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FOSSIL DUGONGIDAE (MAMMALIA, SIRENIA) FROM THE PARANÁ FORMATION (LATE MIOCENE) OF ENTRE RÍOS PROVINCE, ARGENTINA

JORGE VÉLEZ-JUARBE[1,2], JORGE I. NORIEGA[3*] AND BRENDA S. FERRERO[3]

[1]Laboratory of Evolutionary Biology, Department of Anatomy, Howard University, Washington, DC 20059 USA. *velezjuarbe@gmail.com*

[2]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, MRC 121 P.O. Box 37012, Washington, DC 20013-7012 U.S.A.

[3]Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción de Diamante-CONICET, Materi y España, E3105BWA Diamante, Entre Ríos, Argentina. *cidnoriega@infoaire.com.ar; brendaferrero@yahoo.com.ar*

Abstract. Fossil sirenians are well known from the Western Atlantic and Caribbean (WAC) region. Neogene records from the Atlantic coast of South America, although scarce, seem to reflect a similar taxonomic composition to its northern contemporaries. Fossil sirenians from Argentina are known from the late Miocene Paraná and Ituzaingó formations in Entre Ríos Province. An upper third molar housed in the Museo de Paleontología de la Universidad Nacional de Córdoba (CORD-PZ 4301), from the Paraná Formation, was originally described and assigned to the dugongid genus *Metaxytherium* Christol. Subsequent workers suggested it could instead belong to the dugongid genus *Dioplotherium* Cope, a designation that we confirm upon examination of the material. Additionally, we describe new sirenian remains from the Paraná Formation, consisting of two incomplete maxillae with teeth, belonging to one individual, deposited at the Museo de Ciencias Naturales de Paraná (MASP 373). This specimen shows similarities with species of *Metaxytherium* from the northern WAC. The Paraná Formation sirenians represent the southernmost occurrences of these two genera, and the geologically youngest occurrence of dugongids in the southern WAC. *Dioplotherium* and *Metaxytherium* also occur in the early Miocene of northern Brazil. The presence of these taxa as far south as Entre Ríos latitude suggests two possible dispersal routes: (1) across a marginal connection between a southern arm of the Amazonian Sea and the "Paranense Sea"; (2) along the Brazilian coast. Lastly, the occurrence of dugongids, which feed mainly on seagrasses, indicates that these marine angiosperms were present in the region as well.

Keywords. Sirenia. Dugongidae. Miocene. Argentina.

Resumen. FÓSILES DE DUGONGIDAE (MAMMALIA, SIRENIA) DE LA FORMACIÓN PARANÁ (MIOCENO TARDÍO) DE LA PROVINCIA DE ENTRE RÍOS, ARGENTINA. Los sirenios fósiles son bien conocidos en la región del Atlántico occidental y el Caribe (WAC). Los registros neógenos de la costa atlántica de América del Sur, aunque escasos, parecen reflejar una composición taxonómica similar a la de sus contemporáneos del norte. Los sirenios fósiles de Argentina son conocidos desde el Mioceno tardío en las formaciones Paraná e Ituzaingó en la provincia de Entre Ríos. Un tercer molar superior depositado en el Museo de Paleontología de la Universidad Nacional de Córdoba (CORD-PZ 4301), de la Formación Paraná, fue descrito y asignado originalmente al dugongo del género *Metaxytherium* Christol. En trabajos posteriores se sugirió que podría pertenecer al dugongo del género *Dioplotherium* Cope, una designación que se confirma tras el examen del material. Además, se describen nuevos restos de sirenios de la Formación Paraná, correspondientes a dos maxilares superiores incompletos con dientes, pertenecientes a un mismo individuo, depositados en el Museo de Ciencias Naturales de Paraná (MASP 373). Este espécimen muestra similitudes con especies de *Metaxytherium* del norte del WAC. Los sirenios de la Formación Paraná representan los registros más australes de estos dos géneros y la aparición geológicamente más joven de dugongos en el sur del WAC. *Dioplotherium* y *Metaxytherium* también se encuentran en el Mioceno temprano del norte de Brasil. La presencia de estos taxones hasta latitudes tan australes como Entre Ríos sugiere dos posibles rutas de dispersión: (1) a través de una conexión marginal entre un brazo sur del Mar de la Amazonía y el "Mar Paranense"; (2) a lo largo de la costa brasileña. Por último, la aparición de dugongos, que se alimentan principalmente de pastos marinos, indica que estas angiospermas marinas estuvieron presentes en la región.

Palabras clave. Sirenia. Dugongidae. Mioceno. Argentina.

Fossil sirenians are relatively well known from the Western Atlantic and Caribbean (WAC) region and include members of the four known sirenian families, Prorastomidae, Protosirenidae, Trichechidae (manatees) and Dugongidae (dugong) (Domning, 2001). The majority of these fossils are from the Atlantic coast of North America and the Caribbean. They also occur on the Atlantic coast of South America and, although scarce, seem to reflect a similar taxonomic composition to its northern contemporaries (Toledo and Domning, 1991). All the South American occurrences are Neogene in age and include early members of the Family Trichechidae (manatees) (Ameghino, 1883; Pascual, 1953; Domning, 1982, 1997) as well as members of the dugongid subfamilies Halitheriinae and Dugonginae (Reinhart, 1976; Toledo and Domning, 1991; Domning, 2001). *Florentinoameghinia mystica* Simpson, 1932, from

the early Eocene of Patagonia, has been regarded as Sirenia (Sereno, 1982). In his original description Simpson (1932a) mentioned the presence of sinuses, a feature that is absent in Sirenia (Domning, 1994). Therefore, we follow Simpson's (1932a) and Domning's (2001) designation of this species as Mammalia *incertae sedis*.

The fossil record of sirenians from Argentina is so far restricted to the late Neogene Paraná and Ituzaingó formations in Entre Ríos Province. From levels of the Ituzaingó Formation, Ameghino (1883) described *Ribodon limbatus*, an early member of the Family Trichechidae (Pascual, 1953; Domning, 1982). A tooth from the Paraná Formation was described and assigned to the dugongid genus *Metaxytherium* Christol, 1840, by Reinhart (1976). However, subsequent workers (Cozzuol, 1996; Cione *et al.*, 2000; Domning, 2001) considered it, tentatively, as belonging to the dugongid genus *Dioplotherium* Cope, 1883.

In this paper we describe additional sirenian remains from the Paraná Formation and review the morphology of the material described by Reinhart (1976).

MATERIAL AND METHODS

The studied materials consist of two incomplete maxillae with teeth belonging to one individual and an upper third molar, which are deposited at MASP and CORD-PZ collections, respectively.

For identification and comparison of the Paraná fossils we used the following specimens: Dugongidae, Halitheriinae: *Metaxytherium floridanum* Hay, 1922, USNM 356679, 356680; *M. crataegense* (Simpson, 1932b), USNM 16757; and *M. serresii* (Gervais, 1847), 25P115B, 26P66A, 829P34A. Dugongidae, Dugonginae: *Dioplotheirum* cf. *D. allisoni* (Kilmer, 1965), casts of MPEG 64-V (available at the USNM); and *Crenatosiren olseni* (Reinhart, 1976), SC 90.104. Further observations of CORD-PZ 4301 were made on a cast (USNM 412209).

Institutional abbreviations. **CICYTTP-PV**, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción de Diamante-CONICET, Colección de Paleontología de Vertebrados, Diamante, Argentina; **CORD-PZ** (NUC in Reinhart, 1976: p. 272), Museo de Paleontología de la Universidad Nacional de Córdoba, Córdoba, Argentina; **MASP**, Museo Provincial de Ciencias Naturales y Antropológicas "Profesor Antonio Serrano", Paraná, Argentina; **MPEG**, Museu Paraense Emílio Goeldi, Belém, Brazil; **SC,** South Carolina State Museum, Columbia, USA; **USNM**, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Anatomical abbreviations. **ac**, anterior cingular cusp; **hy**, hypocone; **lac**, lingual accessory cusps; **mcl**, metaconule; **me**, metacone; **pa**, paracone; **pc**, posterior cingular cusp; **plc**, posterolingual cingular cusp; **pr**, protocone; **prl**, protoconule; **tv**, tranverse valley.

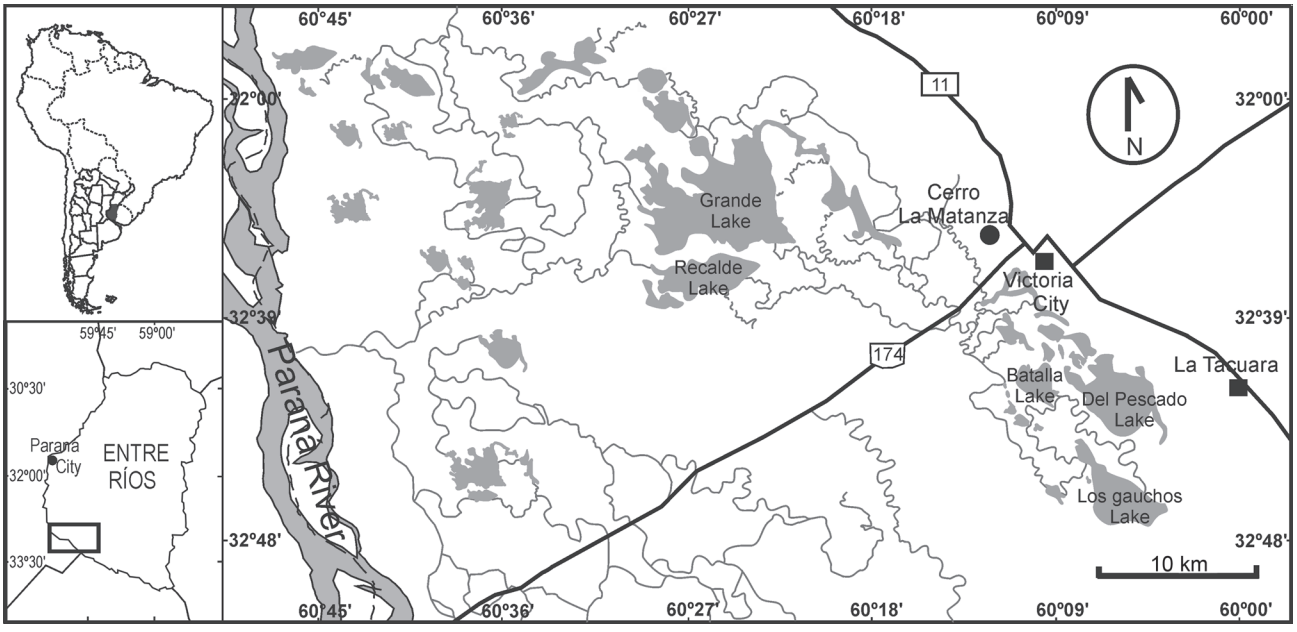

Figure 1. Geographic location of fossil locality Cerro La Matanza, Entre Ríos, Argentina/ *localización geográfica del sitio fosilífero Cerro La Matanza, Entre Ríos, Argentina*.

GEOLOGICAL SETTINGS

The Paraná Formation is the lithostratigraphic expression at southern South America of a widespread Atlantic marine transgression. During the middle and late Miocene this marine incursion covered most of the Chaco–Paraná Basin and eastern Patagonia, the northern portion of the Sierras Subandinas and the north-western Sierras Pampeanas in Argentina, reaching as far north as Bolivia, Paraguay, western Uruguay, and southern Brazil (Uliana and Biddle, 1988; Aceñolaza, 2000, 2004; Hernández *et al.*, 2005; Pascual *et al.*, 1996).

The age of the Paraná Formation has been largely debated on the basis mainly of different biostratigraphic interpretations regarding its included invertebrate fauna, ranging from middle (*e.g.*, Aceñolaza, 2000; Aceñolaza and Aceñolaza, 2000; Del Río, 2000) to late Miocene (*e.g.*, Camacho, 1967; Frenguelli, 1920; Aceñolaza, 1976; Zabert, 1978; Cione *et al.*, 2000). Recent approaches supported on new paleontological evidence and radioisotope dating tend to establish its age in the late Miocene (Pérez and Griffin, 2010; Pérez *et al.*, 2010).

The stratigraphic provenance of fossil dugongids from Entre Ríos Province

MASP 373 comes from the Cerro La Matanza locality (32°35′51″S-60°11′22″W), situated at the surroundings of Victoria city in Entre Ríos Province, Argentina (Fig. 1). Cerro La Matanza is actually part of the riverside cliffs that rises on the left margin of the Paraná River in the southwestern region of the province.

The section exposed there represents an outstanding relict of the mid–late Miocene marine transgression-regression cycle commonly known as "Mar Paranense" or "Entrerriense". The stratigraphic sequence at the fossiliferous locality was described by Bidegain (1991). It is about 8 m thick, being dominated by a thick marine unit (unit B) about 6 m thick, which is discordantly overlain by a loess layer (unit A) and underlain by at least 1.5 m of fluvial sand (unit C) (Fig. 2).

The unit C sand layer consists of medium to fine sand, with cross-bedding occurring in the upper part. It represents fluvio-deltaic depositional conditions (Bidegain, 1991).

Unit B, which contains the fossil-bearing levels, was deposited under shallow marine environmental conditions. The base of this unit is a fossil-bearing (2–3 m thick) calcareous sandstone with dominantly horizontal bedding where mollusc shells are clearly recognized. The sandstone is hard in its middle section, rendering more difficult the recognition of fossil invertebrates, but becomes again less cemented and the grain size is finer towards the top (1 m). There is an oyster bank with *Ostrea patagonica* d´Orbigny, 1842, at the base of the upper part of unit B that consists of greenish sandy-silty clay with $CaCO_3$ precipitates and patches of Fe and Mn oxides (1–1.5 m thick) (Bidegain, 1991). These upper levels of unit B are strongly weathered and contain most of the marine fossil vertebrate bones studied.

From a lithostratigraphic point of view, units C and B of Bidegain (1991) belong to different facies of the Paraná Formation. Unit B is separated by a marked uncoformity, —representing a very long hiatus of time—, from the powdered loess of unit A. The latter is referred to the late Pleistocene–early Holocene Tezanos Pinto Formation.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Sirenia Illiger, 1811

Family Dugongidae Gray, 1821

Subfamily Halitheriinae (Carus, 1868) Abel, 1913

Genus ***Metaxytherium*** Christol, 1840

Type species. *Metaxytherium medium* (Desmarest, 1822)

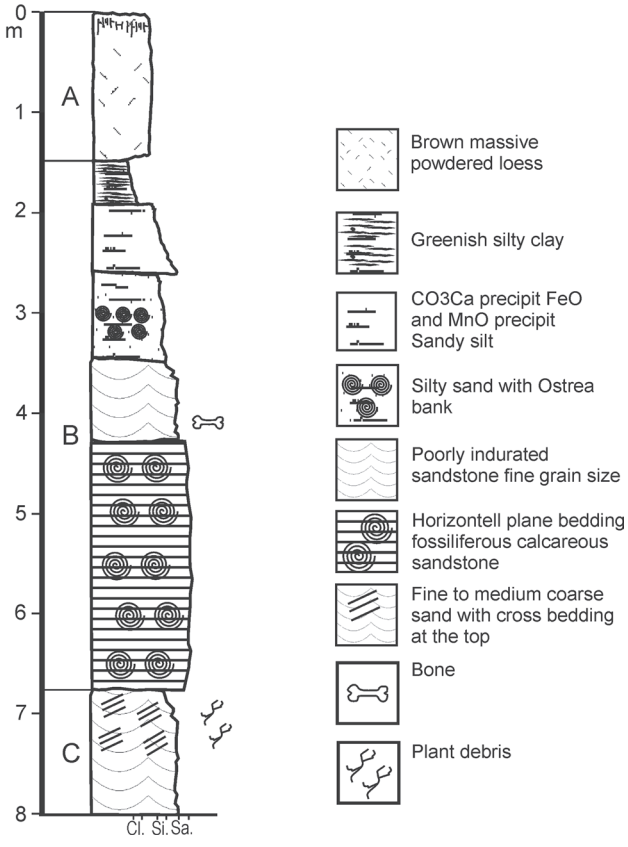

Figure 2. Stratigraphic column/ *Columna estratigráfica*.

Metaxytherium sp.

Figure 3.1–4; Table 1

Referred material. MASP 373, posterior end of both maxillae belonging to a single specimen: left maxilla with M1-3 (Fig. 3.1–2) and right one with M3 (Fig. 3.3–4)

Locality. Cerro La Matanza locality (32°35′51″S-60°11′22″W), Victoria city, Entre Ríos Province, Argentina.

Horizon and age. Paraná Formation, late Miocene.

Description. Only the alveolar portion posterior to the zygomatic-orbital bridge is preserved in both maxillae. As in most known dugongids, with the exception of *Xenosiren yucateca* Domning, 1989a, this part is dorsoventrally thick, being taller than the length of the roots of the molars, and robust, with its lateral surface and posterolateral corner overhanging the molars; posteromedially it thins and the lingual root of M3 is exposed. The posteromedial surface has an interdigitated sutural surface that would have contacted the palatine.

The M1 presents anterior and posterior wear facets (anterior for dP5, posterior for M2); cusps mostly worn, forming a largely confluent lake of dentine. An accessory cusp, located posterolabial to paracone, blocks the transverse valley buccally.

The M2 is a tooth nearly square in outline. Anterior cingulum consists of a ridge, confluent with protocone. An accessory cusp, located mesial to the paracone, closes the precingular valley labially. Protoloph (paracone, protoconule and protocone) worn, forming continuous dentine lake; the cusps seem to have been aligned along a bucco-lingual axis. Protocone subdivided into nearly equal parts by a vertical groove on its lingual surface; alternatively, crevice could be marking the boundary between protocone and an accessory cusp. Protocone extended distally farther aft than protoconule and together with a mesially positioned metaconule, constricts the transverse valley lingually. Paraloph (metacone, metaconule and hypocone) confluent with posterior cingular cusp, forming a continuous lake of dentine. Cusps in paraloph seemed to have been arranged in a semicircle (more like a C). Posterior cingular valley narrower than the anterior one and open buccally. Metaconule and hypocone separated by a notch.

Both left and right M3 nearly identical; not as worn as M1–2 with enamel surface folded and fissured; posteriorly narrower than M2, but overall very similar. Anterior cingulum cuspate and recurved distally on buccal side; separated from protocone by a cleft located mesial to the protoconule. Anterior cingular valley closed by a low cusp from the anterior cingulum and a large mesially-positioned paracone. As with M2, the paracone, protoconule and protocone are arranged in a bucco-lingual axis. Lingual to the protocone there is a couple of accessory cusps in the left molar and one on the right; they are all shorter than the protocone; in the left M3 the more distal accessory cusp is the shortest. Similar to M2, the transverse valley is blocked lingually by a large mesially-positioned metaconule and the posterior slope of the protocone. Metaconule and metacone are arranged nearly in the same bucco-lingual axis. The metacone has an accessory cusp distally of nearly the same size. The hypocone is multicusped and located distolingual to the metaconule. The posterior cingular valley is open distobuccally.

Remarks. MASP 373 displays most of the general features seen in most dugongid molars, such as bucco-lingually oriented protoloph and centrally-located metaconule. Of the dugongid species that we studied, MASP 373 resembled more those within the halitheriine genus *Metaxytherium*, specifically with material referred to *M. floridanum* from the mid–late Miocene Bone Valley Formation in Florida (USA). It resembles this taxon by having in M1–2 an accessory cusp blocking anterior cingular valley; M2 with transverse valley blocked with what could be interpreted as an accessory cusp distal to the protocone; and M1–3 resembling some of the larger *M. floridanum* molars by having accessory cuspules and more complexly folded and fissured enamel surfaces (Reinhart, 1976; Domning, 1988). This pattern of accessory cuspules and more complexly folded and fissured enamel surface has yet to be seen in dugongines (*e.g.*, Domning, 1989a, 1997), and seems to be more distinctive of derived halitheriines. MASP 373 does however differ from *M. floridanum* by being smaller (Tab. 1), with dimensions below the mean values reported for *M. floridanum* (Domning, 1988: tab. 5), being more similar to some *M. serresii* (Domning and Thomas, 1987: tab. 5).

Subfamily Dugonginae (Gray, 1821) Simpson, 1932b

Genus ***Dioplotherium*** Cope, 1883

Type species. *Dioplotherium manigaulti* Cope, 1883

Dioplotherium sp.

Figure 4

Metaytherium, Reinhart, 1976, p. 272.

Dioplotherium, Cozzuol, 1996, p. 327.

Dioplotherium, Cione *et al.*, 2000, p. 198.

cf. *Dioplotherium*, Domning, 2001, p. 29.

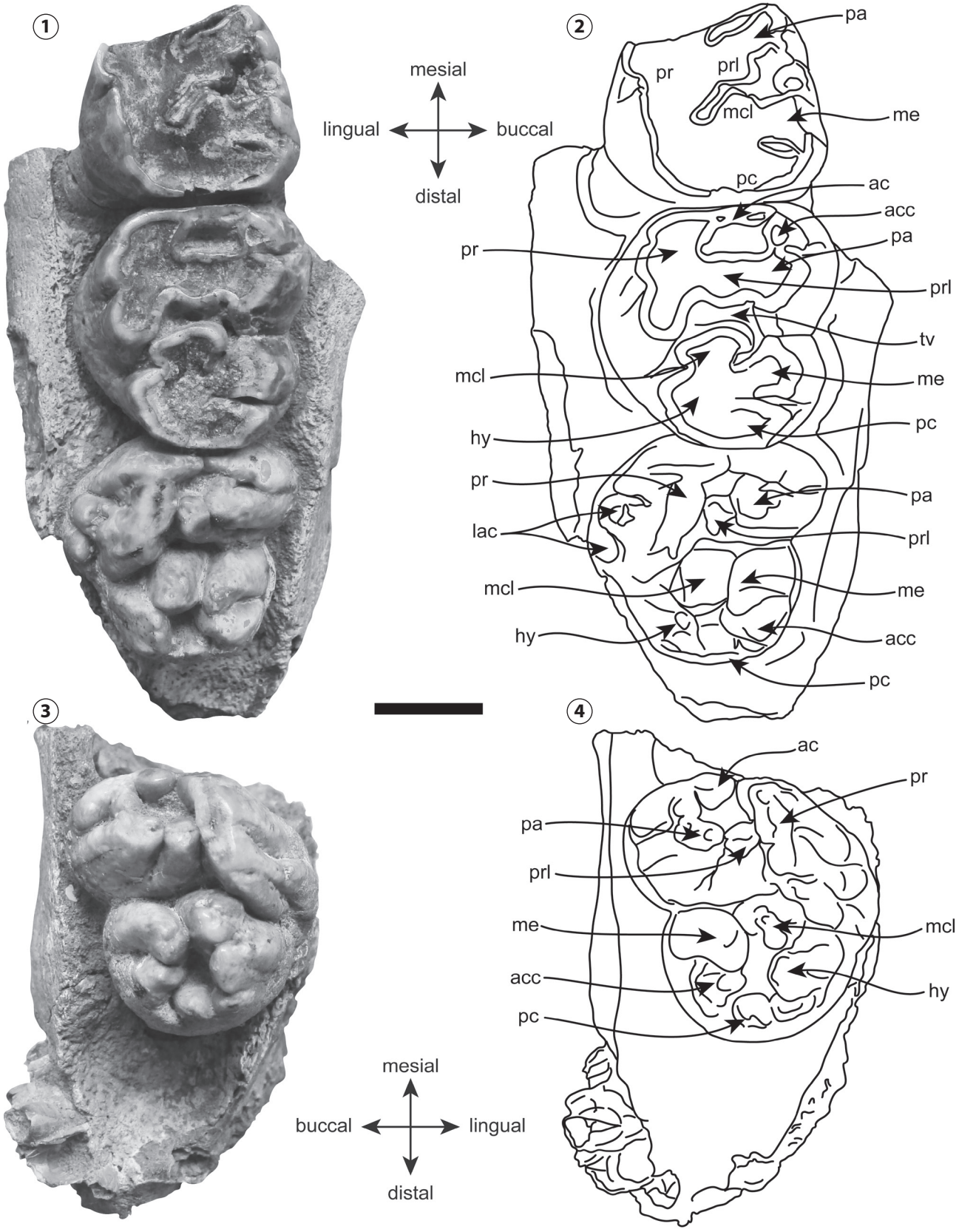

Figure 3. ***Metaxytherium*** sp., MASP 373; **1–2,** occlusal view of left M1–3/ *vista oclusal de M1-3 izquierdos*; **3–4,** occlusal view of right M3/ *vista oclusal del M3 derecho*. See text for abbreviations/ *ver el texto para las abreviaturas*. Scale/ *escala*= 1 cm.

Referred material. CORD-PZ 4301, upper left M3 (Fig. 4).
Locality. Cliffs along Paraná River, Villa Urquiza, Entre Ríos Province, Argentina.
Horizon and age. Paraná Formation, late Miocene.
Description. CORD-PZ 4301 is of similar size to the M3 of the Brazilian *Dioplotherium* (MPEG-64V) (Tab. 1; Toledo and Domning, 1991: tab. 1). However, they differ in that CORD-PZ 4301 has a broader anterior cingular valley, a protocone that projects less far distally, and a metacone that is located distobuccal to the metaconule (see Reinhart, 1976: fig. 32; tab. 7). Both CORD-PZ 4301 and the Brazilian *Dioplotherium* differ from M3 of MASP 373 in lacking accessory cusps, enamel surface not extensively folded and fissured, anterior cingular valley open buccally, and a more lingually located metaconule.
Remarks. This tooth was originally assigned to the dugongid genus *Metaxytherium* by Reinhart (1976). However, since then, several authors (Cozzuol, 1996; Cione *et al.*, 2000; Domning, 2001) have referred it to another genus, *Dioplotherium*. Two species of *Dioplotherium* are known: *D. manigaulti* from the late Oligocene of the east coast of North America (Domning, 1989b) and *D. allisoni* from the middle Miocene of Baja California and California (Kilmer, 1965; Domning, 1978). *D. manigaulti* is known from a nearly complete skull, but only the heavily worn M2 are preserved (Domning, 1989b), making it unsuitable for comparison with the Paraná material. A well preserved skull and mandibles and cranial material belonging to two other skulls from the early Miocene Pirabas Formation of Brazil have been tentatively assigned to *D. allisoni* (Toledo and Domning, 1991). The Brazilian *Dioplotherium* does preserve most of the dentition, which allows the comparison with CORD-PZ 4301 (see description above).

***TABLE 1- Linear dimensions (in mm) of cheek teeth of* Metaxytherium *sp. and* Dioplotherium *sp./* dimensiones lineales (en mm) de dientes mandibulares de *Metaxytherium* sp. and *Dioplotherium* sp. *L, crown length/* largo de la corona*; AW, anterior width/* ancho anterior*; PW, posterior width/* ancho posterior.**

	Metaxytherium *sp.*		Dioplotherium *sp.*
Tooth and dimension	*(Left)*	*(Right)*	*(Left)*
M1 L	*17.3*	–	–
M1 AW		–	–
M1 PW	*19.6*	–	–
M2 L	*22*	–	–
M2 AW	*21*	–	–
M2 PW	*16.1*	–	–
M3 L	*21*	*23*	*25*
M3 AW	*22*	*21*	*18*
M3 PW	*16.1*	*17*	*14.5*

DISCUSSION

The sirenians from the Paraná Formation represent the southernmost occurrence of *Metaxytherium* and *Dioplotherium*, as well as the geologically youngest occurrence of dugongids in the southern WAC. Both genera have been previously reported together from the same age and horizon, *i.e.*, from the early Miocene Pirabas Formation in Brazil (Toledo and Domning, 1991; Berqvist *et al.*, 1999).

From a paleobiogeographic point of view, the presence of these taxa as far south as Entre Ríos in Argentina can be interpreted by dispersal across a connection between the "Amazonian" and the "Paranense" seas or by migration along the marine coast during Miocene times.

Hypotheses about the occurrence of a late Tertiary seaway that connected the Caribbean and the Amazonian regions to the South Atlantic through the Subandean zone have been largely debated (Ihering, 1927; Nuttal, 1990; Boltovskoy, 1991; Webb, 1995; Räsänen *et al.*, 1995; Hernández *et al.*, 2005; Latrubesse *et al.*, 2010). Paleontological and geological evidence seems to be controversial or, at least, not definitive to support this scenario (Rebata *et al.*, 2006; Latrubesse *et al.*, 2010). Based on radiometric dates and analyses of tectonic/eustatic controls during the South American Miocene, Hernández *et al.* (2005) suggested that the 15–13 Ma transgression registered in Argentina by sediments of the Paraná Formation produced no continental connection to the Caribbean or Amazonian transgressions.

On the other hand, Pérez *et al.* (2010) stated that the present and fossil distribution of species of the bivalves *Polymesoda* and *Erodona*, which are known from the Paraná Formation, are indicative of a probably marginal connection between a southern arm of the "Amazonian Sea" and the northernmost reaches of the Paraná Basin. This hypothesis is based on the peculiar ecological requirements of extant members of these taxa, which are restricted to brackish or freshwater environments, making it highly unlikely that they instead migrated along the Atlantic coast of South America (Pérez *et al.*, 2010).

Paleogeographic reconstructions of South America during the interval when the "Amazonian Sea" was present show three main portals into this inland sea (Webb, 1995: 361; fig. 1). It is then tentative to envision a scenario where the Pirabas Formation dugongids, although somewhat older (*i.e.,* early–middle Miocene; see Rossetti, 2001), entered this

inland sea through the "East portal seaway" (Rebata *et al.*, 2006) and migrated down to the Entre Ríos Province where they gave rise to the Paraná dugongids. However, dugongids are tied to the distribution of their main food source, seagrasses, which are largely marine and would not have been present in brackish or maybe even freshwater conditions within the "Amazonian Sea". It therefore seems more probable that the Paraná dugongids dispersed along the South American marine coast, where it is more likely that seagrasses were present, and reached the high latitudes of Entre Ríos Province by entering through the "Paranense Sea" from the south. The presence of this inland sea likely played a major role in the evolutionary history of trichechids as well as other marine-derived taxa (Webb, 1995).

The presence of the dugongids *Dioplotherium* and *Metaxytherium* in Argentina represents the southernmost occurrence of these taxa in the Western Atlantic and Caribbean. These two taxa were probably sympatric, as was the case in the Pirabas Formation and other areas of the WAC region (Toledo and Domning, 1991; Domning, 2001; Vélez-Juarbe *et al.*, 2012). The occurrence of dugongids also serves as a proxy for the presence of seagrasses in an area where they are nowadays absent (Green and Short, 2003). Evidences provided by microfossils and sedimentological facies suggest that the "Paranense Sea" was a shallow embayment, including littoral to sub-littoral environments with transgressive characteristics, and representative of temperate to warm waters (Aceñolaza, 2000; Marengo, 2000). The "Paranense Sea" likely provided an ideal habitat for sirenians and seagrasses, by giving shelter from the open Atlantic Ocean. The extinction of dugongids in this region could have been caused by changes in the depositional environments and reduction of habitat and/or extinction of the seagrasses.

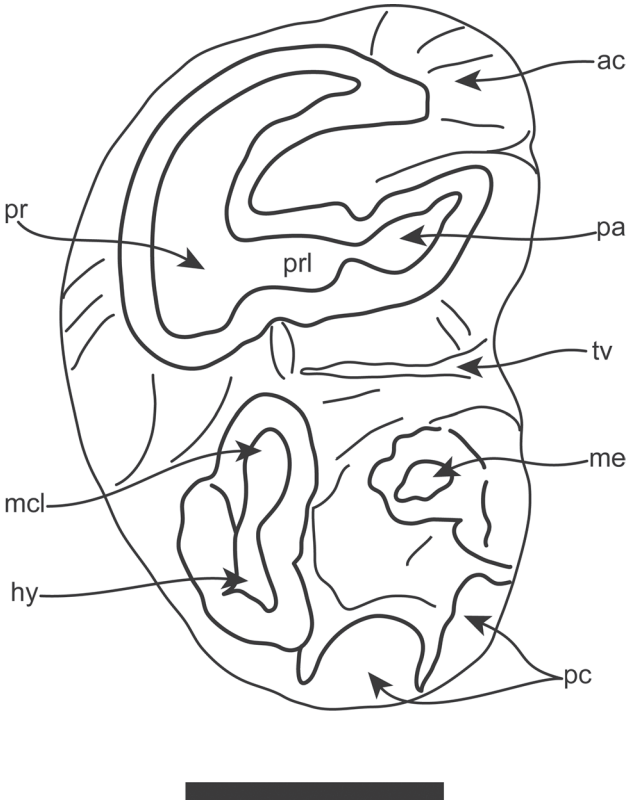

Figure 4. ***Dioplotherium*** sp. CORD-PZ 4301; occlusal view of left M3, modified from Reinhart (1976)/ *vista oclusal del M3 izquierdo, modificado de Reinhart (1976)*. See text for abbreviations/ *ver el texto para las abreviaturas*. Scale/ *escala*= 1 cm.

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