announcements, and other communications are solicited from all readers. Information of general interest will be included in future issues.

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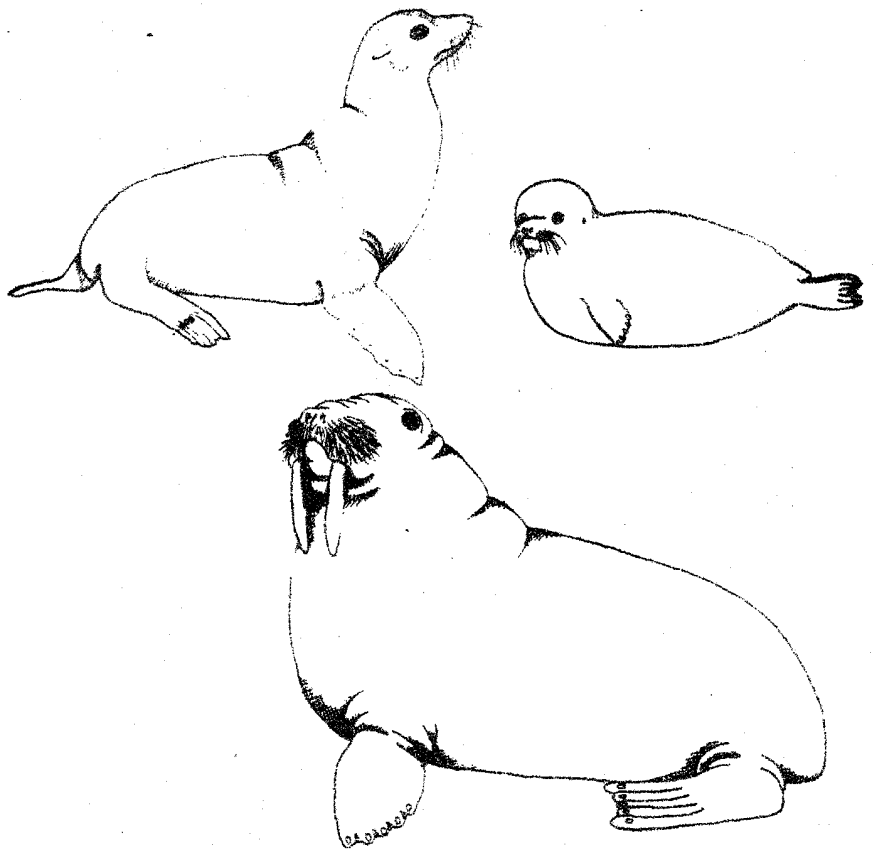

THE FLORIDA STATE MUSEUM

SEALS AND WALRUSES OF FLORIDA

Clayton E. Ray [1]

All marine mammals are descended from terrestrial ancestors that reinvaded the marine environment. They, of course, are warm blooded, nurse their young, breathe air, and have hair. In addition, depending on the group, they do have a greater or lesser overlay of varied aquatic adaptations, including fusiform body, modifications for locomotion in water, and specialized pelage and/or blubber for insulation. The marine mammals include the Cetacea (whales and porpoises); the Sirenia (manatees, dugongs, Steller sea cow; see the *PLASTER JACKET*, Nos. 15 and 25, and *BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES* Vol. 20[4]; the Desmostylia, an extinct order, probably vegetarian hippo-like mammals of Late Oligocene to Early Pliocene age; the sea otter (*Enhydra lutris*), the marine otter (*Lutra felina*), the recently extinct sea mink (*Mustela macrodon*), and the polar bear (*Ursus maritimus*), among fissiped Carnivora; and the Pinnipedia, the subject of this communication.

THE PINNIPEDIA

The pinnipeds, named for their fin- or feather-like feet, include the living seals, sea lions, fur seals, and walruses, and comprise some 34 species, plus an unknown number of extinct relatives. They have been regarded at times as a separate order of mammals, as a suborder coordinate in rank with the land carnivores (fissipeds), and now more and more generally as an artificial group representing at least two independent

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The illustrations in this issue are by Leah Ray.

invasions of the marine environment by land carnivores: the phocoids ("true" seals, "earless" seals, or wrigglers) on the one side, and the otarioids (sea lions, "eared" seals, or walkers, including walruses) on the other. The weight of evidence now suggests that the phocoids evolved in or near the North Atlantic from an otter-like mustelid at or near the beginning of Miocene time, perhaps 18-23 million years ago; the otarioids in the North Pacific from a bear-like amphicynodontid in Late Oligocene time, perhaps 22-25 million years ago. Irrespective of evolutionary conclusions, the name pinniped undoubtedly will continue to be useful to denote informally a group of marine mammals more similar to one another than any is to any other marine mammal.

Phocoids are characterized by reduction or absence of the external ear flap (hence "earless"), by inability to rotate the hind limbs forward in a quadrupedal stance (hence wrigglers), by sausage-shaped body with scarcely discernible neck, short limbs, and internal testes in the male; otarioids by retention of the external ear flap (hence "eared" seals), by ability to rotate the hind limbs forward in a quadrupedal stance (hence walkers), by more typically mammalian body form, with long, flexible neck, long limbs capable of support in terrestrial locomotion, and scrotal testes. Though generally similar to other otarioids, the walrus is divergent in lacking the external ear flap and in having internal testes.

THE PHOCIDAE, "true seals"

After their first appearance some 15 million years ago in the fossil record of the North Atlantic, the true seals dispersed through much of the World Ocean. At their first recognizable appearance they were already highly adapted marine mammals differentiated into the two living subfamilies: the phocines, which are the strictly northern hemisphere, cold-water group, including the living harbor, ringed, Baikal, Caspian, harp, ribbon, bearded, hooded, and gray seals; the mona-

chines, which include the monk seals (the only modern warm-water pinnipeds), of which there are three species, one in the Mediterranean, Black Sea, and eastern Atlantic, one in the Caribbean, and one in Hawaii; plus the the Antarctic crabeater, Ross, leopard, and Weddell seals, and the elephant seals, with one species circum-Antarctic and one eastern North Pacific.

The two subfamilies shared the North Atlantic in Miocene and at least Early Pliocene time, but sometime after that (probably less than 3 1/2 million years ago), perhaps through differing response to deteriorating climate, their evolution and distribution diverged. The phocines seem to have experienced their great modernization and radiation late in geologic time by adapting to cold, highly seasonal climates, and by invading the North Pacific via an Arctic route, to become the dominant phocids of the northern hemisphere. The monachines, by contrast, seem to have responded to deteriorating climates by retaining their generally conservative morphology and receding equatorward following their ancestral habitats. At some point, however, their predilection for warm waters gave them, but not phocines, access to the Middle American seaway and the Pacific Ocean and enabled them to invade the southern hemisphere (a rare event in pinniped history), and thus ironically to give rise to the most southerly of all mammals, the Weddell seal.

THE OTARIIDAE, fur seals and sea lions

The otariids and other otarioid families, including the extinct enaliarctids and desmatophocids, originated in the North Pacific. Their best fossil record is on the west coast of North America in Mexico, California, Oregon, and Washington, but enough specimens, mostly fragments, are known from Japan to indicate that distribution generally must have rimmed the North Pacific, just as in modern times.

At some point, probably in the Late Pliocene, the fur seals and/or sea lions coasted down the Pacific side of Middle America, probably with cooling seas, to invade the

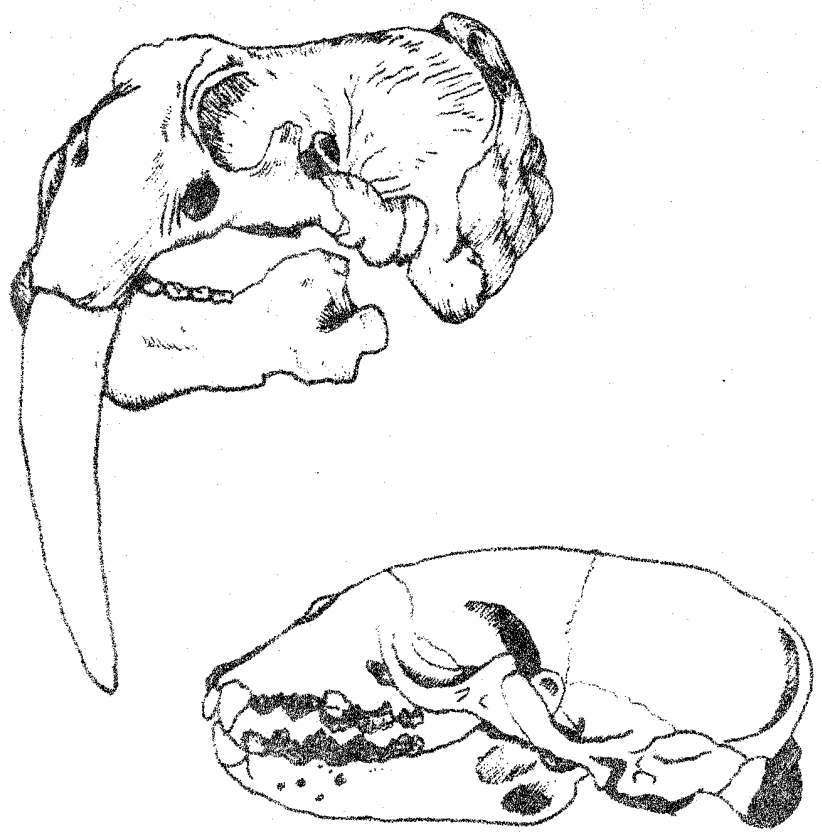

FIGURE 1. Skulls and jaws in left lateral aspect of modern walrus, *Odobenus rosmarus* (upper), and modern Caribbean monk seal, *Monachus tropicalis* (lower). Not to scale; the walrus skull would be approximately 14 inches long and the monk seal approximately 9 inches.

The bone is very dense and heavy (in part pachyostotic) in the walrus skull and jaws, reminiscent of that in sirenians. The postcanine teeth of the monk seal are characterized by highly wrinkled enamel.

southern hemisphere. They apparently were excluded by a land or ecological barrier from entering the Caribbean and thence the Atlantic Ocean. They have occupied the South Atlantic only marginally and only from the south; there is no evidence of their ever having occupied the North Atlantic at any time.

THE ODOBENIDAE, walruses

The walrus family had a rich radiation in the North Pacific during Miocene and Pliocene time, where they apparently occupied many ecological niches now occupied by otariids, judging from their sea lion-like morphology and varied species. The living walrus and its immediate ancestors (odobenine subfamily) are highly atypical of odobenids as a whole in that they are strongly tied to cold water and have enormously enlarged upper canines.

It was assumed until recently that the ancestral walruses entered the North Atlantic via a cold-water Arctic route. The fossil record (especially material from Cedros Island and Baja California) now indicates a southern route via the Middle American seaway, perhaps in earliest Pliocene time (4 1/2-5 million years ago), resulting in distribution to the coastal waters of the southeastern United States, and perhaps following the ancestral Gulf Stream, to northwestern Europe. The modern walrus presumably evolved its northerly adaptations in response to deteriorating climate and thus reinvaded the North Pacific by an Arctic route, essentially completing a counterclockwise circumnavigation of North America.

THE FLORIDA CONNECTION

Now, one well might ask, what does all of this have to do with Florida? Pinnipeds are nonexistent in the present native mammalian fauna of Florida, and in historic times were represented by but a single species regularly inhabiting Floridian waters. Odobenids and otariids are unknown in Florida in Recent times, except for the occasional conspicuous presence of escaped, liberated, or free-swimming trained California sea lions. The only Recent phocid native to Florida is the Caribbean monk seal, now unfortunately almost certainly extinct, but well known in and near Florida from living animals in historic time, and from archeological and Pleistocene fossil records (reviewed recently by then University of Florida graduate student, Stephen Cumbaa).

The pinniped presence is almost equally inconspicuous in the known Tertiary fossil record of Florida. However, enough is known to demonstrate their presence and their potential importance in understanding major features of pinniped evolution and dispersal.

The only phocid specimens of probably pre-Pleistocene age, known to me are a single toe bone in the old collections at Harvard, a partial jaw in the FSM, an isolated tooth collected by Melvin McClean and donated to the Florida State Museum, and a tooth in the collection of Frank Garcia (all from the Bone Valley area); there is also a toe bone collected by Mr. and Mrs. Bill Brayfield from a spoil near El Jobean, Charlotte County.

The first records of fossil odobenids in Florida were published by me in 1960: one from near Sarasota and another from the St. Marys River on the Florida-Georgia border. Since then, at least 15 specimens have been found at scattered localities from Jacksonville to Charlotte Harbor. The collectors and/or donors of specimens to science include Bill and Leila Brayfield, Roy and Helen Burgess, Hazel Cooper, Frank Garcia, Clifford Jeremiah, Bill McDonald, Marian Murray, Mrs. Charles Stapleford, and Margaret Thomas. [It should perhaps be noted here that not a single specimen of fossil pinniped has been found in Florida by a paid professional paleontologist, a reflection one may hope not of malingering on our part, but of the indispensable role of the serious "amateur" at the frontiers of paleontological investigation.

The first records for Florida were thought at the time to be Pleistocene in age, but subsequent discoveries in Florida and elsewhere and advances in stratigraphy and correlation strongly indicate an older Pliocene age for most, if not all, occurrences of fossil walruses in Florida. Interpretation is complicated, however, by the uncertainty of taxonomic discrimination between some fragmentary walrus tusks and by the certainty that modern walruses ranged much farther south during Late Pleistocene glacial ages than during historic time. In the southeastern United States, including the east coast of northern Florida, it is not impossible that extinct Late Tertiary odobenines could occur in the same spoil heaps with Late Pleistocene *Odobenus rosmarus*. Similarly, additional Pleistocene occurrences of northern phocines in the southeastern states are possible and would be of considerable interest (see Ray *et al.* 1968).

The Floridian fossil walruses already contribute significantly to the growing confidence in the probability of Late Tertiary odobenid invasion of the North Atlantic via a warm-water Middle American route, quite in contrast to the traditionally assumed cold-water Arctic route. However, we need to know much more. The geologic occurrence of all specimens is inadequately known--new material collected in place with stratigraphic data or specimens from spoil with adherent matrix would be of great use. All walrus specimens to date are tusks, which afford only limited clues as to relationships. There can be no doubt that other, less durable or less conspicuous hard parts are there to be found or have been found but not yet recognized. Until additional parts are available in some numbers, including parts comparable to type specimens of named fossil walruses, it will not be possible to determine how many species existed in the Atlantic, what their distribution was, how to distinguish between males and females, how they relate to their Pacific relatives, or even which of several possible names may be applied correctly to them.

For the phocids, the state of knowledge is even more primitive, and conversely, the information potential

perhaps even more extraordinary. Discovery of a single well-preserved, well documented specimen could resolve presently unanswerable questions or pose presently undefinable ones. If the Hawaiian monk seal is in fact the most primitive living phocid, how different is it from its Caribbean forebear? How many kinds of monachines inhabited the Caribbean region in the Late Tertiary? Did one stock pass through the Middle American seaway, later to differentiate into the Hawaiian monk seal, elephant seals, and Antarctic monachines, or were these lineages already recognizable in the Caribbean region?

The exceedingly important role of Florida in understanding the historical zoogeography of terrestrial fauna in North and South America has been clearly demonstrated recently by Dave Webb (1976, Mammalian faunal dynamics of the great American interchange. Paleobiology, Vol. 2(3), pp. 220-234). Florida's role in terrestrial zoogeography may be characterized as that of one endpoint in the interchange of fauna between North and South America. For marine mammals, notably for monachine and odobenine pinnipeds, Florida may be characterized not so much as a destination but as a crossroads of global significance between Caribbean and North Atlantic, Atlanto-Caribbean and Pacific, low and high latitudes, and northern and southern hemispheres.

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FIGURE 2. Tooth of sperm whale (left) and tusk of walrus (right) in longitudinal (upper) and transverse (lower) sections. Highly variable in size, but illustrations somewhat smaller than typical natural size.

In both teeth the outermost layer is composed of cementum, which may appear structureless or thinly layered in fossils depending on preservation. The thickness of cementum varies greatly in teeth of sperm whales, less so in walruses. In both cases, it may be wholly or partly exfoliated and lost from fossils.

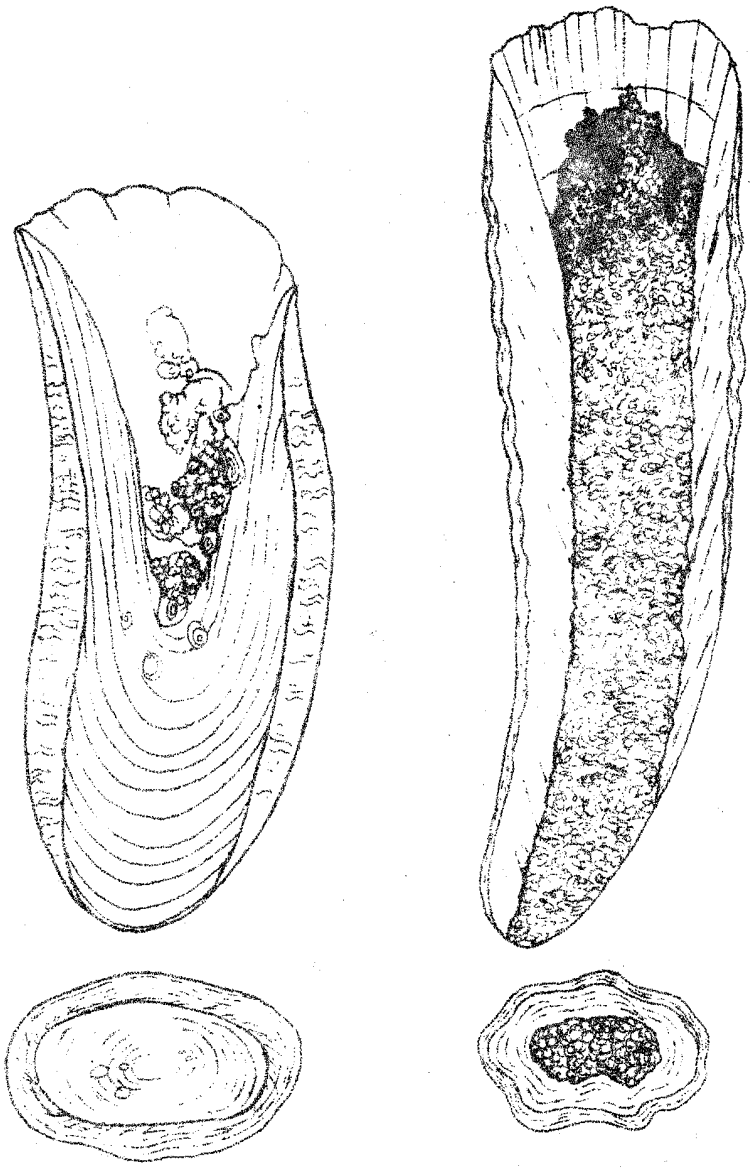
Not represented in the figures is enamel, which may be present thinly and transitorially on the tip of very young walrus tusks, and is variably developed in fossil cetacean teeth, in some persisting in maturity.

The bulk of the tooth in each case is composed of lamellar dentine, laid down in successive layers in the pulp cavity of the tooth, resulting in a structure comparable to a stack of conical paper cups.

Both the cementum and the lamellar dentine are laid down in annual pulses analogous to tree rings, resulting in the possibility of reasonably accurate age determination.

Walrus tusks are characterized by a well organized discrete, columnar core of globular osteodentine extending the full length of the tusk, exposed on the worn tip in all but the youngest tusks, and exhibiting on worn, broken, or polished surfaces the appearance of tightly packed pearls, grit, or finely crackled china.

Globular osteodentine is known in many groups of mammals, including sperm whales, in which it varies from absent altogether to abundantly present in irregularly distributed clumps within the lamellar dentine or loose within the pulp cavity. Although it has been reported in many groups, including humans, it is especially prevalent in tusk-like teeth. In the shovel-tusked mastodonts it forms a discrete core within the tusk, but differs from the globular osteodentine of



walruses in being coarser in texture and in being somewhat organized linearly into irregular intertwined ropy masses.

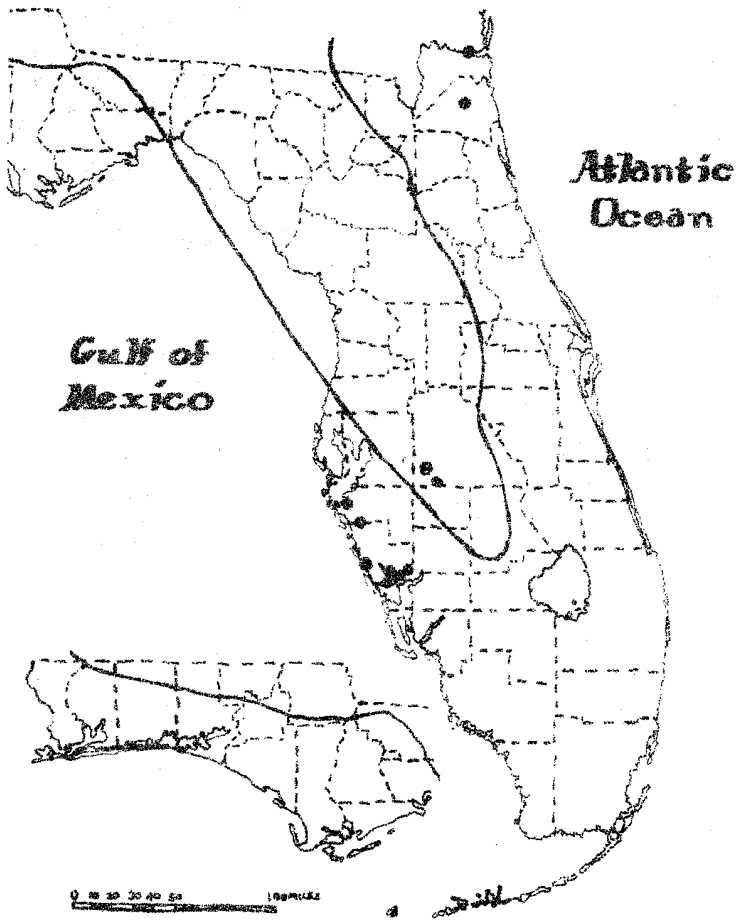


FIGURE 3. Localities from which fossil walrus remains have been recovered in Florida, shown in relation to the Choctawhatchee shoreline. All finds are thought to be pre-Pleistocene in age, with the possible exception of the two at the extreme northeast. Some specimens derive from spoil possibly representing members of the Tamiami Formation, at least in part to be correlated with the Yorktown Formation, now regarded as Early Pliocene in age.