North American Eocene Sea Cows (Mammalia: Sirenia)

Daryl P. Domning, Gary S. Morgan,
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ABSTRACT

Domning, Daryl P., Gary S. Morgan, and Clayton E. Ray.   North American Eocene Sea Cows (Mammalia: Sirenia). *Smithsonian Contributions to Paleobiology*, number 52, 69 pages, 34 figures, 4 tables, 1982.—The record of Eocene sea cows in North America is reviewed in detail, and that of the world is summarized. The North American record includes some 20 localities, mostly yielding fragments identifiable only as sirenian. Of these, the most extensive materials are a partial skeleton from the Cook Mountain Formation of Texas, numerous isolated elements from the Avon Park Formation of Florida, and a partial skeleton and other specimens from the Castle Hayne Formation of North Carolina. The materials from North Carolina and Florida are middle Eocene in age and are referred to *Protosiren* species. These specimens provide further confirmation of the fact that Eocene sirenians had a 3.1.5.3 dental formula and were the latest eutherians known to exhibit five premolars. The implications of this for the higher classification of mammals are discussed. The distribution of sirenians suggests a homogeneous middle Eocene Tethyan fauna and also seems to be a more useful guide to the former distribution of seagrasses than are the distributions of Foraminifera. Eocene sirenians have potential value in intercontinental biostratigraphic correlation.

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Introduction

World knowledge of Eocene sea cows began spectacularly in 1855 with the description by Owen of *Prorastomus sirenoides*, based upon a skull, jaws, and atlas vertebra from Jamaica, still one of the oldest and certainly the most primitive known sirenian. Since then a great deal has been learned about Eocene Sirenia in the Mediterranean region, where discovery and study continue actively at present (Savage, 1977:344–346). In contrast, virtually nothing of consequence has been added for the Western Hemisphere. Thus recent discoveries of assessable, though fragmentary, materials in Florida and North Carolina seem noteworthy.

Our purposes here are to make this new material known; to review other New World Eocene records, published and unpublished (and a few erroneous), in order to bring up to date the meager information on the subject; and to comment upon these records in relation to sirenian relationships, paleontology, biogeography, and paleoecology, in general.

The following abbreviations are used throughout.

BM(NH) British Museum (Natural History)
CGM Cairo Geological Museum, Egypt
ChM Charleston Museum, South Carolina
MCZ Museum of Comparative Zoology at Harvard College
TMM Texas Memorial Museum, University of Texas
TRO Timberlane Research Organization, Lake Wales, Florida
TU Tulane University, Vertebrate Paleontology Collection
UF Florida State Museum, Gainesville
UF/FGS Former Florida Geological Survey collections deposited in the Florida State Museum, Gainesville
UGV University of Georgia, Department of Geology, Vertebrate Fossil Collections
USGS United States Geological Survey
USNM former United States National Museum collections deposited in the National Museum of Natural History, Smithsonian Institution
YPM Peabody Museum of Natural History, Yale University

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Eocene Sirenian Records

ERRONEOUS RECORDS

In 1869 Cope described *Hemicaulodon effodiens*, based on an incomplete tusk, thought to be an upper incisor of an Eocene sea cow, from a marl pit at Shark River, Monmouth County, New Jersey. The specimen has been redetermined as the basal part of the tusk of an advanced, probably Pleistocene, walrus (Ray, 1975).

In 1887, in his catalog of fossil mammals in the British Museum (Natural History), Lydekker (p. 13) listed under *Prorastomus sirenoides*, "M. 3565. Shaft of a humerus; from a Tertiary deposit in the island of Sombrero, near St. Kitts." Kellogg (1966:65) noted the record and remarked that the rocks of the island more recently were regarded as Miocene in age. In 1968 one of us (Ray) examined this specimen and found an unsigned note in its tray, reading as follows: "Probably part of femur of *Testudo sombrerensis* (Leidy)." The handwriting looked like that of Dr. Ernest E. Williams, though he does not now recall writing the note (pers. comm., 1976), but in any event the redetermination appears to be correct. The extinct tortoise of Sombrero Island, *Geochelone (Chelonoidis) sombrerensis*, is regarded as ?Late Pleistocene in age by Auffenberg (1974:150).

In 1917 Palmer reported a neural arch of a sirenian found "freshly fallen, under a cliff of the Calvert Miocene on the western shore of Maryland" and "suggested that the species was living during the period following the first erosion of the Cretaceous and the deposition of the Eocene, as all the specimens so far found in the Miocene were clearly redeposits from an earlier age." Kellogg (1925:59) cited Palmer's report but remarked that Palmer's "view that it was redeposited from an earlier, probably Eocene, formation does not

appear plausible." There is to date no indication of redeposited Eocene sirenian remains among the fairly abundant and in part well-preserved sirenian material from the Miocene Calvert Formation (Kellogg, 1966).

In the course of describing two archaeocete caudal vertebrae (USNM 13856) collected in 1921 by John Navratil and Mark Francis on the J.H. Giessenschlag property, Burleson County, Texas, Kellogg (1936:261, 271) mentioned that they had been "found near 17 vertebrae belonging to an Eocene sirenian and of these 15 were articulated." Stenzel (1938:156) repeated this record on Kellogg's authority, noting that the specimens came from the Mount Tabor Member of the Crockett Formation of the Claiborne Group. Kellogg had indicated the source bed as the Yegua Formation, immediately overlying the Crockett Formation, based on correspondence from Stenzel, who apparently changed his mind prior to publication in 1938 (this and most of the discussion of these specimens are based on the Kellogg-Stenzel correspondence preserved in the Smithsonian Institution Archives). Renick and Stenzel (1931:98) referred to this material, to the locality, and to Kellogg's communications, but only in connection with the cetacean identification, reflecting the fact that only the two archaeocete caudal vertebrae had been studied by Kellogg at that time. These two specimens had been freed by weathering, whereas the 17 associated vertebrae were still embedded in a limonitic matrix. Ball's (1931:110) mention of "a number of vertebrae of *Zeuglodon*" from Burleson County undoubtedly applies to these specimens. In 1935 Kellogg had some of these vertebrae prepared and decided that they were sirenian but exceptionally large for the Eocene. In 1937 Kellogg (letter to Stenzel of 2 November) reiterated his conclusion that the vertebrae represented a large Eocene sirenian, based on his study that year of the Eocene material in the British Museum (Natural History). In the same letter he referred to illustrations of some of the vertebrae, but these have not yet been found among his papers. His file on fossil sirenians includes detailed discussion

and description of the specimens, in part under an unpublished cetacean name. Clearly he vacillated in his ordinal assignment of these tantalizing but unsatisfactory specimens, but they are catalogued as archaeocete vertebrae under the number USNM 13857 and are stored with the Archaeoceti, not the Sirenia. Dr. Kellogg devoted much attention during his retirement (1962–1969) to curation of the fossil marine mammals, and so the physical location and catalogue placement of the specimens probably reflect his definitive opinion as to affinities. In any case, these very poorly preserved specimens do indeed appear to be archaeocete.

In 1969 Voorhies reported as sirenian an isolated cheek tooth from the upper Eocene Ocala Formation in a kaolin mine east of Huber, Twiggs County, Georgia. These beds are now generally referred to the Tivola limestone of the Jacksonian Stage (Huddlestun, Marsalis, and Pickering, 1974:2-3, 2-6). Dr. Voorhies kindly lent the deeply worn tooth, UGV-41, for study, and after considerable difficulty in interpretation, we concluded that it compares most favorably to upper right first or second molars of entelodonts (including *Achaenodon*). Dr. Voorhies tentatively concurred in this and pointed out that at the time of his original identification there were otherwise no land mammals known from the locality and that the tooth was found in place in beds containing a rich marine fauna, but that subsequently a small terrestrial mammalian fauna, including at least one probable entelodont tooth, of Duchesnean age has been recovered from the Twiggs clay overlying the Tivola limestone at this locality (Voorhies, pers. comm., 1975).

NEW WORLD RECORDS

Our intent here is to discuss all of the handful of valid occurrences known to us of Eocene sea cows in the Western Hemisphere in the hope that this will serve as a stimulus to further field efforts and as a baseline for future investigations. A few occurrences of uncertain, but possibly Eocene, age are included as well. The locality numbers

TABLE 1.—World distribution of Eocene sirenians (locality numbers correspond to numbers on maps, Figures 1 and 2)

Local-ity no.	Taxon	Locality	Material	Formation	Age	Sources and remarks
1	*Prorastomus sirenoides* Owen, 1855	Jamaica: river bed "near Freeman's Hall Estate, between the parishes of St. Eliza-beth and Trelawney" (Owen, 1855:541)	skull, mandible, atlas	"Lower Limestone of the Yellow Limestone formation" (Savage, 1977:346)	middle Eocene, Lutetian	Owen, 1855, 1875b; Savage, 1977
2	Sirenia indet	Mexico: Chiapas, between Tumbalá and Yajalón	2 rib fragments		Eocene or Oligocene	Müllerried, 1932
3	Sirenia indet	Texas: Zapata County, 0.8–1.6 km above Falcon Dam on Rio Grande	partial skeleton, including articulated vertebrae and ribs	Cook Mountain	middle Eocene, Claibornian	this report
4	Sirenia indet.	Alabama: Clarke County, Little Stave Creek	rib fragment	Gosport	middle Eocene, Claibornian	Arata and Jackson, 1965
5	Sirenia indet.	Alabama: Monroe County, 3.2 km N of Claiborne	rib fragment	Gosport	middle Eocene, Claibornian	Siler, 1964
6	Sirenia indet.	Alabama: Choctaw County, Puss Cuss Creek	rib fragment	Gosport	middle Eocene, Claibornian	this report
7	Sirenia indet.	Alabama: Geneva County, Samson	rib fragment	Moodys Branch or Ocala	late Eocene, Jacksonian	this report
8	Sirenia indet.	Florida: Levy County, Gulf Hammock quarry	rib fragments	Avon Park	middle Eocene, Claibornian	Reinhart, 1976
9	Sirenia indet.	Florida: Levy County, New Lebanon Dolomite pit near Lebanon	rib fragments	Avon Park	middle Eocene, Claibornian	Vernon, 1951; Reinhart, 1976
10	*Protosiren* species	Florida: Levy County, Waccasassa River	skull and mandible fragments, teeth, and postcranial fragments	Avon Park	middle Eocene, Claibornian	this report
11	Sirenia indet.	Florida: Citrus County, Florida Lime Works quarry near Inglis	rib fragment	Inglis or Avon Park	middle Eocene, Claibornian	this report
12	*Protosiren* species	Florida: Citrus County, Dunnellon Phosphate Co. pit no. 5 near Hernando	two skullcaps	Inglis	middle Eocene, Claibornian	this report
13	*Protosiren* species	Florida: Marion County, Withlacoochee River 4A	skullcap	Inglis	middle Eocene, Claibornian	this report
14	Sirenia indet.	Georgia: Houston County, Clinchfield	rib fragments	Clinchfield Sand?	late Eocene, Jacksonian	this report
15	Sirenia indet.	Georgia: Washington County, Sandersville	rib fragments, vertebral fragment	Tobacco Road Sand; Sandersville Limestone Member	late Eocene, Jacksonian	Flower and Garson, 1884; this report
16	Sirenia indet.	South Carolina: Dorchester County, Giant Portland Cement Co. quarry near Harleyville	rib fragments	Santee	middle Eocene, Claibornian	this report; also a skullcap, now lost (Sanders, 1974)
17	Sirenia indet.	South Carolina: Berkeley County, Mazyck plantation	rib fragments	Santee? greensand?	Eocene?	this report
18	*Protosiren* species	North Carolina: New Hanover County, Martin Marietta Co. Castle Hayne quarry	skullcap	Castle Hayne	middle Eocene, Claibornian	this report
19	Sirenia indet.	North Carolina: New Hanover County, Ideal Cement Co. quarry	rib fragments	Castle Hayne	middle Eocene, Claibornian	this report
20	Sirenia indet.	North Carolina: Pender County, 6.4 km SE of Maple Hill	rib fragment	Castle Hayne	middle Eocene, Claibornian	this report
21	*Protosiren* species	North Carolina: Jones County, North Carolina Lime Co. Comfort quarry	mandible, teeth, and postcranial material	Castle Hayne	middle Eocene, Claibornian	this report
22	Sirenia indet	North Carolina: Craven County, near New Bern	rib fragments	Castle Hayne?	middle Eocene?	Emmons, 1858 (reprinted 1969), 1860

TABLE 1.—Continued

| Local-ity no.	Taxon	Locality	Material	Formation	Age	Sources and remarks
23	"*Halitherium* sp."	Spain: Ebro basin	vertebrae and ribs		middle-late Eocene; Lutetian, ?Ludian, Bartonian	Bataller, 1956; Crusafont-Pairó, 1973
24	*?Protosiren minima* (Desmarest, 1822); *Protosiren* species; *Eotheroides* species	France: Gironde estuary N of Bordeaux	skullcap, teeth, ribs		middle-late Eocene; upper Lutetian, upper Bartonian, lower Ludian	Sickenberg, 1934; Richard, 1946
25	*Eotheroides* species	France: Basses-Alpes, Taulanne	skulls, mandibles, teeth, postcranial material		middle-late Eocene; upper Lutetian-Priabonian	Freudenthal, 1970, pers. comm., 1977; Heal, 1973; Savage, 1977
26	*Prototherium veronense* de Zigno, 1875	Italy: Veneto; Monte Zuello and other locs.	skulls, mandibles, teeth, postcranial material		late Eocene; middle Auversian, Priabonian	De Zigno, 1875, 1880, 1881, and others; Sickenberg, 1934; Piccoli, 1966; Bartolomei, 1969; Savage, 1977; Bizzarini et al., 1977
27	Sirenia indet.	Hungary: Dudar	rib and vertebra fragments		early Eocene, Ypresian	Kretzoi, 1953
28	*Sirenavus hungaricus* Kretzoi, 1941	Hungary: Felsogalla	partial skull, mandible, M₃ fragment		middle Eocene, Lutetian	Kretzoi, 1941
29	*Anisosiren pannonica* Kordos, 1979	Hungary: Vértes Mountains	left maxilla with P⁵-M³ and isolated P		middle Eocene, Lutetian	Kordos, 1979
30	*Protosiren* cf. *fraasi* Abel, 1907	Hungary: Felsögalla	mandible fragment with M₂		middle Eocene	Kordos, 1978
31	*Paralitherium tarkanyense* Kordos, 1977	Hungary: Felsötárkány	mandibles, M₃, vertebrae, ribs		late Eocene	Kordos, 1977
32	*Eotheroides* species	Hungary: Balinka coal mine	mandible and rib fragments		Eocene	Kordos, 1980
33	cf. *Eotheroides*, "*?Halitherium*"	Romania: Transylvania (Siebenburgen)	skullcap, humerus, rib and vertebra fragments		middle-late Eocene; Lutetian, Priabonian	Sickenberg, 1934, Grigorescu, 1967; Fuchs, 1970, 1973
34	Sirenia, new genus and species	Libya: Bu el Haderait	skulls, mandibles, postcranial material		middle Eocene, Lutetian	Savage, 1971, 1977; Savage and White, 1965; Heal, 1973
35	Sirenia indet.	Libya: Dor el Talha	ribs		late Eocene	Savage, 1969, 1971, 1977; Heal, 1973
36	*Protosiren fraasi* Abel, 1907; *Eotheroides aegyptiacum* (Owen, 1875a); *E. abeli* (Sickenberg, 1934); "*Eotherium*" *majus* Zdansky, 1938	Egypt: Gebel el-Mokattam	skulls, mandibles, teeth, postcranial material	Mokattam (= Lower Mokattam)	middle-late Eocene, upper Lutetian-lower Bartonian	Sickenberg, 1934; Zdansky, 1938; Said, 1962, 1963, 1965; Savage, 1977
37	*Eotheroides libycum* (Andrews, 1902); "*Eotherium*" *stromeri* Sickenberg, 1934	Egypt: Fayum	skulls, mandibles, teeth, postcranial material	Qasr el-Sagha	late Eocene; upper Bartonian	Sickenberg, 1934; Reinhart, 1959; Said, 1962, 1963, 1965; Simons, 1968; Savage, 1977
38	Sirenia indet.	Somalia: 25 km SE of Berbera	ribs	Lower Daban Series	middle Eocene; Lutetian	Macfadyen, 1952; Savage and Tewari, 1977
39	Sirenia indet.	Somalia: 20 km SW of Callis	rib	Carcar Series	middle Eocene	Savage and Tewari, 1977
40	cf. *Prototherium*	Somalia: Mogadishu	teeth	Carcar Series	middle Eocene	Savage, 1969, 1977; Savage and Tewari, 1977
41	*Ishatherium subathuensis* Sahni and Kumar, 1980	India: Simla Hills, Subathu	teeth, vertebra, bone fragments	Subathu	early Eocene, Ypresian (probably middle Eocene; see "Old World Records")	Sahni and Kumar, 1980; Sahni, Kumar, and Tiwari, 1980; sirenian identity doubtful (see "Old World Records")
42	*Protosiren fraasi* Abel, 1907	India: Kutch, Harudi, Matanomadh	fragments of innominate, vertebra	Babia Stage	middle Eocene, Lutetian	Sahni and Mishra, 1975; Savage and Tewari, 1977
43	Sirenia indet.	Java: Nanggulan	rib fragment		late Eocene	von Koenigswald, 1952
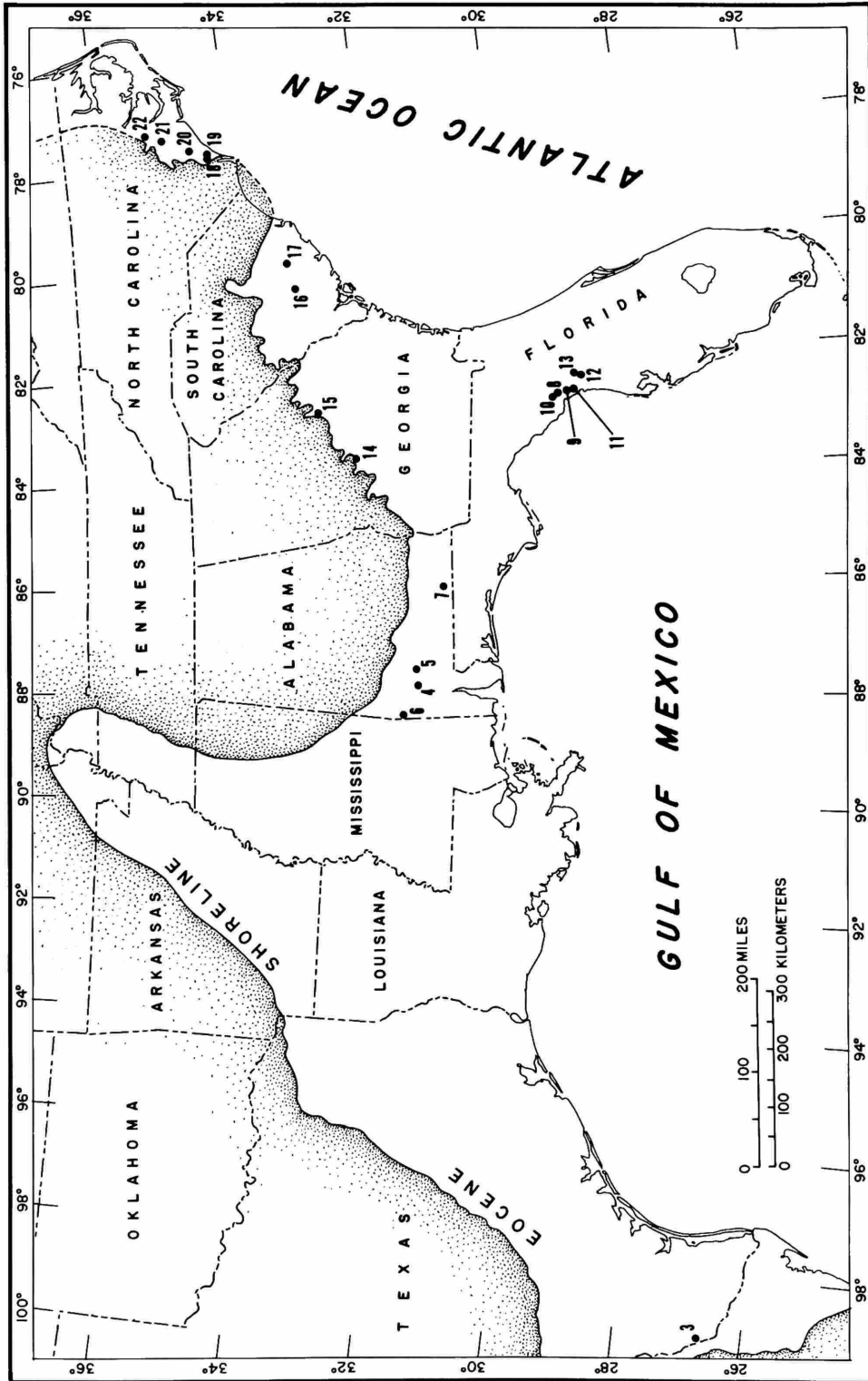
FIGURE 1.—Occurrences of North American Eocene sirenians. (Numbers on map (3–22) correspond to numbered localities listed in Table 1 and discussed in text (localities 1 and 2 are plotted on Figure 2); minimum transgression of Eocene seas (after Cook and Bally, 1975:251) indicated by line with stippling on landward side.)
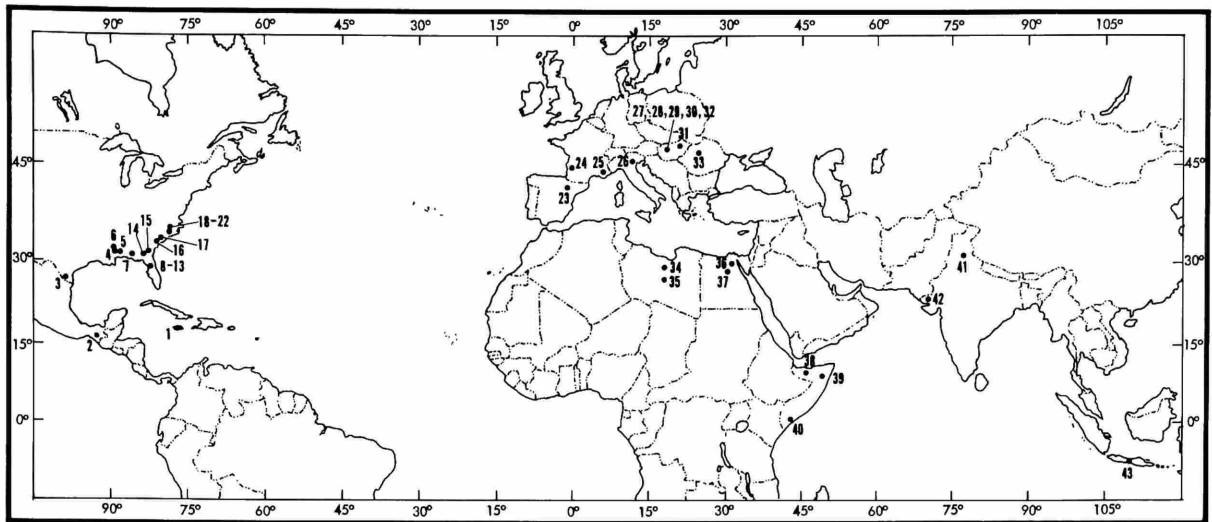
FIGURE 2.—Worldwide occurrences of Eocene sirenians. (Numbers on map (1-43) correspond to numbered localities listed in Table 1 (both New and Old World) and to those localities (New World only) discussed in text.)

correspond to those in Table 1 and Figures 1 and 2. Localities 10 and 21, from which the most extensive new materials are known, are noted briefly here and discussed at greater length under separate headings.

LOCALITY 1.—The holotype and only known specimen of *Prorastomus sirenoides* Owen, 1855, consists of a skull, mandible, and atlas vertebra, BM(NH) 44897, preserved in a calcareous nodule found in a river bed in west-central Jamaica, "near Freeman's Hall Estate, between the Parishes of St. Elizabeth and Trelawney" (Owen, 1855:541). Owen, dissatisfied by the lack of attention given this unusual specimen in the literature, prepared and described it further (1875b). Only recently, however, has the mandible been separated from the skull, and the specimen fully prepared for study (Savage, 1977:346, 347; pers. comm., 1975–1979).

According to Owen (1855:541) the river course in which the specimen was found "is composed of red conglomerate and sandstone, overlaid by limestone, differing from the general tertiary carious limestone of the Island and beneath it." According to Reinhart (1976:265) the specimen

"was collected in the 1400 ft. thick Richmond Formation, from which invertebrate studies . . . are lacking," but according to Savage (1977:346), "it came from the Lower Limestone of the Yellow Limestone formation, which on foraminiferal evidence is of Lutetian (Middle Eocene) age."

LOCALITY 2.—Müllerried (1932) reported two fragmentary sirenian ribs from a locality just south of the Río Hidalgo, about halfway between Tumbalá and Yajalón, Chiapas, Mexico. The beds from which the specimens came were said to contain Eocene pectens and foraminifers, but the sirenian was thought nevertheless to pertain to the Oligocene. Maldonado-Koerdell (1953:146) reported the second occurrence of a fossil sirenian in Mexico, a rib fragment from middle or upper Oligocene rocks of the Palenque region, Chiapas, and noted that the geology of northern Chiapas was poorly known in 1932 and that Müllerried himself seemed uncertain about the age ascribed to his specimens. J.W. Durham (pers. comm.) regards the source beds of Maldonado-Koerdell's specimen as Eocene.

The primary importance of these fragments is in demonstrating the presence of sea cows along

the shores of the Middle American seaway when the Caribbean and Pacific undoubtedly were directly and broadly confluent across southern Mexico (Weyl, 1973) or at least across southern Central America (Woodring, 1966). Well-preserved material of known geologic age from the Eocene or Oligocene of this region would be of great value in clarifying the early history of the Sirenia not only in the Caribbean but also in the North Pacific, where Paleogene sirenians are so far unknown (Domning, 1978).

LOCALITY 3.—Sometime in or near 1950, Mr. Glen Evans collected a partial sirenian skeleton from the middle of the Cook Mountain Formation (Claibornian, Eocene) on the Rio Grande, 0.8–1.6 km (½ to 1 mile) upstream from the Falcon Dam, Falcon Village 7.5 minute quadrangle, USGS, southern extremity of Zapata County, Texas. This specimen, TMM 41843-1, consists of a series of thoracic, lumbar, and caudal vertebrae and some ribs, apparently in or near articulation. Much of the specimen remains largely unprepared in a block of indurated limestone not seen by us; five vertebrae (similar to those of *Eotheroides* in size and shape) and a partial rib (somewhat quadratic in cross-section, 43×39 mm) have been lent for study through the courtesy of Dr. Wann Langston, Jr., who also provided the data on the specimen and permitted our reporting it (pers. comm., 1976).

Although no cranial or appendicular skeletal elements were found, this specimen represents the most extensive part of an Eocene sirenian reported thus far in the Western Hemisphere. Unfortunately there is as yet no basis on which to identify a specimen of this sort more precisely, but its discovery does indicate that associated material of good quality may be expected in North America.

LOCALITY 4.—Arata and Jackson (1965) reported the proximal half of a sirenian rib collected by Dr. Harold Vokes in 1964 from the base of the Gosport Formation (middle Eocene, Claibornian) on Little Stave Creek, approximately 6.4 km (4 miles) north of Jackson, Clarke County, Alabama, where the section was illustrated and described by Rainwater (1955:455–459). The specimen (TU 1004), in the Tulane University Vertebrate Paleontology collection, has been made available to us for study through the cooperation of Drs. Arata and R.H. Reinhart. This rib is oval in cross-section, 31×22 mm.

There is also a rib fragment, said to be Eocene and from Clarke County, Alabama, in the British Museum (BM(NH)35644).

LOCALITY 5.—Siler (1964) reported a sirenian rib fragment from the Gosport Formation in the NE 1/4, SW 1/4, Sec. 24, T. 7 N, R. 5 E, Monroe County, Alabama. This locality is some 35 km (22 miles) due east of locality 4, above, and approximately 3.2 km (2 miles) north of the town of Claiborne. The specimen (TMM 40628-1) has not been examined by us.

LOCALITY 6.—Mr. David C. Mason collected several partial sirenian ribs from a gravel bar in Puss Cuss Creek, SW 1/4 of Sec. 36, T. 10 N, R. 5 W, Choctaw County, Alabama. Two of these ribs have been donated to the Smithsonian Institution and are catalogued as USNM 244363. These sirenian fossils are almost certainly derived from the Gosport Sand of middle Eocene (Claibornian) age, as this is the only formation exposed along Puss Cuss Creek (Dr. Wayne F. Canis, 1978, in litt.).

LOCALITY 7.—Early in 1979 the USNM received from Rick Coffey, David Cramer, and Steve Heaton a small suite of fossils collected by them along a tributary of the Pea River, near Samson, Geneva County, southeastern Alabama. In addition to the characteristic Eocene invertebrates, *Chlamys deshayesi* and *Periarchus lyelli*, the collection included the major part, lacking only the head, of a well-preserved sirenian rib. This specimen, now USNM 321931, is remarkable for its robust, somewhat flattened, banana-like form, tapering abruptly at its sternal end to an irregularly rounded termination some 13 mm in diameter for articulation with the costal cartilage. It is distinctly quadrangular in cross-section (maximum diameters 77.7×49.6 mm).

The only suitable source beds for the specimen in this area are the Jacksonian Moodys Branch

or Ocala Formations, undifferentiated in Geneva County because of deep weathering (Scott, 1966).

LOCALITY 8.—Reinhart (1976:262) reported sirenian rib fragments from the Gulf Hammock quarry of the Dixie Lime Products Company, a dolomite pit in the Avon Park Limestone (middle Eocene, Claibornian), 1.6 km (1 mile) southeast of Gulf Hammock, Levy County, Florida, in the SE 1/4, Sec. 21 and the NE 1/4, Sec. 28, T. 14 S, R. 16 E, Lebanon Station 7.5 minute quadrangle, USGS. Reinhart's (1971:7) mention of middle Eocene sirenians from Florida was based on the rib fragments from this and the following locality. In addition to numerous ostracods and other microfossils, fossil plant material is abundant in the same strata from which the sirenian ribs were derived. Preliminary investigation of these fossil plants by Dixon (1972) indicates that they are closely related to, if not congeneric with, the modern marine angiosperm *Thalassia* (Hydrocharitaceae). The co-occurrence of sea cows and seagrass in the Avon Park Limestone is noteworthy and is discussed in more detail under "Paleoecology of Eocene Sirenians and Seagrasses."

LOCALITY 9.—Vernon (1951:110; repeated by Puri and Vernon, 1959:41) noted a "Manatee" rib in the Avon Park Formation at the New Lebanon dolomite pit in the SW 1/4, NE 1/4, Sec. 12, T. 16 S, R. 16 E, of the Yankeetown 7.5 minute quadrangle, USGS. This abandoned pit lies less than 1.6 km (1 mile) west of the town of Lebanon (not Lebanon Station). Reinhart (1976:262, 264, 265; fig. 26) reported additional sirenian ribs from this locality and illustrated two of them (UF 4503).

LOCALITY 10.—Over a period of several years, beginning in 1968, Robert Armistead accumulated a large collection of vertebrate fossils from the bottom of the Waccasassa River in west-central Florida. Armistead's collection, now deposited in the Florida State Museum, was collected along an 8 km segment of the Waccasassa River north of the town of Gulf Hammock, Levy County, Florida. The exact location of this portion of the Waccasassa River is as follows: Secs.

5, 8, and 17, T. 14 S, R. 16 E; Secs. 20, 29, and 32, T. 13 S, R. 16 E, Bronson SW 7.5 minute quadrangle, USGS. A second collection of fossils from this same part of the river was made in 1971 by John Waldrop, Michael Frazier, and several of Waldrop's students. These specimens are now housed at the Timberlane Research Organization (TRO), Lake Wales, Florida.

At first glance these two collections appear to comprise a typical Rancholabrean (late Pleistocene) fauna, a very common vertebrate fossil assemblage in Florida's fossil-rich rivers. The Waccasassa River assemblage includes mastodon, mammoth, horse, tapir, peccary, camel, bison, deer, several varieties of large edentates, alligator, an unidentified crocodilian, and a large sample of sirenian material. A few fossils indicative of a late Hemphillian (late Miocene to early Pliocene) mammalian assemblage are also present. The most common sirenian element is the dense, thickened skullcap, of which some 30 have been recovered. Ribs and vertebrae are also common. In addition, four isolated teeth, three mandibular fragments, and several cranial fragments are among the identifiable sirenian remains. Comparisons reveal, however, that most of the sirenian fossils are decidedly primitive in structure and quite unlike corresponding elements in the manatee *Trichechus manatus*, the only sirenian known from Florida's Pleistocene and Recent faunas. They are equally unlike *Metaxytherium*, a dugongid common in Florida's Hemphillian faunas. Furthermore, the preservation of these sirenian fossils is very different from that of the late Pleistocene and Hemphillian faunal elements, and one of the skullcaps, a vertebra, and several ribs are either enclosed in limestone or have limestone matrix adhering to them. Mixture of fossils of widely different ages is characteristic of Florida's river-bottom assemblages, and therefore the possibility that the sirenian fossils were derived from an older rock unit was suspected.

The geologic map compiled from Vernon's (1951) study of the geology of Citrus and Levy Counties, Florida, shows that Citrus and Levy counties are underlain almost entirely by carbon-

ate rocks of middle and late Eocene age. In particular, the entire segment of the Waccasassa River in which the vertebrate fossils in question were collected flows on carbonate bedrock of the Avon Park Limestone of middle Eocene (Claibornian) age. Field observations by Morgan confirm that the Waccasassa River in the area of concern does in certain places flow directly on the Avon Park Limestone. Also, numerous outcrops of the Avon Park Limestone up to 1 m in thickness occur along the banks of the river (Vernon, 1951). The presence of limestone matrix on several of the sirenian fossils, identical in lithology to that of the Avon Park Limestone on which and through which the Waccasassa River flows, confirms that these fossils are in fact eroding from the underlying limestone and therefore are Eocene rather than Mio-Pliocene or late Pleistocene. The existence of the Eocene sirenians from the Waccasassa River has been alluded to previously by Domning (1974).

On the basis of mollusks (Richards and Palmer, 1953) and Foraminifera (Applin and Applin, 1944; Applin and Jordan, 1945), the Avon Park Limestone has been correlated with formations of middle Eocene (Claibornian) age. The limestone matrix adhering to one of the sirenian fossils contained fragments of the distinctive scutellid echinoid *Periarchus lyelli*. Included in Waldrop's vertebrate fossil collection from the Waccasassa River were fragments of *Periarchus lyelli* and three complete specimens of the echinoid *Cassidulus globosus*, both of which are characteristic of the Inglis Formation, which overlies the Avon Park Limestone in Citrus and Levy counties (Fischer, 1951). Although the Inglis Formation has been considered to be late Eocene (Jacksonian) by most workers, Richards and Palmer (1953) and Meeder (1976) noted the strong affinities of Inglis mollusks with those of Claibornian age, as well as with mollusks of Jacksonian age. According to these two papers, both the Avon Park and Inglis faunas are Tethyan in affinity and notably different from the faunas of the overlying Williston and Crystal River Formations, of late Eocene age. Meeder (1976) suggested that on the basis of

worldwide faunal affinities, the Inglis Formation probably should be considered late Claibornian rather than early Jacksonian.

The upper part of the Avon Park Limestone and the Inglis Formation, as exposed in Citrus and Levy counties, are very similar in lithology and, in fact, were originally described as a single rock unit, the Gulf Hammock Formation, by Ericson (1945). According to Cole and Applin (1964:14),

As the major break in foraminiferal faunas occurs at the top of the Inglis, and as we cannot discover any criteria in continuous sections of well samples whereby the Inglis could be separated from the Avon Park, in the authors' opinion, the Inglis should be abandoned and these strata included in the Avon Park Limestone.

Cole and Applin (1964:14) commented further that "we consider that the evidence is such that this entire section which we refer to the Avon Park Limestone is middle Eocene in age." Hunter (1976) noted a similar identity in the megafossils of these two formations, with the major faunal change coming at the top of the Inglis Formation. Hunter assigned both the Avon Park Limestone and the Inglis Formation to the same biostratigraphic unit (Gulf Hammock local stage) and correlated them with the Claibornian Stage of the Gulf Coast region. These two formations apparently represent a single regressive-transgressive sequence of very shallow-water limestones and dolomites (Randazzo and Saroop, 1976). The unconformity between the two formations, described by Vernon (1951), appears to be very local in extent and most likely represents a short period of emergence and subsequent erosion during the peak of the regressive phase. Although this is not the place to revise stratigraphic nomenclature, it appears probable that the Avon Park Limestone and Inglis Formation represent a single lithologic unit of late middle Eocene age. A middle Eocene age for these two formations is compatible with the primitive nature of their sirenian remains, which bear a close resemblance to those from the Mokattam Limestone (Lutetian = Claibornian) of Egypt.

From the above discussion, it is clear that the

Waccasassa River assemblage represents an admixture of late Hemphillian and late Pleistocene fossils, probably derived from surficial sands and clays along the banks of the river, to middle Eocene fossils eroded from the Avon Park Limestone on which the river flows. Several dentary fragments and vertebrae of an undescribed crocodilian are also represented, which, like some of the sirenian fossils described above, have adherent matrix of Avon Park Limestone. These fossils, apparently of a marine crocodilian of middle Eocene age, are of unknown affinity and are under study at the present time.

LOCALITY 11.—A partial sirenian rib (USNM 256687) was collected by G.S. Morgan on 21 February 1978 from the base of the Inglis Formation at the Florida Lime Works quarry, 2.5 km south of Inglis, Sec. 11, T. 17 S, R. 16 E, Yankeetown 7.5 minute quadrangle, USGS, Citrus County, Florida. The majority of the stratigraphic section at the Florida Lime Works quarry is composed of massive, porous, tan, unfossiliferous dolomite of the Avon Park Limestone. The top 2–3 meters of the quarry wall consist of chalky, cream-colored limestone with the typical lithology and echinoid fauna of the Inglis Formation. Although there is considerable difference in lithology between the Avon Park Limestone and Inglis Formation in this quarry, there is no definite unconformity between them, suggesting that perhaps the underlying Avon Park Limestone may have been secondarily dolomitized. The sirenian rib was collected from the basalmost Inglis Formation and is extensively abraded and bored, suggesting that it may have been deposited originally in the underlying Avon Park Limestone and subsequently reworked into the base of the Inglis Formation. It is oval in cross-section, 26×15 mm.

LOCALITY 12.—In the vertebrate fossil collections of the Florida Geological Survey (now housed at the Florida State Museum, Gainesville) are two sirenian skull caps (UF/FGS V2282, V2288) collected on 13 February 1913 by Herman Gunter from the Dunnellon Phosphate Company pit no. 5, near Hernando, Citrus County, Florida. Although vertebrates of Hemphillian age (late Miocene) have been collected from the phosphatic rock exposed and formerly mined in this quarry (Vernon, 1951), the sirenian skullcaps were undoubtedly derived from the Inglis Formation, which unconformably underlies the phosphate deposits of the Alachua Formation at the Dunnellon phosphate pit.

LOCALITY 13.—A single sirenian skullcap (UF 24786) in the Florida State Museum collections from the Withlacoochee River 4A site is the only demonstrably Eocene fossil in an otherwise strictly Hemphillian vertebrate fauna. The Withlacoochee River 4A site, an underwater fossil locality in the Withlacoochee River, is located about 12.9 km (8 miles) southeast of Dunnellon in the NW 1/4 of Sec. 30, T. 17 S, R. 20 E, Stokes Ferry 7.5 minute quadrangle, USGS, Marion County, Florida. The fossil vertebrates from the Withlacoochee 4A site were, for the most part, preserved in situ in a massive, green clay of late Miocene age filling a sinkhole developed in the Inglis Formation of late middle Eocene age. Although the majority of fossils from this site were collected from the green clay, some fossils were found loose on the river bottom. The sirenian skullcap was almost certainly derived from the underlying Inglis Formation and subsequently mixed on the river bottom with the Hemphillian-age fossils.

LOCALITY 14.—In the collections of the Smithsonian Institution is a single lumbar vertebra, USNM 13883, identified as *Zygorhiza kochii* by Remington Kellogg and received in 1935 from the quarry of the Pennsylvania-Dixie Cement Corporation at Clinchfield, Houston County, Georgia. In the tray with the cetacean vertebra was an uncatalogued fragment of a sirenian rib. Examination of the registrar's records reveals that there were several fragments of sirenian ribs (identified by Kellogg) in the collection from Clinchfield at the time of receipt. Thus this specimen is undoubtedly one of them and is now catalogued as such under the number USNM 244031. It is oval in cross-section, 31×22 mm.

Also in the collections of the Smithsonian In-

stitution are three fragmentary pieces of sirenian rib, two probably representing a single rib, all now catalogued under USNM 244029, found in a tray with two other fragmentary specimens, not identified as yet, but apparently not sirenian. The largest rib is subquadratic in cross-section, 41×39 mm. In the tray are notes obviously typed by Remington Kellogg, including a detailed geologic section extracted from a letter from Philip E. LaMoreaux, dated 30 July 1945, indicating that the specimens came from the Clinchfield quarries of the Pennsylvania-Dixie Cement Corporation in Houston County, Georgia, and that they were collected apparently in place in the section some 80 feet below ground level, well down in beds assigned by LaMoreaux (letter of 1945) to the Ocala Formation. Beds then assigned to the Ocala Formation in this area would now be assigned by many authors in large part to the Tivola Formation; however, the bed from which the fossils came was described as, "Gray, medium to coarse sand with scattered granules of subangular sand. Fossiliferous. Limy in places." This lithology seems much like that described for the Clinchfield Sand, including that at or near the sirenian locality in the section at the Medusa Cement Company west quarry, Clinchfield (Huddlestun, Marsalis, and Pickering, 1974:2-6, 2-33, 2-34, 2-35). Dr. Paul Huddlestun (pers. comm., 1977) confirms that the Medusa quarry is one and the same as the Pennsylvania-Dixie quarry and, based on examination of LaMoreaux's detailed section, concludes that the sirenian ribs indeed came from the Clinchfield Sand. The Clinchfield Sand, regarded as earliest Jacksonian in age, overlies the Lisbon Formation (Claibornian) and underlies the Tivola Formation.

LOCALITY 15.—In January 1846 Sir Charles Lyell (1850:8, 9) travelled by railway handcar from Savannah to Macon, Georgia, making observations on the geology en route, among which was the following: "Near Sandersville I saw a limestone from which Eocene shells and corals are procured, as well as the teeth of sharks and the bones of the huge extinct cetacean called

Zeuglodon." Flower and Garson (1884:527) listed as *Halitherium* under the number 2725 in the museum of the Royal College of Surgeons, "Transverse process of vertebra and eleven portions of ribs. From Sanderville [sic], Georgia, U.S.A. Presented by Sir Charles Lyell, 1868" and (p. 547) under number 2838, "Body of a dorsal vertebra, probably of a *Zeuglodon*. From Sanderville [sic], Georgia, U.S. America. Presented by Sir Charles Lyell, 1868." Unfortunately these specimens apparently were among the many lost in the destruction of that museum during World War II (E. Allan, pers. comm., 1981). There is, however, neither reason to doubt that specimens listed as sirenian by W.H. Flower were correctly identified, nor that rocks ascribed to the Eocene by Lyell were correctly assigned. Further, Sandersville, Washington County, east-central Georgia, later became the type-locality of the Sandersville Limestone Member, first of the Barnwell Formation (Cooke, 1943:61–63, 65), then of the Tobacco Road Sand of the Barnwell Group (Huddlestun and Hetrick, 1979:27, 46, 48). The Sandersville Limestone was deposited during late Eocene, Jacksonian time.

LOCALITY 16.—Sanders (1974:8) reported a sirenian skullcap from a quarry of the Giant Portland Cement Company, 3.2 km (2 miles) NNE of Harleyville, Dorchester County, South Carolina. The specimen was found on the surface of the Santee Formation after the overlying Cooper Marl had been scraped away in preparation for mining; thus the exact stratigraphic provenience of the specimen is unknown. Further, the specimen unfortunately is not now to be found in the collections of the Charleston Museum.

Nevertheless, the same field work produced another sirenian record, of known horizon, from this locality. According to Albert E. Sanders, the specimen, ChM GPV1306, consists of several fragments apparently of a single rib, found in place in the Santee Formation some 6 meters below the Cooper Marl. This rib is quadratic in cross-section, 46×40 mm.

Ward et al. (1979) have recently studied the stratigraphy of rocks exposed in this quarry,

where the Santee Formation is represented by their (upper) Cross Member, regarded by them as middle Eocene (Claibornian), and directly overlain by their (lower) Harleyville Member of the Cooper Formation, regarded as late Eocene (Jacksonian) in age; however, Baum et al. (1980) have raised the Cross Member to formational rank, and suggested a late Eocene age.

LOCALITY 17.—In the Museum of Comparative Zoology are three sirenian rib fragments probably of Eocene age. All are indicated as coming from greensand and from the Santee Canal, South Carolina. One of these, MCZ 8634, is attributed to R. Mazycks; the other two, MCZ 8767, to R.W. Gibbes. Gibbes (1845:254), in describing the archaeocete *Dorudon serratus*, states that the specimens (now MCZ 8763)

were found in March last, in a bed of Green sand near the Santee Canal, in South Carolina. The locality is on the plantation of R.W. Mazyck, Esq., about three miles from the entrance of the canal from the head waters of Cooper river. The deposit of Green sand is from four to eight feet thick near the surface, lying on a solid yellowish limestone . . . .

Thus there is every reason to suppose that the sirenian rib fragments were obtained at the same place and time and are of the same age as *Dorudon serratus*. If so, then the sirenian specimens are actually from marl diggings, as is *D. serratus*, not from the canal itself.

The Santee Canal, long since abandoned, apparently was excavated shortly after 1800, as the first (Pleistocene) vertebrate fossils were recorded from it in 1802 (see Hay, 1923:119, 156, 162, for a discussion of these occurrences). The canal extended from the head of the West Branch of the Cooper River (approximately 2.4 km (1.5 miles) ENE of Moncks (or Monks) Corner, Berkeley County) NNW for some 32.2 km (20 miles) to the Santee River, just downstream from Lake Marion. Most of its length is mapped on the Chicora 15 minute quadrangle of the USGS, and its southern extremity on the Cordesville 7.5 minute quadrangle.

With the assistance of C. Wythe Cooke, Kellogg (1936:178) determined that the type-locality

of *Dorudon serratus* lay five and three-fourths miles (9.3 km) north of Moncks Corner and one mile (1.6 km) west of MacBeth. This location is now beneath Lake Moultrie.

Kellogg (1936) regarded the source bed of *D. serratus* to be the Santee Formation, but this may be open to some question. As regards the probably associated sirenian rib fragments, their lack of diagnostic morphology, their recovery so long ago from marl diggings, and the opportunity for derivation from younger deposits, together dictate caution in age assignment.

LOCALITY 18.—On 11 April 1981 Vincent Schneider collected a sirenian skullcap from spoil of the Castle Hayne Formation at the Martin Marietta Company's Castle Hayne quarry, in the northern corner of New Hanover County, North Carolina, approximately 3.3 km (2.1 miles) ENE of Castle Hayne, and lying in the NW corner of the Scotts Hill 7.5 minute quadrangle, USGS. This quarry was designated the type-locality of the Castle Hayne Limestone of Baum et al. (1978), and the type-locality of the New Hanover Member and a reference locality of the Comfort Member of the Castle Hayne Formation of Ward et al. (1978).

The specimen is described below, under "North Carolina Eocene Sirenians."

LOCALITY 19.—In September 1977 a Smithsonian field party including Ralph Eshelman and Peter J. Harmatuk visited the quarry of the Ideal Cement Company located in the northern extremity of New Hanover County, North Carolina, immediately south of the junction of Island Creek with the North East Cape Fear River. The quarry lies at approximately 34°22′30″N, 77°50′00″W, straddling the boundary between the Mooretown (on the north) and Scotts Hill (on the south) 7.5 minute quadrangles, USGS. This quarry has been designated the type-locality of the Castle Hayne Formation by Ward et al. (1978) and reference locality of their New Hanover and Comfort Members of that formation. Here they were shown a group of nine fragmentary sirenian ribs and given one of the fragments by Mr. Al Simons. These associated specimens apparently were collected in

place in the Castle Hayne Formation. The bone is compact throughout, hard, and stained uniformly black except for a softer, gray superficial layer approximately one mm thick. Some fragments are quadratic in cross-section, and the maximum shaft diameters are 48×41 mm. Mr. Simons has subsequently presented all of the specimens through Mr. Harmatuk to the Smithsonian, where they are catalogued under USNM 256688.

LOCALITY 20.—In July 1975 Paul Drez collected a partial sirenian rib in an abandoned quarry approximately 6.4 km (4 miles) southeast of Maple Hill, Pender County, North Carolina (Maple Hill 15 minute quadrangle, USGS). The specimen, donated to the Smithsonian Institution and now catalogued as USNM 244030, is embedded in a lump of limestone of the Castle Hayne Formation (Claibornian). It is subquadratic at its larger end, 44×43 mm thick.

LOCALITY 21.—For the past several years, at least since 1970, Peter J. Harmatuk has been prospecting for and collecting fossils in a limerock quarry developed in the Castle Hayne Formation near Comfort, Jones County, North Carolina. This quarry, operated until recently by the North Carolina Lime Company under lease from the land owner, lies a few hundred meters north of State Road 41, approximately 6.4 km (4 miles) by road west of the post office at Comfort, and immediately west of Tuckahoe Church, at approximately 35°01′N, and 77°34.5′W, on the Comfort 7.5 minute quadrangle, USGS. Access to the quarry has been granted by Messrs. A.C. Palmer and Harry E. Jones of the North Carolina Lime Company and by Mr. Linsey Vance Maness, owner of the land.

As is usually the case in commercial quarries, most of the vertebrate remains have been recovered through diligent combing (by Mr. Harmatuk and a few others) of overburden and other residue of mining. In contrast to the macroinvertebrates, vertebrate remains are not sufficiently common to be found often in place or complete under mining conditions. Further, each find of a vertebrate fossil usually represents but a single

small part of the total complement of hard parts of the animal, whereas in many situations essentially whole skeletons of marine macroinvertebrates are found in abundance. Hence the necessity for vertebrate paleontologists to content themselves frequently with float and with fragments and to revisit given sites time and again if they are to accumulate meaningful samples representing even part of the major elements of the skeleton and dentition.

Fortunately, at least some of the vertebrate remains at the Comfort quarry have been found essentially in place. Most important among these are various elements, mostly fragmentary, of what must have been an associated, and at least in part articulated, skeleton of a sea cow. These elements have been recovered by Mr. Harmatuk in the course of numerous visits over a period of several years from a cut bank near the north side of the quarry, through assiduous inspection after rains and through screening, yielding some fragments of teeth, for example, no more than a few mm in maximum dimension. The best specimen recovered to date, a partial mandible, has been reconstituted from many tens of fragments collected in just this manner. Much of the apparently associated skeleton undoubtedly was lost to the bulldozer and dragline.

The section above pond level at this place, excluding irregular hillocks of overburden piled on the original ground surface, is as follows:

Unit	Thickness in meters
1. Gray-green, sticky, glauconitic, sandy clay	1–1.3
2. Tan-yellow, oxidized sand	3
3. Buff-white, shell marl (definitely Castle Hayne Formation)	unknown

The sea-cow skeleton occurred in the uppermost unit. The surface of the bones is off-white, with some superficial dark organic staining. The chalky-white weathered layer typically extends into the bone some 2 mm, beyond which it is replaced abruptly (at least not obviously at any osteologically controlled point such as the demarcation between outer lamellar bone and inner

vesicular bone or marrow cavity) by a dark-brown to gray, hard, mineralized core. The bones are not waterworn or rolled, and retain sharp surface detail in spite of the extremely soft surface that is pasty when wet. There is no indication of boring or encrustation by bottom dwelling invertebrates. Very delicate teeth retain sharp surface detail.

The apparent articulation (largely disturbed, it seems, only in quarrying), preservation of delicate structures, lack of boring and encrustation, and deep weathering combined with retention of surface detail all point toward primary deposition, not reworking. The clearly Eocene aspect of the sirenian skeleton thus would militate against the possibility that the enclosing clay (and its underlying sand) is a much younger unit than the underlying marl and merely contains the reworked debris from earlier episodes of deposition. Thus, in spite of the contrasting lithology, it would seem that these superficial clastics are a part, possibly condensed in place through extreme weathering and leaching, of the same depositional cycle as the underlying marl.

This quarry is the type-locality for the Comfort Member of the Castle Hayne Formation as redefined by Ward et al. (1978:F8, 20, 21), who regarded our uppermost unit in which the sirenian skeleton occurred as (?)Pleistocene. Thus, we are left with somewhat of a dilemma to be resolved only by additional fossils and/or future stratigraphic studies. The lithology of the beds from which the sea cow came is anomalous for the Castle Hayne Formation, but the sea cow seems inescapably Eocene in character.

This section is very similar to that exposed in bluffs of the Trent River approximately 1.6–2.4 km (1–1.5 miles) to the northeast, described by Kellum (1926:10) as USGS locality 10630, three-quarters of a mile NW (not SW as indicated by Kellum) of Comfort on the farm of Miss Sally Simmons (now Eagle's Nest Farm). Kellum, apparently correctly, assigned all of this section (excluding only a surficial sand), from the sticky clay downward, to the Castle Hayne Formation.

Although the Castle Hayne Formation has been assigned by many authors to the Jacksonian (upper Eocene) stage, the most recent students of the problem have reviewed the evidence and history of study, conducted their own field work, and assigned the Formation to the Claibornian (middle Eocene) stage (Ward et al., 1978; Baum et al., 1978). Although the sirenian collection is far too meager to be definitive, its similarity to Egyptian material from beds of the Lutetian stage is more compatible with the Claibornian assignment.

Isolated sirenian elements (other than those apparently pertaining to the associated skeleton) recovered from the spoil of the Comfort quarry include specimens of somewhat different preservation, some of which are of yellowish tinge suggesting derivation from the oxidized sand. No sirenian specimens have been recovered that were definitely preserved in the typical marl. Virtually all specimens reveal the peculiar preservation, with a thin, whitish, chalky outer layer and a thick, dark, hard inner core.

Other vertebrates from the quarry include archaeocetes and bony and cartilaginous fishes, virtually all collected by Mr. Harmatuk. The archaeocete remains consist mostly of isolated teeth (some 20–30 in number), thought to be referable to *Zygorhiza kochii* and under study by Walter Wheeler. Half of a large tooth was collected by Mrs. Gene Mapes and very kindly donated to the Smithsonian Institution, where it has been catalogued under USNM 244043. Some archaeocete cranial fragments were discovered by Mr. Harmatuk and by Yoshikazu Hasegawa on the floor of the quarry in place in the typical Castle Hayne marl, at least 7.6 meters below ground level.

A large suite of fish remains was studied by Robert L. Meyer, then a postdoctoral fellow (1975–1976) with the Paleontology and Stratigraphy Branch of the USGS, who has provided the following report, quoted in part here with permission from him and the USGS.

Preliminary faunal list:
  Selachii:
    Pristis curvidens Leidy—14 rostral spines.
    Rhinoptera sp. 1—worn medial tooth with pronounced

anterior shelf, narrow root; does not differ markedly from the extant *R. bonasus.*

Rhinoptera sp. 2—worn medial tooth lacking anterior shelf, wide root with very narrow grooves. Similar to *R. sherborni* White, but has narrower grooves.

Rhinoptera or *Myliobatis*—worn medial or first lateral teeth (two); broad root with broad grooves, moderately developed anterior shelf.

Myliobatis sp.—two teeth with broad, thick root with wide grooves; possibly upper teeth of *Rhinoptera* or *Myliobatis* referred to above.

Dasyatidae—incomplete caudal spines.

Procarcharodon angustidens (Agassiz)—12 teeth; form very similar to variety called *Sokolowi* Jaekel by Leriche (1942).

Isurus americanus (Leriche)—primitive isurid in the *I. desori* lineage; placed in the genus *Macrorhizodus* by Glikman, 1964; species as yet not securely diagnosed, may be *I. praecursor* (Leriche).

Anomotodon nova (Winkler)—(new combination) three teeth.

Striatolamia macrota—26 teeth.

Odontaspis sp.—four incomplete anterior teeth.

Odontaspis(?) *koerti* (Stromer) as defined by White (1934)—seven teeth.

"*Eugaleus*" *denticulata*? Gibbes—two teeth lacking roots; generic reference very uncertain.

Osteichthyes:

Xiphiorhynchus antiquus Leidy—incomplete rostral complex.

Istiophoridae, genus uncertain—incomplete rostral complex.

Cylindracanthus rectus—incomplete rostral spines.

Carangidae gen. and sp. indet.—incomplete premaxillary bone; also vaguely similar to Pomatomidae and primitive Scombridae without produced snouts.

Indicated Age:

Large *Striatolamia macrota* are indicative of upper Eocene; similar sized teeth are found in the Bartonian of England (based on comparison with USNM collection). *Odontaspis* (?) *koerti* and *Anomotodon nova* have imprecisely known range zones but are most characteristic of middle Eocene. The *Procarcharodon* and *Isurus* are like those from the Jackson Group of Mississippi and Alabama reported by Leriche (1942). These fossils are commensurate with a Bartonian age (Lower Upper Eocene).

Environmental indications:

Relative abundance of pristids indicates rather shallow, warm water; the rest of the constituents of the fauna are widely ranging; nothing indicative of cool or deep water is present.

Matrix samples from both the upper clay at the sirenian skeletal site and the immediately underlying sand have been examined for foraminifers by Thomas G. Gibson and for silicoflagellates by Laurel Bybell, with negative results. Norman Frederiksen analyzed a sample for pollen and spores which yielded inconclusive results but suggested an unexpectedly high level of modern contamination.

The sirenian material from Comfort is enumerated and described in detail under "North Carolina Eocene Sirenians."

LOCALITY 22.—The only published report known to us of a fossil from North Carolina pertaining to an Eocene sirenian is that by Emmons (1858:212, fig. 34, reprinted 1969; figure only, reproduced by Emmons, 1860:213, fig. 181). This report is repeated here in its entirety and the figure reproduced (Figure 3).

The oldest specimen of fossil belonging to the whale or cetacean family, belongs to the genus Physeter, and is regarded as the P. antiquus, (fig. 34). It occurs in the eocene of Craven county. The size of the teeth prove that they belonged to the largest of the class. The largest tooth measures six inches in circumference, and is five and a half inches long, though a portion has been broken from the base. Its form is quadrangular, and presents a curve in front, but is rather straight behind. It shows no conical cavity, but is solid throughout. It shows a tendency to exfoliate concentrically. Many fragments more or less rolled and otherwise defaced, have been seen in the miocene beds upon the Tar River.—It is probable they may have been removed from a lower to an upper formation.

Meaningful comment can scarcely be made on the rolled specimens from the Tar River or on the bulk of those said to be from the Eocene of Craven County; however, the appearance of the one illustrated and characteristics such as large size, "quadrangular" form, "curve in front," "straight behind," "no concavity," "solid throughout," and "tendency to exfoliate concentrically" all seemed equally or more applicable to the distal portion of a rib of a sea cow, rather than to a tooth of a cetacean. Fortunately the illustrated specimen (subsequently broken and in part missing) was preserved in the Emmons collection of Williams College, Williamstown, Massachusetts, and has now been transferred permanently to the Smith-

sonian Institution (USNM 329063). It proves in-deed to be the distal part of a sirenian rib, and thus, if its Eocene age is correct, as seems likely, it constitutes the first record for the Eocene of North Carolina. Its greatest diameters are 35×26 mm.

In discussing the Eocene series, Emmons (1858:102–107; 1860:211) gave special attention to its occurrence in the western part of Craven

FIGURE 3.—Distal portion of Eocene sirenian rib from Craven County, North Carolina (USNM 329063), sternal end up. (Illustration reproduced from Emmons, 1858:212, fig. 34.)

County, on the south side of the Neuse River some 32.2 km (20 miles) above New Bern, in the vicinity of Biddle Landing, Ft. Barnwell, and Core Creek (now generally called Cove Creek), on the Ayden 15 minute quadrangle, USGS, where plantation owners (the Biddle brothers, William Wadsworth, and others) were beginning to use the Eocene marl extensively for agricultural purposes. They were at the same time in com-munication with Emmons, which suggests that the sirenian specimen(s) probably came from this area. Wilson (in Kier, 1980:12) felt that all ref-erences to the Eocene of Craven County by Em-mons pertain to the Wadsworth plantation, but it would seem difficult to exclude the nearby Biddle lands.

OCCURRENCES OF UNCERTAIN AGE.—John T. Thurmond, then of Birmingham-Southern Col-lege, has sent four fragments of sirenian ribs collected by Ronald Rhoads from the lower part of the Citronelle Formation in sand and gravel pits west of Jackson, Clarke County, Alabama, along the Tombigbee River, in Sec. 8, T. 6 N, R. 2 E. These specimens are thought by Dr. Thur-mond to be reworked from Eocene or Oligocene deposits.

A fragmentary sirenian rib was collected by Gerard Case in 1965 at "Marianna, Florida" and said to be of Eocene age, from the "Ocala lime-stone." It is slender, oval in cross-section, and 32×20 mm in diameter. The specimen was do-nated to the Smithsonian Institution, where it is catalogued under USNM 244028. If the specimen is indeed of Eocene age, it undoubtedly came from the Crystal River Formation (Jacksonian), but in view of the widespread development of the immediately overlying, and lithologically similar, Marianna Formation (Oligocene, Vicksburgian), as well as still younger limestones, the record cannot be regarded as unequivocally Eocene in age without more precise field data. Reves (1961) provides a useful introduction to the distribution and exposures of these beds, which are potentially productive sources for fossil sirenians.

OLD WORLD RECORDS

The extensive literature of Eocene sirenians in the Old World spans well over a hundred years, and it is not our purpose here to review it or to discuss Old World materials in any detail, except insofar as it is useful and feasible to compare distribution records and materials with those from North America.

The earliest records of the Sirenia reported to date consist of fragments of ribs and vertebrae from the early Eocene (Ypresian) of Hungary (Kretzoi, 1953) and tooth and postcranial fragments from the early Eocene of India (Sahni and Kumar, 1980; Sahni et al., 1980). As regards the Indian records, however, it should be noted that the mammal-bearing part of the Subathu Formation is more generally regarded as late middle Eocene (Gingerich et al., 1979:113; West, 1980:509), and that the fossils in question may not be sirenian (Savage, pers. comm., 1981; Gingerich and Russell, 1981:237). Savage (1977:344–346) and Savage and Tewari (1977) provide convenient summaries of middle and late Eocene distribution, to which may be added a record of *Protosiren fraasi* from the middle Eocene of India (Sahni and Mishra, 1975) and new records from Hungary (Kordos, 1977, 1978, 1979, 1980). We have mapped world distribution (Figure 2) in order to show visually the striking Tethyan distribution pattern of the Sirenia during Eocene time. The documentation for mapped occurrences in the Old World seems adequately and most succinctly presented in tabular form, which we have done in Table 1, where the numbered entries correspond to the numbered localities on the maps (Figures 1 and 2).

Florida Eocene Sirenians

DESCRIPTION

The Eocene sirenian fossils from the Waccasassa River fauna are represented solely by isolated elements and were mixed on the river bottom with Mio-Pliocene and late Pleistocene ver-

tebrate remains, the latter including the West Indian manatee *Trichechus manatus*. Among the 100 or so identifiable sirenian bones in the Waccasassa River collections, most are totally unlike corresponding elements in *T. manatus*, and no evidence at all has been found of *Metaxytherium* or other late Tertiary forms. The majority of the Waccasassa River specimens, together with those from two other Florida Eocene localities (listed below), seem to represent a single taxon of primitive sirenian.

Locality 10 (Waccasassa River, Levy County, Florida)
  Parietal-supraoccipital skullcaps: UF 14222–14226, 16439, 16441, 16443, 16598, 16607, 21610, 21613; TRO 510, 511, 513–515, 520–524, 529–531, 535–537, 539, 540
  Partial left maxillae: TRO 516, 538
  Sphenopterygoid complexes: UF 16441, 21612
  Upper molars: TRO 518 (left M³); UF 24806 (left), 25708 (right)
  Partial mandibular symphyses: UF 21611; TRO 509, 529
  Vertebrae: UF 25706, 25707, TRO 526, 527
  Rib fragments: UF 16442, 18440, other uncatalogued fragments; TRO 541
Locality 12 (Dunnellon Phosphate Company pit no. 5, Citrus County, Florida)
  Parietal-supraoccipital skullcaps: UF/FGS V2282, V2288
Locality 13 (Withlacoochee 4A Site, Marion County, Florida)
  Parietal-supraoccipital skullcap: UF 24786
Locality unknown
  Parietal-supraoccipital skullcap: UF 3965

PARIETAL-SUPRAOCCIPITAL SKULLCAPS (Figures 4–10).—The sirenian sample from the Avon Park Limestone and Inglis Formation consists primarily of skullcaps, 34 in all. These vary in state of preservation, completeness, and to some extent size, although size is most likely age related. Disregarding broken, waterworn, and immature specimens, the remaining skullcaps are relatively uniform in morphology. As in other sirenians, they consist of the ankylosed parietals and supraoccipital. These were not firmly co-ossified with the frontals and exoccipitals, as most specimens lack the frontals and all lack the exoccipitals. This may indicate that most of these individuals were subadult. Two specimens (TRO 510, 521) retain the posterior portions of the frontals, including most of the frontoparietal suture.

TABLE 2.—Measurements (mm) of Florida skullcaps ($\bar{x}$ = mean, OR = observed range, SD = standard deviation, CV = coefficient of variation)

Variate	N	$\bar{x}$	OR	SD	CV
Maximum width of lambdoidal crest	9	76.1	73.9–80.7	4.5	5.90
Maximum width of parietals anterior to lambdoidal crest	10	63.0	59.1–67.4	2.7	4.31
Minimum width of parietals (just posterior to frontoparietal suture)	10	41.4	35.7–46.4	3.1	7.42
Minimum width at parietal-squamosal suture	13	46.6	42.6–48.9	2.3	4.90
Maximum thickness of supraoccipital	13	20.0	16.5–24.1	2.4	12.13
Maximum thickness of parietals at internal occipital protuberance	13	38.9	35.1–46.6	3.0	7.70
Maximum thickness of parietals at anterior margin	13	27.0	25.0–29.3	1.4	5.05
Angle at which supraoccipital meets parietals, rounded to nearest 5°	23	125°	120°–135°	5.0°	3.98

PARIETALS.—Rather long and narrow in general outline, widest at lambdoidal crest (mean=76 mm; Table 2) and narrowest just posterior to frontoparietal suture (mean=41 mm). Most skullcaps measure approximately 100±10 mm in total length; noticeably more in several specimens, in particular those retaining fragile anterolateral processes of parietals. In most nearly complete specimen (TRO 510), parietals (= total length of skullcap) 127 mm in length. Posterior margin of parietals marked by prominent lambdoidal crest, diverging posterolaterally from midline, and strongly concave posteriorly. Lambdoidal crest seems formed primarily from thickened posterior border of parietals, although supraoccipital may form portion of ventral and lateral borders of crest. Parietals and supraoccipital so firmly coossified that sutural contact between them is at best doubtfully discernible. Location of this suture below lambdoidal crest was reported by Abel (1912) in *Eotheroides aegyptiacum.* Posterolateral prolongation of parietals as lambdoidal crest appears to have precluded contact between squamosals and supraoccipital observed in most si-

renians, but slight contact may have existed in several specimens. Pronounced indentation of parietals present anterior to lambdoidal crest for reception of dorsal margin of squamosal, which seems to have reached level of skull roof. Roof of cranium slightly convex transversely in most specimens but nearly flat in some. Parietals have narrow depression along dorsal midline just posterior to frontoparietal suture, in a few instances reaching nearly to nuchal line (TRO 531). Dorsal surfaces of parietals, roughly midway between frontals and supraoccipital, in some specimens pierced by 1 or 2 prominent emissary foramina on 1 or both sides, well away from midline (UF 21610: TRO 522, 536, 539, 540). Temporal crests poorly developed or absent: where weakly present, they appear to arise from anterior edge of parietosquamosal suture and may have had their origin on dorsal processes of squamosals, none of which are preserved in the Florida specimens. Temporal crests follow dorsolateral borders of skullcaps, becoming weaker on anterolateral processes of parietals. Two specimens which retain small portions of frontals indicate that these
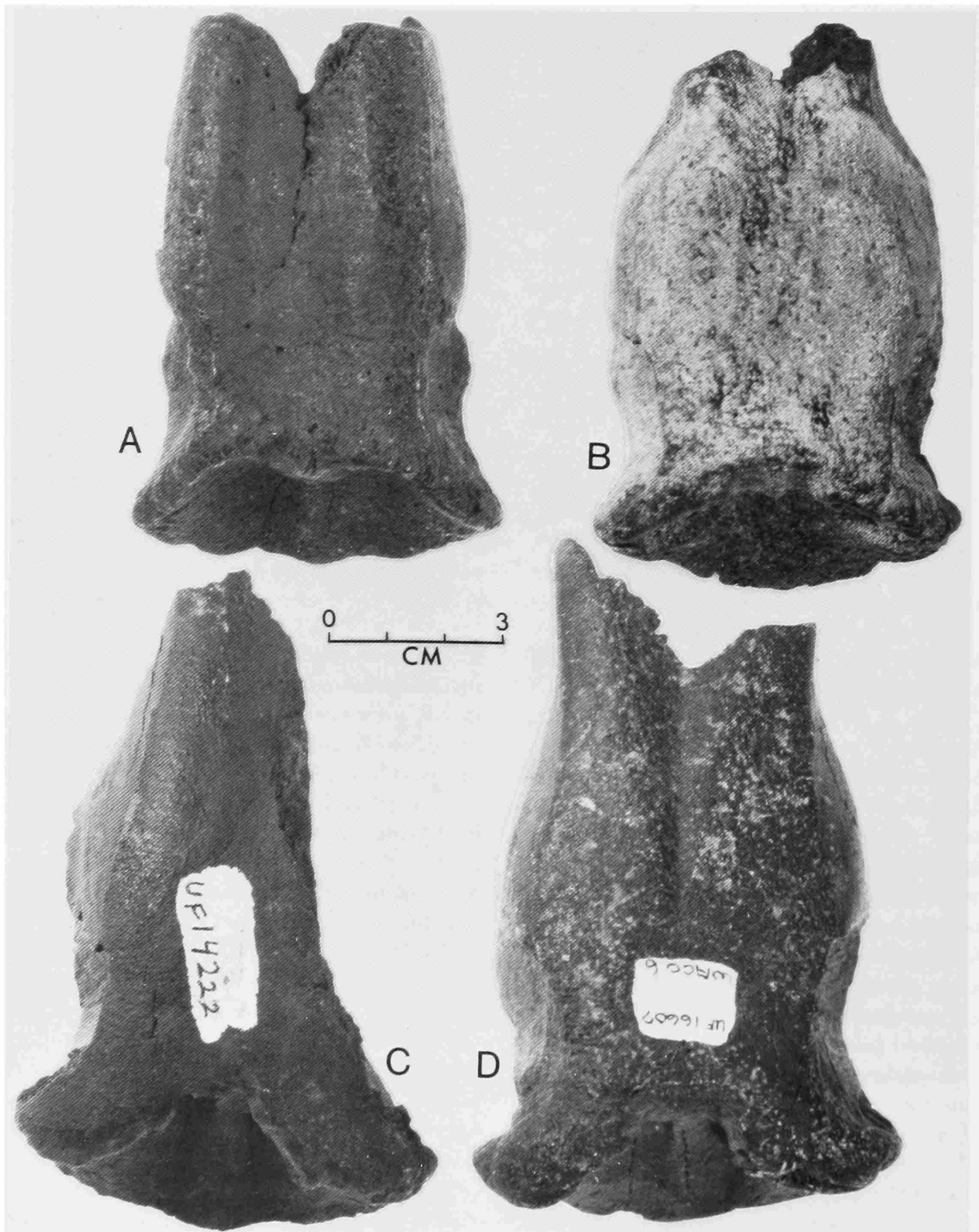
FIGURE 4.—Parietal-supraoccipital skullcaps of *Protosiren* species from Florida in dorsal aspect:
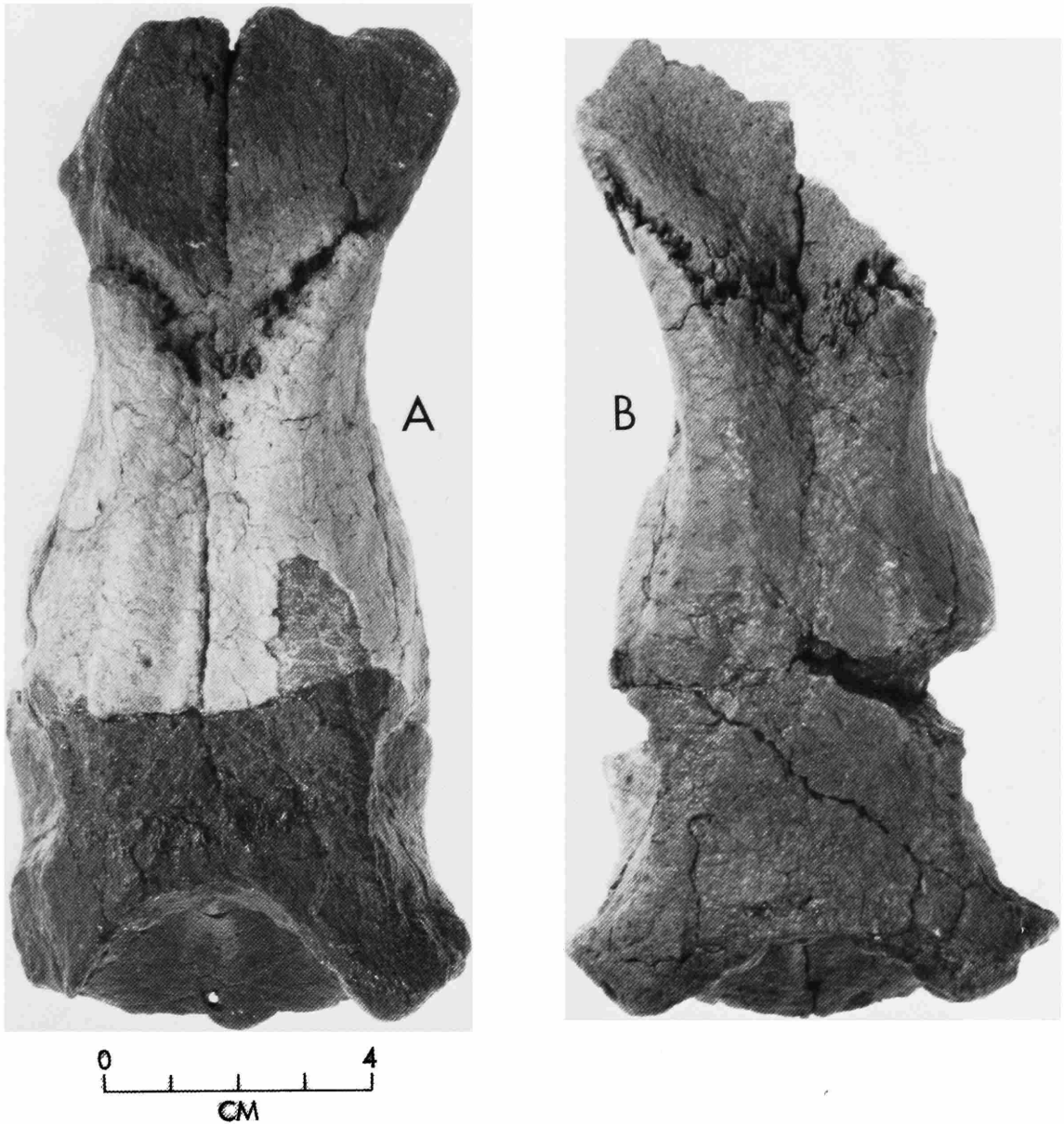A, TRO 531; B, UF 3965; C, UF 14222; D, UF 16607.

FIGURE 5.—Parietal-supraoccipital skullcaps (including portions of frontals) of *Protosiren* species from Florida in dorsal aspect: A, TRO 521; B, TRO 510.

crests were continued anteriorly by overhanging dorsolateral margins of frontals. Lateral walls of braincase meet skull roof at nearly right angles. Internal structure of parietals varies to greater extent than do external features. Braincase bounded anteriorly by ventral process of frontal, posteriorly by supraoccipital and tentorium osseum. Triangular internal occipital protuberance slightly pointed, either broadly confluent with supraoccipital or separated from it by transverse
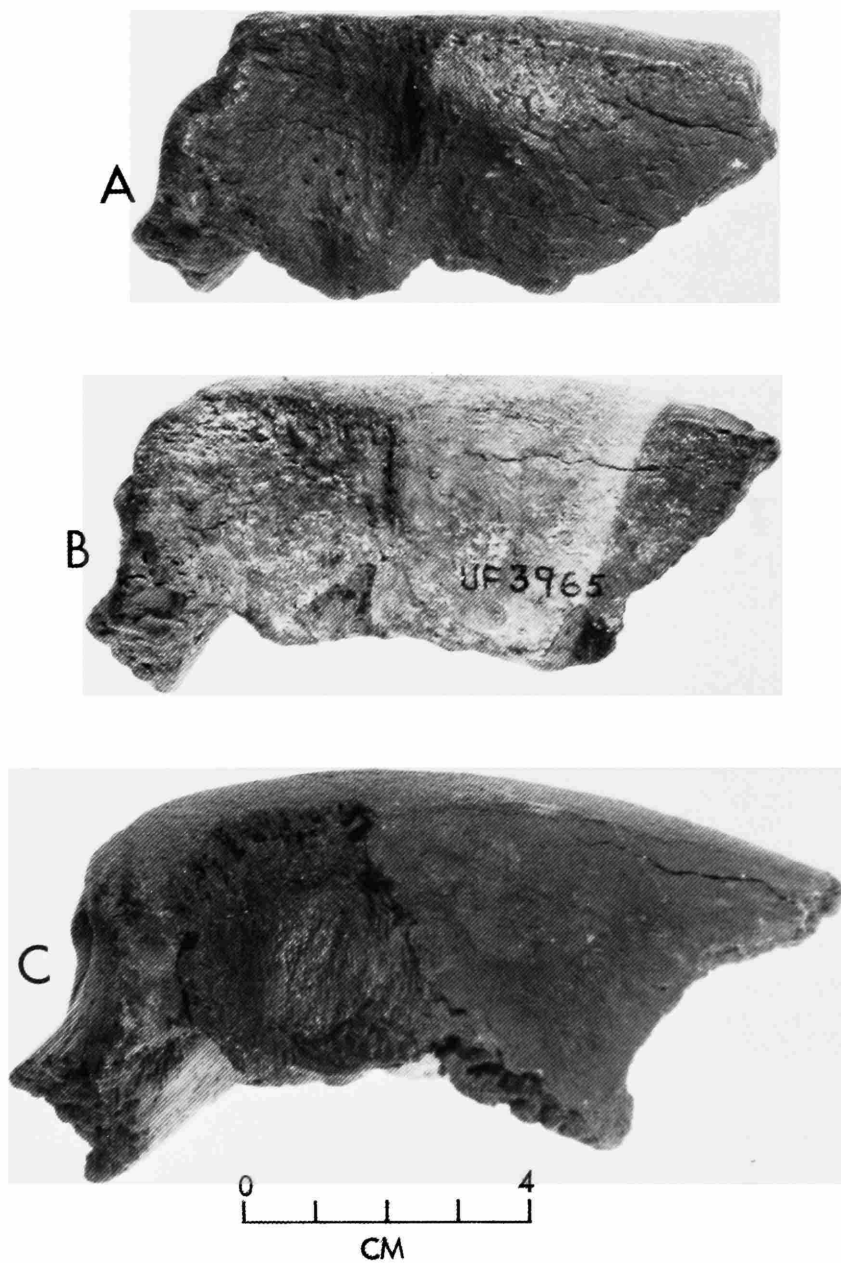
FIGURE 6.—Parietal-supraoccipital skullcaps of *Protosiren* species from Florida (A, B, right lateral aspect; C, left lateral aspect, reversed): A, TRO 531; B, UF 3965; C, UF 14222.
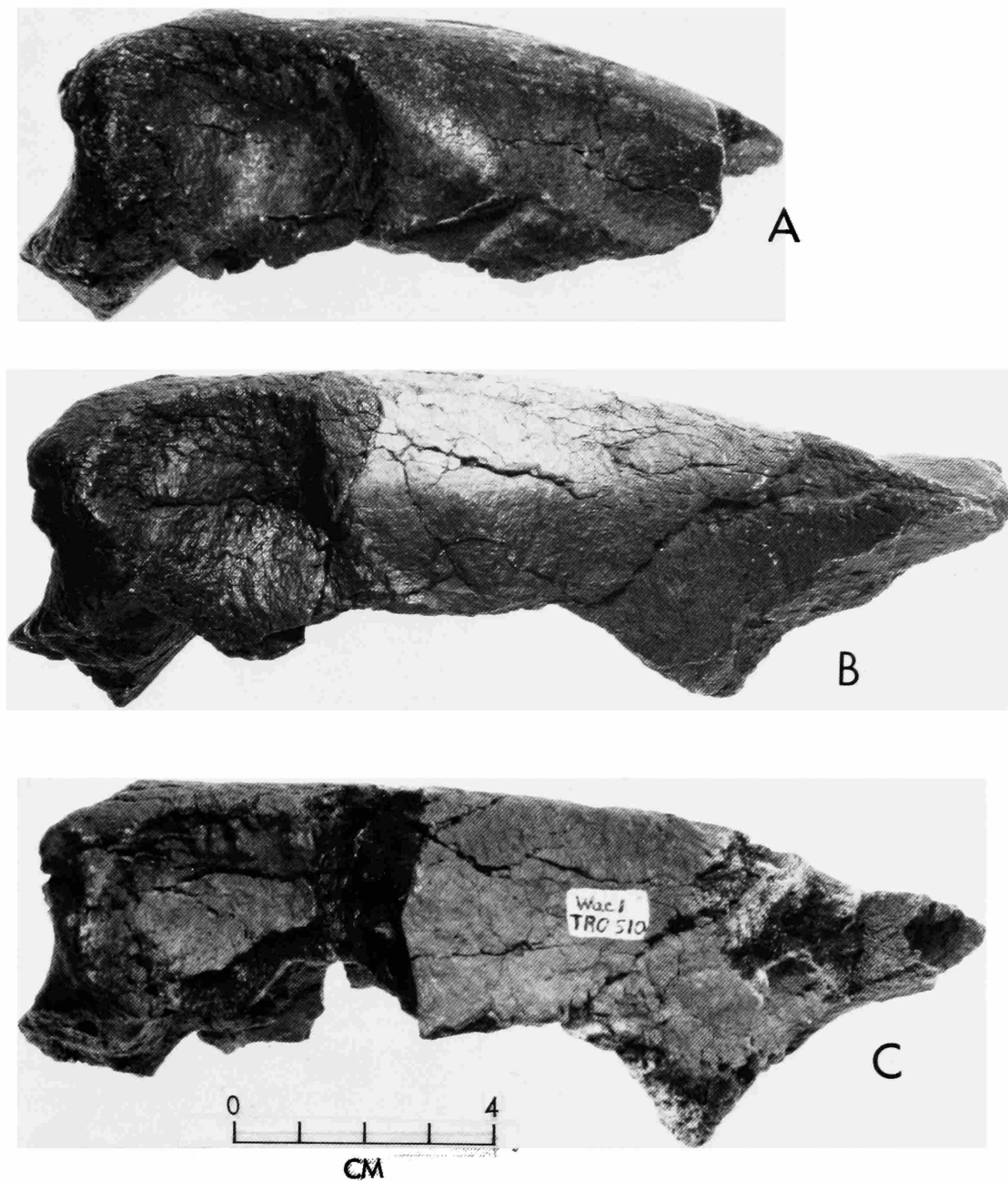
FIGURE 7.—Parietal-supraoccipital skullcaps of *Protosiren* species from Florida in right lateral aspect (B and C include portions of frontals): A, UF 16607, B, TRO 521; C, TRO 510.

FIGURE 8.—Parietal-supraoccipital skullcaps of *Protosiren* species from Florida in ventral (internal) aspect: A, TRO 531; B, UF 3965; C, UF 14222; D, UF 16607.

FIGURE 9.—Parietal-supraoccipital skullcaps (including portions of frontals) of *Protosiren* species from Florida in ventral (internal) aspect: A, TRO 521; B, TRO 510.

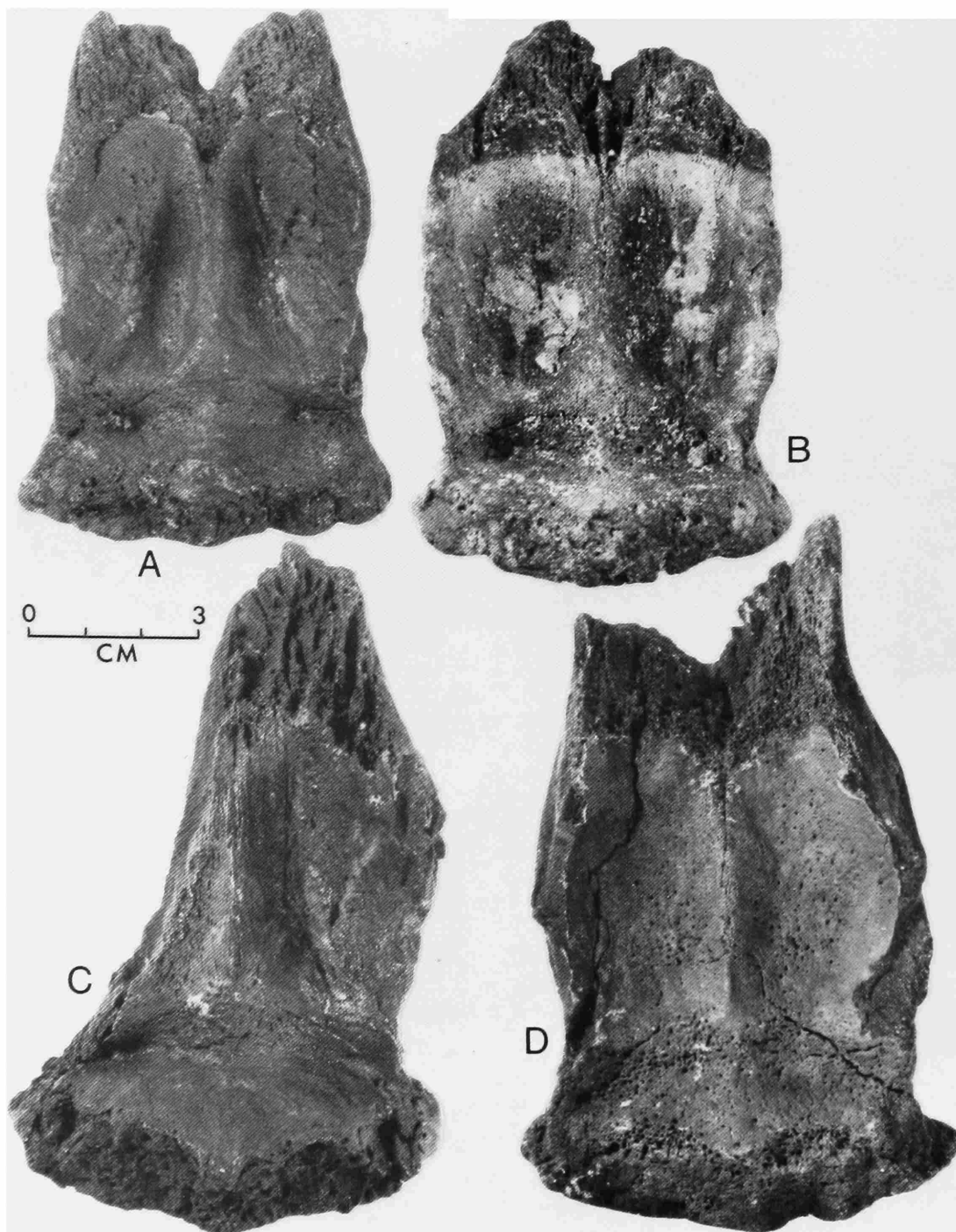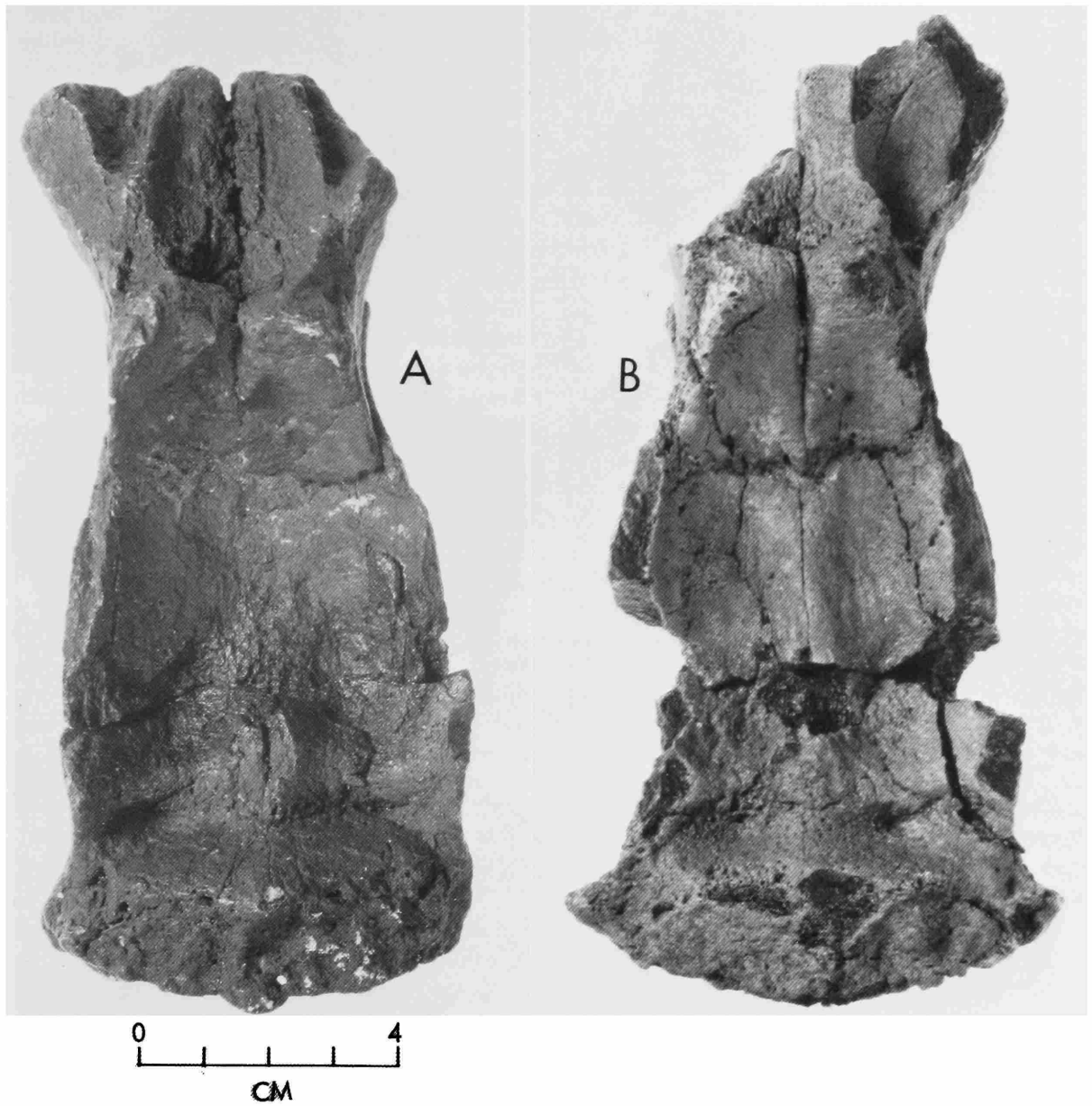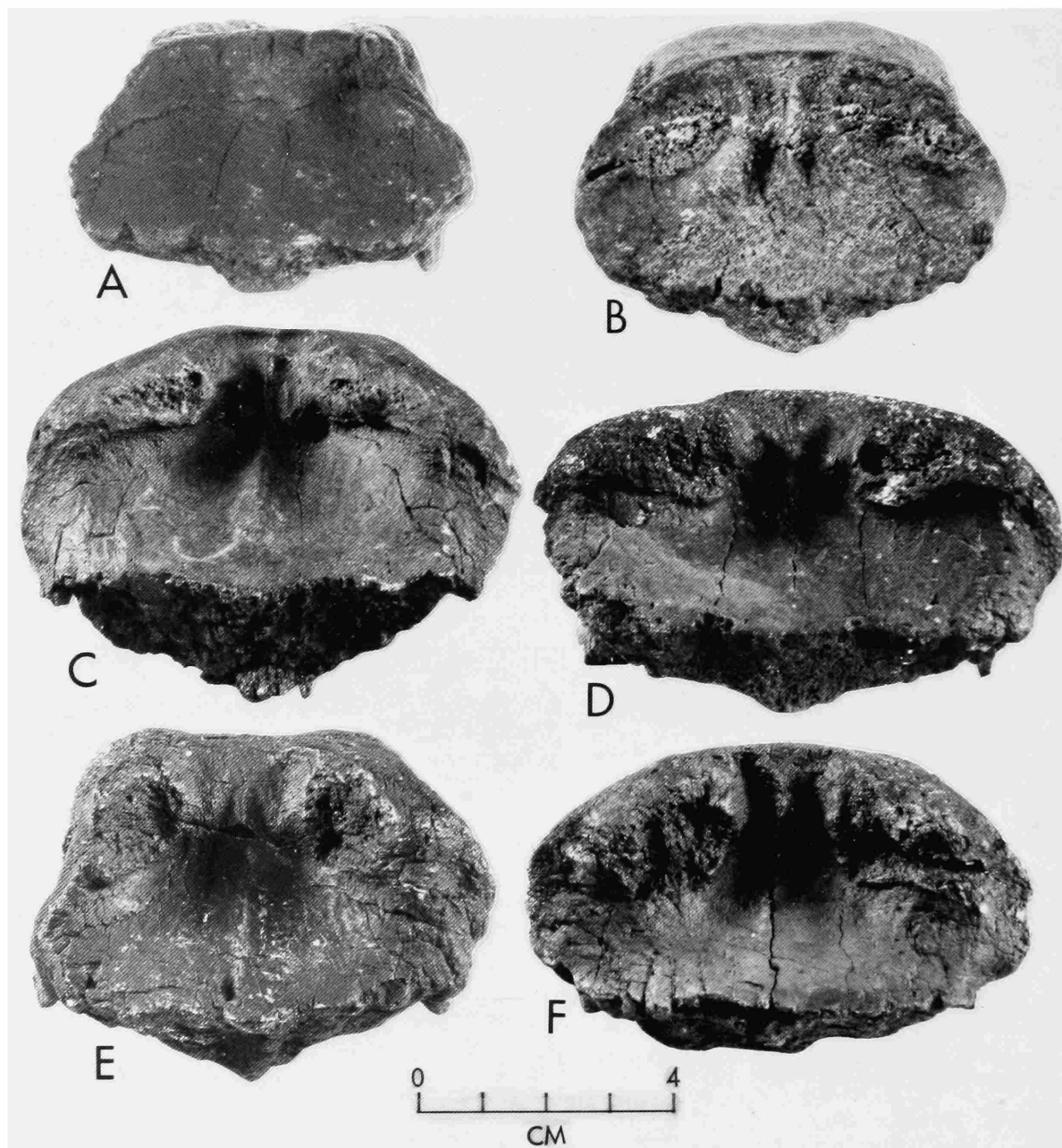FIGURE 10.—Parietal-supraoccipital skullcaps of *Protosiren* species from Florida in posterior aspect: A, TRO 531; B, UF 3965; C, UF 14222; D, UF 16607; E, TRO 521; F, TRO 510.

sulcus. Cerebral hemispheres separated along midline by prominent bony falx cerebri which extends forward from internal occipital protuberance to frontals. Bony falx cerebri sharp, narrow ridge in most specimens but broader and less convex in others; lowest and broadest just abaft frontoparietal suture, where it typically shows median groove. Prominent ridge of bone (tentorium osseum) located perpendicular to bony falx along posterior margin of parietals. Deep transverse sulcus lies just posterior to tentorium osseum and parallel to it, corresponding to suture between parietals and supraoccipital. Transverse sulcus formed in most species by 2 deep lateral concavities and shallow median saddle (internal occipital crest) separating internal occipital protuberance from supraoccipital. Transverse sulcus shallow laterally in several specimens and almost nonexistent along midline, in which case protuberance is broadly confluent with supraoccipital. Bony falx, tentorium osseum, and internal occipital crest typically form strikingly cruciform pattern (cruciate eminence). Portions of parietals and supraoccipital which were in contact with brain smooth, but pierced by numerous tiny nutrient foramina. Dorsal aspect of frontoparietal suture V-shaped, extending anterolaterally at approximately 45° angles to midline. On lateral wall of braincase, frontoparietal suture slopes posteroventrally at about 45° angle. On internal surface of braincase, frontoparietal suture located 20–30 mm posterior to its position on dorsal surface and aligned perpendicular to midline. Parietals further distinguished by extreme thickness of bone (maximum thickness 47 mm along posterior border of parietals, 30 mm farther forward near contact with frontals; N=14).

SUPRAOCCIPITAL.—Supraoccipital firmly fused with parietals, as in other sirenians. Together with parietals, supraoccipital forms prominent lambdoidal crest. Parietosupraoccipital suture obliterated in most Waccasassa River skullcaps, but supraoccipital appears to form lateralmost portion of crest in some specimens and ventral portion of crest in all. In dorsal view, only parietals seem to be present on cranial roof. Deep

median notch in lambdoidal crest visible in dorsal view; notch variably developed and not equally pronounced in all specimens, but in no skullcap does supraoccipital project onto cranial roof. Supraoccipital as broad as or slightly broader than parietals, depending on which bone is interpreted to form lateralmost portion of lambdoidal crest. Overall shape of supraoccipital extremely variable in the Florida sample, although its external surface is broadly concave in all cases. Supraoccipital roughly hexagonal in most specimens; in others it may appear pentagonal, trapezoidal, or almost lozenge-shaped. External occipital protuberance usually weakly developed. In several specimens, weak median ridge extends short distance ventrally from protuberance. As mentioned above, supraoccipital may have contacted squamosals in some specimens. (The large sample of skullcaps from the Florida sirenian, however, indicates that contact between supraoccipital and squamosals is probably not an important morphological feature, as it is dependent on several variable factors, including size of the dorsal process of the squamosal and degree of development and configuration of the lambdoidal crest. The large Florida sample also suggests that these features vary with the size and the age of the animal.) Lateral portions of lambdoidal crest bear prominent rugosities for insertion of semispinalis capitis muscles; these enhance posterad concavity of crest as a whole. Although not so thick as parietals, supraoccipital reaches maximum thickness of 24 mm; on its continuous sutural surface with exoccipitals it is thickest in midline and thins laterad, indicating that supraoccipital did not reach foramen magnum.

FRONTALS (Figures 5, 7, 9, 11).—Posteromost portion of frontals preserved in 2 specimens (TRO 510, 521). Lateral edges of frontals begin to diverge laterad immediately anterior to their dorsal contact with parietals. This is true in most sirenians; however, in this form widening of skull in this region is particularly noticeable due to extreme narrowness of parietals just posterior to frontals. Posterior and median part of frontal skull roof markedly concave; concavity confluent
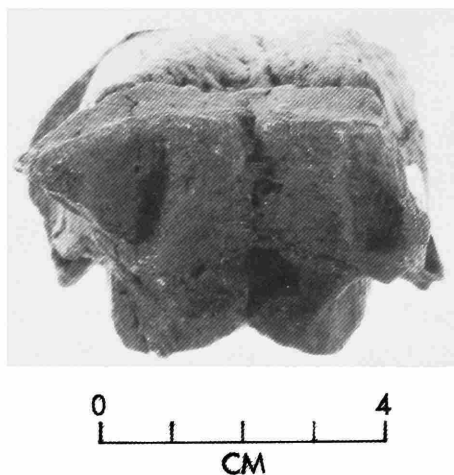
FIGURE 11.—Skullcap of *Protosiren* species from Florida in anterior aspect (TRO 521), showing broken cross-section through frontals.

with narrow groove in parietal midline, which extends posteriorly from frontoparietal suture. Farther anteriorly, dorsal surface of frontals becomes flatter, and in 1 specimen in which this area is preserved, there is a slight frontal boss. Interfrontal suture extends 30–35 mm on cranial surface. Frontal projects ventrally as triangular process, on whose anterior sloping surface is located a deep, transversely oriented elliptical pit, probably for reception of spina mesethmoidalis. This pit appears to approach no closer than 2.5 cm to dorsal surface of frontals. Dorsolateral and anterior to this pit, each frontal bears large concavity which was separated from temporal fossa by thin bony wall; this formed a posterolateral recess of nasal cavity which may have accommodated parts of the ethmoturbinalia (Figure 8).

In summary, the most striking features of the Florida skullcaps are: elongate general outline; deep constriction directly posterior to the frontoparietal suture; deeply incised suture for the dorsal process of the squamosal; prominent, rugose, posterolaterally extended and posteriorly concave lambdoidal crest; slightly convex cranial roof; weak to absent temporal crests; prominent bony falx cerebri, tentorium osseum, and internal oc-

cipital protuberance forming a cruciform pattern; transverse sulcus with deep lateral pits; supraoccipital meeting cranial roof at angle of about 125°; and exceptionally thick bone of the parietals and supraoccipital. The important features of the preserved portions of the frontals include a sharply V-shaped frontoparietal suture diverging from the midline at a 45° angle, a relatively long interfrontal suture on the cranial surface, and prominent posterolateral recesses of the nasal cavity.

MAXILLA (Figure 12).—One of the 2 available edentulous maxillae (TRO 516) is slightly more nearly complete, including alveoli for $?P^4$–M^2 and the entire zygomatic-orbital process. The less nearly complete maxilla (TRO 538) retains alveoli for $?P^4$–M^3 and the posterior half of the zygomatic-orbital process, although the alveoli for $?P^4$ and M^3 are only partially preserved. The only observable differences between the two specimens are in thickness of posterior border of zygomatic-orbital process and shape of M^2 alveolus. In TRO 516, posterior border of process 28 mm thick and essentially flat; in TRO 538 it is only 21 mm thick and more rounded. M^2 alveolus in TRO 516 differs from that in TRO 538 in lacking septa between roots of tooth. These slight differences are easily attributable to individual variation. Zygomatic-orbital process arises directly lateral to point between M^2 and M^3 alveoli and extends anteriorly 60 mm (in TRO 516) to point slightly beyond anteromost alveolus in preserved toothrow. Process thickened along posterior border (28 mm maximum), thins to 8 mm at anterior border. Ventral side of process lies at level of alveolar rim posteriorly and rises anterodorsad at angle of about 20° to palatal plane. Anterior border of process forms floor of infraorbital foramen, which is relatively small (15 mm in mediolateral diameter) in the 1 specimen (TRO 516) in which it is partially preserved. Located approximately 10 mm medial to infraorbital foramen on dorsal side is prominent palatine foramen, which enters rostrum passing anteroventrad. Lateral to toothrow, flattened zygomatic-orbital process slopes gently dorsad to maxillary-jugal suture,
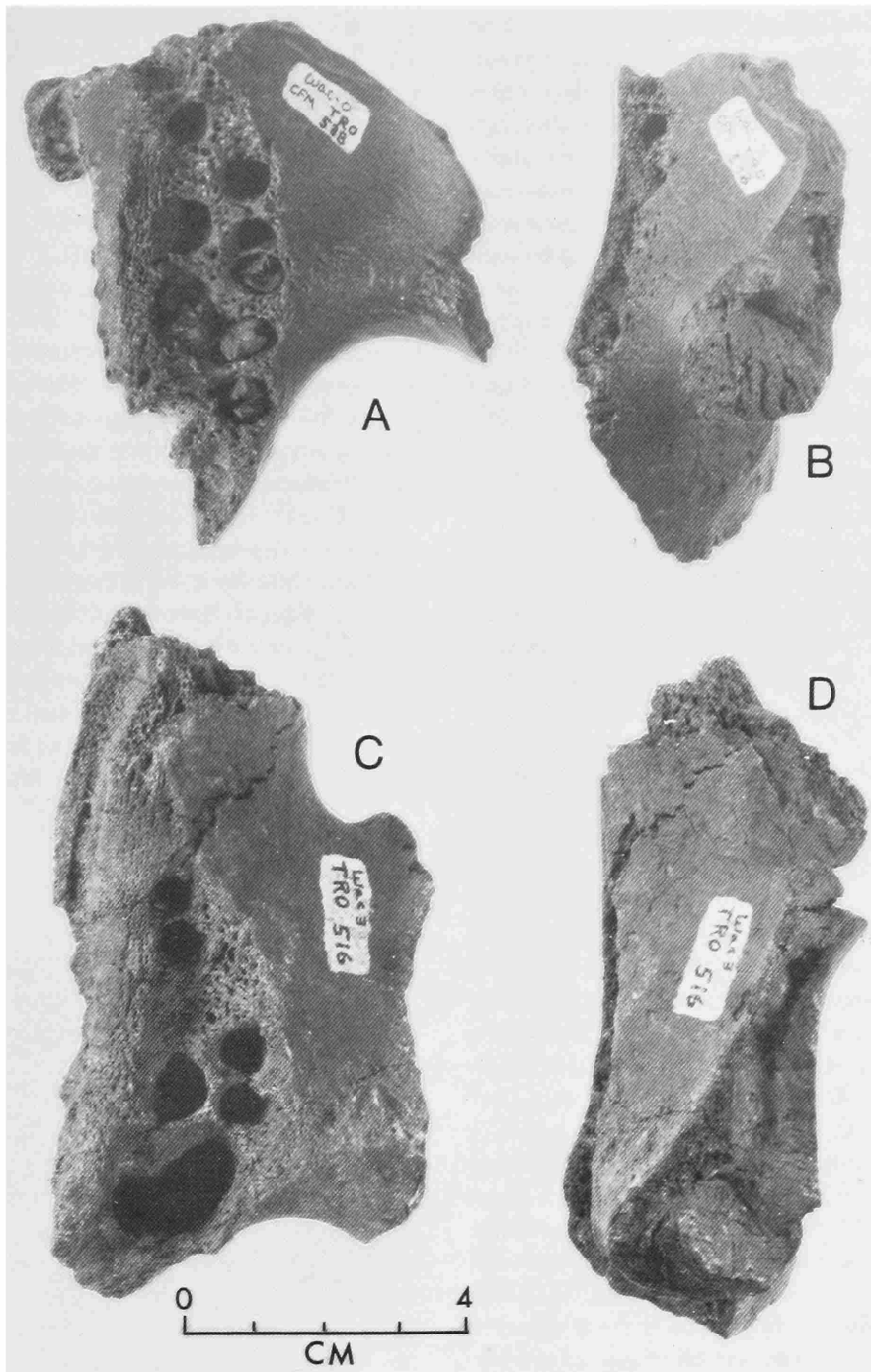
FIGURE 12.—Partial left maxillae of *Protosiren* species from Florida: A, occlusal aspect (TRO 538); B, lateral aspect (TRO 538); C, occlusal aspect (TRO 516); D, lateral aspect (TRO 516). Anterior ends up.

which is more or less parallel to midline and 65 mm in length. Sutural surface very broad posteriorly, narrow more anteriorly, and slightly broadened again at anteromost end; irregularly concave throughout length, with a particularly deep pit in center of broadest (posterior) part, and horizontal interdigitations along posterior edge. Dorsal surface of zygomatic-orbital process forms floor of orbit and is gently concave both anteroposteriorly and mediolaterally. Just medial to maxillary-jugal suture, on dorsal side, rather prominent ridge of bone extends parallel to suture for most of its length. Toothrow rather short; ?P^4–M^2 length = 52 mm in TRO 516, 44 mm in TRO 538. Anteromost premolar and M^3 both relatively near (M^3 perhaps slightly closer to) midline, toothrow in between being bowed outward in gentle arc. Five alveoli present in each maxillary fragment, although TRO 516 retains only anterior wall of M^3 alveolus. Both specimens have 2 small anterior alveoli, which presumably contained single-rooted premolars. These probably correspond to P^4 and P^5 of a skull referred to *Protosiren fraasi* by Sickenberg (1934, pl. 3: fig. 6). Behind these alveoli in each specimen is a slight (~ 10 mm) diastema, evidently a space for a DP^5 alveolus now filled with cancellous bone and being encroached upon by the permanent premolars. A similar condition is observed in specimens of *Eotheroides libycum* (holotype, Andrews, 1906, pl. 20: fig. 1A; also YPM 33852) and *Halitherium schinzi* (Krauss, 1862, pl. 6: fig. 2; Lepsius, 1882, pl. 3: fig. 18). TRO 516 retains enough bone in front of P^4 alveolus to demonstrate that there was at least a 20 mm diastema between it and the next anterior tooth. P^4 and P^5 alveoli circular, equal in size, not separated by a diastema. M^1 and M^2 of TRO 538 appear from the alveoli to have been very similar in shape and size; both were 3-rooted with 2 smaller labial roots slightly flattened anteroposteriorly and a single, larger lingual root circular in cross-section. M^1 alveolus in TRO 516 identical to that in TRO 538, but as described above, M^2 alveolus lacks intra-alveolar septa. M^3 alveolus, though only partially preserved in 1 specimen (TRO 538),

appears to have differed from the 2 anterior molar alveoli in having the posterolabial root socket somewhat enlarged, more posteriorly and lingually placed, and curved forward apically.

SPHENOPTERYGOID FRAGMENTS (Figure 13).—Two examples of the fused basisphenoid-alisphenoid-pterygoid complex are known. In the larger and better preserved (UF 21612), sphenoccipital suture about 34 mm wide; a single ridge descending after side of each pterygoid process begins in contact with edge of suture, unlike *Trichechus* or *Metaxytherium*. No pterygoid fossa present on after side of process. Pterygoid processes converge slightly posteriorly and are at least 40 mm long anteroposteriorly. Alisphenoid canal absent. Optic foramen lies at level of top edge of sphenorbital foramen, which is confluent with large foramen rotundum. Anterodorsal to these on cranial surface, and close to midline at lower edge of cribriform plate, a smaller foramen passes anteroventrad, converging on optic canal. A possible trace of a tiny sinus canal may be discerned dorsolateral to foramen rotundum. Medial sides of foramina rotunda separated by about 23 mm.
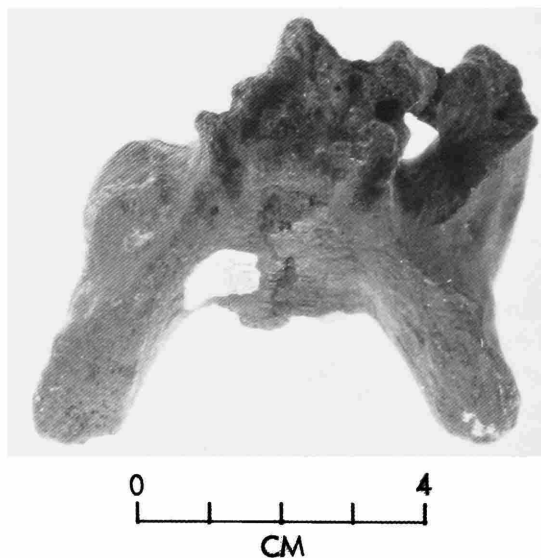

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FIGURE 13.—Partial sphenopterygoid complex of *Protosiren* species from Florida in posterior aspect (UF 21612).

TABLE 3.—Dental measurements (mm) of Florida Eocene sirenians (L = crown length, AW = anterior width, PW = posterior width)

Tooth	L	AW	PW
Right upper M (UF 25708)	11.1	13.2	–
Left upper M (UF 24806)	15.4	–	12.4
Left M^3 (TRO 518)	17.5	14.8	10.6

LEFT M^3 (TRO 518, Figure 14, Table 3).— Tooth very slightly worn. Anterior interdental wear facet present midway between lingual and labial margins. Precingulum consists of prominent noncuspidate transverse crest arising from anterolabial base of paracone and extending lingually slightly more than half breadth of tooth to the point where deep cleft separating protoconule and protocone descends anterior face of protoloph. Precingulum highest at this point, from which it descends at sharp angle toward lingual margin. Lingually, precingulum represented by 2 tiny cuspules at anterolingual base of protocone. Paracone highest cusp on tooth, only very lightly worn but already nearly confluent with protoconule, which is only slightly lower. Paracone and protoconule both compressed anteroposteriorly. Although equidistant from paracone and protocone, protoconule is separated from protocone by prominent cleft which extends down anterior and posterior faces of protoloph to bottom of transverse valley. Protocone largest cusp on tooth, blunt, circular in outline, and slightly lower than paracone, protoconule, hypocone, and metacone. Deep transverse valley open labially but lingually closed by cingulum which extends from posterolingual base of protocone to anterolingual base of hypocone. Lingual cingulum a low ridge consisting of 5 tiny cuspules anteriorly and 1 relatively large cuspule posteriorly, which is separated from hypocone by a cleft. Metacone and metaconule anteroposteriorly compressed and connected to form broad V-shaped ridge with its apex anterior. Metaconule much closer to hypocone than to metacone but separated from former by shallow cleft. Hypocone smallest of the major cusps, blunt, circular in outline, and located near lingual border. From posterolingual base of hypocone a sharp ridge descends posteriorly. This lingual portion of postcingulum is separated from a prominent, sharp cusp located at posteromost point of tooth by a deep cleft extending down lingual margin almost to base of enamel crown. Postcingulum extends anteriorly from large posterior cusp to posterolabial corner of metacone. This labial portion of postcingulum is a low ridge composed of 2 tiny cuspules. Postcingulum and metaloph surround deep circular basin. Tooth has 2 small roots anterolingually and anterolabially and a larger root on posterior margin midway between lingual and labial borders. Small anterolabial root markedly compressed anteroposteriorly; anterolingual root triangular in outline; large posterior root triangular in outline with very deep groove down posterolingual side.

LEFT UPPER MOLAR (UF 24806, Figure 15, Table 3).—This tooth is similar in size and preservation to TRO 518. Labial side of protoloph missing; tips of all major cusps pitted by moderate wear; roots broken. Precingulum confined to labial part of anterior side of crown. Protoloph straight. Slight cingulum present at each end of transverse valley. Metaloph consists of 3 subequal, evenly spaced cusps and is slightly convex forward. Rounded spur of metaconule extends anterolabiad into transverse valley to touch base of protoconule, while another, sharper and bicuspulate spur of metaconule extends posterolinguad, hardly diminishing in height, to stop abruptly at rear of crown in flat, vertical, posteradfacing surface. (This pair of extensions, which gives a +-shaped aspect to the metaloph, is not exactly paralleled in any other sirenian we have seen.) Low posterolabial cingulum encloses a small basin.

RIGHT UPPER MOLAR (UF 25708, Figure 16, Table 3).—Similar in preservation to the above; heavily worn. Precingulum extends across most of anterior side but best developed labially; attached to protoloph just lingual to midline of tooth. Transverse valley open labially, partly blocked in center by spurs of protoloph and metaloph; lingual end damaged. Metaloph
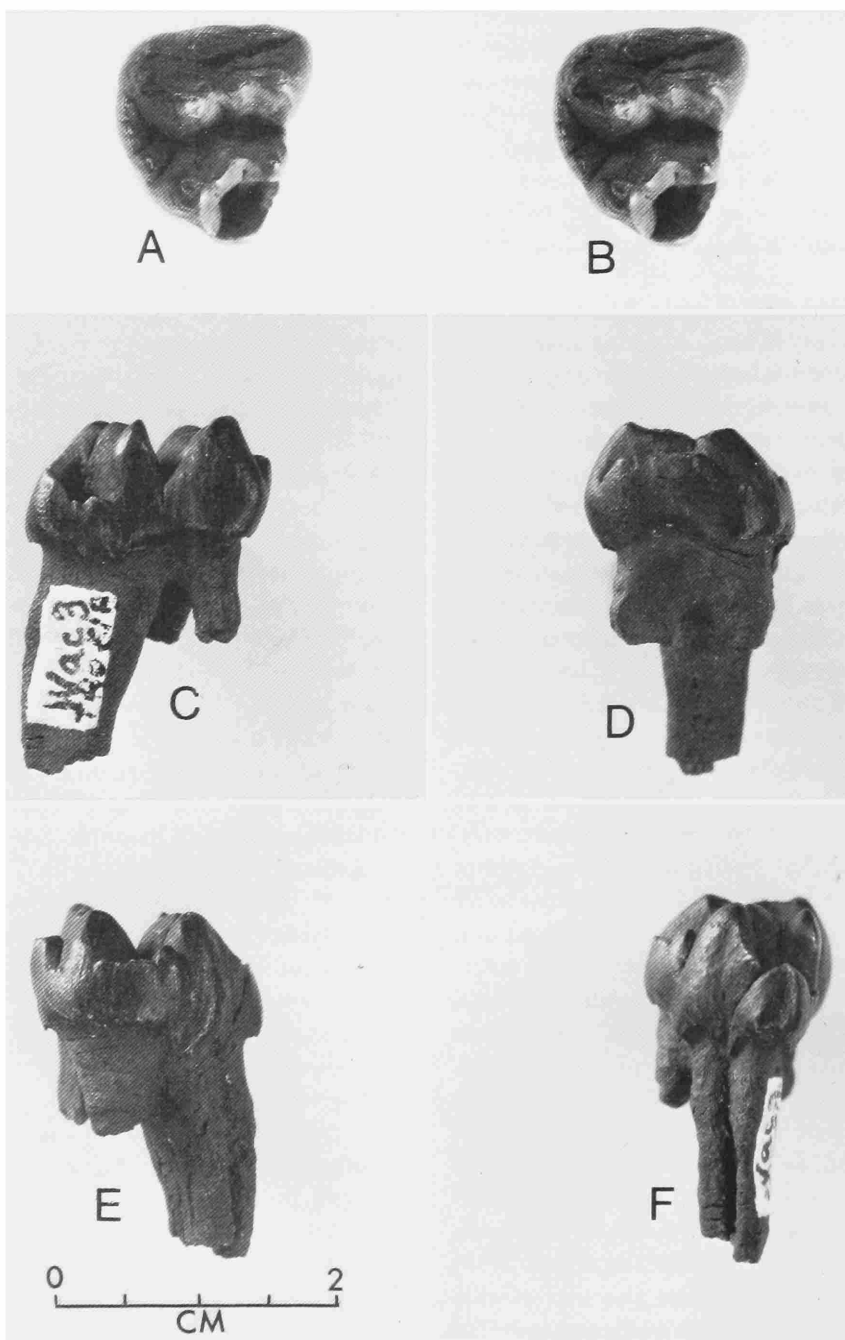
FIGURE 14.—Left M³ of *Protosiren* species from Florida (TRO 518): A, B, occlusal aspect, anterior up (stereophotograph); C, labial aspect; D, anterior aspect; E, lingual aspect; F, posterior aspect.
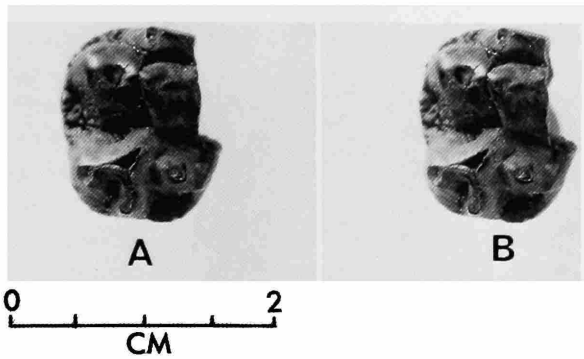
FIGURE 15.—Left upper molar of *Protosiren* species from Florida (UF 24806): A, B, occlusal aspect, anterior up (stereophotograph).
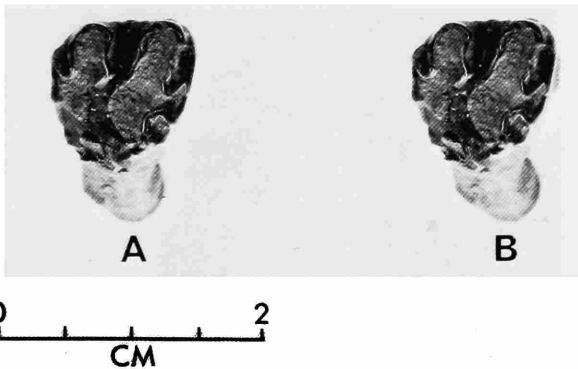

FIGURE 16.—Right upper molar of *Protosiren* species from Florida (UF 25708): A, B, occlusal aspect, anterior to right (stereophotograph).

nearly straight. Small postcingulum attached to metaloph lingually, bounds small posterior basin opening labiad. Posterior interdental wear facet present. Large lingual root preserved, labial roots broken.

MANDIBULAR SYMPHYSES (Figure 17).—All 3 mandibular symphyseal fragments broken off dorsal to mental foramen and lack anteromost portion of symphysis. Two retain enough of horizontal ramus so that abrupt anterior downturning of ventral ramal border is evident. The 3 specimens differ somewhat in size and robustness, but all appear to represent the same form. In the largest (TRO 525) and smallest (TRO 509), the mandibular rami, although solidly fused, are separated ventrally by a cleft. In the third (UF 21611) the rami are fused anteriorly, the cleft persisting only along posteroventral margin of symphysis. Symphyseal regions laterally compressed anteriorly, widen gradually posteriorly in 2 specimens, the smallest being more noticeably compressed anteriorly and hence widening more abruptly. Posteroventral margin of symphysis ascends vertically at almost 90° angle, then turns backward almost as abruptly to form ventral ramal border. In smallest specimen, cleft between right and left rami persists on this vertical posterior margin of symphysis, whereas in other 2 this portion of symphysis fused. Large mental foramen located slightly (about 10–20 mm) forward of posterior border of symphysis. Deep, narrow groove extends forward from mental foramen to point about 10 mm from anteromost margin of symphysis, as preserved in most nearly complete specimen (TRO 509). All 3 symphyses have very small accessory mental foramen, which exits from mandibular canal only a few millimeters posterior and ventral to opening of principal mental foramen. Any other accessory mental foramina which may have been present are obliterated by breakage. Only smallest specimen retains much of mental fossa, which is rather shallow and resembles that of North Carolina mandible described below.

THORACIC VERTEBRAE.—Two examples are preserved. UF 25706, much distorted, has broadly heart-shaped centrum 44 mm high anteriorly, about 50 mm wide, 28 mm thick. Transverse process tapers to irregular point without clear facet for tubercular articulation. Broad, deep fissure occupies ventrolateral surface of transverse process. Neural canal approximately 24 mm wide, 15 mm high posteriorly; apex not slitlike. Anteroposterior length of zygapophyses about 50 mm. Postzygapophyses thin, laterally compressed.

Centrum of UF 25707 of comparable size and shape; transverse process much more robust, quadratic in dorsal view, with articular surface and without fissure. Neural canal approximately 18 mm wide, 24 mm high; apex not slitlike. Anteroposterior length of zygapophyses greater than 45 mm. Neural spine inclined backward slightly but still lies over centrum; posterior edge
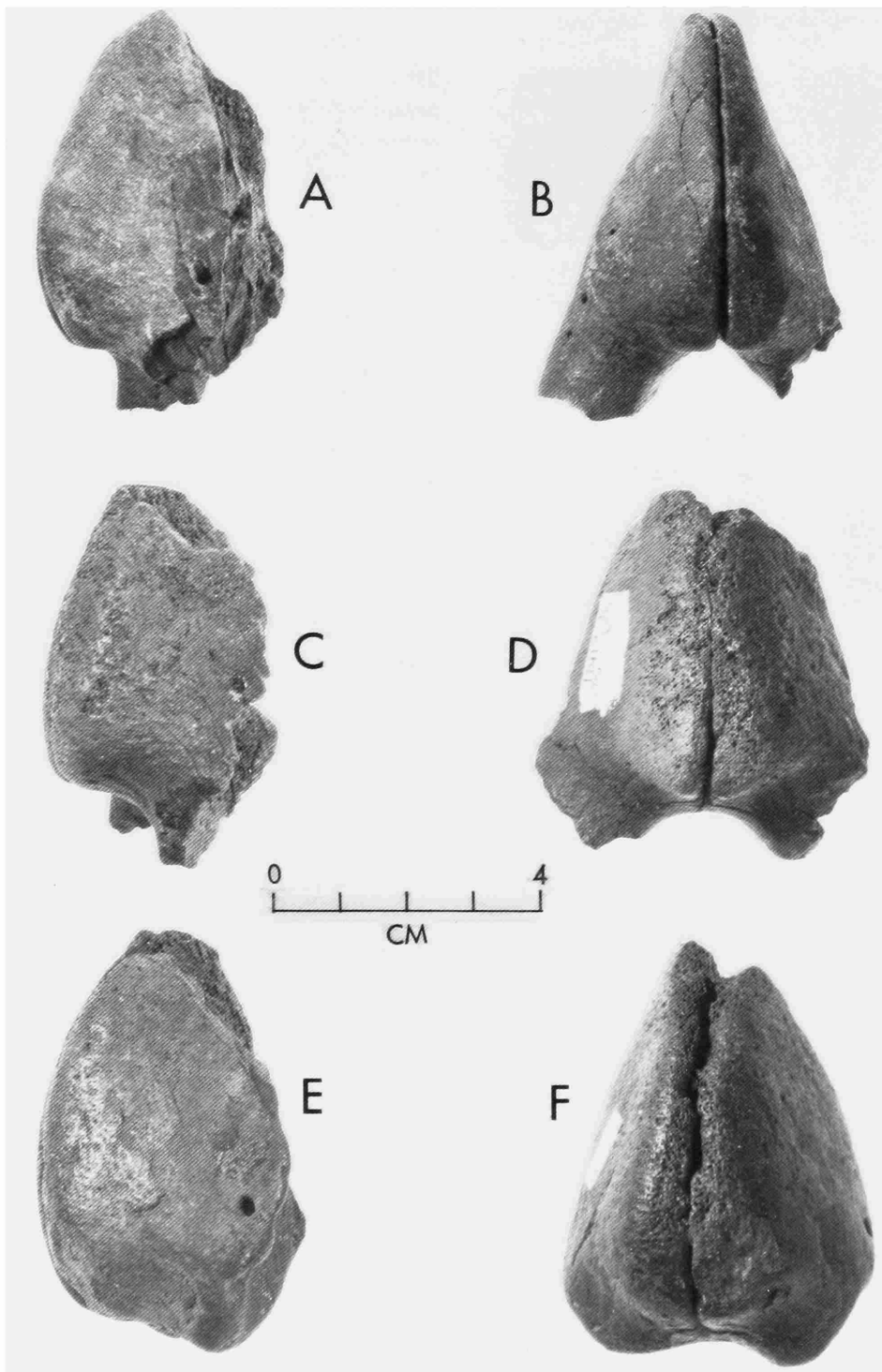
Figure 17.—Mandibular symphyses of *Protosiren* species from Florida in lateral (A, C, E) and ventral (B, D, F) aspects: A, B, TRO 509; C, D, UF 21611; E, F, TRO 525.

only slightly thickened. Both vertebrae composed almost entirely of cancellous bone.

POST-THORACIC VERTEBRAE.—In TRO 527, centrum 62 mm wide and 36 mm high anteriorly, indented at top; overall height about 85 mm; neural canal 19 mm wide, 16 mm high. Transverse processes 36 mm wide, 10 mm thick. Breadth across prezygapophyses 49 mm, anteroposterior length of zygapophyses 62 mm. Neural spine thin, inclined backward, its center lying over posterior edge of centrum. TRO 526 similar, less well preserved. Both vertebrae composed almost entirely of cancellous bone.

RIBS.—Only fragments preserved; cross-sections oval, greater diameter typically 3–5 cm, lesser 2–3 cm. Cancellous bone found only near proximal ends. Distal ends taper abruptly in their last 4–6 cm to truncated subconical tips.

COMPARISONS

Although several genera of Eocene sirenians have been described, considerable doubt and confusion remain concerning their anatomy and proper diagnosis. The three best-known forms—*Protosiren*, *Eotheroides*, and *Prototherium*—have been studied by able workers, including Andrews (1906), Abel (1912), and Sickenberg (1934), yet confusion persists because of the typically dissociated condition of the specimens and the conjectural nature of referrals of isolated elements to a given taxon (Sickenberg, 1934:9, 10). This situation is unlikely to improve until relatively complete, associated skeletons are discovered; certainly we cannot attempt the necessary revision in this paper. On the contrary, the fossils reported herein are prime examples of the frustrating incompleteness of key specimens that continues to plague Eocene sirenian taxonomy. We only can seek to determine whether the North American forms appear referable to any known taxon. The Florida specimens will be considered here, the North Carolina material in a later section.

We regard the diagnostic Florida Eocene specimens as representing a single taxon, whose more important features include: elongate skull roof;

anteriorly constricted, dorsally convex, and extremely thick parietals; massive and posteriorly concave lambdoidal crest; cruciform sculpturing of endocranial roof; lack of an alisphenoid canal; lack of a pterygoid fossa; anteriorly compressed mandibular symphyseal region; sharp anterior downturning of ventral ramal border; restriction of well-developed precingulum to labial part of anterior side of upper molar crown; and presence of cuspules or a small cingulum at lingual end of upper molar transverse valleys. We must determine whether the combination of these and other characters is to be found in any of the previously described taxa.

Prorastomus sirenoides Owen, 1855: The unique type specimen (BM(NH) 44897) of this most primitive known sirenian, from the middle Eocene of Jamaica, reveals many points of contrast with the Florida material. The form of the supraoccipital is quite different (Owen, 1855, pl. 15: fig. 1); an alisphenoid canal is present; and the ventral border of the mandible is nearly straight. (The cranial cavity is unfortunately filled with matrix, concealing details of the braincase.) Although resembling the Florida specimens in some primitive features such as interorbital constriction and lateral compression of the anterior mandibular region, *Prorastomus* is clearly distinct from them.

Sirenavus hungaricus Kretzoi, 1941: This middle Eocene form from Hungary was based on a partial skull and a posterior mandibular fragment, and was considered confamilial with *Prorastomus* by Kretzoi. It resembles the latter and the Florida material in degree of interorbital constriction, and the interorbital region is described as "very massively constructed," as in the Florida form; however, its possession of a "sagittal crest" and lack of pronounced development of the lambdoidal crest distinguish it clearly from our material.

Anisosiren pannonica Kordos, 1979: Another middle Eocene taxon from Hungary, based on a fragmentary maxilla with ?DP^5–M^3 and an isolated permanent premolar. The M^3 closely resembles TRO 518 but is more than a third again

larger, measuring 24.0 mm in length and 22.2 mm in breadth.

Protosiren fraasi Abel, 1907: This important form from the middle Eocene of the Mokattam Hills, Egypt, is more beset with taxonomic confusion than any other we have to consider. Abel first published the name in 1904 but without diagnosis, illustration, or designation of a type. In 1906 he designated as type a skull in the Stuttgart collection (apparently no. 10576 = "Stück V" of Sickenberg, 1934). Also in 1906, Andrews described a skull in the Cairo Geological Museum (CGM C.10171), which Abel then (in 1907) referred to *P. fraasi* and designated as the type in preference to the Stuttgart skull! Abel's 1906 work contained no description or illustration of the latter, however, and "mention of a . . . specimen in a collection" does not constitute an "indication" in the meaning of the 1964 *International Code of Zoological Nomenclature* (art. 16(b) (i)). Therefore, we must with Sickenberg (1934:43, 44) accept Abel's 1907 action as the first valid use of the name and recognize the Cairo skull (CGM C.10171) as the holotype; however, doubtful association of a mandible with this skull (see below) and subsequent referral of other material to this species have clouded the picture further.

The holotype (CGM C.10171), described by Andrews (1906:204–209, fig. 66), closely resembles the Florida sirenians in morphology of the supraoccipital, parietals, and posterior portion of the frontals. Both have relatively elongate skullcaps, massive, strongly concave lambdoidal crests (though these are not rugose in CGM C.10171), weak external occipital protuberances and temporal crests, and slightly convex cranial roofs. Several differences are also apparent. In CGM C.10171, what seems to be a triangular process of the supraoccipital extends onto the skull roof in the midline. This is not matched in any Florida specimen (TRO 531 and UF 16441 come closest) but may be merely an individual variant. The cranial portion of the squamosal fails to extend as high as the level of the skull roof, which it evidently did in the Florida form. The cranial

cavity of CGM C.10171 is unfortunately filled with matrix, leaving in doubt the presence of a bony falx and associated features. An alisphenoid canal, however, is absent from this specimen, as in the Florida sirenians. It further resembles the latter in lack of a pterygoid fossa, in posterior convergence of the pterygoid processes, and in form of the maxilla and toothrow, but differences appear again in regard to M^3. In CGM C.10171, a ridge connects the protocone and precingulum; the cuspidate lingual cingulum connecting protocone and hypocone, and the deep, enclosed posterior basin are both lacking. The molars from Florida and Egypt are similar in having a large, blunt protocone and smaller paracone and protoconule, which are anteroposteriorly compressed and barely separated. Also, both have a blunt hypocone and sharper, more compressed metacone and metaconule.

The mandible thought by Andrews (1906:210–212, fig. 67) to belong to the same species as this skull, and perhaps to the same individual, and which bears the same number (CGM C.10171) in the Cairo Geological Museum, more likely represents a different form. In its ventral outline it resembles both the Florida mandibles and the *Protosiren* mandible of Priem (1907) but contrasts with the latter in its broader dorsal symphyseal surface, which more resembles that of *Eotheroides aegyptiacum* (Abel, 1912, pl. 32: fig. 1).

Abel's original concept of *Protosiren*, however, appears to have been based on Sickenberg's "Stück V" in the Stuttgart collection. Comparison with the latter individual, insofar as its characters can be retrieved from Sickenberg's description of the species as a whole, reveals the following. The degree of development of the lambdoidal crest is not entirely clear from Sickenberg's illustrations (1934, fig. 7; pl. 1: fig. 2) but may fall within the range of variation of the Florida specimens. The supraoccipital, however, is wider in proportion to its height than in any Florida specimen and reaches the foramen magnum, unlike CGM C.10171 or the Florida form (though Sickenberg considered such differences to be age related). The angles formed by the frontoparietal

and the exoccipital sutures, the development of temporal crests, the lack of an external occipital protuberance, and the size of the infraorbital foramen are all points of resemblance. The maxillary tooth row (Sickenberg, 1934, pl. 3: fig. 6) is closely comparable to that indicated by the Florida maxillary fragments; both tooth rows are slightly curved and have two single-rooted premolars anteriorly, which are separated from the next anterior tooth by a diastema. The more anterior premolars of "Stück V" are forward of the level of the infraorbital foramen and would not have been preserved in the Florida material; the most posterior of these, however, may have been absent or more anteriorly located in the Florida form. Sickenberg emphasized the failure of the squamosal to reach up to the temporal crest in Protosiren, but this appears not to have been true in the Florida form. Though there is similarity in the shape of the pterygoid processes and lack of a pterygoid fossa, the presence of a large alisphenoid canal in Sickenberg's specimens is an important difference—not only from the Florida sirenians but also from the holotype skull (CGM C.10171), which Sickenberg apparently did not examine. This casts serious doubt on the identity of his referred material.

Specimens of Sickenberg's hypodigm other than "Stück V" show additional contrasts with the Florida material, chief of which is the absence or weak development of a bony falx cerebri, tentorium osseum, internal occipital protuberance, and transverse sulcus (Sickenberg, 1934, pl. 1: fig. 4). A similarly smooth-surfaced skullcap, also from the Mokattam area, is in the British Museum (BM(NH) M8154), and another from the Eocene of France was referred by Sickenberg (1934:189, 190) to Protosiren. An endocranial cast (Sickenberg, 1934, fig. 8), however, shows the frontoparietal suture perpendicular to the midline as in the Florida sirenians. The mandible described by Priem (1907) (Sickenberg's "Stück L") compares quite closely with the Florida mandibles, particularly the smallest one (TRO 509), in all respects. The M^3 of Sickenberg's "Protosiren" (1934:70, 71, fig. 10), however, is quite different

from TRO 518; the lingual cingulum is absent and the postcingulum and metaloph are different in form. Its outline is quadrilateral rather than tapered and rounded posteriorly. Sickenberg's specimen ("Stück XXXVIII"), however, is described as a "young animal," and the photograph (1934, pl. 1: fig. 8) suggests that the "M^3" is unerupted; hence we may question its identity as a third molar. Though similar in their lack of compact bone, the Florida vertebrae do not otherwise closely resemble those attributed to Protosiren by Sickenberg and show smooth ends without obvious reduction of epiphyses such as he describes.

We conclude that the Florida sirenians most closely resemble the holotype skull (CGM C.10171) of Protosiren fraasi, described by Andrews (1906), and the mandible described by Priem (1907). These latter may differ specifically, if not generically, from "Stück V" and other specimens referred to P. fraasi by Sickenberg (1934), which exhibit alisphenoid canals and smooth endocranial roofs.

?Protosiren minima (Desmarest, 1822) (= ?P. dubia (Cuvier, 1824); see Hooijer, 1952): Based on three isolated teeth from the Eocene of France (Sickenberg, 1934:190, 191, fig. 36), the affinities of this species are indeed dubious. They are somewhat larger than the Florida teeth, and the uppers lack lingual cingula, though their general shape and pattern are similar.

Discovery of good specimens of Eocene sea cows in France was reported by Freudenthal (1969). These were at first tentatively identified as Prototherium or Protosiren; however, examination by Heal (1973) and by one of us (Domning) confirms that they represent not Protosiren but a dugongid, probably Eotheroides. As they have not been formally described and in any case shed no light on the identity of the American specimens, they will not be further discussed here.

Eotheroides aegyptiacum (Owen, 1875a): This middle Eocene form from the Mokattam Hills of Egypt was described solely on the basis of a natural endocranial cast; hence all bones and teeth bearing this name are merely referred spec-

imens (Abel, 1912:308, 309). Abel, however, considered the type to be sufficiently diagnostic for "a certain identification" of his series of topotypic specimens, which included additional endocranial casts.

The endocranial casts illustrated by Owen and by Abel show the frontoparietal sutures diverging anteriorly rather than perpendicular to the midline as in the Florida sirenians.

The parietals and supraoccipital of *E. aegyptiacum*, though quite variably sculpted, are qualitatively similar to the Florida specimens, but they seem from Abel's account (1912) to fall short of the latter in degree of development of the massive, concave lambdoidal crest, median obstruction of the transverse sulcus, and (possibly) thickness of the skull roof. In contrast to other sirenians, probably (but questionably) including the Florida form, the foramen ovale is completely enclosed by bone. A large pterygoid fossa is present, and an alisphenoid canal is lacking, as in other dugongids. The ventral outline of the mandibular ramus resembles that seen in the Florida form, but the anterior symphyseal region of the latter (at least in TRO 509) seems too narrow to have supported the relatively broad symphyseal surface seen in the Egyptian dugongid (Abel, 1912, pl. 32: fig. 1; Andrews, 1906, fig. 67A). The M^3 of *E. aegyptiacum* shares the triangular shape of TRO 518, but a lingual cingulum and posterior basin are lacking. The vertebrae (Sickenberg, 1934) bear no close resemblance to the Florida specimens either in shape or in their relatively high proportion of compact bone, and none of the Florida ribs show quadratic cross-sections like those found in *Eotheroides*.

Eotheroides abeli (Sickenberg, 1934): This middle Eocene Egyptian species was founded on an isolated M^2, with a partial skull and other elements referred. It differs from *E. aegyptiacum* in such features as shorter parietals, higher supraoccipitals, and larger molars, differences which separate it still further from the Florida sirenians.

"Eotherium" majus Zdansky, 1938: This doubtful species from the Egyptian middle Eocene was based on an isolated upper molar, 22 mm long

and 23 mm wide, hence much larger than the Florida specimens. It also lacks a lingual obstruction of the transverse valley.

Eotheroides libycum (Andrews, 1902): This well-known dugongid from the Egyptian upper Eocene likewise differs clearly from the Florida form. Although the bony falx and tentorium osseum are well developed, the parietal roof is bilaterally convex rather than nearly smooth and lacks posterolateral indentations for the squamosals; the lambdoidal crest is not so prominently developed; and the external occipital protuberance is more prominent. A posteromedian depression of the frontal roof is lacking. A pterygoid fossa is present, and an alisphenoid canal absent. The mandibular symphyseal region is very broad and robust (Andrews, 1906, pl. 20: fig. 2; also YPM 38213), unlike the Waccasassa River specimens. The vertebrae show a greater proportion of compact bone, and the neural spines are more massive than in the latter (Sickenberg, 1934).

"Eotherium" stromeri Sickenberg, 1934: This late Eocene nominal species from Egypt was originally proposed by Abel (1912), who designated a type but provided no diagnosis or illustrations, which were not available until the work of Sickenberg (1934). The latter, therefore, rather than Abel, is the author of this name. The holotype is a skull and incomplete skeleton. The parietal roof is relatively short and wide, but otherwise this form closely resembles the other Egyptian dugongids and therein differs from the Florida sirenians.

Prototherium veronense (de Zigno, 1875): This dugongid is known from numerous specimens from the upper Eocene of Italy (Sickenberg, 1934) and is closely allied to *Eotheroides*. Like the latter, it exhibits a bony falx and internal occipital protuberance but lacks the striking development of the lambdoidal crest seen in the Florida skullcaps. It resembles these, however, in apparently lacking a pterygoid fossa as well as an alisphenoid canal. The zygomatic-orbital bridge of the maxilla lies well above the palatal plane, in contrast to the Waccasassa River specimens. The ventral border of the mandibular ramus does not turn down abruptly at the symphysis, and the sym-

physeal masticating surface is broad rather than anteriorly compressed. M^3, however, though relatively large, comes closest to the Florida specimens in having a precingulum developed only labially; a large, blunt protocone somewhat separated from the compressed protoconule and paracone; closely appressed metaconule and hypocone; and (occasionally) a deep posterior basin and lingual cuspules obstructing the transverse valley.

Paralitherium tarkanyense Kordos, 1977: This late Eocene form from Hungary, based on a pair of mandibles with vertebrae and ribs, is excluded from close relationship with the Florida sirenians by its larger size, more massive symphyseal region, dense vertebrae, and quadratic rib cross-sections.

Eocene Sirenians of Transylvania: Fragmentary sirenian remains have been known for over a century from middle and late Eocene rocks of Transylvania (Siebenbürgen), Romania, particularly from the region of Cluj (Klausenburg, Kolozsvár) (Sickenberg, 1934; Fuchs, 1970, 1973, and references therein cited). They have not been formally named but have been thought most closely comparable to *Eotheroides*, *Prototherium*, and *Halitherium*. The best specimen so far reported, a skull roof (Fuchs, 1970), somewhat resembles the Florida specimens in characters of the supraoccipital and the lambdoidal crest but has *Halitherium*-like temporal crests. The skull roof is only 18 mm thick, roughly half the thickness of the Florida specimens and indeed more comparable to *Halitherium*.

Post-Eocene Sirenians: Detailed comparisons with Oligocene and later forms are unnecessary, as none bears a close resemblance to the Florida Eocene specimens. *Halitherium schinzi* from the Oligocene of Europe occasionally shows a similar development of the lambdoidal crest (e.g., MCZ 8829), but thinness of the skull roof, form of the temporal crests, and other features set it well apart from the Florida sirenians. The same is true of *Metaxytherium*, *Trichechus*, and all other later forms, with which there is no danger of confusion.

We conclude that the sirenians from the Avon Park Limestone and Inglis Formation of Florida most closely resemble, and are probably congeneric with, *Protosiren fraasi* from the middle Eocene of Egypt. The Florida sirenians are therefore referred to *Protosiren* species.

North Carolina Eocene Sirenians

DESCRIPTION

The identifiable elements of the North Carolina sirenians complement those of the Florida sea cows almost to the bone. The only bones common to the two samples are ribs, vertebrae, the symphyseal portion of the mandible, and the skullcap (represented in North Carolina by a single isolated specimen). The North Carolina specimens are as follows:

Locality 18 (Martin Marietta quarry, New Hanover County, North Carolina)
    USNM 307609: parietal-supraoccipital skullcap
Locality 21 (Comfort quarry, Jones County, North Carolina)
    USNM 214596: mandible lacking posterior parts of both rami; right P_{3-4}, DP_5, M_1, parts of M_{2-3} and left M_{1-2}; left M_3; left two-thirds of atlas; part of left side of axis; right side of ?first thoracic vertebra; 1 complete posterior thoracic vertebra and fragments of at least 2 more; 5 incomplete post-thoracic vertebrae; 13 rib fragments including parts of at least 3 right and 6 left ribs; fragments of both scapulae; proximal ends of right humerus and ulna; fragment of ?left innominate
    USNM 214597: left M^1 or M^2
    USNM 244491: distal end of right humerus
    USNM 244494-5: lateral portions of atlas
    USNM 244496: partial left periotic
    USNM 256686: fragment of right squamosal
    Numerous uncatalogued rib fragments

PARIETAL-SUPRAOCCIPITAL SKULLCAP (USNM 307609, Figure 18).—Parietals widest (55 mm) at forward edge of parietal-squamosal suture, narrowest (43 mm) just abaft frontoparietal suture; length in dorsal midline about 66 mm, overall length 81 mm. Lambdoidal crest less prominent than in most of the Florida specimens. Lateral indentations for squamosals deep and conspicuous; squamosals reached almost to level of skull roof. Skull roof bilaterally convex with median groove extending entire length of parietals. Tem-
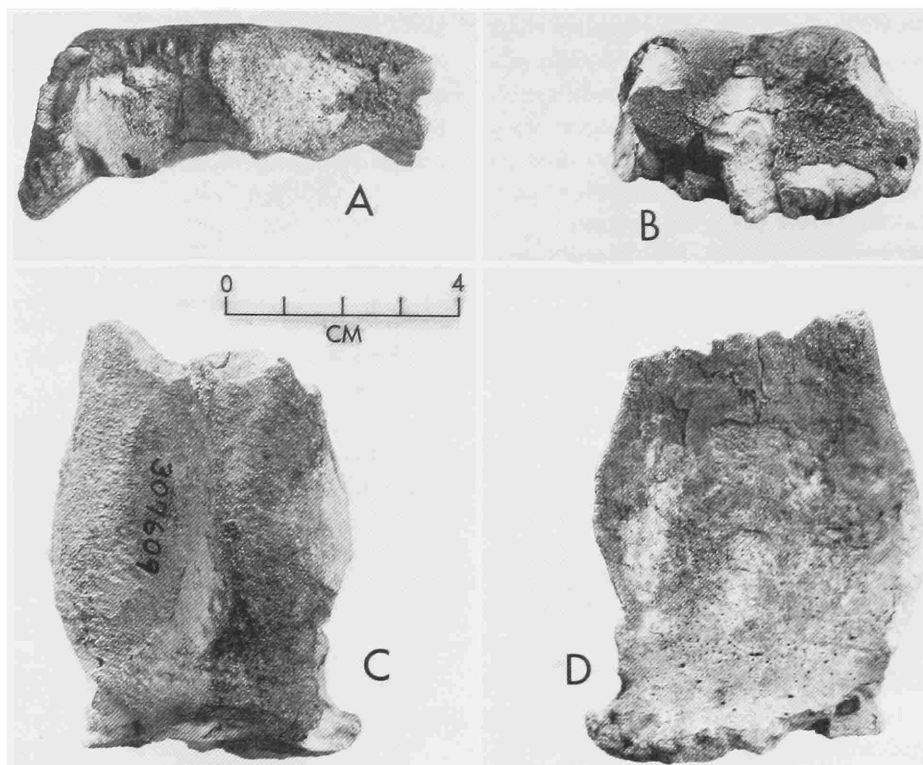
FIGURE 18.—Parietal-supraoccipital skullcap of *Protosiren* species from North Carolina (USNM 307609): A, right lateral aspect; B, posterior aspect; C, dorsal aspect; D, ventral (internal) aspect.

poral crests absent. Lateral walls of braincase meet skull roof at slightly more than right angles, sloping somewhat ventrolaterally. Roof 21 mm thick in midline at frontoparietal suture, 22 mm at parietal-supraoccipital suture. Bony falx cerebri merely a slight median convexity; internal occipital protuberance weak; transverse sulcus and tentorium osseum nearly absent. Internal surface of parietals and supraoccipital pierced by numerous tiny foramina. Supraoccipital 35 to 40 mm high, slightly broader than parietals (estimated width 58 mm), roughly elliptical in outline. Surface of supraoccipital moderately concave, with weak external occipital protuberance and median ridge; lateral and ventral borders damaged, not markedly thickened (about 8 mm in ventral midline). Semispinalis muscle scars not distinctly developed. Parietals and supraoccipital form angle of 115°.

SQUAMOSAL (USNM 256686).—Includes part of root of zygomatic process, area of glenoid facet (which lacks distinct boundaries), and anterior end of socket for periotic. Postglenoid fossa very shallow. Ridge extending anterolaterad from broken postglenoid process short and abruptly sloping. Posterodorsal edge of zygomatic process gently sloping, its posterior end missing.

PERIOTIC (USNM 244496, Figure 19).—Anterior part of pars temporalis (= tegmen tympani) and most of pars petrosa (= pars labyrinthica) missing. Convexity of dorsal surface of pars temporalis continues posteriorly onto pars mastoidea, ending (as in *Dugong*) at a broad, shallow groove passing posterolaterad across dorsal surface of latter. Groove ends in rugose area, which includes a prominent foramen and lies anteromedial to dorsal end of exposed portion of pars mastoidea (processus fonticulus of Sickenberg, 1934:59).
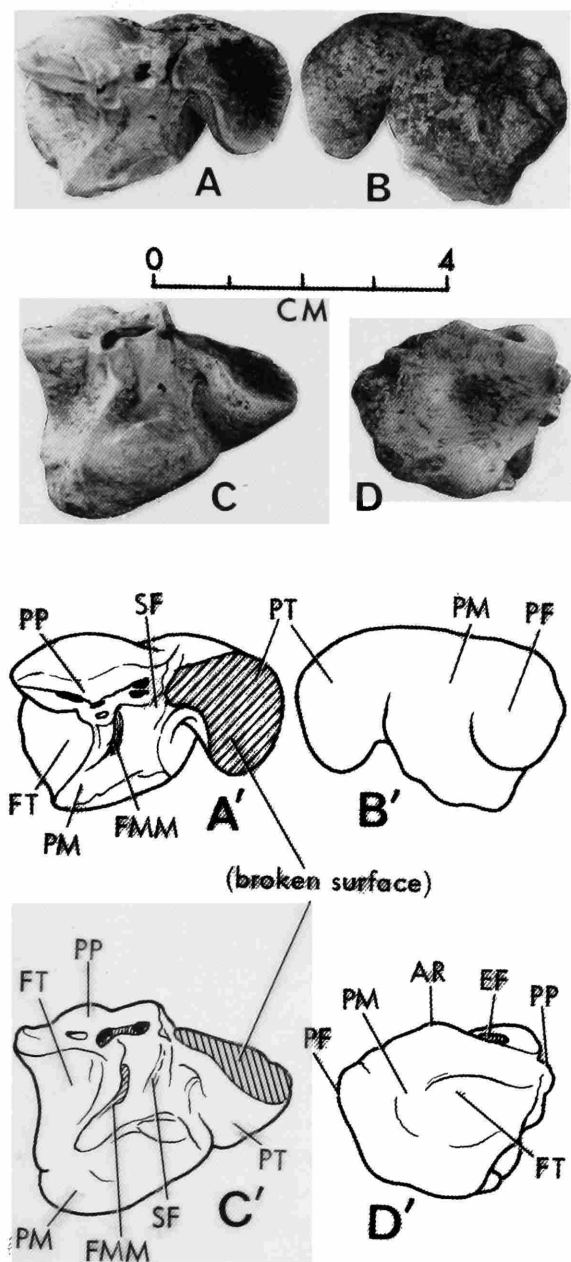
FIGURE 19.—Partial left periotic of *Protosiren* species from North Carolina (USNM 244496): a, a′, medial aspect; b, b′, lateral aspect; c, c′, ventral aspect; d, d′, posterior aspect. (AR = "arête du rocher," EF = endolymphatic foramen, FMM = fossa muscularis minor, FT = fovea triangularis, PF = processus fonticulus, PM = pars mastoidea, PP = pars petrosa (= pars labyrinthica), PT = pars temporalis (= tegmen tympani), SF = sulcus facialis.)

Latter portion forms low, irregular rugosity, somewhat elliptical in lateral view, its anterior part concave, and its posterior part roughly convex, and covering posterior half of lateral side of pars mastoidea. Groove on dorsal side of latter paralleled by a distinct ridge ("arête du rocher" of Robineau, 1969, fig. 4a). Posterior side of pars mastoidea irregularly convex laterally; medially a broadly concave triangular area (fovea triangularis of Abel, 1912, fig. 3) lies beneath overhanging posterior edge of pars petrosa. Ventral end of pars mastoidea curves smoothly inward. Ventrally, pars mastoidea separated from pars temporalis by deep V-shaped cleft, continued onto lateral surface of periotic by a shallow groove. Fossa muscularis minor (for origin of M. stapedius) deep, well marked, somewhat triangular; a very shallow but distinct sulcus facialis is visible anterior to it, passing anteromediad. Endolymphatic foramen well developed. Pars petrosa broken away just lateral to promontory. Anterior edge of pars petrosa laterally forms thin horizontal sheet closely applied to dorsal side of pars temporalis. Height of pars mastoidea from "arête du rocher" to ventral end = 26 mm; maximum dorsoventral thickness of pars temporalis at broken surface = 17 mm.

MANDIBLE (USNM 214596, Figures 20–22).— Symphysis solidly fused, but deep cleft persists ventrally. Masticating surface of symphysis very narrow (16 mm at I_1 alveolus), rugose, without median ridge, and deflected 35° to 40° from occlusal plane. Anterior half of symphysis strongly compressed laterally; symphysis widens posteriorly but without becoming conspicuously bulbous posteroventrally as in *Eotheroides libycum* (Andrews, 1906, pl. 20: fig. 2a). Length of symphysis 72 mm, height 55 mm. Ventral outline ascends abruptly at rear of symphysis, initially passing upward perpendicular to direction of ventral border of horizontal ramus. Large mental foramen (just below canine alveolus) and a single accessory foramen present on each side. At point of divergence of alveolar rows at rear of symphyseal masticating surface, a median foramen passes anteroventrad along suture. Abaft this, dorsal
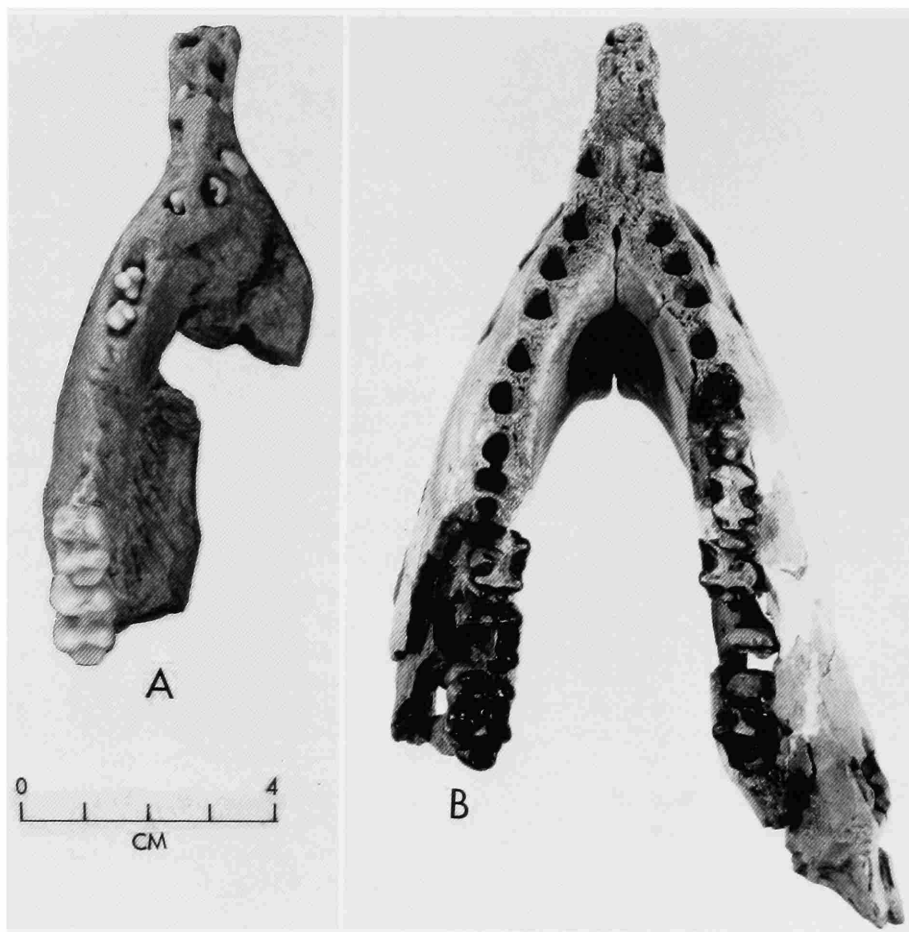
FIGURE 20.—Mandibles of *Protosiren* in occlusal aspect: A, *Protosiren fraasi* from Egypt (USNM 244490, cast); B, *Protosiren* species from North Carolina (USNM 214596).

surface of symphysis curves downward to form thick lip overhanging mental fossa. Latter is broad and well developed but only some 4 mm deep, with a gently convex anteroventral floor. Height of horizontal ramus at P_4 alveolus 37 mm.

DENTITION (USNM 214596, Figure 23, Table 4).—Lower dentition consists of 3.1.5.3. Alveoli of I_1 lie 20 mm from tip of mandible and are separated by 5 mm in midline. I_2 and I_3 alveoli follow after diastemata of about 9 mm each. Canine alveoli closely follow those of I_3 and are separated in midline by 16 mm. Alveoli of P_1 (or DP_1) are likewise close behind those of C but are separated from those of P_2 by 4 mm; subsequent alveoli follow at closer intervals. All alveoli are

deep and well developed. I_1–P_4 are single rooted, DP_5–M_3 double rooted. M_3 is separated by 10 mm from rear of coronoid canal, and dental capsule has atrophied somewhat, indicating (with wear on M_3) adulthood; however, X-ray examination failed to disclose the presence of an unerupted P_5 on either side.

P_3: Bears a single high labial cusp, curved inward at tip, and almost unworn. A much smaller anterolingual and a still smaller posterolingual cusp flank it; between these latter, a crest descends steeply from middle of lingual side of principal cusp and curves past base of posterolingual cusp to form low posterior cingulum. Two
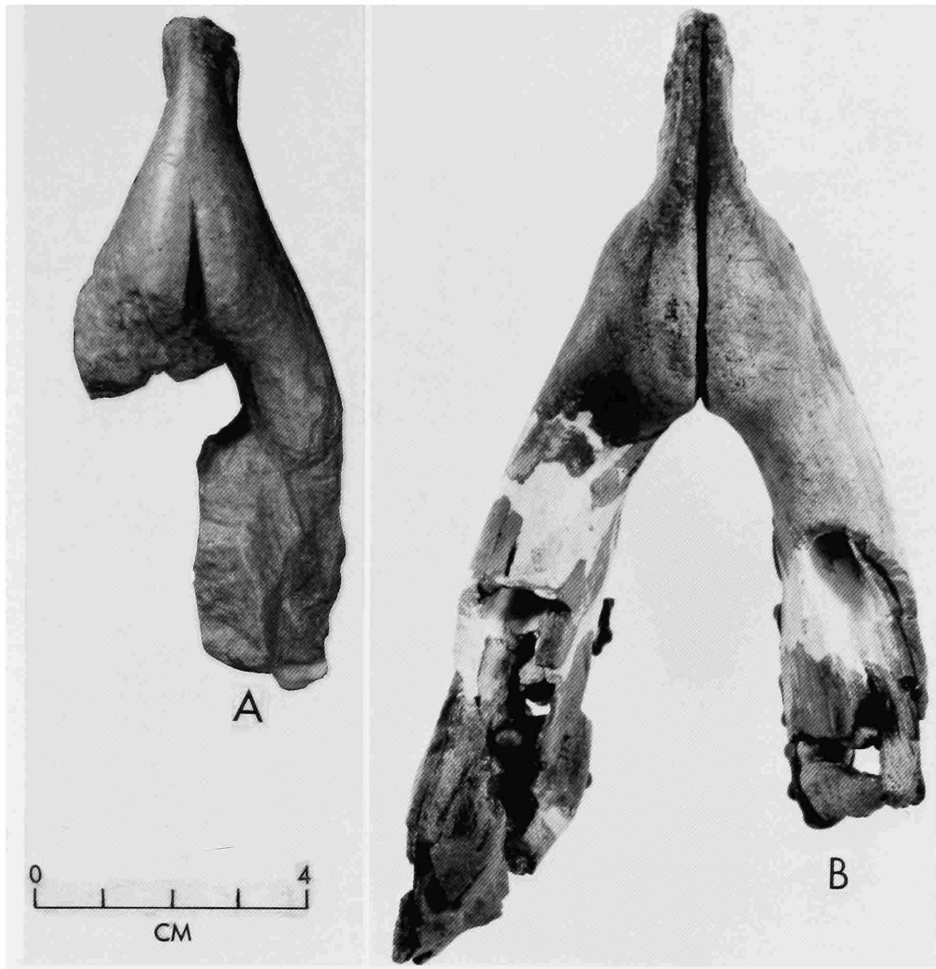
FIGURE 21.—Mandibles of *Protosiren* in ventral aspect: A, *Protosiren fraasi* from Egypt (USNM 244490, cast); B, *Protosiren* species from North Carolina (USNM 214596).

tiny cuspules form anterior cingulum. Root sub-circular in cross section.

P₄: Bears a high labial cusp like that of P₃, enamel slightly breached by wear at tip. A smaller cusp lies directly lingual to it; from tip of latter a ridge descends steeply anterolabiad and then anterad to join highest point of low anterior cingulum. Behind these 2 cusps lies a pair of smaller, subequal cusps, the more lingual lying at edge of crown and forming highest point of minutely cuspate posterior cingulum enclosing the more labial cusp. Root oval, elongate anteroposteriorly, in cross-section.

DP₅: Heavily worn, both lophids and hypoconulid lophule forming a single confluent lake of dentine.

M₁: Likewise heavily worn; broken on both sides. Lingual cusps much higher than labial on all molars, as shown for *Protosiren* by Sickenberg (1934, fig. 11b).

M₂: Broken on both sides. Tips of lingual cusps almost unworn, labial portions of lophids worn. Labiad-descending crest on anterior side of crown ("vorderes Basalband") resembles that seen in *Halitherium christoli* (Abel, 1904, fig. 20) and *Eotheroides abeli* (Abel, 1912, pl. 5: fig. 1).
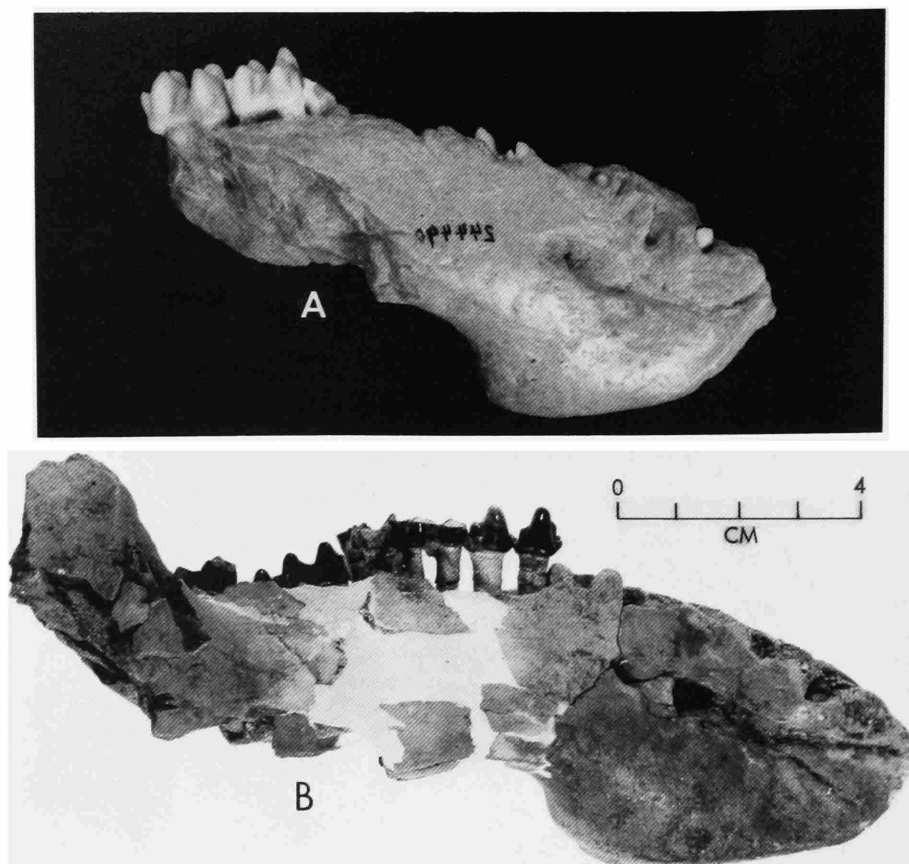
FIGURE 22.—Mandibles of *Protosiren* (A, left lateral aspect, reversed; B, right lateral aspect): A, *Protosiren fraasi* from Egypt (USNM 244490, cast); B, *Protosiren* species from North Carolina (USNM 214596).

Shallow basin present on crest of protolophid between metaconid and protoconid. Transverse valley largely obstructed by indistinctly developed crista obliqua. Hypoconulid lophule small, with single cusp at labial end connected to middle of metalophid by short crest.

M_3: Slightly worn. "Vorderes Basalband" and basin on crest of protolophid like those of M_2. Crista obliqua forms not a distinct crest but a low, bulbous protrusion of metalophid into transverse valley. Hypoconulid lophule prominent, consisting of a single large pointed cusp with somewhat sharpened lingual edge; connected to middle of metalophid by low crest. Anterior root anteroposteriorly flattened, like

roots of other molariform teeth; 27 mm long. Posterior root much larger, longer fore-and-aft than wide, sigmoidal and slightly tapering apically; 24 mm long. Both roots completely closed.

M^1 or M^2 (USNM 214597, Figure 24, Table 4): Moderately worn; posterior interdental wear facet present. Anterior cingulum a simple, non-cuspate ridge, highest at center, contacted lingually by basal swelling of protocone. Protoconule evenly spaced between paracone and larger (but heavily worn) protocone. Transverse valley open. Metaconule appressed to hypocone; from tip of former a ridge (sharpened by wear and forming top edge of anterolabially descending wear facet) descends to intersect anterior side of

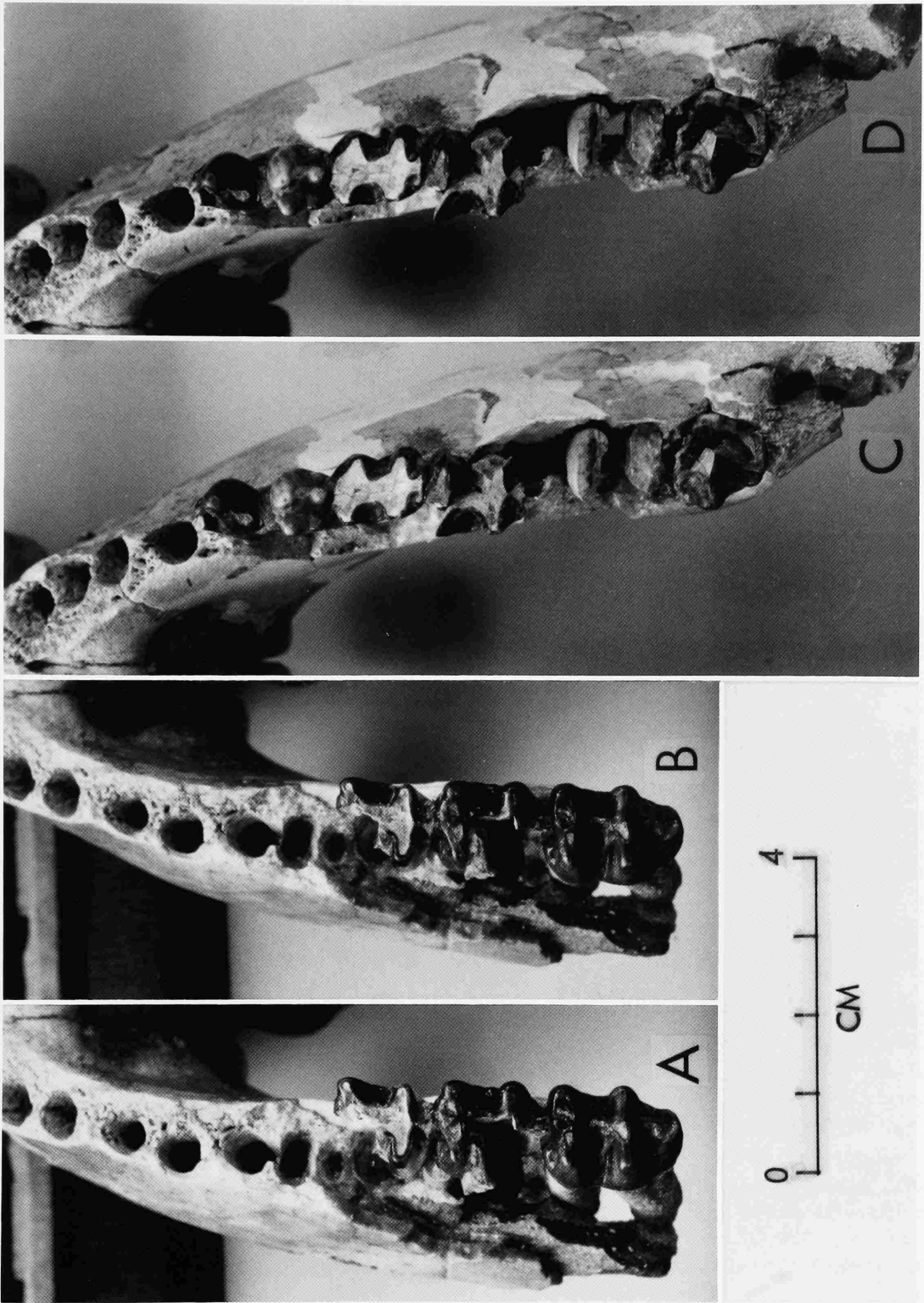FIGURE 23.—Stereophotographs of lower dentition of *Protosiren* species from North Carolina in occlusal aspect (USNM 214596): A, B, left M_1–M_3; C, D, right P_3–M_3.
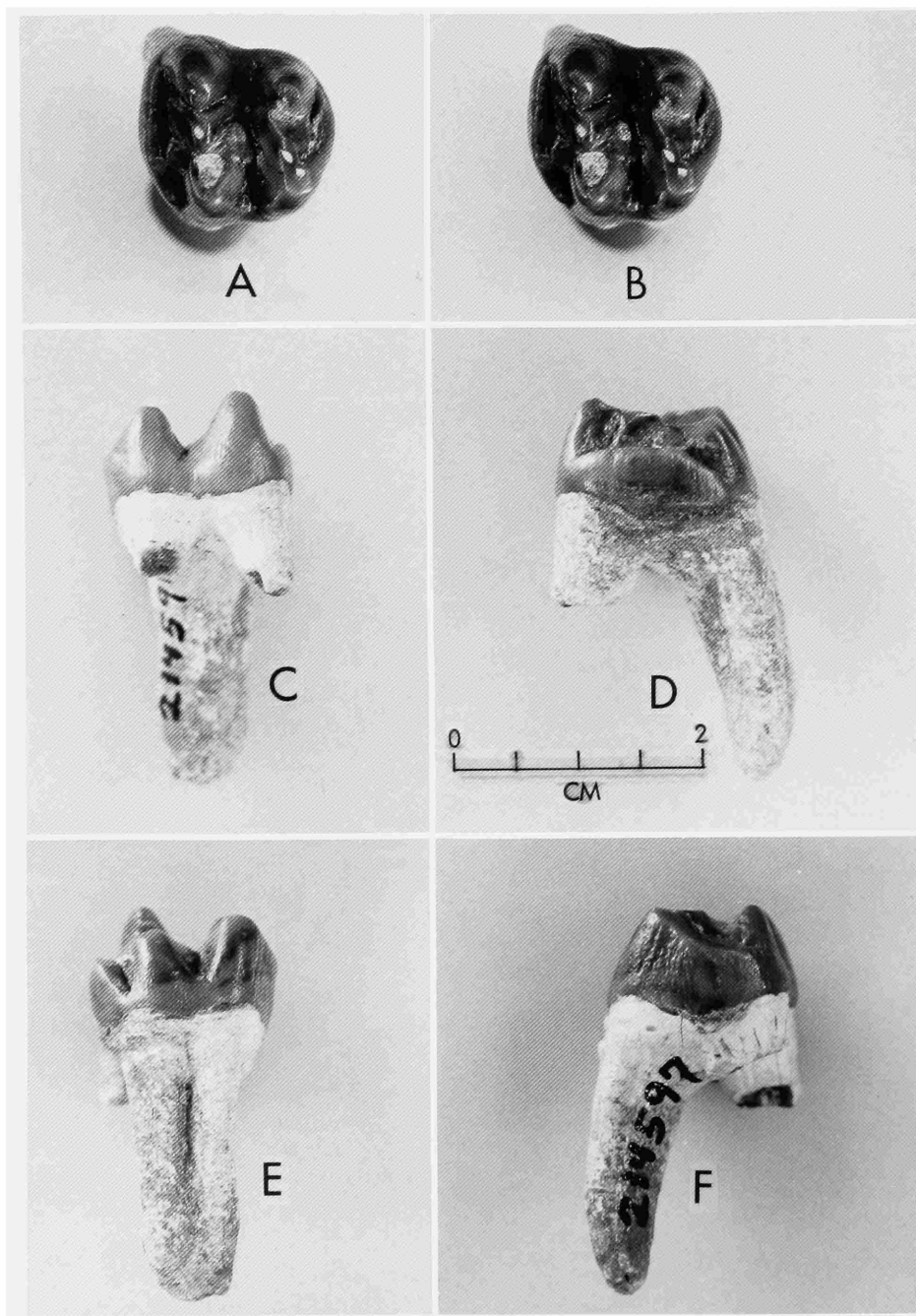
FIGURE 24.—Left M¹ or M² of *Protosiren* species from North Carolina (USNM 214597): A, B, occlusal aspect, anterior to left (stereophotograph); C, labial aspect; D, anterior aspect; E, lingual aspect; F, posterior aspect.

TABLE 4.—Dental measurements (mm) of North Carolina Eocene sirenians (L = crown length, AW = anterior width, PW = posterior width, w = affected by extreme wear, e = estimated, a = alveolar)

Tooth	L	AW	PW
USNM 214597			
Left M^1 or M^2	16.3	16.7	15.1
USNM 214596			
Right P_3	9.0	7.4	
Right P_4	9.7	8.4	–
Right DP_5	12.1w	8.8	9.2
Left M_1	13.4e	–	10.0
Left M_2	14.5	11.7	–
Right M_2	–	–	11.5
Left M_3	18.6	12.2	11.3
Right I_{1-3}	34.6a		
Right $C-M_3$	96.3a		
Right P_1-M_3	90.2a		
Right M_1-M_3	43.5		
Left M_1-M_3	45.4		

metacone at middle of latter's height. From tip of hypocone a thick crest descends across rear of crown, enclosing a narrow, shallow posterior basin. Two labial roots broken; large lingual root 24 mm long, closed, with prominent groove down lingual side.

ATLAS.—USNM 214596 (Figure 25A,C): Dorsal arch robust, topped by single rounded protuberance, without ridges or other sculpturing. Ventral arch thinner, with very weak ventral keel prolonged into irregular posterior process. Dorsal side of arch bears concave depression 21 mm wide for articulation with odontoid process of axis. Anterior cotyle rather deeply concave, with thick, prominent lateral edges and deeply embayed medial edge of articular surface; at level of tubercle for transverse ligament, medial edge of surface lies 15 mm anterolateral to tip of tubercle, and surface itself is 16 mm wide at this point. Arterial canal dorsal to anterior cotyle deep but not bridged over. Posterior cotyle flatter, with broadest part ventral to tubercle for transverse ligament; ventromedial part of articular surface abruptly narrows and turns mediad along rear of ventral arch, reaching level of edge of facet for odontoid process. Transverse process robust and

knoblike dorsally, compressed in posteroventrad-aligned plane; large vertebrarterial canal passes less steeply posteroventrad.

USNM 244494, 244495 (Figure 25B,D): Only lateral portions of atlas preserved; larger than that of USNM 214596. Articular surface of anterior cotyle interrupted by narrow extension of medial embayment, reaching to within 12 mm of lateral edge; total width of cotyle approximately 21 mm at this point (level of tubercle for transverse ligament). Arterial canal dorsal to anterior cotyle was probably bridged. Posterior cotyle as described above. Transverse process with more rugose edge than in USNM 214596; vertebrarterial canal absent on both sides.

AXIS (USNM 214596).—Only left side of centrum and neural arch preserved; resembles other sirenians in structure. Dorsal and smaller ventral arches of vertebrarterial canal broken at roots; unclear whether canal was bridged.

THORACIC VERTEBRAE (USNM 214596, Figure 26).—An anterior, probably first or second, thoracic lacks left part of centrum and transverse process, and tip of neural spine. Centrum is square in sagittal section, composed of cancellous bone, and bears anterior and posterior demifacets. Neural spine dense, inclined backward slightly, but its bulk lies directly above centrum. Cross-section of neural spine at its base resembles that at tip of T2 of *Eotheroides aegyptiacum* (Sickenberg, 1934, fig. 3b) but is more elongated, with sharper projections at posterior corners that may answer to the "Lappen- oder Flügelbildung" described by Sickenberg. Transverse process very massive; greatest transverse breadth of vertebra at level of top of centrum.

A complete posterior thoracic (Figure 27) is preserved. Centrum large relative to neural arch, 45 mm thick, with broadly heart-shaped ends (58 mm wide, 44 mm high), wide, flat ventral keel, and concave sides. Epiphyses thin but fully developed. Articular facets for capitulum and tuberculum of rib not quite confluent. Neural canal small (19 mm wide, 17 mm high), apex pointed but not slitlike. Anterior side of neural arch exhibits broad furrows with thin median crests con-
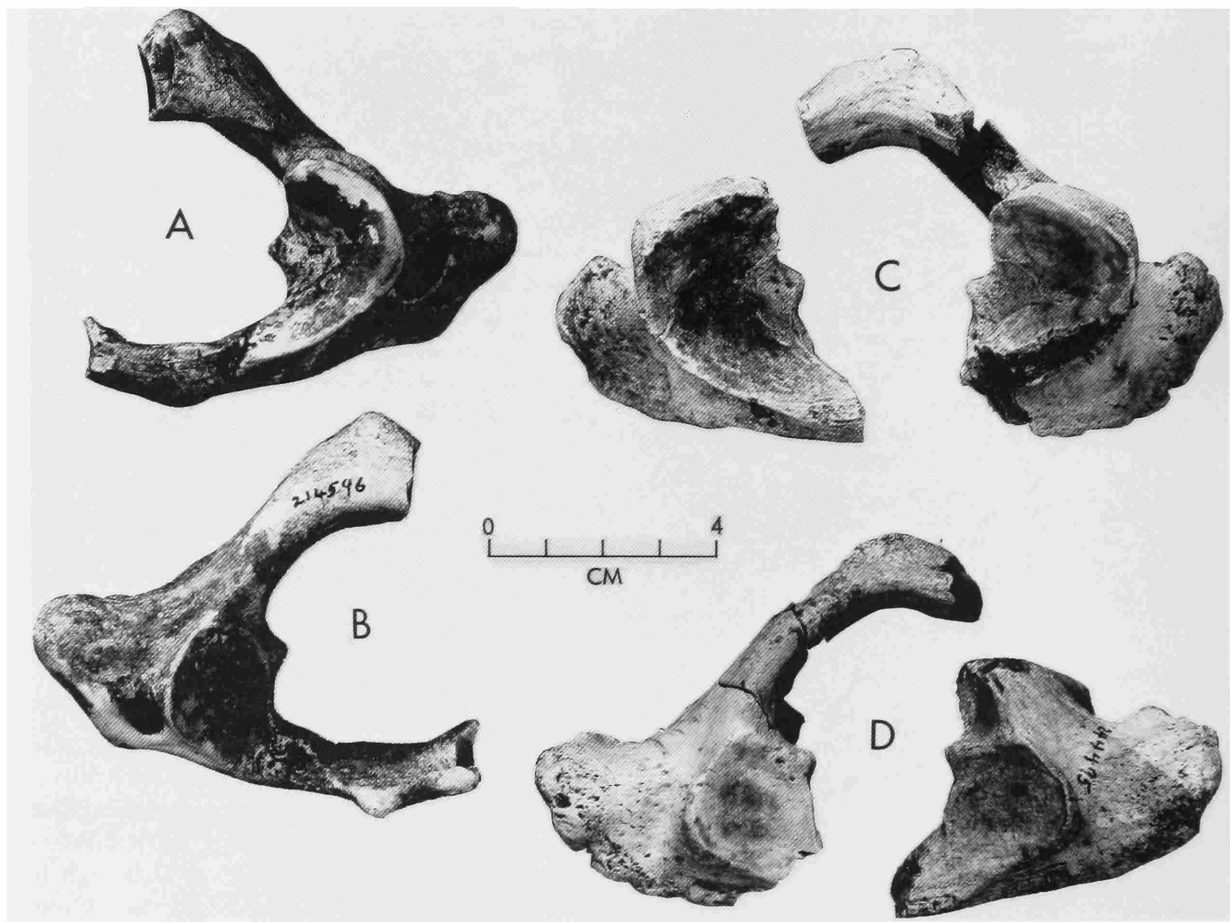
FIGURE 25.—Partial atlases of *Protosiren* species from North Carolina in anterior (A, C) and posterior (B, D) aspects: A, B, USNM 214596; C, USNM 244495 (left) and USNM 244494 (right); D, USNM 244494 (left) and USNM 244495 (right).

verging from either prezygapophysis to join at midline of vertebra (for attachment of ligamentum flavum). Neural spine slightly inclined backward, thicker (14 mm) posteriorly, with sharp anterior and posterior edges, 40 mm long anteroposteriorly. Total height of vertebra 119 mm, transverse breadth 79 mm; anteroposterior length of zygapophyses 61 mm.

Isolated neural spines of other vertebrae variable: one is somewhat swollen posteriorly near dorsal end, with flangelike posterior edges and a low posterior median ridge; another is strikingly swollen near dorsal end, with more prolonged

posterior edge on left but no other ridges or flanges on posterior side.

POST-THORACIC VERTEBRAE (USNM 214596).— A probable first lumbar vertebra is represented by left side of centrum with incompletely fused transverse process. Prezygapophysis well developed; presumed postzygapophysis simple, without distinct articular surface, and located very low on neural arch (evidently below dorsal side of centrum) as described for *Protosiren* (Sickenberg, 1934:85). Transverse process 87 mm long, separated from centrum by broad, deep cleft on posteroventral side; tapers distally and turns sharply posteroventrad at tip. A low ridge, possi-

FIGURE 26.—Partial anterior thoracic vertebra of *Protosiren* species from North Carolina in anterior aspect (USNM 214596).

bly for tendon attachment, passes posterolaterad across middle of ventral side of process. Other fragments of post-thoracic vertebrae show no differences from typical dugongids; thin epiphyses are present as on thoracic vertebrae, and centra are hexagonal in end view.

RIBS (USNM 214596, Figures 28, 29).—Two complete ribs of this specimen are preserved. Neck of left second or third rib inflected posterad; thick dorsoventrally, flattened ventrally, with high semi-circular cross-section. Capitular facets distinct but contiguous; anterior facet elliptical, slightly convex; posterior facet more elongated, convex mediolaterally but flatter anteroposteriorly. Tuberculum elevated, with C-shaped facet opening anteromediad; shallow, irregular ligamentary fossa lies lateral to tuberculum. Shaft
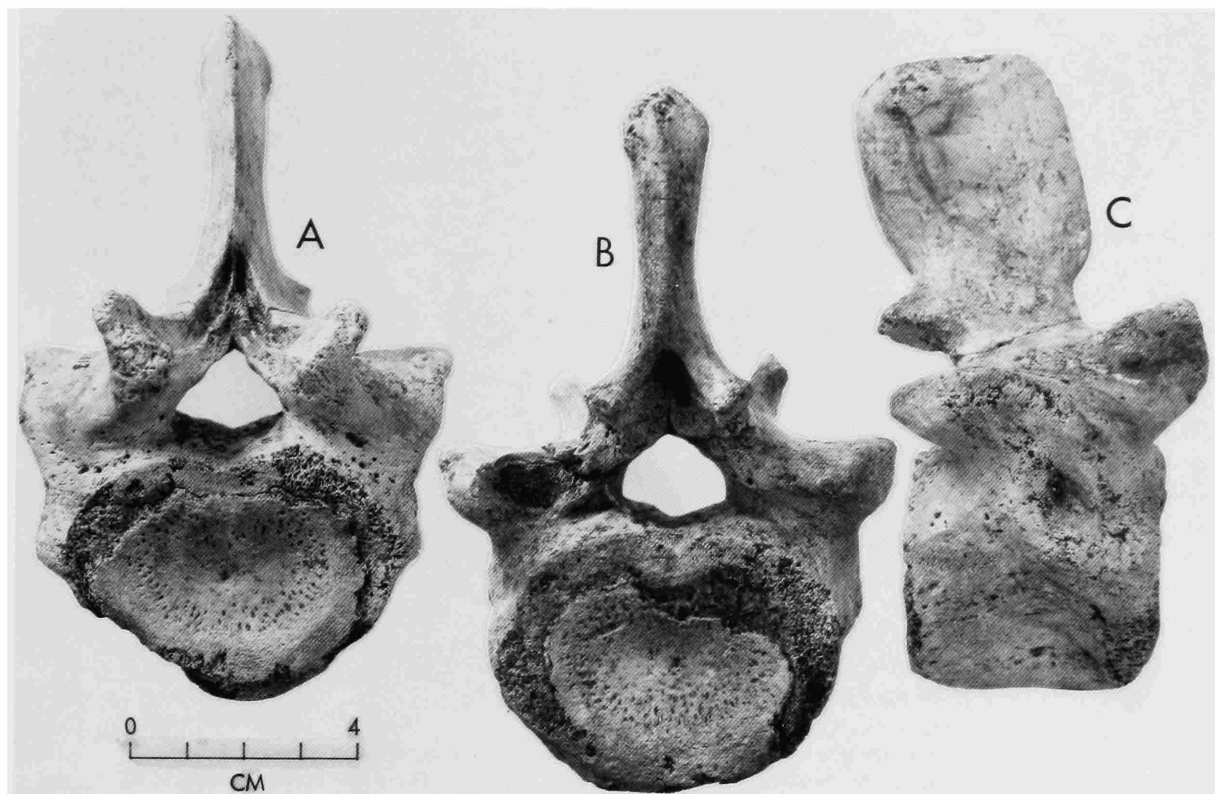

FIGURE 27.—Posterior thoracic vertebra of *Protosiren* species from North Carolina (USNM 214596): A, anterior aspect; B, posterior aspect; C, right lateral aspect.
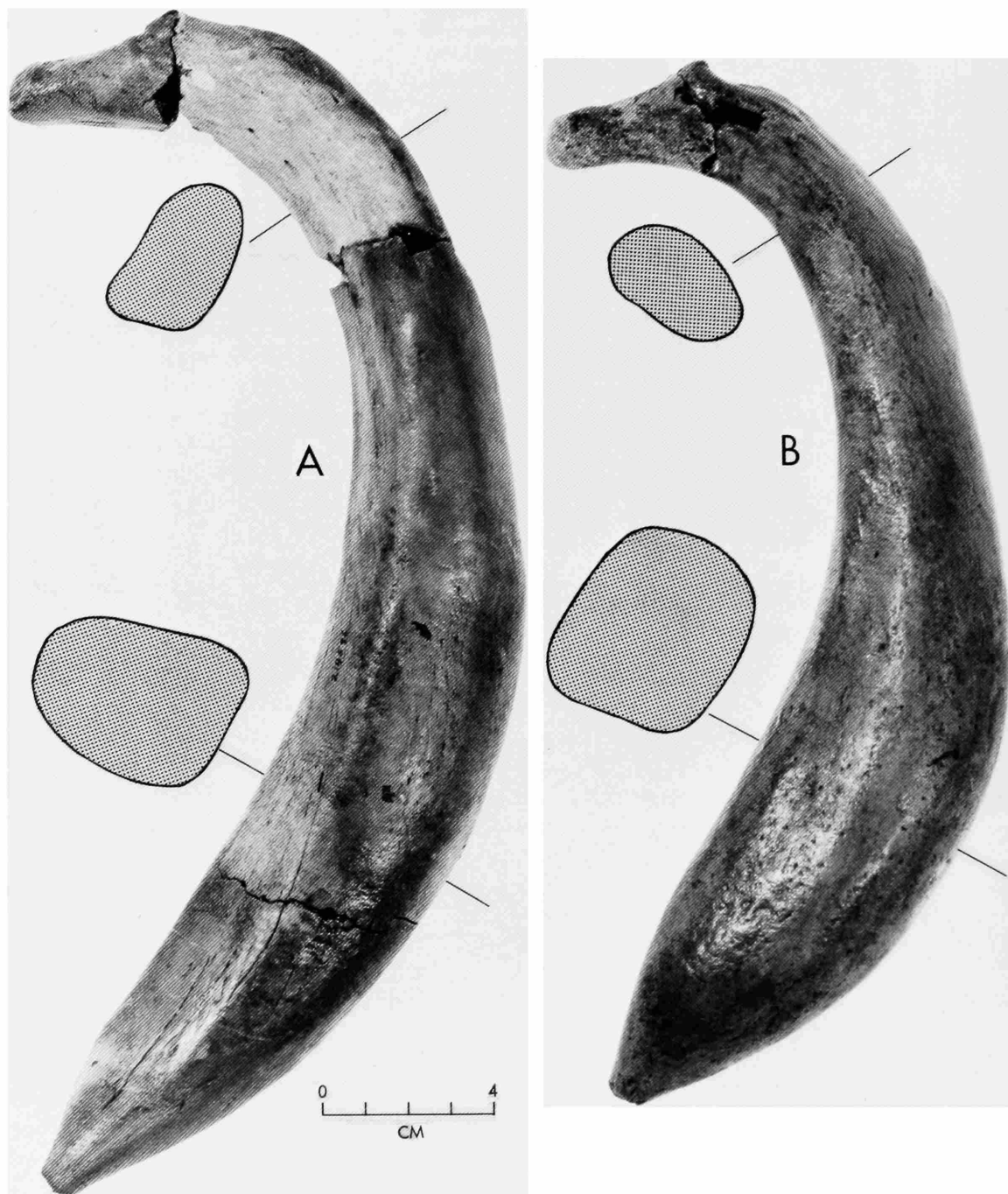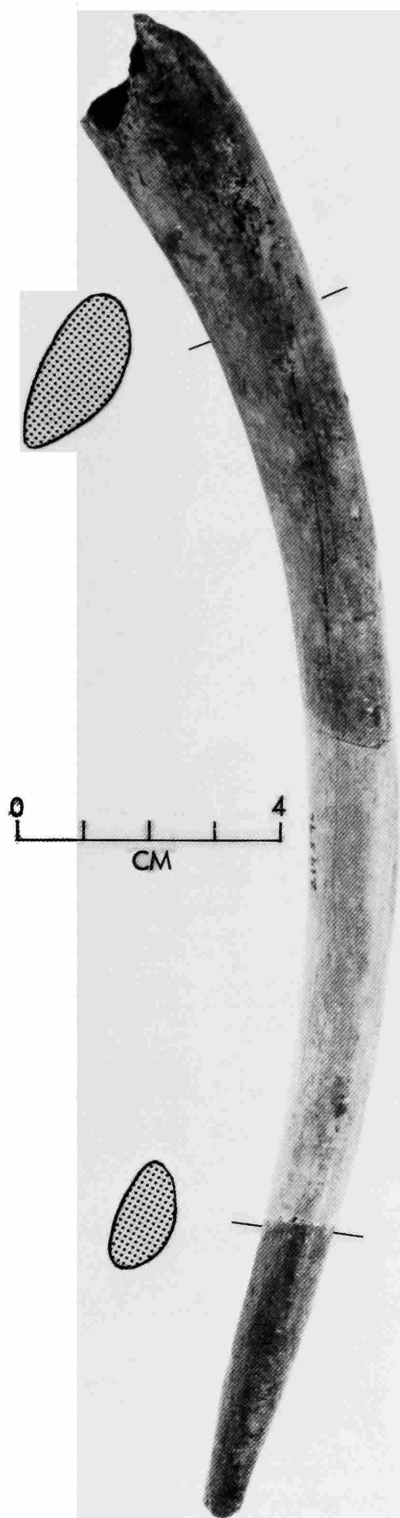
FIGURE 28.—Anterior ribs of *Protosiren* species from North Carolina, showing cross-sections at positions indicated by lines (USNM 214596): A, right 3rd or 4th rib; B, left 2nd or 3rd rib.

somewhat flattened proximally but thick, with anterolateral and posteromedial surfaces broadest. These maintain their widths distally, the latter coming to face more posterad; anteromedial and posterolateral surfaces, however, broaden abruptly beyond middle of shaft to form greatly swollen distal half of rib with quadratic cross-section (greatest diameters 52×49 mm). Anteromedial and posteromedial sides flatter than others, hence medial corner of cross-section somewhat sharper than lateral. Posteromedial side bears 2 prominent foramina proximally and numerous fine parallel furrows for blood vessels distally. Angle of rib indistinct. Distal end of rib banana-shaped, tapering abruptly to small apical area for attachment of costal cartilage.

Neck of right third or fourth rib wider and flatter; capitular facets subequal, roughly semicircular; tuberculum less prominent, with smaller facet; ligamentary fossa deeper. Shaft similar in shape to that described above, but anteromedial side distinctly broadened, even proximal to angle. Greatest diameters 50×44 mm. Posteromedial side bears foramina and furrows as described above. Distal end tapers less abruptly; tip curved backward, bears facet for attachment of cartilage as above.

Fragments of proximal ends of remaining ribs all show distinct tubercular facets; ventral sides of necks noticeably flattened; shallow irregular depressions lie lateral to capitular facets on dorsal sides. Distal ends retain swollen, quadratic shape on some ribs abaft those connected to sternum, but more posterior ones have semicircular distal cross-sections with flat medial sides, while posteromost ribs become quite slender, flat (27×14 mm), and gently tapering distally (Figure 29). All ribs wholly composed of compact bone.

SCAPULA (USNM 214596).—Glenoid fossa deeply concave fore-and-aft, less so transversely; roughly triangular, apex lateral; 31 mm wide, 38 mm long measured from external sides of its borders. Coracoid process simple, blunt, slightly

FIGURE 29.—Partial posterior rib, lacking head, of *Protosiren* species from North Carolina, showing cross-sections at positions indicated by lines (USNM 214596).

deflected mediad; distal end of scapula 42 mm long including coracoid process. Spine extends to within 25 mm of glenoid fossa. Supraspinous and infraspinous fossae gently concave; anterior border sharp, posterior thicker and blunter. Medial side of scapula flat. Posterior vertebral corner of right scapula shows "teres major protuberance" 4 cm distal to corner and well-developed area for attachment of cartilage along vertebral border.

HUMERUS.—USNM 214596 (Figure 30): Proximal end of right humerus lacks articular surface of head and summit of greater tubercle; epiphysis of former may have been unfused. Greatest proximal width 51 mm. Anterolateral surface of greater tubercle smooth, aligned strongly anteromediad; deltoid crest not pronounced or rugose, very similar to that of juvenile *Eotheroides aegyptiacum* illustrated by Sickenberg (1934, fig. 4). Lesser tubercle well developed, irregularly rounded. Bicipital groove deep, narrow. Angle between center of head and extremities of tubercles at sides of bicipital groove = 35°–40° (cf. Sickenberg, 1934:29, 30). Groove turns posteriorly through sulcus intertubercularis into central cul-de-sac of proximal end, bordered by head and tubercles; distal part of groove and proximal cul-de-sac correspond to "vertical" and "horizontal" parts, respectively, of bicipital groove described by Sickenberg (1934:30). This and the following fragment both completely of compact bone.

USNM 244491 (Figure 31): Distal end of right humerus 64 mm wide, has extremely massive entepicondyle reaching as far distad as lateral extremity of trochlea. Trochlea some 41 mm wide anteriorly, inclined at angle of approximately 75° to humeral shaft. Anterolateral surface of trochlea shows severe pitting, perhaps pathological, extending into deep coronoid fossa. Olecranon fossa likewise very deep. Tuberosity for insertion of M. pectoralis major, on anterior side proximal to trochlea, extraordinarily large; a smaller protuberance lies proximolateral and posterior to it. Entocondyloid crest broadly rounded, ectocondyloid somewhat sharper; sagittal diameter of shaft considerably exceeds transverse diameter.

ULNA (USNM 214596, Figure 32).—Proximal

end differs strikingly from those of other sirenians; olecranon aligned coaxially with shaft; outline of posterior edge convex at level of semilunar notch; lateral side has broad, deep longitudinal groove from olecranon to middle of shaft. Summit of olecranon expanded, sloped laterad. Medial side faces posteromediad, gently convex on olecranon, gently concave at middle of shaft. Greatest anteroposterior thickness of olecranon (at upper lip

FIGURE 30.—Proximal part of right humerus of *Protosiren* species from North Carolina (USNM 214596): A, proximal aspect of head, anterior upward; B, anteromedial aspect.
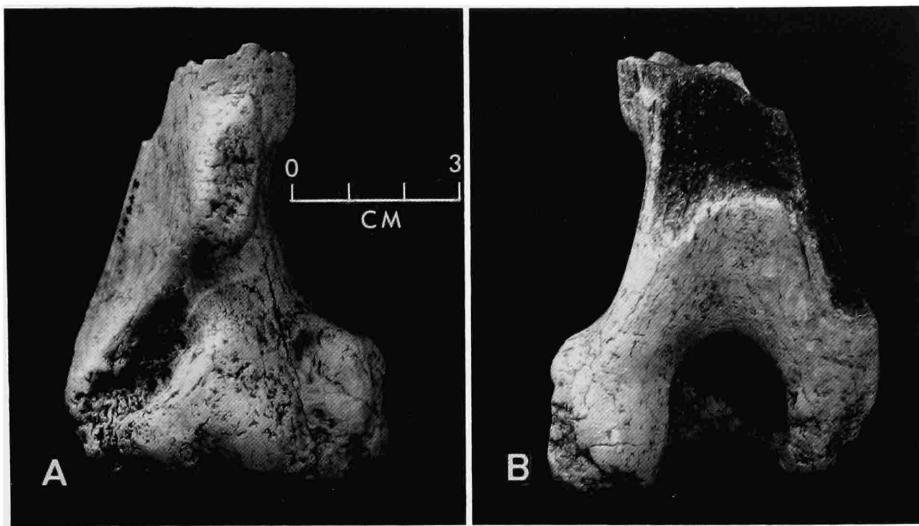
FIGURE 31.—Distal part of right humerus of *Protosiren* species from North Carolina (USNM 244491): A, anterior aspect; B, posterior aspect.
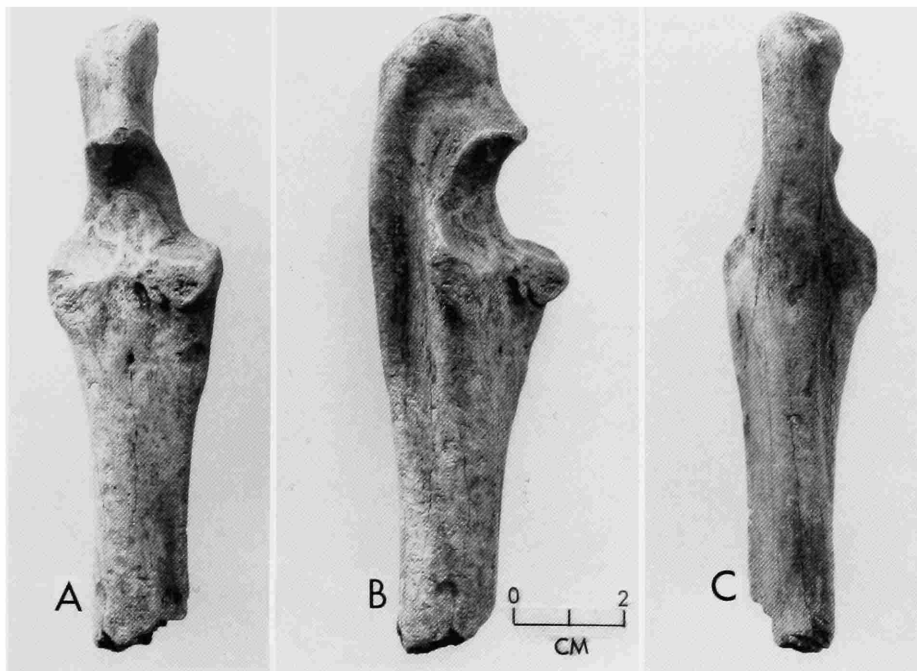

FIGURE 32.—Proximal part of right ulna of *Protosiren* species from North Carolina (USNM 214596): A, anterior aspect; B, lateral aspect; C, posterior aspect.

of semilunar notch) 29 mm; thickness at middle of notch 23 mm. Semilunar notch opens anterad rather than anteroproximad; lateral edge very slightly indented. Proximal part of semilunar articular surface evenly convex mediolaterally; center part occupied by slightly raised, mushroom-shaped area extending up from between radioulnar articular facets; distal part bears separate, slightly concave medial and lateral facets, medial facet facing anteroproximad, lateral facing more proximad. Radioulnar articular facets likewise dual, contiguous with anterior edges of distal semilunar facets; medial radioulnar facet flat, pitted, faces anterolaterad, sharply raised above anterior surface of ulna; lateral facet low, slightly convex, indistinctly demarcated. Maximum width at semilunar notch 32 mm. Shaft where broken composed of compact bone; cross-section has asymmetrical teardrop shape, convex anteriorly and laterally, more acutely convex posterolaterally, and gently concave on posteromedial side, with rather sharp anteromedial point.

?INNOMINATE (USNM 214596, Figure 33).— What appears to be the middle portion of a left innominate bears no very close resemblance to innominates of other known sirenians; orientation uncertain. Shaft of ilium composed of compact bone, oval in cross-section, slightly compressed mediolaterally (19×18 mm), narrower end of cross-section ventral; expanded somewhat proximally, much more so distally. Height where broken proximally = 27 mm. Dorsal third of proximad-facing surface of fragment occupied by distal side of a deep concavity, smooth surfaced except for low median ridge, with rounded dorsal, medial, and lateral rims; lateral rim more pronounced, suggesting an anteromediad orientation of concavity when complete. Lateral surface of ilium occupied distally by longitudinal series of low rugosities. No distinct iliopectineal tubercle present. Distally, fragment broadens abruptly in vertical plane to maximum height of 41 mm; cross-section triangular, medial and dorsolateral sides nearly flat, dorsal edge thickened and
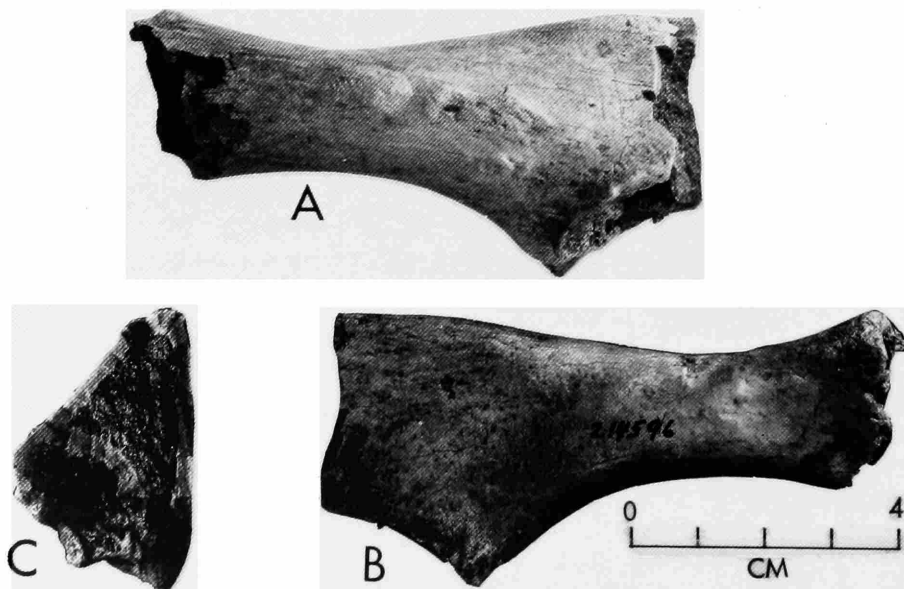

FIGURE 33.—Partial ?left innominate of *Protosiren* species from North Carolina (USNM 214596): A, lateral aspect; B, medial aspect; C, broken cross-section.

slightly overhanging laterally, ventrolateral side occupied by large rugose cavity, apparently acetabulum. Proximodorsal rim of latter irregular, very prominent, causing preserved portion of cavity to face ventrad; cavity separated by approximately 1 cm from anteroventral border of innominate.

COMPARISONS

The North Carolina material is here compared with the previously described Eocene sirenians as was done above with the Florida specimens.

Ishatherium subathuensis Sahni and Kumar, 1980. This species, said to be from the lower Eocene of India, is based on an isolated M_2 which shows almost no resemblance to that of USNM 214596: a prominent anterior cingulum is present; all four major cusps are conical, separate, and distinct, with almost no tendency toward lophodonty; and the posterior slope of the talonid is even, with no suggestion of a hypoconulid lophule. Both the age and the sirenian identity of the species have been questioned (see "Old World Records").

Prorastomus sirenoides Owen, 1855: Resembles USNM 214596 in the extreme narrowness of its mandibular symphyseal region, but the relatively straight ventral border of its mandibular ramus, its condylarth-like ear region (Savage, 1977), and the form of its atlas rule it out of consideration.

Sirenavus hungaricus Kretzoi, 1941: The holotype has almost no elements in common with the American form, but Kretzoi states that the molars are "not lophodont," suggesting a different condition from that observed here.

Anisosiren pannonica Kordos, 1979: M^2 of this form closely resembles USNM 214597 but is considerably larger (21.3×20.8 mm); even its M^1 (17.4×18.0 mm) is larger than the North Carolina specimen. It is not clear from Kordos' illustration whether there is a cuspule at the lingual end of the transverse valley of M^2 as there is on M^3, but at least a cingulum appears to be present, in contrast to USNM 214597.

Protosiren fraasi Abel, 1907: The North Carolina mandible may without hesitation be considered congeneric with the mandible referred to this species by Priem (1907:417, 418, pl. 16) and redescribed and re-illustrated by Sickenberg (1934:63, 64, pl. 1: fig. 9; "Stück L"), a cast of which (USNM 244490) was available to us (Figures 20–22). *Protosiren* alone among known sirenians other than *Prorastomus* has the anteriorly compressed symphyseal region seen in USNM 214596 and also shares with the latter the same ventral outline of the ramus, same degree of rostral deflection, and essentially the same dental morphology, though it lacks an accessory mental foramen. Although it is unknown whether DP_5 was replaced in Priem's specimen, the absence of an unerupted P_5 in USNM 214596 is problematical, for the following reason. Another mandible (YPM 24851, Figure 34) from the late Eocene Qasr el-Sagha Formation of the Fayum, Egypt, although matching the above specimens in most features, clearly shows an unerupted P_5 on each side. This mandible apparently represents a new species of *Protosiren*, advanced beyond the middle Eocene species in at least one respect, greater rostral deflection. If it is presumed to be descended from *P. fraasi*, P_5 can hardly have been lost in the latter. Whether this tooth had yet to develop in USNM 214596, or whether the North American form had eliminated P_5 from its dentition, is unclear; however, Rose and Smith (1979) show that the time of appearance of permanent last premolars in at least some Eocene condylarths was sometimes quite late, so it is not unlikely that in the North Carolina sirenian we see merely a similar case of retarded tooth development.

An M_2 with mandible fragment from the middle Eocene of Hungary was referred to *Protosiren* cf. *fraasi* by Kordos (1978). The photographs of the M_2 are difficult to interpret, but there appears to be an indentation anterolabial to the protoconid which is not well developed in USNM 214596. The fold connecting hypoconid to hypoconulid is present in the American specimen though not in the Egyptian specimen of Priem (1907). The Hungarian tooth is slightly larger than either of the latter. The mandibular cross-section is similar to that of the American specimen; Kordos states that the Egyptian mandible
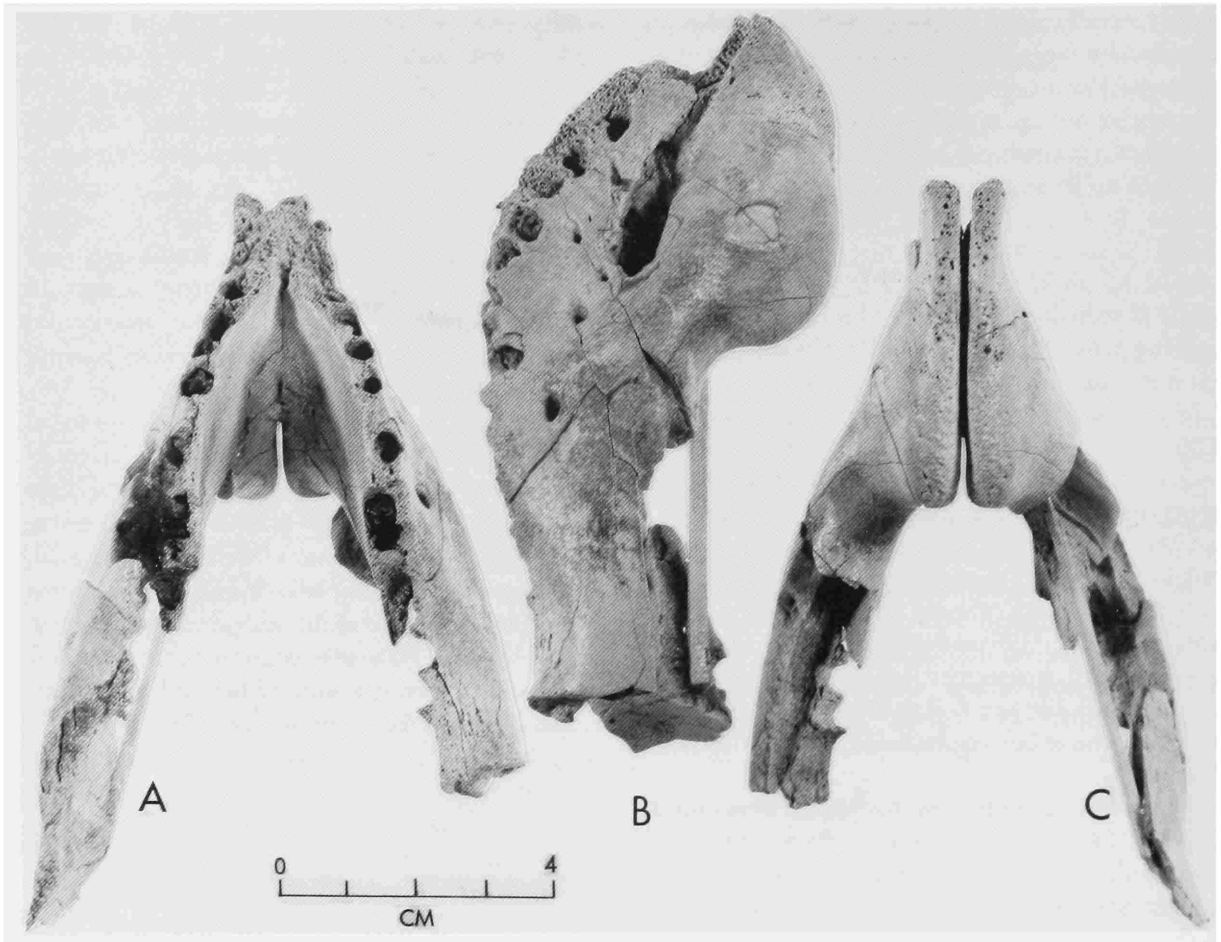
FIGURE 34.—Mandible of *Protosiren* species from the late Eocene of Egypt (YPM 24851): A, occlusal aspect; B, right lateral aspect; C, ventral aspect.

is somewhat different, but this could not be confirmed from the cast we examined.

The North Carolina periotic (USNM 244496) does not show the hypertrophied processus fonticulus of Sickenberg's *Protosiren* (1934, pl. 1: fig. 6). The upper molar (USNM 214597), however, corresponds well with Sickenberg's description of those of *P. fraasi* (1934:69–71). Its dimensions match those of the holotype (Andrews, 1906:209), and it likewise has a ridge connecting the protocone and precingulum, but the latter extends across the whole front of the tooth, not just its labial part. The atlas of USNM 214596 contrasts with that of one *Protosiren* (Sickenberg, 1934, fig.

12) in having an unbridged arterial canal above the anterior cotyle, but the isolated atlas (USNM 244494-5) seems to have had a bridged canal, whereas the vertebrarterial canal through the transverse process is entirely absent (a common variation in sirenians). The fragments of thoracic vertebrae do not closely resemble those referred to *Protosiren* by Sickenberg (1934:79–84) in either overall shape, lack of compact bone, or reduction of epiphyses. A low postzygapophysis on ?L1 seemingly resembles *Protosiren*, but the presence of caudal epiphyses again conflicts with Sickenberg's description. Sickenberg had insufficient material to describe the ribs of *Protosiren* ade-

quately. He did note a peculiarity of this form—absence of tubercular articular facets in the middle thoracic region—which is not evident in the present specimens, though the latter are too incomplete to allow certainty in this regard.

The distal portion of the scapula matches Sickenberg's "St. XLVIII," referred to *Protosiren* (1934, pl. 3: fig. 2), but USNM 214596 unmistakably possessed an unossified scapular cartilage and a "teres major protuberance," contrary to Sickenberg's account of *Protosiren*. The "teres major protuberance" is variably developed in sirenians and may be unreliable here for diagnosis, whereas Sickenberg (1934:92, 93) believed that the scapular cartilage had "already ossified" in St. XLVIII. To our knowledge such ossification has not otherwise been observed in sirenians, but in such primitive forms we should perhaps expect the unexpected. The humerus of the North Carolina form resembles that of *Eotheroides* more than that of *Protosiren*, but as Sickenberg's example of the latter ("St. XLIX") is immature and his referrals were largely based on the slightly smaller body size of *E. aegyptiacum,* they seem open to question. In the ulna of USNM 214596 we indeed encounter the unexpected, as it is quite different from those of *E. aegyptiacum* ("St. XXX") and later sirenians. Its similarity of preservation to and association with the other elements, however, seems to make its identification as sirenian incontrovertible; besides, no alternative identification is apparent. As no ulna has previously been referred to *Protosiren*, it is permissible to conclude that this genus possessed an ulna fittingly primitive for its near-basal position in sirenian phylogeny.

The ?innominate of USNM 214596 differs considerably from the pelvic bone illustrated by Abel (1904, pl. 7: fig. 1) and referred to *Protosiren* by Sickenberg (1934:94) on the basis of the morphology of associated vertebrae. In particular, the acetabulum is well developed and smooth surfaced in the Egyptian form, whereas in the North Carolina specimen it is extremely rough, pitted, and evidently degenerate. In a specimen from India referred to *P. fraasi* by Sahni and Mishra

(1975), the acetabulum also appears to be relatively smooth. The overall impression given by the North Carolina fragment is that of a more reduced condition than seen in the innominates referred to *Protosiren*; its outlines are suggestive of more advanced forms such as *Eotheroides libycum*. The cavity on the dorsal edge of the ilium, however, is not seen in other forms and may be a primitive feature; though Abel (1904) describes no such cavity, he shows (pl. 7: fig. 1) a notch of some sort on the dorsal edge of the ilium in about the same place. Hence the fragment from North Carolina can neither be excluded from *Protosiren* nor referred to it with any confidence.

The North Carolina skullcap (USNM 307609), which may or may not represent the same form as the Comfort quarry material, resembles in its smooth interior surface Sickenberg's "Stück II" (1934, pl. 1: fig. 4). In other respects it falls within the range of variation of the Florida skullcaps.

?Protosiren minima (Desmarest, 1822) (= *?P. dubia* (Cuvier, 1824); see Hooijer, 1952): The $?M^2$ (Sickenberg, 1934, fig. 36c) is somewhat larger than that of the North Carolina form but otherwise indistinguishable from it, and the same is true of the worn $?M_2$ (1934, fig. 36b).

Eotheroides aegyptiacum (Owen, 1875a): This form is distinguished from the Comfort sirenian by its broader mandibular symphyseal surface (Andrews, 1906, fig. 67A; Abel, 1912, pl. 32: fig. 1) and the form of its ulna (Sickenberg, 1934, pl. 4: fig. 6); however, it resembles the latter in several respects: quadratic cross-sections of some ribs, relatively slender build of posterior ribs, presence of a "teres major protuberance" and unossified scapular cartilage (Sickenberg, 1934, pl. 3: fig. 8), and form of humerus (1934:29, 30).

The skullcap of *E. aegyptiacum* differs from the North Carolina specimen in having well-developed falx cerebri and tentorium osseum, and probably a higher supraoccipital.

Eotheroides abeli (Sickenberg, 1934): The hypodigm of this species includes a skull referred by Abel (1912) to *E. aegyptiacum* and on which his description of the latter's otic region was largely based (Sickenberg, 1934:36). The North Carolina

periotic (USNM 244496) resembles this specimen in lacking an enlarged processus fonticulus but otherwise is only generally similar to Abel's illustrations (1912, figs. 3, 4; pl. 30: figs. 3–5). An M_3 (Abel, 1912, pl. 5: fig. 1) referred here by Sickenberg, though slightly larger, closely resembles that of USNM 214596, and an M^2 (Sickenberg, 1934:38, 39, pl. 5: fig. 3) resembles USNM 214597 but for its smaller size and obstruction of the transverse valley by a lingual cuspule. A thoracic vertebra of USNM 214596 also resembles T17 of *E. abeli* (Sickenberg, 1934, pl. 4: fig. 3), but on the whole there are too few preserved elements common to the two forms to allow a satisfactory comparison.

"*Eotherium*" *majus* Zdansky, 1938: Molar much larger than USNM 214597.

Eotheroides libycum (Andrews, 1902): Differs from the Comfort sirenian in its greater size and much broader, more robust, and more deflected mandibular symphyseal region (Andrews, 1906, pl. 20: fig. 2; also YPM 38213). Its M^2 (Sickenberg, 1934:108, pl. 2: fig. 3) resembles USNM 214597 in size and shape, though its M_3 (1934:109, pl. 5: fig. 2) is more complex than the American form. Its atlas (1934, pl. 4: fig. 8) resembles that of USNM 214596, but as indicated above, characters of this element are variable and doubtfully diagnostic. The other vertebrae are likewise similar in the two forms, but Sickenberg does not report the occurrence of quadratic rib sections in *E. libycum*. The expansion of the supraspinous fossa and development of the acromion (1934, fig. 20) are not seen in USNM 214596, though the humeri are similar (1934:127, 128), whereas the ulna of *E. libycum* is unknown. The ?innominate of USNM 214596 resembles that of *E. libycum* in its outlines (Andrews, 1906, fig. 68B) but not in the roughness of its acetabular surface (Sickenberg, 1934:129). The skullcap of *E. libycum* has well-developed falx and tentorium, unlike USNM 307609.

"*Eotherium*" *stromeri* Sickenberg, 1934: Lacks quadratic rib sections but otherwise has too few diagnostic elements in common with the North Carolina material for useful comparison.

Prototherium veronense (de Zigno, 1875): Apart from greater size, this species differs from USNM 214596 in less abrupt downturning of the ventral border of the mandibular ramus, and the symphyseal tooth rows are said to be widely separated (Sickenberg, 1934:160, 161). The premolars are more complex, as is M_3, with its more obstructed valley and massive, multicuspate hypoconulid lophule (1934:170, 171, fig. 27). The supraspinous fossa is broader (1934, fig. 30). A bony falx and internal occipital protuberance are present, in contrast to USNM 307609.

Paralitherium tarkanyense Kordos, 1977: This form is larger than the North Carolina sirenian, with a more massive and strongly deflected (50°–55°) mandibular symphyseal region, but it does exhibit quadratic rib sections (as do also the rib fragments from Transylvania; Sickenberg, 1934:183, 184).

Post-Eocene Sirenians: As with the Florida material, comparison with post-Eocene forms is here unnecessary, as none even remotely resembles the Comfort sirenian in compression of the mandibular symphyseal region, tooth formula, or form of the scapula and ulna. The Oligocene genus *Miosiren* lacks a well-developed falx and tentorium (Sickenberg, 1934:298) but otherwise differs in proportions of the skullcap from USNM 307609.

We conclude that the North Carolina sirenian most closely resembles specimens referred to the genus *Protosiren*, and may be referred to *Protosiren* species. Apparent similarities of many elements to those of *Eotheroides* may in part reflect the sharing of primitive characters by many Eocene sirenians but to a large extent could be artifacts of erroneous referrals of isolated elements to various taxa, including *P. fraasi*.

The conspecificity of the North Carolina and Florida *Protosiren*, however, seems questionable. The former lacks the small accessory mental foramina observed posteroventral to the principal foramen in all three Florida mandibles. The Comfort upper molar lacks a lingual cingulum, and its precingulum extends prominently across the entire front of the tooth. The Florida vertebrae

contain a greater amount of cancellous bone, and quadratic ribs have not been found in the Waccasassa River sample. The North Carolina skullcap lacks the prominent falx and tentorium of the Florida specimens. Only more nearly complete and comparable specimens can reveal whether these differences are significant.

Sirenian Dental Formulae and the Cladistic Classification of Mammals

Although it has been known for more than a century that Eocene sirenians had five instead of the usual eutherian four premolars, this fact has been overlooked by almost all mammalogists. The well-preserved *Protosiren* mandible from North Carolina reported herein, together with an undescribed specimen from Egypt (YPM 24851), provide additional confirmation of this primitive condition. This evidence has gained new significance from recent interest in revising supraordinal mammalian taxonomy. McKenna (1975) outlined a new classification of the higher taxa of mammals based on cladistic analysis. Both proponents and critics of this procedure agree that it has the virtue of vulnerability to falsification. McKenna's cladistic scheme, which did not take into account the presence of five premolars in early sirenians, is in fact partly falsified by these data.

McKenna erected a "Magnorder Preptotheria" to include all known eutherians except edentates, macroscelideans, lagomorphs, possibly rodents, and a few extinct forms. The primitive postcanine dental formula from which preptotheres departed was regarded as DP1 P2 P3 P4 P5 M1 M2 M3. All preptotheres except Deltatheridia and Pholidota were, in turn, placed in a "Superorder Tokotheria," primitively characterized by the postcanine formula DP1 P2 P3 P4 DP5 M1 M2. In other words, McKenna concluded that all tokotheres have lost P5 and M3, and that the teeth traditionally regarded as M1–3 in most orders of living mammals are really DP5, M1, and M2. This hypothesis would be falsified by discovery of a tokothere having five premolars

together with three molars, as in the pre-preptothere condition.

In 1875, Sir Richard Owen redescribed *Prorastomus sirenoides*, a primitive member of the order Sirenia (hence a tokothere) from the middle Eocene of Jamaica having the dental formula 3.1.5.3. Recent repreparation and restudy of the unique type specimen have confirmed this (Savage, 1977). In 1934, Sickenberg described specimens of *Protosiren fraasi*, a more advanced sirenian from the middle Eocene of Egypt, as having I1–3 C1 P1 P2 P3 P4 P5 M1 M2 M3, with a doubtfully present sixth premolar. A mandible of *Protosiren* species from the late Eocene of Egypt (YPM 24851, Figure 34) shows an identical 3.1.5.3 formula, including unerupted P_5s on both sides. Abel (1912) reported *Eotheroides aegyptiacum* (middle Eocene, Egypt) as having P1 P2 P3 P4 DP or P5 M1 M2 M3. In the still more advanced forms *Eotheroides libycum* (late Eocene, Egypt) and *Prototherium veronense* (late Eocene, Italy), Sickenberg (1934) found I1–3 C1 DP or P1–2 P3 P4 DP5 M1 M2 M3, P5 apparently having been lost. This latter formula is also seen in the mandible from the middle Eocene of North Carolina (USNM 214596) referred here to *Protosiren* species.

Therefore, eight postcanine tooth positions are regularly present in all of the four best-known genera of Eocene sirenians. In at least some of these, both deciduous (molariform) and permanent (premolariform) teeth are accounted for at the fifth position, ruling out the possibility that the five apparent premolars include both DP4 and P4. Although late retention of a more anterior DP together with its replacement cannot be absolutely ruled out, the obviously simpler interpretation is that primitive sirenians merely retained the ancestral preptothere condition. The likelihood of discovering early eutherians retaining this condition has, indeed, recently been pointed out by Bown and Kraus (1979:180).

Thus, McKenna's hypothesis of the loss of M3 is falsified for at least the "Grandorder Ungulata," the division of the Tokotheria which includes the Sirenia; hence loss of M3 cannot be used as a defining autapomorphy of the Toko-

theria. The only remaining autapomorphy offered by McKenna for the Tokotheria is reduction of the incisors to 3/3. This feature is shared by the "Superorder Leptictida," which includes most members of the "Magnorder Ernotheria," sister group of the Preptotheria. The Leptictida, however, have lost the DP3–P3 locus and show other autapomorphies not seen in tokotheres, so there is no question of uniting the latter with the former.

The defining autapomorphy of the Preptotheria, according to McKenna's figure 3, is retention of DP 5/5 in the adult. As shown above, this does not apply to the most primitive sirenians; at best it could be a convergence between deltatheridians and some tokotheres. This leaves the Preptotheria without a defining autapomorphy. Thus, of the proposed preptothere-tokothere autapomorphies—retention of DP 5/5, loss of M 3/3, and reduction of incisors to 3/3—the first two have been falsified, and the third, which defines the tokotheres, is shared (convergently) with leptictidans. Apparently, the Preptotheria are defined only as plesiomorphic to ernotheres and are, therefore, in danger of being paraphyletic (if not polyphyletic). If "M 1–3" of any tokotheres are really DP5, M1, and M2, this must have come about separately in one or more clades of tokotheres other than sirenians.

We leave it to specialists in other groups to trace the further ramifications of this situation. Suffice it to say that the Preptotheria and Tokotheria as characterized by McKenna are not adequately diagnosed. It may be further observed, however, that we have here a concrete example of the instability which McKenna (1975:22) warned us to expect from the cladistic method. The "phylogenetic repairs," or at least redefinitions, called for here are at a fairly ancient site, and the classification, if not crumbling, has at least been jarred in some fairly high categories. Whether this is a cause for "rejoicing" will probably depend on whether subsequent "iterations toward a stable . . . system" decrease or increase in amplitude. Meanwhile, we see no reason to make formal classification a tool for identifying

confusion in our phylogenetic concepts when the same result can be achieved, by cladistic analysis, without putting our common taxonomic language so constantly at risk.

History, Biogeography, and Correlation

The earliest geological records of sirenians are in early Eocene rocks of Hungary and India, although both age and identity of the latter have been questioned (see "Old World Records"). Middle Eocene records extend from the Caribbean to India, with a late Eocene occurrence in Java (Table 1; Figure 1). Thus, from almost the beginning of their recorded history, the sea cows have had what can justly be called a "pan-Tethyan" distribution, being found throughout the length of the Tethyan Seaway, which formed the heart of the Paleogene marine tropics. With the exception of *Hydrodamalis*, they have remained essentially tropical animals to this day.

Consideration of the morphology and relationships of Eocene sirenians allows more detailed conclusions to be drawn about their early patterns of dispersal. As by general consensus the order's closest affinities are with moeritheres, proboscideans, and other "subungulate" or "tethythere" groups, we may confidently conclude that they arose in the Old World from an unknown condylarth stock. The rather advanced grade of bone density seen in some early Eocene remains (Kretzoi, 1953) suggests that their aquatic adaptation was well under way by that early date, as would be expected from the diversity already evident in the middle Eocene. (Sahni and Kumar (1980), however, stated that early Eocene specimens which they referred to the Sirenia are not composed of compact bone, possibly a reason to doubt their sirenian identity.) Though the most primitive, adequately diagnosable sirenian, *Prorastomus*, does not appear in the record until the middle Eocene, it is obvious that by then prorastomids were already past their prime and well on the way to being superseded by more derived forms. Perhaps they had already been relegated to a relict, marginal distribution, far from the Old

World center of Tethys (unless *Sirenavus* is in reality a prorastomid). In any case we must place the origin of prorastomid sirenians in pre-Eocene times.

It may be doubted whether *Prorastomus* was even a fully aquatic mammal, rather than amphibious in pygmy hippo- or tapir-like fashion. Sahni and Kumar (1980) stated that limb and girdle elements which they referred to their lower Eocene genus *Ishatherium* (considered by them to be a dugongid yet "ancestral to all later sirenians") showed that this form "was equally adapted to the life in coastal, near-shore conditions as well as on land." They neglected, however, to substantiate this by describing the postcranial elements. By the protosirenid grade, at least, we are much more certain of having an obligatorily aquatic organism, in which the modern sirenian morphotype had appeared in final form save, perhaps, for incomplete reduction of the hind limbs. Protosirenids attained a pan-Tethyan distribution and very likely underwent a modest radiation, giving rise to dugongids (already present in the middle Eocene) and probably, through isolation in South America, to trichechids (Domning, 1982) as well as to apparent post-Eocene protosirenids such as *Miosiren*. By the end of the Eocene, however, protosirenids had already yielded to a third sirenian radiation, that of the dugongids, which have dominated the mammalian marine-herbivore niche down to the present.

The roles that high vagility, low diversity of potential food plants, and relative lack of effective geographic barriers have played in limiting sirenian diversity have already been noted (Domning, 1978:139). Thus the apparent lack of provinciality in Eocene sirenian distribution is not surprising; the Paleocene-Eocene continuity of the Caribbean and Old World Tethyan marine tropics (Berggren and Aubert, 1975) would lead us to expect a relatively homogeneous sirenian fauna. Such a situation has obvious biostratigraphic potential; however, its realization depends on establishment of a sound taxonomic and phylogenetic foundation and on the discovery of relatively complete specimens in farflung

areas. It is certainly encouraging to find evidence of *Protosiren* in middle Eocene rocks of Florida, North Carolina, France, Hungary, Egypt, and India, but until there is some basis for reliable species-level identifications, it would be premature to announce the discovery of a new tool for precise intercontinental correlation.

Paleoecology of Eocene Sirenians and Seagrasses

It is well known that modern sirenians in tropical marine waters eat mainly seagrasses, marine angiosperms of the families Hydrocharitaceae and Potamogetonaceae (Heinsohn et al., 1977; Hartman, 1979; Best, 1981). As nearly all fossil sirenians also appear to have been both tropical and marine, it seems reasonable to conclude that they also depended on seagrasses (Domning, 1977, 1981). What little is known of seagrass evolution does not contradict this; a seagrass flora already existed in the Early Cretaceous, and the distribution of both fossil and Recent seagrasses shows a close association with (and probably origin in) the Tethyan region (den Hartog, 1970; McCoy and Heck, 1976). Cretaceous seagrasses have been reported from Japan, Germany, and the Netherlands (den Hartog, 1970), and there are unpublished records from North America (Ossian, pers. comm., 1981). Thus sirenians most likely fed on seagrasses from the beginning of their entry into the marine environment.

Seagrass fossils, however, are unfortunately rather rare, and some authors have sought to identify other, more common organisms that are regularly associated with seagrasses in order to detect the former presence of the latter. For example, Bałuk and Radwański (1977) and Hoffman (1977) have attempted this with invertebrate faunas, and Brasier (1975) with Foraminifera. Brasier, however, was unaware of the occurrences of seagrasses in Eocene rocks of Florida (see below), and he concluded that seagrasses (and specifically his "*Thalassia* association") did not reach Neotropical waters until the Miocene. This would imply that Paleogene sirenians in the Caribbean

did not eat marine angiosperms. Brasier's reconstruction was criticized by Eva (1980), who concluded (again from Foraminifera) that seagrasses did occur in the Eocene Caribbean, though not as far north as Florida.

Dixon (1972), Randazzo and Saroop (1976), and Saroop (1977), however, reported abundant remains of seagrasses, referred by them to the living genera *Thalassia*, *Syringodium*, *Diplanthera* (= *Halodule*), and *Ruppia*, in the middle Eocene Avon Park Formation of Levy and Citrus counties, Florida—the same unit that yielded many of the sirenian fossils reported herein. The seagrass remains include not only leaf-blade impressions but also entire rhizome mats in growth position, and detailed analysis of the associated fauna, flora, and sediments confirms the existence of a well-developed seagrass community closely resembling the *Thalassia-Syringodium* communities typical of Florida today.

This evidence decisively refutes Brasier's (1975) conclusion and removes the need to postulate that Caribbean Eocene sirenians ate no seagrasses (as suggested by Savage, 1977). It also refutes Eva's (1980) supposition that Eocene seagrasses were absent from Florida. Apparently the relationship between Brasier's "*Thalassia* association" and certain Foraminifera is less obligatory than the dependence of sea cows on seagrasses, and we propose that the latter relationship is the more reliable indicator of areas where seagrasses, though unrecorded, once existed (see, for example, Domning, 1977, 1978, with regard to Miocene seagrasses in California).

This conclusion is also more consistent with McCoy and Heck's (1976:207) thesis that seagrasses, mangroves, and hermatypic corals have shared a common (pan-Tethyan) distribution since the Cretaceous. They predicted that "there should be a number of globally-distributed organisms associated with the three groups which are likely a remnant of Tethyan distributional patterns." Sirenians clearly answer to this description, in addition to the coral-reef fishes, decapod crustaceans, mollusks, and miscellaneous plants cited by McCoy and Heck.

The degree of diversity and pattern of niche partitioning shown by Caribbean Eocene sirenians remain in doubt, however. Two forms (*Prorastomus* and *Protosiren*) are known to have been simultaneously present. Judging by the rostral deflection model (Domning, 1977), they should have been able to coexist sympatrically; the rostral deflection (RD) of the New World *Protosiren* is about 35°–40°, whereas that of *Prorastomus* is a scant 6°, much less than in any other sirenian. Together with its generally very primitive aspect, this might suggest a rather different, and possibly less than fully aquatic, lifestyle in *Prorastomus* than in other sirenians. Certainly *Protosiren* would seem to be the better adapted of the two for feeding on seagrasses. Among modern sea cows, it compares best with *Trichechus manatus* (mean RD = 38.2°; SD = 4.88, N = 72), which has a mixed diet of freshwater plants and seagrasses (Hartman, 1979). It is not known what floating or emergent freshwater plants were available to *Protosiren*, but by analogy with *T. manatus* it seems likely that some were included in its diet. Had it fed exclusively on bottom plants such as seagrasses, we would expect its rostral deflection to have been greater (even up to 70° as in *Dugong*).

No Eocene sirenians with *Dugong*-like snout deflections are known, though by the late Eocene, species of *Protosiren* and *Eotheroides* with somewhat increased deflections had appeared. As we see from the Avon Park Formation that seagrass beds of modern aspect already existed in the middle Eocene, it is not clear why specialized bottom-feeding sirenians with strong snout deflections should not have evolved by that time. It would seem possible for an extreme bottom-feeder to have coexisted with *Protosiren* and *Prorastomus*, as *Dioplotherium* (RD approximately 70°) evidently coexisted with *Dusisiren* (RD approximately 41°) in the Miocene of California (Domning, 1978). Such a specialized middle Eocene form may yet be discovered.

Conclusions

1. Worldwide distribution of Eocene sirenian fossils is limited to the area of the former Tethyan seaway.

2. Identifiable specimens of Eocene sirenians known from the New World represent *Prorastomus sirenoides* from Jamaica and *Protosiren* species from Florida and North Carolina. *Protosiren* is also reported from France, Hungary, Egypt, and India. All the above records are middle Eocene, though *Protosiren* also evidently occurs in the upper Eocene of Egypt. Clarification of the species-level taxonomy of these and other Eocene sirenians may permit their use in intercontinental biostratigraphic correlation.

3. All adequately known Eocene sirenians possessed a dentition including five premolar positions, evidently the primitive eutherian number. They are the latest-surviving eutherians known to have retained this formula. This necessitates revision of some current ideas on the cladistic relationships of the mammalian orders.

4. Distribution of fossil sirenians is evidently a more reliable guide to the past presence of seagrasses than are the distributions of Foraminifera or other organisms whose relationship with seagrasses is less obligatory.

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