

Article VIII.—FOSSIL SIRENIA OF FLORIDA AND THE EVOLUTION OF THE SIRENIA

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INTRODUCTION

Florida is one of the last strongholds of the sirenians in North America, as a small number of manatees there still withstand the onslaught of civilization. It is a matter of peculiar interest that sirenians have long been abundant along its shores. In the shallow-water marine and estuarine deposits of the Miocene and Pliocene of Florida, the almost indestructible and highly characteristic fragments of sirenian ribs are

among the most abundant fossils, and they also occur, although more rarely, in the marine and fluviatile Pleistocene. In spite of this abundance of rib fragments, associated material and more characteristic parts of the skeleton are rare.

This material is now very greatly augmented and permits a first attempt at a general history of the Sirenia in North America and the correlation of this history with the much more numerous data from Europe. These are the aims of the present paper, which was essentially completed in manuscript in the first half of 1930 and has not been extensively revised since then.

The material here studied includes all of that in the possession of the Florida State Geological Survey, kindly lent for this purpose, and other material collected by Herman Gunter, G. M. Ponton and myself in coöperation between the Florida State Geological Survey and The American Museum of Natural History. To Mr. Gunter most cordial thanks are due for making the Survey material available and for many other courtesies, and to Mr. Ponton for his aid in collecting and for much other assistance. The Floridin Company at Quincy, and particularly Mr. R. H. Hopkins, Mine Superintendent, permitted and in many ways greatly assisted the collection of important Miocene specimens. The sources of other material are acknowledged in the descriptive part of the paper.

PREVIOUS KNOWLEDGE OF AMERICAN FOSSIL SIRENIA

It has been known for over a century that remains of fossil sirenians occur along the Atlantic Coast of the United States, the earliest record apparently being that of Harlan in 1825 (*vide* Leidy). DeKay, I. L. Smith, J. A. Allen, Gibbes, Leidy, and Cope also reported various finds during the nineteenth century. These records range from New Jersey to Florida and are almost invariably of uncertain age. The majority probably refer to Tertiary forms, and for the most part they were based on rib fragments.

The occurrence of definitely Pleistocene remains north of Florida is open to question. "*Manatus*" *inornatus* and "*Manatus*" *antiquus* Leidy have been supposed to be Pleistocene, but are probably earlier as mentioned below. Some of the numerous indeterminate fragments may be Pleistocene, but those of known age are all earlier. In Florida, however, the Pleistocene occurrence of the living genus *Trichechus* is established beyond doubt. Leidy (1889) referred rib fragments from Peace Creek to "*Manatus antiquus*," but these were probably derived from

Pliocene beds, and the specific reference, furthermore, lacks foundation. Hay (1919) described an incomplete jaw, without teeth and of uncertain provenience, which he doubtfully referred to "*Trichechus antiquus*." This jaw clearly belongs in *Trichechus*, but the reference to Leidy's species is incorrect. Sellards (1916) and the present writer (1929A) have recorded the occurrence of *Trichechus* in the Floridian Pleistocene of the Withlacoochee River and of the Seminole Field.

Only one species of probably Pliocene Sirenia has previously been described from North America, and it, also, is known only from Florida. This is *Metaxytherium floridanum* Hay (1922) based on part of a right upper jaw with one tooth from the Bone Valley Formation at Mulberry. A badly worn tooth from recent beach deposits at Palma Sola was referred. G. M. Allen (1923) has described a broken humerus, a few vertebrae, and some rib fragments from the same horizon and locality.

Miocene sirenians from the Atlantic coast are more abundant, but have not been represented by better material. "*Manatus antiquus*" Leidy (1860), based on a single tooth from the Ashley River, South Carolina, was almost surely derived from Miocene beds, and the same may be true of "*Manatus inornatus*" Leidy (1873) from the phosphate deposits of South Carolina, the type of which is also a single tooth. In 1883 Cope described a premaxilla from the Wando River, northeast of Charleston. Believing it to have two upper incisors, he called this specimen *Dioplotherium manigaulti*. Subsequent study of the type and of a topotype by Kellogg (1925) did not confirm this supposed generic distinction, and Kellogg provisionally lists the species as *Metaxytherium manigaulti*. Still more recently G. M. Allen (1926) has revised the Miocene Sirenia of South Carolina, describing several cranial fragments, some humeri and a scapula, and mentioning other less characteristic remains. He considers *Manatus antiquus* and *Manatus inornatus* of Leidy as synonymous, and refers to this species, as *Halitherium antiquum*, part of the new material. The remainder of his material he refers to *Metaxytherium manigaulti* (Cope), suggesting that the two genera *Halitherium* and *Metaxytherium* occurred together in South Carolina, although the stratigraphic origin of all of these specimens is highly uncertain.

The Miocene of Maryland has furnished various remains, but none has been exactly determined. Case (1904) described a fused radius and ulna and a rib fragment from the Calvert Formation, erroneously referring them to "*Manatus giganteus*" DeKay—a much larger animal and apparently a cetacean. Palmer (1917) also records sirenian remains from Maryland, a fifth cervical vertebra which he compared with *Hydro-*

damalis and considered as possibly derived from the Eocene, although this seems highly improbable.

Aside from *Desmostylus*, the only fossil sirenian yet described from the Pacific Coast of North America is *Metaxytherium jordani* Kellogg (1925), from the Upper Miocene of California. This species, which is unusually large, was based on an incomplete skull (without teeth), four associated dorsal vertebræ, a metacarpal, and parts of six ribs.

A few specimens are known from the West Indies. Most important of these is a nearly complete skull and lower jaws from the Eocene of Jamaica, described by Owen (1855, 1875) and named *Prorastomus sirenoides*. Also of importance is the posterior part of the left ramus of a lower jaw found by C. A. Reeds in Porto Rico and described by Matthew (1916) as *?Halitherium antillense*. Associated with this were two broken vertebræ, a middle cervical and a first dorsal, and some rib fragments of a second individual were also found. Matthew (1916, p. 23) states that N. R. Cabrero figured, but did not correctly identify, two other sirenian bones from the Porto Rican Tertiary, a scapula and an atlas, in the *Revista de las Antillas* for March, 1914.

The only South American record known to me is that of *Ribodon limbato* Ameghino, based on isolated teeth from the Pleistocene of the Barrancas de Paraná, Argentina, and apparently inseparable from the recent genus *Trichechus*.

The genus *Desmostylus*, found in Tertiary (typically Miocene) beds on both sides of the Pacific, is very unlike any of the European or Floridian sirenians. Abel's recent view that it is a monotreme seems to me to be demonstrably incorrect, but *Desmostylus* surely has only rather distant relationship with the typical Sirenia. Hay (1923, 1924) divides the Order Sirenia into two suborders, the Trichechiformes and the Desmostyliiformes. It is with the former alone that this paper is concerned.

SYNOPTIC CLASSIFICATION OF THE SIRENIA

The following classification omits several genera of doubtful status or uncertain systematic position.

Order SIRENIA

Strictly aquatic eutherian mammals. Hind limbs becoming reduced and functionless, front limbs becoming paddle-like, but with retention of more or less normal articulations. Tail continuing lumbar region, with horizontal fin. External nares dorsal, premaxillæ forming a rostrum, often deflected. Tympanic semicircular, petromastoid mas-

sive, more or less triangular, loosely articulated with basicranium. Incisors becoming reduced in number, one pair forming upper tusks, or lost in adult. Cheek teeth primitively bilophid, may be reduced, degenerate, or lost, may become more complex, bunodont, or may be greatly increased in number.

Suborder **TRICHECHIFORMES**

Upper incisors normal in ancestral types, enlarged to form one pair of tusks or reduced and vestigial in later forms. Cheek teeth, when present, primitively bilophid but becoming complex and more or less bunodont. Skull relatively high, rostrum narrow and usually strongly deflected. Nasals bordering external nares, becoming reduced. Jugals large. No zygomatic or post-temporal foramina in squamosal. External nares relatively posterior.

Prorastomidæ

Complete eutherian dentition. Rostrum little deflected, no enlarged tusks. Functional hind limbs and nearly normal pelvis (at least in *Eotheroides*). A primitive and structurally ancestral group. Eocene.

Prorastomus, Eocene, Jamaica

*Eotheroides*¹, Eocene, Egypt

Dugongidæ

Dentition more or less reduced. Rostrum much enlarged, usually sharply deflected, usually with large upper tusks. Hind limbs reduced, functionless. Ilium and ischium subequal, becoming rod-like. Broad bicipital groove on humerus. Carpals becoming extensively fused. Seven cervical vertebrae, usually 19-20 dorsals. Eocene to Recent.

Halitheriinae

Cheek teeth enameled, closed roots. Rostrum deflected, tusks usually present. M³ unreduced, complex. Nasals present, inserted in frontals. Supraoccipital generally not reaching foramen magnum. Dense ribs. Eocene to Pliocene.

Eosiren, Upper Eocene, Egypt.

Prototherium, Upper Eocene, Europe.

¹The generic names of the Sirenia are the subject of much confusion. *Manatus* is the classic name for the manatee, *Rhytina* for Steller's sea-cow, and *Halicore* for the dugong. None of these names is valid. *Trichechus* Linné, 1758 (*non* 1766), was based on the manatee, not the walrus, and antedates *Manatus* Brünnich, 1772. *Hydrodamalis* Retzius, 1794, antedates *Rytina* Illiger, 1811. *Dugong* Lacépède, 1799, and *Dugungus* Tiedemann, 1808, both antedate *Halicore* Illiger, 1811, and *Dugong* is correct, as it is now held that barbaric names are valid if used binomially. The usual forms *Rhytina* (for *Hydrodamalis*) and *Rhytidus* (extinct European dugong) are also incorrect, as they were intentionally spelled *Rytina* and *Rytiodus* in the original publications. Furthermore, the well-known generic name *Eotherium* Owen, 1875, is preoccupied by *Eotherium* Leidy, 1853, and must be replaced by *Eotheroides* Palmer, 1899. These several genera are here designated by the correct but somewhat less widely used names: *Trichechus*, *Hydrodamalis*, *Dugong*, *Rytiodus*, and *Eotheroides*.

Manatherium, Oligocene, Europe.

Halitherium, Oligocene and Lower Miocene, Europe, North America.

Metazytherium, Miocene, Europe, North America.

Thalattosiren, Miocene, Europe.

Hesperosiren, Miocene, North America.

Felsinotherium, Pliocene, Europe, North America.

Miosireninæ

Cheek teeth enameled, closed roots. Rostrum deflected, large tusks. M^3 much reduced, pattern simple. Occiput broad, cranium rounded. Supraoccipital reaching foramen magnum. [Inadequately described.] Pontian.

Miosiren, Pontian, Belgium.

Rytiodinæ

Cheek teeth enameled, closed roots. Rostrum not deflected, tusks very large, fluted. Molars like *Halitheriina* in proportions, simple in pattern. Skull long and narrow, occiput inclined forward. Oligocene.

*Rytiodus*¹, Aquitanian, France.

Dugonginæ

Only three cheek teeth in adult, no enamel, open roots. Rostrum strongly deflected, large upper tusks in male. Nasals vestigial or absent. Supraoccipital reaching foramen magnum. Ribs slender, with cancellated bone. Recent.

*Dugong*¹, Recent, Red Sea, Indian Ocean, western Pacific.

Hydrodamalinæ

No functional teeth. Rostrum moderately deflected, large, narrow. Nasals present, overlapped by frontals.

*Hydrodamalis*¹, Recent (extinct), Bering and adjacent North Pacific islands.

Trichechidæ

Cheek teeth enameled, rooted, bilophid, continuously replaced from rear. Rostrum small, little deflected, no functional tusks. Ilium reduced or absent, ischium relatively large and triangular. No bicipital groove on humerus. Carpals little fused. Six cervical vertebræ, usually seventeen dorsals. Pleistocene and Recent.

*Trichechus*¹, Pleistocene, North and South America. Recent, Atlantic coast and adjacent parts in North and South America and Africa.

Suborder **DESMOSTYLIFORMES**

Upper incisors small or absent, two lower incisors, procumbent. Cheek teeth hypsodont, closely appressed cylindrical columns, very thick enamel. Skull depressed, rostrum wider than deep and little de-

¹See footnote, page 423.

flected. Nasals well developed, excluded from external narial border by premaxillæ. Jugals reduced. Squamosals pierced by foramina posteriorly. External nares relatively anterior.

Desmostylidæ

Sole family. Miocene.

Desmostylus, Miocene, Pacific coast of North America and Japan.

MIOCENE SIRENIA OF FLORIDA

OCCURRENCE

The Miocene sirenians of Florida are all derived from the Hawthorn Formation. This formation covers a very large area in the peninsula and in northern Florida east of the Apalachicola River. It is approximately equivalent to the Alum Bluff Formation of earlier workers and is a member of the Alum Bluff Group by present usage.¹ It covers a considerable range of time, for various vertebrate horizons have been shown to be of different ages, apparently transitional between Lower and Middle Miocene.² The important sirenian remains are derived from the vicinity of Midway and Quincy in Gadsden County, in fullers' earth mines to which their discovery is due. The horizon at which they occur here is fairly well defined by associated remains of horses and other land mammals and is probably early Middle Miocene. The deposits were laid down in shallow marine, estuarine, or lagunal waters in the immediate vicinity of the mainland to the north. Remains definitely in this formation have not been reported in the peninsula, where it is a more limy and purely marine deposit, although their occurrence there is not improbable. Some of the uncharacteristic remains of the Bone Valley and later formations partly derived from the Hawthorn may be of this older origin, but, as shown below, these formations also contain their own *Sirenia* quite distinct from those of the Hawthorn.

MATERIALS

Sirenian bone fragments are very numerous in the mines at Midway and Quincy, so that it is surprising to find no reference to them in the literature. Previous to 1929 the only considerable mention of the Hawthorn vertebrates was that of Sellards (Florida State Geol. Surv., 8th Annual Rept., 1916), which does not mention sirenians. No identifiable material had, however, been recovered prior to that year.

At the present time the Hawthorn fossil sirenians are the best preserved of any yet found in the Western Hemisphere. In February,

¹See Cooke, C.W., and S. Mossom, 1929, Twentieth Ann. Rept. Florida State Geol. Surv., pp. 98, 115.

²Simpson, 1930B.

1929, Herman Gunter, Gerald M. Ponton, and I visited the mines of the Floridin Company immediately north of Quincy. Previous to our visit a sirenian skeleton had been thrown out of the mine in blasting a sandy stratum between the two commercial beds of fullers' earth. Parts of this badly shattered specimen had been saved and were presented to the Florida State Geological Survey. The missing parts and the stratum itself at this locality had been removed and lost or destroyed in the progress of mining, but on examining the cut bank about fifteen feet from the discovery site, a few ribs of a second specimen were found protruding from the side of the excavation. This was inaccessible because of water in the pit below and uncollectable because of a spur of the mine railway tracks laid on the bench directly above. With the spirit of generous coöperation which has characterized the history of this very important series of finds, the officials of the company, particularly Mr. R. H. Hopkins, and also Mr. R. E. Mawhinney, Mr. C. L. Sowell, and others, removed these apparently insurmountable difficulties. A train-load of dirt was dumped into the water for footing and the track was later removed from above the specimen. Aid was also furnished in the heavier excavation, while Mr. Ponton and I did the actual collecting. After finishing the bandaging of this specimen and finding another in an abandoned part of the mine, other work demanded my departure. Mr. Ponton and Mr. J. H. C. Martens, of the State Survey, completed the packing and shipping of the first two specimens, collected the third, and also found and collected a fourth specimen. The second specimen (type of *Hesperosiren cratægensis*, below) is retained by the American Museum together with supplemental parts from the other specimens. The remainder of the other three specimens, each including associated ribs, vertebræ and in two cases also other parts, are retained by the Florida State Geological Survey. Numerous other isolated bones or small lots of associated fragments were found, but these add nothing to the data of the four more perfect specimens. The Midway material is apparently of the same species but is very fragmentary and need not be specially discussed.

TAXONOMY

All the material here described appears to belong to a single new genus and species.

Hesperosiren, new genus

TYPE.—*Hesperosiren cratægensis*, new species

DIAGNOSIS.—Miocene Halitheriinae. Incisors absent and cheek dentition reduced to four or five teeth in adult. M³ elongate, with accessory cusps, conules dis-

placed, bunodont. Skull mesaticcephalic, relatively shorter than in *Metaxytherium* (*M. cuvieri*), longer than in *Thalattosiren*. Rostrum large, less deflected than in *Metaxytherium* or most other dugongids. Sagittal crests lyriform, well separated on parietals. Prominent median boss on frontals. Supraoccipital nearly or quite reaching foramen magnum, sutures against exoccipitals meeting at about 135°. Probably nine dorsal vertebræ with demifacets (not more than ten nor less than eight), neural spines all triangular in section. Radius and ulna strongly ankylosed, rotation almost completely lost, radius arched forward and ulna outward.

KNOWN DISTRIBUTION.—Middle Miocene horizon of Hawthorn Formation, Florida.

***Hesperosiren cratægensis*, new species**

TYPE.—Amer. Mus. No. 26838, skull, ribs, and vertebræ.

PARATYPES.—Amer. Mus. No. 26839, both humeri, left radius, and ulna. (Associated with ribs, etc., in Fla. State Geol. Surv.).

Amer. Mus. No. 26840, fifth cervical. (Associated with ribs, etc., in Fla. State Geol. Surv.).

HORIZON AND LOCALITY.—Middle Miocene, Hawthorn Formation, Quincy, Gadsden County, Florida.

DIAGNOSIS.—Sole known species of genus as defined above.

MORPHOLOGY

DENTITION.—An outstanding peculiarity is the absence of incisors, present and usually strongly developed in all other known Sirenia except the living *Trichechus*, the recently exterminated *Hydrodamalis*, and the Miocene *Thalattosiren*. In other characters, *Hesperosiren* is distinct from any of these, and the loss of incisors is clearly a character acquired independently at least four times among the Sirenia. Preservation of the premaxillæ is sufficiently perfect to make this observation beyond reasonable doubt. There is, however, a small pit at the extreme alveolar end of a palatal surface of each premaxilla. These are not large enough or of such a character as to hold functional tusks, but are almost exactly similar in size and position to those of *Trichechus*. They probably had the same history; lodging a vestigial tooth or tooth germ either wholly functionless or lost before maturity. It is perhaps possible that this is an individual abnormality or a sexual character, but, judging from other known Sirenia, this is highly improbable. Other normally tuskless genera do occur, and in the tusked genera the female tusks may be somewhat smaller than the male but are always present. The skeleton of *Metaxytherium cuvieri* described by Cottreau (1928) appears to be that of a female. The tusks are small, but much larger than any that can have been present in *Hesperosiren*.

Of the cheek teeth, only the crushed right M³ and a fragment of the left M³ are preserved, with the distorted and obscure alveoli of preced-

ing teeth. The most anterior tooth was opposite the middle or posterior half of the zygomatic root. There were apparently four molariform teeth, as in the *Halitheriinae* generally. P^3 may have been present, but

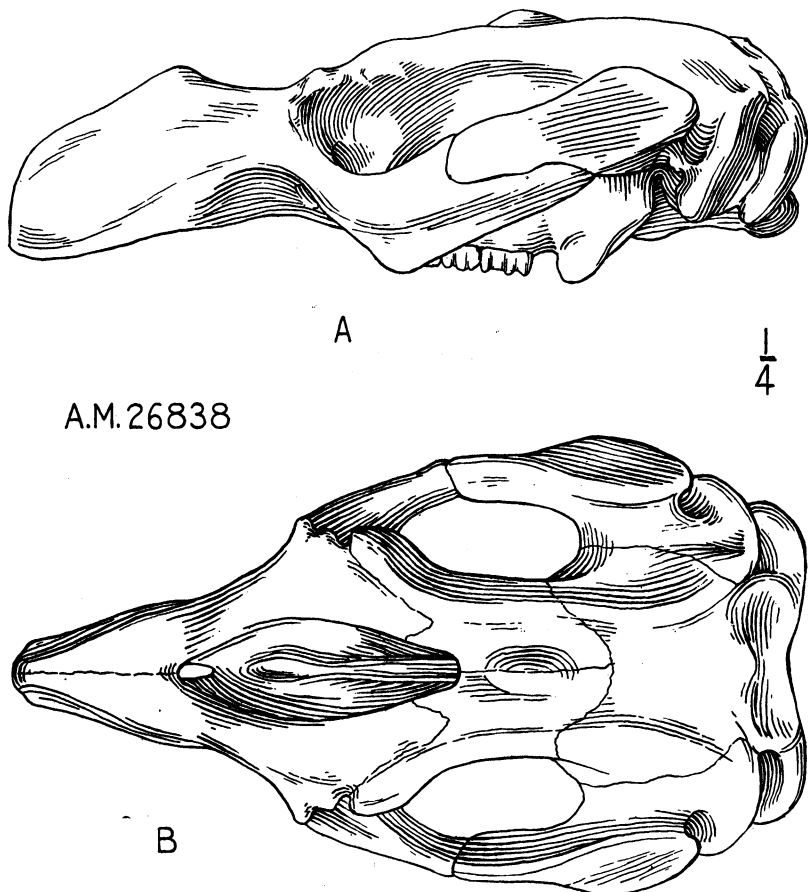


Fig. 1. *Hesperosiren cratægensis*, new genus and species. Reconstruction of skull of type, distortion corrected. The rostrum may have been slightly more deflected than here shown. A, left lateral view. B, Superior view. One-fourth natural size.

the cheek teeth did not number more than five in the adult, and possibly only four.

M^3 is longer than broad and is of complex bunodont type with displaced conules, resembling some species of *Metaxytherium* or *Felsino-*



Fig. 2. *Hesperosiren crataegensis*, new genus and species. Photograph of skull of type, superior view. One-third natural size.

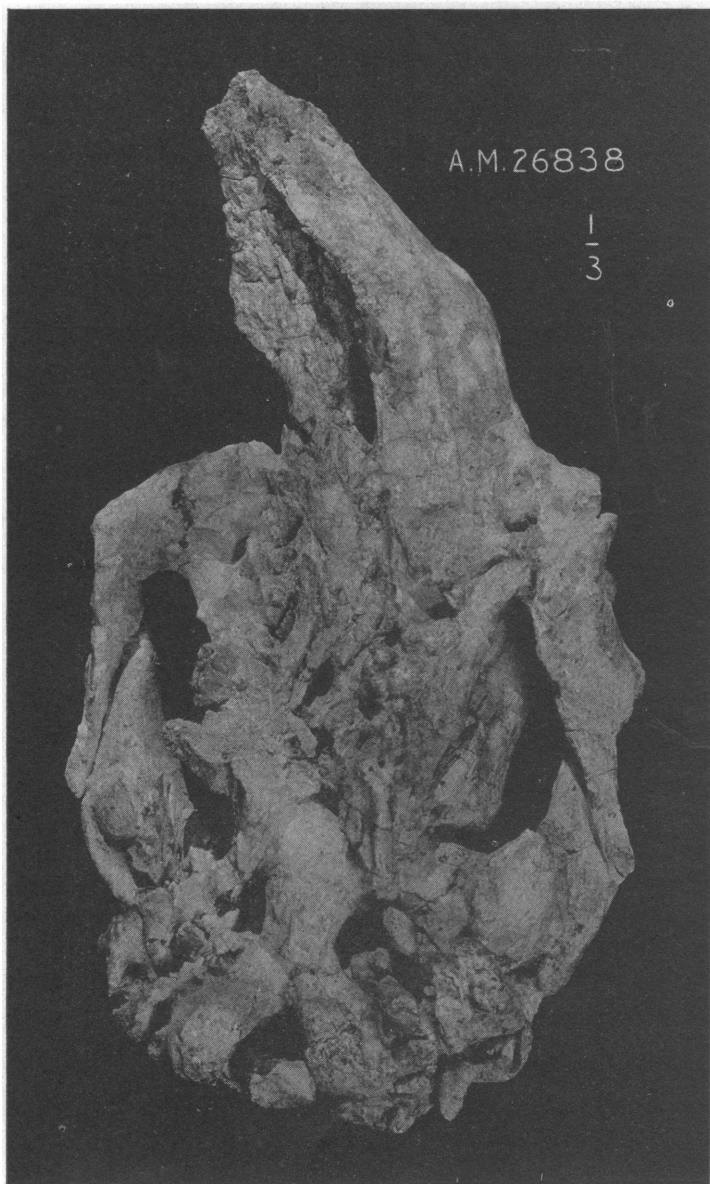


Fig. 3. *Hesperosiren crataegensis*, new genus and species. Photograph of skull of type, inferior view. One-third natural size.

therium but quite distinct from *Halitherium* or *Thalattosiren*. The metacone is definitely anterior to a line between metacone and hypocone, is larger than either of these, and confluent with the latter basally. The valley external to it is closed by a marginal crest. There are two prominent posterior accessory cusps.

SKULL.—The type skull is unusually complete but is rather poorly preserved due to the strong oblique crushing which it has suffered. For this study and for exhibition a model has been prepared by Haakon Dehlin under my direction, in which the distortion is corrected. Every part was carefully measured, and there are few morphological details not determinable on the original with careful study, so that this model probably very nearly represents the original appearance of the skull.

The principal skull parts, cranium, arches, and rostrum, individually resemble various other genera, but their combination is unique and many details are distinctive. The cranium is of medium height and somewhat elongate: about as in *Felsinotherium serresi*, longer than in *Thalattosiren* or *Dugong*, relatively shorter than in *Metaxytherium cuvieri*. The arch, however, appears to have been somewhat less strongly sigmoid than in *Felsinotherium serresi*. The mesorostral fossa is long, comparable to *Metaxytherium*, while the rostrum itself is of fairly stout proportions, although shorter than in most later halitheres. It resembles *Trichechus* in its slight deflection and edentulous character, yet is much more robust. It resembles *Thalattosiren* in the absence of teeth and approximate size, yet is very far from being so sharply deflected. It differs from other and more typical Halitheriinae, *Halitherium*, *Metaxytherium*, and *Felsinotherium*, in all three of its outstanding characteristics, being of somewhat different proportions, less deflected, and toothless.

The palatal surface of the rostrum is lanceolate, the lower borders of the premaxillæ surrounding it produced into thin sharp crests. The surface is highly rugose and vascular and doubtless bore a horny pad as in recent sirenians. This was larger than in *Trichechus* or most halitheres, but comparable in size to the more nearly vertical pad of *Dugong*. Posterior to this the marginal crests become rounded, converge, then diverge to the alveolar margin in the usual way.

The dorsal surface of the rostral part of the premaxillæ is triangular or cordiform, pointed in front, widening and rising to the double swollen prominence immediately anterior to the mesorostral fossa. The latter is long and relatively narrow, the original dimensions (as nearly as can be judged in its distorted condition) being about 155 mm. by 55 or 60 mm. The fossa extends far back, ending at a point well posterior to the

entire supraorbital processes. The posterior processes of the premaxillæ, as in other sirenians, are long and slender and are clasped anteriorly between and above processes of the frontals and maxillæ, posteriorly in grooves in the superointernal side of the supraorbital processes of the frontals. They do not extend back to the posterior end of the mesorostral fossa.

The nasals are obscure. Elements so identified with reasonable probability are rather swollen, vertical bones with a small dorsal exposure. They form the lateral, but not the posterior, margins of the end of the mesorostral fossa, do not meet at the midline, and are inserted posteriorly into the thick frontals.

The supraorbital processes of the frontals have about the relations seen in *Dugong*, but are closer to *Felsinotherium* in being stouter and in diverging at a lesser angle than in the recent genus. They are relatively longer and less expanded distally than in *Halitherium* or *Thalattosiren*. They are similar to those of *Metaxytherium cuvieri*, but diverge more in this less elongate skull. The temporal crests, arising on these processes, are parallel and angular rather than salient on the frontals, lyriiform and moderately salient on the parietals where they are well separated (about 50 mm.). The frontals are characterized by a prominent dorsal median boss, with a relief of about 10 mm. and somewhat elongate antero-posteriorly.

The supraoccipital is about 90 mm. in width by 55 mm. in height. The exoccipital sutures form an angle of about 135° , and the ventral point nearly or quite reached the foramen magnum. The bone (while not in exact agreement with any other form) is thus comparable to relatively progressive Miocene or to Pliocene genera. The median part is not much depressed.

The zygomatic arch is of typical dugongid and halitheriine type and has no particular features of interest aside from its less sharply sigmoid curvature than in *Dugong* or some other forms. The sides of the brain case and the exoccipital and paroccipital regions are crushed and likewise reveal little beyond their essential agreement with most other halitheres.

The palate (badly crushed) agreed with those of related halitheriines. The pterygoids are excavated posteriorly. The basioccipital-basisphenoid suture is closed. The lower surfaces meet at an angle of about 220° . The basioccipital has a sharp but low median keel. The glenoid articular surface is elevated, ovoid, somewhat elongate anteroposteriorly, straight transversely, convex anteroposteriorly.

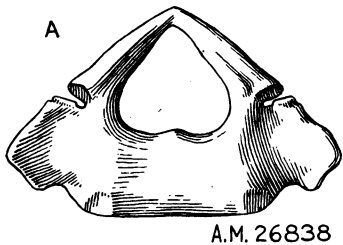
As in all *Sirenia* the tympanic is semicircular and is attached to the periotic at both ends. It is directed anterointerno-posteroexternally. The anterior part is stouter and is produced into an acute angle. The periotics are both preserved but are imbedded in the skull. This element has been so exhaustively described in *Thalattosiren* (Sickenberg, 1928) that it suffices to note the essential agreement of *Hesperosiren* with that genus so far as observed.

The stapes of each side was not found, probably being shattered by the crushing of the skull, but the malleus and incus of both sides are preserved save for the manubria of the mallei. These bones are of the usual sirenian type, described in some detail for the recent and certain of the fossil forms (*Halitherium* by Lepsius, 1881; *Thalattosiren* by Sickenberg, 1928; *Felsinotherium* by Capellini, 1872, and see also below for Florida *Felsinotherium*). In detail they agree rather more closely with *Thalattosiren* than with other genera in which these parts are known. The malleus is very roughly quadrate. The inferior surface bears the large and anteroposteriorly compressed base of the manubrium at its posterior end. The main body is crossed anterior to this by a prominent oblique posteroexternal-anterointernal groove, and the anterointernal angle is produced into a distinctive process. The dorsal surface is divided into a rounded featureless posterointernal part and an articular posteroexternal and anterior part by a sharp groove which forms a notch on the anterointernal margin and communicates with a pit on the internal face. The articular facets (for the incus) are of the tripartite sirenian pattern, save for the very characteristic peculiarity that the double posterior facet has the posterointernal face unusually large and horizontal, the anterior face small, indefinite and at a more open angle than 90° to the other. The separate third facet is elevated and convex.

This last peculiarity is naturally reflected in the incus, which has the posterior articular notch more open than is usual. The whole bone is more slender and less swollen than in *Thalattosiren*. The *crus breve* is of the same peculiarly short type, but is somewhat more produced. It lies in the same plane as the anterior articular surface for the malleus. The structure of both malleus and incus seems fully characteristic of the *Dugongidae* as opposed to the *Trichechidae* and of the *Halitheriinae* as opposed to the *Dugonginae*.

VERTEBRÆ.—Two cervicals are preserved, the sixth of the type specimen and the fifth of a second otherwise unimportant specimen (A. M. No. 26840, this one bone presented by Florida State Geological

Survey). The fifth has a short transverse centrum, great wing-like transverse (+costal) processes, and a slender neural arch. The transverse processes are nearly vertical and extend outward and downward, to a level well below the centrum. The superior and external borders are emarginate and meet at an acute angle. The lower border is expanded anteroposteriorly. In the middle of the process is the large vertebrarterial canal. Pre- and post-zygapophyses are separated by a small notch. The epiphyses on the centrum are complete but thin and spongy.



$\frac{1}{3}$ A.M. 26840

B

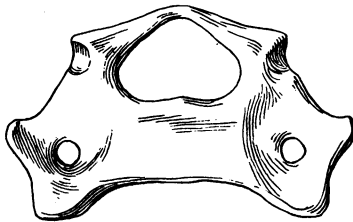


Fig. 4. *Hesperosiren cratægensis*, new genus and species. Cervical vertebrae. A, Sixth cervical of the type, posterior view. B, Fifth cervical of paratype, Amer. Mus. No. 6840, posterior view. Both one-third natural size.

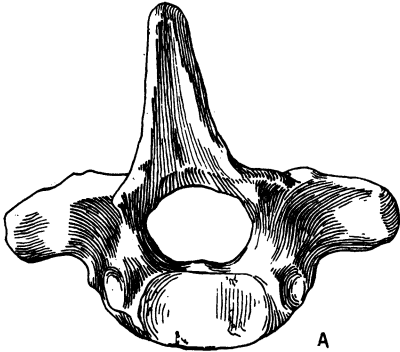
The transverse processes of the sixth vertebra are shorter and extend less downward, not reaching the level of the bottom of the centrum. They are short, bowed forward, especially the upper part, and are not pierced by the vertebrarterial canal but have a pronounced open notch on the lower border. The centrum is thicker (anteroposteriorly) than on the preceding vertebra. The zygapophyses are separated by a large notch.

Eighteen postcervical vertebrae are partly or wholly preserved in the type. These are identified as dorsals 1-3 and 6-16, lumbar 3, sacral, and caudals 2-3. There were certainly nineteen dorsals, probably three lumbar, certainly one sacral, and possibly about twenty-five caudals.

Dollo, in discussing *Miosiren*, has pointed out an interesting progressive character in the rib facets of the dorsals.

Normally the anterior dorsals have three pairs of facets: the tubercular facet and two demifacets, one for the anterior half of the capitulum of the following rib and one for the posterior half of the capitulum of the corresponding rib. The posterior demifacet disappears farther back in the series, the whole capitulum articulation moving onto a single centrum and becoming more central; these vertebrae thus have two facets. Finally the tubercular and capitular facets become confluent and there is but one. In *Halitherium* there are twelve with demifacets

(three facets in all), three with two facets, and four with one. In *Dugong* and *Hydrodamalis* the formula is 7:8:4. In *Metaxytherium cuvieri* there were nine with demifacets, or three facets, but Cottreau does not distinguish those with two and with one. Similarly in *Felsinootherium serresi*,



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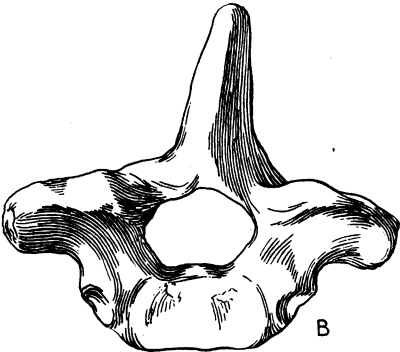
$$\frac{1}{3}$$


Fig. 5. *Hesperosiren cratægensis*, new genus and species. First dorsal vertebra of type. A, Posterior view. B, Anterior view. C, Left lateral view. One-third natural size.

Depéret and Roman state that nine have demifacets. These genera are intermediate between *Halitherium* and *Dugong* in this as in many other characters.

In *Hesperosiren* there were more than seven and less than eleven with three facets, more than three and less than eight with two. The formula was probably 9:6:4, and hence close to, or even identical with,

the formula in *Metaxytherium* and *Felsinotherium*. Reduction of the number of dorsals with demifacets is clearly progressive in this group

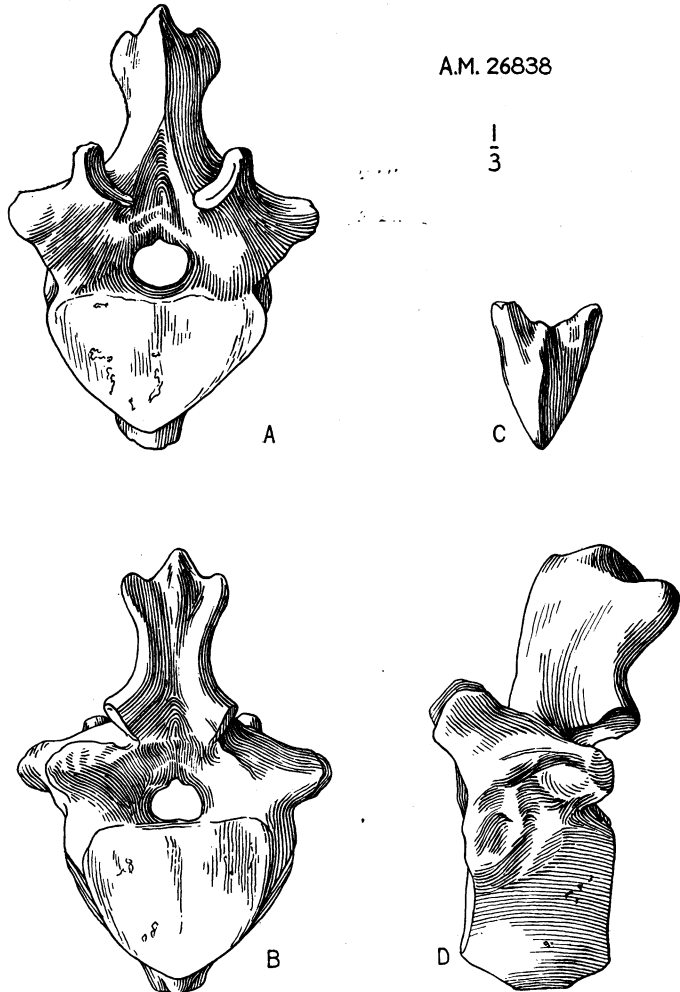


Fig. 6. *Hesperosiren cratægensis*, new genus and species. 14th dorsal vertebra of type. A, Anterior view. B, Posterior view. C, Top of neural spine. D, Left lateral view. One-third natural size.

and *Hesperosiren* certainly had fewer than in *Halitherium* and more than in *Dugong*.

In all their characters the dorsals form a regular graded series. The neural spines increase in height from first to second, decrease very

slowly from second to about sixth, then increase slightly to the end of the dorsal series. The anterior neural spines are inclined back-

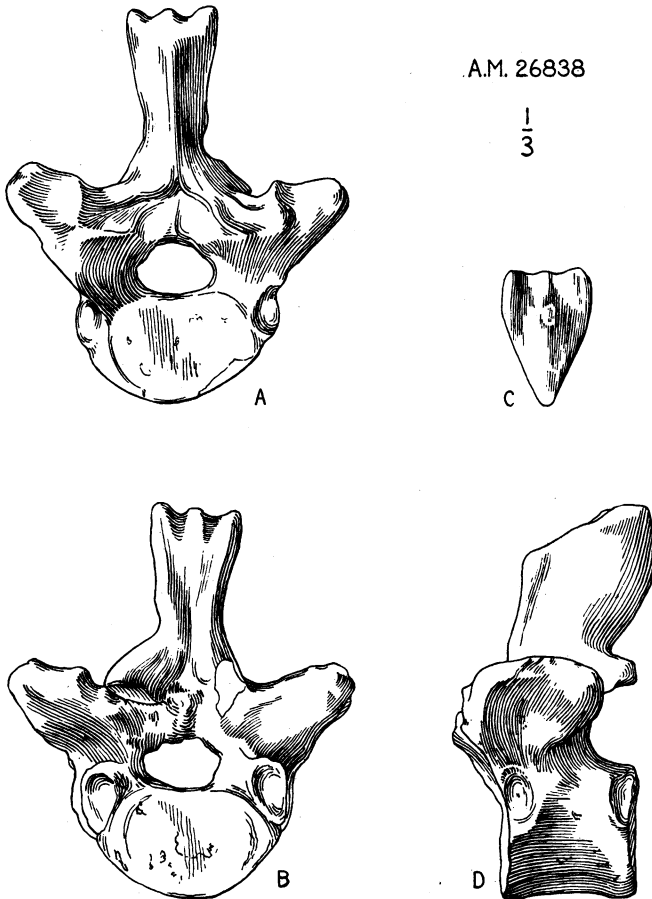


Fig. 7. *Hesperosiren cratægensis*, new genus and species. 7th dorsal vertebra of type. A, Anterior view. B, Posterior view. C, Top of neural spine. D, Left lateral view. One-third natural size.

ward. From about the twelfth they are erect. The first is bluntly pointed. The second and third are progressively more elongate antero-posteriorly and triangular, wider posteriorly. At about the fifth they acquire a highly characteristic pattern, triangular with a sharp anterior

angle, a prominent pair of posterolateral projections, and a smaller median projection. Following this pattern posteriorly, the median projection becomes more prominent, more anterior, more keel-like, until it is higher than the lateral projections and at the anterior angle, and the posterolateral projections become more distinct and more divergent. The transverse processes are well developed on the first dorsal, the distal ends bent somewhat downward. To about the fifth they become progressively longer and directed more upward, then to the end of the dorsal series they become progressively less prominent, being already almost atrophied on the fifteenth. The centrum is transverse, rather small, and shallow on the first dorsal. To about the fifth or sixth these proportions are approximately maintained, but the centrum becomes larger. The next four or five become deeper in proportion to the breadth and the lower surface begins to be keeled or angulate. By the twelfth and thereafter the centra have reached a maximum size, and are about as deep as broad and sharply keeled, so as to have a triangular or cordiform outline in anterior or posterior view. The neural canal, large, transverse, and elliptical in the first vertebra, becomes progressively smaller and more nearly circular (although retaining a dorsal notch or groove). The prezygapophyses face more upward than inward on the first vertebræ and are not elevated above the bases of the transverse processes; more posteriorly they become well separated as distinct processes and face more inward than upward. The postzygapophyses are analogously developed.

The rather peculiar sculpturing of the neural arch is similar in most Miocene and Pliocene *Sirenia* and will be mentioned in discussing Pliocene specimens in which it is more clearly presented.

All of the preserved postcervical epiphyses agree with those of the cervicals in being complete but unfused, thin, and spongy.

Assuming that there were three lumbar vertebræ, which seems highly probable, only the third is preserved. It has long simple transverse processes directed straight outward and somewhat downward. The distal end is expanded much as on the sacral, but to a less degree. The centrum is wider than deep. It is not keeled ventrally but has an anterior and a posterior pair of lateral, marginal projections. There is a median pair of ventral foramina. The neural arch rises from the anterior two-thirds of the centrum and is smaller and simpler than that of the dorsals, although the spine was high. The prezygapophyses are prominent, but the postzygapophyses are insignificant or absent.

The neural spine of the sacral vertebra is high, laterally compressed, the truncate apex simple and not triangular in section. The transverse processes are shorter than on the last lumbar and are expanded dorso-

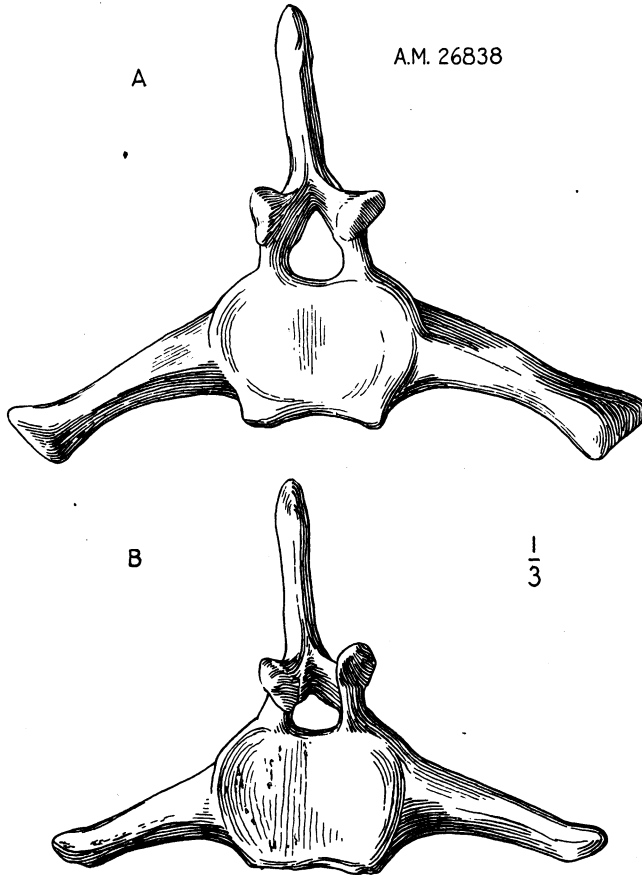


Fig. 8. *Hesperosiren cratægensis*, new genus and species. Post-dorsal vertebræ of type. A, Sacral vertebra. B, Probably second caudal vertebra. One-third natural size.

ventrally at the distal ends so as to have distinct surfaces facing outward and downward, doubtless for ligamentous attachment of the pelvis.

The two preserved caudals are probably the second and third. Except for the lower neural spines and shorter transverse processes, they resemble the sacral.

RIBS.—The ribs are of the types well described by Depéret and Roman for *Felsinotherium serresi* and by Cottreau for *Metaxytherium cuvieri*. I shall confine myself to certain supplemental observations and possibly systematic differences.

In the type specimen, at least parts of all of the ribs of the right side except the fifth are preserved, and there are various ribs from the left side. The first rib is relatively short. The second to sixth are progressively longer, the seventh to fourteenth of about the same length, and the fifteenth to nineteenth progressively shorter. This differs markedly from *Felsinotherium serresi* or *Metaxytherium cuvieri*, in which the posterior diminution in length is not so regular and the eighteenth rib is relatively much longer. The nineteenth rib of the present specimen has about the same length as the first. The curvature and general characters agree fairly well with *Felsinotherium serresi*.

On the external face of the fourth rib near the head there appears a broad shallow anteroposterior groove: on the sixth rib this is a little more distal and it continues at about this level to the eighteenth rib. On the nineteenth rib it is abruptly smaller and more proximal. Above the groove on each rib there is a salient rounded projection or angulation. The definition of the groove and its precise character are irregularly variable. From the twelfth to sixteenth it is rather vaguely bounded and single or obscurely double; on the seventeenth and eighteenth it is more oblique and irregular. On the more anterior ribs it is generally either distinctly or obscurely double, while on the tenth it consists of three distinct and sharply defined parallel grooves in a broad depression or flattening.

Another peculiar point is the presence of certain annular depressions on the external surfaces of the ribs. These look like circles inscribed on the bone, and in some cases they are so regular as to appear to be artifacts, although this is not true. In other cases they are vague or irregular. They do not appear on all of the ribs, but they are present on various individuals. On the fourteenth rib there is a distinct ellipse in the muscular groove previously alluded to, and another of similar size and shape but much less sharp distal and anterior to this. On the thirteenth rib there are likewise two, one on the prominence proximal to the groove, and one, as before, distal and anterior to the groove. On the twelfth there is one on the proximal slope of the prominence, one in the groove, and vague traces of one or two more distal to the groove. They occur variously on other ribs.

Broken rib fragments (both from the Miocene and Pliocene) show the extremely hard, dense substance of the halitheriine ribs. There is

no cancellous tissue. On some weathered fragments, lines of growth can be seen, showing that the bone is added in successive layers. Growth is chiefly on the outer, anterior, and posterior sides, and is most rapid on the outer side, giving the ribs their peculiar swollen appearance.

HUMERUS.—Both humeri are preserved in Amer. Mus. No. 26839 (specimen found by the Florida State Geological Survey, which retains the parts duplicated in Amer. Mus. No. 26838). The humerus is totally distinct from that of a manatee and in itself at once places *Hesperosiren*

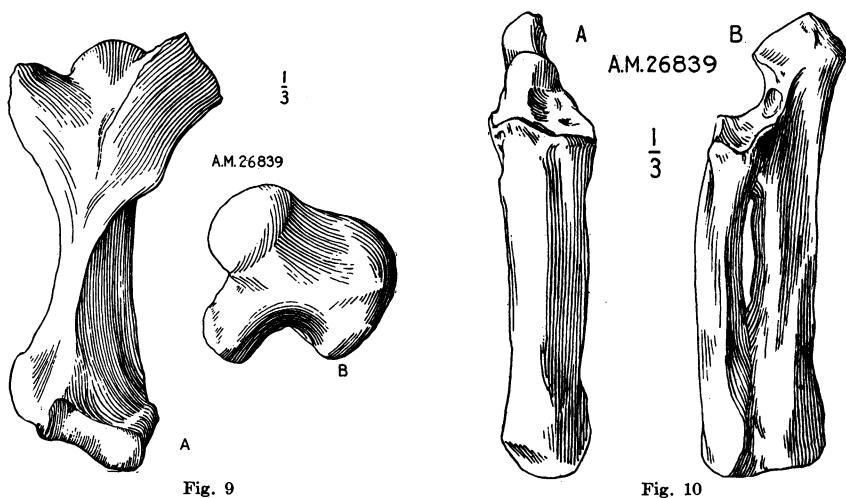


Fig. 9. *Hesperosiren cratægensis*, new genus and species. Left humerus of paratype, Amer. Mus. No. 26839. A, Anterior view. B, Proximal view. One-third natural size.

Fig. 10. *Hesperosiren cratægensis*, new genus and species. Left radius and ulna of paratype, Amer. Mus. No. 26839. A, Anterior view. B, External view. One-third natural size.

among the Upper Tertiary Dugongidæ. The tuberosities are well developed and very unequal. Their axes diverge at an angle of about 85° and the included groove is deep but relatively open. The shaft is short, stout, and tapers to the distal end, which is but moderately expanded. In these characters and in others of the crests, trochlea, and epicondyles, the humerus agrees more nearly with that of *Thalattosiren petersi* (as figured by Abel) than any other European species. It is on the whole more advanced than in *Metaxytherium*.

Although with fused epiphyses, the humeri of this individual are unusually small.

Greatest length.....	172 mm.
Distal width.....	64 mm.
Narrowest diameter of shaft.....	25 mm.

RADIUS AND ULNA.—The left radius and ulna are present in Amer. Mus. No. 26839. Their outstanding characters are the advanced degree of fusion, the very slight torsion, slight arching outward, moderate arching forward of the radius, and relatively little deflection of the olecranon. These features distinguish them from any sirenian radius and ulna hitherto figured.

The bones are completely fused, and the interosseous space is not long and slit-like but short and narrowly lenticular. The interosseous crest is inconspicuous on the radius, sharp and relatively internal on the ulna. The shaft of the radius is compressed anteroposteriorly and has a sharp crest on the external side. The shaft of the ulna is compressed laterally and has sharp anterointernal (interosseous) and posterior crests. The ulna is almost straight, the olecranon nearly continuing the long axis, the shaft bowed outward very slightly. The radius is bowed forward, more than in *Metaxytherium*. The torsion of the two bones is almost completely lost, so that the long diameter of the carpal articulation is almost directly anteroposterior. The region of the biceps insertion is unusually proximal and internal and is marked by two well defined pits. The bones are more slender and elongate than in *Metaxytherium cuvieri*. The radius is much stouter than the ulna. The length of the ulna is about 170 mm.

On the whole, this part is definitely more progressive than in *Metaxytherium* or any earlier form in which it is known and stands on a level with *Felsinotherium*, although of slightly divergent character.

AFFINITIES

It is clear that *Hesperosiren* is a sirenian and of the family Dugongidae. It resembles not the modern sirenians of the same region but those of the same age in Europe and is apparently closer to the now exotic dugong than to the manatee. Among dugongids it differs from *Dugong* itself in the less deflected and the toothless rostrum; complex and enameled cheek teeth, and many other characters which permit comparison only with Tertiary genera. The rostrum, teeth, vertebrae, and other features exclude *Miosiren* and *Rytiodus* and place the Florida fossils in the subfamily Halitheriinae as defined in a previous section of this paper. The absence of incisors, reduction of nasals, complication of the cheek teeth, and other advanced specializations exclude all Eocene

genera. These same advances as well as the less deflected rostrum and more distant sagittal crests exclude *Halitherium*. Closest comparison is with Miocene and Pliocene Halitheriinae, but even here the specimen will not enter a previously established genus. *Felsinotherium* has well developed incisors, a large and more deflected rostrum. *Thalattosiren* has a rostrum of similar size, but much more deflected; the skull proportions are quite dissimilar, and so is the molar tooth pattern. *Metaxytherium* has tusks, the rostrum is somewhat more deflected, the supra-orbital processes longer. Other European genera are inadequately characterized but none appears closer to *Hesperosiren* than is *Metaxytherium*.

The discovery (Sickenberg) that "*Metaxytherium*" *petersi* is very distinct from other supposed *Metaxytherium*, the discovery of the present peculiar genus, the inadequate published data for the remaining species of *Metaxytherium*, the divergent character of species referred to *Felsinotherium*, and the difficulty of any adequate differentiation of the last-mentioned two genera, all show how confused and highly imperfect is any present arrangement of the Halitheriinae. The variation within the subfamily is not great in essential character, yet the different combinations of characters are so numerous and so distinctive that almost every well known species must of necessity be placed in a separate genus on established standards. The less well known species are of doubtful generic affinities in every case. These genera are obviously closely related and do show definite progressive tendencies, yet their arrangement in true phylogenetic series is impossible. They appear to represent a meagre and random sampling of an extremely complex and polyphyletic group.

Hesperosiren represents another and equally isolated member of this group, close to *Metaxytherium* and other approximately contemporaneous forms both in degree of advance and in actual affinity. It appears to be more removed from the main line than is *Metaxytherium*, somewhat more aberrant in specialization. It may tentatively be pictured as diverging from the immediate ancestry of the latter genus.

Hesperosiren shows positive evidence of not being ancestral to later dugongids. The only genus that could conceivably be derived from it is *Hydrodamalis*, and there is no evidence that this was the case.

POSSIBLE MIOCENE SIRENIA OF SOUTH CAROLINA

In his recent study of fossil mammals from South Carolina (1926), G. M. Allen discusses various presumably pre-Pleistocene sirenian remains from the Ashley River deposits near Charleston. As is well

known, these beds contain a mixture of fossils of several different ages. Most of the land mammals are of Pleistocene age, although some are of definitely Pliocene aspect (*Serridentinus obliquidens*, *Hipparion*), some are not later than Miocene (?*Dinohyus mento*), and even recent remains have been listed in the "fauna" (*Sus*, *Bos*, *Ovis*). The marine forms may be largely of Miocene age, although doubtless there is some mixture here as well.

From this very mixed association of faunas, Allen describes a number of fragments, chiefly humeri and cranial shields, which he divides into two groups. To the first group he refers cranial shields with strong and closely approximated sagittal crests and humeri with narrow deep bicipital groove between the prominent tuberosities which diverge at an angle of about 60°. The only closely comparable European forms are referred to *Halitherium*, and Allen's placing of these specimens in that genus seems well justified, although of course it is not certain in view of the inadequacy of the materials. The age is presumably Lower Miocene or earlier, as nothing of this type occurs in later beds of Europe.

Allen considers these specimens as conspecific with *Manatus antiquus* Leidy, which was based principally on a single upper molar tooth from the Ashley River, and he also considers *Manatus inornatus* Leidy, based on a lower tooth from the same deposits, as belonging in this species, called *Halitherium antiquus* (Leidy). This is perhaps a convenient procedure, but the evidence for it is decidedly tenuous.

The type tooth of "*Manatus antiquus*" measures 20 mm. in length and in width. It is simply lophodont, the central cusp of both crests duplicated, the posterior crest bowed forward, no accessory cuspules, anterior and posterior cingula small, non-cuspidate, subequal, united with the inner cusps but nearly separate from the outer. Reference to a distinctive extinct species of *Trichechus* ("*Manatus*") is possible but, as recognized by Allen, improbable. Closer comparison is with the Halitheriinae. Among these the more complex and bunodont teeth of *Metaxytherium* and *Felsinotherium* are not closely comparable. *Prototherium*, *Halitherium*, *Halianassa*, and *Thalattosiren*, on the other hand, all offer definite points of resemblance. Between these genera, and still more between their various species, there is little or no choice. None is exactly similar to "*Manatus antiquus*." Comparison, as suggested by Allen, with *Halitherium schinzi* is hardly as close, either in size, proportion, or structure, as with M² of *Thalattosiren petersi*, for instance. In short, this tooth is indeterminate as to genus, especially as its age is really unknown. The transfer of the species to *Halitherium* and the reference to it of Allen's much more

important *Halitherium*-like skull and limb material seem to me an unfortunate step.¹ I propose to discard Leidy's name as indeterminate and to apply to the referred material of Allen the name ***Halitherium allenii***, new species, type in the Mus. Comp. Zool. Harvard, original of Allen, 1926, Pl. II, Fig. 1, fused supraoccipital and parietals. Allen's recognition of this definitely *Halitherium*-like type in North America is of outstanding importance.

"*Manatus inornatus*" Leidy is based on an equally indeterminate lower tooth.

The second group into which Allen divides his material includes cranial shields with lower, more separate crests and a flatter skull roof and humeri with a broader and more shallow bicipital groove, the tuberosities diverging at an angle of nearly 90°. This form is comparable to *Metaxytherium*, *Thalattosiren*, *Halianassa*, or *Felsinotherium*. It is a Tertiary dugongid, different from *Halitherium* and perhaps of somewhat later type, but otherwise indeterminate. Allen refers it to *Metaxytherium manigaulti* Cope. This may well prove to be correct, but is not capable of demonstration.

Dioplotherium manigaulti Cope was based on a partial premaxilla from the Wando River. Kellogg found that the supposed generic character of two upper incisors is erroneous, and called the species *Metaxytherium manigaulti*. Discovery of more complete material directly comparable with Cope's type and yet, unlike it, generically determinable, may validate the species, but at present even its reference to *Metaxytherium* is a matter of convenience and not of conviction. It is clearly distinct from *Hesperosiren*, in which comparable parts are known.

PLIOCENE SIRENIA OF FLORIDA

OCCURRENCE

The known Pliocene sirenians of Florida are all derived, directly or indirectly, from the Bone Valley Formation, of early Pliocene or latest Miocene age, probably about equivalent to the Republican River of the West. Numerous land mammals of about the same age are found in the Alachua clays and hard-rock phosphates of Florida, but these deposits are terrestrial, and such marine or aquatic fossils as they contain are derived from Miocene or older formations. All of the important sirenian fossils of the Floridian Pliocene have been found in the land pebble

¹Some of the confusion engendered by the attempted redefinition and application of this indeterminate specific name is illustrated by Leidy's using it in Florida for specimens of probably Pliocene age (and in any event not belonging to *Halitherium*) and Hay's placing in it a true Pleistocene or Recent *Trichechus*, also from Florida.

phosphate mines, chiefly in Polk County but also in Hillsborough County. Other specimens, chiefly rib fragments and of little or no value, occur as derived fossils in Pleistocene and Holocene deposits along the Peace River and elsewhere.

MATERIALS

There have previously been described from the Pliocene of Florida a fragmentary maxilla with one tooth and some alveoli (Hay, 1922), type of *Metaxytherium floridanum*, and an imperfect humerus, some incomplete but articulated cervical vertebræ, several other broken vertebræ, and some rib fragments (Allen, 1923). The following more extensive materials are the chief basis for the present research:

F.S.G.S. V3211. Nearly complete cranium, without the facial part of skull. Found and presented by the Amalgamated Phosphate Company (American Cyanamid Company), Brewster, Fla.

F.S.G.S. V3232. Top of cranium. From the mines of the Dominion Phosphate Company, 5 miles south of Bartow. Presented by M. A. Waldo.

F.S.G.S. V4250. Frontals and adjacent parts. Pit No. 2, Coronet Phosphate Company, Pembroke. Collected by Gunter, Ponton, and Simpson, 1929.

F.S.G.S. V2854. Right humerus. Origin uncertain, but from pebble phosphate mine.

F.S.G.S. V656. Axis and parts of third to sixth cervicals in articulation. Found and presented by the Amalgamated Phosphate Company (American Cyanamid Company), Brewster. [This is the specimen described by Allen, 1923, pp. 235-236; 6165 is the old number.]

F.S.G.S. V2730. Distal part of scapula. Found and presented by the Amalgamated Phosphate Company, Brewster.

Amer. Mus. No. 26801. Lower molar. Mines of Coronet Phosphate Company, near Coronet. Presented by H. F. Greene, 1929.

Amer. Mus. No. 26805. Part of left upper maxilla with broken M³ and alveoli. Type of *Felsinootherium ossivallense*, see below.

Amer. Mus. No. 26803. Five articulated posterior dorsal vertebræ. From mines of Phosphate Mining Company near Mulberry. Presented 1929 by the Company through Mr. J. T. Bullwinkel, President.

Three photographs of a skull lacking the posterior portion. From mines of American Cyanamid Company. Present location unknown, see below.

There are also two other skull fragments, an incomplete humerus, several broken vertebræ, and numerous rib fragments which are of minor importance and do not require enumeration.

TAXONOMY

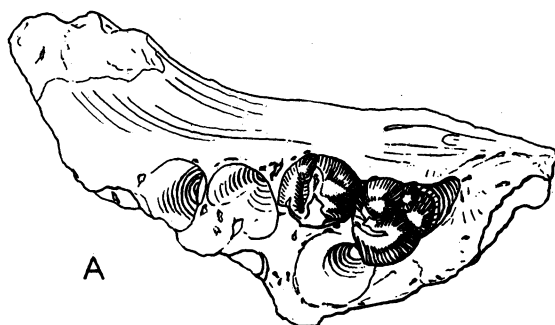
***Felsinothorium floridanum* (Hay)**

Metaxytherium floridanum HAY, 1922, Proc. U. S. Nat. Mus.. LXI, Art. 17, pp. 1-4, Pl. I.

TYPE.—U.S.N.M. No. 7221. Part of right upper maxilla with M^3 and alveoli of dm^4 and M^{1-2} .

HORIZON AND LOCALITY.—Bone Valley Formation. Pit No. 7 of Prairie Pebble Phosphate Company, 1 mile west of Mulberry, Florida.

DIAGNOSIS.— M^3 subquadrate, 26.5 mm. in length on type specimen. Anterior cingulum relatively weak, no anteroexternal accessory cusps. Cingular cusps posterior to hypocone and two of greater size on hinder border of tooth external to this.



A.M. 26805

 $\frac{2}{3}$ 

Fig. 11. *Felsinothorium ossivallense*, new species. Type, part of left maxilla with broken M^3 and other alveoli. A, Palatal view. B, External view. Two-thirds natural size.

Felsinotherium ossivallense, new species

TYPE.—Amer. Mus. No. 26805. Part of left maxilla with broken M^3 and alveoli of M^{1-2} .

REFERRED SPECIMEN.—Skull, lacking the posterior part of the cranium. From mines of American Cyanamid Company at Brewster. Present location unknown.¹

TYPE HORIZON AND LOCALITY.—Bone Valley Formation. Pit No. 42 of the Phosphate Mining Company, Mulberry, Florida.

DIAGNOSIS.—Upper molars about 15% larger than those of *F. floridanum*. M^3 subtriangular. Very strong anterior cingulum crest. Small anterointernal cuspule. Posterior half of tooth relatively narrower, metaconule more anterior to hypocone, two prominent cuspules at posteroexternal angle of tooth.

Felsinotherium spp.

As described below, the available fragments reveal various distinctions which may be in part of taxonomic value. These and the other skeletal parts seem clearly to pertain to a single genus, however, and all are rather uncertain as to species so that it is preferred to describe the osteology of the Floridian felsinotheres all together, although two species are known to be represented. The attribution of these sirenians to *Felsinotherium* rather than to *Metaxytherium*, as heretofore, will be defended after discussing their morphology.

MORPHOLOGY

DENTITION.—The dentition of these Florida felsinotheres is rather poorly known. M^3 of *F. floridanum* has been well described and figured by Hay (1922). It is subquadrate in form, measuring 26.5 mm. in length by 25 mm. in width. There are three anterior cusps in a transverse series, the inner and outer (protocone and paracone) subequal, the middle cusp (protoconule) smaller. Anterior to the protoconule and paracone is a well defined but relatively narrow cingulum. The anterior cusps are followed by another transverse series of three subequal cusps, of which the inner (hypocone) and outer (metacone) are opposite one another, the middle cusp (metaconule) displaced forward and blocking the median valley. This displacement is a characteristic of most later dugongids, such as *Metaxytherium* and *Felsinotherium*, in contrast to the pre-Miocene genera or to the trichechids. On the hinder edge of the tooth between and somewhat posterior to the metacone and hypocone are two prominent cuspules, and a smaller cuspule of the same transverse series is immediately posterior to the hypocone.

¹This skull, one of the finest yet found in the United States, was discovered in 1918. Photographs were taken by Mr. J. C. Driskell and sent to Dr. E. H. Sellards, then State Geologist, by Mr. Anton Schneider, but the specimen itself was not sent to Tallahassee. It is believed to have been sent to some northern museum, and may yet reappear, but prolonged inquiry and search by Mr. Gunter and myself have failed to locate it. Fortunately the three excellent photographs taken by Mr. Driskell are available for study and publication here through the courtesy of Mr. Gunter.

The homologous tooth of the type of *F. ossivallense*, which is complete and well preserved except for part of the protocone, differs considerably from that of *F. floridanum*, although not more than do teeth of separate species of one genus in the European series. It is larger, about 31 mm. in length, and was subtriangular rather than quadrate. The anterior width is not exactly determinable, but from the alveoli and general structure it was little less than the length, while the width across the hypocone, about 20 mm. in *M. floridanum*, contained 1.32 times in the length, is only 17.5 mm., contained 1.77 times in the length. The protocone was apparently very large, while the protoconule and paracone are small and closely crowded together. The anterior cingulum is a high stout crest, separated from the paracone and protoconule by a very deep narrow valley, the outer end of which is blocked by an accessory cuspule. Perhaps consonant with the narrowing of the posterior part of the tooth, the hypocone is more posterior relative to the metacone, while the metaconule is large, almost confluent with the hypocone, and is more nearly directly anterior to the latter. There is no posterointernal accessory cusp, but a large posteromedian cuspule, about as large as the metacone, and a distinct posteroexternal accessory cusp between this and the metacone.

The preceding molars are represented only by alveoli on the two type specimens. These show that in both species M^{1-2} were of nearly equal length and width and that in *F. floridanum*, but apparently not in *F. ossivallense*, M^1 was distinctly narrower than M^2 .

The skull known only from photographs has two teeth on each side, preceded by alveoli for another and followed by alveoli which likewise would seem to have lodged but one root. There are two possible interpretations: The preserved teeth may be dm^4 and M^1 , or they may be M^1 and M^2 . Either is possible, and indeterminable from the photographs, but the latter is perhaps more probable.

On this interpretation the zygomatic process of the maxilla begins to arise opposite the anterior end of M^2 , about as it does in all of the *Felsinotherium* or *Metaxytherium* skulls which have been figured. The alveoli posterior to the preserved tooth seem to have lodged a large triangular tooth, like M^3 of *F. gunteri* and unlike any M^2 known in this group. If this was not M^3 , that tooth was still partly or wholly in its crypt, which is unlikely in view of the advanced wear of the teeth which are preserved. The anterior alveoli would be for dm^4 on this hypothesis, and the true premolar would be lost and its alveoli resorbed, as they are in individuals of *Felsinotherium* (often also in *Metaxytherium*) at an apparently comparable age.

If this interpretation is correct, the dentition agrees with that of *F. ossivallense* more closely than with *F. floridanum*, and the skull may be tentatively referred to the former species.

The first tooth preserved is smaller than the next, and somewhat wider relative to its length. It is so deeply worn that no enamel remains on the crown. The following tooth is less worn and is well preserved on both sides. The absolute dimensions are unobtainable, as the photographs are not to exact scale, but the ratio length-width is about 1.15. The crown consists of approximately equal anterior and posterior moieties, the posterior somewhat the narrower, separated by a sharp valley. The anterior part is rather deeply worn, but had a transverse series of cusps (doubtless three in number as in all related forms) with a prominent transverse anteroexternal cingulum crest. The posterior half has a transverse series of three cusps, the internal the largest, of which the median one is displaced slightly forward and tends to block the transverse valley, although less anterior than on M^3 of either species. Immediately posterior to this cusp, the metaconule, is a stout median posterior accessory cusp, and there may have been another posterior accessory cusp, not clearly visible in the photograph.

The only part of the lower dentition available is the right M_3 listed above. It was just coming into use and is well preserved save for several flakes of enamel. It is uncertain to which of the established species this tooth belonged, if to either. Its length, about 27 mm.,¹ would seem to exclude it from *F. ossivallense*, as in European species M_3 is either equal to or greater than M^3 in length, and it may well belong to *F. floridanum*. The width is 19 mm. As in all sirenian teeth, the internal slope is more nearly vertical than the external. The crown is very complex, the enamel rugose and also with large furrows and ridges giving rise to several minor conules, but the basic pattern is of two transverse crests and a large posterior heel. Each crest is bowed forward centrally and consists of four poorly separated cusps. A large intermediate cusp joins the two crests, depending on the anteroexternal cusp (protoconid) and the second cusp (more external of the two median cusps) of the second crest. A smaller cuspsule adheres to the posterior slope of the anterointernal cusp, but does not join the second crest. The heel consists of three subequal cusps ranged along the posterior border of the tooth and a large median cuspsule wedged tightly between these and the second crest. There are no lateral or anterior cingula, but there is a small deep pit on the vertical anterior face of the protoconid and a smaller pit higher on the crown

¹Estimated maximum. The posterior end is slightly damaged.

just external to the protoconid apex. Deep wrinkled clefts separate the two crests and the posterior crest and the heel externally and internally.

These data regarding the dentition are not very full, but they demand detailed comparison with European species. The unequal development of anterior and posterior cingula, the presence of several accessory cusps, and the blocking of the transverse valleys by these and by anterior displacement of the conules clearly exclude not only *Haliitherium* and all other pre-Miocene forms, but also exclude *Thalattosiren*, *Miosiren*, and *Rytiodus*. Of established genera only *Metaxytherium*, *Hesperosiren*, and *Felsinootherium* come into consideration. *Metaxytherium* and *Felsinootherium* are very difficult genera to distinguish on any basis, even from the teeth. The various species differ about as much as do the genera considered as units. The only supposedly constant dental character is said (Depéret and Roman) to be the fact that the upper molariform teeth are wider relative to their lengths in *Felsinootherium* than in *Metaxytherium*. Taking M^3 as a basis, since this ratio is known in *F. floridanum*, the following figures are calculated from data given by Abel, Bruno, Capellini, Depéret and Roman, and Flot.

	$\frac{\text{Length}}{\text{Width}} \quad M^3$
<i>Metaxytherium krahuletzi</i>	1.24
<i>M. cuvieri</i>	1.23
<i>Felsinootherium serresi</i>	1.14
<i>F. forestii</i>	1.13
<i>F. subapenninum</i>	1.04
<i>F. floridanum</i>	1.06

Depéret and Roman suggest that the difference is especially notable in the anterior molars, but in *Metaxytherium cuvieri* (which is the only species of this genus for which I have been able to find exact figures for M^1 and M^2) the ratio is from 0.9 to 1.1, that is, sensibly the same as for either of the well defined European species of *Felsinootherium*. In *F. ossiwallense*, which may have slightly more elongate molars than *F. floridanum*, the ratio for M^1 (or dm^4) is about 1.0, for M^2 (or M^1) about 1.15.

M_3 also appears to have about the same proportions in *Metaxytherium* as in *Felsinootherium*, the ratio length to width usually about 1.4, as it is in the Florida specimen.

As regards morphology, aside from proportions, there seem to be no constant distinctions in isolated molars between *Felsinootherium* and *Metaxytherium*, although the species vary widely in both genera.



Fig. 12A

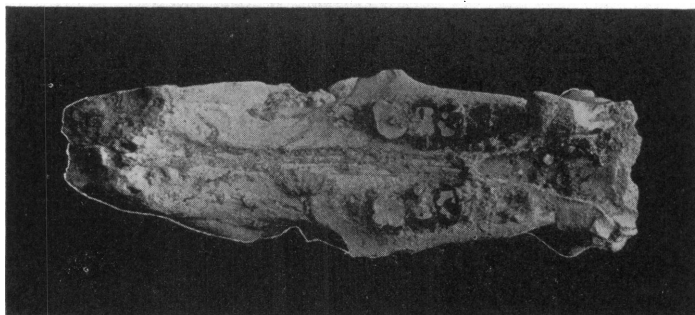


Fig. 12B

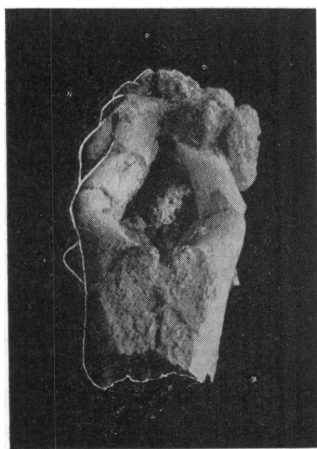


Fig. 12C

Fig. 12. *Felsinotherium ossivalense*, new species. Incomplete skull, referred specimen, present location unknown (see text). A, Left lateral view. B, Palatal view. C, Anterior view. Scale uncertain. Photographs by courtesy of the Florida State Geological Survey.

M³ of *Metaxytherium krahuletzii*, as figured by Abel, differs from *F. floridanum* in the larger anterior cingulum, more closely approximated metacone and hypocone, and more anterior metaconule, from both *F. floridanum* and *F. ossivallense* in the single heel cusp, or anteroposterior series of heel cusps, as well as in its elongate oval form. *F. subapenninum* seems to be closest to *F. floridanum* both in proportions and structure, but it has only one heel cusp—a variable feature, however. *F. serresi* is very close to *F. ossivallense*, in the character of M³, the only constant difference apparently being its smaller size and absence of a cusplule blocking the anterior cingulum valley. The species also closely resembles *F. floridanum* in the character of M² (or of M¹, which is almost identical).

If the various references of European specimens are correct, M₃ is a highly variable tooth, and the distinctions between *Metaxytherium cuvieri* and *Felsinotherium serresi* are slight and inconstant. The isolated M₃ described above is apparently rather more complex. Depéret and Roman cite various differences between the European species (1920, p. 13).

In short, the Florida teeth cannot be referred to any European species and are not diagnostic as to genus but rather closer to species commonly referred to *Felsinotherium* in a few, perhaps doubtful, features.

SKULL.—The rostrum and palate are known only in the lost skull, and like all other features of the Bone Valley Sirenia, they are close to *Metaxytherium* and to *Felsinotherium*. The rostrum is long and sharply deflected. It resembles that of *F. serresi* closely, being stouter, less elongate, and more deflected than in *Metaxytherium cuvieri* and somewhat longer and more slender than in *Felsinotherium forestii*. The general characters are those of all later dugongs. The median boss on the premaxillaries anterior to the mesorostral fossa, although broken, was apparently well developed as in *F. serresi*. The fossa is also similar in proportions to that species, slightly wider than in *F. forestii* but narrower than in the living dugong. The maxillary suture is clearly visible on the side of the rostrum, and shows that this part of the maxilla is more expanded distally than in *Dugong*, although less so than in *F. serresi*. The development of the palate, with its narrow gutter anterior to the cheek teeth, is also much as in *F. serresi*, but it is markedly narrower, especially between the teeth where its width is not greater than that of each tooth. The choanæ extend forward between the last molars. Immediately posterior to M³, the palatines and pterygoids¹ are produced

¹Or alisphenoids. There are no separate pterygoids in recent sirenians, and probably were not in this Pliocene form.

vertically into large processes grooved on their posterior surfaces as in the living *Dugong* or *Felsinotherium forestii*. These processes are more prominent than in *Dugong*, but this apparently is also true of other species of *Felsinotherium*.

The frontal part of the temporal regions is preserved on this skull, but the photographs reveal little not better shown by specimens actually in hand. One of these (F.S.G.S. V4250) has the frontals almost complete, with much of the ethmoidal region also displayed. The nasals are plump bones, somewhat deeper than wide. They did not come in contact with each other on the midline. They are deeply imbedded in the frontals, which surround their posterior ends on all sides, but leave them a small elongate dorsal exposure. As preserved they also are partly exposed in the nasal cavity, but thin plates from the frontal here lap over them and may completely have covered them when unbroken.¹ As preserved, the nasals are smaller than in *Metaxytherium cuvieri* (vide Flot, 1886) and very closely comparable to those of *Felsinotherium serresi*. The nasal passage is marked by two broad grooves on the ventral side of the fragment inclined at about 45°. Between these are two vertical or triangular plates of bone, which doubtless were continuous below when the specimen was entire, and indicate a deep, trough-like vomer. They clasp the ossified part of the mesethmoid between them, and there are traces of ethmoturbinals on each side of this, deep in the olfactory chamber, but their details cannot be made out. In another specimen (F.S.G.S. V3211) the mesethmoid is seen near its posterior end as a large vertical wedge-shaped plate, thin below but widening rapidly above where it is set into the vertical surface of the thick frontals. On the lateral walls of the chamber on each side of the mesethmoid are traces of three or more obliquely inserted turbinals.

The frontals are extraordinary, massive bones surrounding the ethmoidal region above and on each side, forming a relatively small anterosuperior part of the brain case, and produced anteriorly on each side into a stout bar expanded distally into a prominent supraorbital process, the distal end of which is, however, incomplete on all the available specimens. The nasals are inserted between the bones of these

¹Kellogg (1925, pp. 61-62) states that in *Metaxytherium jordani* the nasals are mortised into the top of the frontals, and considers at length the possible origin of the condition in *Hydrodamalis*, with nasals beneath the frontals and exposed in the nasal chambers. Whatever may be true of his species, in the present form the nasals appear definitely not to be above the frontals but inserted into them, very much as shown by Lepsius already to have been established in *Halitherium*, in which the nasals are, however, larger, thinner, and in contact in the midline. The condition in *Hydrodamalis* could be derived from that in *Halitherium* or in the present form by loss of the dorsal exposure (by further reduction or by further overlapping of the frontals, which already overlap them extensively here) and recession of the very thin lower plate of the frontals. This seems to me to be a slight change unattended by any grave mechanical difficulties, contrary to Kellogg's opinion.

processes. The lateral plates, descending into the temporal fossa, are nearly vertical. The suture with the parietals is complex. On the superior surface the frontals extend back into a deep V-shaped notch in the parietals, which here overlap the frontals. Along the sagittal crests there is a narrow extension forward of the parietals. Lateral to this, on the upper part of the vertical wall of the temporal fossa, the frontal is exposed as a blunt projection extending backwards to about the same distance as on the dorsal surface. Along the upper suture of this extension, the superficial part of the frontal somewhat overlaps the parietal, which is thus here clasped in a notch or groove in the thick frontal. Along and below the lower part of the extension of the frontal, the parietal laps forward again over the frontal, with which it has a squamous suture. The condition is very similar in *Dugong*, but in the recent genus, in keeping with the relatively shorter brain case, these various interlocking processes are less produced.

The lower edge of the descending process of each frontal is overlapped by the ascending ramus of the alisphenoid, which also appears to come in contact with the extreme anteroinferior angle of the parietal and with the anterior end of the cranial part of the squamosal. The alisphenoid is broken and badly crushed on the only specimen which shows it (F.S.G.S. V3211), however, and its sutural connections are not wholly clear.

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. Beginning immediately lateral to the nasals on the bases of the supraorbital processes of the frontals, these crests are nearly parallel or slightly convergent backwards on the frontals. Passing onto the parietals, the crests converge to a minimum width at about one third of the length of the parietals, then diverge again until, slightly farther apart than on the frontals, they reach the upper ends of the squamosals, somewhat anterior to the occiput, and disappear. On V3211 the upper surface of the frontals is flat or slightly concave, but on V4250 there is a pronounced, elongate, rounded, median boss, similar to that in *Hesperosiren*. In fact, although this specimen was found in the Pliocene, it may be derived from the Miocene. The point is not very important, since *Metaxytherium*, *Hesperosiren*, and *Felsinotherium* are almost identical in these parts. Measuring from the outer angulation where the temporal wall begins, the minimum width of the cranial roof on V3211 is about 55 mm., on V3232 about 60. 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 skull roof is, of course, considerably broader than in *Halitherium*. The specimen with the less prominent and wider crests suggests *Felsinotherium forestii*. In the other the crests are much

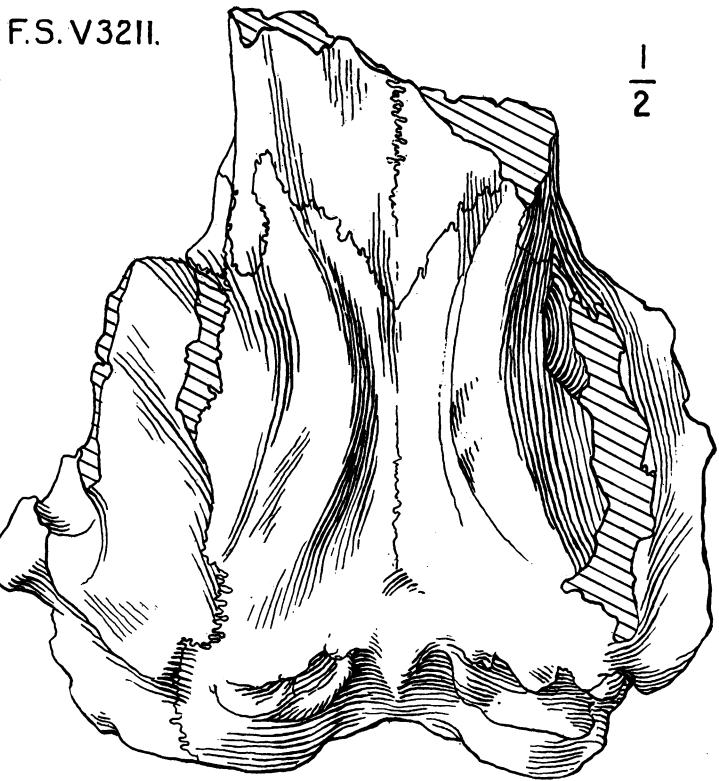


Fig. 13. *Felsinotherium* sp. Posterior part of skull, Florida Survey No. V3211. Superior view. One-half natural size.

swollen, but are otherwise similar in form to various specimens referred to *Metaxytherium cuvieri*, *Thalattosiren petersi*, or *Felsinotherium serresi*.

The two parietals and the supraoccipital are completely fused, forming a single stout bone, the so-called cranial or occipital shield, fragments of which are among the more common sirenian specimens in collections, because, no doubt, they are extremely dense and are recog-

F.S.V32II.

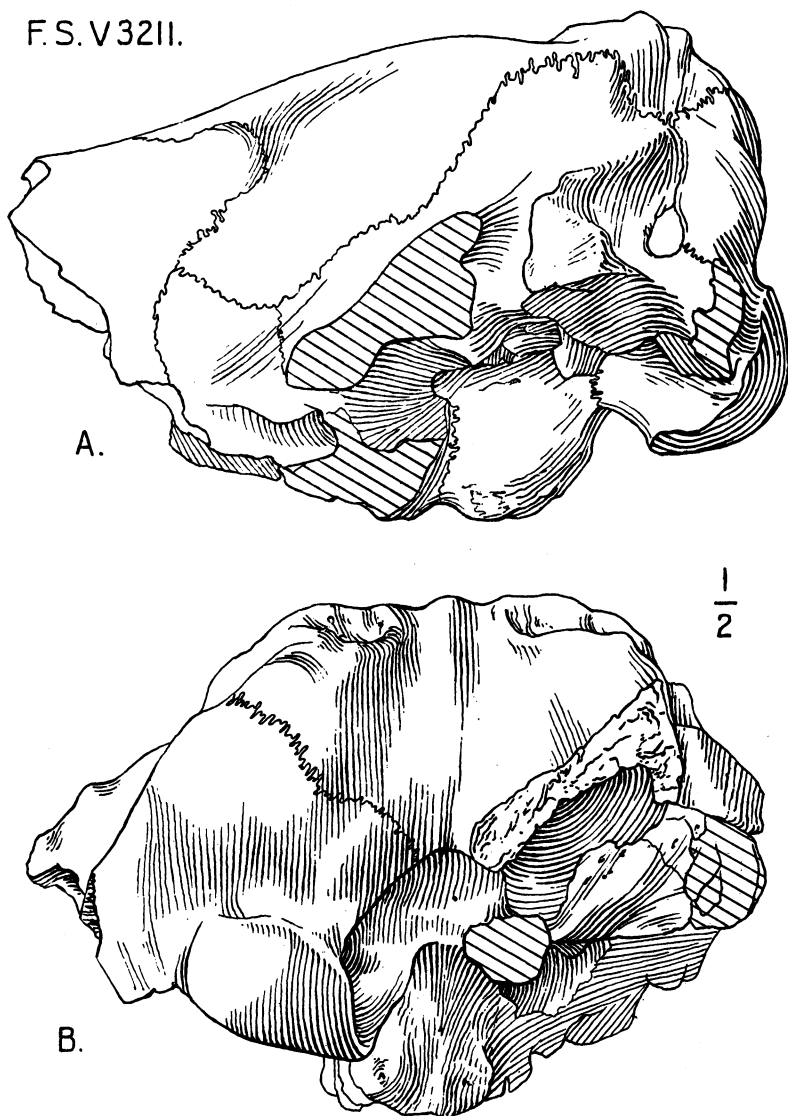


Fig. 14. *Felsinotherium* sp. Posterior part of skull, Florida Survey No. V3211. A, Left lateral view. B, Posterior view. One-half natural size.

nizable even from small fragments. Aside from various unimportant fragments, V3232 consists of this part almost perfect and isolated from other bones, and V3211 includes the entire complex united with the surrounding elements. The complex anterior suture and the dorsal surface have already been described. The descending plate in the temporal fossa, chiefly above the posterior root of the zygoma, is very thick above but rapidly thins out to a sharp edge below. The exposed part reaches its lowest point anteriorly, where it touches the alisphenoid. Above the zygoma the parietal is overlapped by a thin edge of the squamosal. Immediately posterior to the zygomatic root this suture turns abruptly upward, and a thick, blunt process of the squamosal broadly overlaps the parietal, its external surface reaching the posterior angle of the cranial roof, although it is excluded from the endocranial cavity by the parietals.

In the skull, V3211, the central part of the occiput is inclined at nearly 90° to the posterior part of the skull roof, a smaller angle than in *Dugong*, but in the isolated shield, and in the various fragments available, the angle is more open and about as in *Dugong*.

As Abel has pointed out, the shape and relationships of the supraoccipital are very important characters of the Halitheriinae, and, as much as can any single feature, they tend to reveal the degree of evolutionary advance and hence the genus (for *Metaxytherium* and *Felsinotherium* as genera are based rather on structural progress than on phyletic distinctions). Although this part is known in several species of *Metaxytherium*, exact figures seem to have been published only for *M. krahuletsi*. Here, according to Abel, the supraoccipital is separated from the foramen magnum by about 18 mm., and the two exoccipital sutures meet at an angle of about 130° . In *Felsinotherium forestii* and *F. serresi* (Capellini, Depéret and Roman), this angle is slightly smaller, and the supraoccipital may approach within 5 or 10 mm. of the foramen magnum, or may possibly even touch it in *F. forestii* (this part slightly broken in the illustrated materials).

In V3211 the angle is about 115° , and the lower point is not over 5 mm. from the foramen magnum. In V3232, the angle is about 120° , and while the exoccipitals are not preserved, the lower point is tapered in such a way that inner and outer faces are separated only about 4 mm. (on the more lateral part of the suture the thickness is about 15 mm.), from which very close approach to the foramen magnum is clearly indicated. In this, as in various other features, the Floridian specimens are in the most advanced halitheriine stage and are most closely comparable to *Felsinotherium*.

The lateral parts of the supraoccipital are convex, while the central portion is depressed and has a broad concavity separated into two deep narrow grooves in the upper part by a prominent vertical median ridge.

The foramen magnum is subtriangular or cordiform and higher than wide, as in *Felsinotherium forestii* or *Dugong*. The exoccipitals are large bones, surrounding the foramen magnum except for the small basioccipital part below, and forming all of the lateral surface of the occiput. This surface is nearly flat, but with a shallow depression (less pronounced than in *Dugong*) above the condyles. The latter are large, shaped much as in *Dugong* but with the upper part more expanded transversely than in that genus or in *F. forestii*. The general proportions and shape of the occiput (although it is somewhat distorted in the only complete specimen) are clearly very close to *F. serresi*, somewhat broader and lower than in *F. forestii* but relatively higher than in *Dugong*. The paroccipital processes are broken off. The superolateral borders of the exoccipitals are thickened and are separated from the squamosals by a deep groove on each side of the skull.

The zygomatic process of the squamosal is unknown, but the rest of this bone is well preserved in V3211. Its articulation with the parietal has been described. Anteriorly it meets the ascending wing of the alisphenoid, but the course of the suture is not clear. In the basicranium the part opposite the zygomatic root meets the basal part of the alisphenoid in a strong vertical sagittal suture, and posterior to this it surrounds and clasps the petiotic externally. Posteriorly, on the side of the cranium, a prominent groove follows the squamosoexoccipital suture. Deep and narrow in its middle part, this groove becomes very broad below, and there is a small triangular space where its floor is incomplete and the mastoid is exposed, as in *Dugong*, although the groove as a whole is more closed than in any recent manatee or dugong skull that I have been able to examine.

Although this region is somewhat broken, the posttympanic process seems to have had much the same relative size and character as in *Dugong*, but to have been farther from and less intimately related to the paroccipital process. The root of the zygoma is also very like that of *Dugong*, elongate and somewhat elevated posteriorly. Between it and the posttympanic process is a large groove.¹ The articular surface for the mandible is not preserved, but was apparently elevated as in *Du-*

¹In *Dugong* and probably in all of the Halitheriinae (including the present specimen when complete) this groove is almost bridged over by a stout reflected process from the posterior end of the zygoma. It offers a plausible origin for the otherwise highly anomalous piercing of the squamosal in this region in *Desmostylus*.

gong. The fossa between this surface and the postglenoid process seen in *Dugong* is still broader in the fossil and the postglenoid process is somewhat less prominent. The open external auditory meatus lies between it and the posttympanic process, forming a definite groove as in *Dugong* and (like many features of the skull) contrasting sharply with *Trichechus*.

The basioccipital is a larger, stouter bone than in *Dugong*, but otherwise very similar. The condylar foramen is somewhat larger and the bridge of bone which separates it from the auditory recess is relatively stouter. The basioccipital and basisphenoid are completely fused. It is a peculiarity of all of the Sirenia that the lower surfaces of these two bones meet at an angle much greater than 180° , the lower surface of the basisphenoid being bent abruptly upward anteriorly.

The following approximate angles give some idea of the degree of this flexure:

<i>Prorastomus sirenoides</i> (cast of type).....	205°
<i>Halitherium schinzi</i> (Lepsius' figure).....	220°
Florida specimen.....	240°
Recent dugong.....	230°
Recent manatee.....	215°

Like so many others, this character is probably irregularly progressive in the dugongs. The figure for the Florida specimen, apparently higher than even in the recent *Dugong*, may have been increased slightly by crushing.

The greater length throughout of the fossil skull as compared with that of *Dugong*, is correlated with a very distinct difference in the sphenoid region. In *Dugong* the strong pterygoid processes extend as far back as the posterior end of the basisphenoid, but in the fossil their posterior border is 20 mm. or more anterior to the (fused) basioccipito-basisphenoid suture. These processes are broken off in the specimen, but, as already suggested, they are very stout in the photographed skull.

On each side of the basisphenoid, above the front end of the pterygoid processes, is a larger sphenorbital fissure, as in all sirenians. The roof of this fissure is seen to be formed by a separate element, the orbitosphenoid, but the optic canal is not visible on this specimen.

The auditory region is fairly well preserved on the left side of the cranium, V3211, under consideration, and certain features of interest can be clearly made out. In the Sirenia in general the tympanic forms a heavy irregular semicircle fused at both ends with the petrosal; the petrosal part of the periotic is rather loosely set into a large groove in the

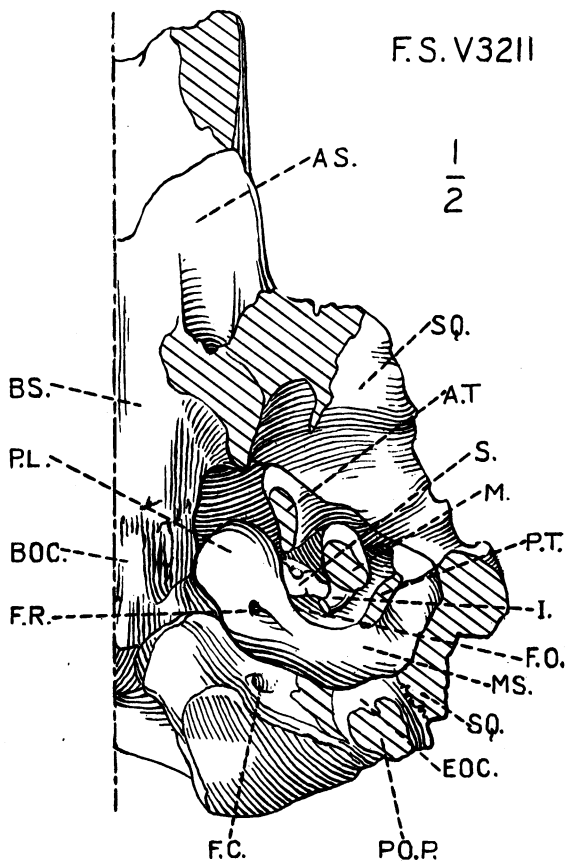


Fig. 15. *Felsinotherium* sp. Posterior part of skull, Florida Survey No. V3211. Inferior view of left side. One-half natural size.

AS.	Alisphenoid.
A.T.	Anterior base of tympanic.
BOC.	Basioccipital.
BS.	Basisphenoid.
EOC.	Exoccipital.
F.C.	Condylar foramen.
F.O.	Fenestra ovale.
F.R.	Fenestra rotundum.
I.	Incus.
M.	Malleus (lower part broken).
MS.	Mastoid.
PL.	Pars labyrinthine.
PQ.P.	Base of paroccipital process.
P.T.	Posterior base of tympanic.
S.	Stapes.
SQ.	Squamosal.

squamosal; the mastoid part of the periotic projects backward and is exposed externally at the bottom of the groove between the squamosal and the exoccipital; and a large open space is left anterointernally on the base of the skull between the periotic, basioccipital, basisphenoid, and alisphenoid. This arrangement, already established in *Eotheroides*, is typically developed in the present fossil and is constant for the Order, but with numerous slight variations in detail.

In the Florida specimen the tympanic ring is gone, but its two attachments to the petrosal are preserved and are quite as in *Dugong*. The lower part of the malleus is missing, but the upper part is present, the incus is complete but poorly exposed, and the stapes is present but slightly broken. The petrosal itself is complete save for numerous small fragments from various parts of the surface. The upper end of the malleus is composed of dense bone and is large and heavy, swollen and clumsy in appearance. The anterior part of the upper surface bears a short \wedge -shaped ridge which is clasped by the incus, articulating with the latter by a steeply oblique anteroposterior surface on each side. The anterior part of the upper surface of the malleus is more elevated and also has a stout articulation with the incus. The body of the incus is stout and bears on its lower surface the complex articular surfaces for the malleus. From its posteroexternal angle, the tapering *crus breve* extends straight upward into the deep and narrow *fossa incudis* of the petrosal. The *crus longum* belies its name by being short and stout. It extends backward, inward, and very slightly downward from the body of the incus and bears at its end the oval, anteroposterior, and almost vertical facet for the stapes. The stapes, which extends inward and slightly upward and forward from the incus, has the form of a thick rod, the basal (internal) end somewhat greater in diameter than the head. Its length is about 11 mm., and the almost vertical stapedial foramen, only about 3 mm. in maximum diameter, is slightly nearer the base than the head. This general structure of auditory ossicles is unique among mammals, highly characteristic of the Sirenia as an order, and closest to *Dugong* in its details.

The tympanic is not preserved, but its points of attachment agree with those of *Dugong* and show that it was semicircular, fused with the petrosal anterior and posterior to the tympanic recess.

The periotic consists of three continuous but fairly distinct parts. The anterior part of the petrosal is irregularly ovoid or roughly hemispherical and is deeply set into the squamosal, so that little of it is visible from any aspect. Its lower surface forms the anterior half of the tym-

panic recess, which lies between it and the posterior part of the petrosal on this side. Externally it is separated from the posterior part by the deep *fossa incudis*, continuous externally with a deep vertical groove, closed to a foramen by the squamosal, just above and internal to the external auditory meatus. The posterior part of the petrosal and the mastoid, which are entirely continuous, together are slightly larger than the anterior part of the petrosal. They are roughly trihedral in form. One face is directed posteriorly and laterally and is covered by the squamosal except for the mastoid exposure already mentioned. Another face is directed backward and abuts against the exoccipital, and another is directed inward and upward and forms part of the endocranial wall. Projecting forward and inward from this part and not clearly separated from it is the labyrinthine part, internal to the vestibular recess and separated by a deep notch from the anterior part of the petrosal. On the base of this part and forming the internal wall of the vestibular recess is a thick high ridge, much more pronounced than in *Dugong*, directed forward and slightly inward. As in *Dugong*, the *fenestra ovale* is on the outer side of this ridge and the *fenestra rotundum* directly opposite on the inner side.

The periotic differs from that of *Dugong* chiefly in being relatively larger and more massive throughout. The posterior and internal parts are also more firmly in contact with the exoccipitals, and the antero-internal vacuity, although large, is smaller relative to the periotic. The whole bone is somewhat more firmly fixed in the skull than in the living sirenians. Since all the essential characters of the sirenian periotic were already fully and typically developed in *Eotheroides*, it is not surprising that *Trichechus* is very similar to *Dugong* in this respect and perhaps even more like the Florida fossil in the superficial character of the massiveness of the periotic than is the latter genus.

VERTEBRÆ.—The cervicals here available for study are those already described by G. M. Allen (1923) and not all of the details need be repeated, although some further comparisons are instructive. The resemblance to *Felsinotherium serresi* is close, closer than to the dugong, for example, and much closer than to the manatee, but there are several unexpected distinctions. The neural canal in the Florida specimen is considerably higher than wide, the reverse of conditions in *F. serresi*; the lateral anterior facets are more nearly equidimensional, and they have the peculiar infero-internal projections noted by Allen, absent in the European species. The posterior zygapophyses, although crushed, appear to have more nearly vertical articular facets. Comparison with

Metaxytherium lovisati, as suggested by Allen, is slightly closer, although the arch here is also relatively broader, the borders of the lateral anterior facets not evaginate laterally, the odontoid facet smaller, the whole bone longer relative to its height. Closest comparison is with *Felsinotherium forestii*, the only significant difference from which seems to be the slightly less produced neural spine.¹ The succeeding cervicals, so far as preserved, are closely similar to those of *Felsinotherium* or *Metaxytherium*. They are unfused. The cervical vertebræ are all quite unlike those of *Halitherium schinzi*.

Post-cervical vertebræ are rather numerous in collections and in the field, but they are usually isolated, fragmentary, and of little interest. Allen (1923) gives measurements of eight centra and figures of two.

Most important of the present materials is a series of five dorsal vertebræ in articulation (Am. Mus. No. 26803), somewhat crushed and lacking the neural spines but otherwise well preserved. The first or second vertebra anterior to these probably had demifacets, and the second or third posterior to them probably had confluent facets. Their position is thus fixed as about the tenth to fourteenth. There were six or seven vertebræ with two facets, in agreement with Miocene and Pliocene Halitheriinae and in distinction from pre-Miocene Halitheriinae and from the other known subfamilies.

The vertebræ agree fairly closely with those of *Hesperosiren* described above, but certain of their characters are better preserved, and there are minor differences. In describing them they will be referred to as the first to the fifth, referring to the individual specimen and not to the complete series.

The more anterior centra are wider than deep and transversely elliptical, the last slightly deeper than wide and triangular. The width is about the same on all, possibly slightly less on the first one or two, but the depth is progressively greater, due principally to the progressive development of a median ventral keel, hardly visible on the first, very prominent on the fifth.

The diapophyses are short, heavy processes, those of successive vertebræ almost in contact. On the first two vertebræ they are turned up slightly at the ends, on the others nearly horizontal. They become progressively shorter (transversely) from the first to the fifth. Each bears a prominent tubercular facet on the lower side of the distal end.

¹The shape of the atlantal facets is not shown in Capellini's figures (1872, Pl. VI), however, and they may also have presented some distinctions.



Fig. 16. *Felsinotherium* sp. Amer. Mus. No. 26803, five dorsal vertebræ, probably tenth to fourteenth, with neural spines broken, dorsal view. One-third natural size.

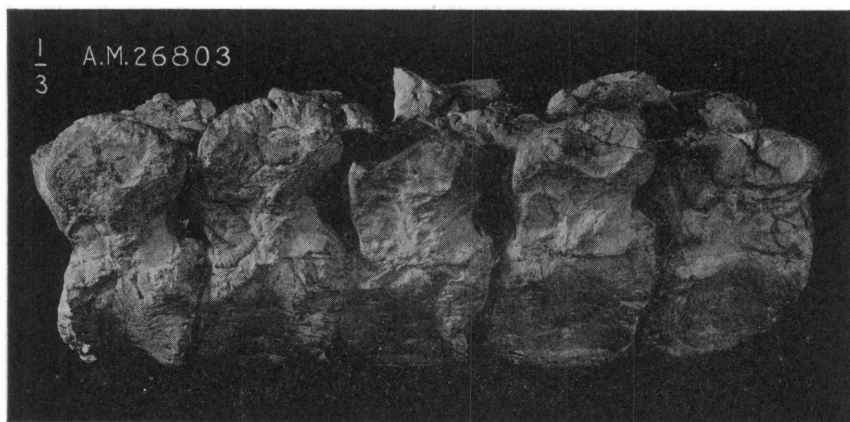


Fig. 17. *Felsinotherium* sp. Same specimen as in preceding figure, left lateral view. One-third natural size.

The capitular facets are on the bases of the diapophyses. On the first vertebra this facet touches the anterior edge of the centrum, so that it doubtless extended onto the preceding centrum on the first or second vertebra anterior to this. On the following vertebræ the two rib facets are progressively closer to each other, the approximate minimum distance separating them being as follows:

1-26 mm.

2-22

3-18

4-16

5-14

The prezygapophysial articulations are concave transversely and slightly inclined inward. From each of these surfaces a groove runs backward, then upward and inward, becoming narrower and almost meeting in a sharp point on the base of the neural spine. Below and between these there is a second set of similar and parallel grooves, separated from the first by a rounded ridge. A similar but larger and less regular pair of grooves appears on the posterior surface of the base of the neural arch below the postzygapophyses. The neural canal is elliptical or ovoid below, but notched above.

Aside from isolated centra and fragments, there are three other dorsal vertebræ in a fair state of preservation among the undescribed available materials. Two of these are posterior dorsals, one about the thirteenth dorsal and the other perhaps the fifteenth or sixteenth. They agree in a general way with those just described, except that the capitular facets on both are deeper and more scar-like. The more anterior of the two seems to indicate a slightly larger animal. They have the epiphyses preserved, and, as already pointed out by Allen on materials from the same formation, these are in a later Tertiary stage of degeneration. Their diameter is slightly less than that of the articular face of the centrum, and while the periphery is fairly thick and well ossified, the central part is thin and spongy.

Another vertebra belongs in the middorsal region, being probably about the seventh dorsal. The centrum is smaller relative to the neural arch and is considerably wider than deep. There are two demifacets of about equal size on each side. The diapophyses are relatively longer and more upturned. The minimum distance from the anterior demifacet to the tubercular facet is about 35 mm.

SCAPULA.—F.S.G.S. V2730 is a somewhat eroded distal end of a right scapula. The distinct, blunt coracoid process, the strong spine

directed backward¹ and about midway between anterior and posterior borders of the shaft, the rather long and slender shaft, fairly straight but bowed outward and diverted backward—all are characteristic of the later dugongs. The borders of the glenoid cavity are broken, but its proportions are also those of the more advanced dugongs. Aside from a definite resemblance to *Metaxytherium* and *Felsinootherium*, there is little that is distinctive.

RIBS.—Pieces of ribs are very numerous, being about the most abundant fossils in the Bone Valley Formation, but no complete or

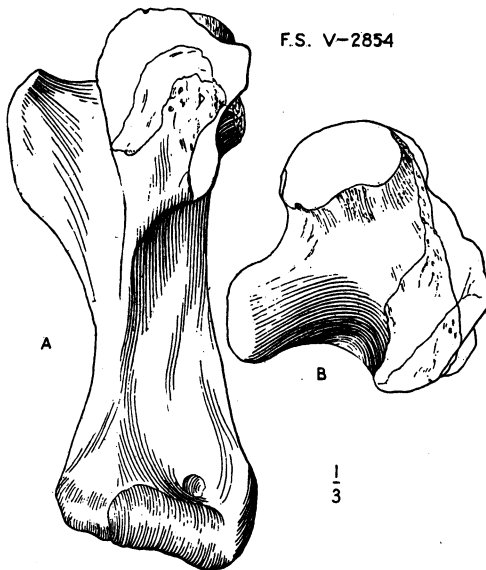


Fig. 18. *Felsinootherium* sp. Left humerus, Florida Survey No. V2854. A, Anterior view. B, Proximal view. One-third natural size.

associated ribs are available, and the fragmentary remains do not warrant description. They are of the universal Middle and Upper Tertiary sirenian type—plump, well rounded, and composed of extremely dense bone with a conchoidal fracture.

HUMERUS.—F.S.G.S. V2854 is a left humerus, nearly complete but with the thin edge of the greater tuberosity mostly broken off. It agrees closely in size and character with the less perfect specimen described by Allen (1923, pp. 233–234) and referred to *Metaxytherium floridanum*.

¹The apex of the spine and the acromion are eroded.

Allen compares his specimen especially with *M. cuvieri* of the Vindobonian. The present material suggests comparison also with *Thalattosiren petersi*, likewise from the Vindobonian (Abel, 1904) and with *Felsinotherium serresi*, from the Plaisancian (Depéret and Roman, 1920). The present specimen is intermediate in size between these two European species, but closer to *T. petersi*.

The greater tuberosity is much larger than the lesser, and had a thin reflected crest, as in the Upper Tertiary dugongs. The angle between the axes of the tuberosities, not exactly determinable because of the somewhat broken greater tuberosity, was between 85° and 90° ¹, and was thus greater than in any European forms save *Felsinotherium*, although approached by *Thalattosiren*. The shaft is relatively more slender than in *M. cuvieri* as figured by de Blainville, more as in *Thalattosiren petersi* or *Felsinotherium serresi*. The other characters of the shaft and deltoid crest are identical with those of these three species, more advanced than in *M. krahuletzi* or other earlier metaxytheres. The obliquity of the trochlea is slightly less than in any figured species of *Metaxytherium*, agreeing more nearly with *Felsinotherium serresi* (or with *Dugong*; this appears to be a progressive character). The width of the trochlea is almost exactly two-thirds that of the whole distal end, in exact agreement with *F. serresi*, relatively longer than in *T. petersi*. The shape and development of the epicondyles, also, are almost exactly as in *Felsinotherium serresi*, slightly different from *T. petersi* and *M. cuvieri*.

Although the humerus is not quite distinctive as to genus, it clearly falls into the European series at an Upper Miocene or Lower Pliocene stage of evolution and seems to be as close to *Felsinotherium* as to any previously described species.

Measurements:

Total length from head.....	223 mm.
Distal width.....	90 mm.
Narrowest diameter of shaft.....	42 mm.

AFFINITIES

It is at once apparent that the Pliocene remains described above belong in the Halitheriinae and are even more typical of that subfamily than is the earlier *Hesperosiren*. So far as present evidence goes, close comparison can be made only with *Metaxytherium* and *Felsinotherium*. These European genera may not be monophyletic units and are to be distinguished with difficulty except from relatively complete specimens

¹Allen gives 85° for his specimen, the proximal end of which is, however, still less complete.

and then chiefly on the basis of evolutionary advances. *Felsinotherium* is, on the whole, the more progressive, as it is the later, form, but at present no single character can be relied on to separate all the species of this genus from all the species of *Metaxytherium*.

From the constant comparison in the preceding pages of the Floridian fossils with the published European materials, the following conclusion seems acceptable until better material may be had: the Bone Valley remains are in some points close to *Metaxytherium*, but in most or all of the principal characters permitting of close comparison they seem rather more advanced and more on a par with *Felsinotherium*. In several respects the more diagnostic of the remains seem particularly close to *Felsinotherium serresi*. It is, therefore, concluded that they should all be placed in the genus *Felsinotherium*, at least until further evidence is forthcoming.

It may not be amiss to devote a few words to the bearing of this evidence on the age of the Bone Valley Formation. Kellogg (1924, p. 765) has considered the Bone Valley as "clearly . . . not later than Upper Miocene" and possibly "at least as old as the Helvetian," on the basis of the cetacean remains and of the supposed presence of *Metaxytherium*. As to the cetaceans I am not qualified to speak and await further revision of the generally very fragmentary and rather unsatisfactory specimens, but the sirenians do not appear to support this view, without absolutely disproving it. It is true that no species of *Metaxytherium* are reported (in contemporaneous literature) from the Pliocene of Europe. But (1) the uppermost Miocene and Lower Pliocene halitheriines of Europe are practically unknown, (2) *Felsinotherium serresi* differs little from advanced species of *Metaxytherium* and was long referred to that genus, and (3) the Floridian remains known when Kellogg wrote were reasonably placed in *Metaxytherium*, but were not really diagnostic as to genus, and the greatly better material now available suggests more probable reference to *Felsinotherium*.

The evidence of the land mammals of the Bone Valley (which is presented more fully elsewhere, Simpson, 1930B) seems to favor placing this formation in the Lower Pliocene. As here interpreted, the evidence of the sirenians is in agreement with this view. This age would be between the known ranges of *Metaxytherium* and *Felsinotherium* in Europe. The sirenians are also in some respects intermediate, but perhaps closer to the latter, Pliocene, genus.

PLEISTOCENE SIRENIA OF FLORIDA

Sirenian bones are common fossils in the Pleistocene deposits of Florida. In the older deposits, sirenians are not recorded in strictly fresh-water beds (such as the Alachua), but occur in greatest abundance in shallow marine or brackish estuarine deposits (as the northern Hawthorn or the Bone Valley). In the Pleistocene, on the contrary, they are most common in the strictly fresh-water strata. They are a normal element in the so-called Melbourne fauna of the east and west coasts and are reported from other fluviatile Pleistocene beds.

Along Peace River and in other deposits deriving material from the Miocene and Pliocene, many of the rib fragments are clearly of Tertiary age, although in Pleistocene or Recent sediments. This is demonstrated by the occurrence in the Peace River Pleistocene of fragmentary humeri identical with those found in the Bone Valley. Like the occurrence of *Hipparion* and *Serridentinus* in these same beds, this does not indicate the survival of the Pliocene genera into the Pleistocene, but only the redeposition of these resistant fossils long after their original burial.

All of the definitely Pleistocene or Recent sirenian remains of Florida belong to the living genus *Trichechus*. Teeth from the Seminole Field and elsewhere are in every respect identical with the living Florida manatee and wholly distinct from the Tertiary Sirenia, all of which are dugongs so far as known.

The most complete post-Tertiary specimen yet discovered was described by Hay (1919). This is a partial lower jaw, without teeth. This was recorded as from the Alachua, but this is clearly erroneous and its origin is unknown. It belongs in the genus *Trichechus*. Hay notes the absence of the concavity on the hinder face of the symphysis, the shorter symphyseal surface, more shallow horizontal ramus, larger mental foramen, and relatively longer tooth series, and concludes that the species is distinct from the recent form. He refers it tentatively to Leidy's "*Manatus antiquus*," which is surely erroneous. There are no directly comparable parts in the two, but "*Manatus antiquus*" proves not to belong in the genus *Trichechus*, while the Florida jaw does belong in that genus. Better material may warrant specific separation.

REVIEW OF OTHER TERTIARY SIRENIA

EOCENE SIRENIA

The following genera of Eocene Sirenia have been described:

Eocene, Jamaica—

Prorastomus Owen.

Middle Eocene, Egypt—

Eotheroides Palmer (= *Eotherium* Owen non Leidy).

Protosiren Abel.

Upper Eocene, Egypt—

Eosiren Andrews.

Archæosiren Abel.

Upper Eocene, Italy—

Mesosiren Abel.

Parahiosiren Abel.

Prototherium de Zigno.

These forms are all in need of revision, and some of Abel's genera are as yet little more than names. Sickenberg is now studying Mediterranean Sirenia, and his results will doubtless supply the needed knowledge. In the meantime a brief résumé of the published work is essential to a general view of Sirenia.

The most primitive known sirenians are clearly *Eotheroides* from the Lower Mokattam of Egypt and *Prorastomus* from the Eocene of Jamaica. They show the following primitive skull characters, among others:

1. Dental formula $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} dm \frac{1}{1} M \frac{3}{3}$.
2. Upper incisors not enlarged to form tusks.
3. Simple, subquadrate, low-crowned molars with two transverse crests, very similar in the two genera.
4. Narrow, elongate premaxillæ.
5. Jugal excluded from anterior border of orbit.
7. Distinct lachrymal, forming anterosuperior border of orbit in notch anterior to supraorbital process.
8. Relatively unspecialized zygomata.

Determination of the validity of various apparent differences would require direct comparison, but the following appear to be the essential known distinctions of *Prorastomus* from *Eotheroides*:

1. Lower incisors and canine apparently larger. Diastema between C and P_1 rather than P_1 and P_2 .
2. Fifth lower cheek tooth said by Owen to have but one fang. (Requires substantiation).
3. Alveolar process of maxilla relatively deeper.
4. Cheek teeth more anterior relative to orbit. In *Prorastomus* a vertical line from the anterior orbital border passes near the anterior end of dm^4 , in *Eotheroides* between P^1 and P^2 .
5. Frontals relatively narrower and apparently not so much arched.
6. Postorbital constriction greater and maximum constriction of cranium farther forward.
7. Cranium relatively slightly longer.
8. Condylod foramina relatively slightly more anterointernal.
9. Occiput probably relatively lower and broader.

10. Symphysis apparently somewhat less deflected and less produced below. (In part due to post-mortem defects, but perhaps partly original).

11. Mandible probably relatively longer.¹

From their numerous points of resemblance, most of which are in characters primitive for the Sirenia as a whole, it appears that *Eotheroides* and *Prorastomus* are rather closely related forms standing on nearly the same lowly evolutionary level. From their differences it seems that they represent early stages of slightly divergent phyla. The common view is that of Abel, that this incipient divergence is that between the Dugongidæ and the Trichechidæ, *Eotheroides* belonging near the former line and *Prorastomus* near the latter. This view, which seems to lack positive evidence, will be further discussed below.

The retention of the family Prorastomidæ, as defined by Cope on primitive characters, is horizontal classification, decried by many authors. At the same time the vertical splitting of the two rather similar genera *Eotheroides* and *Prorastomus* into two distinct families implies a knowledge of phyletic evolution in the Sirenia which is not actually at hand. The family Prorastomidæ must include *Eotheroides* and is the primitive sirenian stock structurally ancestral to the dugongs and probably also to the manatees.

Eosiren Andrews (see Andrews, 1906) from the Egyptian Upper Eocene is of interest in that it apparently shows the definite beginning of the true dugong, or halithere, line and departure from the possible ancestry of *Trichechus* in its advances over *Eotheroides*. It differs from the earlier genus chiefly as follows (Andrews):

- a. First upper incisors more enlarged.
- b. Second and third incisors and canines reduced and displaced outward.
- c. Rostrum more deflected, symphysis thickened.
- d. Nasals reduced.
- e. Supratemporal ridges more marked.
- f. Pelvis reduced, no obturator foramen.

These are all definite advances toward *Halitherium*, and there seems little objection to considering *Eosiren* as approximately intermediate in structure between that genus and *Eotheroides*. As pointed out by Andrews, it is very close to *Prototherium veronense* de Zigno, although slightly less specialized in the dentition. The dugongid line had clearly

¹As restored by Abel (1912, Fig. 5) the mandible of *Eotheroides* is very long. This is due, however, to the hypothetical insertion of a long edentulous part between the known anterior and posterior regions, from M₃ to the coronoid process. This is not present in any other sirenian and there seems to be little evidence that it occurred here.

diverged from the trichechid ancestry in the Upper Eocene.¹ *Prototherium*, although an Eocene form, is a true and typical halitheriine and is discussed in considering that subfamily.

The other Eocene genera are as yet of uncertain structure of affinities so far as published data are concerned.

Protosiren was established by Abel (1904) as a second genus from the Egyptian Middle Eocene. Definitive description is still lacking, but a skull referred by Abel to this genus was described by Andrews (1906, pp. 204–209, 210–212) as "*Eotherium ægyptiacum?*" Abel has published various figures of the skull (1919, Figs. 640–642; 1928, Figs. 325B, 328, 329). He now considers this form as ancestral to *Miosiren*, but the basis for this is not clear. The occiput is broader than in *Eotheroides*, and in Abel's figure, but not Andrews', the foramen magnum is notched above and reaches the supraoccipital. The ribs and vertebræ are said to be less affected by pachyostosis than in *Eotheroides*, the skull roof more rounded, the cerebral hemispheres broader and not separated (on the brain cast) by a median fissure. The dentition and many other structural features appear to be very like those of *Eotheroides*, however, and judgment must be suspended until more adequate publication.

Archæosiren, from the Upper Eocene of Egypt, it considered by Abel as in his *Protosiren*–*Miosiren* line. Little more than the name has been published (Abel, 1912, p. 307), and the genus has apparently not even been validated by diagnosis, description, or figure.

In erecting the genus *Protosiren*, Abel also proposed a new species, *P. dolloi*, from the Upper Eocene of Monte Zuello in Italy. This was later removed to the new genus *Mesosiren* (Abel, 1906). Based on a few upper teeth, the affinities of this form appear doubtful, but it probably belongs with the typical halitheres. Depéret and Roman (1920, p. 40) suggest that these may be milk teeth of *Halitherium* [*Prototherium*] *veronense*.

The genus *Paraliosiren* is also based on milk teeth from Monte Zuello. Inadequately characterized, it remains doubtful. Abel's recent summaries do not mention it.

¹This view of the affinities of *Eosiren* is that of Andrews and of Abel. It is diametrically opposed by that of Depéret and Roman (1920) who consider *Eosiren* as more primitive than the earlier *Eotheroides* and belonging in a divergent line leading to *Prohalicore*. They base this on the smaller size of *Eosiren*, more slender, elongate, and elevated but thicker mandible, quadritubercular superior molars, diastemata between the first two premolars. According to the figures given by Abel and Andrews, *Eosiren libyca* is slightly larger than *Eotheroides ægyptiacum* rather than smaller, and the difference in any event is not great. The lower jaw as figured by Andrews is shorter and heavier in *Eosiren*, the difference again being slight—the lower jaw figured by Depéret and Roman (1920, Fig. 11, IV) is not *Eotheroides* but *Protosiren*, and even it is not significantly heavier than in *Eosiren* and is more primitive in the development of the symphysis. The development of diastemata is a specialization, not a primitive character, in this case, and the molar structure is almost identical. If one may judge by the published data, Depéret and Roman would appear to be mistaken in considering *Eosiren* as the more primitive genus.

EUROPEAN HALITHERIINÆ

The subfamily Halitheriinae includes a varied series of genera, not monophyletic but rather closely related, which runs through the greater part of the European Tertiary, from the Upper Eocene into the Pliocene.

The earliest definitely established form of this group in Europe is *Prototherium veronense* de Zigno, from the Upper Eocene of Monte Zuello in Italy. At first it was placed in *Halitherium* (de Zigno, 1875A), later in the distinct genus *Prototherium* (de Zigno, 1887). Lydekker (1892), on the basis of a wrongly referred specimen, considered the species as congeneric with *Prorastomus sirenoides*, which is certainly erroneous. Depéret and Roman (1920) retain it in *Halitherium*, but the recognition of de Zigno's genus is convenient. A complete skull is known.

The genus *Halitherium* is characteristic of the Oligocene, and the species *H. schinzi*, best known of all fossil sirenians, is widespread in the European Stampian. In the Lower Miocene (Burdigalian), contemporaneous with the earliest species of *Metaxytherium*, occur *Halitherium christoli* Fitzinger of Austria and *H. bellunense* de Zigno, from the base of the Miocene in Italy. Lepsius (1881) placed the former species in *Metaxytherium*, but later work (e.g., Abel, 1904, 1905; Depéret and Roman, 1920) seems to confirm its tentative reference to the earlier genus. The skull is not well known in either species.

Manatherium Hartlaub (1886A) is a second genus of Oligocene halitheres. It is of special interest because of Hartlaub's opinion, unchallenged until recently, that it was a trichechid and not a dugongid. It was based on several skull fragments. Recently Sickenberg (1929) has described a considerable part of the skull of another specimen. He shows conclusively that it has nothing to do with the manatees but is a halithere, closely related to *Halitherium* itself but somewhat more primitive and slightly divergent. The size is small. The skull is higher than in *Halitherium schinzi*, the nasals do not meet in the midline, the frontals are relatively wide, and the teeth are relatively large. Especially primitive characters are the presence of a lachrymal duct and a maxilloturbinal, the relatively strong ethmoturbinals, the relationships of the ascending process of the premaxillæ, and the very primitive tooth pattern.¹

At least three valid genera of this group occur in the European Miocene: *Halitherium* and *Metaxytherium* in the Burdigalian; *Metaxy-*

¹In spite of the universal acceptance of Hartlaub's reference of this genus to the Trichechidae ("Manatidae"), his own figures and description showed that this was erroneous. This conclusion was reached in the present study, written before Sickenberg's paper was published. Fortunately the latter now substantiates and makes unnecessary the discussion of Hartlaub's argument formerly given in this manuscript. Various other Old World specimens, such as "*Manatus coulombi*" Filhol = *Eotheroides ægyptiacum*, have been referred to the Trichechidae in error.

therium and *Thalattosiren* in the Vindobonian. *Metaxytherium* has been used to include a number of species, none of them well known, from the Miocene. Its rather indefinite and polyphyletic character is well shown by the fact that the discovery of a complete skull of *Metaxytherium petersi* Abel proves that this species, originally based on fragments but of unquestioned reference to this genus, is very distinct from the others and referable to a separate genus, named *Thalattosiren* (Sickenberg, 1928). Among more or less definitely established species, this leaves *M. krahuletzii* Depéret, *M. meyeri* Abel, and *M. beaumonti* de Christol in the Burdigalian and *M. cuvieri* de Christol in the Vindobonian. Except for *M. cuvieri*, these are all based on very fragmentary materials, and their interrelationships are doubtful.¹ Knowledge of *Metaxytherium cuvieri*, which must be accepted as the type species, has recently been most fortunately augmented by the description of a nearly complete skeleton by Cottreau (1928).

The genus *Thalattosiren*² has recently been established by Sickenberg for the sole species "*Metaxytherium*" *petersi* Abel of the Upper Mediterranean (Vindobonian) of Austria. The skull and much of the skeleton are known.

A fourth supposed Miocene genus is *Halianassa* von Meyer, with the type species *H. studeri* from the Burdigalian of Germany. Depéret and Roman (1920) consider that the species may be identical with the contemporaneous *Metaxytherium-beaumonti* or *M. krahuletzii*. Von Meyer (1838) believed that this genus included "*Halicore*" [*Metaxytherium*] *cuvieri*, and most authorities have agreed that *Halianassa* is synonymous with *Metaxytherium*. If this is true, *Halianassa* is the prior and valid name, and not *Metaxytherium* as generally supposed, but the generic attributions of these little-known species are so doubtful that both genera may be tentatively retained.

In the Pliocene this subfamily is represented by several closely related or identical species from the Astian of Italy, *Felsinotherium forestii* Capellini (genotype) and related forms. Nearly comparable in evolutionary advance, but sufficiently different in the dentition and some other respects to suggest a distinct phylum, is *Felsinotherium serresi* Gervais from the Plaisancian of France. Both *F. forestii* and *F. serresi* are well known.

The unraveling of the apparently complex phyletic relationships of this confused and not very well differentiated series of genera and species

¹A nearly complete skeleton of *M. beaumonti* was discovered, but it was inadequately described and has since disappeared.

²In Sickenberg's paper (1928) this generic name is spelled "*Thalattosiren*" in the text except on page 321, and "*Thallatosiren*" in the figure and plate legends and on page 321.

is a problem requiring detailed restudy of the originals, which are, however, still inadequate for a complete synthesis. This requires much further work in Europe and lies within the scope of the series of studies inaugurated by Abel and now placed in Sickenberg's hands. The only detailed résumé so far published is that of Depéret and Roman (1920). So far as the forms here included in the Halitheriinae are concerned, they recognize the three genera *Halitherium*, *Metaxytherium*, and *Felsino-therium*. These they place in three phyla, one with two branches. One phylum includes *Halitherium* [*Prototherium*] *veronense*, *H. schinzi*, and *H. bellunense*. The second is the genus *Metaxytherium* (including *Halianassa* and the genus *Thalattosiren* not then established) with two branches, one including the Burdigalian forms and *Metaxytherium* [*Thalattosiren*] *petersi*, the other with only *M. cuvieri*. The third phylum includes the two definitely established species of *Felsinotherium*.

Viewing the subfamily as a whole, there are apparent certain general tendencies towards progressive modification, although these are very unequally exhibited by the various known forms. Among the more important of these progressive features (see especially Abel, 1904) are:

1. Numerical reduction of cheek teeth.
2. Complication of cheek teeth, chiefly by displacement forward of middle cusp of posterior row and addition of accessory cuspules.
3. Broadening of skull roof, temporal crests becoming more parallel.
4. Cranium shortened.
5. Nasal aperture broader.
6. Nasals reduced.
7. Rostrum more deflected and inflated.
8. Lower point of supraoccipital sharper and approaching foramen magnum.
9. Mandible shorter and deeper, more expanded symphysis.
10. Prespinous fossa of scapula larger, spine higher, acromion more prominent, glenoid fossa broader.
11. Lesser tuberosity of humerus smaller, greater tuberosity larger, axes more divergent, deltoid crest stronger.
12. Radius and ulna more nearly in same plane.
13. Fourth metacarpal longer relative to radius.
14. Pubis more reduced, ischium longer and more slender, acetabulum lost.
15. Smaller number of dorsal vertebræ with demifacets for rib capitula.

Most of the known genera and species show various specializations which make this series structural and indirect so far as they are concerned.

Prototherium veronense, judging from de Zigno's figures and descriptions and a cast of the skull, is decidedly the most primitive, as it is the earliest, member of this subfamily in Europe. It could be structurally ancestral in the known parts to the other members of the group.

Halitherium schinzi, although more advanced than *Prototherium veronense*, is still relatively primitive, but it shows several specializations which exclude this species from the ancestry of later forms. } The

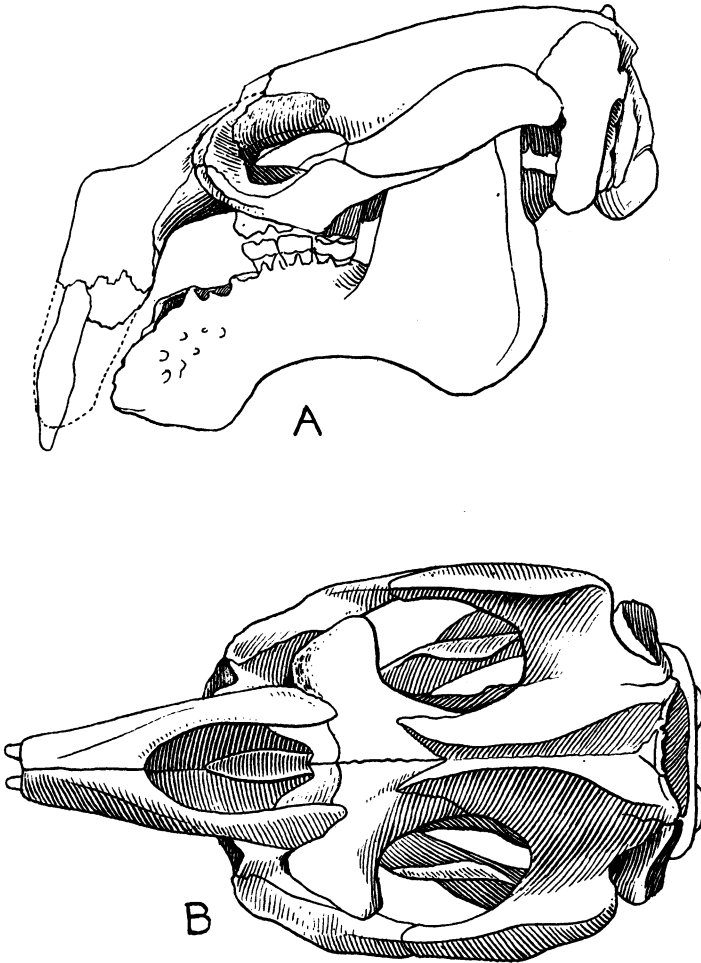


Fig. 19. *Halitherium*. Skull. A, Left lateral view. B, Superior view. After Lepsius.

teeth are still primitive in form and number. They are simpler than in most later halitheriines, but somewhat more complex than in *Thalattosiren*. They show the beginning of bunodont specialization which probably excludes this species from the ancestry of this genus or of *Hali-*

therium bellunense or *Halianassa studeri*. The upper molars are subquadrate, a primitive feature lost in some later forms and retained in others. The nasal aperture is fairly broad, the supraorbital processes short and greatly expanded, partially primitive but here so emphasized as to give rise to a suspicion of aberrancy. The rostrum is more deflected than in *Prototherium*, but it is not clear from the other literature that this is consistently greater than in *Metaxytherium*, as suggested by Depéret and Roman. The postcranial skeleton is in general primitive, but the second and third cervicals are usually fused, an aberrant feature.

Halitherium bellunense and *H. christoli*, as well as the Lower Miocene species of *Metaxytherium*, are very poorly known. So far as these latest species of *Halitherium* are known, they are more progressive than *H. schinzi*, but differ from *Metaxytherium* in much the same way: thicker and less separated temporal crests, simpler teeth without marked blocking of transverse valleys. As pointed out by Sickenberg, the more lophodont teeth of *H. bellunense* may suggest *Thalattosiren*, but not *Metaxytherium* or *Felsinotherium*. *Metaxytherium krahuletzii* shows quite definitely the bunodont tendency which characterizes the teeth of the latter two genera. The teeth are more advanced than in *Halitherium*; the transverse valleys blocked by displacement of ridge cusps and intercalation of accessory cuspules. The ulna and radius may be more specialized than in the later *M. cuvieri* in their close connection and lack of flexion.

Metaxytherium cuvieri, while surely excluded from direct descent from *Halitherium schinzi* and probably from direct ancestry of *Felsinotherium serresi* or *forestii*, is generically intermediate and a member of this structural line. It is on the whole less aberrant than either *Hesperosiren* or *Thalattosiren*. The molars are elongate and complex. The skull is relatively long, high, and narrow, the rostrum well deflected. The supraorbital processes are very long and slender and relatively little expanded. The nasals have little or no median dorsal contact but are fairly large. The lower jaw is deep and heavy. The cervicals are separate. Nine dorsals have demifacets. The tuberosities of the humerus diverge at 85°–90°.

Thalattosiren may, according to Sickenberg's preliminary discussion, find closer relatives among some of the less known earlier forms, but among halitheriines in which the skull or dentition is well known, it is unique. The skull is short and broad, the mesorostral fossa also unusually large, short, and broad, almost as in *Trichechus*. The supraorbital processes of the frontals are moderately long and expanded at

the ends. The nasals have a prominent median suture and surround the posterior ends of the frontal processes of the premaxillæ. The jugal is in contact with the supraorbital process of the frontal. The rostrum is rather thin, very sharply deflected, and there are no tusks in the known skull. The upper molar teeth are simpler and more lophodont than in any contemporary or later halitheriine. These and other peculiarities are not considered by Sickenberg as sufficiently great to exclude *Thalattosiren* from the Halitheriinae, but certainly they stamp it as a member of an aberrant phylum not possibly ancestral to any known later sirenian.

The immediate ancestry of *Felsinotherium forestii*, type of the genus, and *F. serresi* is thus not certainly known, although both are clearly and typically specialized members of the halitheriine group. *Metaxytherium cuvieri* may not be far from this ancestry. *Thalattosiren* can not be considered as very closely related. They represent the last terms in halitheriine specialization along the lines suggested above. The two species are quite distinct although closely comparable. In *F. serresi*, the molars, although of the bunodont type, are strikingly simple and primitive. The six-cusped, two-rowed arrangement is well defined and modified only by relatively slight displacement forward of the median posterior cusp. Complication is almost confined to the cuspules derived from anterior and, especially, posterior cingula. In *F. forestii*, on the contrary, the relatively high-crowned teeth are more complex and the crowded cusps retain little definite evidence of the originally seriate arrangement. The molars are also relatively smaller in this form. *F. forestii* is also the more specialized form in various other respects: the skull is more abbreviated and heavier, the rostrum and symphysis are larger and more sharply deflected, etc.

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, in fact, considered the genera as synonymous.¹ Abel separated them chiefly on the basis of the more bunodont, less lophoid, more complex and more quadrate molars of *F. forestii* and the related or synonymous *F. gastaldii*, and "*Cheirotherium*" *subapenninum*. This would necessitate placing *F. serresi* in *Metaxytherium*, which Abel did. Depéret and Roman place *F. serresi* and *F. forestii* in the same genus, which they distinguish from *Metaxytherium* by "la réduction un peu plus avancée et la forme un

¹In which case, as he does not recognize, *Felsinotherium* is the antedated name, being proposed some twenty-five years later than *Metaxytherium*.

peu plus carrée de M^1 , de M^2 et de P^1 " and by "l'inflexion un peu plus prononcée en bas du rostre prémaxillaire." The teeth of *F. serresi* do not really seem in themselves to offer a valid generic difference from those of *Metaxytherium cuvieri*. The two genera are distinguished by slightly more specialized structure chiefly in proportions and other quantitative characters, rather than by any one or by a few definite qualitative distinctions.

That several, and perhaps many, distinct phyla are included in the Halitheriinae, is apparent. The known species show crossing specializations, and the exact genetic lines cannot now be clearly distinguished. This is a familiar and almost universal condition in palæontologic series, but it does not vitiate the instructive structural sequence, which, regardless of the fluctuating character of the various known species, is generally progressive from *Prototherium* to *Felsinotherium*. As already suggested, still more primitive terms of this structural sequence are probably to be seen in *Eotheroides* and *Eosiren* of the Egyptian Eocene, although, as in the case of the European forms among themselves, the relationship is perhaps not that of direct ancestry.

Judging from this series, the Sirenia are a much more static group than, for instance, the horses. Horses of successive epochs sometimes seem to differ quite as much as do the initial and terminal stages of the Halitheriinae, separated by the greater part of the Tertiary.

DIVERGENT EUROPEAN LINES

In addition to the genera usually referred to the Halitheriinae, a number of other forms have been described from the European Tertiary. So far as valid, these apparently represent more sharply divergent phyla. *Rytiodus* and *Miosiren* are the only ones that are clearly characterized and of outstanding importance.

Rytiodus Lartet, from the Aquitanian of France, is a very large form about equal in size to *Hydrodamalis*. It is known only from the skull,¹ which is elongate, the parietal region very narrow, the occiput inclined forward. The premaxillæ are only slightly depressed, but the incisive tusks are very large, directed forward and slightly downward, subtriangular in section. The upper molars are simple, with two transverse crests separated by a deep straight valley without accessory cusps, the last molar with a strong posterior cingulum. The molar proportions are about as in *Halitherium*. This is a very distinctive genus differing sharply from all other adequately characterized forms. Within the family it

¹A very complete skeleton was discovered in 1861, but all but the skull destroyed (Delfortrie, 1880).

obviously has no special resemblance to *Dugong* itself, but it is a dugongid. Its reference to a distinctive subfamily of Dugongidæ is convenient.

Miosiren Dollo from the Pontian of Belgium is known from a nearly complete skeleton, but has not been fully described or illustrated (Dollo, 1890; Depéret and Roman, 1920). The first three cheek teeth are subequal, simple in structure. The following three molariform teeth ($d^4 M^{1-3}$, according to Abel) are without accessory cusps but with anterior and posterior shelves. M^3 is reduced to a simple cylindrical button. There are twenty ribs with the tuberculum and capitulum separate on all. No acetabulum is present, but there is a rugosity for ligamentous attachment of the vestigial femur. Dollo concludes that this relatively well known and highly distinctive genus is of unknown ancestry and without known descendants. Depéret and Roman emphasize the dental reduction, absence of temporal crests and large size, and they suggest with much hesitation that *Miosiren* may be ancestral to *Hydrodamalis*, although the annectent stages are unknown. Abel considers *Miosiren* as a descendant of the Eocene *Protosiren* and *Archæosiren*, but the evidence has not been given and is not apparent.

OTHER GENERA

About a dozen other generic names for supposed Tertiary European Sirenia have been proposed, but these are all either inadequately known, indeterminate, or incorrectly determined. *Prohalicore* Flot was based on a lower jaw without teeth, apparently a distinctive form but very inadequate and of wholly doubtful significance. Depéret and Roman consider it as quite distinct from the central halitheriine line and perhaps derived from *Eosiren*, although they recognize the lack of evidence for this view. *Pachyacanthus* Brandt was at one time (Van Beneden, 1871) considered as partly based on a sirenian, but is now known to be a cetacean as Brandt originally held. *Crassitherium* Van Beneden is a very doubtful large form, perhaps related to *Miosiren*.

Cheirotherium Bruno is preoccupied and apparently synonymous with *Felsinotherium*; *Furcotherium* and *Pontotherium*, both of Kaup, are apparently synonymous with *Metaxytherium*, and *Pugmeodon* Kaup with *Halitherium*, while *Cyotherium* Kaup, *Halibutherium* Gloger, and *Trachytherium* Gervais are also invalid or of doubtful significance.

RECENT SIRENIA

OSTEOLOGY OF RECENT GENERA

As is well known, there are three very distinct genera of recent sirenians. *Trichechus* ("Manatus") includes the manatees, living along the coasts and in many of the rivers on the western side of the Atlantic, in Florida, the Caribbean Sea and Gulf of Mexico, and northern South America, and on the eastern side of the Atlantic in Central Africa. *Dugong* ("Halicore") lives in the Red Sea, the Indian Ocean from Madagascar to North Australia, and along the shores of many of the Australasian and Malaysian islands. *Hydrodamalis* ("Rhytina" or "Rytina"), Steller's sea cow, was discovered by Bering's expedition in 1741 but was so rapidly slaughtered by this and later parties that it became extinct, perhaps by 1768. Its known range included Bering Island and Copper Island in the North Pacific.

A general résumé of the more striking osteological differences between these genera, with special emphasis on the skull, is here given.¹

ORIGIN OF *Dugong*

Dugong is evidently the closest living relative of the Halitheriinae, but recent writers agree in abandoning the older view of direct derivation through this line. Abel (1904; 1919, p. 833) holds the extreme view that the Dugonginae separated "jedenfalls schon im frühen Eozän," while Depéret and Roman (1920, p. 49) state more conservatively, "Il paraît impossible que le *Dugong* puisse être le descendant direct des gigantesques *Felsinotherium* pliocènes, et il convient plutôt d'y voir un petit rameau parallèle ayant divergé du rameau *Felsinotherium* au moins depuis le Miocène et ayant acquis des caractères un peu particuliers par suite de son isolement géographique."

The more important items of evidence may be briefly given. Many of the characters of *Dugong* are apparently evolutionary advances over *Felsinotherium* or the Halitheriinae in general. Among these are:

1. Cheek teeth further reduced.
2. Rostrum further enlarged and deflected.
3. Nasals absent or vestigial.
4. Supraorbital processes less prominent.
5. Cranium relatively shorter.
6. Supraoccipital reaching the foramen magnum.
7. Mandible shorter and higher.
8. Bicipital groove of humerus broader and deeper.

¹Excellent material of *Trichechus* and of *Dugong* has been studied and also the skull and jaws of *Hydrodamalis*. The skeleton of *Hydrodamalis* is thoroughly figured in Brandt's monumental *Symbole Sirenologicae* (1868) with a very detailed osteological description and comparison of this and the other recent genera.

TABULAR COMPARISON OF OSTEOLOGY OF THE THREE RECENT GENERA OF SIRENIA

	1. <i>Dugong</i>	2. <i>Hydrodamalis</i>	5. <i>Trichechus</i>
SKULL			
Premaxillæ greatly enlarged and sharply deflected.	Premaxillæ slightly smaller and less deflected.	Premaxillæ relatively small and very little deflected.	
Mesorostral fossa relatively wide and margin nearly horizontal.	About as in <i>Trichechus</i>	Narrower than in <i>Dugong</i> and anterior end much lower than posterior.	
Posterior end of premaxillæ stout, lapping far back over frontals.	Somewhat less stout, chiefly abutting against internal side of supraorbital process.	Much as in <i>Hydrodamalis</i> .	
Nasals absent or vestigial.	Nasals present but small, inserted against frontals at internal side of supraorbital process, small dorsal and olfactory exposures.	Nasals normally present, small thick vertical plates inserted into frontals, small dorsal exposure, no olfactory exposure, but highly variable and sometimes absent.	
Jugal expanded vertically below orbit, stout contact with premaxilla.	Much as in <i>Dugong</i> .	Jugal expanded behind orbit, thin and supported on a nearly horizontal maxillary plate beneath orbit, not reaching premaxilla.	
Lachrymal a small bone confined to antero-superior border.	Much as in <i>Dugong</i> .	Lachrymal small and often fused with maxilla.	
Orbit widely open behind.	As in <i>Dugong</i> .	Orbit nearly or quite closed behind.	
Supraorbital processes of frontals not well exposed dorsally and little expanded.	Much as in <i>Dugong</i> , but relatively shorter and more completely exposed (less overlapped by premaxilla).	Widely exposed and broadly expanded on orbital rim.	
Zygomatic process of maxilla intermediate.	Stout, narrow anteroposteriorly.	Thin, expanded anteroposteriorly, tetragonal.	
Frontal region of cranial roof broader than long.	Short as in <i>Dugong</i> , but relatively narrow.	Elongate.	
Temporal crests converging slightly backward on frontal, relatively far apart and nearly parallel on parietals.	Similar but more lyriform, diverging backward on parietals.	Parallel on frontals, relatively close together and lyriform on parietals.	
Occiput relatively narrower, broadly emarginate at ends of exoccipito-supraoccipital sutures.	Broader, not emarginate.	Still broader, sharply emarginate.	
Foramen magnum subtriangular, breadth and height about equal, reaches supraoccipital above.	Transversely elliptical, but not notched and reaching supraoccipital above.	Slightly more transverse than in <i>Hydrodamalis</i> and not reaching supraoccipital.	
Postglenoid region abbreviated making narrow grooves for external auditory meatus between condyles and paroccipital processes.	About as in <i>Dugong</i> .	Considerably more open, broad grooves.	
Angle between lower surfaces of basioccipital and basisphenoid about 230°.	About as in <i>Dugong</i> .	Smaller, about 215°.	
Pterygoid processes deeply grooved behind.	Somewhat more projecting and more widely separated from maxilla.	Stouter palatine portion and very slight grooves.	
Palate sharply elevated above alveolar level, narrow, slight median crest.	Similar but more elongate.	Level with alveolar border, sharp median crest.	
Choanæ intermediate.	Broader than in other genera.	Narrow, slit-like anteriorly.	
Incisive foramen considerably anterior to mesorostral fossa.	As in <i>Dugong</i> .	Beneath anterior end of mesorostral fossa.	
Postzygomatic groove nearly closed by reflected process from zygoma.	More open.	Broad and open.	
Zygomatic process of squamosal much elevated posteriorly, directed forward and downward, tapering anteriorly.	About as in <i>Dugong</i> .	Less elevated, more horizontal, blunt anteriorly.	
Orbit almost without median wall, opening widely into mesorostral fossa.	Orbit with incomplete median wall.	Orbit nearly closed against mesorostral fossa by thin processes of frontals and maxillæ.	
Ascending process of palatine very small, quadrate, poorly exposed.	Relatively much larger and broadly expanded in wall of temporal fossa.	Low but expanded anteroposteriorly.	
Olfactory chamber short, turbinals abbreviated, no ectoturbinals.	Intermediate, but somewhat closer to <i>Trichechus</i> in form and structure.	Elongate. Two ectoturbinals.	
Vomer relatively short, broad anteriorly and separating into two steeply inclined plates.	Short, but slender and single.	Vomer elongate, about reaching anterior end of mesorostral fossa, single, nearly horizontal, little expanded anteriorly.	
Tympanic, periotic, and auditory ossicles relatively small and slender.	Almost identical in structure with <i>Dugong</i> , but relatively larger and stouter.	Similar in structure and stout, as in <i>Hydrodamalis</i> , but with various minor differences, such as the less rugose mastoid, lesser projection of the <i>pars labyrinthiæ</i> beyond the <i>fenestra rotundum</i> , less recurved <i>manubrium mallei</i> , more tumid, less rounded tympanic, the posterior part of tympanic stouter and more distinct.	
MANDIBLE			
Symphysis sharply deflected, deeper than long, anterior surface regularly pitted, nearly vertical.	Symphysis more like that of <i>Trichechus</i> , but still longer and more pointed anteriorly.	Symphysis little deflected, longer than deep. Anterior surface rugose but not regularly pitted, inclined at ca. 45°.	
Horizontal ramus deep.	More like <i>Trichechus</i> , slightly more elongate than either.	Shallower than in <i>Dugong</i> .	
Mental foramen opposite posterior end of symphysis, low.	Mental foramen much farther back.	Mental foramen farther forward than in <i>Dugong</i> and near middle of symphyseal plate.	
Ascending ramus deep and short.	Ascending ramus more like <i>Dugong</i> , slightly longer anteroposteriorly.	Ascending ramus relatively shallow.	
Dental foramen beneath anterior border of coronoid.		Dental foramen farther forward than in <i>Dugong</i> .	
Coronoid process well developed, directed upward.	About as in <i>Dugong</i> but smaller.	Well developed, directed forward.	
Condyle nearly circular; semicircular supracondylar notch.	Broader supracondylar notch.	Condyle transverse; very broad shallow supracondylar notch.	
DENTITION			
One pair of long upper tusks.	No functional incisors.	No functional incisors.	
Three functional cheek teeth in each jaw in adult.	No functional cheek teeth.	Cheek teeth greatly increased in number, continuously replaced from the rear.	
Cheek teeth columnar, no enamel, cement-covered, simple open root.		Cheek teeth low-crowned, two cuspidate cross crests and heels, enameled, no cement, divided closed roots.	
VERTEBRÆ			
Formula usually: C7, D19, L4, S1, Ca 28-29.	C7, D19, L+S+Ca=about 33-35.	C6, D17, L+S+Ca=about 25-27, L2, S1, Ca=22-24.	
Seven dorsals with three rib facets, eight with two, and four with one.	As in <i>Dugong</i> .	Twelve with three, five with two, none with one.	
Neural spines and other processes relatively slender.	Very stout.	Stout, but not quite so much so as in <i>Hydrodamalis</i> .	
Tail long, anterior caudal transverse processes narrower than lumbar; distal caudal processes slightly expanded.	Tail long as in <i>Dugong</i> , and with a slight distal transverse expansion, but anterior caudal transverse processes as wide as or wider than lumbar.	Tail shorter, width evenly tapering from sacral, which is wider than lumbar.	
RIBS [Number and articulations with vertebræ, see above.]			
Slender, with some cancellated bone.	Very stout, all dense bone.	About as in <i>Hydrodamalis</i> .	
STERNUM			
Two bony elements, one rib articulating with anterior part, three with unossified middle part.	Apparently as in <i>Dugong</i> .	One bony element, with which three ribs articulate.	
ANTERIOR GIRDLE AND LIMB			
Scapula: strongly curved, prespinous fossa larger than postspinous, acromion distal, moderately developed, directed slightly backward.	Much as in <i>Dugong</i> , but upper end apparently less well ossified, acromion less distal, larger and more bulky.	Less curved as a whole, postspinous fossa relatively larger, acromion very long and slender and directed backward.	
Humerus: tuberosities diverging at about 90°; greater tuberosity large, expanded crest; broad bicipital groove; strong deltoid crest; wide trochlea, little oblique.	About as in <i>Dugong</i> , but relatively stouter.	Greater tuberosity much reduced, lesser tuberosity large; no bicipital groove; very weak deltoid crest; narrow, strongly oblique trochlea.	
Radius slightly arched forward, long interosseous space, shafts of radius and ulna bowed outward.	Radius and ulna stout, nearly straight, no interosseous space.	Ulna nearly straight, radius strongly arched forward, not bowed outward, short but wide interosseous space.	
Two or three separate carpals.	Unknown.	Five or six separate carpals.	
Fifth metacarpal stout but shorter than third or fourth. (Relative development of other digits and of phalanges, in <i>Dugong</i> and <i>Trichechus</i> highly variable, but comparable in the two genera.)	Unknown.	Fifth metacarpal longer and larger than any other.	
PELVIS			
Pubis absent, ilium long and rod-like, ischium also rod-like, slightly shorter.	About as in <i>Dugong</i> . ¹	Pubis absent, ilium greatly reduced, ischium plate-like, triangular.	

¹Not figured by Brandt, see L. v. Lorenz, Abh. k. k. Reichsanstalt, Wien, XIX, Heft 3; 1904.

9. Radius and ulna not crossed.
10. Carpals more extensively fused.
11. Pelvis further reduced, more rod-like, ischium relatively longer.
12. Seven vertebræ with demifacets and eight with two facets.

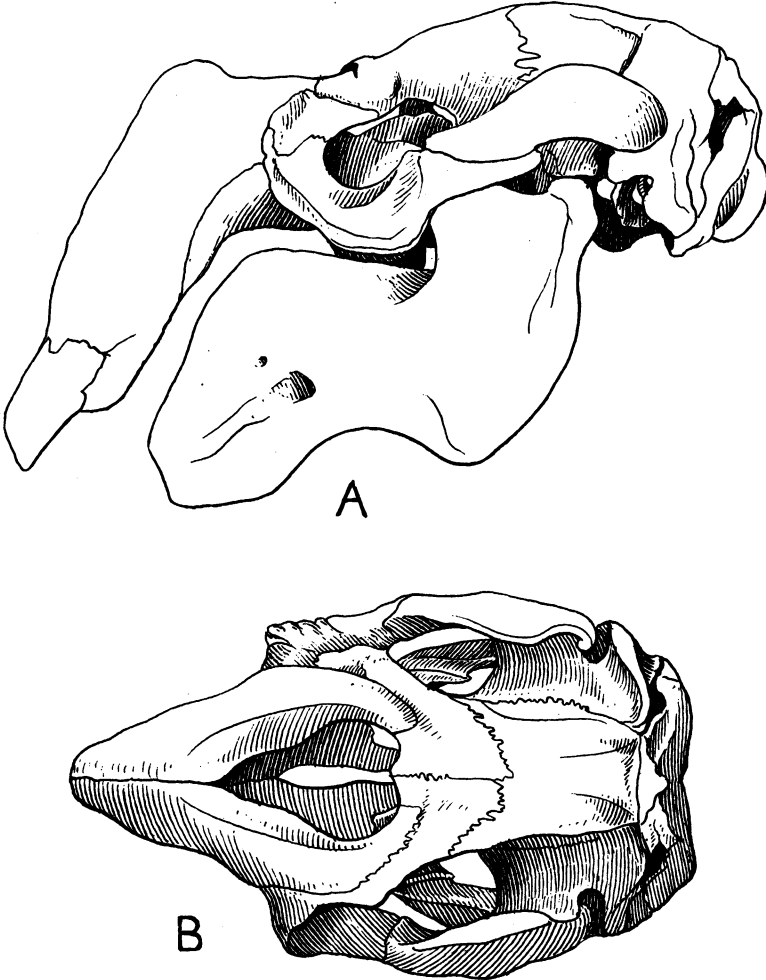


Fig. 20. *Dugong*. Skull. A, Left lateral view. B, Superior view.

These and other differences are the further development of characters progressive in the *Halitheriinae*. With the numerous striking resemblances, they clearly indicate close relationship. In a few char-

acters, however, *Dugong* appears to be specialized in a way not definitely foreshadowed in the Halitheriinae. Among these the most evident are:

1. Cheek teeth degenerate, no enamel, cement-covered, open undivided roots. The halitheriines show reduction but little or no degeneration.
2. Radius slightly more curved, more open interosseous space.
3. Size slightly smaller than in known species of *Felsinotherium*.

None of these characters is of great importance nor does any necessarily exclude divergence from an early species of *Felsinotherium*, the exact ancestry doubtless living in the Indian Ocean or western Pacific and unknown palaeontologically. The principal difficulty, however, lies in the fact that in two characters *Dugong* has been suggested to be actually more primitive than any of the Halitheriinae. These characters are:

1. Rudimentary incisors anterior to upper tusks.
2. Ribs of more normal structure, skeleton generally less massive.

It is on this basis that Abel places the divergence at least in the early Eocene, relying on the so-called law of the irreversibility of evolution. Recent criticisms have shown that this law is not true in its original literal form and that almost any statement of it is open to exception, although in modified form and applied with reasonable judgment as to probability it is a very important phylogenetic principle.

If the anterior incisors were totally lost in the Halitheriinae, then their secondary acquisition in the descendants of that subfamily would be extremely improbable if not impossible. This, however, is not known to be the case. In *Dugong*, they are vestigial and do not normally appear in a macerated young adult skull. There is no assurance that the condition was not the same in the Halitheriinae; in fact, it seems more reasonable to suppose that they did retain vestigial incisors not preserved in the rather limited material available, most of which is of adults and not perfectly preserved in this region. It is impossible to assume that *Dugong* is actually more primitive in this character.

The less massive skeleton and especially the more slender ribs with cancellated bone are not so readily dismissed. In *Eotheroides*, as Abel has shown, the anterior ribs are already dense, the posterior less so. In all post-Eocene forms except *Dugong*, the ribs appear to be entirely massive. Reversion from this swollen but massive condition is not, *a priori*, impossible. It is a developmental character analogous to others in which such apparent reversion has probably occurred.

In the absence of actual annectant fossil types, the question becomes one of personal judgment as to probabilities. On the one hand is the improbability that two lines, separate since at least the Lower Eocene,

would develop with such close parallelism except in this character and one or two others which are inessential and of doubtful significance (as listed above). On the other hand is the improbability that a specialization so firmly fixed since the Eocene should be lost in the interval between about the Miocene or Lower Pliocene and the Recent. I know of no other definitely established case in which lines separate for so long a time have paralleled each other in so many complex and essential characters without a greater distinction arising in other features. In this connection it is also well to remember that all other characters of the ribs themselves are clearly developed or progressively approached by the Halitheriinae.

It seems highly probable that *Dugong* was developed from late Tertiary Halitheriinae structurally similar to the known forms allied to *Metaxytherium* or *Felsinotherium*.

ORIGIN OF *Hydrodamalis*

With his customary brevity, Dollo (1890, p. 421) has stated that *Hydrodamalis* "n'est qu'un *Halicore* [*Dugong*] qui a perdu ses dents." All authorities are agreed that *Hydrodamalis* is related to *Dugong* and sharply distinct from the manatees. There are, however, numerous and important characters, aside from the dentition, which separate *Hydrodamalis* and *Dugong*, and the question is not quite so simple as implied in Dollo's epigram. The degree of separation from *Dugong* and the closer relationship, if any, to the various Tertiary dugongids remain moot questions.

The distinctive characters of *Hydrodamalis* are of two sorts: those which are also found in Tertiary dugongs but are lost or modified in *Dugong* itself, and those which represent divergent specializations. The more important characters in the first category appear to be as follows:

1. Premaxillæ less produced posteriorly, mesorostral fossa longer and narrower.
2. Nasals present.
3. Frontal region more elongate.
4. More projecting and isolated pterygoid processes.
5. Larger and more expanded ascending process of palatine.
6. More elongate olfactory chamber and less degenerate turbinals.
7. Stouter ear bones.
8. Postcranial skeleton, especially ribs, massive, marked pachyostosis.

One does not have to go far back in the Tertiary to find forms from which these characters (with more or less modification consonant with specialization in other respects) could be derived. Forms analogous in degree of evolution with advanced species of *Metaxytherium* could appar-

ently have given rise to *Hydrodamalis* so far as these more or less primitive features are concerned.

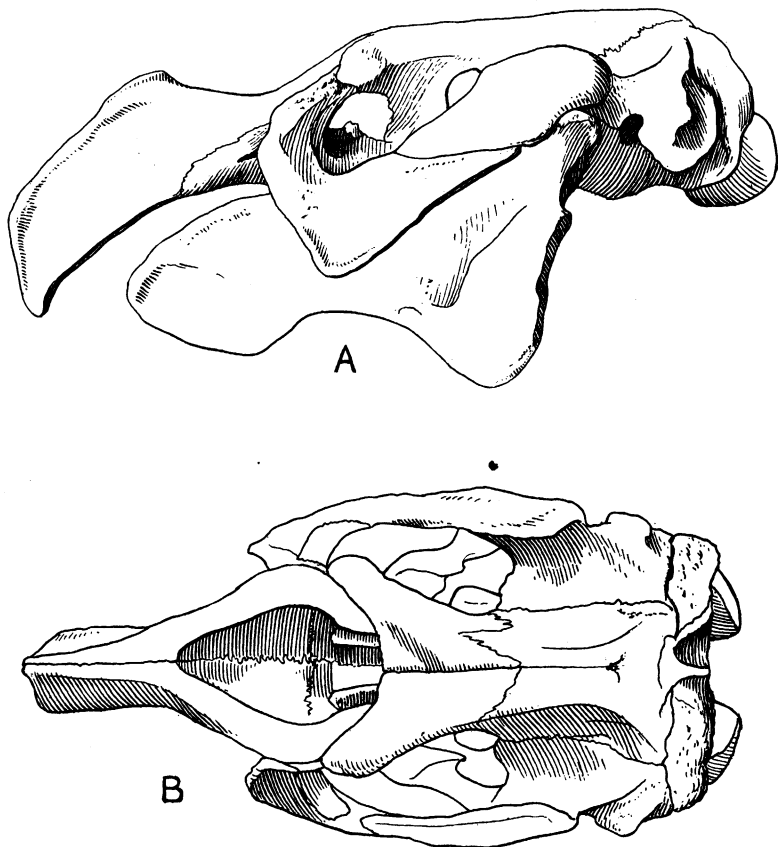


Fig. 21. *Hydrodamalis*. Skull. A, Left lateral view. B, Superior view.

The divergent specializations of *Hydrodamalis* are rather numerous, as suggested by the tabular comparison above. In the skull, the most striking are:

1. Complete absence of functional teeth.
2. Smaller and less deflected rostrum.
3. Olfactory exposure of nasals.
4. Broader and less emarginate occiput, transverse foramen magnum.
5. Broader choanæ.
6. More complete median closure of orbit and anterior part of temporal fossa (perhaps partly primitive).
7. Elongate symphysis and lower jaw in general.

For the most part these and the numerous lesser specializations are directly or indirectly habitus characters, especially related to the loss of teeth and relatively long and low cranium. They seem to raise no special difficulties in deriving *Hydrodamalis* from a Middle or even Upper Tertiary halitheriine.¹

The postcranial skeleton in *Hydrodamalis* is rather similar to that of *Dugong* and still closer to that of the latest halitheriines. The only distinctions seem to be those of proportions and the weighting or development of various processes and crests. Most or all of these can be correlated with the great size of the body of *Hydrodamalis*, both in absolute dimensions and in proportion to the skull.

The true difficulty lies in the absence of a definite foreshadowing of the specializations of *Hydrodamalis* in any known Tertiary dugong. Until such a tendency is more clearly observed, no positive conclusion is possible. The most definite suggestion is that of Depéret and Roman (1920, p. 48). While emphasizing the absence of known intermediates in the Pliocene and Quaternary and expressing much hesitation, they suggest that *Hydrodamalis* is a descendant of *Miosiren*. The only specific evidence given is the rounded form of the cranial roof and the reduction of the molars. No doubt a more complete description of *Miosiren* might reveal other resemblances,² but the evidence seems to be extremely tenuous, too much so to warrant a theory of exact ancestry. Furthermore even the inadequate published descriptions of *Miosiren* reveal some aberrant characters which place *Hydrodamalis* closer to the Halitheriinae than to the Miosireninae. The dental reduction in *Miosiren* is rather in size and form than in number. The cheek teeth are in fact more numerous than in contemporaneous halitheriines or than in *Dugong*, and the simplification of form might better lead to the latter genus (although contradicted by more important osteological peculiarities) than to *Hydrodamalis*. In the number and articulations of the ribs, *Hydrodamalis* agrees with *Dugong* and is readily derivable from the late halitheriines, while *Miosiren* is peculiarly aberrant, having twenty ribs, tubercular and caputular facets distinct on all dorsal vertebræ, and seventeen dorsal

¹Kellogg has supposed the exposure of the nasals to raise such a difficulty. As suggested in a note on a previous page, the nasals of most or all halitheriines are imbedded in the frontals, and the condition in *Hydrodamalis* does not seem to me to be profoundly different.

²The rather diagrammatic outline of skull and skeleton given by Depéret and Roman (1920) is the only illustration known to me aside from that of the upper cheek teeth given by Dollo (1890). Dollo's description of the skeleton is very brief. The only added points of resemblance ascertainable from these publications are the larger size and less deflected, narrower rostrum than in *Felsinotherium*. The size is a superficial resemblance, and the rostrum carries tusks and is hence functionally quite distinct from that of *Hydrodamalis*.

vertebræ with demifacets. In the sternal articulations also (Dollo, 1890, p. 419), *Hydrodamalis* and *Dugong* (and the later halitheriines) agree; *Miosiren* is markedly different. In short, it seems fairly certain that *Hydrodamalis* is closer to the Halitheriinae than to *Miosiren*.

The absence of any definite foreshadowing of *Hydrodamalis* in the Tertiary dugongs is obviously another case of incomplete geologic record and may probably be largely ascribed to its geographic position. Pacific fossil sirenians, except for *Desmostylus*, are almost unknown.

The unique record of *Metaxytherium jordani* Kellogg is of great importance in definitely establishing the presence of the Halitheriinae in the Pacific during Upper Tertiary times, but aside from its large size it does not appear to be definitely closer to *Hydrodamalis* than are other species of *Metaxytherium*.

The conclusion is that *Hydrodamalis* was probably derived from the Halitheriinae in Middle or Later Tertiary time.

ORIGIN OF *Trichechus*

The characters of *Trichechus* might be theoretically divided into the following categories:

A. Normal or primitive mammalian characters not seen in the early Tertiary dugongs. These might tend to suggest that the Sirenia are diphyletic or that the dugongs were derived from the manatees.

B. Characters shared with the Eocene Sirenia but not with the late Tertiary or Recent dugongs. These are primitive characters indicative of common ancestry with the dugongs but opposed to any connection since the Eocene.

C. Characters shared with the later dugongs but not with the earlier forms. These would tend to indicate either convergence or special post-Eocene relationships, depending on their nature, number, and relationship to characters listed under B and D.

D. Characters peculiar to the manatees.

The following are the chief items tentatively assigned to each group:

A. Characters more primitive than in Eocene prorastomids or dugongids,—none observed.

B. Primitive sirenian characters lost in *Dugong*,—

1. Premaxillæ relatively small and little deflected. Smaller than in any dugongids. Perhaps partly secondary.

2. Nasals usually present. As in Pliocene and earlier dugongids.

3. Supraorbital process well developed. As in most early dugongids.

4. Cranium and olfactory chamber (but not rostrum) relatively elongate. Much as in earlier dugongids.

5. Supraoccipital excluded from foramen magnum. As in Miocene and earlier halitheriines.

6. Basioccipital-basisphenoid angle smaller. About as in Oligocene dugongids.

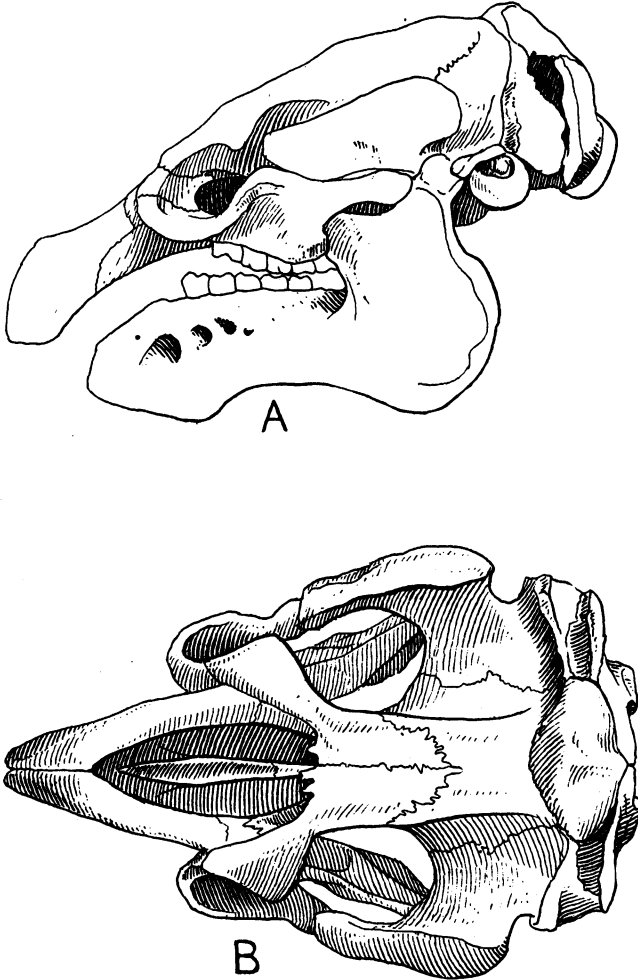


Fig. 22. *Trichechus*. Skull: A, Left lateral view. B, Superior view.

7. Cheek teeth low-crowned, closed and separate roots, enameled crowns of primitive pattern. In these respects about as in earliest dugongids.

8. Mandible relatively slender. In this respect about as in earlier dugongids, but otherwise quite different.

9. Six or seven separate carpals. More primitive than Oligocene dugongids so far as known.

10. Ischium relatively little modified in form. Not derivable from any post-Eocene dugongid condition.

11. Capitulum and tuberculum separate on all ribs. Apparently not true of any dugongids.

Trichechus has many primitive characters, but it is not a primitive genus on the whole, and the important point is rather the association of these characters with others highly and divergently specialized. No post-Eocene dugongid is primitive enough to have given rise to *Trichechus*, and, even apart from other considerations, it is very probable that the two groups diverged in the Eocene.

C. Specializations shared with late Tertiary or Recent dugongids,—

1. Reduction of nasals. About as in Pliocene dugongids.

2. Reduction of the lachrymal.¹

3. Reduction of incisors. As in *Hydrodamalis*.

4. Reduction of vertebral epiphyses. About as in late Tertiary dugongids.

5. Loss of functional hind limbs and reduction of pelvis. About equal in degree to *Dugong*, but very different in character.

6. General pachyostosis of skeleton. Greater than in *Dugong*, but much as in later Tertiary dugongids.

These are all adaptive characters consonant with a similar mode of life and remote similarity of heritage. Taken in conjunction with the specializations, there is no doubt that all are convergent or parallel, not indicative of special affinities. Some of these characters, moreover, are only superficially convergent, the reduction of the incisors and of the pelvis, for instance, taking place in different ways in the two groups.

D. The peculiarities of *Trichechus* are very numerous and have to some extent been detailed above, so that only the most striking are listed here.

1. Rostrum short.

2. Orbit nearly or quite closed and jugal of different form.

3. No functional incisors. (As in *Hydrodamalis*, which has, however, lost the cheek teeth as well.)

4. Cheek teeth greatly increased in number and continuously replaced from the rear.

5. Coronoid process directed forward.

6. Six cervical and seventeen dorsal vertebræ.

7. Acromion long, directed forward.

8. No bicipital groove on humerus, and greater tuberosity much reduced.

9. Reduction of pelvis totally different. Pubis lost, as in dugongs, but ilium also greatly reduced and ischium remaining triangular and plate-like.

¹Gregory, Bull. Amer. Mus. Nat. Hist., XLII, Fig. 143, shows a large lachrymal in *Trichechus*, but this is probably a process of the maxilla. In both *Dugong* and *Trichechus* the lachrymal is a very small bone, easily lost, on the margin of the orbit. Neither genus has a true lachrymal foramen.

These and numerous other peculiarities of *Trichechus*, both in the skeleton and in the soft parts,¹ separate the manatees and the dugongs very sharply.

Weighing these various characters, *Trichechus* retains a few primitive characters already lost in the Upper Eocene *Eosiren*, and it is specialized on a line from which *Eosiren* was already diverging (toward the later dugongs). The manatees cannot be derived from *Eosiren* or any later dugong. On the other hand, they have no characters more primitive than those of *Eotheroides* or of *Prorastomus*, and as those two genera are known, either could be structurally ancestral to *Trichechus*. So far as now possible, the distinctions between *Eotheroides* and *Prorastomus* have been outlined on a previous page. It remains here to inquire into the bearing of the differences on the ancestry of *Trichechus*, which is generally thought to lie nearer the genus *Prorastomus*, although no convincing evidence for this view has been presented.

The first item of this evidence is geographical and has been tacitly recognized rather than categorically stated: that is, the geographic position of *Eotheroides* near the Tertiary and recent home of the dugongs, and that of *Prorastomus* near the present range of the manatees. At present, in so far as geographic distinction has any bearing on the question at all, it is definitely opposed to close genetic relationship between *Prorastomus* and *Trichechus*. The known Tertiary successors of *Prorastomus* in the West Indies and along the shores of North America were not manatees but dugongs. *Trichechus* does not at present appear as the result of continuous antillean evolution but as an invader in the Pleistocene of unknown geographic origin.

The great majority of the features in which *Prorastomus* resembles *Trichechus* are shared with *Eotheroides*. These are quite clearly characters primitive for the Sirenia as a whole. The only circumstance which would make them even suggestive of special relationship between *Prorastomus* and *Trichechus* would be a definitely more recent age for *Prorastomus* than for *Eotheroides*. The exact age of *Prorastomus* appears to be in doubt, but later age than Middle Eocene is improbable.

The great majority of the characters in which *Prorastomus* differs from *Eotheroides* are not points of resemblance to *Trichechus*. On the contrary, they tend for the most part also to distinguish *Prorastomus* and *Trichechus*. Possible exceptions are:

1. The possibly shorter rostrum and relatively large cranium in *Prorastomus*. The rostrum is inadequately known in *Eotheroides*, and this supposed distinction may

¹See especially Weber, 1928, for a résumé of the soft anatomy in the two groups.

not be wholly valid. It does seem to give a slightly *Trichechus*-like aspect to the Jamaican skull, but it is correlated with other features such as the development of the incisors and of the cheek teeth, very different in *Prorastomus* and *Trichechus*. Furthermore, if real, it is a simple difference in proportions which might in any event be considerably modified between the Eocene and the Holocene.

2. The slightly smaller and perhaps more nearly closed orbit. This also may be illusory, and even if real is another simple modification in proportions. The relative size of the orbit in *Trichechus* is very little less than in *Dugong*. That of *Prorastomus* is very little, if at all, less than in *Eotheroides*. The posterior border of the orbit is not completely known in either genus.

A really thorough restudy of *Prorastomus* might reveal some more deep-seated resemblance to *Trichechus* which was at the same time a distinction from *Eotheroides*, but at present none is ascertainable.

The only possible conclusion on the evidence in hand seems to be that *Prorastomus* and *Eotheroides* are slightly divergent members of the most primitive known sirenian group, that they stand near the structural ancestry of all of the Sirenia, but that there is no clear evidence tending to link either one of them with the Trichechidæ rather than with the Dugongidæ. That either one is directly ancestral to any known later forms is, of course, rather improbable. *Protosiren* is another slightly divergent member of the same structurally ancestral sirenian group, again with no special resemblance to *Trichechus*.

No fossil manatees older than the Pleistocene are yet known,¹ and the absence of this ancestry makes further speculation futile. The dugongs and manatees probably separated in the Lower or Middle Eocene, and the prorastomids, as here understood, probably represent their common ancestry in a general way.

AFFINITIES OF THE SIRENIA

The present materials cast no new light on the affinities of the Sirenia as a whole, but a historical résumé may be convenient in this brief general review. A very complete digest of knowledge and opinions up to 1868 is given in Brandt's remarkable *Symbolæ Sirenologicæ*, from which the following sketch is chiefly abstracted so far as concerns this period.

The name "sea cow" and the conception involved may date back to ancient Assyria. Confusion with the Cetacea, current until about thirty years ago, and with the fishes, obsolete for a much longer time, may be equally ancient. In the sixteenth and seventeenth centuries, the numerous theories included supposed relationships with the fishes, the cetaceans, walruses and seals, amphibious fissipeds, and amphibious

¹*Ribodon* is said to be Pliocene, but is probably Pleistocene, and would cast little or no light on the matter in any event.

ungulates¹—the familiar classification by habit, leading to collocations now considered mutually exclusive but not then in apparent conflict. With the exception of supposed piscine affinities, each of these views was variously emphasized by early writers of the modern period. Linnæus at first placed them among the Cetacea, later associating them with the walrus in the neighborhood of the elephants and the edentates. The conception of relationship with the Cetacea continued to be most commonly held, however, as by Buffon, Cuvier, Storr, Daubenton, and many others—usually without any clear distinction from the walruses or the seals. Illiger, to whom we owe the name *Sirenia*, clearly separated them from all other forms, but placed them in the same order as the Cetacea. A distinct, but not wholly opposite, view emphasized relationship to *Ornithorhynchus* or the edentates or both, as by Shaw and by Blumenbach. Blainville, in 1816, did not originate but did most clearly state and emphasize the belief, to which most recent work has returned, that the *Sirenia* are distinct from other aquatic or amphibious mammals, whether monotremes, cetaceans, carnivores, rodents or ungulates, but are closest to the elephants.

The chief gains of the period from about 1820 to 1850 were the weeding out of the most obviously extraneous forms which had been confused with the sirenians and the reduction of well supported theories of relationship to two or three. Belief in Cetacean affinities was almost universal, although a few supported Blainville, notably Owen in his earlier work (1838). About 1845 (Bonaparte, Owen, Gravenhorst and others) the two most widely accepted theories were merged: the *Sirenia* were supposed to be transitional between the Cetacea and the Proboscidea. This apostasy did not leave Blainville's more nearly correct (as we believe) opinion wholly without advocates, however, for Wagner, Eschricht, and others continued to uphold it. Owen eventually (1868) returned to the more or less pure Cetacean school of thought, which continued strong throughout the nineteenth century, Cope (as late as 1898) being one of its most recent adherents.

Brandt's own conclusion was as modern in spirit as was possible with the limited palæontological material then available (1868): "... *Sirenia* Pachydermatum Aquatiliū, Cetaceorum formam æmulantium, titulo designari possent."

Throughout the latter part of the last century, the two views already so widespread continued to be held, that is, that the sirenians were

¹After reviewing this confusing group, one may be grateful for the comprehensive opinion of Th. Hæuser (1731) as quoted by Brandt: "Non reptile est, nec piscis, nec cete, nec amphibion, nec e phocæarum genere et tamen hæc omnia. Nec bovem dicas, nec porcum, nec equum, nec hominem, nec monstrum et tamen hæc omnia."

related to the cetaceans, or that they were related to the ungulates and particularly to the proboscideans. That the group is a very distinctive one was, of course, recognized, and some authorities did not go beyond this point.

Lepsius, in the most detailed study of fossil Sirenia published in the nineteenth century (on *Halitherium schinzi*, 1881), reached the important conclusion that "die Sirenen in keiner Weise mit den Cetaceen, dagegen offenbar mit den Ungulaten eine nähere Verwandtschaft zeigen." He did not support special relationship to the Proboscidea, comparing them rather with the tapirs, but emphasizing the supposed fact that this was due rather to the archaic character of the tapirs than to especial affinity with this one group of ungulates. He placed the Sirenia in the Ungulata as *Ungulata natantia*, opposed to *Ungulata terrestria*.

The changes in viewpoint since that time have been chiefly due to the new or better knowledge of early sirenians and proboscideans from Egypt. The material described by him led Andrews (1906) to advocate common origin for the Sirenia and the Proboscidea. Gregory (1910) agreed that the evidence for this view is strong, and Abel's researches on the Eocene and Miocene Sirenia have led him to support the same view (e.g., 1919, p. 832). This work, and study of the anatomy of the recent animals (references and résumé in Weber, 1928), have definitely excluded the possibility of close affinity with the Cetacea. Osborn (1909) has expressed a belief that "*Mæritherium* is an offshoot of the Proboscideo-Sirenian stock, with slightly nearer kinship to the elephants than to the sirenians." The most detailed study of this point is that of Matsumoto (1923) who gives an elaborate tabulation of the characters of *Mæritherium*. He concludes that *Mæritherium* is definitely in the proboscidean lineage, and well removed from the sirenians, but that the proboscideans, sirenians, and hyracoids are of common ancestry, and that "both the sirenians and proboscideans might have descended from unknown ancestors which stand even before the hyracoids so far as known." Not all of the items of evidence adduced by Matsumoto appear to be equally important or valid, from the standpoint of the Sirenia, but his general conclusion seems fairly to represent the present state of knowledge.

One of the greatest desiderata in mammalian research at present is a wider, yet detailed, study of relationships of the various "subungulates" and "protoungulates." The available data are perhaps inadequate, but the known material has not all been thoroughly studied and correlated. Such a study should cast further light on the sirenians. The

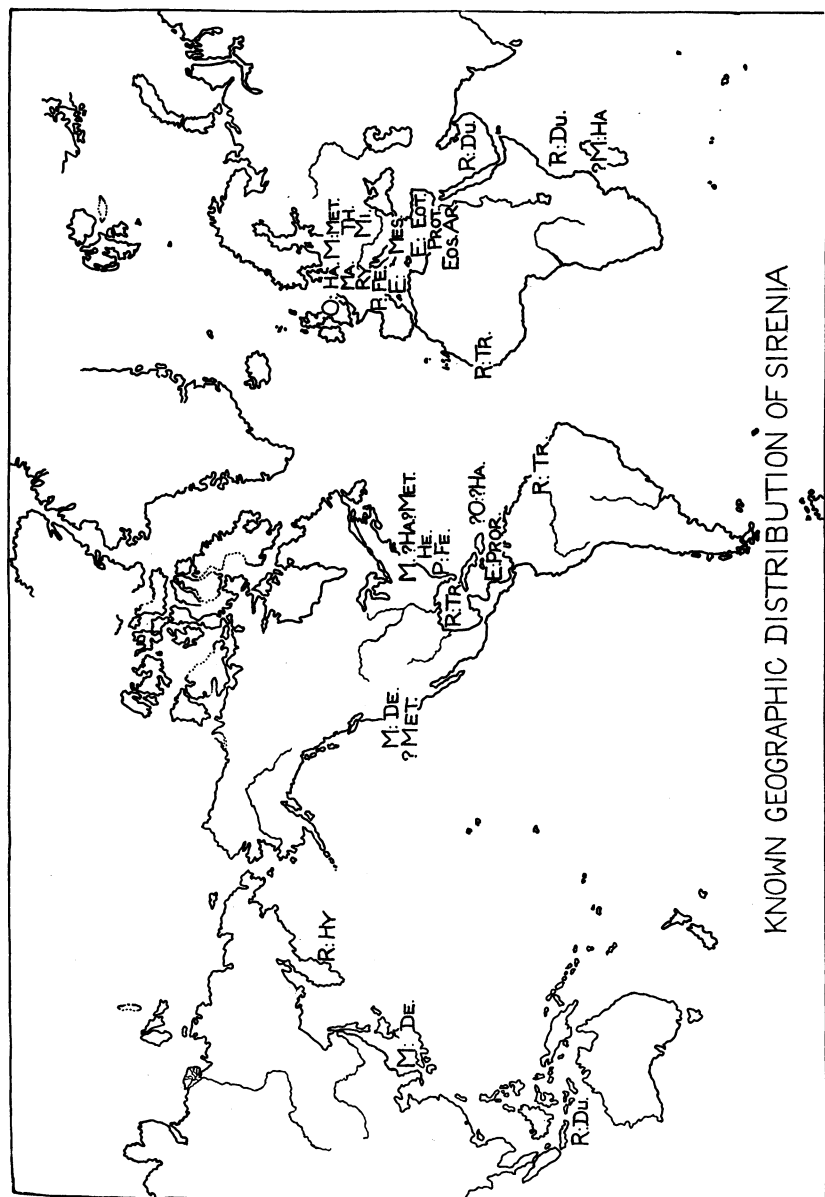


Fig. 23. Known distribution of Sirenia.

Ar.	Archæosiren	Eos.	Eosiren	He.	Hesperosiren	Mes.	Mesosiren	P.	Pliocene	Ry.	Rytiodus
De.	Desmostylus	Eot.	Eotheroides	Hy.	Hydrodamalis	Met.	Metazitherium	Prot.	Protosirenia	Th.	Thalassosiren
Du.	Dugong	Fe.	Felsinotherium	M.	Miocene	Mi.	Miosiren	R.	Recent	Tr.	Trichechus
E.	Eocene	Ha.	Halitherium	Ma.	Manantherium	O.	Oligocene				

knowledge so far won definitely places them in this rather general and confused subungulate complex.

DISTRIBUTION OF THE SIRENIA

The ranges of the three Recent genera do not at all overlap. The manatees occur on the tropical and subtropical shores and rivers of both sides of the Atlantic. The dugongs occur on the tropical and subtropical shores of the Indian Ocean and adjacent seas, to the western shores of the Pacific. Steller's sea cow occurred in the North Pacific. There are no sirenians on the south or east Pacific, Arctic, or Antarctic coasts. Fossil manatees are known only from the Pleistocene, when their distribution, so far as known, was as at present, although slightly more extensive on the western Atlantic coasts. Fossil dugongids occur in great numbers from the Eocene to Pliocene in the Mediterranean region and basins tributary to the eastern North Atlantic, from Eocene to Pliocene along the western North Atlantic coasts and Caribbean, in the Miocene on the northeast Pacific coast, and in the Miocene (probably) of the western Indian Ocean (Madagascar).

Until recently the fossil Sirenia of North America were so inadequately known that it was possible to suppose them all manatees, on zoögeographic grounds. An apparently logical but, as is now seen, quite erroneous theory was developed on this basis by Abel and others. It was supposed that the Sirenia originated in the Mediterranean, that one branch migrated to the Atlantic and developed into the manatees, that another stock developed in the Mediterranean area into the numerous types of dugongids, that a branch of this latter stock emigrated to the Red Sea and Indian Ocean and eventually entered the Pacific, giving rise to *Dugong* itself and to *Hydrodamalis*. The origin of the various groups was thus geographic, along much the same lines as the recent distribution, with the Mediterranean as the center of evolution.

Even *Halitherium antillense* was relegated to the trichechids for the sake of this theory (Abel, 1919, p. 839). With the addition of "*Metaxytherium*" *floridanum*, *Metaxytherium jordanii*, and, more recently, the South Carolina *Halitherium* to the New World list, it became obvious that the history has not been so clear and simple. With these facts before him, Abel has modified his views (1928, p. 502):

"Soweit wir aus den bisher bekannten Überresten ein Urteil gewinnen können, ist das Mittelmeergebiet das Ursprungsgebiet der Sirenen gewesen. Von hier haben sie schon im Eocän, wie der Fund des Schädels von *Prorastomus sirenoides* Owen auf Jamaika beweist, den Weg bis nach Westindien gefunden und vielleicht haben auch noch in späterem Tertiär Untiefen zwischen Europa und Westindien bestanden, die es

Angehörigen des Halitheriinenstammes ermöglicht haben, sich vom Mittelmeergebiet aus bis nach der atlantischen Küste Nord-Amerikas, ja bis nach Kalifornien zu verbreiten. . . . Da der Golf von Mexiko erst in späterer Zeit (Mittelpliocän) gegen den Pazifik abgeschlossen wurde, bis zu dieser Zeit aber eine ungehinderte Verbindung zwischen der atlantischen und pazifischen Küste bestand ist die Entdeckung von *Metaxytherium* an der pazifischen Küste zu erwarten gewesen."

Like the now discredited theory of a Mediterranean sequence of dugongs and a Caribbean sequence of manatees, this view rests largely on negative evidence, and furthermore it does not offer the only or even (I believe) the most probable explanation of such positive facts as are available, especially as augmented by the discoveries here published. The following statements are pertinent:

1. The *Sirenia* originated prior to the Middle Eocene.
2. The ancestry of the *Sirenia* is unknown. This ancestry was probably subungulate in a general sense rather than specifically proboscidean. The subungulates in this sense probably had a very wide distribution. The Proboscidea probably originated in Africa, but this is not certain.
3. Primitive forms, some definitely dugongid, others possibly indifferent between dugongids and trichechids, occur in the Mediterranean region.
4. A primitive sirenian also occurs in Jamaica and so far as present knowledge goes is equally indifferent between the dugongids and trichechids.
5. The known post-Eocene Tertiary *Sirenia* of Europe and of eastern North America are definitely dugongids. The succession is similar in the two regions. There is no good evidence that it was more directly continuous in one than in the other.
6. Fossil sirenians are unknown on the Pacific coasts except for desmostylids and a single typical Middle Tertiary dugongid in California. South Atlantic Tertiary sirenians are unknown. Indian Ocean Tertiary sirenians are unknown except for a single typical Middle Tertiary dugongid in Madagascar. This absence of record is in no way proof or even suggestion of the actual absence of Tertiary *Sirenia* in these regions.
7. Recent *Sirenia* are most characteristic of just those regions (with the small exception of Florida) in which fossil *Sirenia* are nearly or quite unknown, and their differentiation and distribution suggest long residence in these areas.

The theory that Europe or the Mediterranean region was the place of origin and center of dispersal of the *Sirenia* now has little firmer basis than the obviously irrelevant facts that fossil sirenians happen to be rather abundantly preserved there and that the unusually intensive investigation there of marine and estuarine deposits has revealed a great many of them. There is equally good evidence that the American mediterranean sea was the center of dispersal. Probably neither hypothesis is the correct, or at least the complete, explanation.

In spite of the large literature of the subject, the true place of origin is not certainly known for even one mammalian order. The sirenians are no exception to this generalization. The chief center of evolution and dispersal is known or suspected with reasonable assurance for a number of

mammalian groups, such as the Hyracoidea, Toxodonta, Equoidea, or Phalangeroidea, but the Sirenia cannot yet be numbered with these.

One might be tempted to say that the dugongids were of general North Atlantic dispersal, and this would be much more reasonable than specific Mediterranean or Caribbean evolution, but they did occur in the Pacific and Indian Oceans, and the North Atlantic stocks could have been derived from these. The Sirenia are not pelagic and they do not habitually cross large bodies of deep water, but given favorable currents and long periods of time, their ability to do so cannot be questioned. It seems, for instance, highly improbable that the manatees owe their distribution on both sides of the Atlantic to shallow water or coastline migration. From this possibility of wide and geologically rapid migration and from the known ancient and recent distribution, it is reasonable to suppose that, whatever the place of origin, the dugongids have been of world-wide distribution and that their geographic history is one of very complex migrations in numerous directions in at least the North Atlantic, Indian, and Pacific Oceans.

As positive facts slowly accumulate, one negative fact becomes increasingly curious and impressive: the absence of knowledge of Tertiary manatees. They are now Atlantic forms, and, from the very close similarity of the two geographic groups, it is clear that migration has occurred in relatively recent geologic times (probably Pliocene or Pleistocene) between South America and Africa. The direction of this migration is unknown, but the direction of ocean currents and the nature of recent distribution make east to west, Africa to South America, migration seem definitely more probable.

Supposing provisionally that the absence of manatees among the fairly abundant North Atlantic sirenian materials should prove to be due to their real absence, it would be a reasonable although purely speculative hypothesis that the manatees developed in Africa as primarily fluviatile forms while the dugongs became more definitely marine and spread over the world, that the manatees also came to venture into coastal waters, that they were carried across the Atlantic by currents and successfully colonized South America by Middle or Late Pliocene times, that they then spread along the tropical shores of the Americas, and that dugongs became extinct in the Atlantic more or less contemporaneously with the spread of manatees there.

GENUS	Eocene			Oligocene			Miocene			Pliocene			Pleistocene	Recent
	L	M	U	L	M	U	L	M	U	L	M	U		
<i>Prorastomus</i>														
<i>Eotheroides</i>		— ?												
<i>Prolostiren</i>														
<i>Eosiren</i>														
<i>Archaeosiren</i>														
<i>Mesosiren</i>														
<i>Holitherium</i>														
<i>Manatherium</i>														
<i>Rytiodus</i>														
<i>Metaxytherium</i>														
<i>Thalattosiren</i>														
<i>Hesperosiren</i>														
<i>Prohalicore</i>														
<i>Miosiren</i>														
<i>Felsinotherium</i>														
<i>Dugong</i>														
<i>Hydrodamalis</i>														
<i>Trichechus</i>														

Geologic Distribution of the Principal Genera of Sirenia

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