



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

by JAVIER N. GELFO<sup>1,2,3</sup>, THOMAS MÖRS<sup>4</sup>, MALENA LORENTE<sup>1,2</sup>,  
GUILLERMO M. LÓPEZ<sup>1,3</sup> and MARCELO REGUERO<sup>1,2,5</sup>

<sup>1</sup>División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina; e-mails: jgelfo@fcnym.unlp.edu.ar, mlorente@fcnym.unlp.edu.ar, glopez@fcnym.unlp.edu.ar, regui@fcnym.unlp.edu.ar

<sup>2</sup>CONICET

<sup>3</sup>Cátedra Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Avenida 122 y 60, (1900) La Plata Argentina

<sup>4</sup>Department of Palaeobiology, Swedish Museum of Natural History, PO Box 50007, SE-104 05, Stockholm, Sweden; e-mail: thomas.mors@nrm.se

<sup>5</sup>Instituto Antártico Argentino, Balcarce 290, (C1064AAF), Buenos Aires, Argentina

Typescript received 16 April 2014; accepted in revised form 3 June 2014

**Abstract:** New fossil mammals found at the base of Acantilados 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 *Notiolofo* 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 gondwanathere 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 Derorhynchidae (Goin *et al.* 1999). The placental mammals 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 unguinal phalanx (Carlini *et al.* 1992) and an isolated caniniform 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

**TABLE 1.** The terrestrial and marine mammals from the Eocene of La Meseta (Acantilados II, Campamento, Cucullaea I, Cucullaea II) and Submeseta formations in Seymour Island, James Ross Basin, Antarctic Peninsula.

Taxon	Stratigraphy	Age	Source
MAMMALIA			
POLYDOLOPIMORPHIA			
Fam. Prepidolopidae			
<i>Perrodolphys coquinense</i>	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (1999)
Fam. Polydolopidae			
<i>Antarctodolops dailyi</i>	<i>Cucullaea</i> I	Early Eocene	Woodburne and Zinsmeister (1984)
<i>Antarctodolops mesetaense</i>	<i>Cucullaea</i> I	Early Eocene	Chornogubsky <i>et al.</i> (2009)
MICROBIOTHERIA			
Fam. Microbiotheriidae?			
<i>Marambiotherium glacialis</i>	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (1999)
Fam. Woodburnodontidae			
<i>Woodburnodon casei</i>	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (2007)
'DIDELPHIMORPHIA'			
Fam. Derorhynchidae			
<i>Derorhynchus minutus</i>	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (1999)
<i>Pauladelphys juarjoi</i>	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (1999)
<i>Derorhynchidae</i> , gen. et sp. indet.	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (1999)
Fam. indet.			
<i>Xenostylos peninsularis</i>	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (1999)
MARSUPIALIA			
Fam. gen. and sp. indet.	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (1999)
GONDWANATHERIA			
Fam. Sudamericidae			
<i>Sudamerica?</i> sp.	<i>Cucullaea</i> I	Early Eocene	Goin <i>et al.</i> (2006)
XENARTHRA			
Tardigrada indet.	<i>Cucullaea</i> I	Early Eocene	Bond <i>et al.</i> (2006)
LITOPTERNA			
Fam. Sparnotheriodontidae			
<i>Notiolofof arquinoiensis</i>	Acantilados II, <i>Cucullaea</i> I, <i>Cucullaea</i> II, Submeseta Fm.	Early–Late Eocene	Bond <i>et al.</i> (2006) and this paper
ASTRAPOTHERIA			
Fam. Astrapotheriidae			
<i>Antarctodon sobrali</i>	<i>Cucullaea</i> I	Early Eocene	Bond <i>et al.</i> (2011)
INSECTIVORA' or DRYOLESTIDA			
gen. et sp. indet.	<i>Cucullaea</i> I	Early Eocene	Reguero <i>et al.</i> (2013a)
MAMMALIA INCERTAE SEDIS			
gen. et sp. indet.	Campamento	Early Eocene	Vizcaíno <i>et al.</i> (1997)
CETACEA			
Fam. Basilosauridae			
<i>Zeuglodon</i> sp.	Submeseta Fm.	Late Eocene	Borsuk-Bialynicka (1988)
<i>Zygorhiza</i> sp.	<i>Cucullaea</i> I	Early Eocene	Reguero <i>et al.</i> (2013a)
<i>Dorudontinae?</i>	Submeseta	Late Eocene	Fostowicz-Frelik (2003)
<i>Pelagiceti</i> gen. et sp. nov.	<i>Cucullaea</i> I	Early Eocene	Buono <i>et al.</i> (2011)
MYSTICETI			
CRENATICETI			
<i>Llanocetus denticrenatus</i>	Submeseta Fm.	Late Eocene	Mitchell (1989)

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 implica-

tions of their geographical and temporal presence and assign both of them to placental mammals and the tooth to a litoptern sparnotheriodontid.

Litopterna is an extinct order of South American native ungulates which, together with Notoungulata, are among

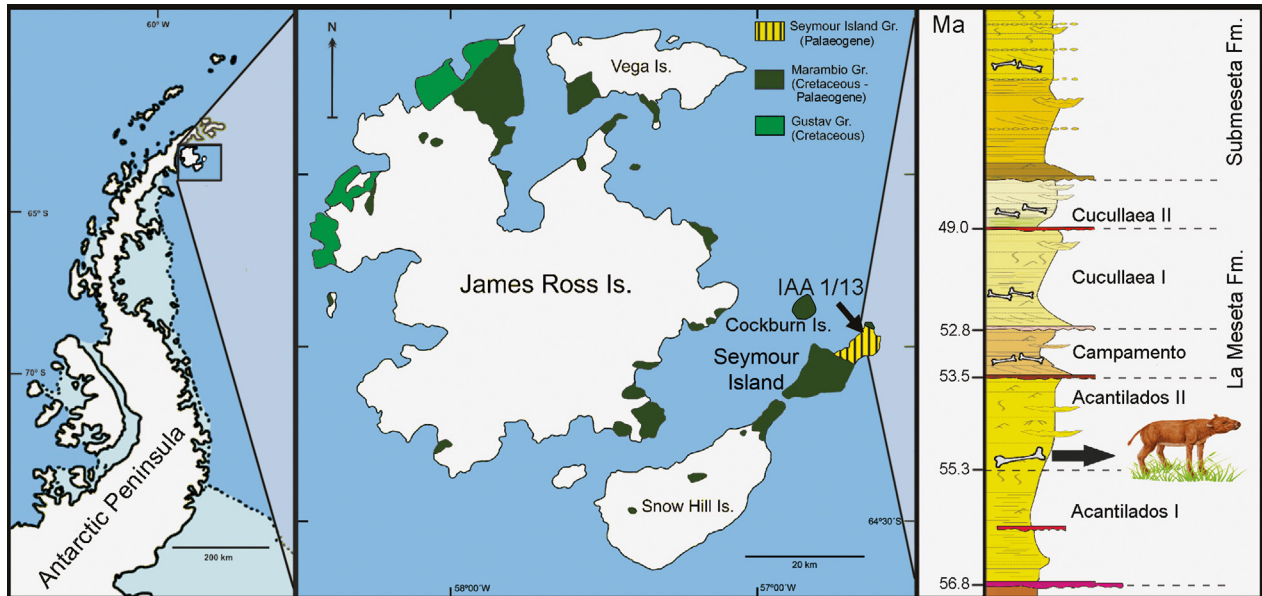


FIG. 1. Geographical and stratigraphical provenance of the remains described here.

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 Holarctic 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* (Macrauchiidae). Sparnotheriodontids were medium- to large-sized ungulates known from the late Paleocene – early Eocene of São José de Itaboraí, 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 (Marensi *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 inter-laminated sand/mud with a large-scale syndepositional deformational feature (Marensi *et al.* 1998). The calcareous siltstones 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 (Marensi 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.



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

*Other abbreviations.* HSB, Hunter–Schreger bands; SALMA, South American Land Mammal Age.

## SYSTEMATIC PALAEOLOGY

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

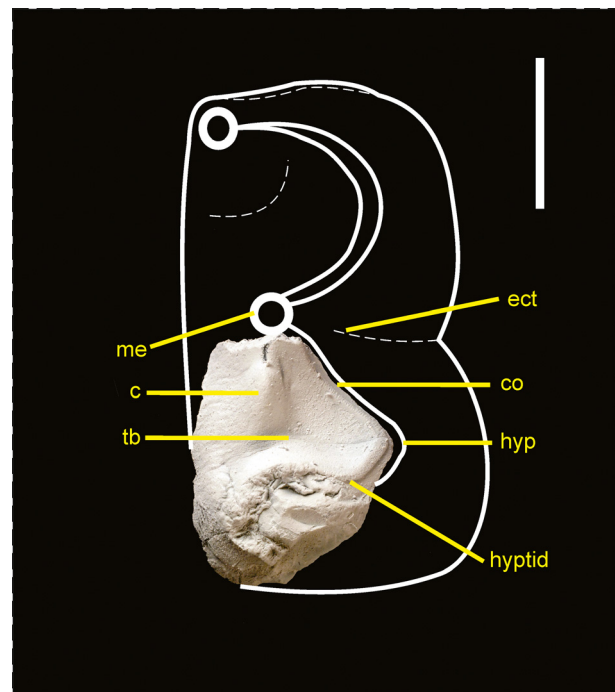
Genus NOTIOLOFOS Bond, Reguero, Vizcaíno, Marensi and Ortiz Jaureguizar, 2009

*Type species.* *Notiolofof arquinoiensis* (Bond, Reguero, Vizcaíno and Marensi, 2006).

*Notiolofof cf. N. arquinoiensis* (Bond, Reguero, Vizcaíno and Marensi, 2006)

Figure 3

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



**FIG. 3.** *Notiolofof cf. N. arquinoiensis* (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 brachyodont 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 Acontilados II Alломember 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, hypoconulid 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 hypocristid that bends lingually mesial to the hypoconulid and probably the entoconid. Even though none of these talonid cusps is preserved, their position can clearly be inferred from the trajectory of the enamel edge. The talonid basin opens lingually 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 fragmentary 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. arquinotiensis*. Noteworthy is the long stratigraphical range of *N. arquinotiensis*, which has been found in the upper levels of the La Meseta Formation (i.e. Campamento, Cucullaea I, Cucullaea II) and in the Submeseta Formation (Table 1). The new specimens come from the basal part of Acontilados II Alломember, which is stratigraphically lower than the above-mentioned units. This is a considerable time range for *N. arquinotiensis*, implying an evolutionary stasis from 55.3 Ma up to 37.8 Ma, following dates of Montes *et al.* (2013). However, the extended biochron of *N. arquinotiensis* might also be a consequence of the nonrecognition of other *Notiolofo*s 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 horizontally around the tooth crowns (Koenigswald 1997). In contrast, the enamel of MLP 91-II-4-1 has vertically oriented 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 (Deperetellidae), Dinocerata and South American Astrapotheria and Pyrotheria (Fortelius 1985, p. 60; Koenigswald 1997).

#### Class Mammalia Linnaeus, 1758

##### *Eutheria incertae sedis*

##### Figure 4

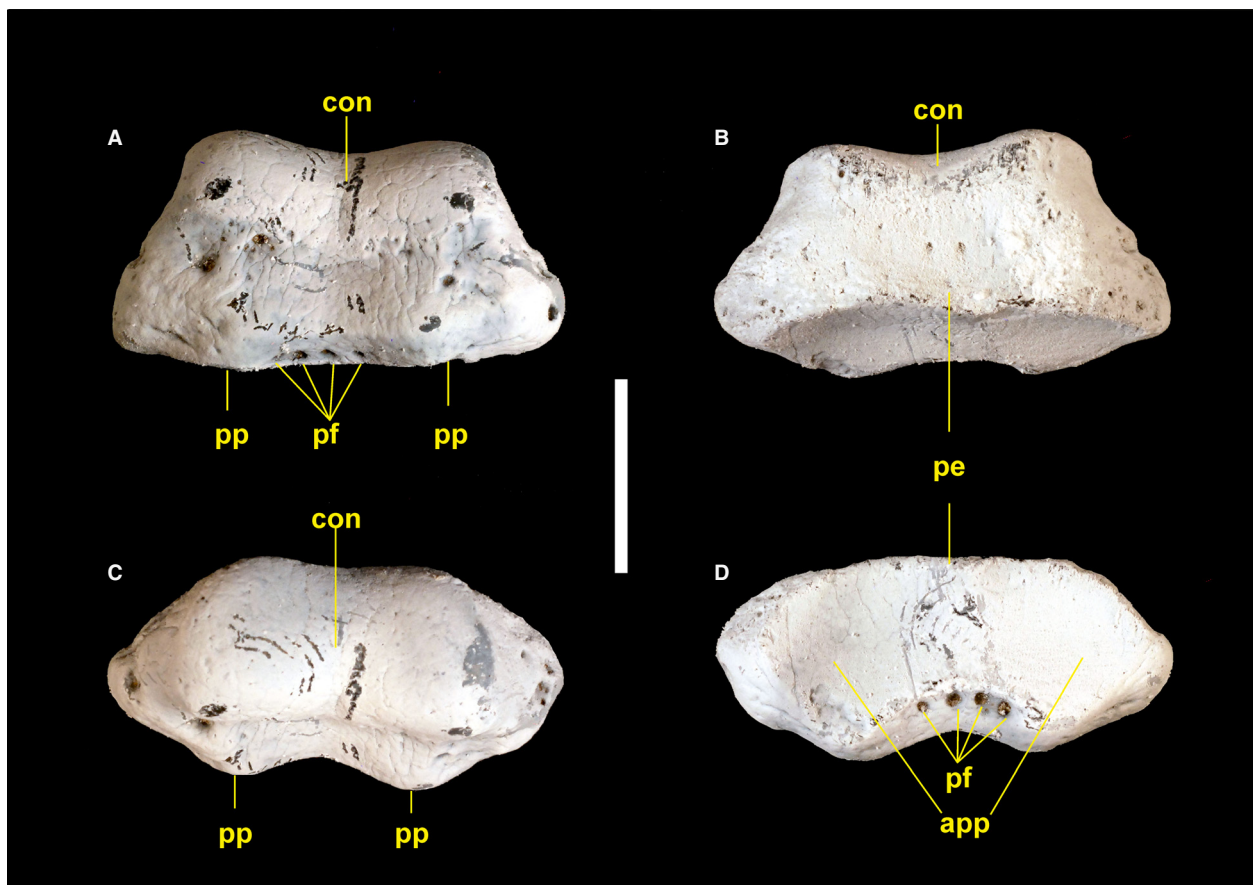
*Referred material.* MLP 13-I-25-2 intermediate phalanx.

*Distribution.* Basal marine horizon of the Acontilados II Alломember 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 surface.

*Comparative description.* On the proximal side, there are two shallow concavities for the articulation with the proximal phalanx, with a marked prominence of the Tuberositas 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 phalanx. 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-posterior 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



**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.

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 juanjoii*, 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 megatheriid 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 *Victorlemoinea prototypica* from the Itaboraian SALMA (late Paleocene – early Eocene) of São José de Itaboraí, Brazil, several postcranial 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

postcranials found in association with dentition belong to *Phoradiadus 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 12-753) from the Miocene of Patagonia (Santacrucian–Chasicuan 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 proterotheriids 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 *Antarcotodon 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 distentus* (AMNH 28906) from the late early 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, *Periphragnis 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 Itaboraí. 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 Acontilados 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 sparnotheriodontids from South America to Antarctica near the Vacan Sub-age (Casamayoran SALMA) or Riochican SALMA during the Eocene (Bond *et al.* 2006). This was based on the alleged morphological size stasis of *Notiolofofos* through most of the Eocene and on the record of *Sparnotheriodon* in Patagonia for the Vacan 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 astrapother palaeobiogeography (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 Acontilados I Allomembers of the La Meseta Formation and also in the Cross Valley Formation.

*Acknowledgements.* Our sincere thanks to both Instituto Antártico Argentino-Dirección Nacional del Antártico and Fuerza Aérea Argentina which provided great logistic support for our Antarctic fieldwork. We thank the support in the PRE-CAV fieldtrip of Luis Bouchet and the rest of Heidi Group: Carolina Acosta Hospitaleche, Sergio Santillana and Jacobo Daniel; and in the CAV fieldtrip of Leonel Acosta, Carolina Vieytes, Juan José Moly, Claudia Tambussi and Alejandra Abello. Cecilia Deschamps improved the English grammar. We thank Michael O. Woodburne, Darin Croft, Hannah O'Regan and Sally Thomas for their valuable comments and suggestions. The authors were supported by PICTO 2010-0093 (ANPCyT-Agencia Nacional de Promoción Científica y Tecnológica), PIP 0462 (CONICET-Consejo Nacional de Investigaciones Científicas y Técnicas), the Swedish Research Council (2009-4447) and the Swedish Polar Research Secretariat (2010-84).

*Editor.* Hannah O'Regan

## 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 ongulés 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 Itaboraí Basin, Brazil. 107–133. In SARGIS, E. J. and DAGOSTO, M. (eds). *Mammalian evolutionary morphology: a tribute to Frederick S. Szalay*. Vertebrate Paleobiology and Paleoanthropology Series, **1**, 440 pp.
- BOND, M., REGUERO, M. A., VIZCAÍNO, 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 palaeoenvironments, James Ross Basin, Antarctica*. Special Publications, Geological Society of London, **258**, 216 pp.
- — — and ORTIZ-JAUREGUIZAR E. 2009. *Notiolofofos*, a replacement name for *Notolophus* Bond, Reguero, Vizcaíno and Marenssi, 2006, a preoccupied name. *Journal of Vertebrate Paleontology*, **29**, 979.
- KRAMARZ, A., MACPHEE, R. and REGUERO, M. 2011. A new astrapothere (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., FERNÁNDEZ, M. S., TAMBUSI, 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**, 149R–150R.
- CARLINI, A. A., SCILLATO-YANÉ, G. J., VIZCAÍNO, S. F. and DOZO, M. T. 1992. Un singular Myrmecophagidae (Xenarthra, Vermilingua) de edad Colhuehuapense (Oligoceno tardío-Mioceno temprano) de Patagonia, Argentina. *Ameghiniana*, **29**, 176.
- CHORNOGUBSKY, L., GOIN, F. J. and REGUERO, M. A. 2009. A reassessment of Antarctic polydolopid marsupials (Middle Eocene, La Meseta Formation). *Antarctic Science*, **21**, 285–297.
- CIFELLI, R. L. 1983. Eutherian tarsals from the late Paleocene of Brazil. *American Museum Novitates*, **2761**, 1–31.
- and 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, Colombia*. 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). *Paleotechniques*. 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, Panameriungulata) and a critic of isolated bone association models. *Bulletin of Geosciences*, **87** (2), 1–11.
- LOPEZ, G. M. and BOND, M. 2008. A new Xenungulata (Mammalia) from the Paleocene of Patagonia, Argentina. *Journal of Paleontology*, **82**, 329–335.
- LÓPEZ, 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., WOODBURNE, M. O., VIZCAÍNO, 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 KOENIGSWALD, W., WOODBURNE, M. O., CASE, J. A., VIEYTES, 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. J. 2007. New mammal from the Eocene of Antarctica, and the origins of the Microbiotheria. *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 latitude continental shelf: Seymour Island, Antarctica. *Geological Society of American Bulletin*, **120**, 659–678.
- KOENIGSWALD, W. V. 1997. Brief survey of enamel diversity 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 BERGQVIST, L. P. 2005. Enamel structure of Paleocene mammals of the São José de Itaboraí 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., VUCETICH, M. G. and KAY, R. (eds). *The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia*. Cambridge University Press, New York, 448 pp.
- MACPHEE, R. D. E. and REGUERO, M. A. 2010. Reinterpretation of the middle Eocene record of Tardigrada (Pilosa, Edentata) from La Meseta Formation, Seymour Island, Antarctica. *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. Paleoambientes sedimentarios de la aloformación La Meseta (Eoceno), 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. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 2219–2235.
- MONTES, M., NOZAL, F., SANTILLANA, S., MARENSSI, S. and OLIVERO, E. 2013. Mapa Geológico de la isla Marambio (Seymour) Escala 1:20.000 Primera Edición. Serie Cartográfica Geocientífica 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 HOSPITALECHE, C., DUTRA, T. and MARENSSI, S. 2013a. *Late Cretaceous/Palaeogene west Antarctica terrestrial biota and its intercontinental 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 Antarctica/South America and the final break-up of Gondwana. 180–182. In LEPPE, 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 WOODBURNE, 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 Casamayorensis. *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-YANÉ, 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 Antarctica Publication, Siena, 1206 pp.
- WOODBURNE, M. O. and ZINSMEISTER, W. J. 1984. The first land mammal from Antarctica and its biogeographic implications. *Journal of Paleontology*, **54**, 913–948.