

FOSSIL SIRENIA (MAMMALIA: DUGONGIDAE) FROM THE PIRABAS FORMATION (EARLY MIOCENE), NORTHERN BRAZIL

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ABSTRACT — *The Pirabas Formation on the Atlantic coast of Pará, Brazil, is evidently of late Early Miocene (Burdigalian) age. It has recently yielded material of three genera of dugongid sirenians: Dioplotherium cf. D. allisoni and cf. Rytiodus (Subfamily Rytiodontinae), and cf. Metaxyltherium (Subfamily Halitheriinae). If the specimen tentatively referred to Rytiodus is correctly identified, this is the first record of the genus in the New World. Sirenotherium pirabense, based on material previously reported from the Pirabas Formation, is a nomen dubium. The new discoveries include the most complete fossil sirenian remains yet discovered in South America, and show that Early Miocene sirenian diversity on the Atlantic coast of South America was comparable to that which existed contemporaneously in North America.*

KEY WORDS: Sirenians, Dugongidae, Early Miocene, Pirabas Formation, Brazil.

RESUMO — *Sirênios fósseis (Mammalia: Dugongidae) na Formação Pirabas (Mioceno Inferior), Norte do Brasil. A Formação Pirabas na costa atlântica no Estado do Pará, Brasil, é considerada como pertencente a porção superior*

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do Mioceno Inferior (andar Burdigaliano). Recentemente, foram descobertos restos de três gêneros de sirênios dugongídeos: *Dioplotherium* cf. *D. allisoni*, *Rytiodus* (Subfamília Rytiodontidae) e *Metaxytherium* (Subfamília Halitheriinae). Considerando-se correta a tentativa de identificação do espécimen referido como *Rytiodus*, este seria o primeiro registro deste gênero para o continente americano. A espécie *Sirenotherium pirabense*, baseada em material registrado para a Formação Pirabas deve ser considerada como nomen dubium. As novas descobertas de sirênios incluem o resto de material craniano mais completo desta Ordem para a América do Sul, e demonstra que a diversidade dos sirênios no Mioceno Inferior na América do Sul foi comparável àquela existente contemporaneamente na América do Norte.

PALAVRAS-CHAVE: Sirênios, Dugongidae, Mioceno Inferior, Formação Pirabas, Brasil.

INTRODUCTION

Discoveries and studies of fossil sirenians have hitherto been largely restricted to Europe, North America, and to a lesser extent Africa. By comparison, the sirenian fossil records of the other continents have barely begun to be investigated. Since a review by Domning (1982) which alluded to all the then-known sirenian occurrences in South America, only a small amount of additional material has come to light in this part of the world. This new material does, however, include by far the best fossil sirenian specimens yet collected from the continent, the first complete cranial material from the continent, and the first dugongid specimens that can be meaningfully related to taxa known from other regions of the globe. These specimens, recently collected from the Early Miocene Pirabas Formation on the northern coast of Brazil, are the subject of this paper. They include representatives of three different and sympatric dugongid genera, following and corroborating the pattern of multiple sympatric dugongid lineages that has emerged from recent North American studies in the same Caribbean-West Atlantic sirenian paleofaunal province (Domning 1989a).

Carlos de Paula Couto (1967) was the first to describe and name fossil sirenian remains from the Pirabas Formation. On the basis of various teeth and bone fragments from Ilha de Fortaleza, Pará (Figure 1), he named *Sirenotherium pirabensis* (properly *S. pirabense*) and referred it to the Family Trichechidae. As pointed out by Domning (1982), only the holotype upper molar is potentially of diagnostic value, and even that is insufficient for a definite family assignment; therefore, he referred *Sirenotherium* only to "Trichechidae or Dugongidae *incertae sedis*."

The name *Sirenotherium pirabense* was resurrected by Toledo (1989) in a preliminary report on a skull from the same geological unit. This skull is here referred to the dugongid *Dioplotherium* cf. *D. allisoni*. It is quite possible that Paula Couto's taxon is in fact identical with this one; alternatively (and more probably, given the small size of the type molar of *S. pirabense*), it may be synonymous with the small *Metaxytherium* also reported here, or some other small sirenian yet to be discovered in the Pirabas Formation. Unfortunately, comparison with

the presently available specimens still does not suffice to clarify the affinities of *S. pirabense*, which must for now remain a *nomen dubium*.

Abbreviations: MPEG — Museu Paraense Emílio Goeldi, Belém, Brazil.

GEOLOGY AND AGE

The Pirabas Formation contains one of the most abundant, diversified, and taxonomically best-known paleofaunal associations in Brazil (Petri & Fúlvaro 1983). Its area of occurrence includes the entire northeastern region of the State of Pará. However, it is found mainly in the subsurface, with only a few outcrops in the coastal zone. Its principal outcrops are found in the municipalities of Salinópolis and São João de Pirabas, and in the limestone mines near Capanema (Figure 1).

The great variety of marine invertebrates, plant remains, pollen, and foraminifers, as well as the diversity of vertebrates, suggests the existence of several sub-environments within the formation's area of deposition. This hypothesis is consistent with the sedimentological data, which indicate that the Pirabas Formation (mainly marine) and the overlying Barreiras Group (mainly continental) form a transgressive-regressive sequence. The Pirabas Formation is basically composed of limestones and, to a lesser extent, marls and shales. According to Góes et al. (in preparation), the formation includes eight distinct facies: biocalcirudites, stratified calcarenites, nonstratified calcarenites, marls, bioherms, black shales, green shales, and micrites. These facies characterize the unit as having been deposited in an open marine environment with warm, shallow, agitated waters, including areas of lagoons, estuaries, and mangroves. The fossil sirenians reported here (*Dioplotherium* cf. *D. allisoni*, cf. *Rytiodus*, cf. *Metaxytherium*) were all collected from the biocalcirudites (Figure 2a, 2b), except for one specimen of *Dioplotherium* (MPEG 65-V) found in the green shales (Figure 2b).

The Pirabas Formation was considered Oligo-Miocene in age by Ferreira (1982), based on the presence of the gastropod *Orthaulax pugnax*, which is found in the coastal outcrops of the Pirabas. According to Vokes (1979), *O. pugnax* is a synonym of *O. inornatus*, and its known occurrences range from the Late Oligocene through at least the late Early Miocene (Burdigalian). Vokes (1979) regarded the Pirabas as correlative with either the Aquitanian-equivalent Tampa Formation or the Burdigalian-equivalent Chipola Formation in Florida, USA. Later, Ferreira et al. (1984), on the basis of foraminifers from well cores concluded that the Pirabas Formation ranges from Late Oligocene to Early Miocene in age. Fernandes (1984), in a paleoecological study of Foraminifera from this formation, dated the Pirabas sediments to the Early Miocene.

The Barreiras Group, which conformably overlies the Pirabas Formation and interfingers with it, has been assigned by Arai et al. (1988) to the Middle Miocene on the basis of pollen, principally the species *Crassoretrilletes vanraadshooveni*. This can be taken as evidence that the Pirabas may have been deposited towards the end rather than the beginning of the Early Miocene.

Consequently, we are inclined to regard the Pirabas Formation as late Early Miocene (Burdigalian) in age. This would make it approximately correlative with the Chipola Formation in Florida, which has been correlated by Akers (1972) with planktonic foraminiferal stage N. 7.

Such a conclusion is consistent with what can be determined from the stage of evolution of the fossil sirenians themselves. As explained below, the *Dioplotherium* material may have greater affinities with the Burdigalian-equivalent *D. allisoni* than with the Aquitanian-equivalent *D. manigaulti*. Likewise, the specimen referred to *Rytiodus* appears to resemble the Burdigalian-age Libyan specimens of that genus more than *R. capgrandi* from the Aquitanian of France. However, it must be emphasized that these identifications and comparisons are tentative and do not form the basis for our age assignment of either the sirenians or the Pirabas Formation itself.

Despite the large amount of data already obtained concerning the Pirabas Formation, work is still needed on its correlation with contemporary units in the Caribbean and North America in order to determine its chronological position more precisely.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Sirenia Illiger, 1811

Family Dugongidae Gray, 1821

Subfamily Rytiodontinae Abel, 1914

Dioplotherium Cope, 1883

Dioplotherium D. allisoni (Kilmer, 1965)

Figures 3-9

Material

MPEG 63-V: Nearly complete skull, mandibles, and atlas. Coll. P. M. de Toledo, from a small outcrop of the Pirabas Formation in the intertidal zone on the beach at Atalaia, Pará.

MPEG 64-V: Fragmentary skull. Coll. P. M. de Toledo, Atalaia, Pará.

MPEG 65-V: Fragmentary skull, vertebrae, and ribs. Coll. P. M. de Toledo, Atalaia, Pará.

DESCRIPTION

The following description pertains to the most complete specimen, MPEG 63-V, except where otherwise indicated.

Skull

The skull of MPEG 63-V is essentially complete and undistorted; it lacks only the left exoccipital, most of the left jugal, the tips of the rostrum and

pterygoid processes, the left tympanic, and fragments of the cranial parts of the squamosals. The cranial cavity and internal nares have not been completely cleared of matrix.

Premaxilla — The premaxilla differs noticeably from that of *Dioplotherium manigaulti* in that the summit of the symphysis is not convex and bulbous, but rather forms a very broad, flat, and indeed slightly concave surface. This unusual form appears to be natural and not the result of erosion; certainly not of post-burial erosion, since patches of matrix are still in place on the surface of the bone. The same form is also observed in a second specimen (see below). The lateral edge of the palatal surface is not thickened; the surface itself is trapezoidal, deeply concave, and much narrower than was estimated for *D. manigaulti*. On each side, the large tusk alveolus is well preserved, and displays the same lozenge-shaped cross section as the tusk. Each alveolus measures about 4 x 2cm in diameter. Just behind the symphysis, each nasal process is markedly swollen on its medial side and has a mediolateral thickness of 4.0-4.5cm; the nasopalatine canal between these swellings is only about 16mm wide. Still further aft, at the level of the anterior ends of the jugals, these swellings diminish rather abruptly and the nasal processes are only about 2.5cm thick mediolaterally. Finally, the processes expand again still more abruptly, flaring inward as they flatten against the frontals to form semicircular terminations about 4cm across. (In MPEG 64-V, the posterior end of the right premaxilla has a more or less straight medial border, and does not flare inward in this manner). The estimated rostral deflection is 63°.

A fragment of the right premaxilla of MPEG 65-V, from the posterior part of the symphyseal region, shows the same structure as that described above: the dorsal surface is flat or slightly concave, and the lateral edge is thick, rounded, and overhanging. The internal structure of this lateral portion (which lies directly above the tusk alveolus, here partly preserved) is completely dense, unlike the more medial and anterior regions of the premaxilla. This zone of dense bone is 4cm wide 3cm high in cross section. The same density of the lateral region was observable in MPEG 63-V along a break which is now glued together.

Nasal — No nasal-frontal sutures are visible. A bone fragment lying against the ventromedial side of the left premaxillary nasal process may represent the process described in *D. manigaulti* as being formed by the nasal bone and/or a large ethmoid concha.

Ethmoidal Region — Not fully prepared. Some partly exposed pieces of bone on the right side of the nasal cavity, at the level of the supraorbital process, may represent one or more conchae.

In MPEG 64-V, part of the nasal septum is preserved; its bottom lies about 5cm below the roof of the nasal cavity at the level of the anterior frontal border. The upper part of the perpendicular plate is only 6mm thick. In lateral view, the perpendicular plate resembles that of *Xenosiren yucateca* Domning, 1989 (Domning 1989c: figura 1A), with fused lateral plates of the vomer discernible below the narial roof on either side.

Vomer — Not prepared or not preserved, except as just stated.

Lacrimal — The lacrimal is not delimited by visible sutures, but appears to be similar in size and position to that of *D. manigaulti*; it forms a segment of the anterior orbital rim about 4.5cm long. There is no knob rising above the supraorbital process, but there is the same strong, laterally-projecting vertical ridge continued downward onto the jugal as in *D. manigaulti* and "*Halitherium*" *olseni* Reinhart, 1976. This ridge is thicker and more rugose on the lacrimal than it becomes farther down on the jugal.

Frontal — The supraorbital processes are very prominent and distinctly hooked, but are relatively thin dorsoventrally and have no protuberance on the underside like that of *D. manigaulti*. The anterior tip of each process forms a blunt point at its junction with the premaxilla and lacrimal; from this point there ascends a high, very prominent, robust ridge that crosses the base of the supraorbital process and is continuous with the temporal crest. No such ridge connects to the posterolateral corner of the process, in contrast to *D. manigaulti* and "*H.*" *olseni*. The dorsal surface of the process slopes steeply ventrolaterad. Below and between the temporal crests lies a very broad and deep concavity like that of *Corystosiren varguezii* Domning 1990; its floor slopes upward posteriorly and becomes level with the temporal crests at the frontoparietal suture. A nasal incisure 2cm wide extends to a level behind the supraorbital process. The temporal crests overhang the temporal walls of the frontal. The lower portion of the temporal wall is recessed slightly, but not delimited by a sharp or distinct crista orbitotemporalis. There are no postorbital apophyses. The frontal roof narrows as it approaches the parietal. The lateral, nearly longitudinally-aligned parts of the frontoparietal suture are marked by slightly raised ridges.

In MPEG 64-V, the nasal incisure is about 2.5cm wide, and is bordered by masses of spongy bone which seem to be part of or fused with the frontals; these may represent nasals. The frontal roof is raised into a convexity along the interfrontal suture, and is 1cm thick in the anterior midline over the nasal cavity.

In MPEG 65-V, the nasal incisure is about 4cm across; it is not clear whether this apparent width is due to an absence of the nasal bones, or whether turbinals are present in MPEG 63-V that make the incisure appear narrower. The sutural surface for the premaxilla on the anterior and dorsomedial side of the supraorbital process is exposed and can be seen to slope ventromedial and anterad; it is not a vertical surface as in *Xenosiren*. The sculpting and contours of the frontal roof are as in MPEG 63-V; the roof is about 35mm thick near the frontoparietal suture.

Parietal — The parietal roof is nearly flat and lacks the prominent temporal crests and other sculpturing seen in *D. manigaulti* and *C. varguezii*. However, it is faintly marked by low, lyrifiform crests with shallow grooves along their medial sides, in substantially the same pattern that is expressed in *Corystosiren* in much stronger relief. The lateral edges of the roof are fairly sharp, and the temporal walls fall away steeply from them. The cranial vault is more or less square in

cross section. The squamosal sutures lie 1.5cm below the parietal roof and so do not indent the latter's outline. Instead, the temporal crests intersect the nuchal crest; no groove separates them.

In MPEG 64-V, the anterior processes of the parietal extend forward to a level 0.5cm or less behind the nasal incisure. The parietal roof is 18mm thick in the midline; in MPEG 65-V it measures about 31mm. On the internal surface, the bony falx cerebri disappears about halfway to the frontoparietal suture in the former specimen, but reaches the suture in the latter. The internal occipital protuberance is high and sharply pointed in both. In MPEG 64-V the tentorium ossium is very faint and broadly V-shaped in plan, and the transverse sulcus is shallow and without lateral pits; in MPEG 65-V both tentorium and sulcus are absent lateral to the internal protuberance. Also in this specimen, the squamosals probably came within 1cm of the parietal roof; the sculpturing, crests, and contours of the roof are as in MPEG 63-V.

Supraoccipital — The supraoccipital forms an angle of about 125° with the posterior part of the parietal roof (about 127° in MPEG 64-V; 120° in MPEG 65-V). The nuchal crest is sharp, thin, and forms a smooth arch on each side above the semispinalis muscle scar. The external occipital protuberance is damaged, but did not rise above the parietal roof; rather, the nuchal crest is slightly depressed in the midline. MPEG 65-V has a small emissary foramen at the summit of the external occipital protuberance; the latter has a sharp median ridge but on the whole is not very prominent. The nuchal crest's lateral edges overhang somewhat in all three specimens. The median crest on the supraoccipital surface is rather weak.

Exoccipital — The supraoccipital-exoccipital sutures form an angle of about 138° . The exoccipitals meet in a suture 1.5cm long. The foramen magnun appears to have been smoothly about rounded dorsally, like that of *D. manigaulti*. The lateral border is somewhat irregular but has no posterior overhang. The supracondylar fossa is deep. The hypoglossal canal is not bifurcated. The paroccipital process is rugose and does not reach as far ventrally as the condyle. The condylar articular surface forms an arc of about 150° .

Basioccipital — Fused with the adjacent bones. The longus capitis muscle scars form a single large rugosity. The ventral surface forms an unusually acute angle (about 110°) with the long axis of the basisphenoid.

Basisphenoid, Presphenoid, Orbitosphenoid — The intracranial surfaces are not prepared; no differences from *D. manigaulti* were observed.

Alisphenoid — The lateral surface of the pterygoid process is fairly smooth. The portion that supports the squamosal is not thickened, laterally protruding, or sculpted as in *D. manigaulti*.

Pterygoid — Fused with the alisphenoid. The pterygoid fossa is very shallow and faces laterad rather than posterolaterad (even more so than in *D. manigaulti*);

its edges become indistinct dorsally before they ever intersect, but the dorsal end of the fossa lies at or slightly above the roof of the internal nares. As in *D. manigaulti*, the posteromedial edge continues dorsally another 3cm (the thickness of the basisphenoid).

Palatine — Only the anterior parts are preserved; they meet in a median suture 1.5cm long and extend to a level forward of the after edge of the zygomatic-orbital bridge. The palatines are clearly separated from the maxillae by sutures, and border the palatal incisure. The latter is some 5cm long and about 1cm wide, and extends to about the after edge of the zygomatic-orbital bridge.

Maxilla — The alveolar portion is heavy and massive. Anteriorly, the palate forms a distinct and moderately deep gutter, and narrows to a width of about 1cm, much narrower than the almost 4.5cm seen in *D. manigaulti* (in MPEG 64-V it is at least 2cm wide; in MPEG 65-V, about 1.2cm). Between this narrow "waist" and the palatines, one or two asymmetrically-arranged palatine foramina are visible on either side. The palate is concave between the tooth rows. At the rear of the intermaxillary suture, its dorsoventral thickness exceeds 24mm in MPEG 65-V. The zygomatic-orbital bridge is elevated less than half a centimeter above the alveolar margin. The infraorbital foramen is 32mm high and 39mm wide (proportionately larger than in *D. manigaulti*). The floor of the infraorbital canal is smooth insofar as it is preserved, but its anterior section is missing where there exists a small spine in *D. manigaulti*. The roof of the canal is not as well preserved, but seems to have borne a transverse ridge similar to (but no larger than) that of *D. manigaulti*. The posterior opening of the maxillo-premaxillary canal is more than 1cm in diameter.

Squamosal — Posterodorsally the squamosal rises to a point 1.5cm below the parietal roof. The posteroventral part of the bone and the sigmoid ridge are missing. The surface dorsal to the zygomatic root is not inflated or bulging. The postglenoid process and postarticular fossa are well developed. The temporal condyle is distinct, elliptical, and obliquely placed. The zygomatic process is fairly long and slender, tapering somewhat anteriorly. Posterior to its broadest point (which is about level with the postarticular fossa), it tapers more rapidly; the posterodorsal border is almost straight in lateral view and moderately concave medially, whereas the posterior part of the ventral border dips downward below the line of suture with the jugal. The processus retroversus has a single, undivided, bulbous posterior termination which is somewhat turned inward ventrally, and forms a very well developed notch at the rear of the zygomatic root. (In MPEG 65-V the rear end of the process is rather sharply pointed instead of bulbous). The underside of the processus retroversus bears a nutrient foramen on the right side which is absent on the left. The posterior end of the squamosal-jugal suture is marked by a blunt downward projection in the lateral outline of the zygomatic process, level with the front edge of the temporal condyle. The squamosal of *D. manigaulti* is not known.

Jugal — Proportionately longer than in *D. manigaulti*; the length of the postorbital (= zygomatic) process (about 7cm) was about equal to the diameter of the orbit. The ventral extremity of the bone lies below the center of the orbit. The ventral part is about 2cm thick mediolaterally; on its posteroventral edge it bears a pair of ridges arranged en echelon for attachment of the masseter. The ventral and anteroventral edges of the orbit overhang slightly. Anterior and anteroventral to the orbit, the bone's surface is slightly concave. The posterior side of the orbit is delimited by a raised process that lies anterior to the tip of the squamosal and is separated from the supraorbital process of the frontal by only 14mm.

Periotic, Tympanic, Auditory Ossicles — Not prepared.

Mandible (Figure 7 — Both mandibles of MPEG 63-V are preserved, lacking only the anterior and posterior terminations, the coronoid processes, and one condyle. The preserved condyle is apparently incomplete, being longer than wide and knoblike rather than transversely expanded as is the case in most adult dugongids. The posterior edge of the ascending ramus is relatively straight, sharp, and curved inward along its whole length. The flat surface between the angle and the internal pterygoid fossa is only about 1cm wide. The ventral extremity of the angle is not thickened, measuring only 8mm mediolaterally. The coronoid arch is thin and has no medial bulge; its ventral edge is sharp. The dental capsule is atrophied, indicating adulthood. The side of the horizontal ramus slopes steeply away from the labial border of the alveoli; the lingual border overhangs. The horizontal ramus is short and deep; its posteroventral edge is thin and somewhat inflected laterad where the masseter inserted on it. The dorsal edge of the ramus is thin forward of the tooth row. On the left side is a single large mental foramen at the level of the posterior end of the symphysis. On the right side the foramen is smaller and farther forward; posterodorsal to it is a sizable accessory mental foramen. The dorsal side of the left mandibular canal is pierced forward of the mental foramen by two anteriorly-directed canals. The anterior masticating surface is narrow, with thin, overhanging lateral edges and a pitted surface; remaining matrix obscures whether distinct vestigial tooth alveoli are present. The symphysis is unfused, and its posterior surface is deeply concave between the lateral convexities formed by each ramus. The mandible's most striking feature is its extreme anterior deflection from the occlusal plane of about 82°, almost 20° greater than the rostral deflection. The ventral arch of the horizontal ramus is not symmetrical; instead its anterior slope is much steeper than the posterior, reflecting this extreme degree of deflection.

Dentition — Together with one of the pair of large upper incisor tusks, MPEG 63-V possesses on both sides M^{1-3} , partly resorbed alveoli for DP^5 , M_{2-3} , and empty alveoli for M_1 . The latter occupy a space 15mm long anteroposteriorly, are 8mm wide anteriorly and 10mm wide posteriorly. All the molars are heavily worn in this adult specimen. No alveoli for premolars anterior to DP^5 seem to be present, in contrast to *D. manigaulti*; in MPEG 64-V the palate is preserved for a distance of 3.5cm anterior to the DP^5 alveoli, and likewise bears no other

alveoli in this region. The anteroposterior space occupied by the alveoli attributed to DP⁵ varies from about 7mm in MPEG 63-V to about 13mm in MPEG 64-V and 22mm in MPEG 65-V.

I¹: Nearly all of the right tusk is preserved; only its tip is lacking. It was found lying in the matrix, free of the skull. Judging from its length, its alveolus (which still contains some matrix) extends almost the full length of the premaxillary symphysis. The tusk displays the lozenge-shaped cross section diagnostic for *Dioplotherium*; its width and thickness do not change appreciably throughout its length. Originally (before slight crushing) it was concave laterally; the lateral side bears a pair of faint longitudinal grooves on its anterodorsal surface. The medial side is covered with very thin black enamel, which contrasts clearly with the light brown dentine. The enamel exhibits the usual fine longitudinal striations and concave-forward growth lines. The most distal 1.5cm of the preserved fragment shows on its lateral side the proximal part of a wear surface, which has reduced the tusk's cross section at its tip from a 4-sided to a 3-sided condition, exactly as in the specimen of *D. allisoni* described by Domning (1978: figure 3B). The root of the tusk is essentially complete and still open; the cavity is filled with matrix. The enamel layer on the medial side extends without variation all the way to the termination of the root.

Molars: In MPEG 63-V the crown pattern of M¹⁻² has been entirely obliterated, and that of M³ nearly so. All that can be discerned in regard to the latter is that the protoloph was broad, the hypoloph narrower, and the posterior basin open posterolabially, with a small cusp or ridge contained in the basin. M₂ has also lost its enamel pattern, while M₃ retains only the remnants of the obliquely placed protolophid and hypolophid, and a large hypoconulid with a lingually situated pit. A posterior spur of the entoconid touches the lingual edge of the hypoconulid.

In MPEG 64-V (Figure 8A), no pattern is left on M¹, but M² is only moderately worn and displays an anterior cingulum joined to the large protocone, a straight protoloph behind which the protocone extends to constrict the transverse valley, a metaconule shifted forward only slightly, a posterior cingulum broadly confluent with the hypocone, and a posterior basin open labially. The slightly worn M³ has an identical pattern, and shows more clearly that the hypocone lies posterolingual to the metaconule and is joined to a single, centrally-located posterior cingular cusp (which is smaller and more closely united with the hypocone than in MPEG 63-V). M³ has a large lingual root 26mm long which curves posterad and labiad near its apex and is completely closed (no open molar roots were observed on any specimen).

In MPEG 65-V (Figure 8B), M² is heavily and M³ moderately worn. The pattern of the latter tooth is the same as that described above, except that the posterior cingular cusp is elongated and closes off more of the posterolabial side of the posterior basin.

These molar patterns are, so far as can be seen, indistinguishable from those of halitheriines such as *Metaxytherium* de Christol, 1840. The large hypoconulid of MPEG 63-V is not matched in the only other lower molars of

Dioplotherium known, those of *D. allisoni* (Domning, 1978: fig. 2); but this structure is highly variable in dugongids in general.

Atlas (Figure 9) — The articular surface for the odontoid process of the axis is circular and concave; no surface for the axis exists on the upper arch. The lower arch has an irregular median protuberance pointing posteroventrad. The upper arch has a median keel flanked by a rounded boss on either side. The canal above each anterior cotyle is well enclosed by bone. The transverse processes curve backward and slightly dorsad; they have distinctly expanded ends, and bases that are slightly grooved or indented along their anterior sides. This groove or indentation extends onto the ventral side of each process, becoming continuous with the vertebrarterial "canal", which in this specimen is a broadly open notch. Ventral to this notch is a low, rugose convexity. Measurements: external height, 86mm; internal height, 47; total breadth, 137; width between processes for transverse ligament, 35; breadth across anterior cotyles, 98e; across posterior cotyles, 78; length in dorsal midline, 29; in ventral midline, 30.

Other Vertebrae — Fragments of 14 thoracics and 7 postthoracics are present in MPEG 65-V. One of the most complete vertebrae, a posterior thoracic, has the following measurements: breadth across transverse processes, 97mm; anterior width of centrum, 65; posterior width, 66; height of centrum in midline, 43; thickness of centrum in midline, 46; width of neural canal, 26; height of canal, 23; maximum length from pre- to postzygapophysis, 55. The neural spine is broken but was rather small in proportion to the arch and centrum. The anterior thoracics have smaller centra. The vertebrae in general resemble those of other dugongids.

Ribs — Numerous rib fragments were associated with MPEG 65-V; their diameters are typically in the neighborhood of 27x20mm.

COMPARISONS

These specimens are clearly referable to *Dioplotherium* by virtue of their large, lozenge-shaped tusks and apparent fusion of the nasals with the frontals. Equally clearly, they are distinct from *D. manigaulti* of the Early Miocene of eastern North America, as this species was redescribed by Domning (1989b). Differences that appear to be of taxonomic importance include the following: enamel is limited to the medial side of the tusk; the summit of the premaxillary symphysis is flattened; and the nasal process of the premaxilla is greatly thickened and strengthened just behind the symphysis. Other differences, such as the more flattened supraorbital process, less pronounced parietal sculpturing, and longer postorbital process of the jugal in the Brazilian specimens, are of uncertain taxonomic value given the lack of adequate samples (particularly of *D. manigaulti*) to illustrate the range of individual variation.

The only other named species of *Dioplotherium* is *D. allisoni* from the Early to ?Middle Miocene of the west coast of North America. This species is known only on the basis of tusks, fragmentary mandibles, and lower molars (Domning,

1978). Its only known distinction from *D. manigaulti* is that enamel is confined to the medial side of its tusk, as in the Brazilian specimens. The latter differ from the previously described specimens only in the presence of a large hypoconulid on M_3 , which (as noted above) is of doubtful significance. Until topotypic cranial material of *D. allisoni* becomes available for comparison, therefore, the referral of the Brazilian material to this species is best made provisional. However, the fact that the Brazilian specimens appear to be chronologically later than the *D. manigaulti* skull from Florida (Domning 1989b) and more nearly correlative with the North Pacific material is consistent with the referral of the Brazilian form to *D. allisoni* and with the hypothesis (Domning 1989b) that this species is more derived and hence later than *D. manigaulti*.

A further implication of this hypothesis is that *D. allisoni* should be phylogenetically as well as chronologically intermediate between *D. manigaulti* and *Xenosiren yucateca*. The available evidence is not inconsistent with this, but unfortunately the parts of the skull most critical for comparison (in particular the premaxillae) are not known for the latter species. All that can now be said is that the Brazilian form possesses no derived characters known to be absent in *Xenosiren*, while it lacks most of the latter's striking autapomorphies.

Subfamily Rytiodontinae Abel, 1914 cf. *Rytiodus* Lartet, 1866
(Figures 10-11)

Material

MPEG 206-V: Fragmentary skull. Coll. A. C. Nogueira, from the Limestone Quarry B5 from CIBRASA Co., Capanema, Pará.

DESCRIPTION

Skull

Several fragments of an adult skull (MPEG 206-V), including a tusk, have been recovered. The open root of the tusk suggests that the animal had not reached extreme old age.

Premaxilla (Figure 10) — The symphyseal region is bulbous and convex rather than flattened at its summit, although it is abraded. The side of the symphysis, like the tusk, is strongly concave laterally along its long axis. The nasal process is not thickened mediolaterally, and seems to have been shorter than the symphysis. Near its rear end, the lateral surface of the process slopes steeply ventrolaterad as the process curves mediad and reaches a mediolateral width of about 3cm. The rostral deflection was 60° or more.

Nasal (Figure 11b, 11c) — The nasal is a massive, subcylindrical, spongy bone more than 8cm long, 2.5cm wide, and 2cm high, set in a socket on the medial side of the anterior prolongation of the frontal. Its boundaries are distinct; its anterior end is missing. In medial view, its dorsal surface is flat and its posterior

end curves downward. The posterior end lies a few millimeters forward of the anterior frontal border. The medial side of the nasal is partly covered by a thin sheet of ethmoid, and lies about 1cm from the midline, making the nasal incisure about 2cm wide and about 7cm deep.

Ethmoidal Region (Figure 11c) — The mesethmoid forms a mass of bone, 5cm wide when complete, which rises to 15mm below the frontal roof. At this level it sends a slender conical median spine (the spina mesethmoidalis) directly backward, paralleling the roof for a distance of 2.5cm. Posterolateral to the main mass of the ethmoid and 4cm below the frontal roof, there is preserved the hemispherical posterior end of a cavity in the frontal; this is probably an extension of the nasal cavity. It is separated from the braincase by a wall of bone only 2mm thick.

Vomer, Lacrimal — Not preserved.

Frontal (Figure 11) — The anterior frontal border seems to have been thin and sharp. The frontal roof is very narrow and fairly flat, including its anterior part between the temporal crests. These begin near the frontoparietal suture, are 0.5cm high at the level of the anterior frontal border, and rise to a maximum height of 1cm above the dorsal surfaces of the nasals. Where highest, each crest is less than 1cm thick mediolaterally, and has a smooth, sloping lateral surface and an overhanging medial wall. Three to four cm forward of the anterior frontal border, the crest rather abruptly turns down and laterally onto the dorsal surface of the supraorbital process, which is missing. The frontoparietal suture is acutely V-shaped (forming an angle of about 40°). The temporal wall is vertical and lacks orbicular apophyses.

Parietal (Figure 11) — The anterior processes extended to within 2cm of the anterior frontal border. The roof is about 20mm thick in the anterior midline. At the level of the frontoparietal suture, the parietal roof is almost parabolic in cross section, beginning its steep ventrolateral slope right from the midline.

Supraoccipital, Exoccipital, Basioccipital, Basisphenoid, Presphenoid, Orbitosphenoid — Not preserved.

Alisphenoid, Pterygoid, Palatine — The left pterygoid process is preserved, consisting of the fused alisphenoid and pterygoid, sutured to a portion of the palatine. The lateral (= alisphenoid) side of the process bears at its lower end a vertically elongated boss 3cm long. The pterygoid fossa is broad (2cm) but shallow; the intersection (if any) of its lateral and medial edges is not preserved. The medial edge projects farther aft.

Maxilla — The zygomatic-orbital bridge is long anteroposteriorly, and bears no transverse ridge on its dorsal surface.

Squamosal — The zygomatic process consists mostly of dense bone except for some cancellous bone toward its medial side near the anterior end. It is broad posteriorly, flattened mediolaterally, convex medially, and concave laterally due to a lateral protuberance on its ventral edge at the level of the temporal condyle.

This protuberance may mark the posterior limit reached by the jugal. The zygomatic process has a sharp ventrolateral edge and a smoothly rounded ventromedial edge. Its posteroventral and posterodorsal edges are concave in lateral view; the latter is not convex laterad. The processus retroversus is single, is turned inward ventrally, is elevated about 1cm above the level of the ventral edge of the zygomatic process, and forms a shallow notch at the rear of the zygomatic root. The postarticular fossa and postglenoid process are very pronounced. The elliptical temporal condyle sits on a "pedestal" that protrudes 0.5cm below the level of the ventral edge of the zygomatic process. The temporal fossa is narrow and deep above the zygomatic root; here the surface of the cranial portion is concave. The sutural surface has a deep oblique pit anteriorly for the alisphenoid, as in *Xenosiren* (Domning, 1989c: figure 5A).

Jugal — The jugal is fragmentary but was an extremely broad, flat bone; its depth below the orbit (= measurement ab) was probably 8cm or more. This suborbital part is less than 2cm thick; its posteroventral edge is quite thin. The ventral margin of the orbit overhangs slightly. The orbit measures about 7.5cm in anteroposterior diameter. The preorbital process is about 2.5cm thick mediolaterally, and bears a socket at its upper end for the lacrimal; the anterolateral surface of the process is flat. There is a raised process in front of the squamosal zygomatic process.

Periotic, Tympanic, Auditory Ossicles — Not preserved.

Dentition — Only the large left incisor tusk (Figure 10) is preserved. Both ends are complete; the root is open and full of matrix, and lies 2-3cm abaft the rear end of the premaxillary symphysis, with its lower part enclosed by the maxilla. The pulp cavity was between 8 and 13cm deep; this middle section of the tusk is extensively damaged. The entire medial side of the tusk is covered from root to tip by paper-thin brown enamel, which bears concave-forward growth lines, longitudinal striations, and several very broad, shallow grooves. Two or three of the latter are about 1cm wide; there are also some narrower, fainter ones that do not extend the full length of the tusk. The wear surface on the lateral side extends about 6cm from the tip; the cutting edge is located posteroventrally. The tusk protrudes 9cm from the alveolus, so the wear surface lies 3cm or more outside the alveolus. However, the root lies about 2.5-3.0cm from the rear of the alveolus (which is about 20cm deep measured in a straight line), so the tusk may have slipped forward slightly in the alveolus.

COMPARISONS

Despite its shattered condition, this large dugongid skull of striking appearance is clearly assignable to the Subfamily Rytiodontinae on the basis of its downturned supraorbital processes, deep nasal incisure, and nasals appressed against the sides of this incisure. With reference to the preliminary cladogram of rytiodontines presented by Domning (1989b: Figure 6), we can see that it also shares the following derived characters: tusks mediolaterally compressed (character IV), frontal roof deeply concave (VI), enamel only on

medial side of tusk (XI), tusk extremely flattened (XIV), and (apparently) nasal processes of premaxillae shortened (XV). It lacks characters XII-XIII (peculiar to "*Halitherium*" *olseni*) and VIII-IX (which distinguish the *Dioplotherium* lineage). It also lacks the specializations of the maxillary zygomatic-orbital bridge and the preorbital process of the jugal found in *Xenosiren yucateca* (Domning, 1989c), as well as the extremely broad frontal roof and the enormously thick parietal roof with trapezoidal cross section seen in *Corystosiren varguezii* (Domning 1990). This leaves only one rytiodontine genus with which to compare it: *Rytiodus* itself.

The type species *Rytiodus capgrandi* Lartet, 1866, from the Early Miocene (Aquitanian) of France, has been illustrated in part by Lartet (1866), Delfortrie (1880), and Pilleri (1987), but a modern description of its cranial anatomy is lacking. From the published illustrations there appear to be some points of contrast with the Brazilian specimen: the frontal roof looks proportionately broader; the temporal crests seem more pronounced; the temporal fossa appears wide; the processus retroversus of the squamosal is less elevated; and the jugal does not seem to be as deep (though it is unclear which, if any, of the latter's margins are undamaged in Delfortrie's specimen).

The only other available description of *Rytiodus* is Heal's (1973) unpublished account of specimens from the later Early Miocene (Burdigalian) of Libya. Based on this account and notes of an examination of some of the specimens by one of us (DPD), the Libyan material seems to have somewhat more in common with the Brazilian specimens. Although the temporal crests are again more prominent than in the latter and the frontal roof appears wider, the skull roof is similarly narrow in the anterior parietal region and has the same parabolic cross section. The temporal fossa is also narrow. The processus retroversus appears to be elevated. The ventral extent of the jugal, as before, is unclear; but several other details match those seen in our specimen: the rostrum has the same vertically deep base; the lateral profile of the frontal and its downturned supraorbital process is similar; the nasals are separate bones (although they appear more triangular in dorsal view; the squamosal zygomatic process is similarly thin mediolaterally and has a similarly shallow notch at the rear of its root; and the pterygoid fossa is also shallow though perhaps not quite so broad. While these resemblances are more tantalizing than decisive, they at least allow us to conclude that the Brazilian specimen may well be congeneric with others that have been identified as *Rytiodus*. Pending further collecting and study, it may conveniently be referred to as cf. *Rytiodus*.

Subfamily Halitheriinae (Carus, 1868) Abel, 1913 cf. *Metaxytherium* de Christol, 1840

(Figure 12)

Material

MPEG 66-V: Skull fragment. Coll. P. M. de Toledo, Atalaia, Pará.

DESCRIPTION

A fragmentary pair of frontals (MPEG 66-V) appears to be referable to a small member of this genus. The frontal roof is strongly convex. The bases of the supraorbital processes begin to flare outward at the apparent level of the anterior frontal border, which is broken (although not much is missing since the broken edge is less than 4mm thick). The forward extremities of the parietal lay at least 43mm behind this edge. No orbicular apophyses or crista intratemporalis are present; the temporal walls are vertical. At least two pairs of conchae are visible in the nasal cavity, together with the perpendicular plate of the ethmoid. Frontal-nasal sutures are not discernible, but it is probable that the nasals are fused with the frontals and form the sides of the apparent nasal incisure. The width of the frontal roof (= measurement GG') is 65mm; the interfrontal suture (partly missing at both ends) was more than 53mm long.

Dugongidae gen. et. sp. indet.

Material

MPEG 67-V: Isolated left ?M². Coll. P. M. de Toledo, Capanema, Pará.

MPEG 205-V: Isolated lumbar or sacral vertebra. Coll. P. M. de Toledo, Atalaia, Pará.

DESCRIPTION

The heavily worn upper molar (MPEG 67-V) retains no enamel pattern at all. Its measurements (in mm) are: crown length, 18.7w; anterior width, 23.4; posterior width, 21.8w.

The vertebra (MPEG 205-V) is larger than those associated with one of the *Dioplotherium* skulls from Atalaia (MPEG 65-V), and may represent a larger form such as cf. *Rytiodus*. Its measurements are: anterior width of centrum, 97; posterior width, 93; height of centrum in midline, 62; thickness of centrum in midline, 63; width of neural canal, 27; height of canal, 22.

DISCUSSION

The first result of this study is its demonstration that Miocene sirenian faunas on the Atlantic coasts of South America displayed a diversity comparable to those in North America. In the southeastern United States, more than three dugongid lineages appear to have coexisted during the Miocene, and at least three sympatric genera have been collected from the Early Miocene (Aquitanian-equivalent) Parachucla Formation in Florida (Domning, 1989a). Two of those (*Dioplotherium* and *Metaxytherium*) have now been discovered in the somewhat later Pirabas Formation, plus a third not previously known in the New World. This also confirms that the pattern of diversity seen in the north (one halitheriine lineage together with two or more rytiodontine lineages) was typical of the entire Caribbean-West Atlantic sirenian faunal province, although the available record is still too spotty to determine whether there existed any taxonomic endemism within this province.

If the specimen we have tentatively referred to *Rytiodus* is correctly identified, it provides the first evidence of occurrence of a rytiodontine genus on both shores of the Atlantic. Although this sort of cosmopolitan distribution appears to be the rule for halitheriines, up till now the Rytiodontinae have displayed a purely endemic pattern, with *Rytiodus* isolated in the Old World and the other members of the group known only from the New. This biogeographic difference between the subfamilies may be more apparent than real. In any case, the known diversity of large-tusked rytiodontines in the West Atlantic, and the consequent difficulty of explaining their coexistence in ecological terms, is now greater than ever.

The new specimens of *Dioplotherium* on the Atlantic coasts of South America, however, throw some interesting light on the functional anatomy of these animals, and it tends to support Domning (1989b,c) interpretation of how rytiodontines used their tusks. The pronounced thickening of the premaxillary nasal process just behind the symphysis in the Brazilian specimens can be seen as a response to increased shear and/or compressional forces in this region of the skull. These would be the inevitable result of forcing the tusks downward and backward against the substrate (in attempting to cut seagrass rhizomes), which would tend to bend the rostrum upward and create a compressional stress field along the top of the rostrum. The muscle best adapted for such a purpose was the masseter, when used to approximate the rostrum and mandible while the front of the latter was held against the substrate (Domning 1989c). In this light it is interesting to observe that there is a disparity of almost 20° between the rostral and mandibular deflections, in contrast to most sirenians in which the rostral and anterior mandibular masticating surfaces are more nearly parallel. Perhaps an anterior gap between these surfaces was useful in allowing the lower jaw to gain a purchase on the substrate; or perhaps the different deflection of the mandible simply adapted it to transmit force more efficiently to the sea bottom. In any event, the strong mandibular deflection of the Brazilian *Dioplotherium* is reflected in an extreme degree of curvature of the ventral mandibular border. An identical condition is seen in the Libyan specimens of *Rytiodus*, where an apparently strong mandibular deflection likewise occurred in paradoxical association with a more moderate rostral deflection (Heal, 1973). It will be interesting to see if this pattern repeats itself in other advanced rytiodontines such as *Corystosiren* and *Xenosiren*.

ACKNOWLEDGMENTS

We thank Dr. R. J. G. Savage for the opportunity to examine *Rytiodus* specimens from Libya. Domning thanks his parents, Mr. & Mrs. Emile F. Domning, for support of his travel expenses for this study. His work on West Atlantic fossil sirenians has also supported by National Science Foundation grants DEB-802026540. Toledo thanks the CIBRASA CO. that permitted field studies in the limestones quarries B-5 and D-11, and the student Afonso C. Nogueira in collecting vertebrate fossils for the Goeldi Museum.

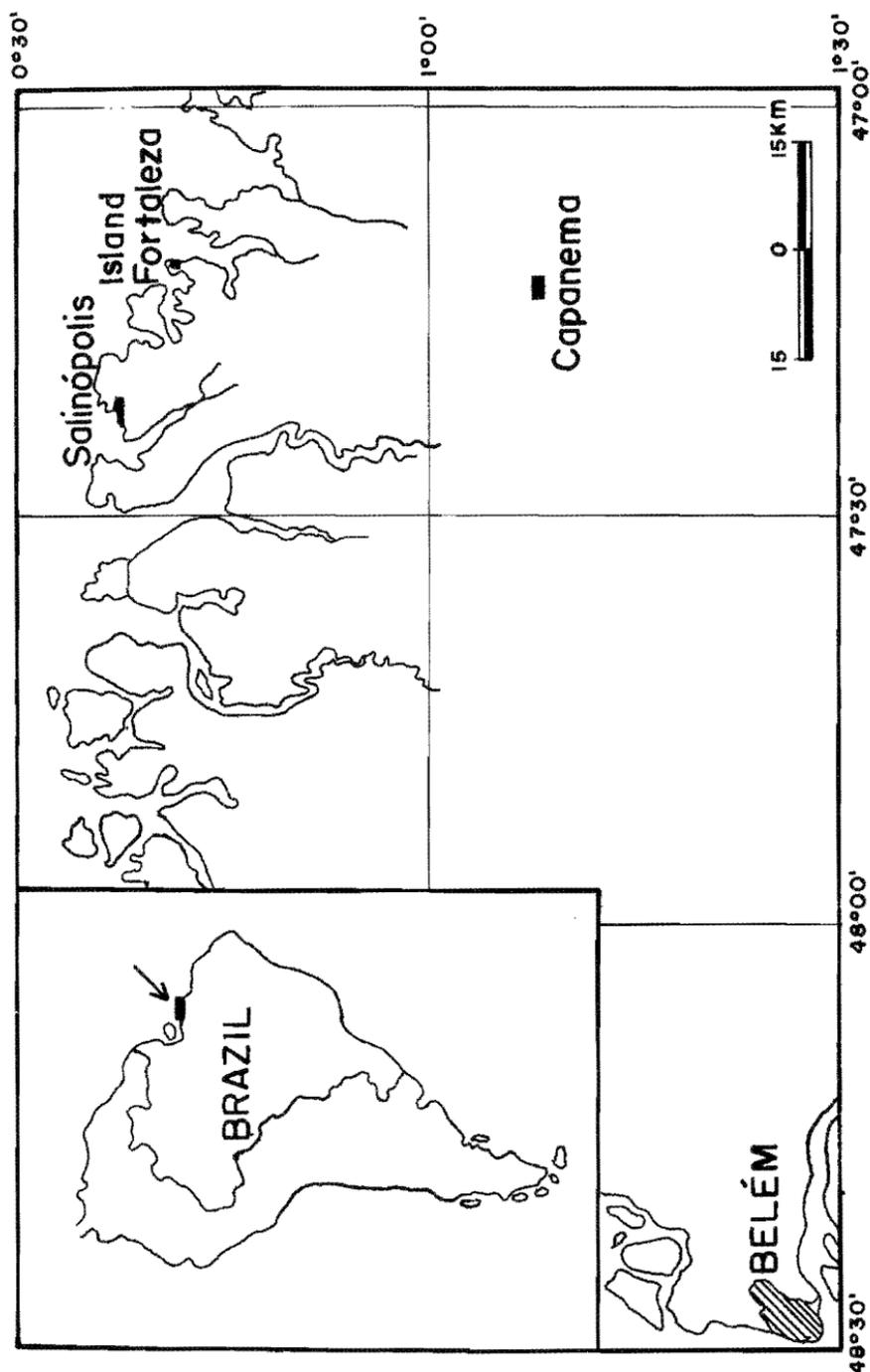


Figure 1 — Map showing localities referred to in the text.

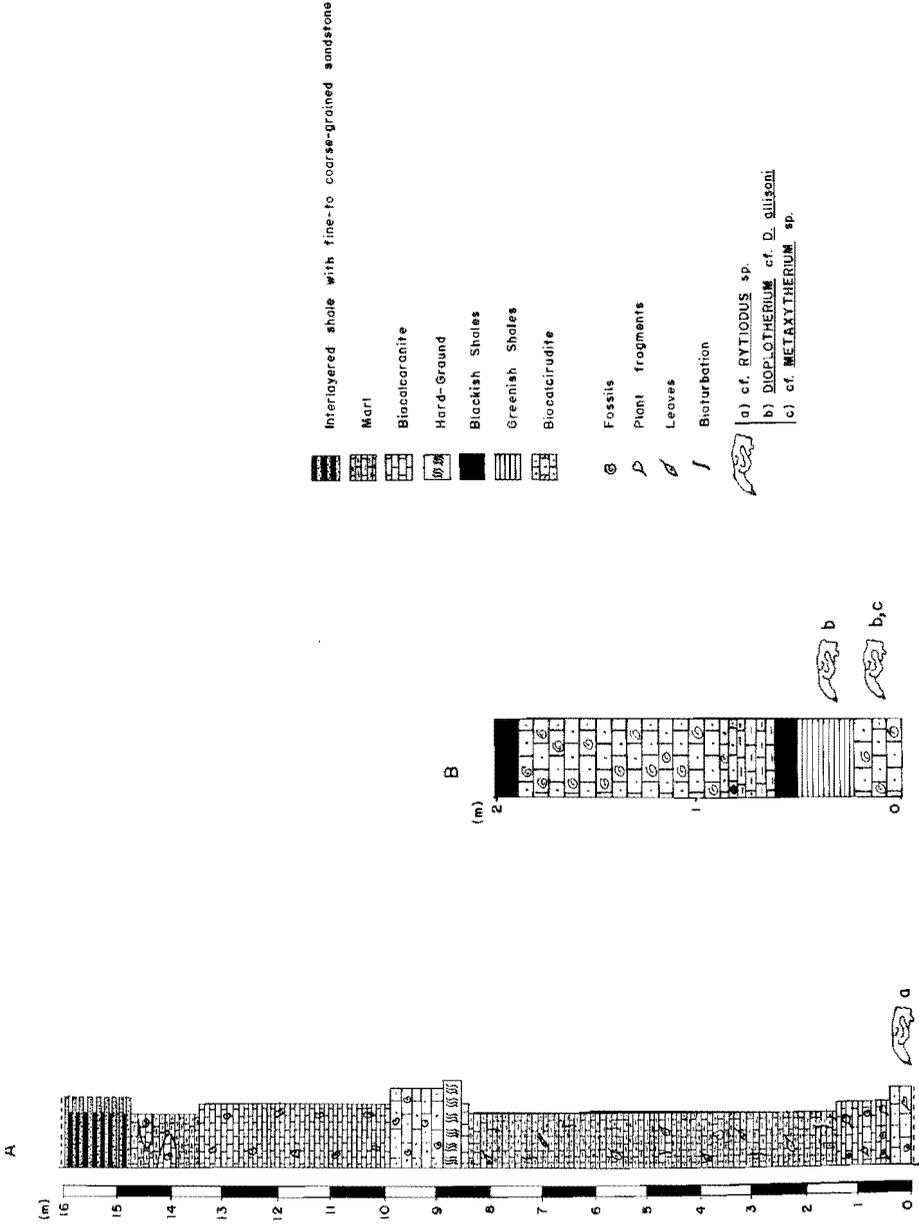


Figure 2 — Geologic section of the Pirabas Formation. A = CIBRASA QUARRY B-5, Capanema Country. B = Atalaia BEACH, Salinópolis Country (modified from Goes et al., in preparation).

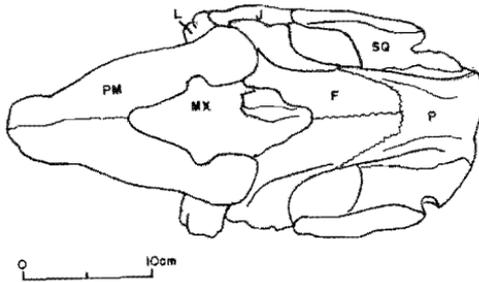
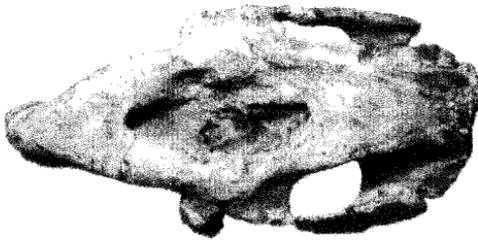


Figure 3 — *Dioplotherium* cf. *D. allisoni* (MPEG 63-V), photograph and sketch of skull in dorsal view (partly restored in sketch). Abbreviations used in this and subsequent figures: A, alisphenoid; BO, basioccipital; BS, basisphenoid; EO, exoccipital; F, frontal; J, jugal; L, lacrimal; ME, mesethmoid; MX, maxilla; N, nasal; P, parietal; PL, palatine; PM, premaxilla; SO, supraoccipital; SQ, squamosal.

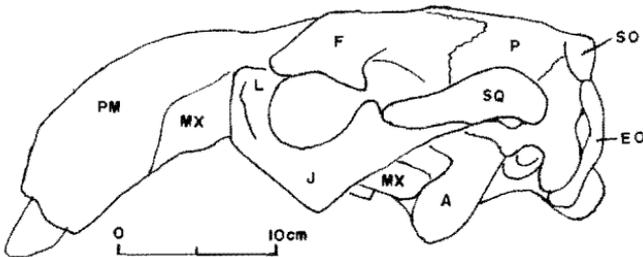


Figure 4 — *Dioplotherium* cf. *D. allisoni* (MPEG 63-V), photograph and sketch of skull in lateral view (partly restored in sketch). See Figure 3 for abbreviations.

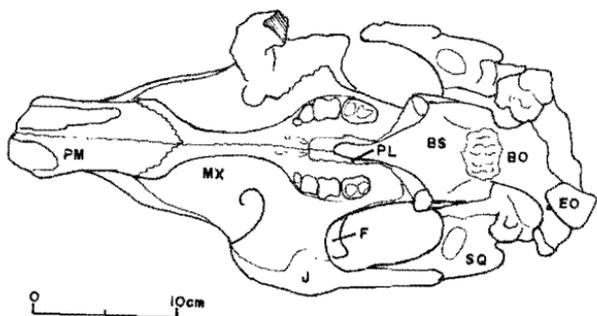
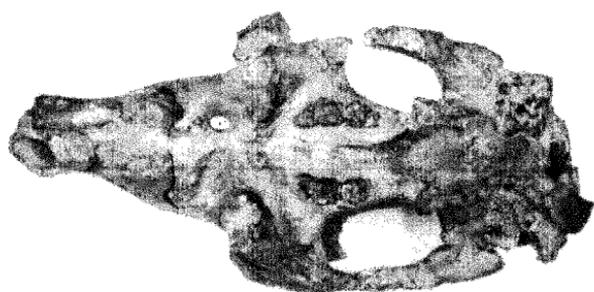


Figure 5 — *Dioplotherium* cf. *D. allisoni* (MPEG 63-V), photograph and sketch of skull in ventral view (partly restored in sketch). See Figure 3 for abbreviations.

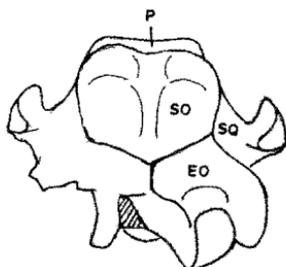


Figure 6 — *Dioplotherium* cf. *D. allisoni* (MPEG 63-V), photograph and sketch of skull in posterior view. See Figure 3 for abbreviations.

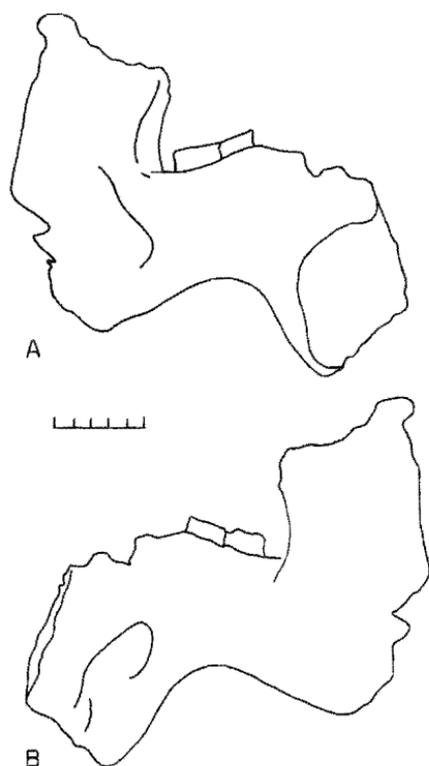


Figure 7 — *Dioplotherium* cf. *D. allisoni* (MPEG 63-V), left mandible in (A) medial and (B) lateral views. Ascending ramus partly restored from right mandible. Scale = 5cm.

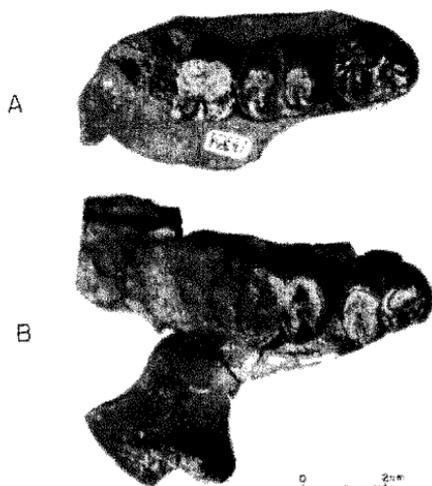


Figure 8 — *Dioplotherium* cf. *D. allisoni*, photographs of molars in occlusal view: A, MPEG 64-V; B, MPEG 65-V.

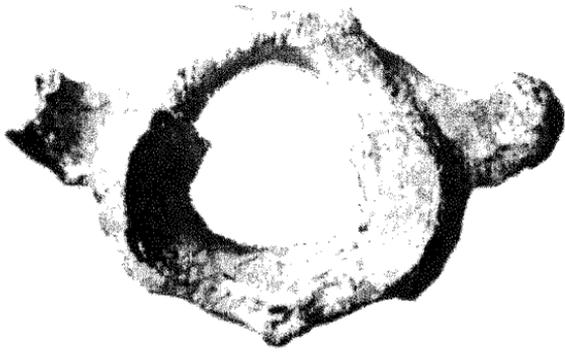


Figure 9 — *Dioplotherium* cf. *D. allisoni* (MPEG 63-V), photograph of atlas in posterior view.

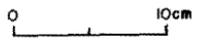
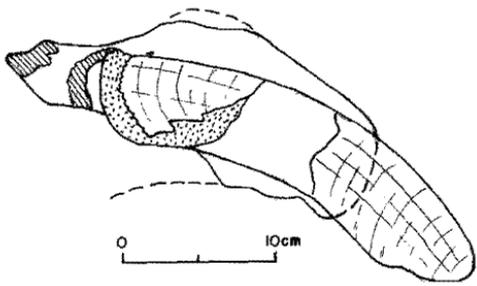
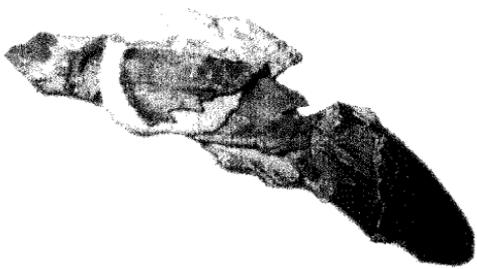


Figure 10 — *Rytiodus* (MPEG 206-V), photograph and sketch of left premaxilla and tusk in medial view. Stippling denotes matrix behind the end of the root and in the pulp cavity. Ridges and growth lines on the enamel are indicated. The midsection of the tusk is damaged; its outline and that of the premaxilla are restored in the sketch.

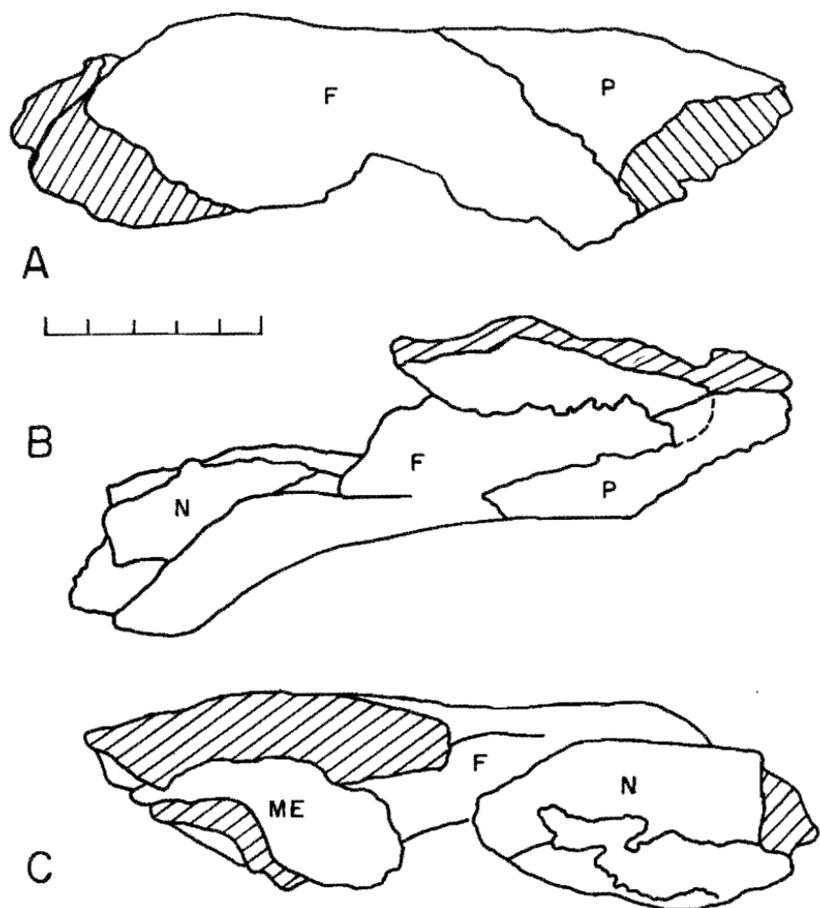


Figure 11 — *Rytiodus* (MPEG 206-V), sketches of frontal section of skull roof (partly restored): A, lateral view; B, dorsal view; C, medial view. Scale = 5cm. See Figure 3 for abbreviations.



Figure 12 — Cf. *Metaxytherium* (MPEG 66-V), photograph of frontals in dorsal view.

Table 1 — Measurements on skulls and upper molars of *Dioplotherium* cf. *D. allisoni* and cf. *Rytiodus* from the Pirabas Formation, Brazil, in mm. Letters in parentheses denote measurements used by Domning (1978: tab. 2). e = estimated, L = left, R = right, w = measurement affected by wear.

	<i>Dioplotherium</i>			cf. <i>Rytiodus</i>
	MPEG 63-V	MPEG 64-V	MPEG 65-V	MPEG 206-V
Condylbasal length, excluding tusks (AB)	415 ⁺	—	—	—
Height of jugal below orbit (ab)	42	35 ⁺	—	73 ⁺
Length of premaxillary symphysis (AH)	144 ⁺	—	—	174e
Rear of occipital condyles to anterior end of interfrontal suture (BI)	193	—	—	—
Zygomatic breadth (CC')	200	—	—	—
Top of supraoccipital to ventral sides of occipital condyles (de)	129	—	—	—
Length of frontals, level of tips of supraorbital processes to frontoparietal suture (F)	146	128e	148e	—
Length of interfrontal suture	68	57e	69	70e
Breadth across supraorbital processes (FF')	176	172e	—	—
Breadth of cranium at frontoparietal suture (GG')	80e	65e	70e	60e
Length of mesorostral fossa (HI)	148	—	—	—
Height of foramen magnum (hi)	35	—	—	—
Width of mesorostral fossa (JJ')	75	—	—	—
Maximum height of rostrum (KL)	82	—	—	105 ⁺
Posterior breadth of rostral masticating surface (MM')	56	—	—	—
Anteroposterior length of zygomatic-orbital bridge of maxilla (no)	45e	—	—	—
Length of zygomatic process of squamosal (OP)	112	—	119	—
Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen (OT)	139e	—	—	—
Length of parietals, frontoparietal suture to rear of external occipital protuberance (P)	78 ⁺	90e	83e	—
Length of row of tooth alveoli (pq)	R: 62 L: 65	74	90	—
Anteroposterior length of root of zygomatic process of squamosal (QR)	49	—	—	60
Maximum width between labial edges of left and right alveoli (rr')	78	—	—	—
Width between lingual sides of M ² s	36	—	—	—
Width of supraoccipital	84e	—	93	—
Height of supraoccipital	63	50	65	—
Minimum width of skull roof between squamosal notches	73e	—	69	—
Maximum width of braincase (level of middle part of parietal-squamosal suture)	84	75e	77e	—
Length of cranial portion of squamosal (ST)	82e	—	—	—
Dorsoventral thickness of zygomatic-orbital bridge (T)	16	—	14	20

continue

TABLE 1 (conclusion)

	<i>Dioplotherium</i>			cf. <i>Rytiodus</i>
	MPEG 63-V	MPEG 64-V	MPEG 65-V	MPEG 206-V
Anterior breadth of rostral masticating surface (tt')	38e	—	—	—
Dorsoventral breadth of zygomatic process of squamosal (WX)	34	—	37	62
Maximum width between pterygoid process (yy')	55e	—	—	—
Length of jugal (YZ)	154e	—	—	—
Crown length of M ¹	R: 16.4w	—	—	—
	L: —	—	—	—
Anterior width of M ¹	R: —	19.1	—	—
	L: —	—	—	—
Posterior width of M ¹	R: —	18.8	—	—
	L: —	—	—	—
Crown length of M ²	R: 21.4	22.0	23.8	—
	L: 22.1	—	—	—
Anterior width of M ²	R: 20.7	20.2	24.3	—
	L: 20.7	—	—	—
Posterior width of M ¹	R: —	18.8	—	—
	L: —	—	—	—
Crown length of M ²	R: 21.4	22.0	23.8	—
	L: 22.1	—	—	—
Anterior width of M ²	R: 20.7	20.2	24.3	—
	L: 20.7	—	—	—
Posterior width of M ²	R: 19.3	19.9	23.7	—
	L: 18.3	—	—	—
Crown length of M ³	R: 23.5	23.0	24.7e	—
	L: 24.3	—	—	—
Anterior width of M ³	R: —	20.9	21.8	—
	L: 19.4	—	—	—
Posterior width of M ³	R: 17.7	19.3	19.6	—
	L: 17.7	—	—	—
Combined length of M ¹⁻³	R: 60w	—	—	—

Table 2 — Measurements of mandible and left lower molars of *Dioplotherium* cf. *D. allisoni* (MPEG 63-V) from the Pirabas Formation, Brazil, in mm. Letters in parentheses denote measurements used by Domning (1978: tab. 2). e = estimated; w = measurement affected by wear.

Distance between anterior and posterior ventral extremities (DF)	130e
Height at mandibular notch (DK)	156
Height at condyle (DL)	171
Height at deflection point of horizontal ramus (EF)	136e
Minimum anteroposterior breadth of ascending ramus (GH)	77
Front of ascending ramus to rear of mental foramen (GP)	85e
Top of ventral curvature of horizontal ramus to line connecting ventral extremities (MN)	42
Minimum dorsoventral breadth of horizontal ramus (MO)	66
Maximum breadth of masticating surface (RR')	37
Rear of symphysis to front of mandibular foramen (SQ)	75
Length of alveolar row (TU)	66e
Crown length of M ₂	21.4v
Anterior width of M ₂	13.6e
Posterior width of M ₂	15.3ev
Crown length of M ₃	24.5
Anterior width of M ₃	16.3
Posterior width of M ₃	15.5

Table 3 — Measurements of tusk fragments of rytiodontine dugongids from the Pirabas Formation, Brazil; in mm. e = estimated.

	Length of Fragment	Maximum Width	Maximum Thickness
<i>Dioplotherium</i>			
MPEG 63-V	150	35	17
MPEG 65-V	70	36	20
cf. <i>Rytiodus</i>			
MPEG 206-V	271	61	19

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