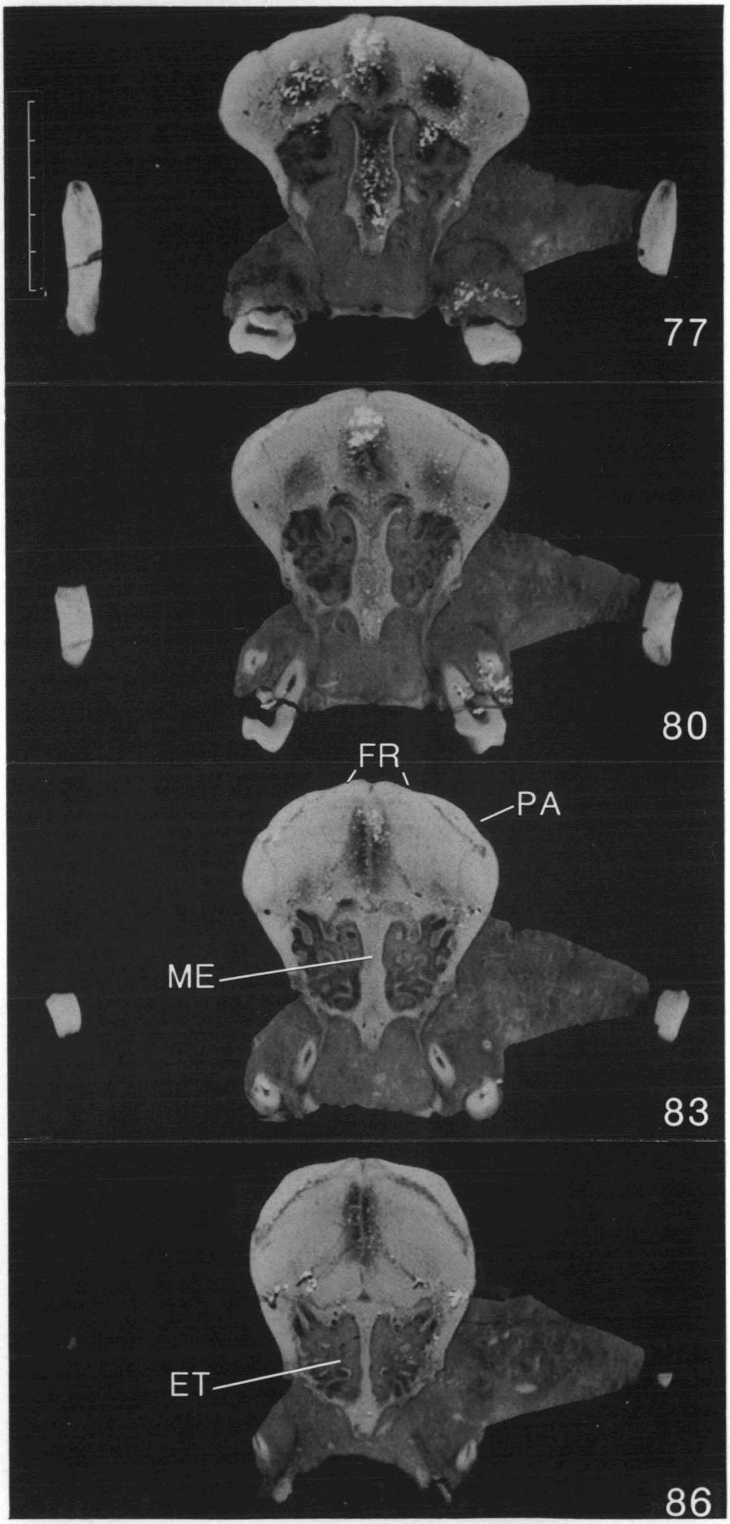
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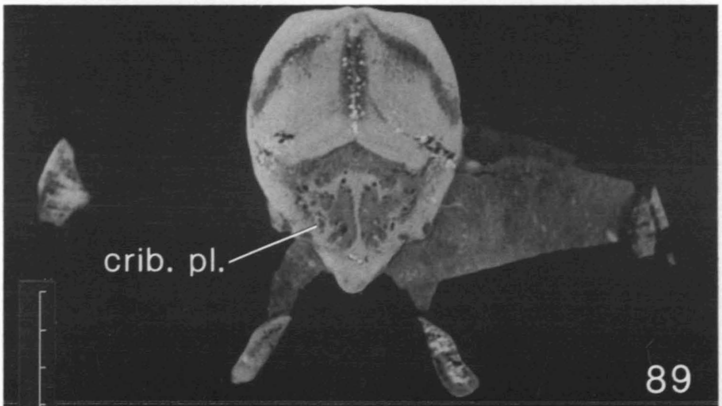

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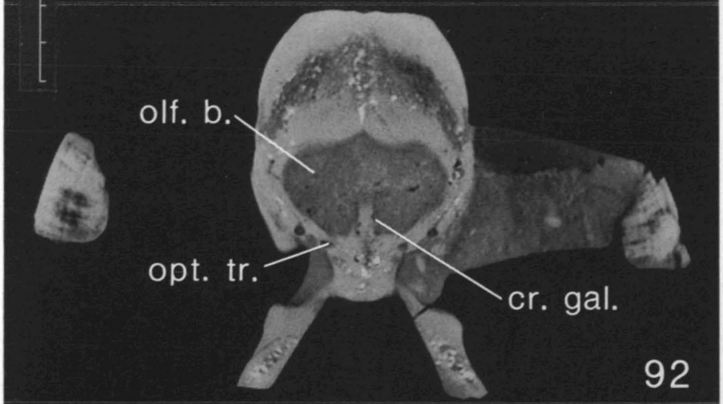

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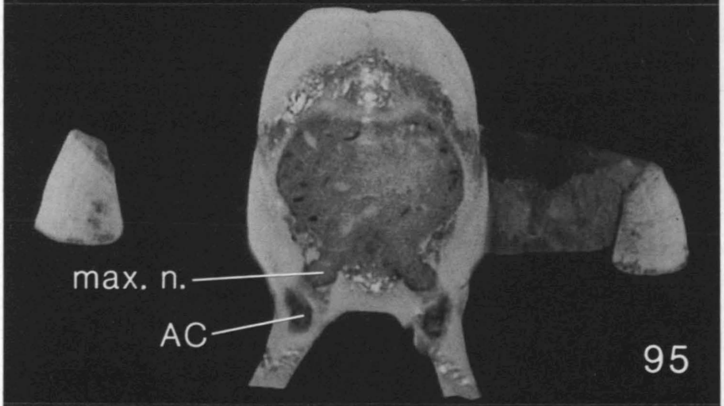

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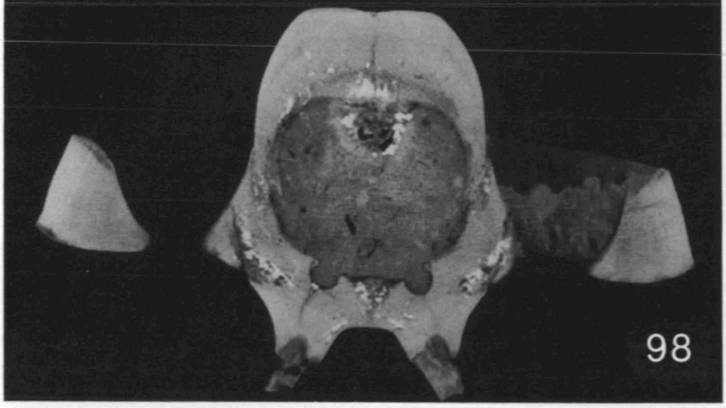

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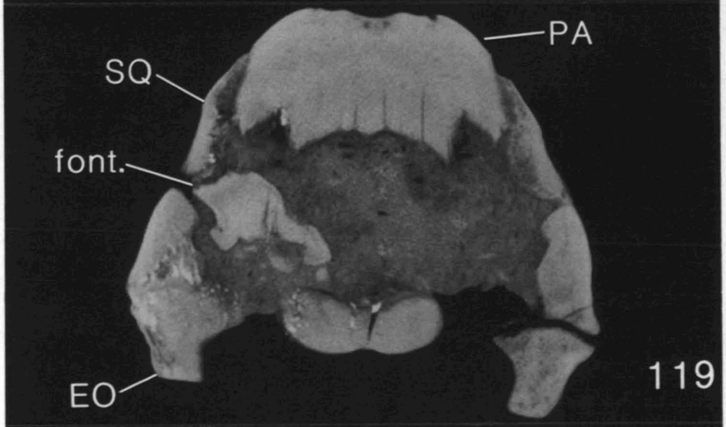

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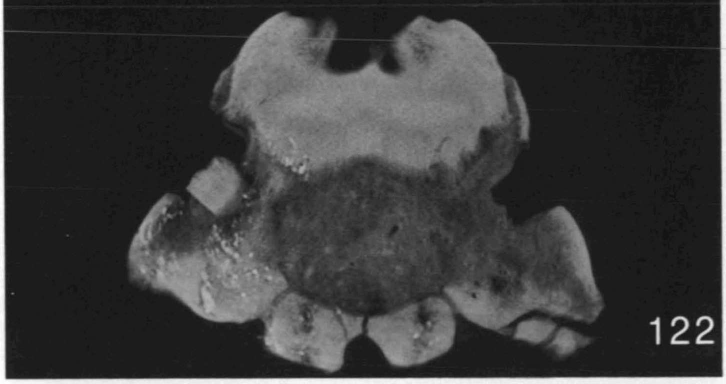

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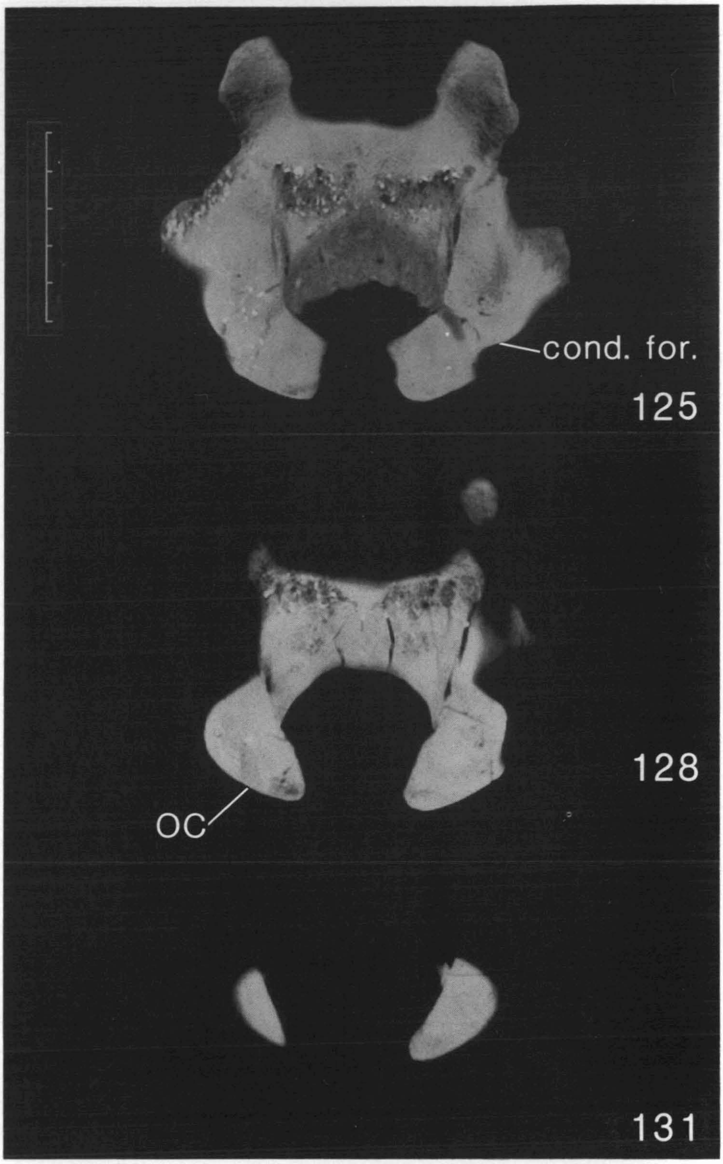

4.029 and 4.032 . Alveoli for left and right canines appear as matrix-filled spaces ventral to the dense rod-like posterior processes of the premaxillae (oval in cross-section).

Alveoli for left and right $P^1$ in the maxillae are shown in images 4.041 and 4.044, alveoli for $P^2$ are shown in image 4.047, alveoli for $P^3$ are shown in 4.053, alveoli for $P^4$ are shown in 4.056, and alveoli for $P^5$, larger but still single-rooted, are shown in images 4.059 and 4.062. Left and right $M^1$ are just visible in image 4.062. Distinct infraorbital foramina [*FIO*] for large maxillary arteries and maxillary divisions of the trigeminal nerves are visible on the left and right sides of the skull in 4.050 and 4.053. Anterior tips of the vomer [*V*], separated by an anterior incisure, are visible overlying the maxillary palate near the midline in image 4.047. The vomer, U-shaped in cross-section, continues backward in successive images. It is trough-like and hollow above where it embraced the lower thickened border of the mesethmoid cartilage. Dorsally, the matrix-filled opening of the external nares, first visible in image 4.026, is roofed over by nasals [*N*] in image 4.059. The nasals become massive and largely overlain by frontals [*FR*] in 4.062. The skull is compressed dorsoventrally at this point, which affects interpretation of the size and shape of the matrix-filled narial passages.

Image 4.065 shows crowns of left and right first molars ($M^1$), images 4.071 and 4.074 show crowns of left and right second molars ($M^2$), and images 4.077 and 4.080 show left and right third molars ($M^3$). Dense posterior processes of the left and right nasals, tear-shaped to oval in cross-section, and overlain by frontals, are clearly visible just under the dorsal surface of the skull in images 4.065, 4.068, and 4.071. These are replaced in image 4.074 by an open 'alveolus'-like space or sinus for each, which in life was probably filled by cartilage (cf. mesethmoid cartilage in image 4.074). The frontals in images 4.062, 4.065, and 4.068 appear also to include spaces of reduced density lateral to the nasals on the left and right sides, which may be vestigial frontal sinuses (otherwise unknown in Sirenia).

The vomer that was small and U-shaped in images 4.050 through 4.062 becomes elongated dorsally to embrace the mesethmoid cartilage, beginning in 4.065, and the narial passages are constricted laterally. From this point the narial passages are floored by palatine bones [*PAL*]. It is not clear exactly where the vomer is replaced by ossified ethmoid, but the lamina perpendicularis of the mesethmoid [*ME*] appears well developed and fully ossified in images 4.080, 4.083, and 4.086. Ethmoturbinal scrolls [*ET*] are present in left and right olfactory chambers. The olfactory chambers each appear to measure about 18 × 25 mm in cross-section and about 30 mm in length. Note that the frontals [*FR*], by themselves, are as much as 3 cm thick in images 4.080 and 4.083, where they are overlain by thin anterior projections of the parietals [*PA*]. The frontals here appear to contain a narrow midline space that probably housed a cartilaginous dorsal part of the ethmoid, including the spina mesethmoidalis.

Image 4.089 includes the cribriform plates [*crib. pl.*] of the exethmoids for passage of branches of the olfactory nerves (cranial nerve I) to the nasal fossae. This marks the anteriormost part of the braincase. In the following image, 4.092, the ventral parts of the spaces for the olfactory bulbs are visible, separated by a robust ossified crista galli [*cr. gal.*]. The roof of the braincase directly above the crista galli has a midline sulcus impressed in it that is not visible in more posterior sections. Three small circular foramina about 2 mm in diameter are visible in cross-section on each side lateral to the crista galli. The most medial appears to represent the optic tract (*opt. tr.*; cranial nerve II). Image 4.095 shows the courses of the large maxillary divisions of the trigeminal nerves (*max. n.*; cranial nerve $V_2$) diverging at the ventral corners of the braincase to exit through a large foramen rotundum that measures 8 mm in diameter. Below these, alisphenoid canals [*alis. can.*] are visible, 6 mm in diameter, which are characteristically present in the genus. In life these carried left and right external carotid arteries forward into the temporal and orbital fossae. The inside of the braincase is 50 mm wide at this point, which represents the width across the frontal lobes of the cerebral part of the endocast (Table 2).

Image 4.101 is the first CT section in which the entire roof of the braincase is parietal [*PA*]. Here and in following images there is very little ventromedial deflection of the roof of the braincase, and there is no indication of the prominent bony falx cerebri characteristic of Owen's *Eotheroides aegyptiacum* (or Andrews' *Eosiren libyca*). Section 4.101 is approximately the position of the sylvian sulcus separating frontal and temporal lobes of the brain, and following sections flare conspicuously. The base of the parietal part of the endocranial vault is 64 mm wide in image 4.110, and this is taken as the width across the temporal lobes of the cerebral part of the endocast (Table 2). Note that dorsoventral compression after burial has pushed the squamosals [*SQ*] on both sides a short distance up and over the parietals, decreasing the height of the endocranium. Image 4.107 is the first to show the large left and right basal vacuities accomodating the periotics [*P*] and isolating first the basisphenoid [*BS*] and then basioccipital medially from the alisphenoids, squamosals, and exoccipitals laterally.

The left periotic is clearly visible in the left basal vacuity in images 4.110 through 4.119, which show the dense petrosal surrounding the inner ear to have been displaced slightly, ventrally and medially, into the braincase, from a formerly tight-fitting connection to the squamosal (the right periotic evidently fell out of the right basal vacuity and was lost before burial). Image 4.113 shows the ventral extension of the tympanic ring [*T*]. Image 4.119 shows the processus fonticulus [*font.*] of the mastoid portion of the periotic inserted into the mastoid foramen between the squamosal [*SQ*] and exoccipital [*EO*]. Note also the strong ventral processes of the exoccipital visible in this section (truncated by saw cuts in the original). Sections 4.122 through 4.128 show a pronounced dorsal concavity of the supraoccipital; this represents the space between the posterolaterally-projecting ends of the nuchal crest (Fig. 1D).

Section 4.119 shows parietals [*PA*] that are slightly thicker than those in the previous section, with an unusual dorsal endocranial profile. This laterally-truncated profile suggests tentorial swelling across the medial part of the ventral surface of the skull roof, marking the point at which the cerebrum and cerebellum join. The distance from section 4.089 (showing the cribriform plate) to section 4.119 (30 × 2.5 = 75 mm) is taken as the length of the cerebrum (Table 2). Section 4.125 is the first image to show a cross-section of the braincase that is not filled with sedimentary matrix, and image 4.128 is a cross-section through the occipital condyles [*OC*]. Together these represent the foramen magnum, and the distance from section 4.089 to section 4.128 (39 × 2.5 = 97.5 mm) is taken as the length of the entire endocranium (Table 2). The condyloid foramen [*cond. for.*] for the hypoglossal nerve (cranial nerve XII) is visible perforating the right condyle in image 4.125.

## ENDOCRANIUM OF *PROTOSIREN FRAASI*

Abel (1928, p. 503), in a brief overview of sirenian evolution, characterized *Protosiren* as one of a small group of sirenians lacking the deep median cleft imposed by a 'bony falx' separating left and right cerebral hemispheres of the brain that is found in *Eotheroides* and most other sirenians. However, brain morphology of *Protosiren* was not well known until Edinger (1933) described six natural stone endocasts attributed to *P. fraasi*. Edinger started her description by citing a paragraph on the brain of *Protosiren* then in press by Sickenberg (later published on p. 62 of Sickenberg's 1934 monograph; see also Table 1 here). She followed this with several pages of additions, clarifications, and qualifications. A later paper of Edinger (1939) is also important. Edinger published measurements of endocasts of *Protosiren* in both papers, which are summarized here in Table 2.

The principal features of the brain and skull of *Protosiren fraasi* that are visible in endocranial casts can be summarized as follows (Abel, Sickenberg, and Edinger's observations are printed in italics, followed by our comments based on CT scans and external morphology of CGM 10171):

(1) *The brain of* P. fraasi *is larger than that of* Eotheroides aegyptiacum, *but the two overlap in some measurements.* New linear measurements reported in Table 2 tend to confirm this. Note that the linear dimensions of the CGM 10171 endocast measured here using CT scans fall within the range of measurements reported by earlier authors in every instance.

(2) *The olfactory bulbs are small, separated by a distinct crest of bone or crista galli, located at the rostral pole of the brain, and, evidently, positioned at the end of long flat olfactory tracts underlying the frontal lobes like the flat olfactory tracts found in extant sirenians (compare Edinger's, 1933, text-fig. 5 and her Plate 1 figs. 3b and 3c).* CT image 4.089 confirms that the cribriform surfaces of the olfactory bulbs are small, and image 4.092 confirms that these are separated by a distinct crista galli.

(3) *The optic tract is characteristically very narrow in sirenians, and it cannot be traced on endocasts of* Protosiren *(Edinger, 1939, p. 46).* CT image 4.092 shows what appears to be a cross-section of the optic canal about 2 mm in diameter.

(4) *There is a distinct angle between frontal and parietal surfaces of the brain.* This cannot be studied using transverse sections alone.

(5) *Frontal and temporal lobes of the brain are separated by a sylvian sulcus, the frontal lobe is not as broad as the temporal lobe, and it narrows anteriorly.* This is confirmed by comparing sections 4.095 through 4.101 and section 4.110.

(6) *The cerebrum and cerebellum are sometimes poorly divided and there is little or no development of a bony tentorium.* Section 4.119 suggests that the bony tentorium may be a little better developed within the skull than is suggested by most endocasts.

(7) *There is no median sagittal bony falx cerebri dividing left and right cerebral hemispheres like that in* Eotheroides aegyptiacum *(Fig. 2).* This is clearly confirmed by the flat ventral surface of the parietals roofing the braincase shown in cross-section in sections 4.101 through 4.116.

(8) *There is some indication anteriorly of a longitudinal dorsal sagittal venous sinus traversing dura mater between cerebral hemispheres, but evidence of this disappears posteriorly suggesting that it was situated less close to the bony skull roof.* The only suggestion of a longitudinal dorsal sagittal venous sinus is in section 4.092, but this does not rule out the presence of a venous sinus lying within the dura.

(9) *The foramen magnum is large, measuring 33 mm high and 41 mm in breadth (Edinger, 1933, p. 16).* Sections 4.125 and 4.128 are oblique to the course of the medulla oblongata, precluding measurement of foramen magnum height from CT scans. Our measurements of the foramen magnum taken from the type skull show it to be 23 mm high and 38 mm wide.

(10) *The fossa in the floor of the braincase for the hypophysis appears to have been very shallow and it is bordered laterally by a large ophthalmic ramus of N. trigeminus (cranial nerve $V_1$) and possibly a finer cord for N. abducens (cranial nerve VI) running just medial to this.* The probable position of the hypophyseal fossa is obscured by radio-opaque minerals in CGM 10171, and there is no evidence of N. abducens in the CT scans. What Edinger (1933, text-fig. 5) labelled the ophthalmic ramus of N. trigeminus ($V_1$) is almost certainly the maxillary ramus ($V_2$): the maxillary ramus is normally the larger of the two, and, in innervating a large and specialized muzzle, the maxillary ramus is the division one would expect to be enlarged in sirenians. Furthermore, the maxillary ramus usually leaves the braincase travelling forward through the round window in mammals, providing further confirmation that the enlarged ramus in *Protosiren* is the maxillary ramus ($V_2$).

Edinger (1933) concluded that the brain of *Protosiren fraasi* was larger than that of *Eotheroides*, and this is indicated by linear measurements of the lengths and widths of endocasts (Table 2). In addition, we calculated the endocranial volume of the braincase of CGM 10171 by digitizing a trace of the inside edge of the braincase in all CT sections in which the braincase appears (restored slightly when necessary to correct for dorsoventral compression). The area of each closed trace was computed, and this was multiplied by the 2.5 mm spacing between traces to represent the volume associated with each trace. A total volume was obtained by adding volumes associated with individual traces. This technique has been validated in human organ volume estimation (Heymsfield et al., 1979; Henderson et al, 1981; Breiman et al., 1982; and Schlesinger et al., 1993). Three estimates of endocranial volume based on independent traces totalled 185.4, 185.7, and 186.3 cc, respectively, with a mean of 185.8 cc and a standard deviation of about 0.5 cc. Rounding to the nearest 5 cc yields an estimated endocranial volume of 185 cc for the type specimen of *Protosiren fraasi*. The error of this mean estimate is certainly greater than the standard deviation of the three independent estimates and the estimate may be biased downward because of the difficulty of correcting for dorsoventral compression, but 185 cc is not likely to underestimate endocranial volume by any great amount.

An endocranial volume of 185 cc estimated for the type specimen of *Protosiren fraasi* is about 23% greater than the endocranial volume of 150 cc reported above for *Eotheroides aegyptiacum*, confirming that the endocranial volume of *P. fraasi* is greater. There are two problems in interpreting the possible significance of such a difference: (1) brain size is usually directly proportional to body size, and differences in brain size between *P. fraasi* and *E. aegyptiacum* may simply reflect differences in body size of the two species (the former has larger teeth, a larger skull, and larger postcrania); and (2) Edinger (1939, p. 45) reported that as much as one-quarter of the braincase of sirenians is filled with coarse dura mater, lymphatic spaces, and blood vessels, and she suggested that there was less intimate contact of the brain and braincase in *Protosiren* than in *Eotheroides* because the brain did not fill as much of the endocranium.

## TOOTH SIZE AND ASSOCIATION OF DENTARIES

Skulls of early middle Eocene *Protosiren fraasi* are larger than those of contemporary *Eotheroides aegyptiacum*, and this is reflected in their larger tooth size. Upper molars preserved in the type skull of *P. fraasi*, CGM 10171 (Fig. 1), have the following measurements (in mm, estimates marked with asterisks; measurements in parentheses are those given by Andrews, 1906, p. 209):

| | Length | Ant. width |
|---|---|---|
| $M^1$ | 16.2 (1.6 cm) | 16.8 (1.7 cm) |
| $M^2$ | 18.1* (1.8 cm) | 18.5 (1.9 cm) |
| $M^3$ | 19.3* (1.9 cm) | 17.9 (1.8 cm) |

For comparison, upper molars of a referred skull, SMNS 10576 (Fig. 5) measure (mm, estimates marked with asterisks):

| | Length | Ant. width |
|---|---|---|
| $M^1$ | 14.5* | --- |
| $M^2$ | 15.2* | 16.1 |
| $M^3$ | 16.7* | 14.9 |

Andrews wrote that the dentary of CGM 42297 (Fig. 6; originally part of 10171) "probably belongs to the same species and perhaps to the same individual" as the type skull of *Protosiren fraasi*. This dentary too has large teeth, which have the following measurements (in mm, estimates marked with asterisks; measurements in parentheses are those given by Andrews, 1906, p. 212):

| | Length | Post. width |
|---|---|---|
| $M_1$ | 15.2* (1.6 cm) | 12.8 (1.3 cm) |
| $M_2$ | 19.0* (1.9 cm) | 14.5 (1.5 cm) |
| $M_3$ | 21.6* (2.2 cm) | 13.7 (1.4 cm) |

The teeth of CGM 42297 are large by comparison to those in most dentaries known from the Mokattam Limestone of Cairo. For example, Priem (1908, p. 418) reported the last molars of a smaller dentary collected by Teilhard de Chardin to measure (mm):

| | Length | Width |
|---|---|---|
| $M_2$ | 12.5 | 9.5 |
| $M_3$ | 15.5 | 11.0 |

One of the distinctive features of Andrews' dentary, CGM 42297 (Fig. 6), is its broad rostrum with large well-spaced alveoli for all anterior teeth. This contrasts markedly with the smaller subadult dentary with a very narrow rostrum described and illustrated by Priem (1908).

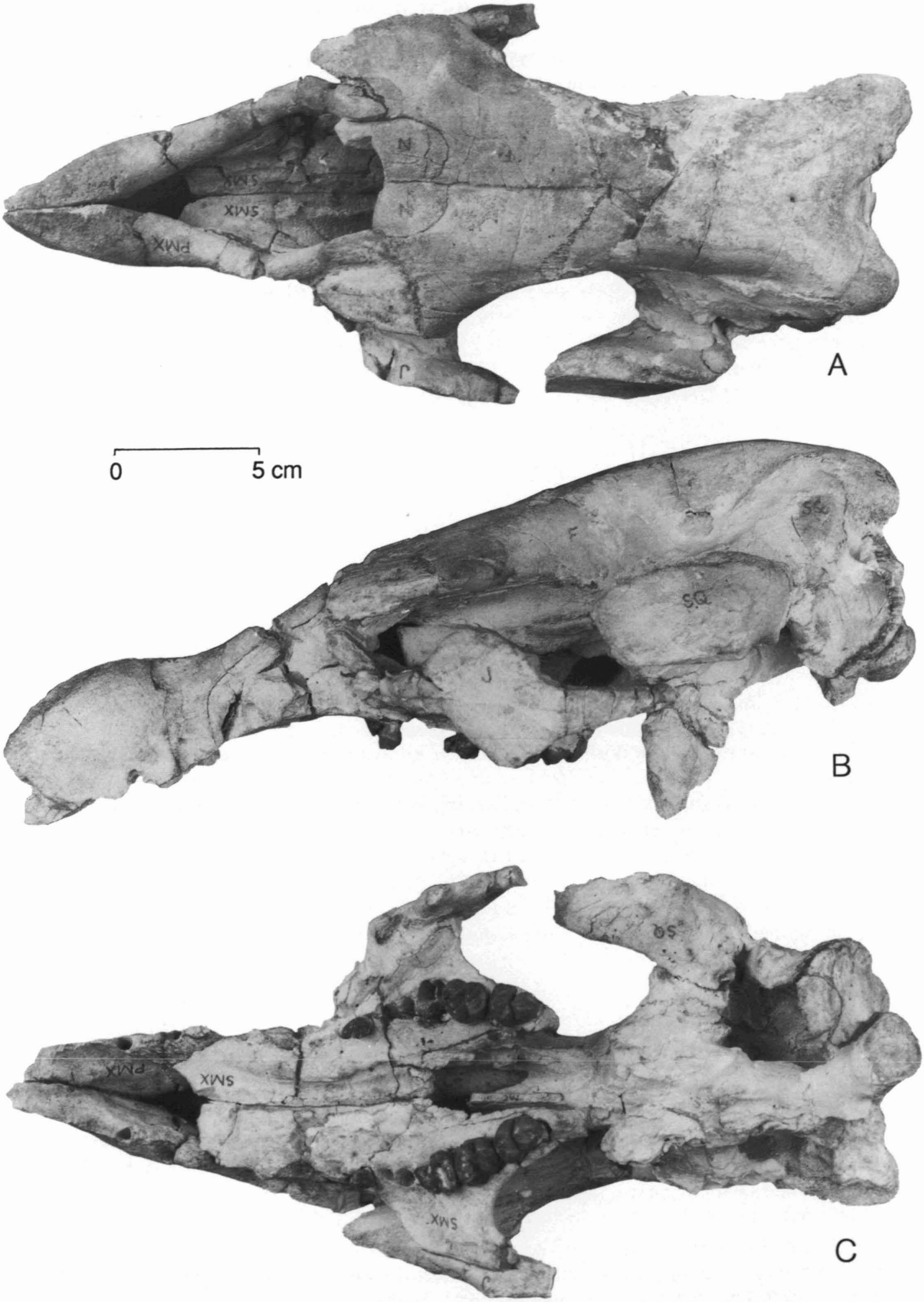

FIG. 5—Cranium of *Protosiren fraasi*, SMNS 10576, in A, dorsal; B, left lateral; and C, palatal views. Note break in rostrum and well preserved pterygoid processes. Reproduced about 0.45× natural size.

Priem referred his dentary to the same taxon as Andrews' CGM 42297, possibly anticipating that it would look like CGM 42297 when fully adult. Then Priem, citing Abel (1904, 1906), called Andrews' specimen, and hence his own, *Protosiren fraasi*. Later Sickenberg (1934) considered Priem's dentary "probable" to represent *P. fraasi* and referred no other dentaries to this species (inexplicably ignoring CGM 42297). Thus small dentaries with very narrow symphyses have come to typify *Protosiren* (compare Domning et al., 1982, figs. 20, 21, and 34). However, specimens collected in Wadi Hitan (Zeuglodon Valley) in Egypt in recent years show that *Protosiren* there has a large dentary with large molars, and a wide mandibular rostrum with well-spaced alveoli for all anterior teeth (Domning and Gingerich, 1994), while *Eotheroides* has the smaller dentary with smaller molars and a narrower rostrum (like Priem's dentary). Andrews was correct to place CGM 42297 in the same taxon as CGM 10171, and it might even be part of the type specimen (fide Andrews, 1906, p. 210). Both represent *Protosiren fraasi*.

Accordingly, the data matrix of Domning (1994: table 1) should be corrected to read as follows for mandibular characters 121-129: *Protosiren fraasi*, 11111100; *Eotheroides aegyptiacum*, 010???0?. This does not change the resulting geometry of the consensus tree.

## ROSTRAL LACUNA

The type skull of *Protosiren fraasi*, CGM 10171, is unique among sirenians in having a conspicuous rostral lacuna or midline concavity in the dorsal surface of the premaxillary symphysis (Fig. 7, see also CT images 4.011 through 4.029 in Fig. 4). Andrews mentioned (1906, p. 206) that "the upper surface of the rostrum in front of the narial opening is gently concave from side to side," but offered neither any comparative nor any functional interpretation of this. Sickenberg (1934, p. 47) mentioned that the upper surface of the rostrum is broad ("*etwas verbreitert*") in the type skull and in the Frankfurt specimen illustrated in his text-fig. 6, but he did not note the presence of a rostral lacuna in the type (which he never studied first-hand). There is no suggestion of a rostral lacuna in the Frankfurt skull illustrated by Sickenberg, nor in other skulls of *Protosiren* known to us (e.g., SMNS 10576 shown in Fig. 5).

While the rostral lacuna of CGM 10171 is well developed and seemingly cannot be a consequence of natural erosion nor artifact of preparation, its uniqueness complicates interpretation. A rostral lacuna is present in virtually all Proboscidea (including *Palaeomastodon* but not *Moeritherium*; see Andrews, 1906), where it is associated with development of the muscular proboscis or trunk. Andrews (1906, p. 139) called a rostral lacuna-like concavity in the conjoined premaxillae of *Palaeomastodon* "the first indication of the form so characteristic of the later Proboscidea."

Proboscideans also commonly have a semicircular line on the frontals arcing above the external nares. This marks the limit of the area of origin of anterior longitudinal muscles lifting the trunk. The rostral lacuna on the dorsal surface of the premaxillae fills the area between the tusks. This is the area of origin of posterior longitudinal muscles anchoring and depressing the trunk (Miall and Greenwood, 1878). It is possible that the rostral lacuna in CGM 10171 indicates presence of a small proboscidean-like trunk of some kind in *Protosiren fraasi*. The type has a raised area on the left frontal suggestive of a semicircular line that might mark the area of origin of muscles to raise a trunk but this raised area is *not* evident on the right frontal, which means, again, that interpretation is complicated. Consequently, we defer interpretation of the rostral lacuna present in CGM 10171 until such a feature is found in another sirenian skull.

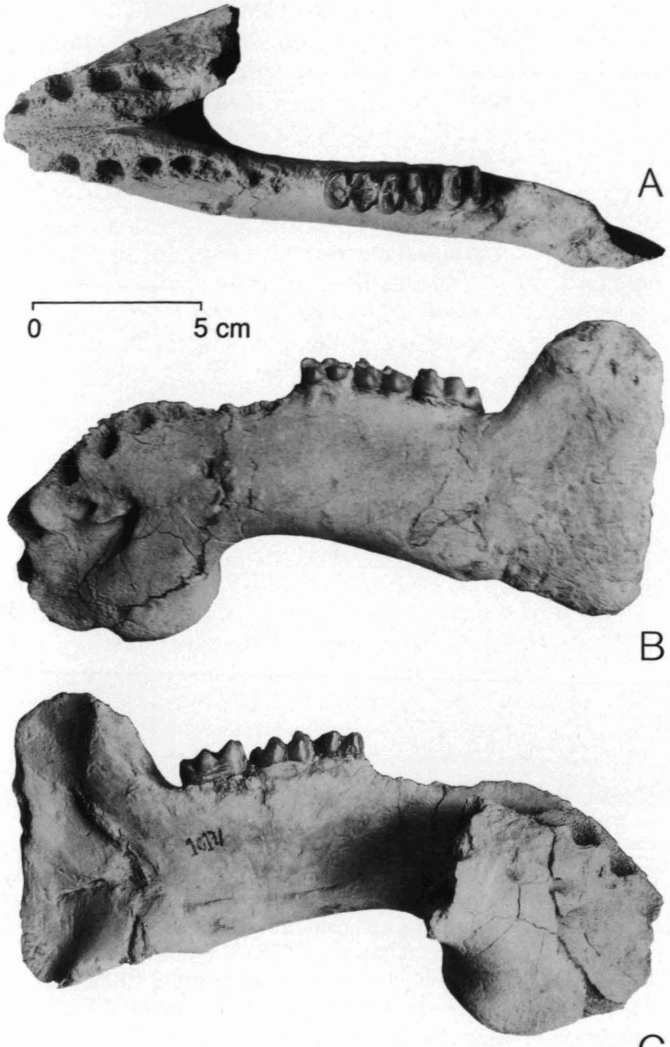

FIG. 6—Dentary of *Protosiren fraasi*, CGM 42297, originally considered by Andrews (1906) to be, possibly, part of type specimen; dentary has been renumbered from CGM 10171. Dentary is shown in A, occlusal; B, left lateral; and C, right lateral (symphyseal region) and medial views (left dentary). Note broad mandibular rostrum with large well-spaced alveoli for all anterior teeth. Reproduced about 0.45× natural size.

## DISCUSSION

Direct comparison of the natural endocast of the type specimen of middle Eocene *Protosiren fraasi* Abel (using CT scans) with that of the type specimen of contemporary *Eotheroides aegyptiacum* (Owen) confirms that the two endocasts differ markedly in the development of a bony falx and bony tentorium, as Abel (1928), Edinger (1933, 1939), and Sickenberg (1934)

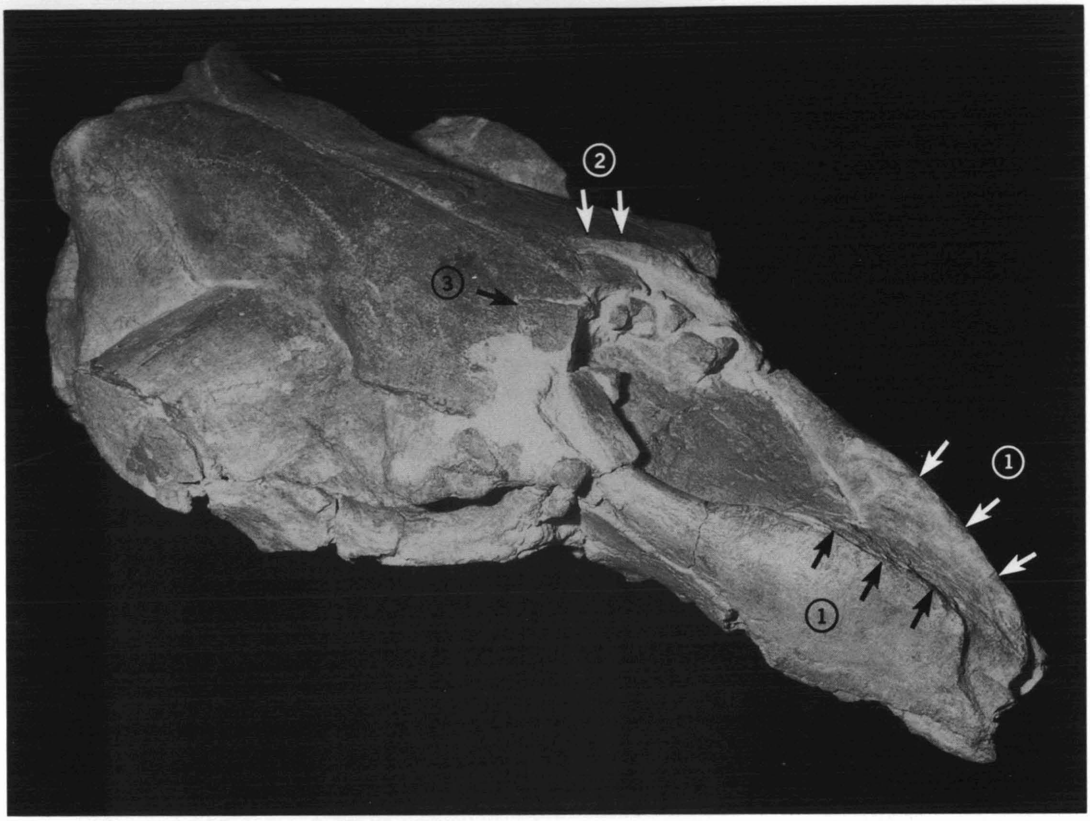

FIG. 7—Unusual features of the type cranium of *Protosiren fraasi*, CGM 10171. Arrows on premaxillae (1) mark lateral margins of well developed rostral lacuna or sulcus. Arrows on the left frontal (2) mark raised area possibly corresponding to a semicircular line. Arrow on right frontal (3) marks position where raised area corresponding to a semicircular line would be expected, based on left frontal (2), but no raised area is evident. Andrews (1906) shows the raised semicircular line on the left side and the rostral lacuna in his drawing of *Protosiren* (see Fig. 2 here; neither was labelled by Andrews). The rostral lacuna is also clearly shown in cross-section in CT images 4.011 through 4.029 of Figure 4. Interpretation is problematical (see text).

inferred without being able to make any direct comparison of the types. New cranial and postcranial specimens currently under study indicate that *Protosiren* and *Eotheroides* differed in many other ways as well, and these new remains show that Andrews' conservative idea that CGM 10171 belonged to Owen's *Eotheroides* (echoed by Carroll, 1988, p. 544; and by Gingerich, 1992, p. 75) is clearly erroneous.

Previous restorations of the lateral profile of *Protosiren fraasi* were based largely on SMNS 10576 (Abel, 1928, p. 499; Sickenberg, 1934, p. 49). Here we present a new lateral restoration (Fig. 8) based on the type skull, which has never been illustrated in lateral view before, carried out with the aid of photographs of SMNS 10576. Restoration required (1) raising the dorsal surfaces of the frontals and parietals slightly to correct for dorsoventral compression of the cranium; (2) slight deflection of the rostrum to close a gap through the alveoli for left $P^1$ and right $P^2$; (3) slight additional curvature of the rostrum to currect for its dorsoventral compression, making it match better the outline of the CGM 42297 dentary; and (4) reconstruction of the anteriormost part of the rostrum to connect the crowns of the $I^1$ tusks, illustrated by Andrews (but now lost), to their roots preserved in the front of the type skull as

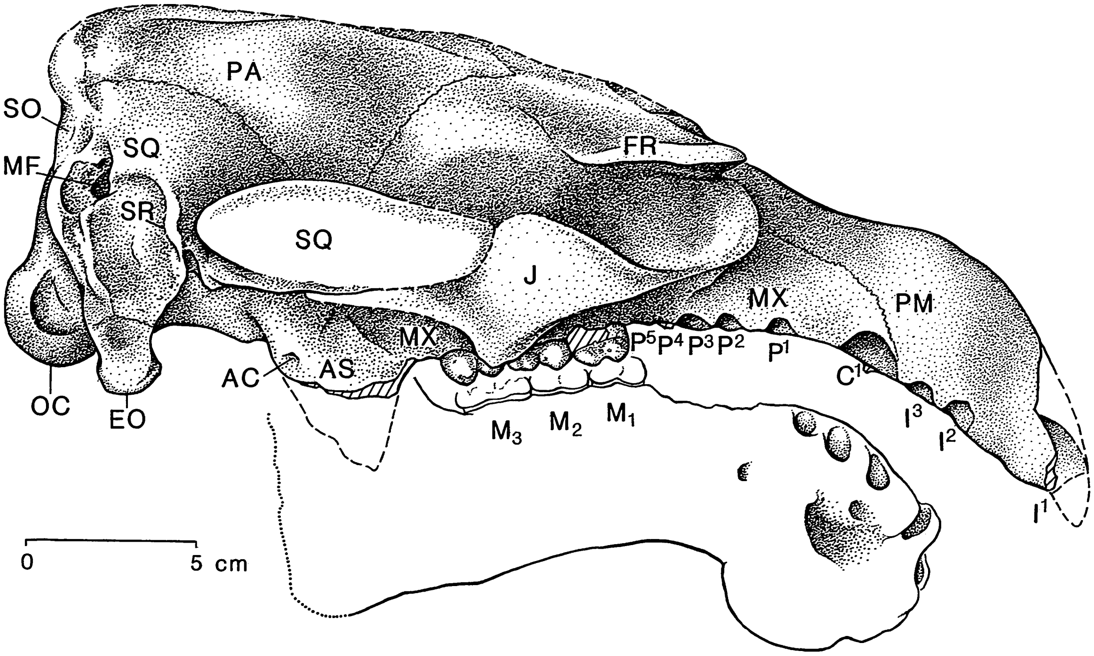

FIG. 8—New reconstruction of type skull of *Protosiren fraasi*, CGM 10171, with additions from SMNS 10576. Dentary is shown in outline, based on CGM 42297, which may be part of type specimen (see Andrews, 1906). Reproduced ca. 0.45× natural size. Abbreviations (after Domning, 1978, with additions): *AC*, alisphenoid canal; *AS*, alisphenoid; $C^1$, upper canine alveolus; *EO*, exoccipital; *FR*, frontal; $I^1$ etc., upper incisor alveoli; *J*, jugal; $M_1$ etc., lower molars; *MF*, mastoid foramen; *MX*, maxilla; *OC*, occipital condyle; $P^1$ etc., upper premolar alveoli; *PA*, parietal; *PM*, premaxilla; *SO*, supraoccipital; *SQ*, squamosal; *SR*, sigmoid ridge.

it now exists. Andrews noted cryptically (p. 204) that the anterior ends of the premaxillae were separated by a fracture, making them appear to be more elongated than was actually the case in life. This "fracture" appears to have been repaired by inserting 3-4 cm of plaster in the original before Andrews' illustrations were prepared (this plaster, cross-hatched in Fig. 1, is now missing from the specimen, exposing the roots of left and right $I^1$). This artificial elongation of the rostrum was removed in preparing the restoration of Figure 8. Thus character number 3 of Domning (1994) should be scored 0 rather than 1 for *P. fraasi*, eliminating a supposed autapomorphy of this species.

Comparison of the new lateral restoration of *Protosiren fraasi* with those published by Abel (1928, fig. 328) and Sickenberg (1934, fig. 7), based on SMNS 10576 (Fig. 5), is complicated by the fact that Abel and Sickenberg provide oblique dorsolateral views in order to show the orbital and temporal fossae of the skull. This lowers the zygomatic arch considerably, and obscures the molar dentition. Abel reconstructed *Protosiren* as having four premolars, but Sickenberg correctly determined that five were present. Figure 5 shows SMNS 10576 to be compressed dorsoventrally, with the rostrum broken through $P^2$, suggesting that the rostrum was straightened by compression as in CGM 10171. Restoration of rostral curvature in SMNS 10576 would require articulation of a dentary of *P. fraasi*, which was not available to either Abel or Sickenberg, and we expect that it will look more like Figure 8 here when this is done. We provisionally conclude that *P. fraasi* had a rostral deflection in the neighborhood of 40°-50°, slightly greater than previously thought.

The type, CGM 10171, is unique among *Protosiren* (and sirenian) specimens in having a well developed rostral lacuna. The earlier species *Prorastomus sirenoides* does not have this lacuna (Savage et al., 1994), conspecific SMNS 10576 does not have it (Fig. 5), and the later *P. smithae* does not have it either (Domning and Gingerich, 1994), which, as outlined above, makes any interpretation problematical.

Integration of CT scans shows that the endocranial volume of the type specimen of *P. fraasi* was 185 cc, which is about 23% larger than that of *Eotheroides aegyptiacum*. It is difficult to interpret the meaning of brain size without good estimates of body size, which are not yet available for *Protosiren* or *Eotheroides*. The position of the brain in the skull is similar to, but slightly lower than, the position reconstructed from SMNS 10576 by Edinger (1933, fig. 10a). Specializations of the brain in *Protosiren* include small olfactory bulbs, small optic tracts, and large maxillary nerves, which are all consistent with diminished importance of olfaction and vision in an aquatic environment, and consistent with enhanced tactile sensitivity of the large downturned rostrum characteristic of most Sirenia.

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