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FROM FLORIDA AND ELSEWHERE

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GAINESVILLE

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## FOSSIL SIRENIANS AND DESMOSTYLIDS FROM FLORIDA AND ELSEWHERE

ROY H. REINHART<sup>1</sup>

**SYNOPSIS:** Florida is the only part of the world in which extensive sirenian remains have been recovered from each epoch, beginning with the Eocene and continuing into the Recent. The evolutionary stage of the Mio-Pliocene sirenians from Florida parallels that of similarly aged European sirenians, in which a puzzling complex of specimens assigned to *Metaxytherium*, *Halianassa*, and *Felsinotherium* exists. From this study a proposal for synonymy of the above genera into the genus *Metaxytherium* is made. Florida metaxytheres are subdivided into three species with retention of trivial names now in use. Amplification and clarification of these species are made through a description of a number of new specimens.

Changes in interpretation of the cranial morphology of *Hesperosiren* are suggested, with the result that this form appears to be closely related to *Metaxytherium*, rather than the highly aberrant form it has been considered.

The presence of *Halitherium* in continental North America is now established beyond question in the new species *H. olseni* from Florida. Although of a similar evolutionary stage, this specimen is from beds of Middle to Upper Miocene, as compared to the Middle to Upper Oligocene European *Halitherium*.

Ribs of Middle Eocene sirenians have been substantiated from a number of Florida localities, but no diagnostic elements have been found.

Comments are made on Sirenia from areas other than Florida. These include a review of Sirenia from Java, the second report of a dugongid from South America, the validity of the Argentine trichechid *Ribodon*, and a report on the nomenclatorial status of *Manatus* and *Trichechus*.

Desmostylid remains have been authenticated only from the circum-North Pacific region, but reports on fragmentary teeth, incorrectly identified, have been attributed to *Desmostylus* from various localities. Two such proposals, *Cryptomastodon* from Java and *Desmostylus* from Texas, are discussed. Reports on new specimens of *Cornwallius* from the Aleutian chain, and *Desmostylus* from California and Florida are made, the latter being the first desmostylid authenticated outside of the Pacific. Discovery of *Desmostylus* in Florida extends its upper stratigraphic range from Late Miocene to Mio-Pliocene or to Middle Pliocene (Hemphillian), according to the age designation given to the Bone Valley Formation.

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## INTRODUCTION

Recent finds of Sirenia in the western hemisphere show that some modifications of our vague, but generally accepted, concepts of this order are necessary. As a carryover from older European literature, the origin of the Order Sirenia is often speculated to have occurred in the Middle Eocene Fayum region of Egypt because of the relative abundance of primitive Sirenia from this area, plus the earliest known representatives of the closely allied Order Proboscidea. A Middle Eocene sirenian with equally prototypic structural characteristics is also found in Jamaica, while less diagnostic specimens from Florida, Alabama, and possibly Java suggest a wide geographic distribution during this epoch, with no positive evidence for initiation of the group in any single region. The ancestral breeding ground is therefore unknown, as is true with most mammalian orders. The general paucity of early sirenians from much of the world likely results from insufficient investigation of Eocene marine and estuarine beds, rather than from their true absence. An interesting fact, but one that casts no information on ordinal origin, is that Florida is the only area with evidence of continuous sirenian habitation

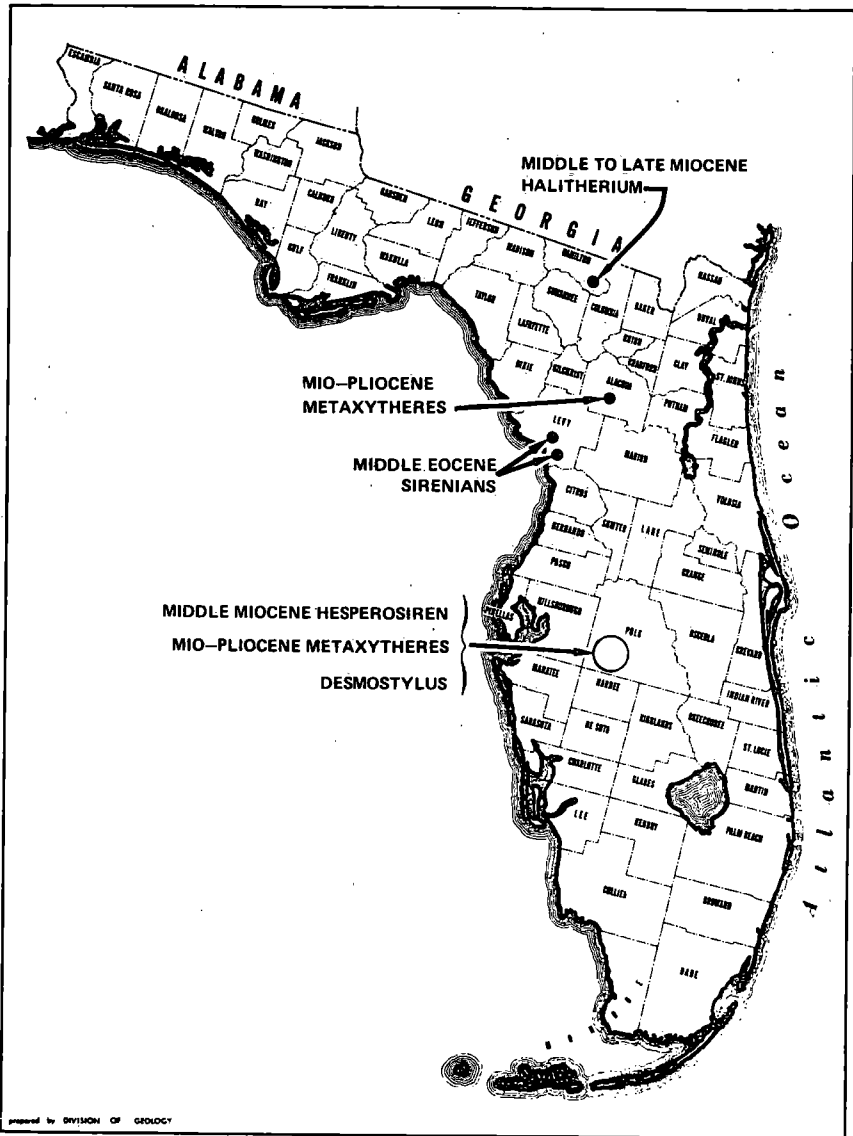


FIGURE 1.—*Sirenia* and *Desmostylus* localities in Florida.

from Middle Eocene to Recent time. If Europe and Egypt are combined, a similar time range exists for this more geographically-widespread region, with the exception of an absence of Pleistocene and Recent forms.

Higher in the geologic column, the evolutionary stage of Oligocene as well as Mio-Pliocene sirenians from Florida parallels that of European

sirenians that are similar in age. Existence of a stratigraphic problem is immediately obvious when these almost identical representatives are compared. European specimens are invariably placed in a slightly older unit of geologic time than their North American counterparts. Whether this reflects a true picture of the genesis of the order or a fault of intercontinental correlation is a matter of conjecture.

Also included in this study is new information on the Sirenia of South America, where recent discoveries have revealed their presence in the western Atlantic region, from Colombia to Argentina. The find of a lower Miocene trichechid in Brazil (Couto 1967), in addition to the Middle to Upper Miocene dugongid from Argentina reported in this study, indicates trichechids existed with dugongids in the Caribbean Sea and in South America throughout the Miocene, and possibly through Pliocene time. Not knowing of any Trichechidae from areas other than the Caribbean and the coastal rivers of the South Atlantic is an enigma. Because the Dugongidae are geographically widespread from Middle Eocene to Recent time, one would expect the Trichechidae to have a somewhat greater range than the narrow distribution evidenced by the fossil record. The considerable cranial and postcranial differences between Pleistocene and Recent Trichechidae and Dugongidae, plus evidence of similar separation back through Lower Miocene, suggests the possibility of a separate phyletic line for each since Eocene time.

#### ACKNOWLEDGMENTS

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Robert O. Vernon, chief of the Florida Geological Survey, was particularly helpful in my securing the excellent specimen of Florida *Halitherium* and provided funds for its preparation. J. C. Dickinson, Jr., director of the Florida State Museum, aided in numerous ways, and, with William Reimer, former chairman of the Department of Natural Sciences of the same museum, was in charge of financial aid received from the University of Florida to make the study possible. Later funds were received through the office of Walter Auffenberg. H. Kelly Brooks of the University of Florida, Gainesville, proved to be an indefatigable and enthusiastic field worker whose time and knowledge of Florida stratigraphy was given generously. In the closing stages of the study David Webb contributed comments and his efforts most willingly.

To Clayton Ray of the U. S. National Museum, Washington, D. C., (and formerly of the Florida State Museum), must go my deepest thanks for initiating the project and providing stimulation throughout the study. Both Ray and Stanley Olsen of the Florida Geological Survey sent many specimens, provided field data, and continually added encouragement in our many meetings. For the varied exhaustive help from these two colleagues I am most grateful.

### Materials Examined

Material examined is from the following collections: American Museum Natural History (AMNH), Field Museum of Natural History (FMNH), Florida State Geological Survey (FGS), Los Angeles County Museum of Natural History (LACM), Museum Comparative Zoology Harvard, (MCZ), National University of Cordoba, Argentina (NUC), University of California Museum Paleontology (UCMP), University of Florida, Gainesville (UF), United States National Museum (USNM), University of Texas, Austin (UT). All measurements throughout the text are in millimeters.

### Abbreviations Used in Figures

Abbreviations used in figures are as followed: DENTAL: Anterior cingulum (A.c.), Hypocone (Hy), Metacone (Me), Metaconule (Ml), Median valley (M. vi), Paracone (Pa), Posterior cingulum (P.c.), Protoconule (Pl), Protocone (Pr); CRANIAL: Exoccipital (Ex), Frontal (Fr), Jugal (Ju), Lacrymal (La), Maxillary (Mx), Nasal (Na), Parietal (Pa), Premaxillary (Pmx), Supraoccipital (So), Supraorbital processes of frontals (S. or Pr.), Squamosal (Sq), Zygomatic arch (Zy).

There is no doubt that the evolutionary stage of the Mio-Pliocene sirenians from Florida parallels that of the European sirenians of a similar age. A puzzling complex of European specimens were originally ascribed to the genera *Metaxytherium*, *Halianassa*, and *Felsinotherium*. These genera have never been clearly defined. Herein lies the problem of comparing specimens from Florida, assigned to these three genera, with European forms, which are not distinctly defined nor differentiated morphologically.

The close similarity of *Metaxytherium* and *Halianassa* has long been recognized, and Simpson (1945), in his excellent taxonomic paper, regarded *Metaxytherium* Christol (1840) as a junior synonym of *Halianassa* Meyer (1838). The writer and most recent students have followed the work of Simpson; however, Kellogg (1966: 68-70), in his detailed review of the problem, showed that the name *Halianassa* Meyer (1838) was not originally accompanied by a description and is therefore a *nomen nudum*. Kellogg's well documented work traces the type species of this genus to *Halianassa studeri* Studer (1887), thereby giving *Metaxytherium* Christol

(1840) precedence. This has long been a difficult nomenclatorial problem, but on the basis of documentation by Kellogg I am changing my usage of *Halianassa* to *Metaxytherium*.

#### METAXYTHERIUM-FELSINOTHERIUM

The frustrating problem of generic distinction of the Mio-Pliocene *Metaxytherium-Felsinotherium* complex has been emphasized by a number of authors, including Gregory (1941: 40), who stated, "Possibly the most feasible solution of the taxonomic problem would be to regard the differences between Miocene and Pliocene Halitheriinae as too slight and variable to be worthy of generic recognition, and to place the species now referred to *Felsinotherium* in *Metaxytherium*, recognizing that some species of that genus showed certain evidence of advancement over their earlier relatives." The problem of separation of the genera *Metaxytherium* and *Felsinotherium* was further emphasized by Simpson (1932: 479) when he stated in his discussion of two species (*F. ossivalense* and *M. floridanum*) of Florida felsinotheres: "Even if neither species of *Felsinotherium* be directly derivative from any known species of *Metaxytherium*, the differences are really so slight and unimportant that no thoroughly satisfactory diagnoses separating the two genera have been proposed. Capellini (1872), in fact, considered the genera to be 'synonymous'."

Depéret and Roman (1920: 48) distinguished *Felsinotherium* from *Metaxytherium* by the presence in the former of a slightly more advanced reduction<sup>1</sup> and more quadrate shape of M<sup>1</sup>, M<sup>2</sup>, and P<sup>4</sup>, plus an inflection slightly more pronounced in the base of the premaxillary rostrum. Of two species referred to *Felsinotherium*, the large *F. foresti* has slightly more quadrate teeth than does *F. serresi*. This was previously deduced by Abel who, on the basis of this difference, placed *F. serresi* in the genus *Metaxytherium*. If the degree of premaxillary flexure is regarded as a valid distinction between the two genera, one finds a very similar expanded downturned rostrum in *F. foresti*<sup>2</sup>, *F. serresi*, and *M. cuvieri*, as opposed to a less deflected and less expanded rostrum in *Metaxytherium jordani* (= *Halianassa vanderhoofi*) from California. Expansion of the rostrum is most pronounced in the old, tusk-bearing adults. While not necessarily old individuals, the European Sirenia mentioned bear well developed tusks, as opposed to the California metaxytheres, which have nonfunctional incipient incisors. Degree of rostral flexure, however,

<sup>1</sup> Other authors have pointed out this statement but fail to comment on the meaning of "a slightly more advanced reduction." To me it means fewer cheek teeth, but in all cases I know there appears to be a maximum of five cheek teeth in all adult Sirenia attributed to *Metaxytherium* and to *Felsinotherium*. If this is the meaning, I fail to see a difference between the genera.

<sup>2</sup> Dorsal portion of rostrum missing.



appears to be somewhat greater in the European *Sirenia* mentioned than in *M. jordani*.

In a recent generalized, but completely summarized, review of *Metaxytherium* and *Felsinotherium*, Dechaseaux (1958: 353) recognized the difficulty of generic distinction, but nevertheless differentiated *Felsinotherium* in this manner:

“Il differe de *Metaxytherium* par une accentuation des tendances évolutives marquées par le genre miocène plutôt que par la possession de nouveaux caractères, aussi est-il très difficile de donner ses caractéristiques; plusieurs auteurs considèrent même ces deux genres comme synonymes.

“Il y a d'assez grandes variations dans les caractères du crâne et de la dentition selon les espèces (voir fig. 33); les molaires peuvent être simples, primitives, quoique de type bunodonte, ou bien posséder des tubercules accessoires et un arrangement en séries des cuspidés.”

The difficulty of working with two genera that can be differentiated only by vague criteria by the many competent students who have compared them leads me to propose that the species of *Felsinotherium* be placed in the genus *Metaxytherium*. This procedure is not suggested as a matter of convenience to end the confusion experienced by many students of the subject, but rather it is an attempt to frame the many isolated specimens attributed to a bewildering number of species into what appears to be a natural genetic group. Animal affinities are therefore considered primary, but the secondary result of cosmopolitan communication is also highly important and can no longer be ignored in this taxonomic problem.

The principal source of Mio-Pliocene metaxythere specimens in Florida is the Bone Valley district. The name “Bone Valley” is derived from exposures of fossiliferous phosphatic gravels in Polk and Hillsborough counties in south-central Florida. Prior to the use of the term *formation*, exposures had been referred to as Bone Valley gravel, “land pebble phosphates,” or “pebble phosphates.” Matson (1915: 36) described the Bone Valley sediments thus:

“The Bone Valley gravel consists of rounded pebbles of phosphate embedded in a matrix of sand or clay overlain by varying thicknesses of loose or semi-indurated sand. The maximum thickness of this formation is probably more than 50 feet, but only about one-third of this thickness should be assigned to the phosphate.

"The phosphate-bearing portion of the Bone Valley formation is a gravel containing rounded and subangular pebbles of phosphate of varying degrees of coarseness intermingled with more or less sand and clay. In general the deposit shows distinct stratification, some beds being wonderfully persistent over a distance of several hundred yards though others are lenticular and extend only short distances. There are numerous alterations of coarse and fine material and many of the layers are distinctly undulating—the entire formation bears evidence of having been deposited in shallow water where conflicting currents gave rise to irregular bedding and rapid alterations of sediments of varying coarseness."

Most exposures of the unit are the result of phosphate mining operations, rather than natural outcrops, with the result that lithologic descriptions are largely limited to regions where phosphatic concentrations are relatively thick.

A general consensus of opinion is that the Bone Valley sediments are in part estuarine and in part shallow marine in origin, an environment with which most fossil and living sirenians have usually been associated. There are also stratigraphic indications that periods of time existed when meandering streams crossed lowland and swampy areas. The Bone Valley was considered Pliocene in age by the United States Geological Survey (Cooke 1945: 197-210), much of the evidence being based on Simpson's determination of the age of fossil vertebrates found in the unit. Because the methods of phosphate mining often involve mixing of the underlying formations (usually Middle Miocene Hawthorne Formation), as well as overlying Pleistocene material, care must be taken to determine the faunal elements contemporaneous with deposition. Based on the land mammals determined by Simpson (1930: 180) to be indigenous to the Bone Valley, this stratigraphic unit is referred to the Hemphillian by Stirton (1936) and Wood *et. al.* (1941). More recent work by Olsen (1959: 40) and the Florida Geological Survey sums up the present questionable use of the term "formation" in relation to the Bone Valley sediments: "Perhaps no area in Florida has caused the concern, in regard to dating the vertebrate fauna it contains, as has the Bone Valley of Polk County. The term "Bone Valley" should be used to define a geographic boundary, rather than a stratigraphic unit, as beds ranging from Upper Miocene through the Lower Pleistocene are known to occur in the "Bone Valley" as defined by earlier workers. These beds, in some cases, show a lithologic change and are not clearly mapable units." Olsen (1959: 42) states the Bone Valley fauna is Mio-Pliocene in age, corresponding

to the upper Barstovian and lower Clarendonian. Recent study of a faunule collected from the Bone Valley Formation in Manatee County indicates a Hemphillian age (Webb and Tessman 1968).

The first important record of a sirenian from the Bone Valley Formation of Florida is that by Matson (1915), in which he referred a portion of an upper right maxilla to a "manatee." This specimen was later refigured and described by Hay (1922) as a new species, *Metaxytherium floridanum* (holotype: USNM 7221), a taxonomic assignment that correctly removed it from the Trichechidae. Allen (1923) subsequently referred a humerus and a number of vertebrae and ribs that had been collected in the "land-pebble phosphate deposits" near Mulberry, Florida, to *M. floridanum*. The postcranial material was not associated with teeth or other diagnostic cranial elements; therefore, the taxonomic assignment remains in some doubt. Simpson (1932) compared the humerus and vertebrae with other more complete specimens and referred Allen's material to *Felsinotherium*. Other sirenians from the sedimentary unit were described by Simpson under the name *Felsinotherium ossivalense*, the holotype (AMNH 26805) of which is a relatively unworn but fragmented M<sup>3</sup>. An important specimen referred to this species by Simpson is the anterior half of a cranium in the Florida Geological Survey collection (FGS V5454) that lacks the anterior end of the rostrum and the zygoma (Simpson 1932: 452, fig. 12 A-C). The dentition of this cranium was later described more fully by Gregory (1941), and certain cranial elements were further amplified. The only other figured specimen from the Bone Valley sediments (the posterior half of a cranium) is present in the Florida Geological Survey collection (FGS 3211), and lacks teeth, rostrum, and the anterior half of the frontals. Another specimen (FGS 3232), consisting of a well-preserved, fused parietal-supraoccipital element, was discussed by Simpson (1932) but not figured.

With the fossil material found to date, the most feasible method of differentiating Florida sirenians is to correlate two of the more common diagnostic elements, the cranial caps with upper cheek teeth. To date the only figured specimen from the Bone Valley beds in which these elements are found associated is a relatively complete cranium (FGS V5454). This paper will add three more specimens in which various cranial elements and teeth are associated, as well as a number of isolated cranial caps, individual upper and lower teeth, mandibular specimens bearing teeth, and varied postcranial elements. On rare occasions where postcranial elements have been found definitely associated with a cranium this relationship is described; however, because such elements appear to be more conservative in change than the cranium, they have limited value in determining relationships. An exception to postcranial

conservatism is the sacral elements, but these bones are unknown in the Florida Mio-Pliocene sirenians, undoubtedly due in part to their reduction in size and difficulty of recognition.

#### CRANIAL ROOF

Evaluation of cranial and dental characters, including their assignment to genus and species, age of individual, or dimorphic status, has long plagued European and North American students of Sirenia, particularly when the study concerned the relatively abundant specimens of Mio-Pliocene age. Among the more common specimens are cranial shields composed of ankylosed supraoccipital and parietals. Two major shield types are readily distinguished, one of which consists of swollen temporal crests that are lyriform (i.e., approach each other in the midline), and the other being a more squared-up cranial shield. Temporal crests in the latter are essentially lacking, not swollen, and widely separated, with lateral boundaries varying from a gentle rounding to a prominent upraised sharp edge.

Depéret and Roman (1920) considered *Metaxytherium* as having two parallel ramifications. *M. cuvieri* with lyriform temporal crests and of Vindobonian age represents one stock. The second, more abundant, stock is represented by forms with separated crests: *M. krahuletzki* and *M. beaumonti* of Burdigalian age and *M. petersi* and *M. aff. petersi* of Vindobonian age. Sickenberg (1928), on the basis of a complete young specimen of Tortonian age from the Vienna basin, referred *M. petersi* to a new genus, *Thalattosiren*. *M. aff. petersi* is then to be referred to *T. aff. petersi*; however, I would refer this specimen, as illustrated by Depéret and Roman (1920: pl. VII, figs. 3 and 4), to *M. cuvieri* because of geographical and geological proximity and osteological similarity. *T. petersi* of the Vienna basin is of similar age as the Mont-de-Marsan *M. aff. petersi* from France, but there are no good adult parietal specimens of the Austrian *T. petersi* (no figured specimens known to me) with which to compare the French specimen. The parietals of *M. cuvieri* from France, on the other hand, are both reasonably abundant and well preserved and do not differ from the Mont-de-Marsan specimen. Furthermore, Depéret and Roman (1920: 29) stated that the reference of the Mont-de-Marsan cranial roof to *M. aff. petersi* was tentative.

Simpson (1932: 455) found a condition in the cranial roofs of specimens from Florida, which he referred to the genus *Felsinotherium*, similar to that in the European *Metaxytherium*. He described this as follows: "The sagittal crests and general contour of the cranial roof differ considerably in the several available specimens, but the degree to which this variation is individual or specific is not clear." Later, in a

discussion of specimens V3211 and V3232 Simpson stated (1932: 455-456): "In the former specimen the crests on the parietals are very prominent, elevated and swollen, while on the latter they are very weak, little more than the sharp angle between the superior and lateral parts of the parietals. This distinction may be in large part due to age or sex, or may characterize the two species."

The progressive development of crests and rugosities with increasing age of individuals has been noted many times in various mammalian groups. This process applies to the degree of development in the temporal crests of the two living genera, *Trichechus* and *Dugong*, and has been recorded to some extent from the fossil record. In the young *Trichechus* and *Dugong* the crests are virtually nonexistent, and therefore are described as lacking to widely separated. Prominent crests progressively develop on males and females of both genera, an indication that such rugosities are probably attachments for muscle insertion and to a large extent a factor of age. Neither temporal crests nor accompanying portions of the cranial roof are seen to differ between sexes, and if this condition is applied to metaxytheres, two species or other taxa are represented by the differentiation of cranial shields.

#### INCISOR TUSKS

Tusks of a variety of marine mammals have been found in North America since Cope's 1869 proposal of *Hemicaulodon effodiens*, but no exacting dental study has been made of these isolated specimens. A series of five specimens consisting of partial premaxillaries with tusks or individual tusks are ascribed by Kellogg (1966: 78) to dugongids from as early as Miocene. Following the well documented study by Ray (1975) I consider the lost *Hemicaulodon* tusk to belong to the walrus *Odobonus rosmarus* and the three individual tusks (USNM 9457; USNM 23110; AMNH 9852) studied by Kellogg (1966) to belong to physeterid sperm whales. The two remaining specimens identified as Sirenia by Kellogg, the type right premaxillary of *Dioplotherium manigaulti* Cope, and a left premaxillary (YPM 21334) dredged from the Wando River, South Carolina, may belong to this order, but the fragmented specimens do not permit generic assignment. The only North American sirenian with a complete cranium bearing tusk-like incisors is the Middle to Late Miocene *Halitherium olseni* from Florida. Other cranial specimens such as *Caribosiren* from the Middle Oligocene of Puerto Rico and *Hesperosiren* from the Middle Miocene of Florida lack tusks, whereas *Metaxytherium jordani* (= *Halianassa vanderhoofi*) from the Late Miocene or Early Pliocene of California reveals two small pits at the end of the snout, which likely housed nonfunctional incisors.

Of the Recent Sirenia, the genera *Hydrodamalis* and *Trichechus* are edentulous, each having two minor pits housing nonfunctional incisors, whereas the genus *Dugong* possesses strong tusks in both sexes, with those of the females being slightly smaller. These examples suggest that the presence of tusks in sirenians does not indicate dimorphism, since both sexes seemingly either bear or lack tusks. Unfortunately this suggestion raises a paradox when one considers the following European and North American metaxytheres, which have in common geologic age, similar number of cheek teeth, almost identical cusp pattern of cheek teeth, and similar cranial construction throughout. A comparison of several pertinent cranial and dental characters can be seen in Table I.

TABLE I.—COMPARISON OF CRITICAL CRANIAL AND DENTAL CHARACTERS IN MIO-PLIOCENE DUGONGIDAE.

Species	Separated		Tusks	No Tusks
	Crests	Lyriform Crests		
<i>Felsinotherium forestii</i>	X		X	
<i>F. serresi</i>		X	X	
<i>Metaxytherium cuvieri</i>		X	X	
<i>M. jordani</i> (= <i>H. vanderhoofi</i> )	X			Pits, nonfunctional
<i>M. calvertense</i> (UF 11579 <sup>1</sup> )		X		Pits, nonfunctional

<sup>1</sup> Finest preserved cranium yet found in North America. From Florida, probably Late Miocene or Early Pliocene age. Not reported upon in this paper.

From this small sample of closely related Sirenia it may be seen that both types of cranial shields, whether separated or lyriform temporal crests, may bear or lack tusks. The first three species are European forms and bear tusks; the latter two tuskless species are from North America. *Thalattosiren*, a closely related European sirenian of comparable geologic age, lacks tusks. It may be noted that in the European Sirenia both types of cranial shields are associated with tusks, a feature that can be interpreted as representing either two separate species or merely sexual dimorphism. In the two North American specimens both types of cranial shields lack tusks, which would result in an analogous interpretation. Although the few well-preserved specimens suggest tusked European versus tuskless North American metaxytheres, it seems unlikely that the North American Mio-Pliocene forms would be virtual structural duplicates of their European counterparts, except for the absence of tusks. In a number of museums and small private collections in Florida, fossil sirenian tusks have occasionally been noted, and chance alone makes it seem unlikely that all belong, or can be assigned, to a tusked genus such as *Halitherium*. Whether *Dioplotherium* Cope 1883, a partial premaxillary with tusk, will eventually prove to be a metaxy-

there remains a question. Kellogg (1925: 59) placed *Dioplotherium* in the synonymy of *Metaxytherium*, a reasonable assignment but one that cannot yet be proved. Later Kellogg (1966: 91) re-elevated *Dioplotherium* to a distinct genus, which I also prefer until synonymy is demonstrated.

#### ORDER SIRENIA

#### FAMILY DUGONGIDAE GRAY

#### GENUS *Metaxytherium* CHRISTOL 1840

The Florida Mio-Pliocene metaxytheres are separable into three species, the distinction being basically contingent upon the degree of separation, size, and shape of the parietal temporal crests, coupled with variances in the shape and complexity of the upper cheek teeth, particularly  $M^3$ , which is always less worn than preceding teeth. Total morphologic features are also naturally considered, but the cranial roof and  $M^3$  are among the more common characters that can be used to demonstrate relationship. The three Mio-Pliocene species are *Metaxytherium ossivalense*, *M. floridanum*, and *M. calvertense*.

#### *Metaxytherium ossivalense* SIMPSON 1932

DIAGNOSIS:— $M^3$  obovate (egg shape) to subtriangular;  $M^2$  subquadrate to obovate;  $M^1$  quadrate; small cuspule blocks anterior cingular valley on buccal side of  $M^3$ ; metaconule displaced forward but median transverse valley relatively straight on  $M^3$ , unblocked by cuspule on either buccal or lingual side; low broad anteroposterior boss on frontals; parietal with temporal crests thin, upraised, widely separated; supraoccipital probably touched border of foramen magnum.

DISCUSSION.—Specimens assigned to this species by Simpson are the type (AMNH 26805), which consists of part of the left upper maxilla with broken  $M^3$  and alveoli, and the referred anterior two-thirds of a cranium; FGS V5454, which lacks the downturned extremity of the premaxillaries and the zygoma. The latter specimen is assigned by me to *Metaxytherium calvertense* Kellogg 1966. Specimens referred by me to *M. ossivalense* are FMNH P27227, an essentially complete posterior two-thirds of a cranium broken vertically at a point immediately anterior to  $M^1$ ; MCZ 4062, a parietal-supraoccipital cranial cap; UF 2847, an upper left  $M^1$  or  $M^2$ ; UF 11575-77, three  $M^3$ ; UF 3596, consisting of a partial rostrum, two fragmented unworn  $M^3$ , a partial mandible with teeth, an atlas, and a fragmented scapula. Other specimens tentatively assigned to this species are UF 3281, an upper left  $M^3$ ; FMNH P27228, a palate and maxillaries containing  $M^{1-2}$  and the alveolus of  $P^4$ ; FMNH PM155,

EPOCH	NORTH AMERICAN PROVINCIAL AGES	FLORIDA EQUIVALENT
PLIOCENE	BLANCAN	
	HEMPHILLIAN	BONE VALLEY GRAVELS <sup>1</sup>
	CLARENDONIAN	
MIOCENE	BARSTOVIAN	BONE VALLEY FAUNA <sup>2</sup>
	HEMINGFORDIAN	HAWTHORNE
	ARIKAREAN	

FIGURE 2.—Correlation of Hawthorne and Bone Valley strata with North American provincial ages. <sup>1</sup> Bone Valley Gravels of Sturton (1936), Wood *et al.* (1941), and Webb and Tessman (1968). <sup>2</sup> Bone Valley Fauna of Olsen (1959).

a plaster cast of right and left maxillaries containing on either side (exception left M<sup>1</sup>) alveoli for P<sup>4</sup>, a worn M<sup>1</sup> and M<sup>2</sup> and partially erupted M<sup>3</sup>, FGS V5953, a right M<sup>3</sup>.

PREMAXILLARIES.—No evidence of incisors is present in the premaxillaries of UF 3596. This feature is characteristic of all North American metaxytheres reported to date, in contrast to European metaxytheres,



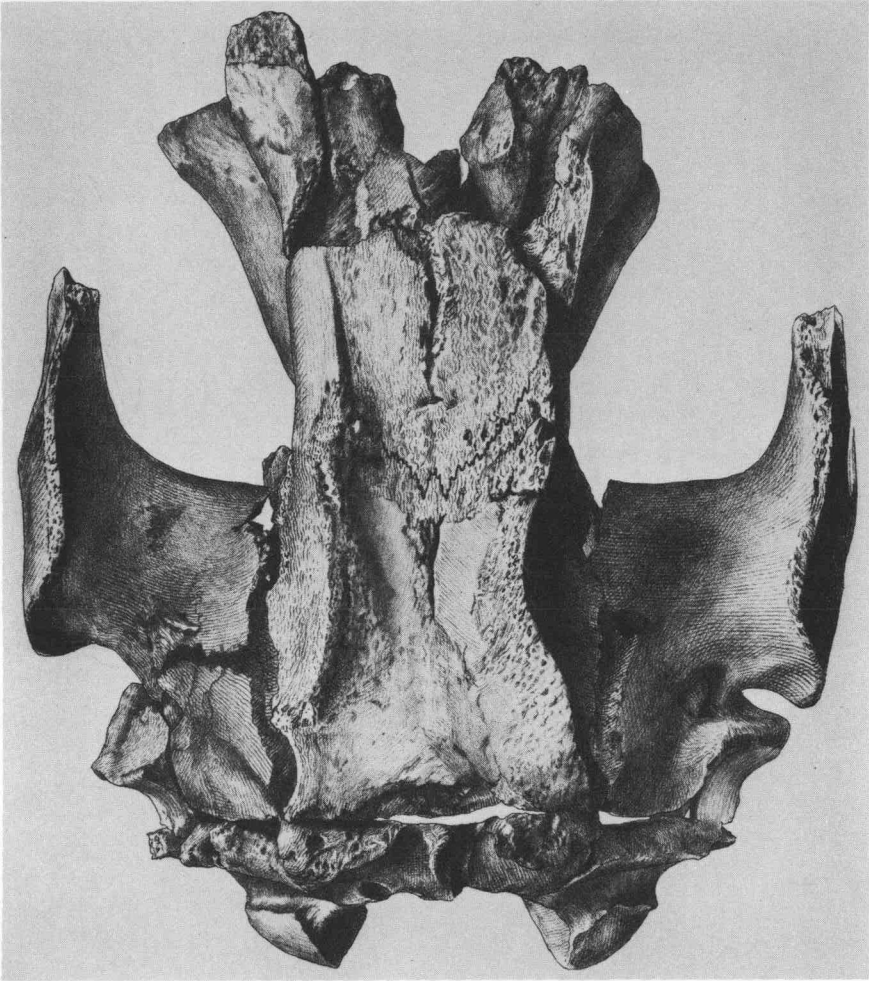


FIGURE 3.—*Metaxytherium ossivalense* (FMNH P27227): dorsal view of cranium.

which have well developed incisors. Owing to the general paucity of rostral specimens, it remains a question whether future finds will continue to support present information concerning lack of all but incipient tusks in North American forms. As stated previously, this lack of incisors is also characteristic of the European *Thalattosiren*, the North American *Caribosiren*, *Hesperosiren*, and *Metaxytherium*, the recently extinct *Hydrodamalis*, and the living *Trichechus*. A moderately broad, swollen boss found on either side of the rostrum of *M. ossivalense* lacks the prominent development present in *Dugong*. In an accentuated manner, similar to the development in *Dugong*, a double arch exists in the anterior border



FIGURE 4.—*Metaxytherium ossivalense* (FMNH P27227): ventral view of cranium.

of the mesorostral fossa. The smaller anterior arch, also peculiar to *Thalattosiren petersi* (Sickenberg 1928: 297, fig. 1) and *Dugong*, appears to have its incipient development in *Eotheroides*. Such a double arch is absent in Eocene Sirenia (exception, *Eotheroides*) and in the Oligocene *Halitherium*, appears to be present but not prominent in *Hesperosiren*, and is developed to a moderate degree in the Oligocene *Caribosiren* (Reinhart 1959: 10, fig. 26) and the Mio-Pliocene metaxytheres. The degree of arch development seems to be associated with a well-developed and wide nasopalatine canal and most prominent in those genera having wide grooves for the nasopalatine cartilaginous canal.

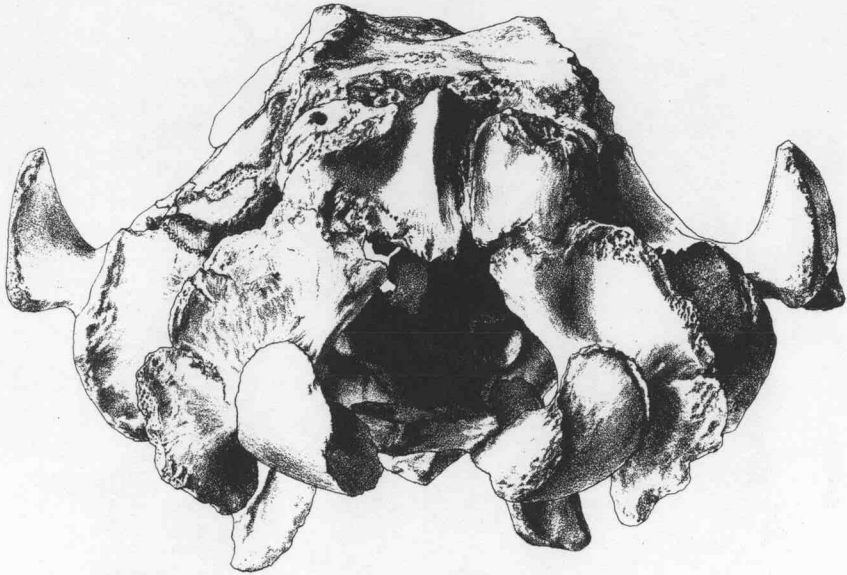


FIGURE 5.—*Metaxytherium ossivalense* (FMNH P27227): posterior view of cranium.

**NASALS.**—Because the nasal-frontal sutures were fused, the boundary between these elements is indeterminate, and it cannot be ascertained whether the nasals were separated or met in the midline. Closely related forms in the same geographical area and stratigraphically equivalent sediments have nasals separated by a forward extension of the frontals; a condition characteristic of the metaxytheres and the referred felsinothers. The only sirenian recorded from the North American-Caribbean area that is believed to have nasals meeting in the midline is the Florida *Halitherium* reported upon in this paper. Although the nasal region is largely missing in this halitheriine, it is comparable in all other features to the European genus and therefore considered to have similar bony relationships in this area. Among European genera in which the nasal-frontal relationship is known, only the metaxytheres and referred felsinothers are characterized by nasals that are not united in the midline. An exception to this statement is *Metaxytherium* n. sp., which has nasals meeting in the midline (see illustration by Kaltenmark [1942: 107]). All other metaxytheres that show the nasal region are in disagreement with this reported condition. For a more complete discussion of the nasal-frontal relationship see Reinhart (1959: 59-62).

**FRONTALS.**—The frontals of metaxytheres vary from forms with squared lateral boundaries and a relatively rectangular outline to those exhibiting a gradual anterior expansion of these elements from the



FIGURE 6.—*Metaxytherium ossivalense* (MCZ 4062): dorsal view, parietal-supraoccipital cap.

parietal-frontal contact. *M. ossivalense* features elongate, squared frontals bounded by weakly developed temporal ridges that parallel each other back to the parietals. A low broad anteroposterior elongate boss is present in the anterior midline, a condition that appears to characterize all species of *Metaxytherium*, as well as referred felsinothers. Gradual expansion of the postorbital processes begins at a point lateral to the anterior end of the frontal boss, but the distal ends are broken. When the frontals and parietals are found separated, the frontal-parietal sutures are marked by a complex series of slanting ridges, a condition often well expressed in both young and mature individuals.

PARIETALS.—The configuration of the parietal-frontal suture, seen on

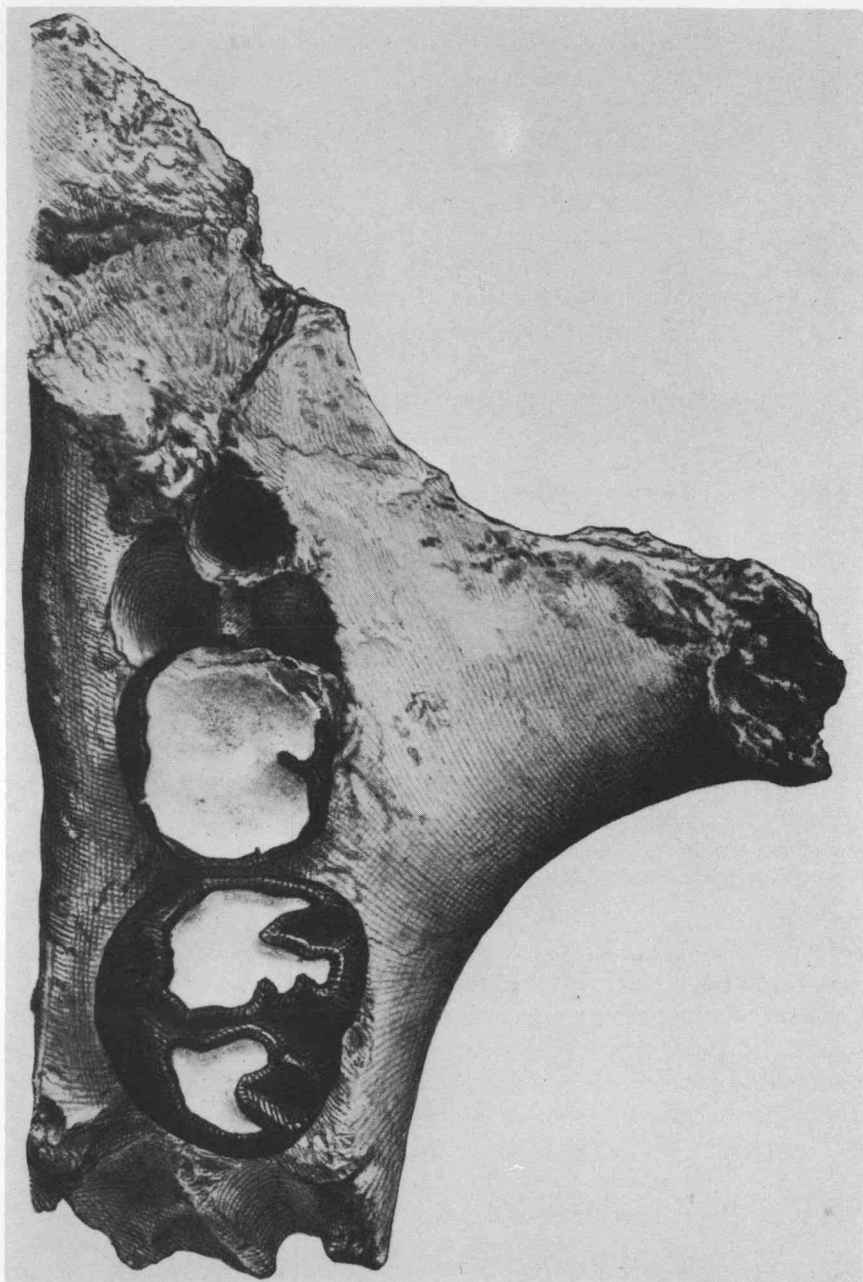


FIGURE 7.—*Metaxytherium ossivalense* (FMNH P27228): occlusal view of left maxillary containing M<sup>1-2</sup> and P<sup>4</sup> alveolus.

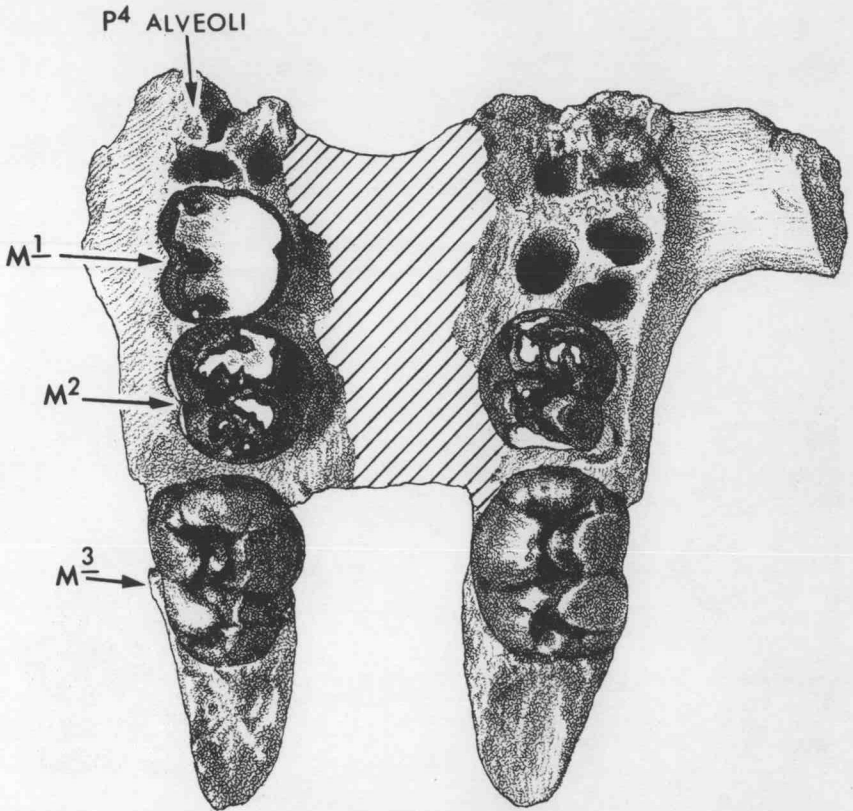


FIGURE 8.—*Metaxytherium ossivalense* (FMNH PM155): occlusal view of M<sup>1-3</sup> and P<sup>4</sup> alveolus (M<sup>3</sup> partially erupted).

both dorsal and dorsolateral surfaces, is approximately the same as that found in other metaxytheres and in all Sirenia in general (*i.e.* long narrow arms of the parietal project forward over the frontal on either side of the midline). Lyriform temporal crests are relatively thin, sharply upraised, and widely separated. Outline of the crests is similar to those attributed to *Metaxytherium* aff. *petersi* Abel (Depéret and Roman 1920: pl. 8, fig. 4). One element of distinction among the Florida metaxytheres is based upon variations in the degree of development and shape of the parietal temporal crests, as found in adult specimens. The difference in shape of temporal crests is probably not due to age but may instead be a sexual, or perhaps specific difference that developed in populations separated in geologic time. The last theory is advanced despite the assumption that animals existing during the years encompassed by deposition of the Bone Valley sediments are thought to be essentially

contemporaneous. Temporal crests are often moderately developed on young adults, with growth progressively accentuated with increased age. The general unworn quality of the crania would seem to rule out the possibilities of removal of the crests by abrasion or solution, either of which would leave some indication of such actions.

The parietal-supraoccipital element is stoutly fused into a single bony unit, as is characteristic of the Sirenia. This ankylosed condition is present even in the fetal stages of *Dugong* and *Trichechus*, but there is no complete union between the supraoccipital and other adjacent bones until the adult stage is reached. In FMNH P27227 the parietal-supraoccipital complex meets at an angle of 101 degrees, which is comparable to the 105 degrees of similar elements in FGS V3232, referred to *M. floridanum*. In this instance the slight difference in degrees between the two species may be the result of preparation in the former specimen or to age difference, a greater angle being characteristic of youth. Measurements in the union of the parietal-supraoccipital shield in the metaxytheres are in contrast to *Dugong*, in which these elements meet at a much higher angle (122 degrees in the young specimen at hand).

Internally the parietals form the greater portion of the braincase in the superior and posterior areas. The cerebral hemispheres are elongate, laterally compressed, and separated by a very prominent longitudinal median carina, which forms an internal occipital protuberance posteriorly and ends abruptly, abutting against the supraoccipital. The median carina divides into two separate ridges about 15 mm posterior to the frontal-parietal suture in the braincase. These continue forward as two low-rounded ridges, become progressively smaller anteriorly, and spread out on either side of the crista galli. This same bony condition is true in the large *Metaxytherium jordani* of the Pacific coast, in *M. calvertense*, and in FGS V5947 (*Metaxytherium* indet.); in contrast to *Trichechus* and *Dugong*, in which the median carina continues anteriorly to the crista galli as a single ridge that spreads out just before contact with this bony complex. The relationship of the parietals to other bony elements within the braincase is about the same as that found in all Sirenia; however the elongate shape of the cerebral hemispheres differs from those in certain other genera, which are more subquadrate in this region.

**SUPRAOCCIPITAL.**—In FMNH P27227 an unusually well developed external occipital protuberance, resembling that of *M. jordani*, is bounded on either side by deep grooves, which in turn are bordered by an oblique rugose area. The prominent degree of development of tuberosities and rugosities, as well as the large size of the parietal, suggests the cranial specimens assigned to this species are adults, perhaps tending toward old age. Specimen MCZ4062 displays a broadly rounded lambdoidal

crest, in front of which lies a small but noticeable boss in the midline of the parietals.

**EXOCCIPITALS.**—The condyles are semilunar in shape, with the articular surfaces convex both transversely and vertically. Condylar foramina are similar in size to those of *Metaxytherium jordani* (= *M. vanderhoofi*) and are comparably much larger than those in *Dugong*. The supracondylar fossa is broad and shallow and terminates in sharp crests at its lateral borders, in contrast to the gently rounded borders of comparable areas in *Dugong*. *Exoccipital* borders are unusually prominent, overriding the posterior end of the post-tympanic processes that abut against it. Inferiorly, the paroccipital process is very thin and is characterized by the deep concave surface formed by a border that curves back toward the median line. Accentuation of the paroccipital process is shown by their extension below the ventral surface of the condyles.

Sutures between the supraoccipital and exoccipitals are indeterminate in FMNH P27227, but judging from the angle at which the exoccipitals rise to form the dorsal portion of the foramen magnum, it is quite possible that the supraoccipital closely approached or touched this foramen. If the supraoccipital formed part of the dorsal border of the foramen magnum, it lacked the high dorsal indentation illustrated for "*Metaxytherium* nov. spec." (Kaltenmark 1942: 105, fig. 1). The foramen magnum of FMNH P27227 is a flattened transverse outline, with a suggestion of a very slight rise in the dorsal midline. A dorsal indentation in the border of the foramen magnum is present to some degree in practically all sirenians, the only exceptions being those of *Trichechus* and of *Felsinoitherium serresi* (Déperet and Roman 1920: 5, fig. 4), the later illustrated from a cast. On the same page, however, it is stated that the occipital foramen is oval and higher than wide, which is in agreement with the illustration but different from all other metaxytheres. Both Abel (1904) and Simpson (1932) attributed considerable taxonomic importance to the proximity of the supraoccipital to the dorsal margin of the foramen magnum and to the sutural angle formed by the supraoccipital and exoccipitals. I am in complete agreement with this conclusion.

Beginning with Eocene sirenians in the family Dugongidae, there has been an irregular progressive tendency for the ventromedial portion of the supraoccipital to be near, or to form a minor part of, the mid-dorsal border of the foramen magnum. An exception is the Eocene *Protosiren fraasi* (Sickenberg 1934: pl. 1, fig. 2), in which a character of the recent *Dugong* had already appeared (*i.e.* the supraoccipital touches the foramen magnum and the supraoccipital-exoccipital angle is approximately 160°). This condition is in contrast to that of *Trichechus* and the Eocene



*Eotheroides* (= *Eosiren*) *libyca* (Andrews 1906: 198-199, pl. XX, fig. 16); in *Eotheroides* the supraoccipital is separated from the foramen magnum by 23 mm, and the supraoccipital-exoccipital angle is  $160^\circ$ . The Oligocene *Halitherium schinzi* has a similar supraoccipital-exoccipital relationship as is present in *Eotheroides*; the exoccipital angle is  $167^\circ$  and the supraoccipital approaches to 21 mm of the foramen magnum. Separation of the supraoccipital from the dorsal border of the foramen magnum in *Trichechus* is considered retention of a primitive feature.

Exclusion of the supraoccipital from the foramen magnum has been considered a prototypic arrangement, but participation of the supraoccipital in the foramen margin of the otherwise structurally primitive Middle Eocene *Protosiren* cannot be overlooked. Perhaps *Protosiren*, as do most other Sirenia, bore a combination of osteological advances and a retention of primitive phases in its construction.

Abel (1904) has given figures for *Metaxytherium krahuletzki* in which the supraoccipital is 18 mm from the foramen magnum, and the exoccipitals meet at an angle of about  $130^\circ$ . *Metaxytherium jordani* (= *Halianassa vanderhoofi*) (Reinhart 1959: 26) is in essential agreement, with a separation of 10 mm and an angle of  $136^\circ$ . Coupled with the California Middle Miocene *M. jordani* is the immature Baja California *Metaxytherium reinharti*, which bears a comparable  $137^\circ$  exoccipital angle and an estimated 5 mm supraoccipital-foramen magnum separation. According to Kaltenmark's figure (1942: 105, fig. 1), the exoccipitals of *Metaxytherium* nov. spec. meet at an angle of about  $130^\circ$  and the supraoccipital reaches the foramen magnum. In *Felsinotherium foresti* Capellini, the supraoccipital may just touch the foramen magnum and the exoccipital angle is about  $124^\circ$ . The supraoccipital may either touch or be excluded from the foramen magnum in *Felsinotherium serresi* Gervais. Depéret and Roman (1920: fig. 2) illustrated *F. serresi* with the supraoccipital excluded and an oval rather than the more characteristic cordiform outline of the foramen magnum. Simpson (1932: 457) described two specimens that he referred to *Felsinotherium*; FGS V3211 with an exoccipital angle of about  $115^\circ$  and the supraoccipital not over 5 mm from the foramen magnum<sup>1</sup>, and FGS V3232 with an angle of about  $120^\circ$  and the supraoccipital closely approaching the foramen magnum. From the specimens at hand the supraoccipital of *Dugong* touches the foramen magnum and the exoccipital angle is  $140^\circ$ . Comparable elements of the adult *Trichechus* display a 12 mm separation and an angle of  $136^\circ$ .

<sup>1</sup> Simpson's illustrations of this specimen (1932: 457, fig. 14B) differs from the text measurements, and I agree with the illustration, which shows that the supraoccipital formed the dorsal border of the foramen magnum. Sutures of the specimen are not distinct in the dorsal midline of the foramen magnum; therefore this feature is a matter of interpretation.

There may be a slight discrepancy in angles as a result of variation in the preservation or preparation of the fossils.

It is interesting to note the similar configuration of the parietal-supraoccipital complex between the young Pleistocene trichechids and certain older Mid-Oligocene-Pliocene sirenians. A series of water-worn parietal-supraoccipital elements (UF 3965 and UF 14222-14226) referred to *Trichechus* sp. display a narrow cranium with convergent lyri-form crests. The thin elongate roof distinguishes these specimens from the larger metaxythere crania but suggests affinities with *Hesperosiren* (MCZ 4432), *Halitherium*, and *Caribosiren*. Coupled with this important feature, a rugose sutural surface on the supraoccipital indicates this element met the exoccipitals at an angle of  $146^\circ$  and was separated from the foramen magnum. In crania where the supraoccipital approaches or takes part in the foramen magnum, the element usually thins in the ventral midline and bears a small dorsal indentation. The referred specimens thicken at this point and show no indentation; the supraoccipital was therefore well separated from the foramen magnum. The occiput is unknown in *Caribosiren*, but the lack of contact between the supraoccipital and the foramen magnum differentiates the Florida trichechids from *Hesperosiren*. The supraoccipitals of these specimens are readily distinguished from *H. olseni* in the more posterior thrust of the ventral midline and the much thicker medial ventral area, which lacks the central fossa of *Halitherium*.

Unfortunately the only locality data given for UF 3965 is "Florida." UF 14222-14226 were collected in Pleistocene sediments in the Waccasassa River, Levy County, Sec. 16, R15E, T15S.

**SQUAMOSAL.**—The posterior portion of the cranial part of the squamosal is not in contact with the exoccipital dorsally, the two bones being separated by a narrow, elongate fontanelle which in its ventral portion leaves the mastoid exposed. The corresponding squamosal-exoccipital in *Dugong* is wider but of similar length. As in all sirenians, the squamosal forms a small circle directly above the post-tympanic process and around the periotic, thus leaving the latter bone exposed externally. In contrast to *Dugong*, the post-tympanic process is well developed, with the ventral portion directed anteriorly and terminating abruptly in a blunt ovoid. The squamosal-parietal relationship shows a detailed similarity to that of *Dugong*, particularly in the angulation of these bones along the temporal wall of the braincase. The cranial wing is set into and topped by a thin overlap of the parietals. The zygomatic root and arch has the same general configuration as other specimens of *Metaxytherium*, except *M. jordani*, which has a pronounced anterior inclination. The zygomatic root is elongate, vertically thin, and terminates posteriorly in

a deep-U that is open in a posterior direction. Immediately behind, and parallel to, either broken glenoid surface is an elongate transverse depression, which is much deeper than in *Dugong*. A high narrow triangle is formed by a cross-section of the sinous arch, with all borders ending in thin crests except the ventro-anterior which is broadly rounded.

**AUDITORY REGION.**—All of the ear bones are of a dense composition and have a swollen appearance, particularly the periotic and mastoid. As in the Sirenia in general, the periotic lies in a hollow cup formed in the base of the squamosal, with the more swollen and posterior mastoid lying in a shallow basin formed chiefly within the paraoccipital processes. The tympanic ring is missing, but its attachments to the petrosal are similar to those in *Dugong*. Two of the ossicles, the incus and the stapes, are present. The incus is a stout bone, with complex articular surfaces for the malleus on its inferior side and a convex smooth surface on its superior side. The upper portion of the incus lies in the deep groove of the fossa incudus. The crus breve is shorter and stouter than that of *Dugong dugong* (= *D. australis*) (Doran 1879: pl. LXIII, fig. 29); the crus longum is broken. The left stapes, which extends inward and lies slightly below the incus, is a stout cylindrical bone perforated by a minute stapedia foramen near the base; the right stapes appears to have been imperforate or nonfunctional. This ossicle is 12.2 mm long with the foramen 3.7 mm from the base. These measurements are comparable to the stapes of *M. jordani*, which is 14.8 mm long with the stapedia foramen 4.4 mm from the base, and to that of *M. jordani* (= *H. vanderhoofi*), which is 12.6 mm long with the foramen also 4.4 mm from the base. The entire group resembles in detail that of *Dugong* as illustrated by Doran (1879: pl. LXIII, fig. 30).

**BASIOCCIPITAL.**—There is little to distinguish the basioccipital from similar elements in other metaxytheres or from Sirenia in general. The ventro-anterior surface is greatly thickened, rugose, and roughly rounded; the dorsal surface is flat, with a thin spatulate extension overlying the basioccipital. The maximum thickness of this element at the anterior end is 39 mm; the minimum width, 30.3 mm, is at the center.

**BASISPHENOID.**—The basisphenoid of FMNH P27227 is comparable in size to that of *Dugong*, being larger only because of a larger cranium. Apparently this element maintains a relatively constant size, depending upon the size of the cranium. Between the base of the pterygoid processes, the ventral surface of the basisphenoid is approximately 30.5 mm wide; from the ventral surface of the basisphenoid the pterygoid processes are inclined laterally and measure about 68 mm between the inner surface of their ventral tips. The ventral surface of the basisphe-

noid and basioccipital meet at an angle of about  $120^\circ$ . Unlike most other sutures in the cranium, the basisphenoid-basioccipital suture is not fused. This condition is the same in *M. calvertense* (FGS V5454), whereas the suture is thoroughly fused in FGS V3211, also referable to *M. calvertense*. Sickenberg (1931: 428) notes the general occurrence of a nonfusion of this suture, discusses its relationship to other conditions in the Sirenia, and attributes these to hypothyroid metabolism. Nonfusion of this suture occurs in *Caribosiren* and *M. jordani* (= *H. vanderhoofi*), but both specimens studied are young adults, as judged by the general open sutures throughout the cranium of each. Dilg (1909: 115) stated that the two bones are separated in *Trichechus* up to the ninth year, indicating that the state of fusion revealed in FGS V3211 marks it as a very old individual.

Endocranially, a prominent olfactory groove on either side of the crista galli leads anteriorly into a perforated fossa, partially destroyed in FMNH P27227 but well displayed in *M. calvertense* (FGS V5454). Behind and ventral to these grooves are the optic foramina, separated by a thin crest of the presphenoid. In a transverse line between the optic foramen the bones are perforated by many minute foramina.

PTERYGOIDS.—A comparison of the pterygoids of *M. ossivalense* and *M. calvertense* reveals no differences. Well-developed pterygoid processes begin at the posterior portion of the basisphenoid and slant anteriorly. They are characterized by stout bases and are deeply grooved posteriorly from base to tip; the lateral and medial margins of the grooves are more nearly equal than in *Dugong*, in which the medial is much the more prominent of the two. The postero-lateral and medial

TABLE 2.—CRANIAL MEASUREMENTS OF *Metaxytherium ossivalense* (FMNH P27227).

CRANIUM	
Length, posterior end of occipital condyle to anterior end of M <sup>2</sup> .....	258.0
Length, posterior border of mesorostral fossa to posterior end of external occipital protuberance .....	202.4
Maximum width between lateral extremities of zygomatic arches .....	252.2
Maximum width of exoccipitals at lateral margins .....	176.5
Maximum width, foramen magnum .....	72.2
Maximum width, lateral border of occipital condyles .....	123.0
Length, midline of parietal-frontal suture to posterior border of external occipital protuberance .....	110.0
Maximum width of parietal temporal crests at juncture with squamosal wing ...	97.2
MEASUREMENT OF MCZ 4062	
Length, midline of parietal-frontal suture to posterior border of external occipital protuberance .....	94.5
Maximum width of parietal temporal crests at juncture with squamosal wing ...	93.4

TABLE 2.—CONTINUED

DENTITION					
M <sup>3</sup>	Length	Width Anterior loph	Length Anterior loph	Width Posterior loph	Length Posterior loph
Type AMNH 26805	30.5	28.8 <sup>e</sup>	1.06	17.2	1.77
FMNH P27227	30.0	25.7	1.17	21.5	1.40
UF 11576	30.5	24.0		17.0	
UF 11575	32.2	24.0		18.3	
UF 11577	31.0	26.7		20.3	
FMNH PM155	29.2	23.5	1.24	20.0	1.46
UF 3596	25.0	22.0	1.14	20.6	1.21
UF 3281	29.3	22.9	1.28	19.0	1.54
FGS V5953	29.7	24.2	1.23	21.0	1.41
M <sup>2</sup>					
FMNH P27227	29.4 <sup>e</sup>	25.9	1.14	23.0	1.28
UF 2847	20.5	17.9	1.15	15.0	1.37
FMNH PM155	21.8	24.2 right	.90	18.6	1.17
		21.8 left	1.00		
FMNH P27228	25.0	24.0	1.04	20.0	1.25
M <sup>1</sup>					
FMNH PM155	20.2	20.2	1.00	18.2	1.11
FMNH P27228	19.7	18.8	1.11	17.7	1.11

e = estimated

margins of *M. ossivalense* are thin and have sharp crests, whereas the medial margin of *Dugong* has a broadly-rounded crest and relatively no crest at the lateral margin. On either side of and above the pterygoids is the large sphenorbital fissure, the anterior end of which descends abruptly downward and continues by a broad groove into the anterior portion of the base of the pterygoid process. In *Dugong* this fissure is formed by the posterior margin of the palatines and the internal portion of the alisphenoid, roofed by the inferior margin of the orbitosphenoid, and connected postero-internally with the postero-dorsal edge of the base of the pterygoid process. Although in an excellent state of preservation, the bony relationship of the elements forming these fissures in FMNH P27227 is indeterminate.

**ORBITOSPHEOID.**—The orbitosphenoid is essentially the same as in *Dugong*. It is pierced in an antero-posterior direction by the optic canals that open anteriorly just above and in front of the sphenorbital fissure. The optic canals of FMNH P27227 (*M. ossivalense*) differ from those in FGS V5454 (*M. calvertense*) only because they are larger.

## DENTITION

Stages of life represented by the studied specimens range from approximately early adult to a point that precedes old age. Cusps of the teeth are lophodont or essentially arranged in transverse rows, a condition typical of the Sirenia.

M<sup>3</sup>.—A perplexing number of minor cusp variations with transitional gradations occur in the M<sup>3</sup> of the metaxytheres. In the norm of the specimens a prominent anterior cingulum is closed on the lingual side by a juncture of the protocone and cingulum, and an accessory cuspule blocks the buccal side of the anterior cingular valley. A variation from this condition is found in UF 11577, where the anterior loph appears to have been formed by two separated cusps. A second loph is formed by a large protocone and a medium-sized protoconule and paracone. A deep median valley separates the anterior and larger portion of the tooth from the posterior part. Behind the transverse median valley the lophodont character is modified as the middle cusp (metaconule) and is displaced forward to block the valley, a feature characteristic of the metaxytheres. The degree of anterior displacement of the metaconule varies from the metaconule lying completely in front of the hypocone and metacone to a very minor advance. A lingual hypocone is generally confluent with the metaconule, and either cusp is usually slightly larger than the metacone. Without exception the hypocone lies posterior to the metacone. A posterior cingulum composed of two or three small cusps is usually adherent to the hypocone, with a fossa between metacone and accessory cusps opening on the buccal side. The border of this cingulum is broadly rounded in all specimens but the type, in which the round outline is much narrower. Two unworn M<sup>3</sup>'s of FMNH PM155 are in the process of eruption and extend to a point about half-way down the crown of M<sup>2</sup>. The arc-like eruption of these teeth follows the pattern of tooth succession of other Sirenia, in which the anterior cusps come into use first and at eruption extend out of the jaw farther than the posterior portion of the tooth.

M<sup>2</sup>.—Comparison of the ratio of length/width in M<sup>2-3</sup> reveals that M<sup>2</sup> is more nearly subquadrate and is usually of shorter length but of relatively greater width. Like M<sup>3</sup> it is lophodont and divided subequally by a transverse median valley into a large anterior and a smaller posterior portion. A thin prominent anterior cingulum is separated by a deep valley that is closed by a small accessory cuspule at the buccal side of the tooth (see UF 2847), and is blocked at the inner margin by the tightly adhering protocone and cingulum. A transverse loph is formed by the protocone, protoconule, and paracone, of which the former may

be slightly larger than the other two cusps. As in  $M^3$ , the metaconule is closely appressed to the hypocone and is anterior to this cusp and the metacone, which are on a transverse line. The transverse median valley is near closure on the lingual side but widely separated at the buccal extremity. One large cusp, in close contact with the hypocone, usually forms the posterior cingulum. A fossa between the metacone and cingulum opens at the outer posterior border of the tooth. One obvious difference between  $M^2$  and  $M^3$  is the lack of minor accessory cusps in  $M^2$ .

$M^1$ .— $M^1$  has a quadrate outline and is much smaller than  $M^2$ . The available specimens are deeply worn, but it can be seen that the transverse median valley divided the tooth into two equal parts. A thin transverse anterior cingulum is inferred from the presence of a small external enamel lake, which marks the buccal opening of the cingular valley. A similar condition is present at the posterior end of the tooth, where a fossa formed between the posterior cingulum and the hypocone opens buccally. Because of the worn condition of the tooth, it is not known if accessory cusps were present.

$P^{3-4}$ .—The crown pattern of these teeth is unknown in the Florida specimens, but the alveoli for the teeth are present. FMNH P27228 bears alveoli for  $P^4$ , but there is no evidence for  $P^3$ .  $Dp^3$  may have been present in a very young stage of this individual and later shed, but there is no suggestion of this condition. Gregory (1941: 36) states that ". . . an indistinct smaller anterior region which lodged  $Dp^3$  may be observed on the right side in FGS V5454." This specimen, originally identified as *F. ossivalense*, is now referred to *M. calvertense*.

$P^4$ .—The manner of cheek tooth replacement from a posterior to anterior position indicates some pressure is being applied from rear teeth to those anterior. Evidence of this pressure is revealed by the noticeable indentations in the enamel between teeth, and the manner in which the most anterior teeth are worn and pushed out of the jaw. Such an anterior progression would suggest a possible slant to the root system, but FMNH 27228 clearly reveals vertical  $P^4$  alveoli. Following the loss of  $P^4$ , the anterobuccal root of  $M^1$  moves forward into the alveolus of the posterobuccal root of  $P^4$ . The other two alveoli of  $P^4$  are then gradually filled with cancellous bone and become indistinct.

ROOT SYSTEM.— $M^{1-3}$  are firmly anchored in the maxilla by one large, centrally-located lingual root and two transversely broad buccal roots, which display incipient bifurcation. As is the usual case in metaxytheres, the single lingual root when exposed is found to be sharply recurved posteriorly at the base, which acts as a hook to lodge teeth in their sockets. In contrast the two buccal roots are straight.

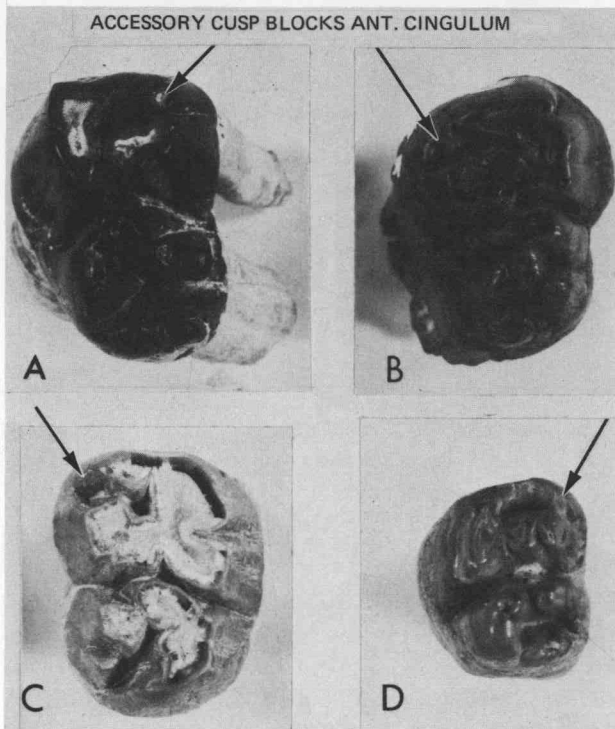


FIGURE 9.—*Metaxytherium ossivalense* occlusal views: (A) (UF 11575) left M<sup>3</sup>; (B) (UF 11576) right M<sup>3</sup>; (C) (FGS V5953) right M<sup>3</sup>; (D) (UF 2847) left M<sup>1</sup> or M<sup>2</sup>.

*Metaxytherium floridanum* HAY 1922

DIAGNOSIS.—M<sup>3</sup> anterior cingulum and loph transversely expanded; central portion of anterior border of tooth just forward, indicating incipient development of an anterior cingulum separate from anterior loph; anterior cingular valley deep, pronounced, not blocked buccally by accessory cusps; metaconule displaced forward, completely blocking transverse median valley; posterior border transversely straight, composed of variable number of supernumerary cusps; M<sup>2</sup> subquadrate to broadly egg-shaped, and although worn the M<sup>3</sup> cusp description essentially applies (except for posterior border missing in M<sup>2</sup>); cranial roof "squared up;" low, broad, elongate boss on frontals; temporal crests widely separated, the lateral border terminating in sharp edge on parietals, low and gently rounded in medial direction.

DISCUSSION.—I believe that the generic designation given by Hay (1922) to *Metaxytherium floridanum* is correct, and that later references





FIGURE 10.—*Metaxytherium floridanum*: (A) (FGS V3232) dorsal view of parietal-supraoccipital cap; (B) (UF 2199) occlusal view of right  $M^1$ - $3$ ; (C) (UF 2199) dorsal view of cranium.

of this species to *Felsinotherium* are incorrect. For the sake of accuracy, it should be added that in the holotype, the anterior border of  $M^3$  is worn through contact with the preceding  $M^3$ ; therefore the length 26.5 mm would be slightly greater in an unworn specimen. The width of the  $M^3$  given by Hay as 25 mm is the maximum width across the anterior loph formed by the protocone, protoconule, and paracone. UF 2199 is referred to this species and consists of portions of the cranial roof, exoccipitals, squamosal, jugal, ear bones and maxillary, the last containing an  $M^3$  on either side, an  $M^2$ , and a fragmented  $M^1$ . Also referred is a cranial cap of fused parietals and supraoccipital (FGS V3232), a specimen discussed as *Felsinotherium* sp, but not figured by Simpson (1932: 455-458). Reference of UF 2199 to *M. floridanum* is done with some reluctance, because the holotype is a worn specimen that does not present the diagnostic qualities of the species as distinctly as would be desired.

**CRANIAL CAP.**—Varied cranial remains of UF 2199 indicate that it represents a large adult, but not a form as massive in construction as the larger *M. jordani* of the California Miocene. The angle at which the posterior end of the premaxillary arm joins the postorbital process indicates a mesorostral fossa with a very wide posterior border. Nasal boundaries cannot be determined because of nasal-frontal fusion and fragmentation. A low, broad, elongate frontal boss is present, as in *M. ossivalense* and *M. calvertense*, but unlike the latter the frontals are "squared up" and essentially lack temporal crests. The undulatory lateral border of the postorbital processes is almost identical to that of *M. jordani*. Temporal crests on the parietals are widely separated and weakly developed in comparison to the condition present in other Florida metaxytheres, and end in a sharp lateral edge with a gentle medial rounding. The almost complete lack of temporal crests on adult specimens may prove to be a specific distinction differentiating this species from *M. ossivalense*, which bears relatively narrow upraised sharp crests, and from *M. calvertense*, which is characterized by broadly swollen temporal crests that closely approach each other in the midline.

**JUGAL.**—The anterior end of the zygomatic arch is fragmented and does not reveal the bony contacts of the maxilla and jugal. The jugal is vertically expanded beneath and posterior to the orbit, with a gradual diminution of this bone posteriorly. The malar process, which bears a wide shallow groove on the lateral surface, extends back to a point about 17 mm anterior to the glenoid plate. This process is either rarely preserved or perhaps less readily recognized and collected as an isolated bone than are most other cranial elements of fossil Sirenia. There are no features that differentiate this element from those found in better preserved metaxytheres. When compared to the three recent genera, the general configuration of this element most nearly approximates *Hydrodamalis*; also, the outline differs little from the Eocene *Protosiren*.

An important element that suggests degree of evolution is the progressive approach of the ventral midline of the supraoccipital to the foramen magnum. In FGS 3232 the exoccipital-supraoccipital contacts are diverted at an angle of 125°, and the supraoccipital closely approaches the foramen magnum. This is the general condition found in all Florida metaxytheres.

**M<sup>3</sup>.**—One of the distinguishing qualities in UF 2199 is the great width across the anterior loph, as compared to the length in M<sup>2</sup> and M<sup>3</sup>. The result is a length-width ratio that indicates a more squared-up tooth than the usual elongate M<sup>3</sup> present in other metaxytheres. The width across the protocone, protoconule, and paracone of 30 mm, in both M<sup>2</sup> and M<sup>3</sup>, is by far the greatest recorded width for this portion of either



Three large roots are present in  $M^3$ . Beneath the protocone a large long root is curved dorsally toward the buccal side of the maxillary. The root beneath the paracone follows a dorsal course, with a strong curve to the buccal side of the maxillary. This root is much shorter than that beneath the protocone, displays an incipient bifurcation throughout its length, and ends distally at the buccal border of the maxillary. Beneath the hypocone and the posterobuccal portion of the posterior cingulum, a large root is strongly bent posterobuccal toward the elongate, laterally-flattened, grooved knob formed by the ventroposterior extension of the maxillary. Because of exposure on the buccal side of the maxillary, it can be noted that the distal extension of the root is open, and during life was covered by a very thin, moderately-porous covering of the maxillary.

$M^2$ .—As in a number of sirenians, the  $M^2$  of UF 2199 has an equal or greater width across each major transverse loph than has  $M^3$  and is but slightly shorter in length. Only minor differences in cusp pattern are present between  $M^2$  and  $M^3$ , but in less worn specimens there is invariably an increase in the number of accessory cusps from anterior to posterior teeth. The anterior border of  $M^2$  is broadly rounded, probably is less undulatory than in  $M^3$ , and the hypocone is proportionally larger. Because of wear, it is impossible to determine the number of cuspules in either the anterior or posterior cingulum. Three large roots are present in a position similar to those in  $M^3$ . A break in the specimen between  $M^{2-3}$  indicates that the posterior root is essentially vertical.

As in larger Sirenia, the cheek teeth have a forward displacement in relationship to the zygomatic-orbital bridge. The anterior border of  $M^2$  of UF 2199, the  $M^1$  in young specimens of *Metaxytherium* and the assigned felsinothere, the transverse valley of  $P^4$  in *Dugong*, and the anterior end (approximately) of the sixth cheek tooth in adult *Trichechus* all lie lateral to the same part of the bridge. In the case of UF 2199, this is 9 mm anterior to the posterior border of the bridge.

$M^1$ .—Fragmented remains of a subquadrate tooth mark the presence of  $M^1$ . Like *M. ossivalense* the width appears to be greater than the length, although both measurements in UF 2199 are estimated. The anterior border of  $M^1$  lies lateral to the anterior border of the zygomatic-orbital bridge in a well advanced position; this characteristic apparently is age-dependent, the border being farther advanced in older specimens.

#### *Metaxytherium calvertense* KELLOGG 1966

CRANIAL DIAGNOSIS.—Four cheek teeth;  $M^{2-3}$  subquadrate;  $M^1$  quadrate; transversely straight anterior and posterior border on  $M^{1-2}$ ; borders on  $M^3$  straight to slightly rounded; anterior cingular valley deep, pro-

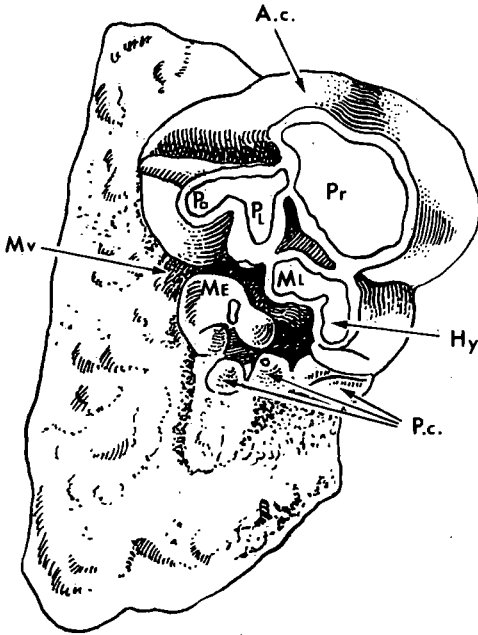


FIGURE 11.—*Metaxytherium floridanum* (UF 2199); right M<sup>3</sup>.

nounced, this feature being accentuated from M<sup>1</sup> to M<sup>3</sup>; large well developed cusplule on lingual side blocking transverse median valley in M<sup>1-3</sup>, this character not well developed on partially erupted, unused M<sup>3</sup>; variable number of supernumerary cusps; incisors, if present, nonfunctional; rostrum acutely downturned, as in all metaxytheres; nasals separated by frontals in midline; frontals elongate; squared-up, low, elongate boss; temporal crests on parietals swollen, rounded, and closely approaching each other; supraoccipital touching dorsal border of foramen magnum.

REFERRED SPECIMENS.—A study of the relatively complete cranium of the holotype of *M. calvertense* reveals no differences with FGS V5454, an anterior two-thirds of a cranium lacking the ventral half of the rostrum. FGS V5454 had previously been attributed to *Felsinotherium ossivalense* by Simpson (1932) and by Gregory (1941). This specimen and the holotype have already been adequately described, and further amplification will be made only where information is added by comparative study. Also here assigned to *M. calvertense* is an important half of a cranium (FGS V3211), well described by Simpson (1932) and referred to *Felsinotherium* sp.; the undescribed MCZ 4218, consisting of a left portion of the maxilla with M<sup>1-3</sup> implanted; and a parietal (UF 11574). The holotype is from the Middle Miocene Calvert Formation of Maryland,

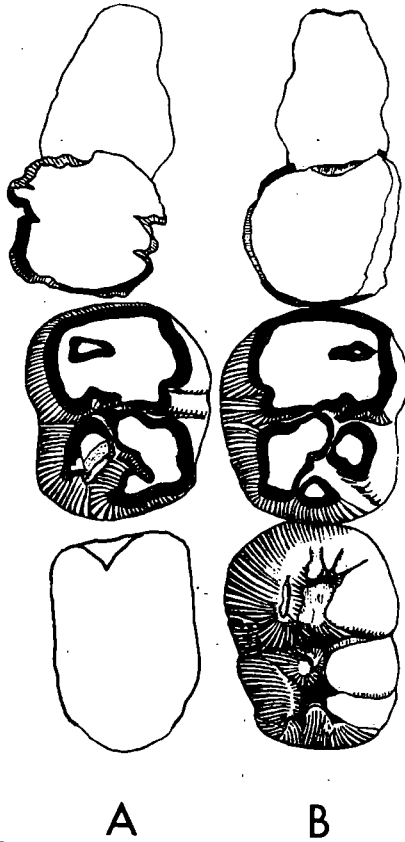


FIGURE 12.—*Metaxytherium calvertense* (FGS V5454); occlusal view of (A) right  $M^{1-2}$  and (B) left  $M^{1-3}$  from Gregory, 1941.

and the referred specimens are from Mio-Pliocene or Middle Pliocene Bone Valley Formation of Florida.<sup>1</sup>

**CRANIUM.**—A review of the specimens suggests that a series of growth stages is represented. The holotype (USNM 16757) is a very young adult; FGS V5454 is a young adult, more advanced in age than the holotype; MCZ 4218 and FGS V3211 are mature adults. Incisors are absent in the holotype and FGS V5454, the two specimens in which the rostrum is preserved; but most of the anterior ends of the premaxillaries are missing in the latter form. It is unknown if the tuskless condition is a dimorphic quality in which only females lack tusks, or if *M. calvertense* is a tuskless species. The rostrum is downturned, as in other metaxy-

<sup>1</sup> UF 11579, an excellent cranium, is referred here also but could not be included in this study. (see Table 1).

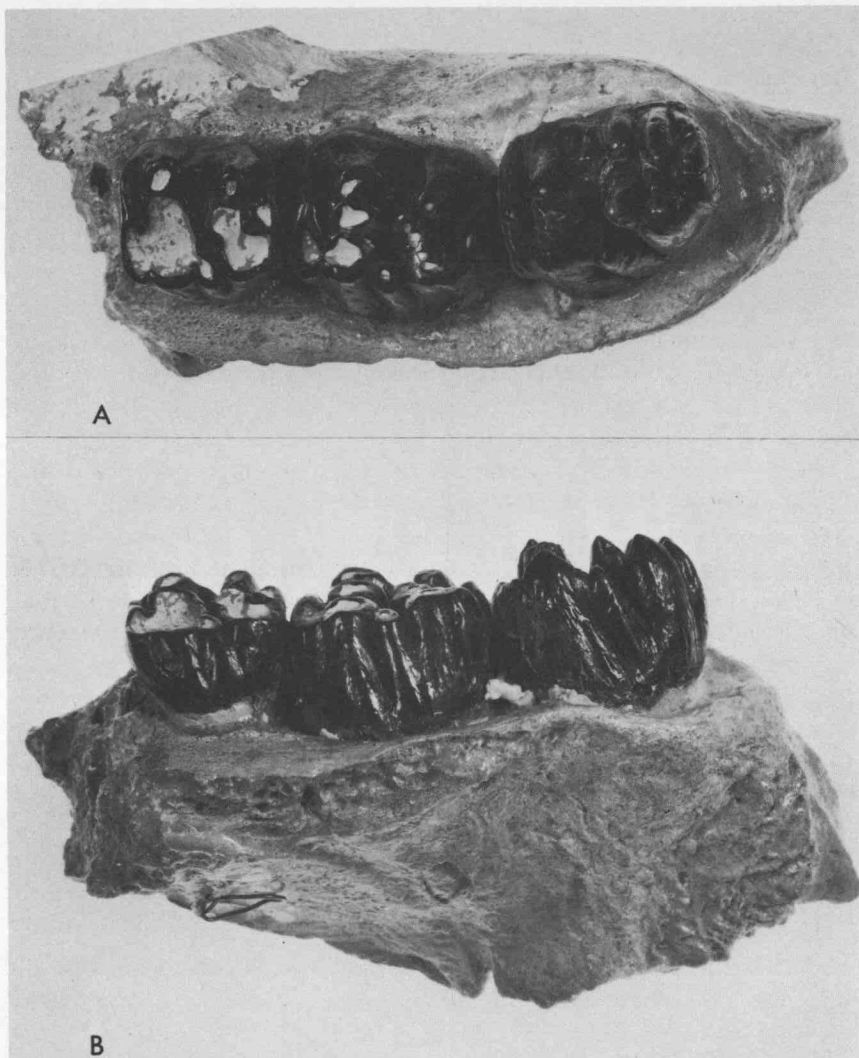


FIGURE 13.—*Metaxytherium calvertense*: (A) (MCZ 4218) occlusal view of left  $M^1-3$ ; (B) (MCZ 4218) lingual view of left  $M^1-3$ .

thers, but not so pronounced as in *Halitherium schinzi*, *Caribosiren*, or *Dugong*.

In both the holotype and FGS V5454 the nasals are separated by the frontals, a condition often not clearly detected in older specimens due to a fusion of the nasal-frontal sutures, which obliterates the contact

between these elements. In the latter specimen the closest approach of the nasals to each other at the posterior end of the premaxillary arms is 10 mm, with this distance increasing slightly in width both anteriorly and posteriorly. Separation of the nasals by the frontals is a condition characteristic of *Eotheroides aegyptiacum*, *E. libyca*, *Caribosiren*, *Hesperosiren*, and the metaxytheres. In *Thalattosiren* the frontals do not separate the nasals (Kellogg 1966: 73), but a forward projection of the frontals pushes into and partially overrides nasals in the midline. Sickenberg (1928: 200) stated that the nasals of *T. petersi* were joined medially along a suture 11 mm in length, which lies along a line of continuation of the sagittal suture. The frontals of *M. calvertense* are moderately elongate, squared up, bear a low elongate boss, and have a slight expansion of the postorbital processes. Expansion of the postorbital processes is a factor of age, with progressive expansion coinciding with growth of the frontals.

General size and configuration of the parietal temporal crests of FGS V5454 (Gregory 1941: pl. 11) closely resembles *Metaxytherium* (= *Felsinotherium*) *foresti* Capellini (1872: pl. 2, fig. 1). Crests present in FGS V3211 (Simpson 1932: fig. 13) are also swollen but project higher than in the aforementioned specimens, and posteriorly exhibit a gradual, rather than a sudden increase in expansion and swelling. Close approach of the crests in the midline is reminiscent of *Halitherium*, but in this genus, unlike metaxytheres, the parietal crests are thinner and extend posteriorly to the lateral edges of the supraoccipital, rather than terminating near the anterior half of the squamosal ring.

The outstanding structural condition in the rear of the cranium is the prominent supraoccipital (which forms the dorsal border of the foramen magnum), a feature considered progressive in the metaxytheres. The same essential relationship of posterior cranial elements is present in FGS V3211, as well as in other Florida metaxytheres and *Hesperosiren*.

DENTITION.—In  $M^3$  the anterior cingular valley is open buccally from the base of the crown; in  $M^1$  the initial opening is midway down the crown; and in  $M^2$  the condition is intermediate between these two teeth. The lack of an accessory cusp to block the anterior cingular valley is a feature shared by *M. calvertense* and *M. floridanum*, and generally serves to distinguish fully erupted adult cheek teeth from those of *M. ossivalense*. When present, the blocking cusp is normally confined to  $M^3$ . This observation must be tempered by the fact that in the specimens available the crown of  $M^2$  is moderately worn, and the crown of  $M^1$  is usually worn down to a point that the cusp, if present, would be obliterated. It should also be noted that partially erupted third molars often have crowded, indistinct cusps rather than clearly



TABLE 4.—MEASUREMENTS OF THE DENTITION OF *Metaxytherium calvertense*.

M <sup>3</sup>	Length	Width Anterior loph	Length/ width Anterior loph	Width Posterior loph	Length/ width Posterior loph
MCZ 4218	32.0	25.6	1.25	20.4	1.57
FGS V5454	30.1	24.2	1.24	22.0	1.37
USNM 16757	28.5	18.5	1.54	18.5	1.54
M <sup>2</sup>					
MCZ 4218	28.4	27.5	1.03	24.2	1.17
FGS V5454	28.4	26.2	1.08	23.0	1.23
M <sup>1</sup>					
MCZ 4218	23.5	23.5	1.00	21.2	1.11
FGS V5454	20.0–20.5 <sup>e</sup>	22.+	.91	20.0 <sup>e</sup>	1.00–
USNM 16757	18.5	19.6	.94	15.5	1.19

e = estimated

separated entities that characterize an M<sup>3</sup> ready for use, or but slightly worn. Many also retain abundant, fine, vertical striations on and between cusps and are pitted as the result of physiological effects on the enamel. Both of these latter features quickly disappear with wear.

The transverse anterior loph is composed of the protocone, protoconule, and paracone as in all sirenians. Although all three are of similar size, the protocone is largest and the paracone smallest. To a degree comparable to *M. ossivalense*, the transverse median valley is blocked by the forward displaced metaconule, but this cusp is not as closely adjoined to the protoconule as in *M. floridanum*. The M<sup>3</sup> in the large *M. jordani* from California has a straight, open, median valley; a feature shared to a degree by *M. ossivalense* (FMNH PM155). Confluent with the protocone a large accessory cusp blocks the lingual side of the transverse median valley in M<sup>1-3</sup>. This feature, coupled with the rounded temporal crests on the parietals, distinguishes *M. calvertense* from other North American metaxytheres. In MCZ 4218 a smaller cuspule, which is appressed to the paracone, partially closes the same valley buccally in M<sup>1</sup> through M<sup>3</sup>. A separate accessory cusp situated lateral to the metaconule and anterior to the metacone on M<sup>3</sup> further blocks the valley on the buccal side. Positions of the forward metaconule, the large, closely-appressed hypocone, and the smaller metacone are typical of all species of Florida *Metaxytherium*. The transversely straight posterior boundary in M<sup>3</sup> is formed by three distinct cusps, with that of M<sup>1-2</sup> essentially forming one large transverse cusp. The posterior cingular

valley is open in  $M^{1-2}$  but closed by accessory cusps in  $M^3$ . It must be emphasized that supernumerary cusps are far more common on the large posterior molars, so variance of such cusps must be treated conservatively before establishing a new species on this basis. If accessory cusps are present on  $M^3$  but lacking on anterior molars, such cusps are considered by the writer to be of no systematic value; but if accessory cusps are a prominent part of all the molars, as in MCZ 4218, the features are considered to be morphological differences of taxonomic value. Strong vertical ridges and wrinkling are unusually well developed on this specimen. Such wrinkling is found to some degree on many unworn sirenian teeth and is most prominent on the larger teeth.

Three root sockets, two on the buccal side and one on the lingual side, mark the position of the missing  $P^4$  in MCZ 4218, and indicate a tooth only slightly smaller than  $M^1$ . Bone enclosing the terminus of the root is thin, and a minimum of erosion will expose these elements, as has occurred in five points on this specimen. In FGS V5454 the alveoli are essentially filled with a cancellous bony tissue, and it is difficult to ascertain if one or two premolars were present when this animal was immature.

#### CONCLUSIONS ON DENTAL CHARACTERISTICS OF FLORIDA METAXYTHERES

In this study the following limiting factors applied: (A) The small number of specimens studied from Florida represents an accidental remnant or a local morphologic sample range rather than a species range; (B) The lack of stratigraphic data limits information on the former extension of the sample in time and space and renders interpretation of evolutionary trends difficult:

1. From a dental study of Florida's Mio-Pliocene Sirenia it cannot be determined if the metaxythere group was evolving from simple bunodont to more complex hypsodont.

An increase in complexity of enamel due to infolding and growth of accessory cusps has accompanied the history of many successful terrestrial herbivores and has usually been accompanied by a growth from bunodont to hypsodont teeth. The question that arises is: Were metaxythere cheek teeth evolving a complex triturating surface by folding of enamel and growth of accessory cusps, or were cheek teeth of this group becoming simplified? Evidence suggests both conditions of dental change occurred, but each in a different geographic area. The increase in complexity is indicated by the European metaxytheres, which, on the basis of stratigraphic evidence, show an increase in accessory cusps in geologic time.

2. There appears to be a development toward a strong anterior cingulum that tends to become an independent transverse loph with loss of attachment even to the protocone. To some extent an independent anterior cingulum is found as far back as Eocene genera, as well as in the living *Trichechus*, but in neither of these cases does the loph extend up to the height of the loph formed by the protocone, protoconule, and paracone. This feature is well expressed in *M. ossivalense* (UF 11576-11577), *M. calvertense* (MCZ 4218 and FMNH PH155), and the European *H. krahuletsi*.

3. Through Miocene and Pliocene time (Burdigalian through Astian), the metaconule is gradually displaced forward to block the transverse median valley and eventually lies completely anterior to the hypocone and metacone. Expression of this feature is displayed in all North American metaxytheres, as well as in European metaxytheres and assigned felsinothers.

4. Closure of the lingual side of the transverse median valley is accomplished in *M. calvertense* through growth of a prominent accessory cusp posterolingual to the protocone. Incipient development of the cusp appears in *M. ossivalense*. To my knowledge, no other metaxythere or assigned felsinothere of North America or Europe bears this cusp.

5. An accessory cusplule blocks the buccal side of the valley of the anterior cingulum in *M. ossivalense*. This condition is believed to have developed from an ancestry having the more typical open valley.

6. I believe that metaxytheres of Europe and the Atlantic coast of North America during Miocene-Pliocene time slowly evolved a more complex triturating surface, but conversely, during Pliocene time, a loss of dentition developed in North American Pacific coast metaxytheres.

If one examines the entire history of the sirenians, it is evident that, with the exception of the living *Trichechus*, there is a gradual loss in number of functional teeth from the almost complete Eocene eutherian dentition to the reduced number of simple peg-like teeth in *Dugong* and the complete loss in *Hydrodamalis*. Until a recent study by Domning (1972, unpub. Ph.D. disser.), no fossil adult with fewer than four functional cheek teeth (16 teeth) had been found, and these failed to show loss of accessory cusps or any dental degeneration that one would expect in an ancestor of *Dugong* or *Hydrodamalis*. Domning, however, provided conclusive proof of the relationship of the geographically widespread *Metaxytherium* to the recently extinct (ca. 1768) Bering Sea *Hydrodamalis gigas*. A similar relationship had been proposed by Simpson (1932), Vanderhoof (1941), and Reinhart (1959), but diag-

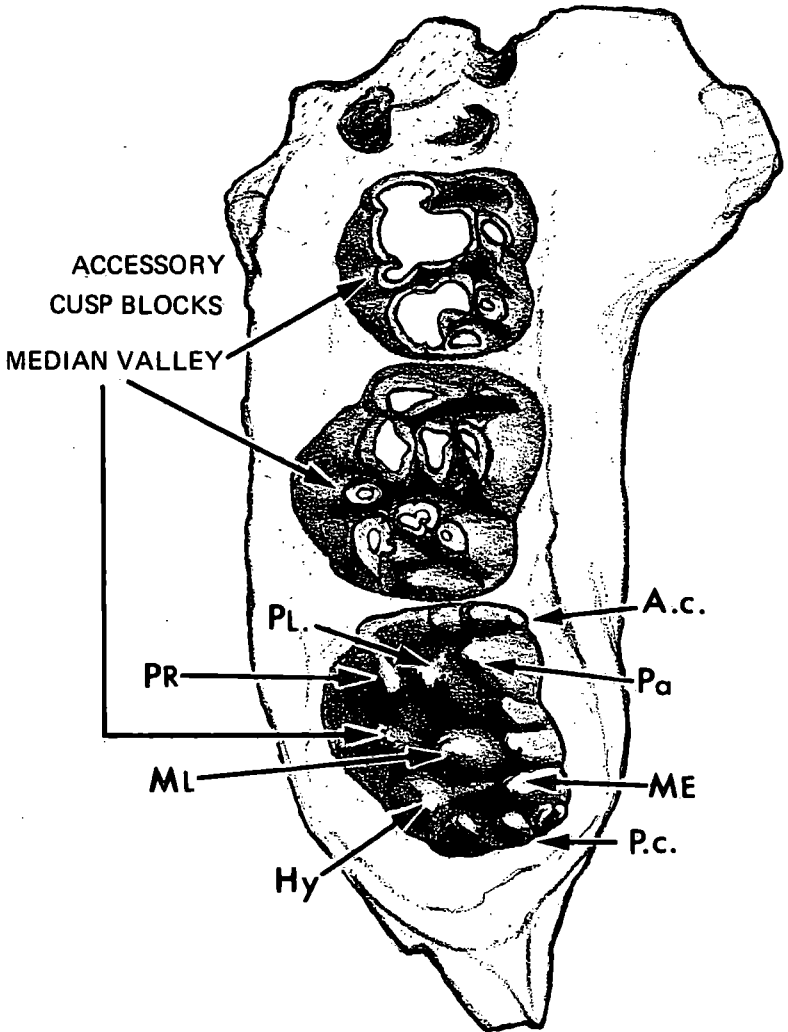


FIGURE 14.—*Metaxytherium calvertense* (MCZ 4218): occlusal view of left  $M^{1-3}$ .

nostic evidence was lacking. A well-preserved new species of *Hydrodamalis*, intermediate between *Metaxytherium* and *H. gigas* both in time and morphological characteristics, clearly displays a close affinity to these genera.

It should be noted here that *Felsinotherium gunteri*, which appeared in Simpson's (1932: 449) review of sirenian metaxytheres, is a *nomen nudum*, and should be referred to *F. ossivalense* (G. G. Simpson, pers. comm., 14 December 1959).

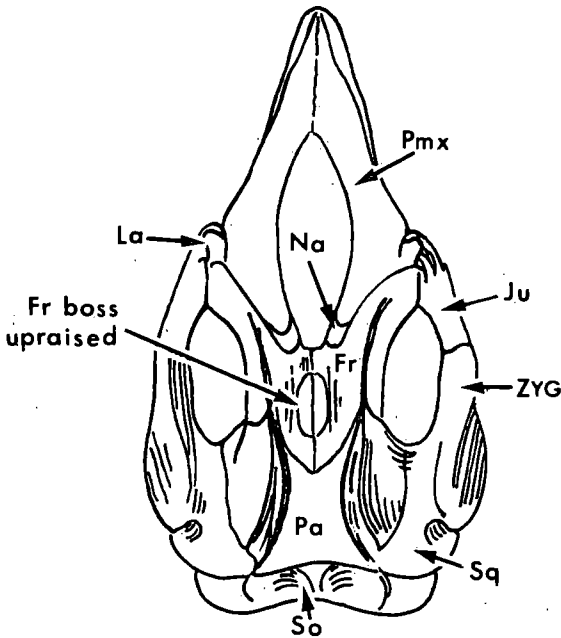


FIGURE 15.—*Hesperosiren crataegensis* (AMNH 26838): dorsal view of cranium. Modified from Simpson, 1932.

#### *Hesperosiren* SIMPSON 1932

As is often the case in the taxonomic history of the Sirenia, the relative scarcity of diagnostic remains results in many monotypic genera, whereas a larger number of specimens available for comparison may indicate that synonymization of some of these genera is called for. *Hesperosiren* is regarded as a rare sirenian, possibly because it actually is rare or, of equal likelihood, because its bony elements are not readily distinguished from the more common metaxytheres found in the same geographical area or in sediments of similar geologic age. Despite the moderate number of sirenian remains discovered in Florida since 1932, only two new specimens are referable to *Hesperosiren*. These are MCZ 4432, a relatively complete posterior half of a cranium, and FGS V4250, a well preserved specimen of the mid-cranium. The latter specimen was designated a plesio-type of *Felsinotherium ossivalense* by Simpson (1932: 454). Also tentatively referred to *Hesperosiren* is USNM 181550, a parietal-supraoccipital complex from an old individual that features an unusual vertical thickness. Although the holotype cranium is complete, its crushed condition requires judgments to be made concerning the configuration and contacts of a number of bony elements as they

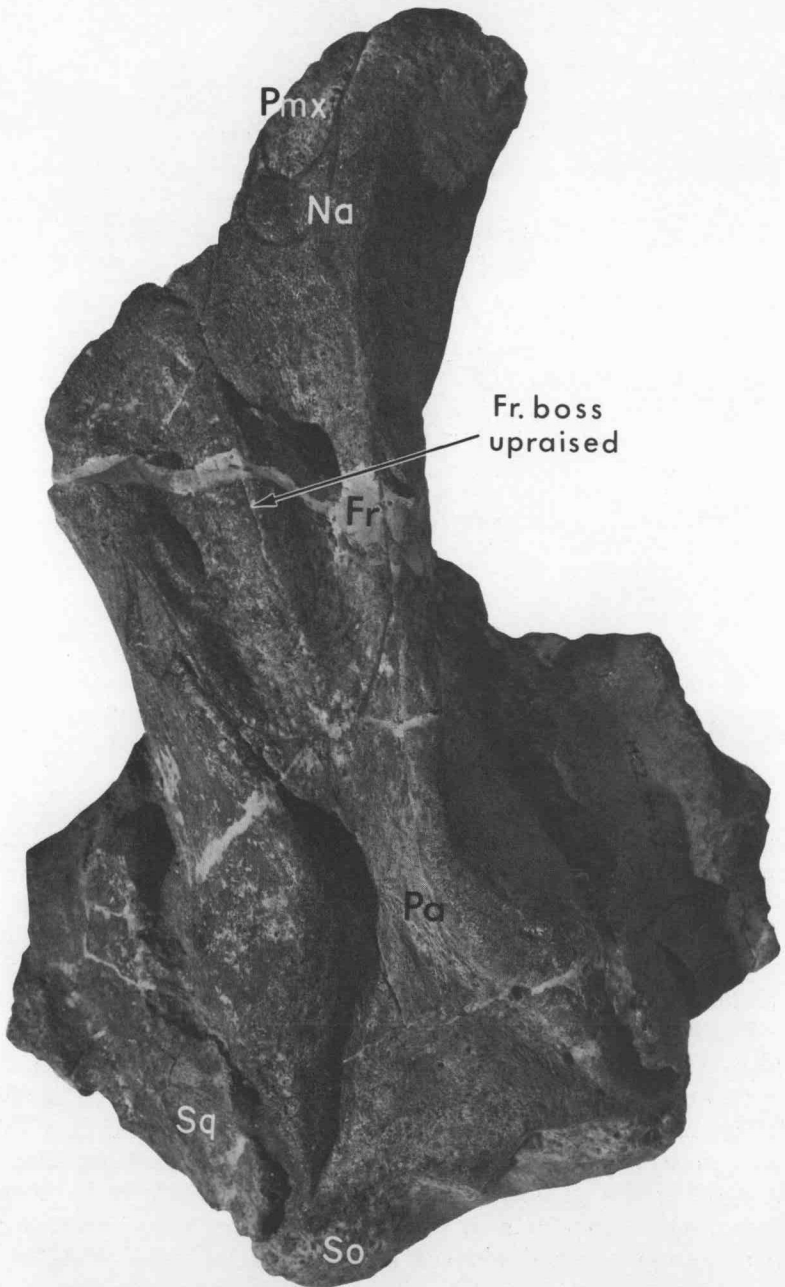


FIGURE 16.—*Hesperosiren* sp. (MCZ 4432): dorsal view of cranium.

TABLE 5.—CRANIAL MEASUREMENTS OF *Hesperosiren*.

	AMNH 26838 (Holotype)	MCZ 4432	FGS 4250
Width across postorbital processes	140	186 <sup>e</sup>	
Minimum separation between inner border of nasals, posterior end	20.2	30 <sup>e</sup>	21.4
Width of frontals across middle of boss	75	74	64
Height of frontal boss	10	10	8
Anterior midline of parietals to posterior border of nasals	75	107	76.5
Posterior border of external occipital protuberance to anterior midline of parietals	75	94.7	
Minimum separation of temporal crests on parietals	41	17.7	

e = estimated

existed in a pre-crushed condition. The referred specimens, therefore, while displaying some variation from the holotype, may aid in the clarification of the interpretations. Whether these variations will eventually be found attributable to age, sex, individual differences in the same species, or to different species, is a matter that can only be determined by more specimens. Based on the present information, I prefer to retain all the specimens in a single species.

On the dorsal cranial surface the rounded posterior borders of the nasals are inserted under the overriding frontals and are separated in the midline by the same bones. Thin anterolateral extensions clasp the posterior end of the premaxillary arms in the same fashion as in the metaxytheres. Within the narial passage the inner half of the nasals is thin, compressed laterally, extends deeply into the frontals, and thins out anteriorly as a long extension lying against the premaxillary. Various turbinals lie immediately adjacent to the inner side of the nasals, but the relationship is not clear. The size and shape of the nasals are the same as in metaxytheres of similar size.

A notable difference between the type of *Hesperosiren* and the referred specimen may be seen in the width between the lateral extremities of the postorbital processes of the frontals, which is estimated to be 140 mm for the holotype and 186 mm for the referred MCZ 4432. The great lateral divergence of the postorbitals in the latter specimen is similar to that found only in the very largest sirenians, such as *Metaxytherium jordani* (198 mm) and *Hydrodamalis* (192 mm, but will vary with age). The distance from the posterior margin of the parietal to the anterior angle of the postorbital process of the frontal is 316 mm

in the specimen of *Hydrodamalis* at hand, and 248 mm in MCZ 4432. In the referred *Hesperosiren* the posterior measurement was taken from the midline of a small transverse ridge immediately anterior to the external occipital protuberance. Because of the complete fusion of the supraoccipital and the parietals in all fossil and living sirenians, except during the fetal stage, it would be difficult to determine the exact posterior boundary of the parietals. A comparison of the width across the postorbital processes is made to demonstrate that *Hesperosiren* has a width in this area comparable to that of such large sirenians as *M. jordani* and *Hydrodamalis*, and yet it has a much shorter skull with much smaller dimensions throughout its posterior half. Certainly one of the outstanding features of *Hesperosiren* must be the widely divergent postorbital processes and, possibly in conjunction with this feature, a wide mesorostral fossa. Anterolateral divergence of the frontal processes is more exaggerated in the two specimens referred to *Hesperosiren* than in the holotype, because of the distinctive narrowing of the frontals posteriorly, which culminates in a pinched-in parietal-temporal area. Lateral divergence of the postorbital processes may be most prominent in FGS V4250, as suggested by the sharply branching base of the processes, and in this respect it shows some resemblance to *Halitherium* and to *Manatherium*.<sup>1</sup>

All specimens of *Hesperosiren* bear an elongate, prominently upraised dorsal median boss on the frontals, a feature similar to *Dugong* but completely unlike *Trichechus*. In *Dugong* the bone joining the boss is not thicker than the bone immediately bordering the upraised area but is merely arched upward. *Hesperosiren* (FGS V4250) reveals a condition suggesting that the bone forming the boss was thicker, whereas *Metaxytherium floridanum* (UF 2199), which clearly displays the area, shows a low broad boss composed of unthickened bone. A question arises as to whether the boss is formed solely by the frontals, or if other cranial elements add to its formation. A lateral section in *Metaxytherium* (UF 11573) displays a spine that rises above the crista galli and becomes deeply entrenched to within 4 mm of the dorsal surface of the frontals at a point just behind the midline of the boss. Another specimen (FGS V5947), which essentially lacks a boss, also has a spine that rises to within 3 mm of the dorsal surface of the frontals. Lepsius (1882: table 5, fig. 58) reveals a cross-section of the frontal-ethmoid contacts in *Halitherium*, but no entrenchment of the ethmoid is shown. Despite its proximity to the boss, the ethmoid bone does not appear to be a factor in the elevation of the bone in the median frontal region.

<sup>1</sup> Sickenberg (1934: 274) refers the genus *Manatherium delheidi* to *Halitherium schinzi* f. *delheidi*.



Another aspect to be considered is why the frontal boss is so prominent in *Hesperosiren*, but not in other genera. Conceivably it is prominent in young individuals, then spreading out with growth of the frontals, and disappearing in adults. Dilg (1909), working with the growth stages of *Trichechus inunguis*, has shown that in young sirenians the frontals are short, and the parietals long. Further growth in the cranium takes place to a great extent in the frontals, but parietal growth is relatively limited. In MCZ 4432, which appears to be an adult, the boss remains well elevated above the cranial roof. Formation of the boss may be due to a telescoping of bones in the nasal region; a condition that frequently occurs in the evolution of aquatic mammals as they become better adapted to a water environment. Such a suggestion may be plausible in the case of *Dugong*, but not for *Trichechus*, which has a broad concavity in the frontals, bordered by high squared-up crests. Sirenians in general show a reduction in size of the nasal bones from Eocene to Recent forms.

Lyriform temporal crests on the parietals converge moderately in the midline of these elements, with an estimated minimum separation of about 41 mm on the holotype. This is in essential agreement with metaxytheres, which vary somewhat in the degree of separation, although most are more squared-up in this region. Unlike the holotype, MCZ 4432 has a minimum separation of well developed parietal temporal crests of only 17 mm, and in this respect greatly resembles the convergent crests characteristic of *Halitherium*. FGS V4250 also shows indication of bearing strongly convergent crests, but inasmuch as only the anterior ends of the parietals are present the degree of convergence is unknown. Separation of the temporal crests on FGS V4250 at the posterior border of the frontals in the midline is 22 mm. The crests are tapered so that they undoubtedly came closer together at a more posterior point. Although some degree of relationship is shown with *Halitherium* in this individual character, it would necessarily be with a more conservative member of this genus. A young *Halitherium* sp. individual from the island of Madagascar has parietal crests in contact for a distance of 55 mm. In *Halitherium schinzi* the parietal crests are in close proximity, but not touching, for an estimated 40-42 mm. Dorsally the anterior ends of the parietals in *Hesperosiren* extend forward to a point midway across from the center of the frontal boss (Fig. 15). Although the degree of parietal crest convergence in the two specimens referred to *Hesperosiren* is quite similar to that in *Halitherium*, a number of other cranial relationships reveal important differences. In *Halitherium* the nasals are larger and meet in the midline; in *Hesperosiren* the smaller nasals are separated in the midline by these bones. The supraoccipital is separated

from the foramen magnum by the exoccipitals in *Halitherium*, but it forms a small portion of the dorsal-central border of the foramen magnum in *Hesperosiren*. There is no prominent upraised median boss present on the frontals of *Halitherium*, as is present in *Hesperosiren*.

From a dorsal view the cranial roof of the referred MCZ 4432 is superficially like that of *Metaxytherium cuvieri*, the resemblance being based largely on a thin elongate cranial cap with swollen temporal crests. The pronounced medial boss on the frontals, characteristic of *Hesperosiren*, is lacking in *M. cuvieri*. A low broad boss or convexity is present, however, as in all Miocene and Pliocene metaxytheres. The minimum degree of separation of the temporal crests of *M. cuvieri* ranges from that of Flot<sup>1</sup> (1886), who gives a figure of 92 mm, to the type of *M. cuvieri* (listed as 73 mm), to the 70 mm on the excellent specimen described by Cottreau (1928), to a specimen from Maine-et-Loire region with a minimum separation of 69 mm. Cottreau believed the separation of the temporal crests to be a character that varies with both age and sex. Dilg (1909), working with growth stages of *Trichechus*, showed that in the younger stages the temporal crests are less distinct and more widely separated than in the older stages. I agree that crests, as well as other rugosities, are less distinct in the younger forms, and because of the lack of development the relatively flat cranial roof bears such small crests that indeed there is a wide separation of these elements.

Again, in reference to the dorsal surface of the cranial roof, the holotype bears a superficial appearance to *Thalattosiren*, rather than to *M. cuvieri*. It differs (a) from *Thalattosiren* by the division of the nasals by the frontals, (b) from *M. cuvieri* in having a less elongate cranium and less prominent temporal crests, and (c) from both genera by the presence of a prominent frontal boss.

The general configuration of the supraoccipital is more rounded in *Hesperosiren* than in *Metaxytherium* and *Dugong*, but less so than in *Trichechus*. Essentially all fossil Sirenia, but not recent forms, have a prominent external occipital protuberance in the dorsal midline of this element. In *Hesperosiren* (MCZ 4432) the protuberance is a very broad triangle, with the apex ventral. This shape contrasts in several ways to that present in *Dugong*, *Trichechus*, *Halitherium*, and adult metaxytheres.

In *Hesperosiren*, as with many crushed specimens, various interpretations can be made concerning the correction of distortions. In the case of the holotype, the only illustrations are those from Simpson (1932:

<sup>1</sup> Abel (1904: 13) places *Halitherium fossile*, depicted by Flot (1886: pls. 26-27), in the synonymy of *Metaxytherium cuvieri*.

Figs. 1 A and B). My interpretation of the boundaries of various cranial elements differs from Simpson as follows:

- 1) In Fig. 1B (a dorsal view), the anterolateral extensions of the parietals should be moved anteriorly to a point lateral to the middle of the frontal boss. These dimensions would then be in agreement with the specimen, as well as virtually all other Sirenia.
- 2) The boundaries of the nasal bones should appear much more clearly in the illustration, particularly in view of the fact that the relative size and configuration of these bones, in relation to the anterior midline of the frontals, is of considerable taxonomic importance.
- 3) The juncture of the lacrymals, jugals, postorbital process of the frontals, and posterolateral arms of the premaxillaries is not at all in accord with the illustration of the holotype. In the illustration, there are no undulating rugosities on the premaxillaries immediately anterior to the postorbital processes, and the posterolateral configuration of the premaxillary arms is completely incorrect. The anterior border of the orbital ring is formed by what appears to be a lacrymal, identified by its position and characteristic lateral protuberance, and a jugal whose relationship is not distinct. Whether the maxilla separates the jugal from the premaxillary arm cannot be determined. The illustration of these elements, as rendered by myself, would have a configuration that would not digress strongly from the condition present in Eocene to Recent forms.
- 4) In Figure 1A (a lateral view of *Hesperosiren*) the pterygoids undoubtedly extended below a point lateral to the occlusal surface of the cheek teeth, as they do to some degree in all Sirenia.
- 5) The dorsoanterior end of the zygomatic arch of the squamosal has a greater forward extension than the ventroanterior end, which is opposite the condition in Figure 1A.
- 6) The outstanding superficial criterion for distinguishing *Hesperosiren* is the interpretation that this genus bore a straight rostrum, as opposed to all other Sirenia in which this region is acutely downturned. Because of the crushed condition of the premaxillary arms, it is difficult to ascertain the degree of flexure. In my opinion there is little to distinguish between the rostra of *Thalattosiren petersi* Sickenberg (1928: pl. 1) and *Hesperosiren*. Whether *Hesperosiren* bore a flexure as acute as this form is a matter of conjecture, but no more questionable than the interpretation of a straight rostrum. It appears unlikely that the rostrum was as acutely downturned as the condition found in *Halitherium schinzi*, *Caribosiren*, or *Dugong*.

GENUS *Halitherium* KAUP 1838

The presence of *Halitherium*, long represented by a number of fine specimens from Europe and a cranial cap from Madagascar, has now been definitely established in North America on the basis of Florida Oligocene material. The term "established" is important, for poor specimens from the Atlantic coast of the United States have been attributed to this genus previously. Most sirenians from the eastern coast of the United States have come either from the Calvert Formation of Maryland or the Ashley River Formation of South Carolina. Both formations contain a mixture of reworked faunas, and the sirenians found usually have been not only fragmentary but of uncertain age. In Leidy's (1856) short description of an isolated upper molar from the Ashley River deposits he mentioned fragments of ribs. These specimens, of which the tooth was the type, were referred to *Manatus antiquus*. The same tooth was later figured by Leidy (1860) in Holmes' *Post Pliocene Fossils of South Carolina*. A second name, *Manatus inornatus*, was proposed by Leidy in 1873, based upon the crown of a relatively small isolated lower cheek tooth from the same deposits. The specific names *antiquus* and *inornatus* are therefore based on teeth of indeterminate genera and unknown age.

In reviewing the fossil mammals from the Ashley River deposits near Charleston, South Carolina, Allen (1926) noted that the beds contained a mixture of fossils from several different epochs. He considered the land mammals to be chiefly of Pleistocene age (although some range from Miocene to Recent), but, on the whole, the marine forms are from the Miocene. From these deposits Allen collected a number of sirenian remains, with the more diagnostic remains being cranial roofing composed usually of some combination of the frontals, parietals, and supraoccipital. Some water-worn humeri were also described. He divided the skulls and humeri into two groups, referring those with strongly convergent temporal crests and the small humeri with proximal tuberosities (which diverge at an angle of  $60^\circ$ ) to *Halitherium antiquus*. Allen also referred *Manatus inornatus* to *H. antiquus*, although the teeth are generically indeterminate. Simpson (1932) proposed discarding Leidy's names (*M. antiquus* and *M. inornatus*) as indeterminate, proposed a new name (*Halitherium alleni*) based on Allen's (1926: pl. 11, fig. 1) figure of fused parietals and supraoccipital. Whether the cranial material is referable to *Halitherium* or to another genus is not known, but I agree with Simpson that Allen's specimens (cranial roofs and humeri) cannot be referred to Leidy's indeterminate teeth.

Allen's second division of sirenian specimens was composed of larger, flatter, wider cranial roofs, with the temporal crests not so well developed

as in the smaller crania. The proximal tuberosities of this second group diverged at an angle of approximately 85 to 90 degrees. Allen referred his second group to *Metaxytherium* (= *Halianassa*) *manigaulti* Cope. Reference of this material to *Metaxytherium* is reasonable, although the specimens are so waterworn as to make a generic allocation somewhat questionable. The type of *M. manigaulti* is a fragmentary premaxillary from the Wando River, South Carolina, and was described by Cope (1883) as *Dioplotherium manigaulti*. The generic distinction, according to Cope, was that each premaxillary contained two incisors. Kellogg (1925) showed this supposed differentiating character to be incorrect and subsequently referred *Dioplotherium* to *Metaxytherium manigaulti*. Since well-preserved specimens of *Metaxytherium* found to date in the western hemisphere lack incisors, this premaxillary with its well-developed incisor may be referable either to a male individual of the genus *Metaxytherium* or to another genus.

A similar generic proposal was made by Lydekker (1887), who postulated that a vertebral centrum and two ribs from the Ashley River deposits belonged to *Halitherium*. A taxonomic assignment based on such clearly indeterminate material is premature.

Matthew's (1916) reference to this genus may possibly be correct. The type (from Juana Diaz, Puerto Rico) is a fragmentary mandible bearing three heavily worn molars and the alveoli from three premolars. The sediments around Juana Diaz are largely of Oligocene age, and this, plus the number of teeth, gives credence to the determination. *H. antillense*, however, might equally well be synonymous with *Caribosiren turneri* Reinhart 1959, which was collected in the same general locality in undoubted Middle Oligocene strata, but which is distinctly different from *Halitherium*. Unfortunately no common elements involving these specimens exist.

Subsequent information gained from specimens indicates that cranial caps with narrowly separated parietal-temporal crests cannot automatically be referred to *Halitherium*. Similar bony elements from *Hesperosiren*, from young individuals of the Pleistocene *Trichechus*, and to a lesser extent *Metaxytherium calvertense* and *Caribosiren turneri* are virtually indistinguishable from those of *Halitherium* when parietals alone are examined. To distinguish between *Hesperosiren* and *Halitherium* it is necessary to have adjoining bones where distinctive differences exist as follows:

- 1) A large prominent domal boss characterized the frontal midline of *Hesperosiren*, but is lacking in *Halitherium*.
- 2) Postorbital processes of the frontals in *Hesperosiren* have a com-

paratively greater distal expansion and are not abruptly recurved posteriorly, as in *Halitherium*.

- 3) Nasals join anterior to the frontals in *Halitherium*, but are separated in the midline by a forward extension of the frontals in *Hesperosiren*.
- 4) The rostrum of *Halitherium* is abruptly downturned. The degree of flexure in the rostral region of *Hesperosiren* cannot be properly assessed because of the crushed condition of the holotype, but I believe it is more deflected than shown in reconstruction.
- 5) Well developed tusk-like incisors characterize the snout of *Halitherium*, whereas *Hesperosiren* either lacked tusks or bore only minute vestigial incisors, as is found in some Florida metaxytheres. Such incisors would have been shed before maturity, were probably nonfunctional, and the area covered by a horny pad in the young adult.
- 6) In *Hesperosiren* the exoccipital sutures form an angle of about  $135^\circ$ , and the ventral midline of these elements almost touches or borders the foramen magnum in a fashion typical of metaxytheres and referred felsinotheres. A similar point in *Halitherium schinzi* displays an exoccipital angle of  $167^\circ$  and a 21 mm separation from the foramen magnum.

Perhaps other distinctive differences could be determined between the two genera, but the above can be readily evaluated with a cursory examination. Variance between *Halitherium* and the genus *Metaxytherium*, plus related felsinotheres, is well known, so a review of differences would not add to the readily available information. Comparison of *Halitherium* with *Caribosiren* was made by Reinhart (1959: 8-21).

#### *Halitherium olseni* new species

TYPE (FGS V6094).—Cranium and mandible, essentially complete; postcranial elements present from anterior half of left side; cervical vertebrae present; thoracic vertebrae partially present; fragments from right side.

TYPE LOCALITY.—FGS Locality No. 82, E bank Suwannee River at water level, approximately 1.6 mi. below White Springs, Sec. 11, T2N, R15E, Hamilton Co., Florida, 11 December 1961. Specimen found in sand, fine to medium quartz in a matrix of clay, containing hard nodules of sandy limestone. Bed is approximately 5 ft. above Suwannee (Oligocene) limestone and contains impressions of pecten-like shells, too fragmentary for an accurate determination to be made.

AGE.—Middle to Late Miocene.<sup>1</sup>

<sup>1</sup> Age assigned by Dr. Robert O. Vernon, Division Director and State Geologist, Florida Geological Survey, 18 March 1965.

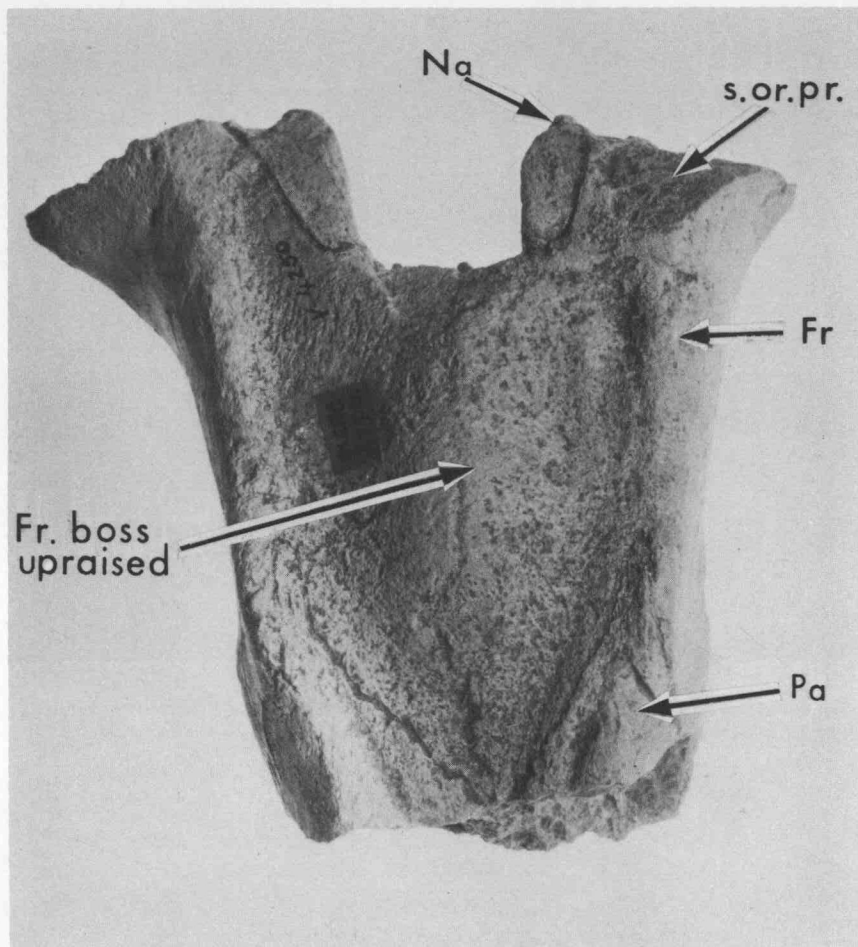


FIGURE 17.—*Hesperosiren* sp. (FGS V4250): dorsal view of nasals, frontals and anterior end of parietals.

DIAGNOSIS.—Acute ventral bend to rostrum; functional tusklike incisors present; supraorbital processes of frontals abruptly recurved; swollen, rounded parietals with temporal crests narrowly separated; unusually large lacrymal, with duct and well developed lateral tuberosity; supraoccipital-exoccipital sutural contact  $132^\circ$ ; supraoccipital separated from foramen magnum by 16.5 mm; dental formula:

$$\begin{array}{r} 1-0-1-3 \\ \hline 2 \text{ or } 3^1-0-1-3 \end{array}$$

<sup>1</sup> Nonfunctional.



FIGURE 18.—*Halitherium olseni* (FCS V6094): dorsal view of cranium.





FIGURE 19.—*Halitherium olseni* (FGS V6094): lateral view of cranium.

#### DESCRIPTION AND DISCUSSION

**PREMAXILLARY.**—The premaxillaries have a strong ventral deflection similar to that of *Halitherium schinzi* and *Metaxytherium* (= *Felsinothorium*) *serresi*. The downward deflection is intermediate between that found in the larger metaxytheres and referred felsinotheres and the more acute angle present in *Caribosiren* and *Dugong*. From a dorsal view the overall construction of the rostrum most closely resembles that of *M. serresi* and *Miosiren kocki*. As in all Sirenia, the rostrum narrows ventrally, but the large alveoli and prominent incisors preclude a slightly expanded rostral area necessary to house such tusks. This is in contrast to such genera as *Caribosiren*, *Hesperosiren*, and North American metaxytheres in which the lack of incisors results in a narrow wedge-shaped rostrum. A moderately swollen dorsal boss is present on either side of the rostrum, a feature found to some degree in all Sirenia, even in *Trichechus*, which bears the least developed rostrum of living or fossil members of the order. The ventral surface of the premaxillaries is of a general sirenian construction. It is concave, centered with a narrow continuation of the palatal gutter, and bordered by thin, sharp, overhanging sides. Its rugose surface is pitted with many small foramina, and no doubt it bore a horny pad when the animal was living.

The mesorostral fossa is elongate, similar to that in *Halitherium schinzi* (Lepsius 1882: fig. 92), but apparently differs from the specimen illustrated in having a slightly developed anterior arch. Development of this small anterior arch ranges from strongly pronounced in *Dugong* to virtually absent in *Trichechus*. An incipient development of the arch may be noted in *Eotheroides* (Reinhart 1959: 54, fig. 8-B), but it is absent in *Prorastomus* (Owen 1875), *Protosiren fraasi* (Andrews 1906, [= *Eotherium aegyptiacum*]), and in Sickenberg's (1934) stylized or generalized illustrations of various Eocene forms. It is quite likely that

TABLE 6.—MEASUREMENTS OF *Halitherium olseni*.

	UF 3965	<i>H. olseni</i>
CRANIUM		
Length of cranium		367.5
Maximum width mesorostral fossa		50.5
Postero-central border of frontals to anterior border of mesorostral fossa		
Length of zygomatic arch		99.0
MANDIBLE		
Length, cheek tooth row		62.0
Length M <sub>3</sub>		17.9
Width M <sub>3</sub> , anterior loph		13.5
Width M <sub>3</sub> , middle loph		11.5
PARIETAL		
Maximum width at posterior end, above squamosal wings	53.5 <sup>e</sup>	53.7
Minimum width between temporal crests	12.0	12.0
Maximum width at anterior end of frontal-parietal suture		39.0
Maximum length		86.0 <sup>e</sup>
SUPRAOCCIPITAL		
Maximum width	67.7 <sup>e</sup>	71.0
Maximum height	48.2 <sup>e</sup>	48.2
Thickness of ventral medial border	17.0	—
Width between lateral borders of supraorbital processes		122.5
Postero-central border of frontals to anterior end of supraorbital processes		136.0
Postero-central border of frontals to posterior end of supraorbital processes		102.5
ATLAS		
Width between lateral extremities of transverse processes		110.0
Height of transverse processes		32.7
Ventral surface of atlas to dorsal border of anterior cotyle		47.0
Width between lateral extremities of posterior cotyles		58.0
Estimated height if uncrushed		64.5
AXIS		
Maximum height		74.0
Anterior margin of odontoid process to posterior margin of centrum		42.0
Length of facet on ventral side of odontoid process		24.3
Maximum width of facet on ventral side of odontoid process		22.8
Maximum width between lateral extremities of cotyles		62.7
Height of anterior cotyle		23.5
Maximum width anterior cotyle (right)		21.6
Maximum width, neural canal		28.6
Height of neural canal, anterior border		24.5

TABLE 6.—CONTINUED

	UF 3965	<i>H. olseni</i>
Width between lateral extremities of postzygapophyses		48.5
Width between lateral extremities of dorsal transverse processes		74.7
Width between lateral extremities of ventral transverse processes		52.1
THIRD CERVICAL		
Height		60.8
Width, estimated		77.0
Width between lateral borders prezygapophyses		56.1
Height, neural canal		23.6
Maximum width neural canal		29.7
FOURTH CERVICAL		
Height, estimated		60.3
Width between lateral borders prezygapophyses		65.3
Height, neural canal		23.3
Width, neural canal		31.0
SIXTH CERVICAL		
Minimum distance between ventral protuberances		46.0
SCAPULA		
Border of coracoid process to ventral edge of glenoid cavity		52.3
Ventral border of glenoid cavity to projection for teres major		128.6
HUMERUS		
Dorsal border of greater tubercle to ventral border of trochoid		136.3
Lateral border of dorsal head to lateral border of greater tubercle		48.7
Anterior border of dorsal head to posterior border of lesser tubercle		46.7
Maximum width between lateral extremities of entocondyle and ectocondyle		45.5
Maximum width of trochoid on medial side		20.0
Maximum width of trochoid on lateral side		27.7
Minimum distance between border of greater and lesser tubercles		7.7
RADIUS AND ULNA		
Length of radius		111.5
Maximum height of radial epiphysis		5.2
Length of ulna		134.0
Maximum height of ulna epiphysis		5.9
Length of interosseous space		50.0
Width across semilunar and radial notch		28.0

e = estimated

the apparent absence of the incipient arch in most of these early animals results from lack of detail in illustration.

Insertion and posterior termination of the premaxillary rami are located at a point lateral to the posterior end of the supraorbital process. Although sutural contacts are not prominent in this area, those present lead one to interpret that the frontals and nasals covered the posterior ends of the rami, and therefore dorsal exposure of these arms was close to the forward edge of the supraorbital process.

**NASAL CHAMBER.**—A well preserved perpendicular plate, the lamina perpendicularis, merges posteriorly with an indistinct crista galli and cribiform plate. Dorsally the rugose surface of this plate bears evidence of cartilaginous extensions. The ventral border is a thin, sharp edge, clasped on either side by thin ascending plates of the vomer. From either side of the posterior terminus of the perpendicular plate, prominent nasoturbinals rise dorsad, and if these elements are in their correct position and not crushed upward the following two nasal structure possibilities exist: 1) the nasals would probably be short in an anterior-posterior direction, and 2) the anterior border of the nasals would rise noticeably to override part of the nasoturbinals. Contacts between the nasals and the adjacent frontals cannot be determined; therefore, the configuration of these bones is unknown. Based on remains of the bones in the area, however, I believe that if nasals were present they would not have so great a forward extension as in the illustration of *H. schinzi* Lepsius 1882: pl. 9, fig. 92), which shows the anterior nasal border well in advance of the supraorbital process. In view of the actual specimen shown by Lepsius (1882: pl. 2, fig. 5), it is quite possible that his interpretation of this extension is incorrect. Extension of the anterior nasal border slightly in front of, or even with, the forward edge of the supraorbital process is found in Eocene Sirenia because of the relatively large, well-developed nasals. A reduction in size of sirenian nasal bones occurs through time, ranging from the large Eocene forms, which have well developed nasals that meet in the midline, to Mio-Pliocene metaxytheres with reduced nasals lying behind the premaxillary rami and separated in the midline by the frontals, to the virtually non-existent nasals of the recent *Dugong*, *Trichechus*, and *Hydrodamalis*. A reduction in size of nasals by telescoping occurs in all land mammals that have become acclimated to marine water and is clearly seen in the Cetacea.

The posterior half of the nasoturbinals is closely appressed to the lateral borders of the nasal region, with the anterior half terminating in a pronounced hooked processus hamatus lying well out into the mesorostral fossa. The nasoturbinals are thin, laterally compressed, concave medially, convex laterally, and in general shape are similar to those of

*Caribosiren*. These are in contrast to the more stoutly built elements present in the later Mio-Pliocene metaxytheres.

**FRONTALS.**—In overall configuration the cranial roof of *H. olseni* is thin and elongate, and most closely resembles the European *Halitherium christoli* (Spillman 1959: fig. 10), although it differs in certain details. Elongation of the cranial cap is also characteristic of the lesser known European Upper Oligocene *Halitherium pergense*, but the Florida specimen differs from this species by the presence of more strongly developed and convergent temporal crests and by a flat, vertical temporal region, rather than a gentle lateral widening in this area. Both *H. olseni* and *H. christoli* differ from *H. schinzi*, which has foreshortened frontals and less recurvature of the supraorbital processes.

The unique shape of the supraorbital processes of *H. olseni* serves to distinguish it readily from all other sirenian genera and species. Recurved processes identify the specimen as *Halitherium* (Fig. 18), but no other published specimen has been noted with such prominent recurved posterolateral borders. This feature is further accentuated by a thin sharp crest that, as a continuation of the temporal crests, extends along the lateral borders of the frontals to the middle of the supraorbital processes. At this point the crests diminish in height and recurve to the posterolateral borders of the processes. The lateral borders of the processes are strongly directed ventrally and are divided by a small central indentation. These two features are present to some degree in all Sirenia but usually are not as accentuated as in this specimen.

Unfortunately the anterior central portion of the frontals is missing, and no contacts between frontals and nasals are available. From adjacent fragments, a gentle rise in the midline of the frontals is suggested. In the posterior portion of the midline, the frontal-parietal contact forms the typical V-shaped juncture, with the parietals overriding the frontals and extending well forward along the temporal borders.

**LACRYMAL.**—The lacrymal is a short thick semilunar shaped bone, whose main configuration can be attributed to a prominent anterolateral knob. Ventrally it is in contact with the jugal, dorsally with the postorbital process of the frontal and the premaxillary arm, and anteriorly and lingually with the maxillary. These lacrymal contacts are essentially the same from the Eocene *Eotheroides* sp. through the Recent genera, although the element is reduced, nonfunctional, and essentially lost in *Dugong*, *Trichechus*, and *Hydrodamalis*. Behind the anterolateral knob, a small lacrymal duct passes toward the orbital region, a state that indicates a functional duct. The presence of a functional duct suggests that *Halitherium olseni* is not far removed from a terrestrial ancestor in which an efficient tear duct was a necessity. Though a small sirenian,

*H. olseni* has a much larger lacrymal than do either the European halitheres or *Caribosiren*, and despite different proportions this bone is closer in size to those of *Metaxytherium cuvieri* and *Metaxytherium jordani* (= *H. vanderhoofi*). The latter two metaxytheres probably reached about twice the body size of the Florida *Halitherium*, thus emphasizing again the exceptional size of the lacrymals in this relatively small animal. Evolution of the lacrymal through time was reviewed by Reinhart (1959: 57-58), so only the main points will be mentioned here.

- 1) There was an irregular progressive loss of function in the sirenian lacrymal. It had already reached this stage in the Middle Oligocene *Caribosiren*, but was still functional in the later Pontian *Miosiren*. Neither *Trichechus*, *Dugong*, nor the recently extinct *Hydrodamalis* retained a true functional lacrymal duct.
- 2) The lacrymal bone has become progressively smaller and shows much variation in size and shape in various phyletic lines.
- 3) As the lacrymal has lost some contact with the maxillary, it has correspondingly gained contact with the jugal. The position of the lacrymal has remained relatively constant, with consistent maintenance of contact to the postorbital process of the frontal.

Measurements of the lacrymal are: maximum height, 33.5 mm; maximum anteroposterior length, 21.5 mm; and maximum lateral width at anterolateral tuberosity, 24.4 mm.

**PARIETALS.**—A planum parietal is almost non-existent, due to the well developed lyriform temporal crests tending to meet in the midline. As mentioned earlier in the study, cranial caps with narrowly separated parietal temporal crests cannot automatically be referred to *Halitherium*. If parietals alone are examined, such specimens could be referable to *Hesperosiren* and, to a lesser extent, certain metaxytheres, (*Caribosiren* and *Trichechus*). Because of this, Simpson's (1932: 445) referring the two parietal-supraoccipital elements to *Halitherium alleni* cannot be completely accepted, although the generic designation is quite plausible and probable. Validity of the specific name *alleni* is questioned, since it is virtually impossible to distinguish the parietal from those of various European halitherines.

The lyriform crests of *H. olseni* are broadly rounded, but bear a thin sharp crest at the dorsolateral edge. A deep groove present at the dorso-posterior border follows the medial side of the lyriform crests forward and is the cause for accentuation of the crests in this area. In general appearance the parietals are intermediate between the cranial caps of *Halitherium antiquum* (Leidy) which were illustrated by Allen (1926: pl. 11, figs. 1-2) and later referred by Simpson (1932) to *H. alleni*.

Internally the parietals form the greater part of the superior, lateral,

and posterior walls of the braincase. Extending forward from a pronounced triangular internal occipital protuberance is the wedge-shaped falx cerebri, which bifurcates immediately in front of the protuberance, thins to a crest, and ends on either side in contact with the dorsal part of the crista galli. In most adults (except *Hydrodamalis*), regardless of genera, the parietal protuberance is separated from the supraoccipital by a moderately deep, thin, transverse sulcus or groove, which marks the contact between the bones. In *H. olseni* the groove is wide and not noticeably incised, a factor believed to result from the youth of the individual.

**MAXILLA.**—Ventrally, with the exception of the anterior end of the maxillary-jugal contact, sutural relationship of the maxillaries with surrounding elements is in all respects like that of *Halitherium schinzi* (Lepsius 1882: pl. 10, fig. 96). In contrast to *H. schinzi*, the forward edge of the orbital ring has a pronounced posterior slant on the lateral border, as compared to the prominent anteriorly directed orbital ring of the European form. In front of P<sup>4</sup> the anterior continuation of the palatal gutter is narrowly constricted almost to a point of closure, then expands with a gradually widening taper that culminates in a maxillary ridge swinging abruptly outward to the ventrolateral margins of the rostrum. A very similar palatal condition is also present in *Metaxytherium serresi* (Depéret and Roman 1920: pl. 2, fig. 1c), in contrast to other members of the metaxythere-felsinothere line (*Caribosiren* and *Dugong*), in which the palatal gutter is less lyriiform, more open, with lateral termination of this groove formed by overhanging parallel borders.

A broad, flat, horizontal zygomatic-orbital bridge extends laterally, its posterior border beginning at a point lateral from the rear end of M<sup>2</sup>. The anterior border of the bridge cannot be determined exactly because of missing fragments. Laterally the maxillary meets the jugal in a broadly arched and expanded vertical plate. The exact nature of the posterior termination of the maxillary-jugal suture is believed to be shown by a circular rugose surface on the inner surface of the jugal at a point immediately posterior to the beginning of the vertical expansion of the jugal. The bony relationship in this region is quite similar to that in *Caribosiren* (Reinhart 1959: p. 10, figs. A-C).

**VOMER.**—There is a general similarity of this element to that of *Metaxytherium* and *Dugong*, but it differs markedly from the condition in *Trichechus*, which bears a flat anterior processus maxillaris, in contrast to the thin vertical parallel plates present in the Florida form. Because of the delicate construction of this bone and its general loose sutures with surrounding elements, it is not usually preserved. As a result of its rarity in the fossil record, there is a lack of specimens avail-

able for comparison, and most illustrations either fail to show the vomer or it is displayed in a very generalized manner unusable for comparison.

The lower anterior half of the elongate U-shaped vomer lies in a deep indentation of the maxillary, and it is bordered on either side of the base by a small canal leading from the anterior incisive foramen to its disappearance on the sides of the processus maxillaris. The dorsal anterior half of this element extends upward into two thin parallel bones, with the greater accentuation posterior. If the thin vertical plates are in place, as they appear to be, then the dorsal extension is unusually high. The posterior half of the vomer is indistinct, except for the thin ascending plates that clasp the perpendicular plate.

**SUPRAOCCIPITAL.**—As is true even in advanced fetal stages of *Dugong* and *Trichechus*, the supraoccipital parietal complex in *H. olseni* is firmly ankylosed. Juncture of the dorsal surface of the parietal and the posterior surface of the supraoccipital is  $115^{\circ}$ . The anterior border of the superior nuchal line is upraised and arched forward. On the medial nuchal line the triangular external occipital protuberance diminishes to a thin crest, which extends two-thirds of the way down this element and merges with a broad-grooved, indented ventral sulcus. The medial crest is bounded on either side by an oblique rugose fossa. Sutural contact with the exoccipitals forms an angle of  $132^{\circ}$ , and the ventromedial portion of the supraoccipital is separated from the foramen magnum by an estimated 16.5 mm. These measurements are similar to those of the large European *Metaxytherium krahuletzki*, which has complementary figures of  $130^{\circ}$  and 18 mm, but is otherwise structurally different and readily distinguishable. The irregular progressive tendency for the supraoccipital to touch the foramen magnum and for the supraoccipital-exoccipitals to meet at a more closed or small angle is considered fully on page ——. From this discussion it will be noted that the measurements given for the Florida specimen are about intermediate between those of Eocene forms and the living *Dugong*.

**EXOCCIPITAL.**—Articular surfaces of the condyles are convex (as in all Sirenia), have a semi-lunar outline, and, due to the excellent state of preservation, bear sharp borders as in living forms. The lateral border of the condyles is paralleled by the outermost borders of the exoccipitals, with a deep supracondylar fossa separating the two parts. Borders of the foramen magnum form a transverse flattened oval, with a slight rise in the midline. Such a description fits the shape of the foramen magnum in the bulk of fossil Sirenia, but differs from the broader, flatter oval form of *Trichechus*, which also lacks a dorsal indentation and can be differentiated from *Dugong*, which bears a triangular foramen. In this same feature, *Halitherium schinzi* Lepsius (1882: pl. 5, fig. 52; pl. 10, fig. 97)



differs in the presence of an abrupt small dorsal arch. Another point of contrast between the Florida specimen and *H. schinzi* is the paroccipital process, which in the latter, as in metaxytheres and referred felsinothers, lies below the ventral surface of the condyles, as compared to a higher placement in *H. olseni*.

The condyloid foramen, a short, thick canal that provides an exit for the hypoglossal nerve, is present on the lateral side of either condyle, at which point it ascends dorsally and medially, bifurcating into two branches on the inner surface of the cranium. As would be expected, this foramen maintains a relatively constant size; that is, it enlarges as the animal grows and reaches greatest size in the largest genera.

**BASIOCCIPITAL.**—A review of this element in Eocene to Recent Sirenia reveals no basic change in shape and but minor superficial differences. Fusion has obliterated the basioccipital-basisphenoid contact, a moderately unusual condition. Sickenberg (1931: 428) notes the general occurrence of a nonfusion of this suture, discusses its relationship to other neotenic conditions in the Sirenia, and attributes these to hypothyroid metabolism. Nonfusion of this suture occurs in *Caribosiren*, *Halitherium schinzi*, *H. christoli*, *Metaxytherium jordani*, *Hesperosiren*, and many other forms. From examination of living and fossil specimens, it is suggested that, as with most other sutures, the basioccipital-basisphenoid contact tends to remain open in young animals and to fuse in old age.

The sella turcica is a shallow depression that is moderately well developed considering the small size of the individual. It was reported to be present by Lepsius (1882) in *H. schinzi*. It is absent in the adult specimens of *Dugong* I have examined, an observation in keeping with those of Freund (1908). Sickenberg, however, reported a gentle depression in this area in very old individuals of *Dugong*. Adult trichechids show this minor feature well developed; it is relatively less conspicuous in *Hydrodamalis*. A small ridge, the dorsum sellae, is present, but it is not known if the lateral clinoid processes were ever present. As in *Metaxytherium jordani* (= *H. vanderhoofi*), the typical upraised rugosity found on the anteroventral surface reveals some details not generally preserved. A narrow median ridge in the posterior half divides the rugosity into two oval rugose areas, which in turn are split by an anteroposterior directed sulcus.

**PTERYGOID.**—Posteriorly the pterygoid processes are deeply incised by a broad groove, which widens ventrally, terminates laterally in thin edges, and ends dorsally in a small lateral spine. Rugose surfaces on the lateral and anterior surfaces of the processes indicate that sutural connections with the alisphenoid and palatines are missing. Although the

pterygoid processes are not exactly like those of other sirenians, neither are they distinctive from other halitheres or the metaxythere-felsinothere line.

**JUGAL.**—The anterior-dorsal part of the maxillary separates the lacrymal and jugal from the premaxillary arm, a condition also found in the Eocene *Eotheroides* sp. (Reinhart 1959: fig. 8). Abel (1912: 312) illustrated the maxillary of *Eotheroides aegyptiacum* as forming the entire lateral ring of the orbit. Weber (using Abel's reconstruction [1928: fig. 330]) illustrated, and Sickenberg (1934: 196) stated, that in *Eotheroides libyca* the forward end of the orbit is composed of the lacrymal and jugal. *H. olseni*, like *Eotheroides* sp. above, is intermediate between the position interpreted by Abel and that of Weber and Sickenberg. It has the lateral surface of the orbital ring composed of the jugal instead of the maxillary, which differentiates it from *E. aegyptiacum* as described and illustrated by Abel. Furthermore the forward border of the orbital ring is composed of the maxillary, jugal, and lacrymal, rather than exclusively of the two latter bones, as Sickenberg and Abel have interpreted for *E. libyca*.

The maxillary-jugal contact at the anterior end of the orbital ring, as seen in the illustration of *H. schinzi* by Lepsius (1882: pl. 8, fig. 87), is basically the same as in the Florida halithere, except that a lacrymal is not present in the former. The same series of illustrations by Lepsius is used by Dechaseaux (1958: 350, fig. 25), but here the maxilla is labeled as the jugal, and the jugal bears no designation. Because the lacrymal is loosely sutured to the surrounding bones, it is rarely present, and for this reason I place strong emphasis on the interpretation of the bony relationships displayed in this area in both *H. olseni* and *Eotheroides* sp. This is in contrast to many illustrations that I feel are incorrectly interpreted and illustrated, due to lack of clarity in the specimens.

Dorsoanteriorly the jugal abuts abruptly into the ventral end of the lacrymal. The orbital rim is laterally widened and flat, as is true of Sirenia in general. The ventral surface beneath the orbit is broadly rounded; dorsally the orbital ring ends in a thick rugose surface, and it appears that this area abutted abruptly into the zygomatic arch. As a result of crushing during preservation, a strong skew exists in the orbital ring. Nevertheless, it is interpreted that the posterior end of the orbit was more closed than in *H. schinzi*, but less so than in *Trichechus*. Behind the orbit there is a marked vertical expansion, which thins rapidly posteriorly and terminates as a thin vertical plate. An indentation and general rugose ventral surface of the zygomatic arch indicates that the malar process ended at a point lateral to the middle of the glenoid plate.

**SQUAMOSAL.**—The overall configuration of this element is similar to

that of *Halitherium schinzi* and *Metaxytherium serresi*. Should it differ from any Eocene through Pliocene sirenian, it would be in the more posterior extension of the malar process, which in this instance is opposite the center of the tuberculum articulare. The articular plate is roughly oval, with the long axis transverse, and (with the exception of a slightly upraised border) it is flush with the ventral surface of the zygomatic root. A deep postarticular fossa, of the same size and shape as that in *Dugong*, is also present.

Above the posttympanic process, the squamosal swings in a small irregular circle around the mastoid part of the petiotic, thus leaving this bone exposed externally. Internally the petrosal part of the petiotic is loosely enclosed in a large groove of the squamosal.

EAR BONES.—The ear bones are dense and compact, as is true of most marine mammals. An irregular ovoid to reniform petiotic is set in a deep groove of the squamosal. The petrosal is separated from the malleus by a wide fossa incudus, which is broadly rounded dorsally, as compared to the condition in *Dugong* and *Trichechus* in which the dorsal termination is a narrow V. The posteroexternal face bears a flat rugose surface, which is exposed externally and partly enclosed by the squamosal and exoccipital. Because of the skewed condition of the cranium in this area, the relationship of the supraoccipital to the exposed mastoid is not known although the general condition appears to have been very similar to that in *Dugong*. Both pars labyrinthiae are missing, as well as the various foramina located at the juncture with the main body of the mastoid.

In *H. olseni* both tympanic rings are detached. These are of typical horseshoe shape, with the anterointernal arm bearing several small, weak points for attachment to the petrosal, and the larger posteroexternal attachment is missing. The ventral margin terminates in a thin crest, similar to that in *Trichechus*, with a ventroanterior edge produced into a prominent spine. In general outline there is a close resemblance to *Halitherium schinzi* (Lepsius 1882, pl. 2, fig. 12).

#### AUDITORY OSSICLES

LEFT MALLEUS.—A vertical, transversely thin, helmet-shaped manubrium extends ventral from the main body of the malleus, and is uniquely different in details from that in *Dugong* and *Trichechus*. It is noticeably thinner than in *Dugong*, more like that of *Trichechus*, and although slightly broken it clearly lacks the prominent ventroposterior extension of the manubrium present in the two living genera. The main body is twisted and bears a conical, internally directed prominence termed the lateral process. On the outer side, the spur of the malleus is slightly

twisted and directed inward as in *Dugong*. Anteriorly the general configuration also resembles *Dugong*, but posteriorly *H. olseni* has a simpler construction (*i.e.* fewer and less accentuated undulations).

**RIGHT INCUS.**—The incus in its entirety is almost an exact replica of that present in *Dugong*. The crus breve and crus longum diverge from one another nearly at right angles. The crus breve is short and conical, and extends dorsally into the fossa incudis. On the anterior face of the body is a concave oval facet, which articulates with the head of the malleus. Lying immediately dorsal to this is the V-shaped facet, into which the spur of the malleus is inserted. As an extension of the body the crus longum is twisted medially and terminates in a small oval facet against the stapes.

**RIGHT STAPES.**—Although the stapes is separated from its articulation with the incus, a small oval articular facet (the lenticular process) is present on the incus, and a corresponding articular surface is undoubtedly present on the head of the stapes. The base is a flat oval plate, and the general proportions of the stapes are similar to those of all Dugongidae. The stapes is 8.2 mm long, with a distance of 3 mm separating the base from the center of the stapedia foramen. As near as can be ascertained from living and fossil specimens, no taxon is distinct because of unusually large, or small auditory apparatus, but rather the sizes of ear bones and ossicles are in proportion to the size of the individual.

The value gained from a description of the auditory ossicles is limited, because of the difficulties involved in interpreting distinctions among such intricately constructed elements, based on descriptions and/or illustrations in the literature. A detailed study of actual specimens covering the time sequence from Middle Eocene to Recent might reveal features characteristic to various taxa that are not readily perceivable except by direct examination.

**UPPER INCISOR.**—As with all tusked Sirenia, the upper tusk-like incisors appear almost too large for the cranium, and seem grotesquely inconsistent with other cranial proportions. They are similar to incisors of the European *Halitherium*, *Metaxytherium*, and referred felsinotheres in having a laterally compressed oval outline and a heavily-striated, rough surface. Extending down from the base for approximately 21 mm and encircling either incisor is a series of rings formed by small rugose round knobs. A small, laterally compressed dental cavity is present in the base of the tusk. In cross-section the occlusal end is roughly triangular, and the lateral face sharply beveled with a chisel-like termination. Throughout the length of the tusks there is a gently lateral diver-

sion, the maximum separation of the incisors occurring at the occlusal end. Maximum length of the incisor is 93.7 mm.

**DENTITION.**—An oval alveolar region is present in *H. olseni*. Very similar counterparts are found in *H. schinzi*, *Caribosiren*, *Metaxytherium serresi*, and *M. foresti*, as compared to some of the anteroposterior straight alveolar rows present in *Trichechus* and occasionally in some of the larger Sirenia, such as *Metaxytherium calvertense* (FGS V5454). Four heavily worn cheek teeth, interpreted as being  $M^{1-3}$  and  $P^4$ , reveal little detail, due to obliteration of cusp structure. Although *H. olseni* is a young individual, the worn condition of the teeth suggests an animal of old age. It suggests either an inability to efficiently masticate vegetation, or the consistent presence of hard, abrasive sediments mixed with the food. The worn molars could well have been a factor contributing to the apparent premature death of the individual.

$M^3$  is subquadrangular, with the three anterior teeth quadrangular. In  $M^{2-3}$  minor remains of enamel on the occlusal surface show that an anterior cingular valley was present on the buccal side, and a transverse median valley present in  $M^{1-3}$ .  $P^4$  also appears to have been lophodont. The right  $M^3$  has two roots that recurve anteriorly and one or possibly two vertically straight roots.  $M^2$  through  $P^4$  bear one root on the lingual side and two on the buccal. The condition of recurved or hooked roots is typical in fossil Sirenia, as opposed to straight roots in *Trichechus*, vertical pegs in *Dugong*, and an absence of teeth in *Hydrodamalis*.

**MANDIBLE.**—Torsion during preservation has warped the mandibles, but dental differences between the North American and European *Halitherium* are readily recognizable. A long diastema separates four cheek teeth from 2-3 alveoli in the symphyseal plate. Broad, shallow alveoli reveal the former presence of three nonfunctional incisors in the left mandible and two in the right. The small number of symphyseal teeth is reminiscent of the metaxythere-felsinothere Mio-Pliocene line rather than of *Halitherium*, which normally bears alveoli for three incisors and one canine. Whether this is an individual anomaly or a trend similar to the loss of incisors, as in *Trichechus* and *Hydrodamalis*, is not known. Innervation of the symphyseal face is accomplished by a medial foramen, which enters the dorsoposterior margin, then becomes a moderate furrow from which minor grooves branch throughout the symphysis. Lateral to the incisor alveoli the lateral borders of the symphyseal region flare out to a thin edge, the degree and prominence of flare corresponding to the development of the incisors. A thin-edged diastema separates the  $P_4$  from the symphysis. It can be clearly ascertained that  $M_3$  is trilophodont, the size of the fragmented  $M_2$  suggests a similar construction, and two lophs are discernible for  $M_1$ . All cheek



FIGURE 20.—*Halitherium olseni* (FGS V6094): posterior view of cranium.

teeth are anchored by two roots: those of  $M_{1-2}$  are thin anteroposteriorly and transversely broad; the  $M_3$  roots are more rounded; and the alveoli of  $P_4$  suggest small round roots. No comparison of cusp details is possible because of the heavy wear. Except for their small size, the cheek teeth of *H. olseni* cannot be distinguished from those of the European *H. abeli* or *H. christoli*. The ventral border of the horizontal ramus forms a broad symmetrical arc, similar to that in *Dugong*, *H. abeli*, and *H. christoli*. The comparable region in *Halitherium schinzi* is less arcuate; that is, it is more elongate and straight as the angle is approached. Remains of the angle appear to be typically dugongid and not arched anteriorly, as in *Trichechus*.

ATLAS.—There is, in general, a dearth of fossil atlases with which to compare *H. olseni*, but the atlas of *Halitherium abeli* is essentially an exact duplicate, and that of the Eocene *Protosiren fraasi* has the same type of transverse processes and general proportions. The major difference existing between FGS V6094 and forms such as *M. jordani*, *M. cwieri*, *M. foresti*, and *M. serresi* is the much greater height and prominence of the transverse processes in the former. This condition results from the development of the base of the transverse processes lateral to the ventral arch, rather than midway up the atlas as in other fossil specimens and recent genera. Unlike the distinct vertebrarterial canal

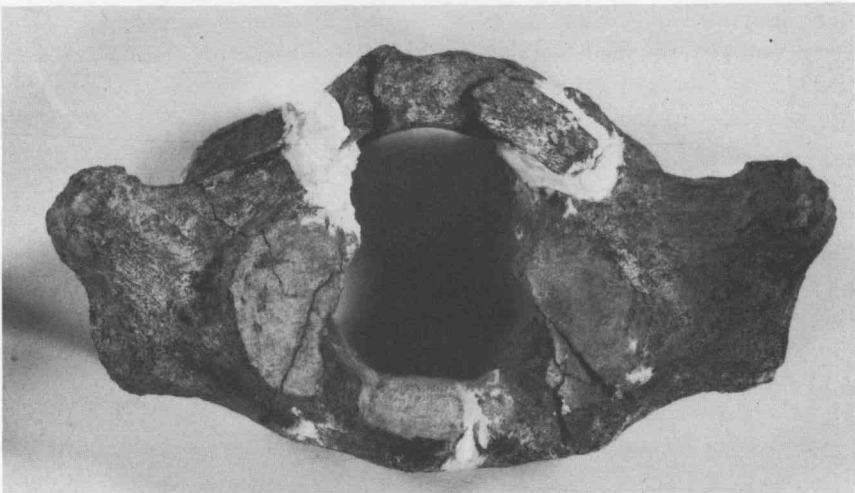
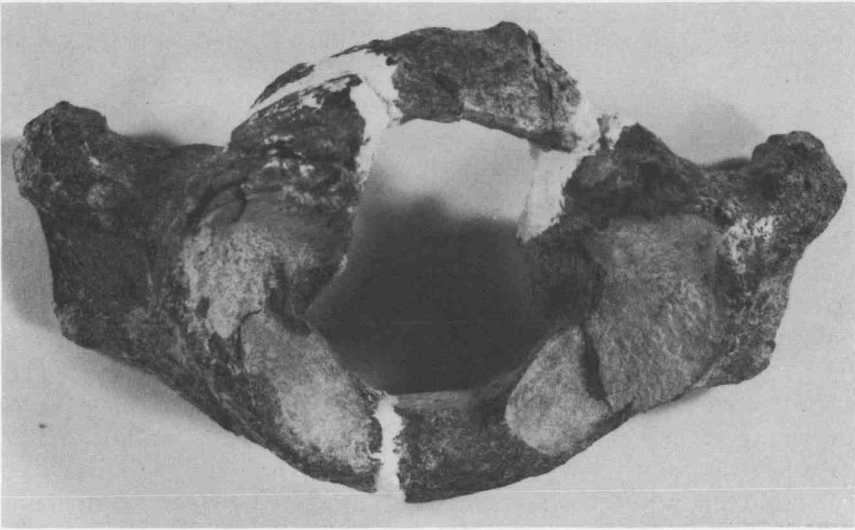


FIGURE 21.—*Halitherium olseni* (FGS V6094): (A) anterior view of atlas; (B) posterior view of atlas.

foramina, which pierce the transverse processes in *H. abeli*, those of the Florida specimen are incipient and hardly functional. Presence of these foramina is highly variable, often being well developed on one side and closed on the other, sometimes not developed on either side, or incised at the base of the process by a deep groove as in *M. jordani* (= *H. vanderhoofi*). The double arch for the odontoid process and the neural

canal is in the shape of a figure 8, which is the state found in Oligocene-Pliocene sirenians, in contrast to the laterally expanded, open neural canal in *Trichechus*. The neural arch is crushed, so the correct height of the element can only be approximated.

AXIS.—Except for details, the axis of *H. olseni* does not differ from that of *M. serresi*. The base of the odontoid process is bounded dorsally and laterally by a deeper groove than any illustration or specimen known to the writer, but this condition is undoubtedly due to the juvenile stage and the excellent degree of preservation. Beneath the process the outline of the articular epiphysis is similar to an exaggerated egg, with the anterior half pinched and the posterior half expanded suddenly into a bulbous posterior border. This articular facet, well separated from the anterior cotyles and lacking a prominent articular platform, is in contrast to the condition present in adult metaxytheres and *Trichechus*, in which the facet is elevated on a short platform, and a proximity of cotyles to the facet is the rule. In general outline the epiphysis not only differs from the more oval border of various metaxythere axes on hand and from the round epiphysis of *Trichechus* but, most interestingly, it is as large as those in axes 50-75% larger in overall proportions. Anterior cotyles are quadrangular and more like those of Florida metaxytheres than those of *M. serresi* or *Metaxytherium cuvieri*, both of which are vertically elongate. The border of the neural canal has a rounded arch, as in *Trichechus*, rather than the condition typical of Oligocene-Pliocene sirenians in which the dorsal half of the neural canal is more quadrate. A rugose surface marks the dorsal surface of the neural arch upon which a central weakly developed spinous process is present. The anterior tubercle of the neural canal is roughly oval in outline, and rugose where a pad of cartilage lays between this face and the atlas. Postzygapophyses are as large as in the larger *Trichechus*, a feature in keeping with the large articular facet on the ventral side of the odontoid process. The base of the centrum is broadly concave, as opposed to the usual flattened condition of both fossil and recent forms. Laterally the centrum is flanked by two pairs of transverse processes; a thin, prominent dorsal extension directed lateroposteriorly; and a small ventral pair. These are present to a minor degree on a number of well preserved fossil specimens and in *Trichechus*, but in no instance do any display the development of *H. olseni*. Whether this is a character of taxonomic value or the result of excellent preservation is not known.

CERVICAL VERTEBRAE.—The cervical vertebrae from 3 through 7 bear slender neural arches that are nested within one another, and have the reduced thickness characteristic of all mammals that have become adapted to an aquatic environment. A triangular spinal canal is similar



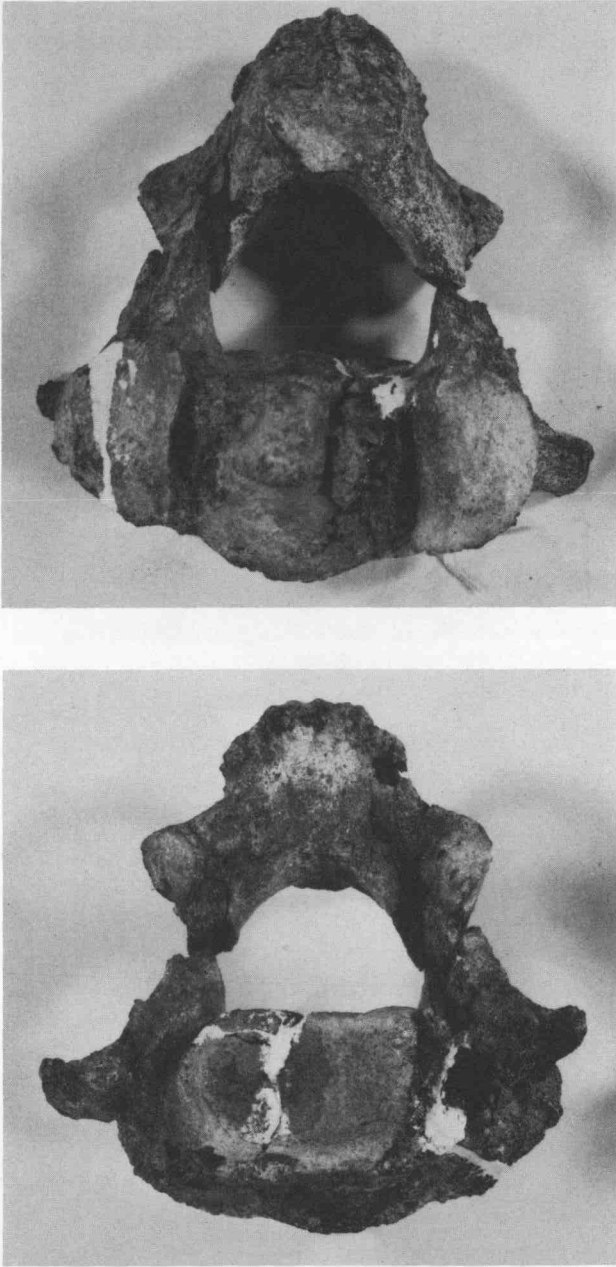


FIGURE 22.—*Halitherium olseni* (FGS V6094): (A) anterior view of axis; (B) posterior view of axis.

to that of virtually all living and fossil sirenians, but is different from the more rounded arch of *M. serresi*. The cervical centra form a broad transverse ellipse, are of equal thickness in numbers 3, 4, and 5, and increase in thickness rapidly in 6 and 7. Broad, posteriorly directed transverse processes, pierced by a vertebrarterial foramen, are present on number 3 and are believed to have been present on numbers 4 and 5. A similar situation is found in cervical vertebrae of European halitheres. Peculiar to the sixth cervical is a powerfully constructed, ventrally directed knob at either ventrolateral corner of the centrum. The base of each of these tuberosities is pierced by a foramen. The seventh cervical bears large thick transverse processes that begin laterally from the flat base of the centrum, a feature also true of *M. serresi* and *M. foresti*. A similar knob, but of different shape, is present on the sixth cervicals of the Egyptian Eocene *Eotherium aegyptiacum* and *E. libycum*, and on the third cervical of *M. foresti*. Generally such protuberances are missing on fossil cervicals and are completely lacking in *Trichechus*. No definite criteria that can be used for generic or specific distinction appear to be among the reduced cervicals. Perhaps more information concerning the size and shape of the transverse processes will prove to be of value in such a diagnosis. The first thoracic, or eighth, vertebra bears the typically wide transverse processes with distinct facets for articulation with tuberculum and capitulum. No vertebrarterial foramen pierces either the seventh or eighth vertebra.

SCAPULA.—The overall outline and proportions of the scapula agree best with *Halitherium abeli*, *Metaxytherium krahuletzki*, and *M. serresi*, except that in *H. olseni* this bone is smaller. The glenoid cavity is deeply concave, with an egg-shaped articulate surface, and the coracoid process is well developed for a juvenile individual. Beginning at the ventral edge of the glenoid cavity, the curving axillary border becomes gradually thinner, ending in a prominent projection for reception of the teres major muscle. This projection, which is also pronounced in *Dugong*, is seldom found preserved, but where it is not destroyed, as in scapula of *M. serresi* and *M. foresti*, the projection is poorly developed. The border remains thin posterior to this projection. The only spine seen was fragmented, but appeared to be short, as in *Halitherium christoli*.

HUMERUS.—The humerus is fore-shortened, as in all Sirenia, but it nevertheless lacks the massiveness of the larger metaxythere humeri. It is relatively slender, and in this regard resembles both the European *Halitherium schinzi* f. *delheidi* (Sickenberg 1934: pl. 9, fig. 2a-b) and *M. serresi* (Depéret and Roman 1920: pl. 2, fig. 3) in some detail. The dorsal head is hemispherical, is joined to the body by the short, restricted anatomical neck, and assumes a relatively greater size in the distal end

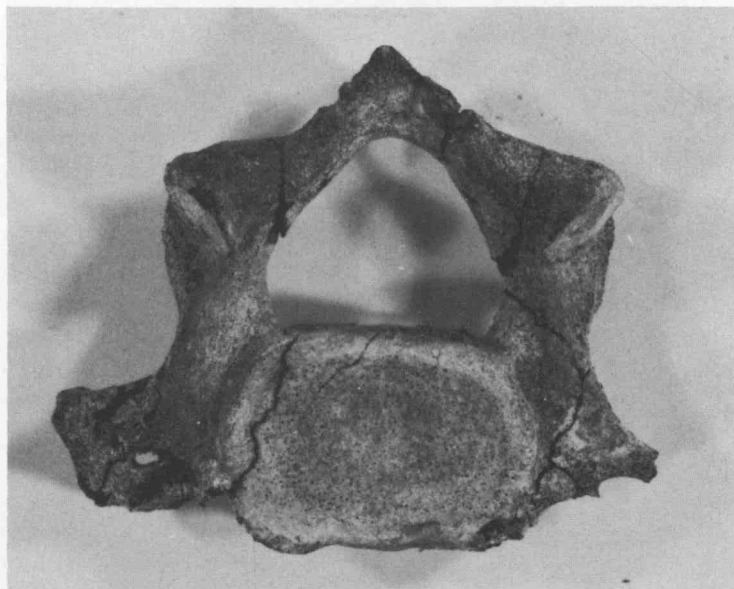
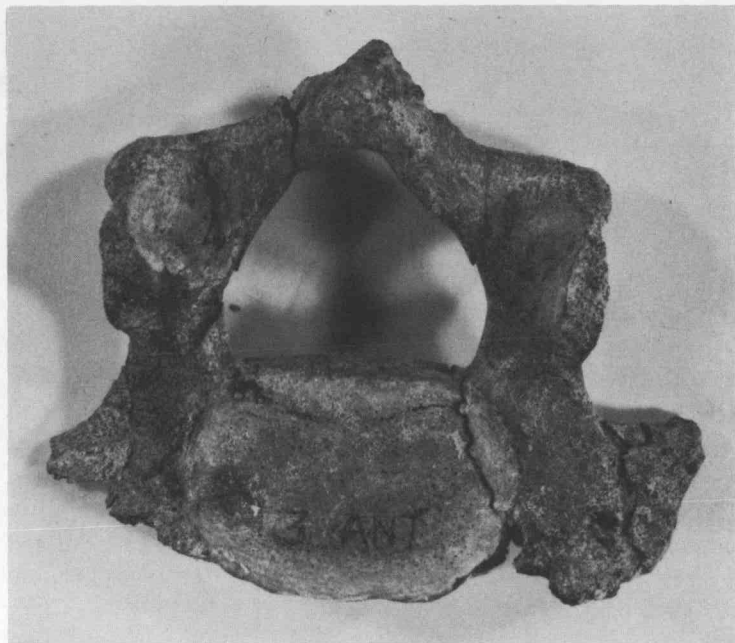


FIGURE 23.—*Halitherium olseni* (FGS V6094): (A) anterior view of third cervical vertebrae; (B) posterior view of third cervical vertebrae.

of the humerus than in the large metaxytheres. The long axis of the greater tubercle lies lateral and parallel to the dorsal head, the two separated by a deep U-shaped sulcus. A continuation of this bicipital groove between the greater and lesser tubercles becomes deeper, with the accentuation greatly increased where the border of the greater tuberosity curves abruptly toward the lesser, and partially closes the U-shaped sulcus or groove. Closure of this intertubercular groove is greater than in any illustration or description known to me, although the more massive *Metaxytherium krahuletzki* (Abel 1904: pl. 14, fig. 4b) and *Metaxytherium* sp. (UF 3619) approach this condition. Juvenile humeri of *Metaxytherium cuvieri* display a relatively open notch, with more closure occurring as the lesser tubercle develops a larger size with age. The head of the greater tubercle is a modified semilunar outline, the entire surface apparently having served for muscle insertion.

A small circular area for muscle insertion lies at the base of the greater tubercle, immediately above the sharply recurved deltoid process. This thin process is usually worn or broken in fossil humeri, but the sharp curvature is present to a similar degree in *H. schinzi* f. *delheidi*, *M. serresi*, *M. cuvieri*, and *Dugong*. Below the distal head the triangular shaft displays a slight degree of curvature, which is similar in the humeri of all sirenians. The proximal third of the humerus is virtually the same in *Sirenia* from the Oligocene through the Pliocene. A semicylindrical, oblique trochoid is bounded laterally by a prominent entocondyle and a small ectocondyle. Both the olecranon and coronoid fossae are deep and well developed. In metaxytheres the olecranon fossa remains a deep depression throughout the adult stage, but the coronoid fossa tends to fill with bone, with the result that only a shallow depression marks the site.

**RADIUS AND ULNA.**—The coronoid process of the ulna is well fused in the upper extremity, but unfused at the distal end, except for a small internal area immediately above the epiphyses. The usual crossed torsional position between these bones is less developed than in any other sirenian specimen known to me, regardless of genus. This relatively straight relationship could be a function of age with torsion and a greater bony opposition occurring as it becomes necessary for the animal to propel a larger body. A long, thin interosseous space is present that is similar to that in *Halitherium* and *Metaxytherium*, more closed than in *Dugong*, and lacks the outward bowed radius of *Trichechus*. Shafts of the radius and ulna are slightly bowed, with the only major change in configuration being a deep depression running the length of the internal face of the ulna. Semilunar and radial notches form a concave, transversely broad semicircle. The olecranon process of

the ulna is the same as that in *M. serresi*. The distal epiphysis of the ulna is larger than that of the radius, as is usual in sirenians. The epiphyseal surface of the ulna is concave, rounded, and elongate, whereas the corresponding articular surface of the radius is transversely broad, somewhat flatter, and kidney-shaped. Lack of fusion of the epiphyses, plus the cellular structure of these elements, indicates a young animal. In general proportions it appears to show closest affinities to the European *Halitherium schinzi* f. *delheidi* and to *M. serresi*.

**METACARPALS.**—Remains of the proximal ends of the left metacarpals 3, 4, and 5, and the distal portion of metacarpal 2, reveal partially broken articular surfaces, but provide no new information regarding the genus or species. A partially combined element of the intermedium and radiale is, as near as can be ascertained, the same as that of *Halitherium schinzi* f. *delheidi*.

**RIBS.**—Heads of ribs 1 through 3 are missing or fragmented, but remaining portions strongly suggest the usual condition of the anterior ribs (i.e. a tuberculum and capitulum separated by a broad groove). As in *Trichechus*, the first rib is anteroposteriorly flattened, acutely curved at the proximal end, and bears a small tuberosity on the distal termination. Articular facets on the seventh cervical and first thoracic vertebra indicate the usual angular, two-sided capitulum characteristic of a number of interior ribs.

The second rib is much more robust than the first and is terminated distally by a flattened thin end, the inner posterior face being formed by a flat plane. The third rib is marked by an increasingly robust construction, a noticeably larger size than the two anterior ribs, a typically banana-like shape, and a distal termination that ends in a flat plane like that of the second rib.

No difference in size of ribs 4 through 9 is evident. Separation of tuberculum and capitulum is essentially unchanged, but the double face of the capitulum tends to become a single facet in a posterior progression of the ribs. An obvious change is noted in the angle, which is marked by a minor groove in the first rib and becomes a gentle round protuberance bounded on either side by a broad shallow groove. Flattening of the distal end is evident in ribs 1 through 7, but thereafter the rib termini become more rounded. The distal portions of ribs 10-12 are enlarged, bulbous, and were probably attached to a cartilaginous or bony sternum, as suggested by the rugose medial termination. Scattered remains of many rib fragments near the posterior end and possibly right side of the specimen are heavily weathered and add no new information.

## EOCENE SIRENIA FROM FLORIDA

MATERIAL.—Two ribs (UF 4053).

LOCALITY.—Abandoned quarry of New Lebanon dolomite pit, Sec. 12, T 16 S, R 16 E, SW Lebanon Station, Levy Co., Florida.

FORMATION.—Avon Park limestone.

AGE.—Late Middle Eocene.

Sirenian ribs are found abundantly in a number of north African sites; however, the ribs here reported from the Middle Eocene of Florida are considered a rarity. Vernon (1951: 108-110) substantiated this record in his brief mention of a "Manatee rib" from the above dolomite pit, which is accompanied by a detailed stratigraphic section. Because of the significance of the discovery and the importance of eventually establishing a stratigraphic relationship among Eocene sirenians, the section by Vernon is included here:

On November 15, 1947, and July 11, 1948, boulders of this limestone, completely dolomitized, were mined in the north side of the pit, and these contained the large *Lucinia* of L-123, a Manatee rib, and numerous dolomite casts of "*Cerithium*" n.sp.

A visit to the site of the abandoned quarry produced a number of rib fragments from scattered boulders composed of massive tan sugary dolomite, as well as a dolomite conglomerate. In what appeared to be rocks of comparable altitude and lithology 10 mi. north of the New Lebanon dolomite pit, more sirenian rib fragments were found. The second collecting site (SE  $\frac{1}{4}$  Sec. 21, T14S, R16E, 1 mi. SE Gulf Hammock, Levy Co.) is being actively worked as a dolomite pit. Since Owen's record of the Jamaican *Prorastomus* in 1875, two recent reports have been made on Middle Eocene sirenians in the western hemisphere. Siler (1964) provided the first information of Eocene Sirenia in the United States. This is a rib of typical dense structure, found in place in the Gosport sandstone, Monroe Co., Alabama (assigned to Middle Eocene, Auversian age, by Stenzel *et al.* 1957). The second record (Arata and Jackson 1965) is a distal half of a rib from Little Stave Creek, base of the Gosport sandstone, Clarke Co., Alabama (*see* Russell 1955: 454-457, 469). In neither case was the described rib figured. The Gosport sandstone of Alabama and the Avon Park limestone of Florida are equivalent in age.

Upper-Middle Eocene beds of the Fayum bear moderate numbers of sirenian specimens and, largely because of the relative abundance of fossils from this region of Egypt, some students, such as Kurten (1969),



FIGURE 24.—*Halitherium olseni* (FCS V6094): articulation of humerus with radius and ulna, left side.

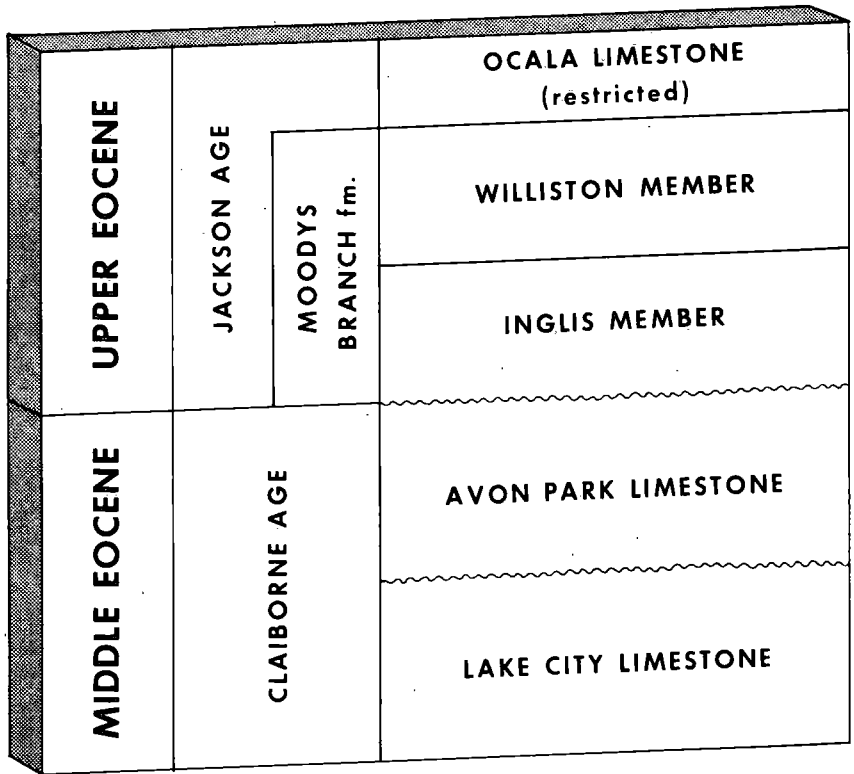


FIGURE 25.—Stratigraphic correlation chart of Florida Eocene.

believe that the order had its genesis in this region. Although it is true that few remains of these early beasts are known from the West Indies region, and there is an almost complete absence from the remainder of the world, this probably results from insufficient investigation of Middle Eocene beds rather than from a lack of fossils. The earliest sirenians with representatives in Jamaica, Florida, Alabama, Egypt, and possibly Java would obviously have had a wider geographic range than these isolated regions.

From the two illustrated Florida specimens, it can be seen that the head and articular facets are missing in the more complete rib, but the remainder is present from a point immediately anterior to the angle to the ventral termination. Curvature of the shaft is moderate throughout, with a slightly more acute curve at the angle. The other rib consists of the lower half of the shaft, from which the distal terminus is missing. Both the density of the bony structure and plumpness of the ribs immediately suggest sirenian affinity, but beyond this no specific reference





FIGURE 26.—(UF 4053) Middle Eocene sirenian ribs from Avon Park limestone, Florida.

can be given. Ribs from the uppermost Middle Eocene sirenians of the Egyptian Fayum also demonstrate the typical sirenian massiveness at an early geological stage. Andrews (1906: 217) stated: "This specimen shows that in *Eosiren* the ribs had attained the great thickness and generally massive structure characteristic of some of the later Sirenians." A cylindrical marine boring and a number of circular, nickel-size indentations (probably echinoderm or limpet depredation) indicate that the more complete rib either was not immediately covered by sediment after death or was later uncovered after fossilization occurred. Similar borings or markings by marine invertebrates on sirenian ribs are moderately common throughout the fossil record of this order. The greatest diameter of the larger rib fragment is 30 mm at a point just ventral to the angle.

Other than the ordinal designation, no taxonomic relationship to the Middle Eocene *Prorastomus* from Jamaica is proposed or even contemplated. The West Indian specimen was collected in the 1400 ft. thick Richmond Formation, from which invertebrate studies (which could be used to correlate between this formation and the Florida Avon Park limestone) are lacking. Absence of comparable bony elements further complicates any suggestion of relationship between the sirenians from these two sites. The rib fragments from Florida can be readily identified as sirenian, but to provide them with a taxonomic designation below that of order is unwarranted. A concentrated collecting effort in Florida and Alabama Eocene formations would undoubtedly produce material that would permit a taxonomic diagnosis.

## JAVA SIRENIANS

Inasmuch as the Recent *Dugong* ranges throughout large areas of the Indian and southwestern Pacific oceans, one would expect to find remains of fossil specimens from this region. Continental shores and islands in this area, however, have not been consistently investigated geologically or paleontologically, except in isolated sites, and knowledge of fossil Sirenia is most fragmentary. Fossil Dugongidae are well known from North Africa, Europe, and North America. From a study of the distribution of this family through various Cenozoic epochs, and from a consideration of the genera common to Europe and North America, one might assume that these forms crossed the Atlantic, thus accounting for the trans-Atlantic distribution of the genera and what appears to be parallel development. An east-west distribution of the sirenians by way of a Pacific route is seldom, if ever, mentioned as a possible dispersal route, perhaps due to a lack of knowledge of trans-Pacific forms. Lack of such information has made the work of Koenigswald (1952) on the fossil sirenians of Java of unusual importance.

Koenigswald (1952: 610) listed the earliest sirenian remains as a thick pachyostotic rib from Upper Eocene beds. To this he added, "too fragmentary for description, this find must be mentioned here, as it is the oldest indication for the presence of sirenians in the East Indies." The age of the rib fragment is of marked significance in providing a possible link between the North African Eocene sirenians and the Middle Eocene *Prorastomus* from Jamaica. The importance, however, is lessened by the fact that the rib is too fragmentary for description or illustration and no catalogue number is given.

Javanese sirenian remains from the Lower Miocene include a "fragment of a heavy bone in a marine limestone" and two tusks referred by Riggs (1839) to the genus *Sus*. In reference to the tusks, Koenigswald states, "As the formations in that neighborhood are marine, and also 'tusks' are typical for *Halicore*, these teeth most probably indicate a Sirenian. The original specimen seems to be lost." Doubt was subsequently expressed as to the proper reference of the tusks (Riggs 1839: 612) ". . . the 'tusks' from the Lower Miocene of Djasinga—if they really belong to a Sirenian . . ." The assignment of the Lower Miocene specimens to a sirenian appears vague and indefinite to me. The "heavy bone" is not illustrated or described in any manner and the "tusks" are lost. Identification of marine mammal tusks is a special problem and little has been accomplished toward differentiating the myriad of sizes and shapes with their varied triturating surfaces. Tusks of marine mammals are found unidentified in many private collections and in all large museums.



FIGURE 27.—Fossil sirenian localities in Java and Australia.

A most important sirenian is *Indosiren javanense* (von Koenigswald 1952) from the Upper Miocene (probably Sarmatian) of western Java. This is a small, unknown, bilophodont, upper milk molar that completely lacks development of roots. The anterior cingulum is typical in  $M^1$  of most sirenians from Eocene forms up to *Trichechus*. Some variation, however, may block an opening or the anterior loph and cingulum may be worn low, thus giving the impression of an open cingular valley. In most fossil Dugongidae,  $M^3$  is more likely to bear an open cingulum on the buccal side, with  $M^2$  intermediate in this character between the closed  $M^1$  and the open  $M^3$ . The anterior loph consists of a transverse arrangement of the paracone, protoconule, and protocone, all of which are similar in size. A very straight transverse median valley divides a slightly larger and wider anterior part of the tooth from the posterior. An unusual feature for a tooth of this age is the absence of any major or accessory cusp blocking the median valley. An open median valley is characteristic of the Eocene *Eotheroides*, *Prototherium*, and the living *Trichechus*. Miocene and Pliocene metaxytheres of a similar age as *Indosiren* are characterized by a forward displacement of the metaconule. The posterior loph is composed of a closely appressed and equal-sized hypocone and metaconule, which are separated from a shorter stout

metacone. The posterior cingular valley is open on the buccal side, a molariform trait common to most fossil sirenians.

In general appearance the occlusal surface bears a resemblance to *Trichechus* and to the Upper Eocene *Prototherium*. A lateral view again suggests *Trichechus* and also the tapir *Tapirus*. The tooth, as Koenigswald (1952) states, differs from other genera of similar age (*Halianassa*, *Miosiren*, and *Felsinotherium*), and reference to Eocene forms is unlikely. In addition, the tooth, which lacks any sign of abrasion, cannot be logically reworked from older strata. In the analysis of this tooth, certain developmental changes in sirenian teeth should be remembered. Fossil sirenian milk molars are rare, the usual finds being adult cheek teeth that usually differ from their lacteal predecessors. Because there are few milk teeth of comparable development with which to compare *Indosiren*, its significance remains unknown. With a single tooth a number of questions remain unanswered: Would the permanent adult tooth differ from the lacteal counterpart, or would it bear the same cusp occlusal pattern? In a number of fossil Dugongidae a greater number of accessory cusps appear in successive molars in the same individual as it grows older. The question may be asked whether an adult molar of *Indosiren* would be comparable to other genera of similar geologic age or a distinct entity, as the milk molar appears to be? More specimens are needed before the correct taxonomic assessment of *Indosiren* can be made.

Measurements of the upper left molar of *Indosiren javanense* are (in mm): length, 14.6; maximum width, 13.5 and height of entire loph, 10.6.

#### AUSTRALIAN SIRENIAN

The only other figured sirenian from this general sector of the world is a parietal-supraoccipital complex (De Vis 1883), which bears the proposed name of *Chronozoon australe*. This specimen is from the Chinchilla Drift, Darling Downs, New South Wales, in the southeast sector of Australia. The age of the element is not known, but it may be Pliocene. Associated land and freshwater vertebrates indicate a freshwater deposit.

Based on the illustration, there is some suggestion of similarity of this specimen to comparable elements of *Metaxytherium serresi* and *Halitherium antiquum* (Leidy), the latter of which was later referred by Simpson (1932: 445) to *Halitherium alleni* and assigned possibly to *Metaxytherium* or *Felsinotherium* by Kellogg (1966: 91). Other than this general observation, there is no indication of the relationship of this form to other genera. Because diagnostic qualities of a new genus are lacking in this specimen, the name is of little value other than to serve

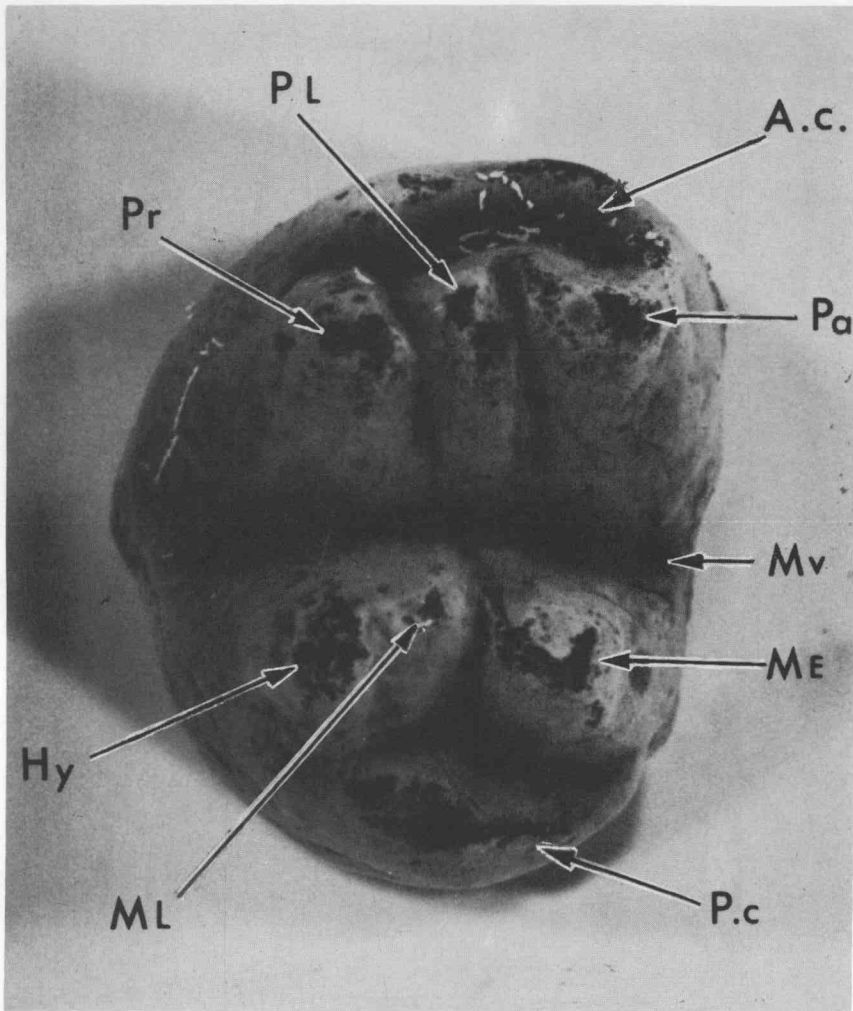


FIGURE 28.—*Indosiren javanense*: occlusal view of upper left milk molar.

as a reminder of the presence of a sirenian from this isolated geographic area.

#### INCISOR ANOMALY IN *Dugong*

The recent specimen of a young *Dugong* (FMNH 68781) used for purposes of comparison reveals an interesting anomaly in the symphyseal portion of the mandible. Four alveoli for three incisors and a canine are present on the left side, but five alveoli are found on the right. If

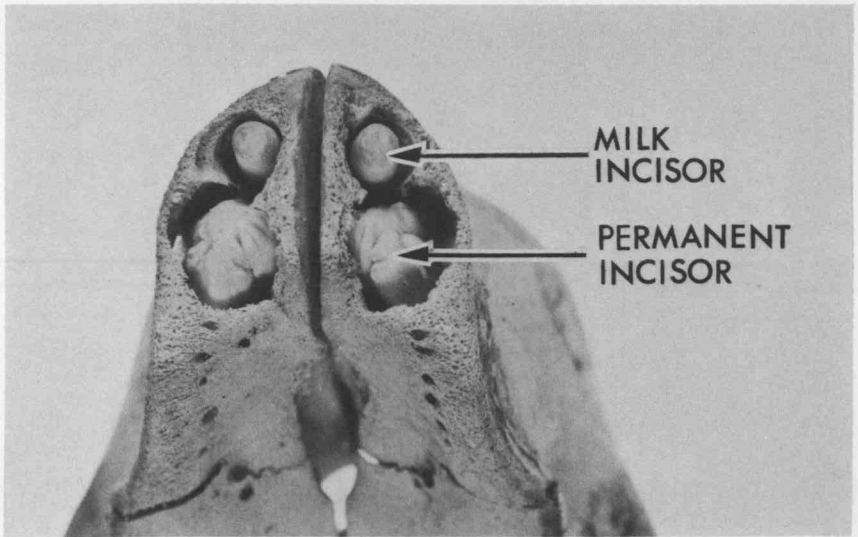


FIGURE 29.—*Dugong* (FMNH 68781): premaxillary incisor tusks in young *Dugong*.

the three ventral alveoli on the right are ascribed to the incisors, the upper two would then have contained a canine and a premolar. To attribute the dorsal alveolus to the premolar would be odd indeed, for this would necessitate separation of an anterior premolar from the cheek teeth by an elongate diastema. Separation of canine and premolar is a condition found in many animals and this is possibly the situation in FMNH 68781. If this postulate should be accepted, however, some explanation must be given to account for an extra incisor. Holmes and Harrison (1892: 790) may possibly have found a *Dugong* with five alveoli on either side of the mandibular symphysis, but their explanation is brief, vague, confusing, and lacks illustrations. Since all mandibular alveoli, except  $I_2$  on the right side, are shallow and essentially filled with a cancellous bony growth, presumably there was but one vestigial incisor that in life was undoubtedly covered by a horny pad. The alveolus of  $I_2$  probably held a milk tooth that was absorbed during early adulthood. The alveolus for  $I_2$  is elongate (14.5 mm), cylindrical (7.5 mm diameter), bears a round posterior termination, and is slightly expanded anteriorly.

Several other accounts mention vestigial incisors in *Dugong*. Home (1820: 153, pl. 14) stated that in a young female the third alveolus on each side of the jaw bore a small tooth. Owen (1840-45: 366) and later Lyman (1939: 229) noted an adult male *Dugong* in which the third alveolus in the left mandible bore a vestigial tooth. Kükenthal (1897: 68) reported four teeth-bearing alveoli in each mandible of an embryo.

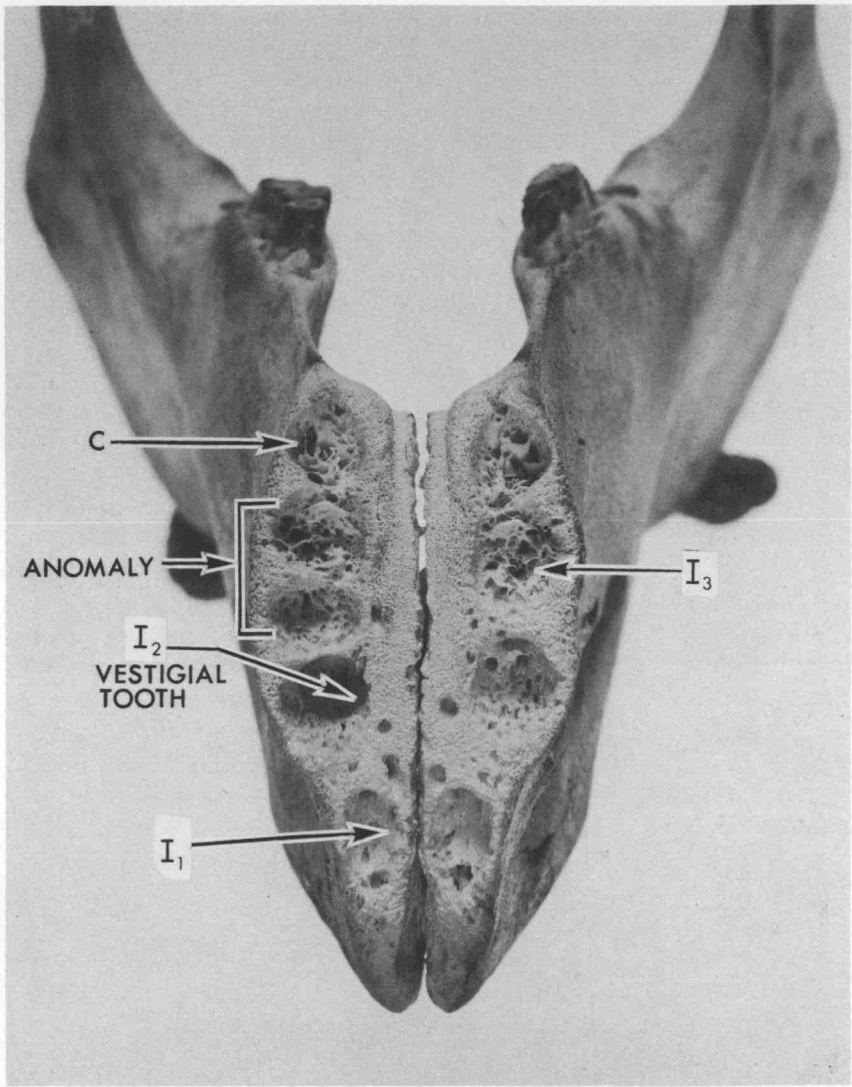


FIGURE 30.—*Dugong* (FMNH 68781): mandibular incisor anomaly.

From these few cases one would surmise that in *Dugong* there is in progress an irregular reduction of incisors in which  $I_3$  is generally the most stable and the last to disappear. This condition of  $I_3$  stability was pointed out by Heuvelmans (1941: pl. 4), who stated that the last rudiments of the labial teeth are always found in the third alveolus. FMNH 68781 differs from what might be the usual condition by the presence of

the right  $I_2$  alveolus that is believed to have contained a milk incisor. The primitive condition of a vestigial incisor can occasionally be expected in the young of an animal species in an evolutionary stage intermediate from one in which the adults had functional incisors and one in which the incisors are replaced by a horny pad for mastication. The uneven number of five alveoli, however, is an oddity not attributable to this general evolutionary trend but rather to an individual anomaly.

In the cranium of the same individual the maxillaries reveal two sets of incisors, a condition described by a number of authors in some detail. The milk incisors are smaller, anterior, and are firmly attached in their sockets. The larger posterior permanent incisors are short (27 mm), stout, roughly triangular, longitudinally striated, incipiently cuspid, and lie loose in their alveoli (sockets). The layer of enamel and dentine is very thin, and the teeth are hollow, with the vacuity extending throughout the tooth. This condition differs from that reported by Heuvelmans (1941: 2, fig. 1), in which the internal vacuity is short and the dentine well developed. It is possible that the specimen at hand was a young female, in which the permanent incisors would not have become well developed. The posterior termination of the permanent incisors lies in a broadly swollen recess of the premaxillaries. The swollen sockets are thin and open, thus revealing internally the cancellous bony tissue through which the permanent incisors were innervated. A thin transverse bony plate separates the anterior and posterior incisors. In contrast to the larger permanent incisors, the lacteal counterparts are strongly rooted, cylindrical, more elongate, lack striations and enamel, and bear no signs of cusps. The etched condition of the anterior incisors appears not to be the result of use, but rather of physiological resorption. The usual number of five cheek teeth are present in both upper and lower jaws of this specimen.

PRESENCE OF *Metaxytherium* IN ARGENTINA  
*Metaxytherium*, SPECIES INDETERMINATE

REFERRED SPECIMEN.—Upper left  $M^3$ . NUC 4301, Department of Paleontology, Physical and Natural Sciences of the National University of Cordoba, Argentina.

AGE.—Collected immediately below strata of Mesopotamian age. Upper Paranaian age, equivalent to Middle or Upper Miocene.

LOCALITY.—Cliffs along Parana River, Villa Urquiza, Province of Entre Rios, Argentina. Stratigraphic marine sequence provided by Dr. Florencio G. Aceñolaza.  
UPPER MIOCENE

Parana Formation (= Paranense + Entrerriense.<sup>1</sup> Frenguelli 1920-1947).

The Tertiary marine section outcropping in the Villa Urquiza region is composed of two members.

Overlying: "Mesopotamiense-Rionegrense<sup>2</sup> fluvial" (Frenguelli 1920-1947).

<sup>1-2</sup> See Paacual, R., et al. 1965, p. 174, table 11.



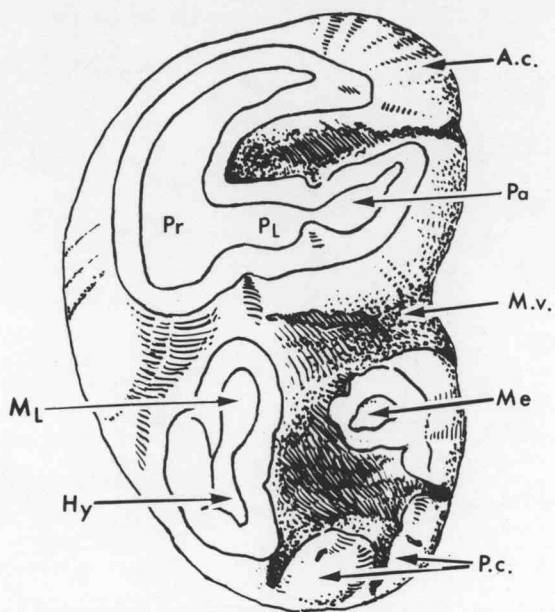


FIGURE 31.—*Metaxytherium* sp. indet. (NUC 4301): occlusal view, left M<sup>3</sup>.

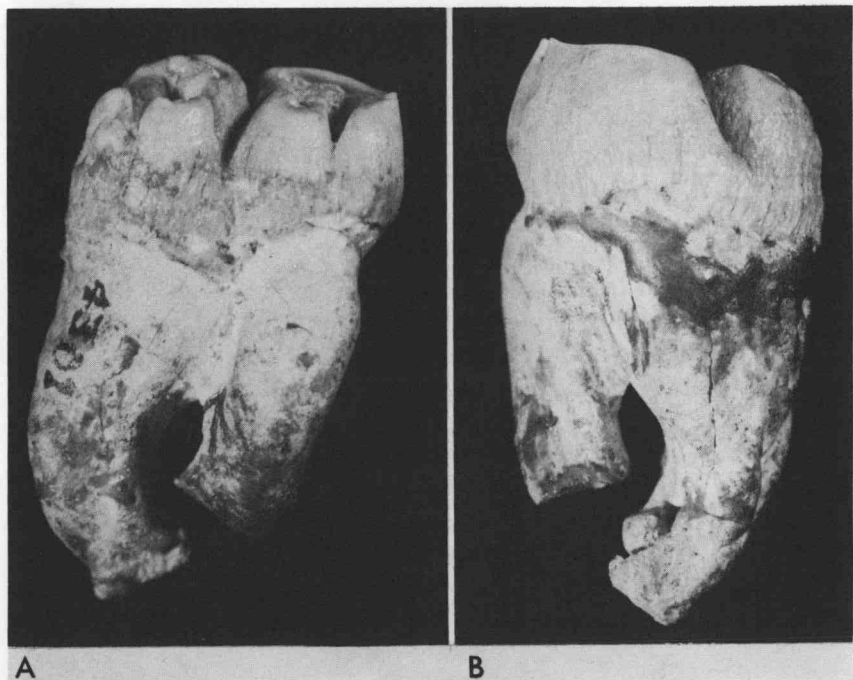


FIGURE 32.—*Metaxytherium* sp. indet. (NUC 4301): (A) Buccal view; (B) Lingual view.

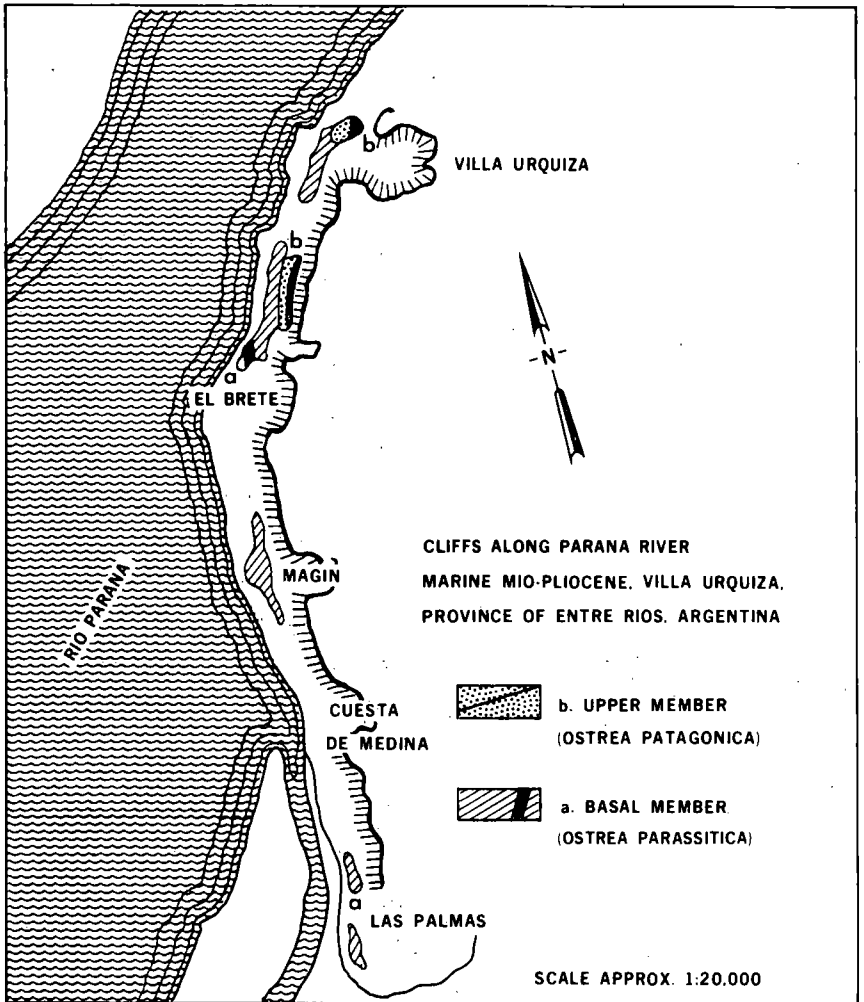


FIGURE 33.—Argentina, collecting site of *Metaxytherium* sp.

#### UNCONFORMITY

**UPPER MEMBERS:** Thickness 1½-3 m. Yellowish and whitish sand, clayey; massive in lower level; a fossiliferous bed in the upper level, contains: *Ostrea patagonica* D'Orb, *Ostrea alvarezii* D'Orb, *Chlamys paranensis* (D'Orb), and *Amusium darwini-anus* (D'Orb).

The best outcrop of these members is situated in the Port Villa Urquiza area. In the sand and clay there are abundant vertebra, fish-scales, and teeth of selachians (*Carcharodon*, *Carcharias raja*, etc.).

**BASAL MEMBERS:** Thickness 8-10 m. Green and green-yellowish clay, with thinly bedded, fine white-yellowish sand in the upper part.

Clay with an intercalation of whitish fossiliferous limestone (thickness 25 cm)

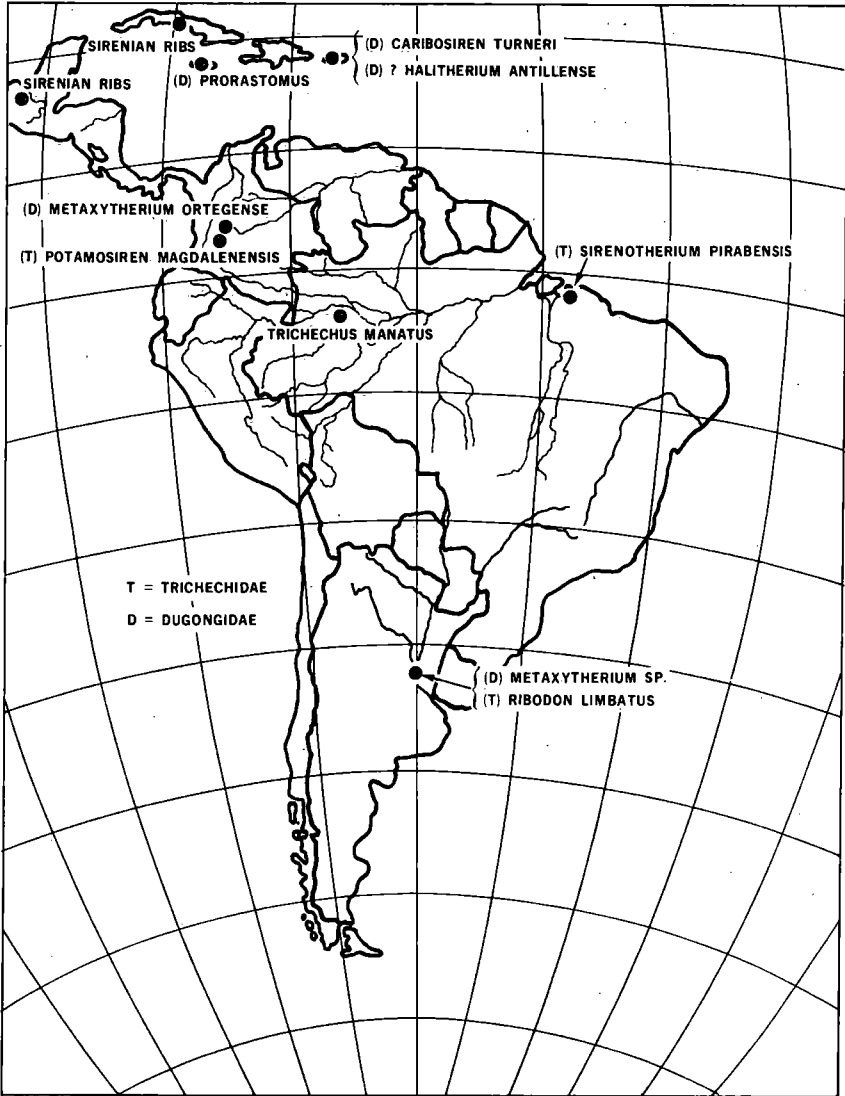


FIGURE 34.—Fossil sirenian localities in South America and the Caribbean.

outcrops in El Brete area; containing: *Ostrea parassitica* Gm., *Morophoraster darwini* (Desor), and *Sirenia indet.* (tooth).

In the Las Palmas area an oyster bed 30 cm. thick, intercalated between dark green clay, contains: *Ostrea parassitica* Gm. and *Placunanomya (Pododesmus) papiro-racea* (Phil)

BASE: "Not seen."

Although fossil sirenians achieved their greatest range and probable zenith in Late Miocene time, it is significant that a dugongid has been

identified as far south (latitude 30° 38' south) on the east coast of South America as Argentina. A report of another dugongid (Kellogg 1966), *Metaxytherium ortegense* from Colombia, further corroborates the co-existence of dugongids and trichechids in the Caribbean, and probably the entire coast of South America, south to the Parana River Basin during Late Miocene-Early Pliocene time. What factors caused the demise of the more widespread dugongids, but permitted the continued existence of the trichechids? Except for *Hydrodamalis*, the most obvious limiting factor affecting recent Sirenia is the narrow range of water temperature that the animals can withstand. Increased death of Florida *Trichechus* is notable during short periods of unusual cold weather. This fact applied to cooling marine currents of Pliocene and Pleistocene time may have accounted for a drastic reduction in numbers, as well as an associated change of flora due to cooler temperatures. Cooler temperatures may also have caused a crowding of herbivorous marine mammals in a narrow range of latitude, causing increased competition for food, as well as encouraging predators to feed on this concentrated food supply. Both living genera of Sirenia are basically shoreline and river-dwelling inhabitants, but reports on the sightings of recent dugongids suggest that they are more likely to be found in the open ocean than are trichechids. This gives rise to the thought that dugongids would be affected more by cooling marine currents than would their relatives. The above premises are interesting, but offer no explanation for the presence of the living *Dugong* from the Solomon Islands in the east, to the gulfs of Suez and Aquaba and the north coast of Kenya in the west.

TABLE 7.—MEASUREMENTS OF M<sup>3</sup> IN *Metaxytherium*.

	<i>Metaxytherium</i>		
	sp. indet. NUC 4301	<i>calvertense</i> USNM 23409	<i>ossivalense</i> UF 3281
Length	25.0	28.5	29.3
Width across protocone	17.7	18.5	22.9
Width across hypocone	13.9	18.5	19.0
Length M <sup>3</sup> /width M <sup>3</sup> across protocone	1.41	1.54	1.28
Length M <sup>3</sup> /width M <sup>3</sup> across hypocone	1.80	1.54	1.54

Stage of development of the M<sup>3</sup> from Argentina is similar to that of metaxytheres and the assigned felsinothers from Middle Miocene through Lower Pliocene of both Europe and North America. The lophodont molar is an elongate oval, subequally divided by a moderately-open, transverse median valley into a large anterior and a small posterior. The

prominent anterior cingulum is open on the buccal side, rather than closed by an accessory cusplule, and but for this difference most closely resembles *Metaxytherium ossivalense* (UF 3281) from Florida and *Metaxytherium calvertense* (USNM 23409) from Maryland. As in typical metaxytheres, the second loph is formed from a large protocone that is fused with the lingual portion of the anterior cingulum and the approximately equal-sized protoconule and paracone. The transverse median valley is deep, and essentially straight transversely, being interrupted by the forward displacement of the metaconule, a feature characteristic of the Mio-Pliocene metaxytheres. In most specimens attributed to this lineage, the anterior end of the metaconule has a more central location than that present in the Argentina specimen; however, the holotype of *M. ossivalense*, except for its larger size appears almost identical in this character. The hypocone is confluent with the metaconule, and the two cusps form a single unit about twice the size of the metacone. The posterior cingulum is formed by two small cusps, of which the larger is lingual and unattached to the hypocone. The posterior series of cusps, metaconule, hypocone, metacone, and two posterior cusps form a small circle that encloses an open lake in this section of the tooth.

Despite its small size, the South American specimen is well developed, and the occlusal surface shows much wear. Tooth size indicates an immature individual, but this cannot be substantiated without more evidence. Certain specimens of *Metaxytherium* (= *Felsinotherium*) *serresi* bear a cusp and size resemblance to NUC 4301, and these are considered to have belonged to a group in which the mature adult was small in contrast to its larger contemporaneous relatives.

A determination that the tooth is an  $M^3$  is made on the length/width ratio, the  $M^3$  being elongate, the  $M^2$  more quadrate.

Typically the  $M^3$  through the  $P^4$ , inclusive, of North American and European metaxytheres bear two roots on the buccal side and one on the lingual. In the South American  $M^3$  the anterobuccal quadrant is underlain by a root that spirals and turns in a posterolingual direction. The posterior and smaller portion of the molar is completely underlain by a large root that curves abruptly in an anterolingual direction near the tip or base. In similar teeth from North America another root would underlie the protocone and curve in a posterobuccal direction. The small tooth size may account for the lack of a third root.

The question to be resolved is whether or not the  $M^3$  from Argentina, which closely resemble similar teeth from North America, can be judged a new species. Basis of determination must be reached on two criteria:

(1) minor morphological variations, and (2) spatial relationships (*i.e.* geographical separation of the teeth in question).

In terms of morphological variation, the sample under consideration obviously is inadequate. In neither case (North or South America) can the specimens be classed as representative of the former population or populations that existed in these present widespread geographic communities. A comparison of the  $M^3$  from Argentina with molars of similar age from the south Atlantic coast of the United States indicates minor differences in occlusal cusp pattern, length/width ratio, and size, but not more than what would be expected within members of a species. This, of course, is my subjective concept inferred from the specimens at hand, a knowledge of the order, plus information available from literature.

Based largely upon the distance separating Florida and Maryland from the Parana River Basin, can one with any certainty assume that two different species are involved, or are we dealing with a species having a north-south range on the east coast of North and South America extending from approximately  $40^\circ$  N to  $31^\circ$  S? This is not an unusual range for certain living marine mammals, such as the larger whales, but it is a moderately broad range for a near-shore form. Among living Sirenia in the Atlantic region, *Trichechus inunguis* occurs from the Amazon River and its tributaries and *Trichechus manatus* from the Antilles, the Gulf Coast, and Mexico. The latter species is divided into the following subspecies by various authors: *T. manatus manatus* from the Antilles, and *T. manatus latirostris* and *T. manatus americanus* from the continental gulf coast. I do not know if the latter names are now regarded as synonymous nor the basis for their separation into subspecies. *Trichechus senegalensis* occurs along the West African coast and associated major rivers. Though the supposed diversity of living trichechids in a relatively small geographic area suggests the possibility that the Late Miocene dugongids in question were separate species, this cannot be proved from the specimens. Finally, one must consider continental drift and the possibility that South American and North American Sirenia are now separated by greater distances than in the past.

My conclusion is to withhold description of a new species until other specimens are found that will permit a clearer determination to be made than is now possible. Should the small tooth represent an adult rather than an immature individual, a new species would be justified. Because the  $M^3$  is in the general metaxythere lineage it is referable to *Metaxytherium* sp.

TRICHECHIDAE  
VALIDITY OF THE GENUS *Ribodon*

STRATIGRAPHIC

In 1883 Florentino Ameghino established a new genus, *Ribodon*, based on several trichechid teeth from the cliffs along the Parana River, Argentina, and referred the specimens to the Order Perissodactyla. Since that time the taxonomic reference to these fossils, as well as the sedimentary strata from which they were collected, has been the subject of much discussion.

The earliest investigators of the fossils in the cliffs along the Parana River were D'Orbigny (1842) and Darwin, neither of whom did much to differentiate between the sedimentary units composing the cliffs. Later, Ameghino, in his 1883 study of the Pampean Formation, attributed the major portion of this sedimentary unit to a Pliocene age and suggested that the lower Pampean sediments that formed the cliffs along the Parana River would be of an older age and therefore at least Miocene. Doering (1881), however, established three stratigraphic horizons within the formation, a lower marine that he correlated with the Eocene, a middle unit of fluvial terrestrial origin placed in the Lower Oligocene, and an upper marine that corresponded with the upper Mesopotamian strata from which the molars of *Ribodon* were collected. Ameghino (1906) placed the Mesopotamian in the Upper Oligocene. Here the subject of stratigraphic equivalency rested until Frenguelli (1920a,b), on the basis of (a) ichthyological and (b) invertebrate evidence, established the area from which the fossils were collected as belonging to the Upper Miocene, and he further corroborated the age (Frenguelli 1922) on the basis of structural evidence, which suggested an Upper Miocene-Lower Pliocene age. Later, Simpson (1932), in his review of the Sirenia, synonymized *Ribodon* with the genus *Trichechus*, and the sediments in which it was found to be Pleistocene. However, Pascual (1953), in a well documented review of the genus *Ribodon*, revalidated the genus and placed it in a Mio-Pliocene age.

TAXONOMIC

The genus *Ribodon* has had a history of varied taxonomic assignments, which may well account for its former general lack of acceptance as the important pre-Pleistocene trichechid it has proved to be. On the basis of an upper molar collected in the cliffs along the Parana River, *Ribodon limbatus* was proposed in 1883 by Ameghino, who placed it in the Order Perissodactyla, Superfamily Tapiroidea. In 1885 Ameghino also referred a lower molar and three upper molars to this taxon, and continued to attribute it to the tapirs. In the following year Burmeister

(1886) mistakenly assigned *Hyrachyus agrarius* Leidy (1873), to *Ribodon*, an excusable error since the teeth of the small running rhinoceros, *Hyrachyus*, bear a close resemblance to the teeth of the South American tapirs. Ameghino (1886: 147), although accepting the taxonomic assignment of *Hyrachyus* to *Ribodon*, emphasized throughout the paper the many differences existing between the two genera, rather than the close relationship suggested by Burmeister. By 1891 reservations as to the relationship of *Ribodon* begin to appear in the writings of Ameghino. In a letter to H. V. Ihering he stated (translation) “. . . The *Ribodon* known only by isolated molars could have completely different affinities from those that I previously supposed.” A short time later he stated (Ameghino 1893: 448), “While I am speaking of the fossils of that region, I must add that the doubts which I had concerning the real nature of *Ribodon* are now at rest. The new material at hand shows *Ribodon limbatus* belongs to the Sirenia, and is one of the family of Halitheriidae.”<sup>1</sup> The same year Lydekker (1893) also referred *Ribodon* to the Sirenia, suggesting that it had close relationship with the European *Halitherium* or with *Prorastomus*. Later, Ameghino (1906: 481) correctly removed *Ribodon* from the family Halitheriidae and placed it in the Trichechidae. Little more was written on this genus until Simpson (1932) determined that the teeth belonged to the Pleistocene *Trichechus*. I (Reinhart 1951) followed Simpson in this matter, and it was not until better specimens (a mandible and more lower and upper molars) were described by Pascual (1953) that the generic validity of *Ribodon* could be categorically substantiated.

#### BRAZILIAN *Trichechus*

Another interesting South American trichechid was reported upon by Couto (1956). This consists of the typical cranial remains, a fused parietal-supraoccipital element, from the Jurua River, Acre Territory, in northwest Brazil. Though referred to *Trichechus manatus*, a Pleistocene and Recent species of North and South America, it was collected from river sediments that may possibly have been reworked from older beds. Couto (1956: 110) had indicated this possibility:

“The fossil mammals from the upper Jurua and Purus rivers regions are, in part, of Tertiary (Upper Miocene, Pliocene), and in part, of Pleistocene aspect. Their stratigraphical origins are, for the most part, doubtful (most of them were collected on the edges or banks of the rivers, after having been transported from

<sup>1</sup> Dugongidae Gray 1821 (=Halitheridae Gill 1872).



their original sediments and rolled down river). Only the exploration of those regions by competent paleontologists can give us safe information concerning the stratigraphical origins of the fossils, and their relative ages, as well as the correlation of the respective strata with other South American Cenozoic deposits of which the geological age is more or less known."

With present information it is not possible to correlate the Cenozoic deposits of the upper Juruá with those of the Mesopotamian of Argentina, but it is an interesting speculation in view of the fact that *Ribodon* is known to be from the Mesopotamian and the specimen referred to *T. manatus* may possibly have been reworked from beds of similar age. *Potamosiren* from the La Venta fauna, Upper Miocene, of Colombia, is of a similar age range as *Ribodon*, and Pascual (1965) and Couto (1956) believe it may be referable to that genus. Location of the Brazilian specimen, approximately 1200 miles from the present ocean, is not unusual when one considers the present dispersal of *Trichechus manatus*<sup>1</sup> in the Amazon River valley. The river and its tributaries are readily navigated by such water dwellers today, and it is believed that physiographic conditions for this region were similar in late Cenozoic time.

An earlier occurrence of a fossil sirenian was reported by Dilg (1909) to have been found in Pliocene beds near Para (Belem), at the mouth of the Amazon. This form was named *Trachypleurotherium*, but failure to describe or figure the material has rendered the name a *nomen nudum*.

#### *Manatus* IN SOUTHEAST EUROPE

Because of the restriction of fossil and living Trichechidae to the West Indies, southeastern United States, the east coast of South America, and the west coast of Africa, it is of unusual interest to note that Macarovic and Oescu (1941) have referred remains of sirenians from Bessarabia (southern Russia) to *Manatus maeoticus* Eichwald 1853. The specimens consist of 15 ribs of adults and 8 ribs attributed to young individuals. From the characteristic bulbous shape of the ribs, one would readily agree to the sirenian assignment, but whether they belong to the Trichechidae or to the Dugongidae I cannot ascertain. Identifying the ribs to genus and species is impossible on the basis of morphologic features. The authors gave specific assignment to the ribs because they were found in the limestones of Chisinau, where Eichwald (1853) found the bones he referred to *Manatus maeoticus*. This reference, while

<sup>1</sup> Often referred to as *T. inunguis*.

specifically and probably generically incorrect, has the advantage of keeping the specific name consistent for all indeterminate sirenian specimens found at a given locality. Following Eichwald, Nordmann (1860: 330-333) described and referred to *M. maeoticus* ribs, two scapulae, and 26 vertebrae from the stone quarries of Kischinew (now Kishinev [Chisinau when under Roumanian rule], capital of the Republic of Moldavia, Russia, at the northwest end of the Black Sea). Unfortunately Nordmann classified the sirenians as belonging to the whales. Since 1771, when Brunnich proposed the genus *Manatus* (which was preceded by *Trichechus* Linnaeus 1758 nec 1766), the generic name has continued to be widely but incorrectly used in reference to both recent and fossil forms. Hemming (1952) recently presented a well documented report on the nomenclatorial usage of *Manatus*, both as a generic and trivial name. His recommendations are as follows:

- (1) place the generic name *Manatus* Brunnich, 1771, an objective junior synonym of the name *Trichechus* Linnaeus, 1758 (already placed on the *Official List of Generic Names in Zoology* by the decision taken in *Opinion* 112), on the *Official Index of Rejected and Invalid Generic Names in Zoology*;
- (2) place the trivial name *manatus* Linnaeus, 1758 (as published in the binominal combination *Trichechus manatus*) (trivial name of the type species of *Trichechus* Linnaeus, 1758) on the *Official List of Specific Trivial Names in Zoology*.

I have been unable to find any reference to the geologic age of the referred collecting sites. In the general nearby region of Europe the most common genera have been *Metaxytherium* and *Halitherium*, and the postcranial materials from this area should be compared to these genera. The geographic area strongly suggests that the specimens belong to the family Dugongidae rather than to the Trichechidae, and quite possibly to one of the two genera mentioned above.

ORDER DESMOSTYLIA  
*Cryptomastodon* FROM JAVA

Vertebrate paleontologists have discussed on numerous occasions the possible relationship of *Cryptomastodon* and *Desmostylus*. I believe *Cryptomastodon* is a proboscidean, the category in which it is classified at the present time, and thus *Desmostylus* would have no closer relationship to this genus than to any other proboscidean. The rare remains of

*Cryptomastodon* consist of teeth fragments, of which one tooth is almost complete, and a questionable distal end of a humerus. A series of short columns inclined toward each other at the occlusal surface give the tooth a superficial resemblance to *Desmostylus*; this characteristic being shared with many proboscidean teeth, particularly fragmented columns. The individual columns differ from those of the desmostylids in (1) being broader at the base, (2) having a less circular outline, (3) being appressed less closely, (4) having more cement between the columns, and (5) lacking a small upraised boss in the center of the occlusal surface in unworn columns. The thickness of the enamel may offer some comparison, as would the outline of a perfect tooth, but the former aspect of the Java specimens is unknown to me and the latter remains to be found. Comparisons between *Cryptomastodon* and desmostylids can be made using the works of Stehlin (1925), Es (1931), Koenigswald (1933), and Dietrich (1934).

#### ALASKAN DESMOSTYLID

A 1961 report by Drewes *et al.* on Unalaska Island, in the Aleutian chain, contains the interesting report on the presence of *Cornwallius*<sup>1</sup> from the Unalaska Formation, Lower Miocene. Inasmuch as this area is at the geographic center of the desmostylid range from Japan to the west coast of North America, this find is not unexpected. The known range of latitude for this genus during the Lower Miocene is therefore from 53° 40' north (at Unalaska) to 25° 20' north (Baja California site). Using this broad geographic range as a base, a number of points of information on the life habits and taxonomy of this genus can be surmised. If one assumes that a single species of *Cornwallius* lived approximately concurrently at both localities, and climatic conditions were similar to those at present, a eurythermal physiological condition might have been a necessity. General climatic conditions in the Miocene are believed to have been more cosmopolitan than at present, however; a fact that is indicated by widespread seas and many far-ranging marine vertebrates and invertebrates. If this were the case, ocean currents may have caused similar climatic conditions in the broad swampy bays and estuaries in the widely separated regions. A single species would have a wide range of latitude and even a similar diet. It is equally possible that within the two regions a southern and a northern species are represented, although scarce dental remains and a complete lack of cranial and postcranial bones give no such clue.

<sup>1</sup> Identified by Dr. G. E. Lewis (Drewes *et al.* 1961: 606). Lewis further states that identification as *Desmostylus* is possible, however, the manuscript indicates a preference for *Cornwallius*.

Japanese fossil remains similar to *Cornwallius* include teeth of *Paleoparadoxia* (*Cornwallius*) *tabatai* Tokunaga (1939), from the Middle Miocene of Sado Island, Japan, and a very fine cranium of the same species from South Sakhalin Island (Ijiri and Kamei 1961). Based on examination of a plaster cast of a tooth of the Unalaska *Cornwallius*, the identification by Lewis appears plausible since the tooth lacks the well developed cingulum characteristic of *Paleoparadoxia*. The Unalaska tooth appears to be an upper molar; if so, placement of the cusps is much like that of *Paleoparadoxia* (Ijiri and Kamei 1961: pl. 2, fig. 7). If the tooth is unbroken it consists of six cusps. The anterior portion presents a large central and anterior column flanked by two smaller columns. Three cusps of equal size form a rough triangle behind the anterior row. The large roots are broken as is common in the desmostylids.

Together with the *Cornwallius* tooth reported by Drewes, other very fragmentary teeth and skeletal material from the same location at Unalaska are housed at the National Museum of Natural History. No remains other than rare isolated teeth of this genus have been described, but it is unlikely that the associated skeletal material, even if prepared, would be complete enough to add any information to the taxon.

#### FLORIDA DESMOSTYLUS

During examination of the collection of vertebrate remains made by Mr. F. R. Berquist, Superintendent of the American Agricultural Company, Fort Pierce, Florida, five columns of *Desmostylus* were noted. All are the typical color of the specimens from the phosphate pits of Florida, and all specimens were collected from the American Agricultural phosphate pits near Brewster, Florida.

All columns are hypsodont, none showing the cingulum or low-crowned character of *Cornwallius* or *Paleoparadoxia*. Three heavily worn columns (UF 3962, and two in the collection of F. R. Berquist) represent adult molars. The unworn columns (UF 3961, 3963) apparently belong to teeth in the process of eruption and, on the basis of size difference, degree of tooth development, amount of wear, and color of preservation, evidently belonged to different individuals. An analysis of these criteria suggests that three individuals are represented by the five columns. Because these teeth were collected from the Bone Valley Formation, their exact age is in question. As expressed earlier, the Bone Valley may contain reworked specimens from the underlying Middle Miocene Formation, as well as a confused blending of overlying Pleistocene sediments. Whether these columns, which lack signs of abrasion, are

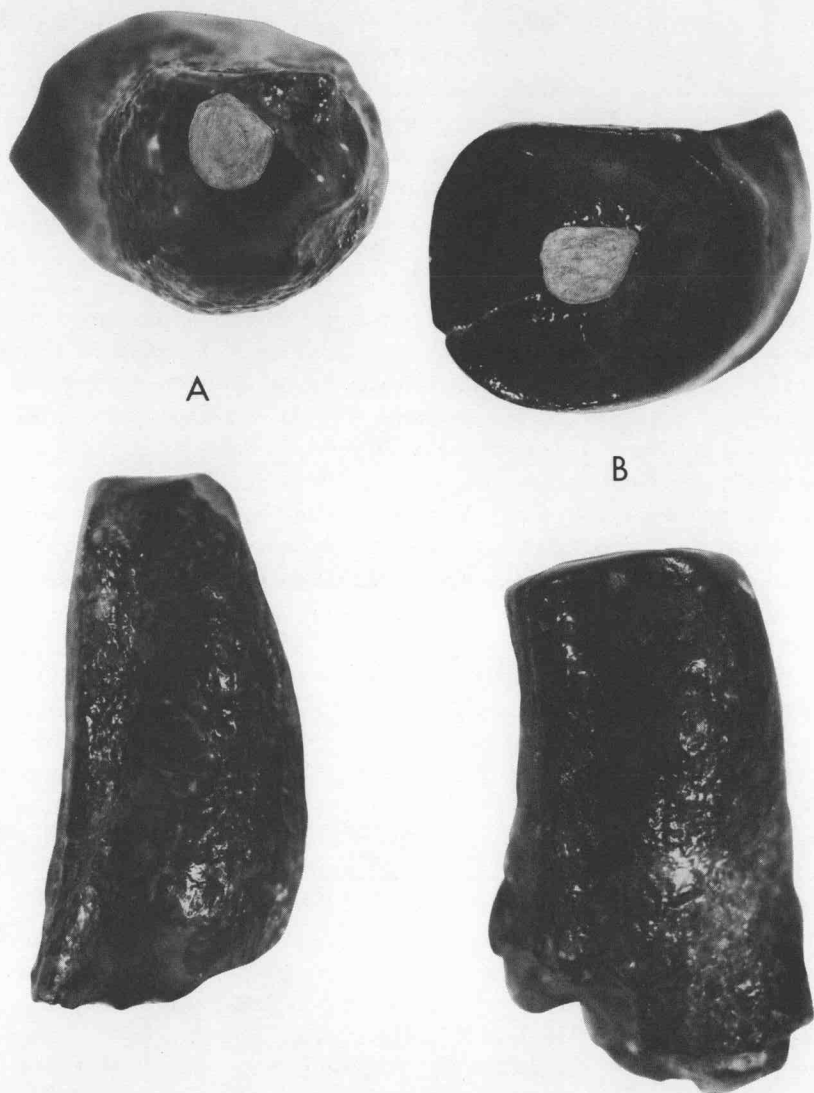


FIGURE 35.—*Desmostylus* cheek teeth, probably from the Hawthorne Formation underlying the Bone Valley Formation, Polk Co., Florida. Occlusal and lateral views of (A) UF 21312, and (B) UF 21311; both X 2.

from the Hawthorne Formation or from younger deposits is not known. If they are construed to be of the same age as the known sediments in the Bone Valley District (Late Miocene to Middle Pliocene), the sediments are of comparable age to the Cierbo and underlying Briones mega-

faunal stages of the North American Pacific coast, and Fujinan and the underlying Iwamiotan West Pacific Japanese stage of Tai (1959). Extension of the geographic range east of Florida indicates strongly the possibility of the former presence of desmostylids all along the swampy coastline, estuaries, and large rivers of the Gulf of Mexico and the Caribbean. With the presence of *Cornwallius* in Baja California during the Lower Miocene (Durham and Allison 1960), it is not surprising to find desmostylids between the boundary of the Gulf of Mexico and the Atlantic Ocean. Indeed it is more puzzling that other specimens have not come to light. The presence of *Desmostylus* in Florida no longer limits the desmostylids to the Pacific Ocean. The gradual expansion of geographic range follows the pattern of extension of the vertical range. For many years *Desmostylus* has been considered restricted to the Middle Miocene; however, recent stratigraphic work indicates a geologic range for this genus from earliest Miocene, and with the Florida specimens a possible extension into Early Pliocene. Also there has been a general consensus that a brachyodont *Cornwallius* gave rise to a hypsodont *Desmostylus*. *Cornwallius* so far is restricted to the Lower Miocene<sup>1</sup>; therefore, in order to be ancestral, it should be present in Upper and possibly Middle Oligocene.

This is not the first report of a desmostylid outside of the Pacific region. Earlier Hesse (Stenzel *et al.* 1944) reported finding fragments of desmostylid tooth columns from the Miocene beds along the Sabine River, Burkeville, Texas (Texas-Louisiana border). I have examined these fragments (U.T. 2888-2889) and believe they can be referred to proboscidean teeth, or as an alternative should be classified as indeterminate. The proboscidean reference coincides with the belief Hesse first held but later changed (Stenzel *et al.* 1944: 1005-06): "Early in the present investigation of the Burkeville area certain thick enameled tooth fragments were found. These were regarded as proboscidean, although it was evident that there was something peculiar about the fragments. Further collecting failed to disclose any definite proboscidean material and the conviction grew that the fragments were not of that order." The Burkeville fauna is a mixed assemblage of terrestrial, fresh water, and brackish water forms considered Upper Miocene (Barstovian) in age. General conditions of the facies from which the fragments were collected are quite similar to *Desmostylus* collecting sites in California, a point that influenced Hesse's decision. Partial columns of desmostylid teeth are readily identifiable, but the Burkeville specimens fail to reveal any diagnostic characteristic of *Desmostylus* teeth. No triturating sur-

<sup>1</sup> A question remains as to the age of the sediments in which *Cornwallius* has been found. They are either latest Oligocene or earliest Miocene.

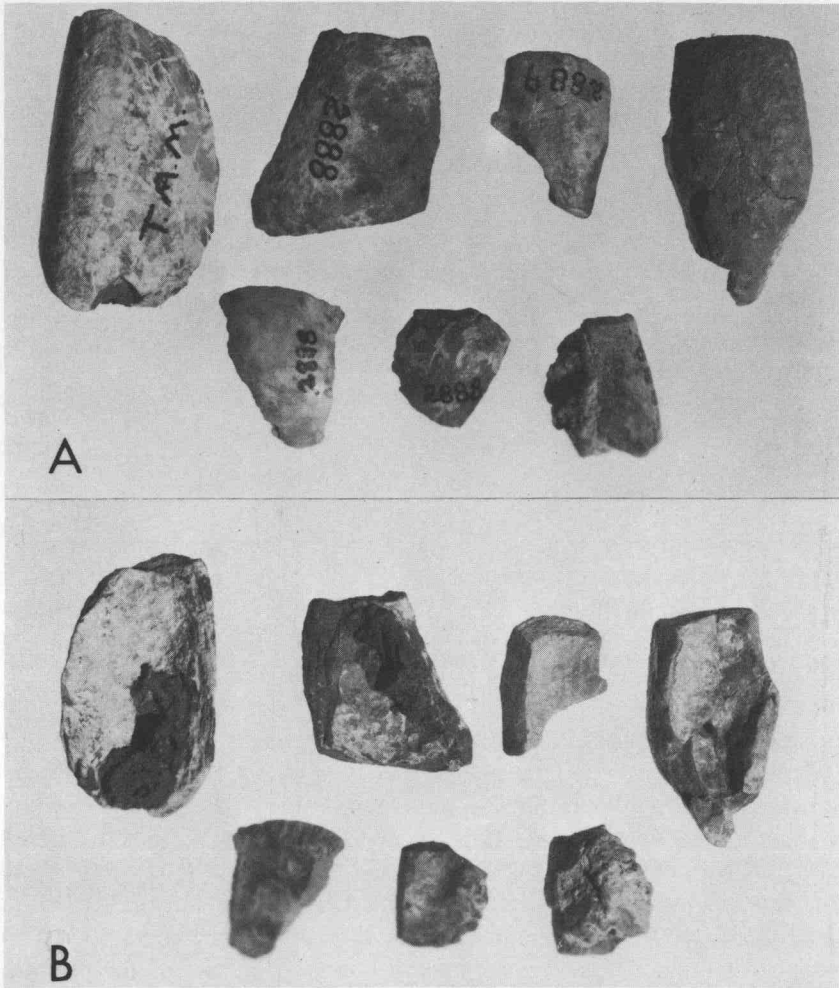


FIGURE 36.—UT 2888-2889, indeterminate thick enamel tooth fragments from Texas: (A) lateral view; (B) internal view.

faces are present, and none of the supposed columns show signs of being appressed to an adjacent column. On the two largest fragments the circumference is too great and the enamel too thin to be referable to *Desmostylus*. The specimen upon which Hesse relied for positive identification is called an "incomplete cone," but it is as readily (and far more probably) referable to a proboscidean as to a desmostylid. Future collecting may reveal specimens that can be positively identified as either proboscidean or as desmostylid. The known material is so fragmentary that it might properly be referred to as indeterminate rather than placing it in a definite category.

CALIFORNIA *Desmostylus*  
ORDER DESMOSTYLIA REINHART 1953  
FAMILY DESMOSTYLIDAE OSBORN 1905  
*Desmostylus hesperus* MARSH 1888

REFERRED SPECIMEN.—LACM A. 6363.53.1. Three specimens pertaining to one individual: weathered cranium lacking bony covering over much of surface; brain and rostrum exposed as casts; part of right mandible with three cheek teeth, broken off vertically immediately anterior and posterior to cheek teeth; and left mandible broken off vertically at anterior end of most posterior cheek tooth, base of ramus and outer half of condyle present. All specimens exhibit one molar in process of eruption.

LOCALITY.—LACM 1099. On Palos Verdes Corp. property; 1.8 mi. NW junction Greshaw Blvd. and Crest Road; See San Pedro Hill quad. ed. 1940 USGA Professional Paper 207 overlay dated 11 June 1953.

FORMATION.—Altimira shale member, Monterey Shale Formation.

AGE.—Middle Miocene (ref.: Woodring, Bramlette, and Kew 1946, USGS Prof. Paper 207).

#### CRANIAL ELEMENTS

ROSTRUM.—The rostral section is filled by a complicated mass of scrolled turbinals that are surrounded ventrally and laterally by the maxillaries and dorsally by the premaxillaries, nasals, and the forward extension of the frontals. The posterior base of the turbinals is on the lingual side of the cheek teeth and has its beginning just anterior to the dental capsule. Here a division into two broad, equal-sized units divides the lower maxilloturbinals from the upper ethmoturbinals. Ventrally the maxilloturbinals rise into a slight arc, then course forward and downward. In mid-height the arc becomes more abrupt, with the short half of the arc posterior and a gentle elongate arm anterior. Dorsally, where the ethmoturbinals underlie the nasals and the frontals, the base of these elements begins in a posterior direction, then curves abruptly forward and follows the gentle configuration of the ventral turbinals. In cross-section the ethmoturbinals dip beneath the anterior part of the frontals, and between these bones and the part of the maxillary overlying the dental capsule. They were apparently separated from the brain through the crista galli-cribiform plate region.

FRONTALS.—All cranial roofing bones are missing, with the exception of fragments of the frontals; however, the general dorsal configuration of the cranium suggests no differences between this specimen and that of other similar remains of *Desmostylus hesperus*. The dorsal surface of the frontals is missing. The lack of surface covering by dense bones reveals that the internal part of these elements is formed by an internal diploe of anteroposterior elongate chambers, separated by thin bony extensions. This swollen condition of frontal, as well as more anterior, facial bones is also true of the proboscideans and most ruminants. It is usually the



result of growth in size of skull, and an anterior prolongation that causes a greater mechanical burden upon the neck of the animal. An adjustment to this problem is solved by a reduction in weight without loss of bulk and by inflated passages in the cranium, more often than not in the nasal-frontal region.

**BRAIN CAST.**—Unfortunately the cast of the brain is heavily weathered and only the general configuration can be approximated. The posterior part was bordered by the almost vertical supraoccipital; the dorsal surface beneath the parietals and frontals is rectangular in outline, with a gentle rounding at the edges. A thin line of demarcation exists between the parietals, as does the V-shaped lambdoidal crest which marks the medial parietal-supraoccipital juncture.

**VENTRAL OCCIPITAL REGION.**—Remains of the broken occipital condyles reveal only a large condylar foramen that originates in the dorsal half of the foramen magnum, and in a posterior direction pierces, ventrally and laterally, the ventral part of the basioccipital. Suggestive of an osteological condition similar to that of the Sirenia, the base of the squamosal is a thick bone that encircles what must have been a very prominent periotic.

**BASISPHENOID-BASIOCCIPITAL.**—Sutural contact between the basisphenoid-basioccipital is broadly open, a neotenic condition also shared by *Paleoparadoxia* and sirenians. The ventral surface of these elements is very broad and flat, with the lateral borders of the basioccipital broadly rounded. This same condition is found in *Paleoparadoxia*, but differs from that of the sirenians in which the antero-ventral surface of the basioccipital is expanded into a prominent rugosity, and the posterior end is expanded into a broad Y. In the Sirenia the basioccipital is Y-shaped, with the single axis pointed anteriorly; in *Desmostylus* this element is more rectangular, with the long axis transverse. Two minor pairs of foramina are present on the ventral surface of the basioccipital, the more anterior pair being slightly closer to the lateral extremity of the cranium.

**PALATINES.**—The palatines are crushed by lateral compression and have buckled outward at the median suture. As in *Desmostylus hesperus* (VanderHoof 1937: 221, fig. 10; Ijiri and Kamei 1961: pl. 1, fig. 2), the sutural contact between the maxillary and palatine occurs at the posterior border of the dental capsule and gradually inclines medially along the palate, with the anterior contact ending at a point lateral to the anterior border of  $M^3$ . In *Paleoparadoxia* (Ijiri and Kamei 1961: pl. 3, fig. 2) the contact of palatines with the maxillary is lateral to a point just anterior to  $M^2$ . A minor postpalatal foramen is present at the anterolateral borders of the palatines. Like the Sirenia in general, the thin rear border divides into a thin vertical wedge of bone, which appears

to have been clasped by the alisphenoid externally and the pterygoid processes of the basisphenoid internally. In contrast to the usual situation in this order, however, the rear border of the palatines extends back relatively much farther. A large sphenorbital canal lies immediately behind and about midway up the posterior border of the dental capsule.

MAXILLARIES.—In conjunction with the palatines, the maxillaries continue anteriorly to form a maxillary gutter, which is gently raised in the midline and bordered on each side by shallow elongate basins. In cross-section the midline is composed of a thick bone that diminishes in thickness laterally toward the basined areas. Within the rostral cavity, at a point near the forward end of the nasals, the complicated scrolls of maxilloturbinals and the configuration of the maxillaries closely resemble that of the cross-section of the rostrum of *D. hesperus*, as illustrated by Hay (1924: pl. 1, fig. 3).

TABLE 8.—CRANIAL MEASUREMENTS OF *Desmostylus hesperus*.

CRANIUM	
Length of broken cranium	568.0
Height of dental capsule	86.8
Estimated anterior-posterior length dental capsule	78.5
Estimated width basisphenoid-basioccipital suture	78.0
RIGHT MANDIBLE	
Estimated anterior-posterior length dental capsule	75.5
Estimated height dental capsule	82.0
Length $M_3$	66.0
Maximum width $M_3$	46.6
Length $M_2$	48.4
Maximum width $M_2$	36.4
Length $M_1$	27.7
Maximum width $M_1$	22.0
LEFT MANDIBLE	
Estimated anterior-posterior length dental capsule	82.5
Estimated anterior-posterior length unerupted tooth	75.5
Length $M_3$	65.7
Anterior border $M_3$ to posterior border worn condyle	205.0

MANDIBLE.—The buccal surface of the mandible is relatively vertical, and contains a broad deep indentation beginning near the bottom of the mandible at a point directly under the most posterior molar, with a gradual deepening of this trough in the direction of the angle. The lingual side (which should be concave) fails to present a correct picture, because much of the bony surface is missing. Beneath the cheek teeth the bottom of the right mandible narrows and deepens posteriorly. A

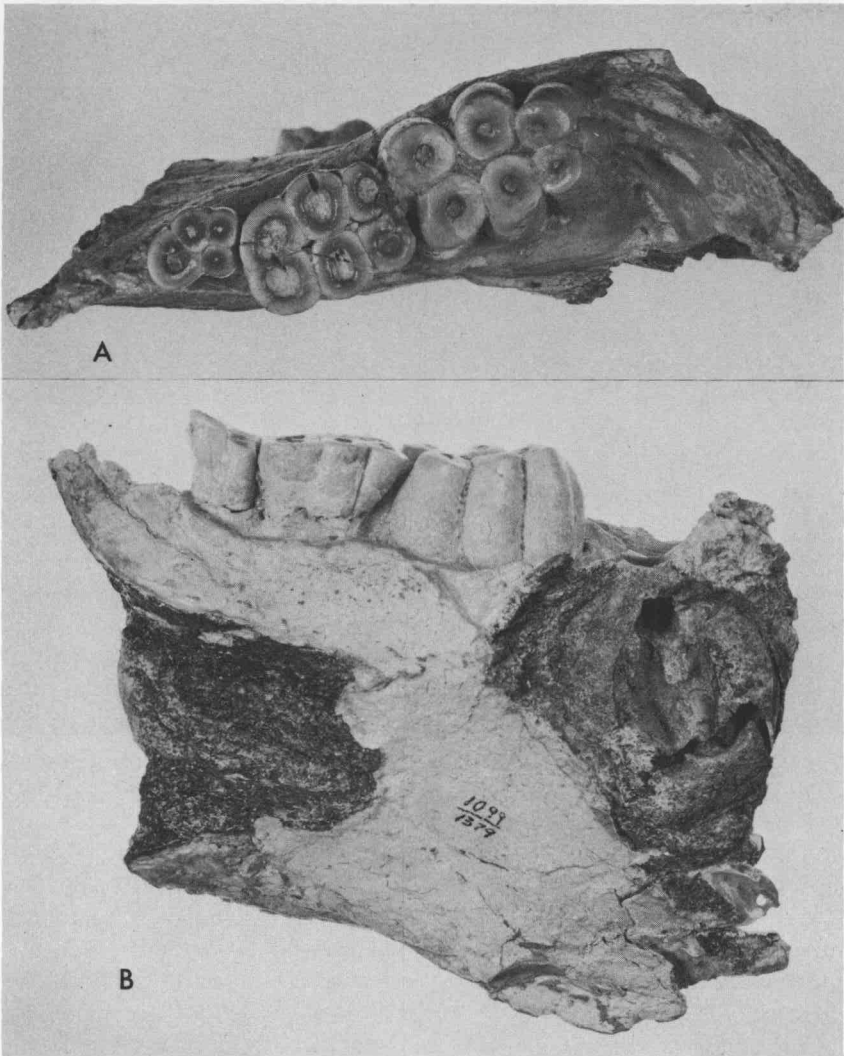


FIGURE 37.—*Desmostylus* (LACM A. 6363.53.1): occlusal (A) and lingual (B) views of right mandible (note unerupted molar in jaw bone).

vertically compressed oval mandibular canal underlies the teeth and appears to have communicated with them by extension of the roots into the canal. The condition of the condyle, which is present on a horizontal line behind and on a direct elevation with the cheek teeth, differs from that in *Vanderhoofus* in which the condyle is above the cheek teeth. The neck of the condyle is constricted and is moderately delicate in this

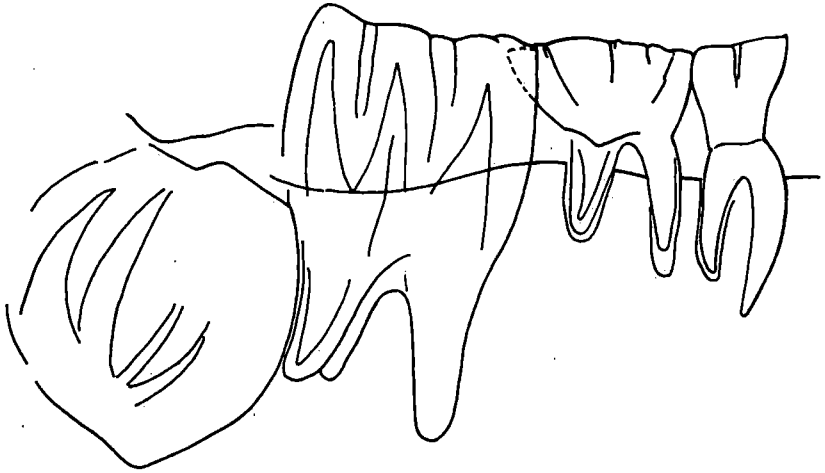


FIGURE 38.—*Desmostylus* (LACM A. 6363.53.1): x-ray through right mandible, labial view.

region for a jaw of this size. The head of the condyle has a concave surface, but details are lacking.

**TEETH.**—Three cheek teeth in the right mandible of LACM A.6363.53.1 apparently comprise the full complement of functional teeth. The anterior tooth is composed of five columns that lack a definite pattern of arrangement, other than a rough alternation of offset cusps as opposed to the usual transverse rows. The largest cusp is the most anterior and is so closely appressed by a small lateral cusp that the two appear as one. Two moderate-sized cusps form a middle row, with the cusp on the buccal side larger and displaced forward. A cusp of similar size to either column of the middle group forms a talon. The middle tooth can be termed the typical adult molar and follows the usual mandibular molariform pattern of transverse rows of cusps in a 2-2-2-1 sequence.<sup>1</sup> The same pattern of cusps is present in the rear functional molar, which is approximately 10 percent wider and 15 percent longer than the middle molar. Within the dental socket a still larger tooth of apparently the same 2-2-2-1 pattern would eventually have come into use and probably would have caused the most anterior tooth to be shed. This would have permitted three functional molars of the same pattern and of progressively larger size (from front to back) to form the surface of trituration. A similar condition, which is found in both the Sirenia and Proboscidea, has the teeth generally increasing in size with each

<sup>1</sup> With less frequency this may appear in adult lower molars as a 2-2-2 or a 2-2-2-2 sequence or in varied patterns of 7 columns. See VanderHoof (1937: 227) and Nagao (1935: pl. 18).



FIGURE 39.—*Desmostylus* (LACM A. 6363.53.1); lingual view of left mandible. Note unerupted molar.

successive replacement and retaining the same or (more often) a similar primary cusp pattern, with an addition of more secondary cusps.

Wear between the posterior end of the middle molar and the anterior end of the rear molar is heavy and displays a pattern that most likely was formed by the two teeth coming into contact during the process of eruption of the posterior molar (see fig. 35). Matsumoto (1918: 63) attributed this type of wear to "compression;" it is discussed more fully by VanderHoof (1937: 183-184) and by Reinhart (1959: 79-81). This presents the possibility that prior to the eruption of the posterior molar the functional teeth consisted of the seven-columned middle tooth, the anterior five-columned tooth, and possibly one or more teeth of fewer columns that lay forward in the tooth row and were shed nearly concurrently with the eruption of this large molar.

A posterior molar on the right side of the cranium is composed of columns in the typical *Desmostylus* sequence for this tooth (*i.e.* 3-2-2-2 anterior to posterior). This pattern also occurs with about equal frequency as 3-2-2-1. It is probable that the fragmented dental socket

present on the left side of the cranium was in the process of moving into a position of eruption with a similar patterned tooth.

**ROOT SYSTEM.**—Roots of the cheek teeth of *Desmostylus* are usually missing, because the difference in hardness between the tough enamel pegs and the relatively soft roots is so great that erosion or a slight blow during collecting readily separates the crown from the roots, or causes the roots to crack and completely disintegrate. It had been thought previously that some pliability of the roots would be accounted for by a posterior slant to them as the tooth moved forward. Such a condition is present in proboscideans and results from the horizontal succession of teeth. However, an X-ray of the three implanted molars in the right mandible reveals no slant, but rather vertical roots with a long single root anteriorly and a shallower, and to some degree bifurcated posterior root. The condition of a single or a shallow bifurcated posterior root in  $M_{1-2}$  is not revealed by the X-ray. In other teeth in which such roots have been examined, the anterior root is triangular with a broad round terminus, and the posterior is a short, broad, transverse root that may show increased bifurcation from the  $M_1$  to the bifurcated  $M_3$ . Single-rooted teeth appear to be premolars, and I know of none that bear any noticeable slant. I suspect that such structures are milk teeth implanted in a vertical fashion, then shed in the adult stage with no replacement.

**DENTAL CAPSULE.**—In the adult the dental capsule is round in cross-section and only slightly compressed in width, being similar in size and shape to a lopsided tennis ball. A contrast is exhibited in the thin dense layer of bone surrounding the unerupted molar with the immediately adjacent cancellous bone through which the tooth will move to become implanted as a functional tooth in the jaw. A tooth in either an upper or a lower dental capsule lacks roots and exhibits the coalescing of all of the enamel pegs to a centralized grouping. Bone overlies the top of the unworn crown and extends between the separations of the occlusal surface of the columns. After eruption of the tooth, cement replaces the bone between the dorsal portions of the columns. The pulp cavity and dentine core, broadly expanded at the base of the tooth, are also filled with bone, which extends up into the dentine and precludes the possibility of roots forming while the tooth remains within the capsule. These conditions are well expressed in all three specimens of LACM 1379, but are more diagrammatically exhibited in UCMP 40003 (Reinhart 1959: 80-81).

**TOOTH REPLACEMENT.**—The posterior-anterior horizontal succession of molars from the dental capsule into a functional point in the jaw is exceptionally well exhibited in both the cranium and the mandibular specimens. Because the dental capsule lies on the lingual side of the

jaw, it is necessary for an erupting tooth to move toward the outside or buccally to align itself behind the molar, which will be moved forward. In both mandibular specimens the most posterior molar shows moderate wear and is in the process of being pushed forward by a molar of slightly larger size (estimated 10-15% longer), which is in the process of eruption. An increase in size of succeeding molars would be expected in animals that were still growing, the larger teeth providing a broader grinding surface for the necessary increased quantity of food. The left mandible displays a cross-section of the rootless molar, still within its thin bony capsule, that underlies and pushes up against the three most posterior cusps of the rear functional molar. Curvature of the peglike tooth columns would not permit a vertical movement of such magnitude as to allow an erupting molar to push a functional molar out of the jaw; however, it would undoubtedly exert great pressure upon the worn molar, and would cause it to move forward as room was gained for the new molar. The relationship of the erupting and functional molar in this specimen is such that the incoming tooth might tilt the posterior end of the worn molar upward and the anterior end slightly downward. As in other adult specimens of *Desmostylus*, the crowns of the teeth in the entire grinding tooth row are in contact and forward pressure on the most posterior tooth will cause a small pressure to be placed on the entire tooth row. The osteoclasts react to this pressure by partially destroying the bone immediately preceding each tooth, a condition that will allow the teeth to move forward and thus relieve the pressure. At the time the osteoclasts are destroying the bone, the mesenchyme cells (osteoblasts) immediately in front of the teeth deposit bone that prevents the cheek teeth from becoming loose as they progress forward. The advancement of the teeth in this manner continues until the dental capsule no longer erupts a new tooth. The number of molars or molariform teeth erupted from the dental capsule in *Desmostylus* is unknown.

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