THE OLDEST MAMMALS FROM ANTARCTICA, EARLY EOCENE OF THE LA MESETA FORMATION, SEYMOUR ISLAND

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Abstract: New fossil mammals found at the base of Acan-tilados II Allomember of the La Meseta Formation, from the early Eocene (Ypresian) of Seymour Island, represent the oldest evidence of this group in Antarctica. Two specimens are here described; the first belongs to a talonid portion of a lower right molar assigned to the sparnotheriodontid litoptern Notiolofos sp. cf. N. arquinotiensis. Sparnotheriodontid were medium- to large-sized ungulates, with a wide distribution in the Eocene of South America and Antarctica. The second specimen is an intermediate phalanx referred to an indeterminate Eutheria, probably a South American native ungulate. These Antarctic findings in sediments of 55.3 Ma query the minimum age needed for terrestrial mammals to spread from South America to Antarctica, which should have occurred before the final break-up of Gondwana. This event involves the disappearance of the land bridge formed by the Weddellian Isthmus, which connected West Antarctica and southern South America from the Late Cretaceous until sometime in the earliest Palaeogene.

Key words: West Antarctica, Palaeogene, Ypresian, tooth and bone morphology, ungulates, Sparnotheriodontidae.

Today Antarctica is the only continent with a complete lack of terrestrial mammals; their seas and shores are inhabited by only a small number of marine mammals adapted to extreme polar conditions. But in the geological past, and more precisely in the early Palaeogene, the climatic conditions and southern palaeogeography (during the final break-up of Gondwana) were very different. The record of fossil mammals is restricted to the Eocene of West Antarctica. Located east of the Antarctic Peninsula, Seymour (or Marambio) Island has produced marine and terrestrial mammals from shallow marine horizons of the Cucullaea I (Ypresian) allomembers of the La Meseta Formation and Submeseta Formation (Bartonian) (Montes et al. 2013; Reguero et al. 2013a).

In addition to cetaceans, the terrestrial mammal fossil record (Table 1) includes a gondwanatherе with close affinities to Sudamerica ameghinoi from the Selandian of Patagonia (Goin et al. 2006) and a wide diversity of therian mammals including a suite of ‘opposum-like’ metatherians (Goin et al. 1999) referable to ‘Didelphimorphia’ (Goin et al. 1999), Microbiotheria (Goin et al. 2007), Polydolopimorphia (Woodburne and Zinsmeister 1984; Chornogubsky et al. 2009) and Derozrynchidae (Goin et al. 1999). The placentals are represented by sparnotheriodontid litopterns (Bond et al. 2006) and astrapotheriids (Bond et al. 2011). Two other groups were possibly present in Antarctica but need further confirmation: xenarthrans were initially recorded based on an ungual phalanx (Carlini et al. 1992) and an isolated ca-niniform tooth (Vizcaíno and Scillato-Yané 1995), which later was reclassified as Mammalia incertae sedis (MacPhee and Reguero 2010). A possible insectivoran was identified based on a specimen that is now lost and not available for further comparison (Reguero et al. 2013a).

During the 2012–2013 austral summer, an Antarctic campaign organized by the Dirección Nacional del Antártico – Instituto Antártico Argentino (DNA–IAA) in collaboration with the Swedish Polar Research Secretariat (SWEDARP 2012/13) prospected for terrestrial vertebrates in the La Meseta Formation of Seymour Island (Fig. 1) and collected several mammalian remains. Among them, an isolated broken tooth and an intermediate phalanx of a terrestrial mammal from the lower levels of the formation at the ‘Channel Site’, south of Cape Wiman. These
two specimens come from a basal marine shell layer of the Acantilados II Allomember of La Meseta Formation (Montes et al. 2013). This level is stratigraphically lower than any other mammal-bearing unit in Antarctica. Here, we describe the two specimens, discuss several implications of their geographical and temporal presence and assign both of them to placental mammals and the tooth to a litoptern spartheriodontid.

Litopterna is an extinct order of South American native ungulates which, together with Notoungulata, are among
the main orders of the Cenozoic South American ungulate radiation (Simpson 1948). The Paleocene and Eocene forms show close affinities with didolodontid archaic ungulates, retaining a bunodont dentition (Protolipternidae) or at least low-crowned teeth (Notonychopidae). Litopterns from the Miocene up to the Pleistocene convergently resemble several Holartic ungulates in their adaptations, showing a tendency to reduce their number of digits (Proterotheriidae) comparable to equids, or, with a large size and a nasal proboscis, a camel-like aspect in Macrauchenia (Macraucheniidae). Sparnotheriodontids were medium- to large-sized ungulates known from the late Paleocene – early Eocene of São José de Itaborai, Brazil, several Eocene localities of Patagonia and Antarctica (Bond et al. 2006), and the middle Eocene of Mendoza, Argentina (López 2010).

MATERIAL AND METHODS

All the fossils and casts used for the comparisons are cited or mentioned with their corresponding repository number in the text. For photographing, the phalanx and the tooth were whitened with ammonium chloride (Feldmann 1989). Measurements were taken with a point digital calliper (Schwyz) and given in millimetres.

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

The tooth and the phalanx were collected on Seymour Island, east of the Antarctic Peninsula, at a locality informally called ‘Channel Site’ and here named as IAA 1/13 (or NRM locality 7) S 64°13.264′ W 056°38.196′ (Fig. 2). It was found in the Acantilados Allomember of the La Meseta Formation, in levels with Cucullaea and brachiopods. The Acantilados Allomember is composed of cross-bedded sands and silts, and shell beds and lenses with a dominance of veneroid bivalves (Marenssi et al. 1998). The fossiliferous level is equivalent to Acantilados II with its base dated as 55.3 Ma (Ivany et al. 2008; Montes et al. 2013), representing a fraction of the earliest Eocene epoch.

Besides the two specimens described here, vertebrates are represented by numerous shark and ray teeth, and penguin bones. This section of the La Meseta Formation, which is well exposed along the sea cliffs facing the López de Bertodano Bay and extends inland towards the south-east, was characterized by Sadler (1988) as having a high mud content, a paucity of shell beds and a well-preserved fine stratification. Its maximum thickness is 210 m, comprising a coarsening upward sedimentary succession made up of interlaminated sand/mud with a large-scale synsedimentary deformational feature (Marenssi et al. 1998). The calcareous silstones locally contain abundant molluscs, echinoderms, leaves, arthropods and fishes. Small wood fragments are often concentrated in the muds or in thin ferruginous concretionary seams. The depositional setting is interpreted to be an outer and middle estuary (Marenssi 1995).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, NY, USA; FMNH, Field Museum, Chicago, IL, USA; IGM, Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Museo Geológico, Bogotá, Colombia; MLP, División Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina; NRM, Swedish Museum of Natural History, Stockholm, Sweden.
SYSTEMATIC PALAEONTOLOGY

Sparnotheriodontidae classification is controversial. Dental evidence suggests that they are closely related to litopterns such as Anisolambdidae which, in turn, could be derived from the primitive Didolodontidae (Soria 2001). However, studies based on the association of isolated tarsals with sparnotheriodontid teeth placed them within ‘Condylarthra’ (Cifelli 1983; Bergqvist 2008), which now are no longer considered a valid order or a natural group. The classification of Sparnotheriodontidae used here follows Bond et al. (2009) in which they are considered as part of the Litopterna.

Class MAMMALIA Linnaeus, 1758
Order LITOPTERNA Ameghino, 1889
Family SPARNOTHERIODONTIDAE Soria, 1980

Genus NOTIOLOFOS Bond, Reguero, Vizcaíno, Marensi and Ortiz Jaureguizar, 2009

Type species. Notiolofos arquinotiensis (Bond, Reguero, Vizcaíno and Marensi, 2006).

Notiolofos cf. N. arquinotiensis (Bond, Reguero, Vizcaíno and Marensi, 2006)  
Figure 3

2006 Notolophus arquinotiensis Bond, Reguero, Vizcaíno and Marensi, pp. 166–174, figs 2–5.

FIG. 2. View of the north-west side of the Seymour Island. The arrow indicates the position of locality IAA 1/13.

FIG. 3. Notiolofos cf. N. arquinotiensis (Bond, Reguero, Vizcaíno and Marensi, 2006). Occlusal view of the talonid fragment of the lower right molar, MLP 13-I-25-1, and reconstruction of the complete tooth based on MLP 91-II-4-1 adjusted to fit with the fragmentary specimen. Scale bar represents 10 mm. Abbreviations: c, crest; co, cristid obliqua; ect, ectoflexid; hyp, hypoconid; hyptid, hypocristid; me, metaconid; tb, talonid basin. Top and left of the figure, mesial and lingual side, respectively.

Referred material. MLP 13-I-25-1 fragment of a brachydont lower right molar, probably m1 or m2, which preserves a portion of the talonid with most of the lingual side.
Distribution. Basal marine horizon of the Acantholados II Allo-
member of the La Meseta Formation. Early Eocene (Ypresian) from Seymour Island, Antarctica. Locality IAA 1/13 (or NRM locality 7).

Dimensions. The preserved portion of the tooth is 18.44 mm
long (mesiodistal) and 15.32 mm wide (labiolingual).

Comparative description. The distal side of the tooth is
represented by only a faint dentine rim limited by a labial enamel edge. The dentine margin matches with a small portion of the central part of the worn V-shaped 'labial lophid', formed by the cristid obliqua, hypoconid, hypo-
conulid and entoconid. The enamel edge is the lingual side of the above-mentioned lophid. The cristid obliqua
descends from the distal side of the metaconid up to the hypoconid; projecting from it, there is a shorter hypocrist-
tid that bends linguosaginal to the hypoconulid and probably the entoconid. Even though none of these talo-
id cusps is preserved, their position can clearly be inferred from the trajectory of the enamel edge. The talo-
id basin opens linguosaginally and mesially, and a rounded
crest descends from the distal part of the metaconid. The base of the lingual side of the tooth shows a wrinkled enamel structure.

The portion of the talonid is comparable to the same structure in N. arquinotiensis, particularly MLP 91-II-4-1 which represents a complete molariform (Bond et al. 2006). The new specimen differs from the latter only in having a smoother enamel surface and a more rounded crest descending from the metaconid. Because of the frag-
mentary nature of MLP 13-I-25-1, there is not enough information to differentiate the specimen properly from other taxa or to corroborate its assignment to N. arqui-
notiensis. Noteworthy is the long stratigraphical range of N. arquinotiensis, which has been found in the upper lev-
els of the La Meseta Formation (i.e. Campamento, Cuca-
lae I, Cucullaea II) and in the Submeseta Formation (Table 1). The new specimens come from the basal part of Acantholados II Allomember, which is stratigraphically lower than the above-mentioned levels. This is a consid-
erable time range for N. arquinotiensis, implying an evolu-
tionary stasis from 55.3 Ma up to 37.8 Ma, following dates of Montes et al. (2013). However, the extended bi-
chron of N. arquinotiensis might also be a consequence of the nonrecognition of other Notiolofos species due to the lack of knowledge of this form, which is represented only by isolated teeth and tooth fragments. New remains could falsify either of these hypotheses.

The teeth of many placental mammals, in contrast to those of most marsupials, show an enamel type characterized by layers of decussating enamel prisms, known as Hunter–Schreger bands (HSB). The change in prism orientation can be observed under low magnification from the outside and in sections as alternating light and dark bands. Usually, the slightly undulating HSB run horizontal-
ly around the tooth crowns (Koenigswald 1997). In contrast, the enamel of MLP 91-II-4-1 has vertically ori-
ented HSB like those described for N. arquinotiensis, other Sparnotheriodontidae, and bunolophoselenodont South American native ungulates (Line and Bergqvist 2005; Bond et al. 2006).

Vertical HSB are also present in extant Rhinocerotidae (Koenigswald 2000), and they are even more frequent in fossil rhinocerotids, some Asian tapiroids (Deperetelli-
daes), Dinocerata and South American Astrapotheria and Pyrotheria (Fortelius 1985, p. 60; Koenigswald 1997).

Class Mammalia Linnaeus, 1758
Eutheria incertae sedis
Figure 4

Referred material. MLP 13-I-25-2 intermediate phalanx.

Distribution. Basal marine horizon of the Acantholados II Allo-
member of the La Meseta Formation. Early Eocene (Ypresian) from locality IAA 1/13 (or NRM locality 7), Seymour Island, Antarctica.

Dimensions. The phalanx is well preserved, 20.45 mm wide and 11.4 mm in length, with a trapezoidal outline and a rough sur-
face.

Comparative description. On the proximal side, there are two shallow concavities for the articulation with the prox-
imal phalanx, with a marked prominence of the Tuberos-
itas flexoria. The dorsal edge of the proximal epiphysis is
convex, and the ventral side shows a central concavity in the position of the prominence mentioned above. There is a faint furrow over the latter concavity, with four-
rounded aligned foramina. Under each of the articulation fossae for the proximal phalanx, there are two ventral projections. The left and right borders of the epiphysis form a moderate acute angle that points out of the pha-
lanx. On the dorsal side of the bone, above the epiphysis,
there is a very small shelf that belongs to the Processus extensorius, the insertion of the tendon of the extensor
muscle of the fingers (Extensor digitorum communis in the hand and Extensor digitorum longus in the foot). The condyle is smaller than the epiphysis, being less than two-
thirds of the epiphysis width, more expanded over the ventral side of the phalanx and divided by an antero-pos-
terior sulcus marking the sagittal plane of the bone. There are two foramina in the dorsal part of the phalanx.

MLP 13-I-25-2 is symmetrical and compressed along the antero-posterior axis, so probably represents part of the third digit of the forelimb, because the other
Phalanges tend to be asymmetrical to varying degrees, and pedal phalanges tend to be longer. There are no derived characters that allow an unquestionable determination of the phalanx. Two different lines of evidence are used here to interpret and assign this specimen: the abundance and size of taxa already known to be present in the Antarctic fossil record and their general structure.

Marsupials are the most abundant and diverse mammals in the Antarctic fossil record. Among them, derorhynchids are relatively small sized, with m3 ranging from 1.25 mm long and 0.8 mm wide (*Derorhynchus minutus*, MLP 96-1-5-44) to 2.64 mm long and 1.84 mm wide (*Pauladelphys juanjoi*, MLP 95-1-10-2; Goin et al. 1999). The largest microbiotherian is *Woodburnodon casei* with an M2 or M3 (MLP 04-III-1-2) 4.96 mm long and 5.58 mm wide (Goin et al. 2007). The Antarctic polydolopids are referable to a single genus *Antarctodolops*, the largest sizes of which belong to A. dailyi with an m3 (MLP 96-1-5-2) 4.07 long and 2.49 mm wide (Chornogubsky et al. 2009). The phalanx described here is too large to be related to any known Antarctic marsupial, and a similar conclusion may be reached considering gondwanatherian mammals.

The presence of xenarthrans in Antarctica was based on an ungual phalanx (MLP 88-I-1-95) assigned to a megatherioid or a myrmecophagid (Carlini et al. 1992). A direct comparison of the intermediate phalanges of extant *Myrmecophaga tridactyla* (MLP 1232) and the fossil mylodontids *Lestodon* (MLP 3-3), *Glossotherium* (MLP 3-138) and *Scelidotherium* (MLP 3-401) shows that they have a very distinct morphology with a dorso-ventrally high and pronounced proximal articulation, very different from what is observed in MLP 13-I-25-2. Notwithstanding that the taxa available for comparison are Neogene, we reject xenarthrans as a probable assignment for the phalanx.

Litopterna are represented by several families in the South American Cenozoic. Sparnotheriodontidae are known only by dental remains. Even though, in *Victorlemonia prototypica* from the Itaborai SALMA (late Paleocene – early Eocene) of São José de Itaborai, Brazil, several postcranal elements have been questionably assigned to this taxon using equation regression models and relative abundance (Cifelli 1983; Bergqvist 2008; Gelfo and Lorente 2012), no phalanx is available to compare with this specimen. The only sparnotheriodontid

**FIG. 4.** Phalanx, MLP 13-I-25-2, in A, plantar; B, dorsal; C, distal; D, proximal views. Scale bar represents 10 mm. **Abbreviations.**

app, articular surfaces for proximal phalanges; con, condyle; pe, Processus extensorius; pf, proximal foramina; pp, plantal projections.
postcranials found in association with dentition belong to *Phoradius divortiensis* (MLP 87-II-20-72) from the Eocene of Mendoza province, but no phalanges are present either, preventing a direct comparison with this family.

Among litopterns available for comparison, macraucheniids like *Theosodon* (MLP 12-740 up to 12-735) from the Miocene of Patagonia (Santacrucian–Chasicoan SALMAs) have tridactyl feet with intermediate phalanges from digit two and four almost square in dorsal view and with an asymmetric proximal side. The third digit is longer but differs from the Antarctic specimen in the stronger distal condyle and the dorso-ventrally higher epiphysis. In prototheriids such as *Diadiaphorus* or *Thoatherium*, in which the third digit is the main support of the hindlimb (Soria 2001), the intermediate phalanx is never so wide and the ventral side of the epiphysis is strongly projected. The Antarctic phalanx resembles the third digit phalanx of *Megadolodus* (IGM 183544) from the Miocene of Colombia in its proportions and in having a proximal epiphysis wider than the distal one (Cifelli and Villarroel 1997).

The Antarctic Astrapotheria are represented by *Antarcodon sobrali*, known only by a right p4 or m1 (Bond et al. 2011). No postcranials of basal astrapotherians like trigonostylopids are known. In the middle Miocene *Astrapotherium* (FMNH P14251), the intermediate phalanx of the second digit differs from the one described here in being longer than wide (Riggs 1935).

Even though no Notoungulata are known from Antarctica, they are the most diverse ungulate group in the South American Cenozoic (Simpson 1948). In contrast to MLP 13-I-25-2, pentadactyl notoungulates like *Thomas-huxleya externa* (AMNH 28905) and *Anisotemnus distensus* (AMNH 28906) from the late Eocene of Patagonia (Vacan SALMA) show quadrangular intermediate phalanges, with the length of the bone as the longest axis. The proximal articulation is flat and their size almost the same as the distal articulation (Shockey and Flynn 2007). In these taxa, the proximal articulations of the intermediate phalanges in the second and third digit are slightly asymmetrical, and in the first and fifth digit, these phalanges are considerably longer. Another pentadactyl notoungulate, *Periaphragn harmeri* (MLP 12-2197) from the late Eocene (Priabonian age, Mustersan SALMA) of Patagonia, has wider intermediate phalanges, particularly the one of the third digit. It resembles the phalanx described here, but in contrast, it is transversally shorter and without the prominent ventral projections. Tridactyl notoungulates like the Miocene *Nesodon* (MLP 12-90) have a comparable outline of the intermediate phalanx of the third digit as the longer axis is also transverse, but in contrast, it is proportionally higher in dorso-ventral view, it is not as wide, and it shows a prominent and rounded condyle.

The Xenungulata are also unknown from Antarctica, and they are not a very diverse group in the Palaeogene of South America (Gelfo et al. 2008). Nevertheless, despite its smaller size, MLP 13-I-25-2 resembles *Carodnia vierai*, a pentadactyl form from Itaborai. The intermediate phalanx of the third digit of *C. vierai* (cast AMNH 49850) is wider than long and with the distal end shorter than the proximal articulation as in the Antarctic phalanx.

In sum, considering the diversity of Antarctic metatherians and gondwanatherians, and particularly their size, the phalanx MLP 13-I-25-2 cannot be undoubtedly assigned to any taxonomic group. In consequence, it is considered as a placental mammal *incertae sedis*, even though its main affinities suggest that it probably belongs to a South American native ungulate. The symmetry of the phalanx resembles more those of the intermediate phalanx of the third digit of litopterns, notoungulates and xenungulates, than those from other digits. The proportions of the phalanx are similar to the intermediate phalanx of the third digit of graviportal taxa such as *Elephas* and *Rhinoceros*. However, the size of the new specimen described here is of a smaller animal and not of one adapted to support great weights; but proportionally, it could have had an exceptional weight for its size. Mediportal mammals include animals with limbs primarily adapted to solve the problems of bearing weight but with some cursorial elements (e.g. digitigrade stance, loss of lateral digits and interlocked or fused metapodials), usually retained from a more cursorial ancestor (Coombs 1978). An objection to consider MLP 13-I-25-2 as a mediportal mammal could be its similarity to *C. vierai*, which has no cursorial adaptations but relatively short and somewhat robust limbs, with pentadactyl extremities.

**DISCUSSION**

The remains described here represent the oldest mammals known from Antarctica. The basal marine shell layer of the Acantilados II Allomember of the La Meseta Formation, where the tooth and the phalanx were found, is dated at 55.3 Ma (Montes et al. 2013). The phalanx is assigned to an indeterminate Eutheria, but it should be noted that after dismissed gondwanatheres, metatherians and xenungulates affinities, and considering the similarity with some South American native ungulates (i.e. *Carodnia, Megadolodus*), it probably belongs to one of them. In contrast, the sparnotheriodontid affinities of the tooth are clear. Sparnotheriodontids were medium- to large-sized ungulates, with a wide geographical distribution that includes several distant Palaeogene localities. They were already known to occur in younger units of the Eocene of Seymour Island in Antarctica (Bond et al. 2006) and
Eocene localities in South America such as São José de Itaboraí of Brazil (Paula Couto 1952), several Patagonian outcrops (Ameghino 1901; Soria 1980) and Divisadero Largo in Mendoza, Argentina (Simpson et al. 1962). These South American records and the presence of an Antarctic sparnotheriodontid at 55.3 Ma lead to the question of the minimum age at which the group spread over both the continents. This should have occurred before the final break-up of Gondwana, an event that involved the disappearance of the land bridge formed by the Weddellian Isthmus that connected West Antarctica and southern South America from the Late Cretaceous until sometime in the earliest Palaeogene (Eagles and Jokat 2014). An immigration event was suggested for the spar- notheriodontids from South America to Antarctica near the Vaca Sub-age (Casamayoran SALMA) or Riochican SALMA during the Eocene (Bond et al. 2006). This was based on the alleged morphological size stasis of Notolofos through most of the Eocene and on the record of Sparnotheriodon in Patagonia for the Vaca Sub-age. Phylogenetic and palaeobiogeographical analyses of sparnotheriodontids (Gelfo et al. 2013; Reguero et al. 2013b), taking into account the newly presented findings here, indicate that the minimum divergence date of Antarctic and Patagonian litopterns should be around 57–58 Ma. A similar value (58–59 Ma) was obtained based on astrapotheres (Gelfo et al. 2013; Reguero et al. 2013b), using a previous phylogeny (Bond et al. 2011). This minimum phylogenetic divergence time could indicate that isolation of terrestrial vertebrates in Antarctica had occurred 5 Ma prior to their known fossil record. This suggests that sparnotheriodontids and astrapotherians would not be unexpected in the upper Paleocene sediments of Valle de las Focas and Acantilados I Allomembers of the La Meseta Formation and also in the Cross Valley Formation.

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REFERENCES

AMEGHINO, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas Academia Nacional de Ciencias en Córdoba, 6, i–xxxii, 1–1027.

1901. Notices préliminaires sur des ongués nouveaux des terrains crétacés de Patagonie. Boletín de la Academia Nacional de Ciencias en Córdoba, 16, 350–426.

BERGQVIST, L. 2008. Postcranial skeleton of the upper Paleocene (Itaboraian) ‘Condylarthra’ (Mammalia) of Itaborai Basin, Brazil. 107–133. In SARGIS, E. J. and DAGOUSTO, M. (eds). Mammalian evolutionary morphology: a tribute to Frederick S. Szalay. Vertebrate Paleobiology and Paleoanthropology Series, 1, 440 pp.

BOND, M., REGUERO, M. A., VIZCAINO, S. F. and MARENSSI, S. A. 2006. A new ‘South American ungulate’ (Mammalia: Litopterna) from the Eocene of the Antarctic Peninsula. 163–176. In FRANCIS, J. E., PIRRIE, D. and CRAME, J. A. (eds). Cretaceous–Tertiary high-latitude palaeo-environments, James Ross Basin, Antarctica. Special Publications, Geological Society of London, 258, 216 pp.

— — and ORTIZ-JAUREGUIZAR, E. 2009. Notolofos, a replacement name for Notolophus Bond, Reguero, Vizcaín and Marenssi, 2006, a preoccupied name. Journal of Vertebrate Paleontology, 29, 979.

— — KRAMARZ, A., MACPHEE, R. and REGUERO, M. 2011. A new astrapother (Mammalia, Meridiungulata) from La Meseta Formation, Seymour (Marambio) Island, and a reassessment of previous records of Antarctic astrapotheres. American Museum Novitates, 3718, 1–16.

BORSUK-BIALYNICKA, M. 1988. New remains of Archaeoceti from Palaeogene of Antarctica. Polar Research, 9, 437–445.

BUONO, M. R., FERNANDEZ, M. S., TAMBUSSI, C., MÖRS, T. and REGUERO, M. A. 2011. Un arqueoceto (Cetacea: Archaeoceti) del Eoceno temprano tardío de Isla Marambio (formación La Meseta), Antártida. Ameghiniana, 48, 1499–1508.

CARLINI, A. A., SCILLATO-YÁNEZ, G. J., VIZCAÍNO, S. F. and DOZO, M. T. 1992. Un singular Myrmecophagidae (Xenarthra, Vermilingua) de edad Colhuehuapense (Oligoceno–Mioceno temprano) de Patagonia, Argentina. Ameghiniana, 29, 176.

CHORNOGUBSKY, L., GOIN, F. J. and REGUERO, M. A. 2009. A reassessment of Antarctic polydontoid marsupials (Middle Eocene, La Meseta Formation). Antarctic Science, 21, 285–297.

CIFELLI, R. L. 1983. Eutherian tarsals from the late Paleocene (Itaboraian) ‘Condylarthra’ (Mammalia) of Itabora. 133. In CIFELLI, R. L. and FLYNN, J. J. (eds). Vertebrate Paleontology Series, 285–297.

— — VILLARROEL, C. 1997. Paleobiology and affinities of Megadolodus. 265–287. In KAY, R. F., MADDEN, R. H., CIFELLI, R. L. and FLYNN, J. J. (eds). Vertebrate paleontology in the neotropics: the Miocene fauna of La Venta, Colomia. Smithsonian Institution Press, Washington, DC, 608 pp.

COOMBS, W. P. J. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. Quarterly Review of Biology, 53, 393–418.

EAGLES, G. and JOKAT, W. 2014. Tectonic reconstructions for paleobathymetry in Drake Passage. Tectonophysics, 611, 28–50.
FELDMANN, R. M. 1989. Whitening fossils for photographic purposes. 342–346. In FELDMANN, R. M., CHAPMAN, R. E. and HANNIBAL, J. T. (eds). Palaeotecniques. Paleontological Society Special Publication, 4, 358 pp.

FORTELIUS, M. 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. Acta Zoologica Fennica, 180, 1–76.

FOSTOWICZ-FRELIK, L. 2003. An enigmatic whale tooth from the upper eocene of Seymour Island, Antarctica. Polar Research, 24, 13–28.

GELFO, J. N. and LORENTE, M. 2012. The alleged astragalar remains of Didolodus Ameghino, 1897 (Mammalia, Pana- meriungulata) and a critic of isolated bone association models. Bulletin of Geosciences, 87 (2), 1–11.

LOPEZ, G. M. and BOND, M. 2008. A new Xenungula- ta (Mammalia) from the Paleocene of Patagonia, Argentina. Journal of Paleontology, 82, 329–335.

LOPEZ, G. M., ABELLO, M. A., REGUERO, M., SANTILLANA, S. N. and MARENSSI, S. 2013. The record of Palaeogene Ungulates and the demise of the South America–Antarctica land connection. 53. In LOBO, F. J., PÉREZ, L. F. and MARTOS, Y. M. (eds). Symposium: The Scotia Arc: geodynamic evolution and global implications. Granada, España, 129 pp.

GOIN, F. J., CASE, J. A., WOODBURN, M. O., VIZ- CAÍNO, S. F. and REGUERO, M. A. 1999. New discoveries of ‘opossum-like’ marsupials from Antarctica (Seymour Island, medial Eocene). Journal of Mammalian Evolution, 6, 335–364.

REGUERO, M. A., PASCUAL, R., VON KOENIGS- WALD, W., WOODBURN, M. O., CASE, J. A., VIET- TES, C., MARENSSI, S. A. and VIZCAÍNO, S. F. 2006. First gondwanatherian mammal from Antarctica. 135–144. In FRANCIS, J. E., PIRRIE, D. and CRAME, J. A. (eds). Cretaceous-Tertiary high-latitude palaeoenvironments, James Ross Basin, Antarctica. Geological Society of London, Special Publications, 258, 216 pp.

ZIMICZ, N., REGUERO, M. A., SANTILLANA, S. N., MARENSSI, S. A. and MOLY, J. L. 2007. New mammal from the Eocene of Antarctica, and the origins of the Mi- crobiotheria. Revista de la Asociación Geológica Argentina, 62, 597–603.

IVANY, L. C., LOHMANN, K. C., HASIUK, F., BLAKE, D. B., GLASS, A., ARONSON, R. B. and MOODY, R. M. 2008. Eocene climate record of a high southern lati- tude continental shelf: Seymour Island, Antarctica. Geological Society of American Bulletin, 120, 659–678.

KOENIGSWALD, W. V. 1997. Brief survey of enamel diver- sity at the schmelzmuster level in Cenozoic placental mammals. 137–161. In KOENIGSWALD, W. V. and SANDER, P. M. (eds). Tooth enamel microstructure. Balkema, Rotterdam, 288 pp.

2000. Two different strategies in enamel differentiation: Marsupialia versus Placentalia. 107–118. In TEAFORD, M., FERGUSON, M. W. J. and SMITH, P. (eds). Development, function and evolution of teeth. Cambridge University Press, New York, 328 pp.

LINE, S. R. P. and BERGGVIST, L. P. 2005. Enamel structure of Paleocene mammals of the São José de Itaborai basin, Brazil. 'Condylarthra', Litopterna, Notoungulata, Xenungulata, and Astrapotheria. Journal of Vertebrate Paleontology, 25, 924–928.

LINNAEUS, C. 1758. Tomus I. Systema Naturae, Tenth Edition. Laurentii Salvii, Holmiae, [1–4], 1–824.

LÓPEZ, G. M. 2010. Divisaderan: land mammal age or local fauna? 410–420. In MADDEN, R., CARLINI, A., VUCE- TICH, M. G. and KAY, R. (eds). The paleontology of Gran Barranca: evolution and environmental change through the Mid- dle Cenozoic of Patagonia. Cambridge University Press, New York, 448 pp.

MACPHEE, R. D. E. and REGUERO, M. A. 2010. Reinter- pretation of the middle Eocene record of Tardigrada (Pilosa, Edentata) from La Meseta Formation, Seymour Island, Ant- arctica. American Museum Novitates, 3689, 1–21.

MARENSSI, S. A. 1995. Sedimentología y paleoambientes de sedimentación de la formación La Meseta, Isla Marambio, Antártida. Unpublished PhD Thesis, Universidad de Buenos Aires, 502 pp.

SANTILLANA, S. N. and RINALDI, C. A. 1998. Paleo- ambientes sedimentarios de la alofomación de La Meseta (Eocene), Isla Marambio (Seymour), Antártida. Instituto Antártico Argentino, Contribución, 464, 51 pp.

MITCHELL, E. D. 1989. A new cetacean from the late Eocene La Meseta formation, Seymour Island, Antarctic Peninsula. Can-adian Journal of Fisheries and Aquatic Sciences, 46, 2219–2235.

MONTES, M., NOZAL, F., SANTILLANA, S., MARE- NSSI, S. and OLIVERO, E. 2013. Mapa Geológico de la isla Marambio (Seymour) Escala 1:20.000 Primera Edición. Serie Cartográfica Geoscientífica Antártica. Madrid-Instituto Geológico y Minero de España; Buenos Aires-Instituto Antártico Argentino.

PAULA COUTO, C. 1952. Fossil mammals from the beginning of the Cenozoic in Brazil. Condylarthra, Litopterna, Xenungulata and Astrapotheria. Bulletin of American Museum of Natural History, 99, 355–394.

REGUERO, M., GOIN, F., ACOSTA HOSPITALCHE, C., DUTRA, T. and MARENSSI, S. 2013a. Late Creta- ceous/Palaeogene west Antarctica terrestrial biota and its inter-continental affinities. Springer Briefs in Earth System Sciences, London, 120 pp.

ABELLO, M. A., GELFO, J. N., LÓPEZ, G. M., CANDELA, A. M., SANTILLANA, S. N. and MARENSSI, S. A. 2013b. Land vertebrates biogeography of West Ant- arctica/South America and the final break-up of Gondwana. 180–182. In LEPPÉ, M. (ed.). Avances en Ciencia Antártica Latinoamericana: VII Congreso Latinoamericano de Ciencia Antártica. Estudio Avanzado de Zonas Áridas (CEAZA) e Instituto Antártico Chileno, La Serena, Chile, 598 pp.

RIGGS, E. 1935. A skeleton of Astrapotherium. Geological Series of Field Museum of Natural History, 6, 167–177.

SADLER, P. 1988. Geometry and stratification of uppermost Cretaceous and Palaeogene units of Seymour Island, northern Antarctic Peninsula. 303–320. In FELDMANN, R. M. and WOODBURN, M. O. (eds). Geology and paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America, Memoir, 169, 566 pp.

SHOCKEY, B. J. and FLYNN, J. J. 2007. Morphological diversity in the postcranial skeleton of Casamayoran (Middle
to Late Eocene) Notoungulata and foot posture in notoungulates. *American Museum Novitates*, 3601, 1–26.

SIMPSON, G. G. 1948. The beginning of the age of mammals in South America. Part 1. Introduction. Systematics: Marsupialia, Edentata, Condylarthra, Litopterna and Notioprogonia. *Bulletin of the American Museum of Natural History*, 91, 1–232.

—— MINOPRIO, J. L. and PATTERSON, B. 1962. The mammalian fauna of the Divisadero Largo Formation, Mendoza, Argentina. *Bulletin of Museum of Comparative Zoology*, 127, 239–293.

SORIA, M. F. 1980. Una nueva y problemática forma de ungulado del Casamayorense. *Actas II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología* (Buenos Aires, 1978), *Actas II*, 193–203.

—— 2001. Los Proterotheridae (Litopterna, Mammalia), sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales*, 1, 1–167.

VIZCAÍNO, S. F. and SCILLATO-YANEZ, G. J. 1995. An Eocene tardigrade (Mammalia, Xenarthra) from Seymour Island, west Antarctica. *Antarctic Science*, 7 (4), 407–408.

—— REGUERO, M. A., MARENSSI, S. A. and SANTILLANA, S. N. 1997. New land mammal-bearing localities from the Eocene La Meseta Formation, Seymour Island, Antarctica. 997–1000. In RICCI, C. A. (ed.). *The Antarctic region: geological evolution and processes*. Terra Antartica Publication, Siena, 1206 pp.

WOODBURN, M. O. and ZINSMEISTER, W. J. 1984. The first land mammal from Antarctica and its biogeographic implications. *Journal of Paleontology*, 54, 913–948.