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An Early Eocene Sirenian from Patagonia (Mammalia, Sirenia)

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ABSTRACT

Two mammalian maxillary fragments from the Lower Eocene of Argentina were described as *Florentinoameghinia mystica* (Simpson, 1932) and were designated as Mammalia, *incertae sedis* (Simpson, 1945). These specimens are here restudied and reassigned to the order Sirenia. They are shown to have many similarities with the den-

tition of *Protosiren fraasi* Abel (1904), a sirenian from the Middle Eocene of Egypt. These fragmentary remains represent the earliest dental record of fossil sirenians and extend the trans-Atlantic distribution of sirenians back to the Lower Eocene.

INTRODUCTION

Florentino Ameghino, premier South American paleontologist and biostratigrapher, is well known for his acute observations and trustworthy accounts, but his long and productive career is remembered as well for its sometimes spectacular unorthodoxy. In 1906 he announced to an unbelieving audience the association of mammals of Tertiary type with dinosaurs in beds he claimed were of Cretaceous age. His claim was often belittled in subsequent literature, but it was not until the Scarritt Patagonian Expedition of 1930–1931 that a serious attempt was made

to determine the accuracy of his statement. In the course of settling this issue, G. G. Simpson revisited all of Ameghino's localities and amassed a large collection. Simpson's thorough examination convincingly dispelled Ameghino's association, but also brought to light fragmentary remains of uncertain affinity. Ironically, Simpson himself felt that these mammalian cheek-teeth were possibly associated with a caniniform, "more or less dinosaur-like tooth" found in the same block of matrix (Simpson, 1932). The caniniform tooth (AMNH[R] 3162), of large size

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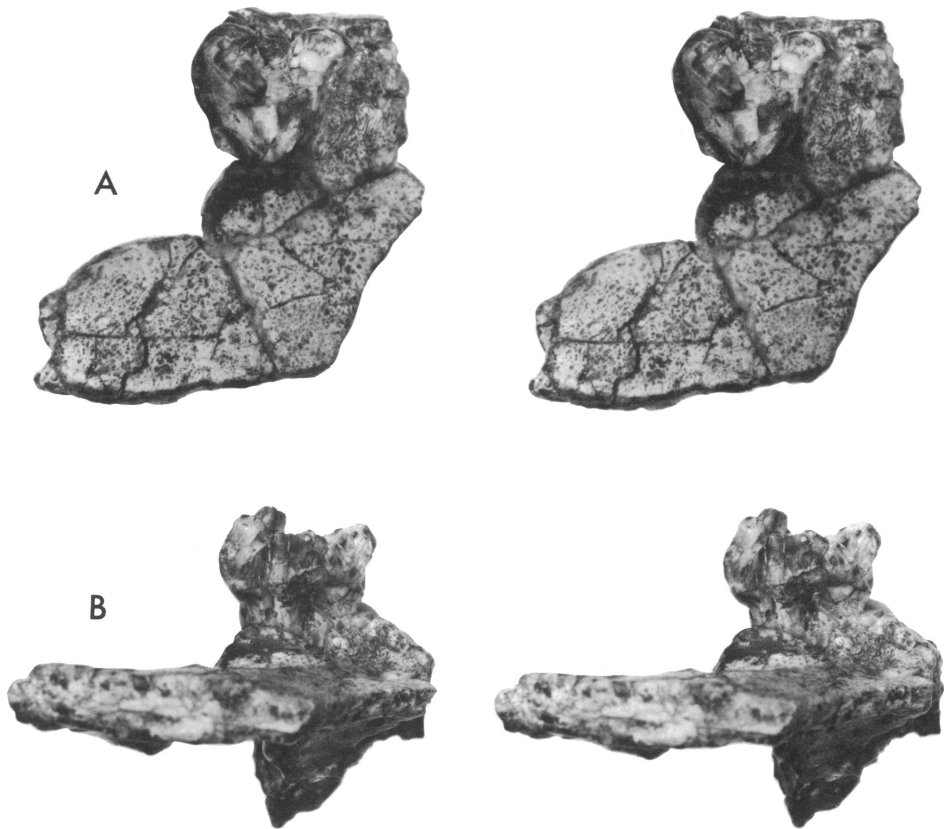


FIG. 1. *Florentinoameghinia mystica*, AMNH 28402. A. Stereopair of occlusal view of upper premolar, anterior side at right, lingual side at bottom. B. Stereopair of lingual view of upper premolar, anterior side at right.

relative to the cheek-teeth, has since been attributed to *Sebecus* along with many similar crocodile teeth from the same beds. The maxillary fragments containing the cheek-teeth suffered a more obscure fate—designated as *Mammalia, incertae sedis*, by Simpson (1945) and *Marsupialia, incertae sedis*, by Romer (1966). Recently McKenna (1980) has revived interest in this regard by suggesting a sirenian relationship. The present paper redescribes and discusses the possible affinities of these curious remains, quite appropriately named *Florentinoameghinia mystica* Simpson, 1932.

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ABBREVIATIONS:

AMNH, Fossil mammal collection, American Museum of Natural History.

AMNH(R), Fossil reptile collection, American Museum of Natural History.

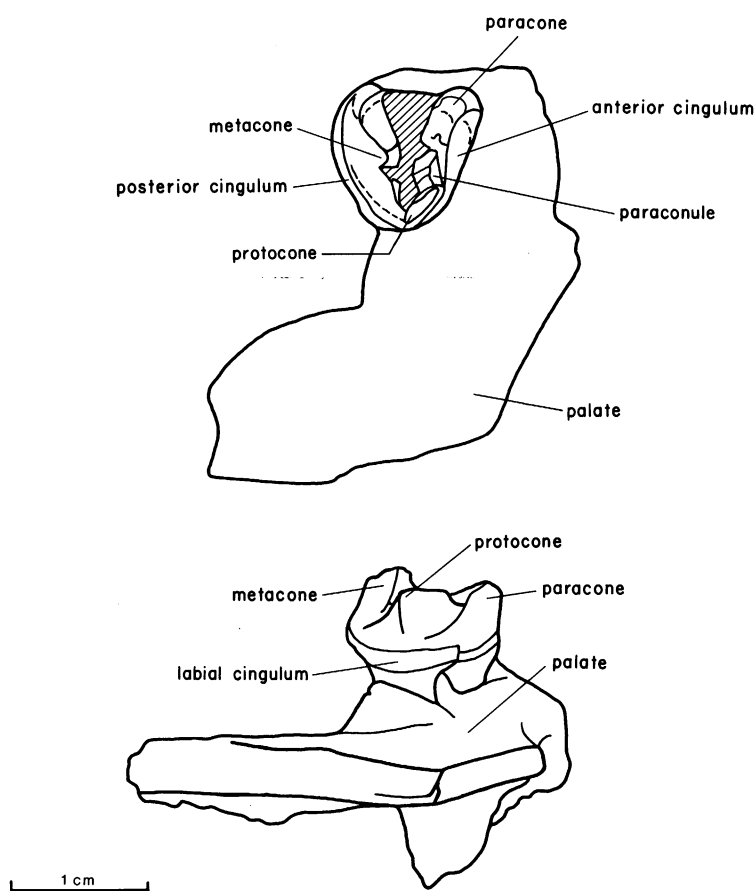


FIG. 2. *Florentinoameghinia mystica*, AMNH 28402. Labeled drawings of the premolar of figure 1 with the same orientation.

SYSTEMATICS

ORDER SIRENIA, *INCERTAE SEDIS*
FLORENTINOAMEGHINIA SIMPSON, 1932
FLORENTINOAMEGHINIA MYSTICA

SPECIMENS: AMNH 28402, two maxillary fragments with three cheek-teeth.

HORIZON AND LOCALITY: *Notostylops* Beds, Oficina del Diablo, Cañadón Vaca, near Paso Niemann of the Río Chico del Chubut, Chubut Territory, Argentina.

REVISED DESCRIPTION

The remains of *Florentinoameghinia* consist of two right maxillary fragments (AMNH 28402) containing three cheek-teeth and several small, indeterminate skull fragments, emplaced in roughly a cubic decimeter of matrix (*vide* Simpson, 1932). There is no direct contact between the maxillary fragments but their association is implied by comparable size, similar texture and state of preservation of the bone, and close proximity.

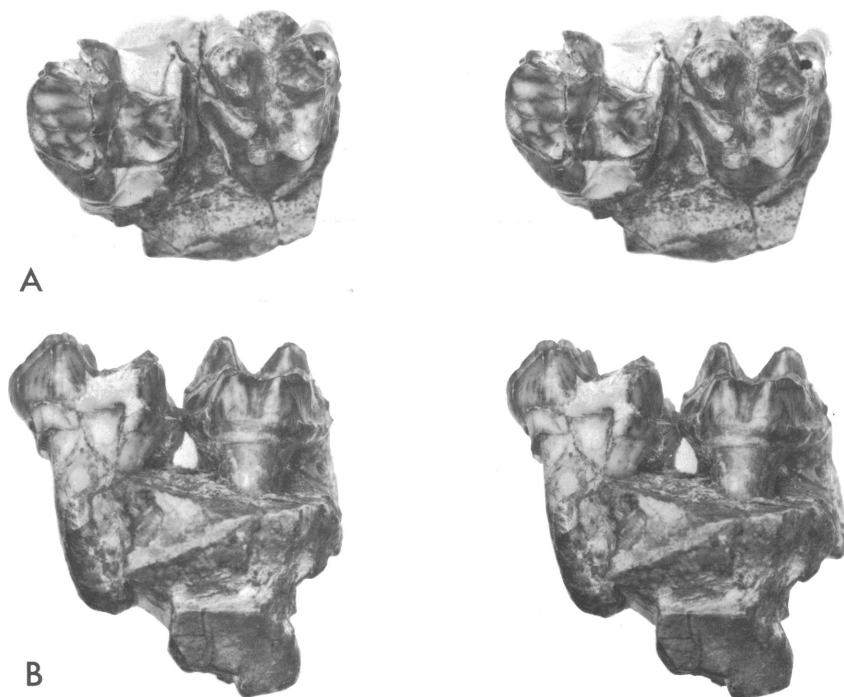


FIG. 3. *Florentinoameghinia mystica*, AMNH 28402. A. Stereopair of occlusal view of upper molars, anterior side at right, lingual side at bottom. B. Stereopair of lingual view of upper molars, anterior side at right.

The single tooth of the first fragment (fig. 1A, B; fig. 2) is the most imperfect, missing a large portion of the central basin and external margin. It is premolariform and triangular in shape, measuring 10 mm. in length and 9 mm. in width. Although the apex of the protocone is absent, the truncated base is sizable, already equaling the metacone in height. The subconical metacone is positioned far to the interior of the tooth and has anterolabial and posterolabial crests. Possible missing material at the posterior surface of the metacone, perhaps, has accentuated the posterolabial crest. The paracone is broken away but would have been more labial in position than the metacone, as indicated by the juncture of the anterior cingulum and the base of this cusp. Closely allied with the protocone is a small paraconule, damaged on

the anterior surface. The metaconule is broken away but must have been smaller, if present at all, for there is little space between the protocone and metacone. Well-developed anterior and posterior cingula curve upward toward the paracone and metacone, respectively. A moderate labial cingulum is also present. Except for a slight bulge in the posterior cingulum, there is no development of a hypocone. Three roots are positioned under the major cusps, the labial pair more robust than the lingual root. The tip of the latter is deflected labially, toward the posterolabial root.

It is probable that a diastema preceded this tooth; an anterior alveolar border, nearly 4 mm. in length, is preserved with no indication of an adjacent tooth. This tooth, therefore, probably represents an anterior pre-

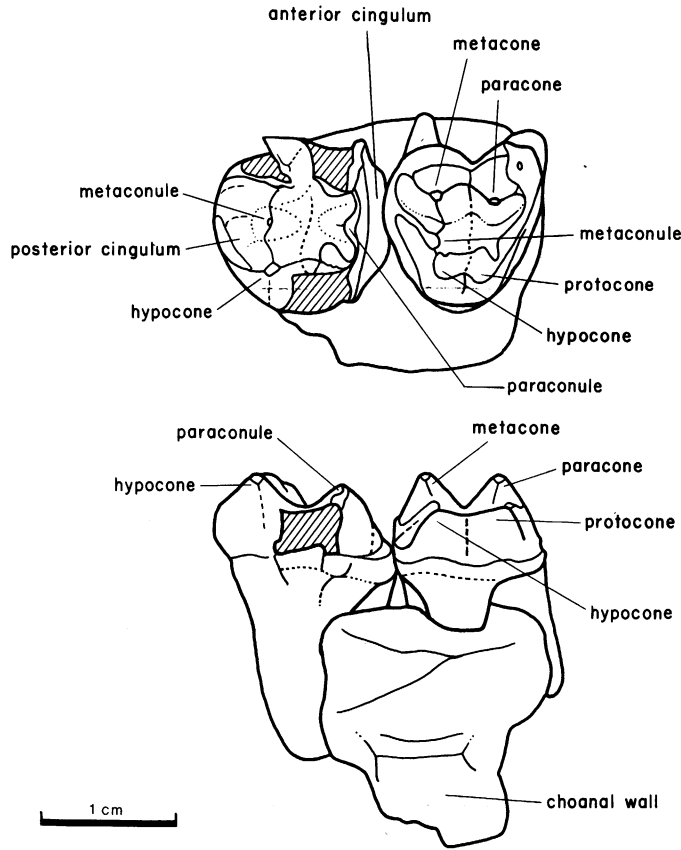


FIG. 4. *Florentinoameghinia mystica*, AMNH 28402. Labeled drawings of the molars of figure 2 with the same orientation.

molar, with several missing teeth between it and the other maxillary fragment.

A strong hypocone is present in the remaining teeth (fig. 3A, B; fig. 4). The most anterior of these is trapezoidal in shape and sublophodont, with the metaconule shifted behind the hypocone. A strong notch divides the paracone and metacone as well as the weak labial cingulum. The damaged protocone and hypocone, on the other hand, remain closer and more connate than the paracone and metacone. Closely applied to the protocone and hypocone are the paraconule and metaconule, respectively, which form incipient lophs. In addition, there are anterior and posterior cingula of moderate development.

The second tooth lacks most of the protocone and paracone, but its major features are discernible. It is composed of two parallel rows of cusps nearly equal in height, with connate bases. The well-developed hypocone is clearly separated from the protocone, in contrast to the condition in the preceding molar. There is noticeable development of the posterior cingulum, the crest of which arches from the metacone to the tip of the hypocone, with a slight basin between itself and the adjoining row of cusps. The anterior cingulum is well-developed but remains low, and lingual and labial cingula are absent. The second tooth measures 12 mm. in length and 11 mm. in width and is greater in overall

dimensions than the first, which is approximately 10 mm. in length and width.

About 15 mm. of the palate is preserved lingual to the first, premolariform tooth. It is flat, not arched or grooved, and relatively thin, thickening only near the alveolar border. The second maxillary fragment preserves a section of the wall of the choanal passage. The position and proportions of these maxillo-palatine fragments indicate a rather lightly built palate and dental margin.

Above the two posterior teeth are two cavities separated by a thin partition. There is a sizable foramen at the bottom of each cavity which, however, does not pierce the palate, as suggested by Simpson (1932). These cavities could represent the crypts of successional teeth positioned above what are perhaps deciduous molars. I concur with Simpson, however, in rejecting such an hypothesis, for the teeth are not heavily worn and do not exhibit any other lacteal characteristics. In addition, the cavities are not directly above the teeth in question; the partition between the cavities is positioned above the posterolabial root of the anterior tooth, not between the roots of these teeth. Therefore, it is likely that we are dealing with permanent teeth, most likely M^1 and M^2 , for there is a distinct facet on the posterior cingulum of the more posterior tooth, presumably for M^3 .

DISCUSSION

There has been very little comment on the systematic position of *Florentinoameghinia*. Simpson (1932) pointed out vague resemblances to certain South American ungulates, but the supposed association of the crocodile tooth only added to the singularity of these remains. By placing *Florentinoameghinia* in Marsupialia, *incertae sedis*, Romer (1966), we must assume, was misled by the erroneous association of the caniniform tooth. He probably interpreted these fragments as the remains of a previously unknown carnivorous marsupial. Simpson (1932) had remarked on the presence of "sparassodonts" (borhyaenids and thylacosmilids) in the same beds.

Cuspidate cross lophs are the most distinctive feature of the specimen, best developed on what is probably M^2 . The metaconule has shifted entirely behind the hypocone and lost any former connections with the protocone. Thus there is an immediate resemblance to other lophodont groups such as macropodids, tapirs, some South American ungulates, and some tethytheres (Proboscidea, Desmostylia, and Sirenia).

A diverse fauna of diprotodonts was already present in Australia by the late Oligocene (Tedford et al., 1975), the first known macropodids occurring in as yet undescribed faunas of medial Miocene age (Archer and Bartholomai, 1978). In *Dorcopsoides*, perhaps the most primitive member of the Macropodidae, conules are absent (Ride, 1971). Styral cusps, though reduced, are present and the premolars are sectorialized. None of these characters are present in *Florentinoameghinia*. Beyond incipient lophodonty, which has developed independently in many lineages, early macropodids do not share any of the distinctive features of these molars.

At the time of their first appearance in the fossil record in the late Paleocene, perissodactyls already had developed incipient transverse crests. In *Homogalax* and *Hyrachtherium* (see Radinsky, 1969, fig. 2) an ectoloph is formed by the paracone, metacone, and parastyle although these cusps retain their individuality. Lingually, the protocone and paraconule and the hypocone and metaconule form two oblique transverse crests. Again the resemblance to *Florentinoameghinia* is superficial. There is no hint of an ectoloph or parastyle in *Florentinoameghinia*. The incipient lophs in *Florentinoameghinia* are parallel, or slightly convergent (M^1), and the metaconule is distinct and clearly associated with the metacone in the second loph. Only in more derived tapiroids does the metaloph terminate in the position of the metacone on the ectoloph. Similarities between *Florentinoameghinia* and tapiroids are thus convergences in the development of a bilophodont dentition.

Unlike other South American ungulates, the Pyrotheria and Xenungulata are charac-

terized by simple bilophodont molars. Simpson (1932) noted similarities between *Florentinoameghinia* and *Carolozittelia*, a primitive pyrothere also from the Casamayor Formation of Patagonia. Only M^{2-3} are known and are very similar to M^{1-2} of the xenungulate *Carodnia* (Paulo Couto, 1952). The upper molars are brachydont with two somewhat oblique lophs. The lophs are lower at their centers and concave anteriorly, quite unlike *Florentinoameghinia*. In *Carolozittelia* (see Simpson, 1967) the protocone and hypocone participate in the lophs but are larger than the metacone and paracone and retain their individuality. In M^1 of *Florentinoameghinia*, in which both metacone and paracone are preserved, the notch in the loph dividing the metacone and paracone is deeper than that for the protocone and hypocone. It would seem that the metacone and paracone, not the protocone and hypocone, would be the last cusps to merge completely in the formation of lophs. A noticeable feature of *Florentinoameghinia* is the prominence of the metaconule and paraconule. *Carodnia* and *Carolozittelia* retain a remnant of the metaconule as a bulge in the posterior loph, but the paraconule is not visible. Other pyrotheres such as *Griphodon* (Patterson, 1942) or *Propyrotherium* have crenulations or variable cusps, but there are no regular conules or conulids. *Colombitherium*, from the Gaulanday Formation of the Eocene of Columbia, has nearly straight lophs like *Florentinoameghinia*, but conules are absent and the anterior and posterior cingula are poorly developed. In *Carodnia* the premolars are preserved and are highly derived. In P^{1-2} the roots are single and laterally flattened. In P^{3-4} the protocone is V-shaped and a strong mesolingual paracone is present. There are not, however, any shared-derived characters with the three-rooted premolar of *Florentinoameghinia*. The resemblances in the molars, nevertheless, may be indicative of a more remote relationship.

Bilophodonty is an early development in tethytheres. In Eocene *Moeritherium* (see Tobien, 1978), lophs are formed in typical fashion from the protocone and paracone and

the metacone and hypocone. A sulcus persists between the cusps of each loph in unworn molars. Unlike *Florentinoameghinia*, the cusps are low and blunt, and conules are entirely lacking. There is, in addition, a strong lingual cingulum and an extra cuspsule behind the hypocone, neither of which are present in *Florentinoameghinia*.

Well-preserved dentitions of early sirenians are scarce. *Prorastomus*, from the Middle Eocene of Jamaica, is clearly the most primitive known sirenian; the ear region lacks the conspicuous modifications observed in all other sirenians (Savage, 1976). The dentition, unfortunately, is very poorly preserved. It can be determined, however, that the earliest sirenians primitively possessed five (or possibly six) premolars and that the incisors were all small (Sickenburg, 1934; Savage, 1976; Domning, 1978). *Sirenavus*, from the Middle Eocene of Hungary (Kretzoi, 1941), consists only of cranial roof and mandibular fragments (possibly also the posterior half of M^3) which have yet to be described in detail. *Eotheroides* and *Protherium*, from Middle to Upper Eocene deposits of Europe and Africa, are represented by more adequate material (Sickenburg, 1934). The upper molars are bilophodont with three cusps on each loph. The cusps are lower than in *Florentinoameghinia* and the metaconule has begun to invade the transverse valley. The blunted cusps and position of the metaconule in *Eotheroides* and *Protherium* probably already represent dugongid specializations. Other clear dugongid features of these genera include a deflected rostrum and the development of small tusks.

Middle Eocene *Protosiren*, described and figured by Sickenburg (1934), remains the best-known primitive sirenian dentition. The resemblance to *Florentinoameghinia* is remarkable. The cusps are trenchant with connate bases that form two parallel lophs, much as in *Florentinoameghinia*. Unlike *Eotheroides* and *Protherium*, *Protosiren* has not developed the strongly deflected dugongid rostrum. If the molar structure of *Protosiren* is primitive among known sirenians, then we

TABLE 1
Eocene Sirenia^a

Stage	Location	Fossil Material	Original Description	Current Taxonomy
U. Eocene	Italy	Skull	de Zigno (1875)	<i>Prototherium</i>
U. Eocene	Egypt	Skull and postcrania	Andrews (1902)	<i>Eotheroides</i>
U. Eocene	Egypt	Skull and postcrania	Abel (1913)	<i>Eotheroides</i>
U. Eocene	Libya	Ribs	Savage (1971)	?
U. Eocene	Java	Ribs	Koenigswald (1952)	?
M.-U. Eocene	Somalia	Ribs	Savage (1969)	?
M.-U. Eocene	France	Skull and postcrania	Freudenthal (1970)	? <i>Eotheroides</i>
M.-U. Eocene	Egypt	Skull and postcrania	Owen (1875)	<i>Eotheroides</i>
M. Eocene	Jamaica	Skull	Owen (1855)	<i>Prorastomus</i>
M. Eocene	Hungary	Maxillary frag. and ribs	Kordos (1977)	<i>Anisosiren</i>
M. Eocene	Hungary	Jaw fragment and ribs	Kordos (1978)	? <i>Eotheroides</i>
M. Eocene	Hungary	Cranial and mandib. frag.	Kretzoi (1941)	<i>Sirenavus</i>
M. Eocene	Egypt	Skull	Abel (1904)	<i>Protosiren</i>
M. Eocene	Libya	Skull and postcrania	Heal (in prep.)	New Genus
M. Eocene	France	Molar	Richard (1946)	?
M. Eocene	Somalia	Teeth and postcrania	Haas and Miller (1952)	?
M. Eocene	Romania	Humerus	Fuchs (1973)	?
M. Eocene	Florida	Ribs	Vernon (1951)	?
M. Eocene	Alabama	Ribs	Siller (1964)	?
Eocene/Oligocene	Mexico	Ribs	Müllerreid (1932)	?
L. Eocene	Hungary	Ribs	Kretzoi (1953)	?
L. Eocene	India	Fragmentary molar	Sahni and Kumar (1980)	<i>Ishatherium</i>
L. Eocene	India	Vertebra	Sahni et al. (1980)	?
L. Eocene	Patagonia	Maxillary fragments	Simpson (1932)	<i>Florentinoameghinia</i>

^a There has been some question concerning the assignment of European Marine stages to Lower, Middle, and Upper Eocene. I follow Berggren et al. (1978) in regarding both the Lutetian and Bartonian stages as Middle Eocene, and the Ypresian and Priabonian as Lower and Upper Eocene, respectively. The majority of the references listed above as Middle Eocene are of Lutetian age.

can list several shared-derived characters that unite Sirenia and *Florentinoameghinia*:

1. Upper molariform teeth composed of two roughly parallel, tricusped cross lophs divided by an unobstructed transverse valley;
2. Molar cusps composed of protocone, paracone, metacone, hypocone, paraconule and metaconule, all approximately equal in height;
3. Metaconule and paraconule positioned closer to the protocone and hypocone, respectively, in adjacent cross lophs, and
4. Well-developed anterior and posterior cingula; the posterior cingulum higher and much stronger than the anterior cingulum, the former anteriorly basined with a crest

arching from the metacone to the tip of the hypocone.

The molars of both *Florentinoameghinia* and *Protosiren* increase in size posteriorly, but this may be primitive for Sirenia. In *Protosiren* the premolars are triangular with three cusps and a surrounding cingulum, as in *Florentinoameghinia*. The metacone and paracone of the premolars of *Protosiren* are lower and more variable in position relative to the protocone (Sickenberg, 1934). The most noticeable difference between the premolars of *Protosiren* and that of *Florentinoameghinia* is that the former have only one root while the latter has three.

The number of premolars in early sirenians is particularly interesting in light of recent

controversy regarding the primitive therian dental formula (McKenna, 1975). *Eotheroides*, *Protosiren* (Sickenberg, 1934), and *Prorastomus* (Savage, 1976) clearly retain at least five premolars as adults.

A tabulation of the earliest known sirenians reveals that by the Middle Eocene fossil sirenians had both a New World and Old World distribution (see table 1). The earliest traces of fossil sirenians are rib fragments from the Lower Eocene of Hungary (Kretzoi, 1953) and possibly a fragmentary molar (Sahni and Kumar, 1980) and isolated vertebra (Sahni et al., 1980) from the Lower Eocene of India. *Florentinoameghinia*, from the Lower Eocene of Argentina, extends the trans-Atlantic distribution of sirenians into the early Eocene and casts some doubt on the traditional view that the origin and early evolution of the Sirenia occurred on the shores of the Tethys.

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