The fossil record of Antarctic land mammals: commented review and hypotheses for future research

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Abstract   The fossil record of terrestrial mammals in Antarctica is temporally and geographically constrained to the Eocene outcrops of La Meseta and Submeseta formations in Seymour (Marambio) Island in West Antarctica. The faunal assemblage indicates a clear South American imprint since all the groups have a close phylogenetic relationship with Cretaceous and Paleogene mammals from Patagonia. Despite the presence of several mammalian taxonomic groups: Dryolestida, Gondwanatheria, Eutheria and Metatheria, the presence of other major mammalian taxa should be expected and will probably be confirmed by new findings. Placental mammals with an inferred body mass between 10 to 400 kg in size, are represented by xenarthrans, and two groups of the so called South American native ungulates: Astrapotheria and Litopterna. The Metatheria are the smaller (less than 1 kg) and most abundant components of the fauna. Marsupials are represented by derorhynchid ameridelphians, several microbiotherian australidelphians (both microbiotheriids and woodburnodontids), and ?glasbiid prepidolopod and polydolopid polydolopimorphians. Plus, there are remains of several mammalian teeth of indeterminate phylogenetic affinities. The present knowledge of the Southern Hemisphere mammalian evolution and paleogeographic change through time, indicates that Antarctica played a major role for land mammals, at least since the Jurassic. The actual representation of Paleogene terrestrial mammals in Antarctica is most probably biased, as all the evidence indicates that australosphenidan mammals should be present in this continent since the Jurassic.

Keywords   **Antarctica, James Ross Basin, Jurassic, Paleogene, Eocene, Mammalia**

1   Introduction

In the last 35 years, two paleontological discoveries have changed our assessment and understanding of mammalian evolution. One is the discovery of Mesozoic mammals on Gondwanan continents (Kielan-Jaworowska et al., 2004), particularly in South America (Bonaparte and Soria, 1985) and Australia (Archer et al., 1985; Rich et al., 1997). The other is the presence of Paleogene land mammals in Antarctica (Woodburne and Zinsmeister, 1982, 1984), a fact that not only reinforces previous paleobiogeographic statements, but also triggers new questions about

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mammalian evolution. Today, with a surface of almost twice that of Australia and a polar climate, Antarctica is the only continent that experienced a complete extinction of terrestrial mammals. Extant mammals are solely represented by whales which inhabit the circumpolar seas around it, and seals which, while breeding on the coasts of Antarctica, completely depend on marine resources for their feeding.

The history of land mammals in Antarctica is constrained by a poor and scarce fossil record due to the existence of a huge ice sheet that covers the continent. This record is restricted to the Paleogene outcrops at Marambio (Seymour) Island (Figure 1) in the James Ross Basin

(Reguero et al., 2013) and allows just a brief glimpse into the evolution of mammals in Antarctica, as well as of the role played by this continent in mammalian evolution. The diversification of Mesozoic mammals (e.g. Gondwanatheria and Australosphenida) on the Gondwanan continents suggests that Antarctica was either a centre of origin and/or a main paleobiogeographic corridor.

In the present article, we review and update the knowledge of the fossil record of Antarctic terrestrial mammals, the main geological features of the localities where they were found, and discuss several hypotheses of what could be expected in future research.
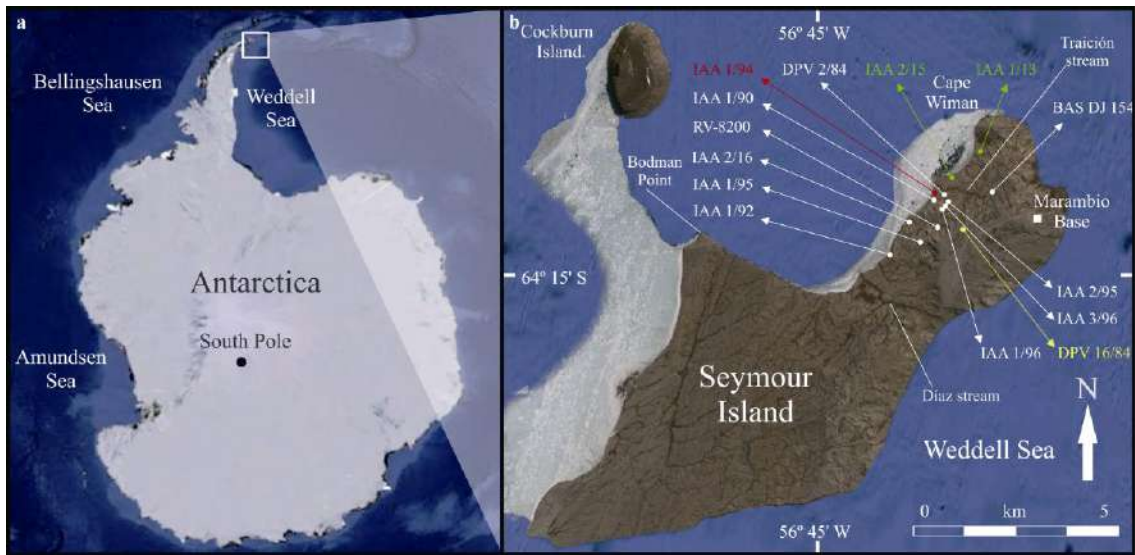
Figure 1 **a**, Map of Antarctica; **b**, Location of fossil land mammals localities on Seymour (Marambio) Island.

2 Geology and paleontological localities with land mammals

The geology of James Ross Basin, and particularly of Seymour Island, includes an important stratigraphic sequence of Upper Cretaceous and Palaeogene marine sedimentary rocks which, from base to top, comprise the Gustav (Aptian–Coniacian), Marambio (Santonian–Danian) and Seymour Island (Selandian–Rupelian) groups (Montes et al., 2013; Reguero et al., 2013). The terrestrial mammal fossil record is restricted to the last group, and particularly to particular levels of La Meseta and Submeseta formations.

The first geological studies of the sedimentary sequence outcropping in Seymour Island were made by the Swedish South Polar Expedition 1901–1903 led by Otto Nordenskjöld. Andersson (1906) distinguished at the south part of the island the Cretaceous "Older Seymour Island Beds" and in the northwest the Tertiary "Younger Seymour Island Beds". Part of these latter beds were named as La Meseta Formation and divided into three units by Elliot and Trautman (1982). The formation is composed of sandstones and mudstones with interbedded shell-rich conglomerates. Sadler (1988) divided

the formation into seven numbered units from Telm 1 through Telm 7, and later Marenssi et al. (1998) organized this sequence into erosionally based internal units or allomembers, which are the basis for the present stratigraphic framework. The recognized allomembers of the La Meseta Formation include from base to top: Valle de Las Focas, Acantilados I, Acantilados II, Campamento, *Cucullaea* I and *Cucullaea* II (Montes et al., 2013 and Figure 2). During the Eocene, these units were deposited in deltaic, estuarine and shallow marine settings, mostly within a NW–SE trending valley.

The Submeseta Formation of Montes et al. (2013) was first identified as another allomember of La Meseta Formation (Marenssi et al., 1998), equivalent to Telm 7 of Sadler (1988).

2.1 Acantilados II Allomember localities

IAA 1/13, informally called 'Channel Site', is a small flat pocket of no more than 25 m^2 at 64°13'15.84" S, 56°38'11.76" W (Figure 1), around 200 m from the coast at López de Bertodano Bay (Gelfo et al., 2015). 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); this composition is equivalent to the lower part of Telm 3 of Sadler (1988). The fossiliferous level is
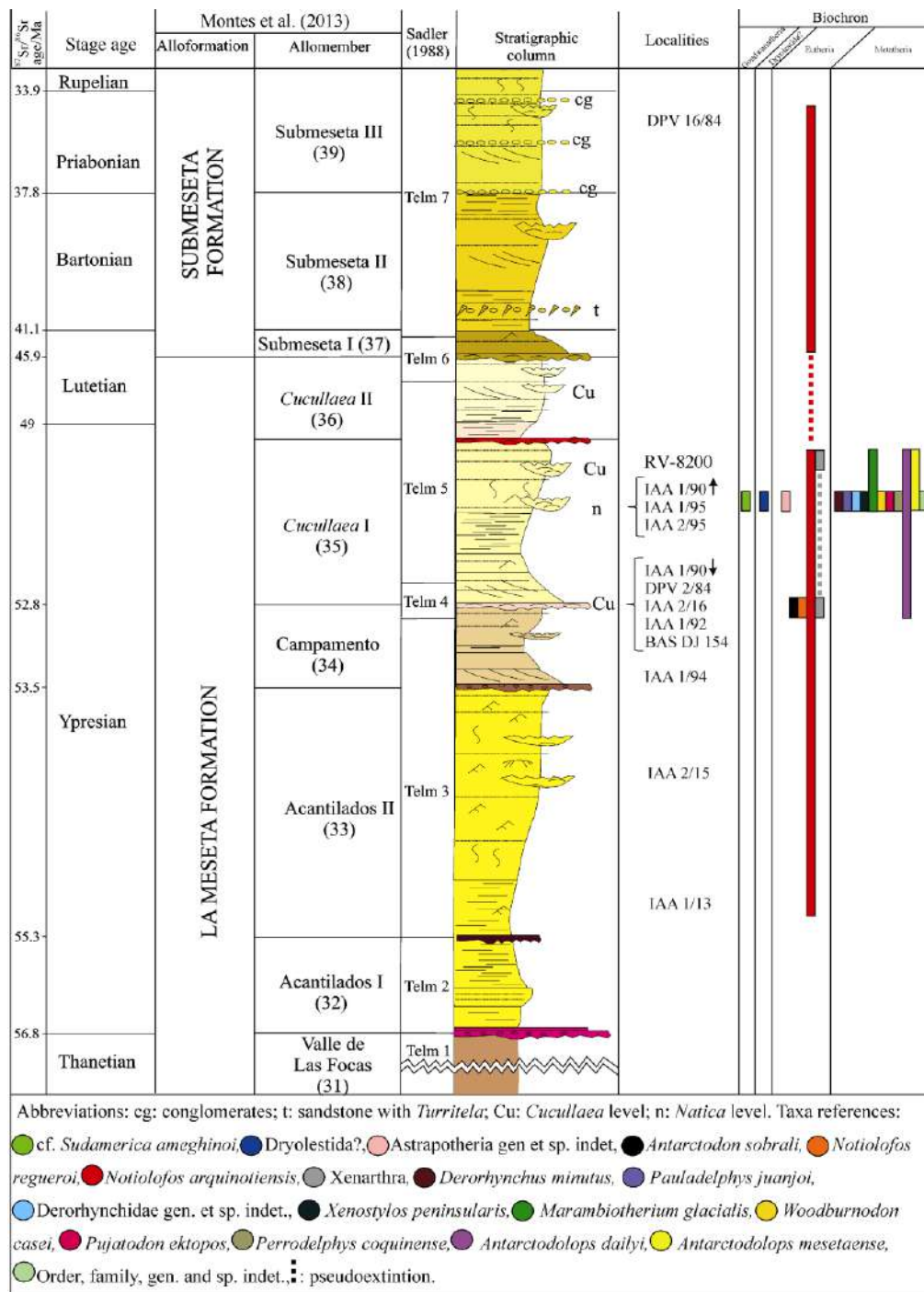
Figure 2 Stratigraphic column of La Meseta and Submeseta formations, showing the age of the fossiliferous localities and the biochron of the land mammals (modified from Montes et al., 2013). The precise stratigraphic positions of IAA 1/96 and IAA 3/96 in the *Cucullaea* I Allomember are not clear.

equivalent to Acantilados II, with its base dated at 55.3 Ma (Ivany et al., 2008; Montes et al., 2013) which is the oldest level where land mammals have been found in Antarctica.

IAA 2/15 is at 64°13'33.4" S, 56°39'06.4" W, around 480 m E-NE from the mouth of the Traición stream, in a flat surface round 30 m elevation and close to a cliff near the coast of López de Bertodano Bay (Figure 1). This

level represents a channel fill and is comparable to IAA 1/13, also from the same allomember, even though it is located stratigraphically higher in the sequence.

2.2 Campamento Allomember locality

IAA 1/94 is placed near the usual location of Geomarambio camp at 64°13'53.253" S, 56°39'51.239" W (Figure 1). This

place is located in the upper part of a 10 meter-thick, cross-bedded, sandy facies of fine to medium grained, massive to cross-bedded strata with mud drapes (Vizcaíno et al., 1998). The Campamento Allomember, crops out from sea level at López de Bertodano Bay and extends inland toward the east, along the northwest edge of the island. The unit was described by Marenssi (1995) and Marenssi et al. (1998) as 50 m of shelly channel fills and mud/sand interlamination with current and wave structures. The depositional setting was considered to be that of outer and middle estuary.

2.3 *Cucullaea* I Allomember localities

DPV 2/84 is located around 27.42 m above sea level, around 110 m of the left margin of Traición stream at 64°13'51.195" S, 56°39'21.992" W (Figure 1). This level constitutes the base of this unconformity-bounded allomember, equivalent to part of Telm 4 (Sadler, 1988), and represents the transition between Campamento and *Cucullaea* I allomembers. It has an erosive base, with a thickness of 4 m that could be traced laterally for several kilometers (Marenssi et al., 1998). An intense reworking and winnowing of the underlying deposits of Campamento Allomember, was detected in this lower coquina bed of the *Cucullaea* I Allomember (Sadler, 1988; Marenssi, et al., 2002).

BAS DJ 154, also known as "Hooker site" is located at 64°13'51" S, 56°37'36" W (Figure 1), near the nascence of the Traición stream in its right margin, and near the transect of Sadler's (1988: Fig. 3) north section. The level outcropping here is the basal and reworked coquina bed of *Cucullaea* I Allomember, equivalent to Telm 4 of Sadler (1988).

IAA 2/16 is a site of low hills SSW of Sergios Point near the coast of López de Bertodano Bay, at 64°14'16.5" S, 56°40'38.6" W (Figure 1). From base to top, the low hills include the Campamento Allomember and the basal conglomeratic shell bed of the *Cucullaea* I Allomember, equivalent to Telm 4 of Sadler (1988). This unit is the top of the exposed sediments and forms an extensive and flat surface over the mentioned hills, which are mapped as "level 35 Cu" in Montes et al. (2013).

IAA 1/92 is 75 m above sea level and is located at 64°14'43.9" S, 56°41'9.9" W, around 1000 m NW of the mouth of Díaz stream (Figure 1). Marenssi et al. (1994) mentioned the locality around 1500 m south of DPV 2/84 and indicated that both are part of the shell bed marking the base of the section of *Cucullaea* I Allomember, equivalent to Telm 4 of Sadler (1988). There are two misunderstandings about this locality. In the field one of the authors (JNG) confirmed that the stake placed at these coordinates indicates the name as IAA 2/92, a name never used in publications, rather than IAA 1/92. The other issue deals with the locality of the specimen MLP 92-II-2-135, mentioned in Bond et al. (2006) as IAA 1/92; contrary to its original description, it is regarded as Campamento

Allomember, and equivalent to Telm 3. This specimen was collected during the Antarctic summer campaign 1991 around 300 m from the Geomarambio camp, therefore, it is highly probable that the correct formal locality for it is IAA 1/94, which matches with the geographical coordinates (Vizcaíno et al., 1997).

IAA 1/90 is located at 64°14'06" S, 56°39'57.1" W, approximately 300 m north-west of locality RV-8200, at an elevation of about 50 m overlooking the coast (Figure 1). It was informally mentioned as "Ungulate site" (Marenssi et al., 1994), and there outcrop two different levels of *Cucullaea* I Allomember of La Meseta Formation. The lower conglomeradic shell bed, which unconformably overlies the Campamento Allomember, is equivalent to Telm 4 (Sadler, 1988) and was mapped as "level 35 Cu" by Montes et al. (2013). This level was interpreted as reworked from Campamento Allomember (Sadler, 1988; Marenssi et al., 2002). The upper level at IAA 1/90 belongs to the naticid conglomerate bank, mostly composed of *Polinices* sp., which is equivalent to Telm 5 of Sadler (1988). This level is over half of the allomember that was mapped by Montes et al. (2013) and can be followed through different hills where other land mammal localities are present. The reference IAA 1/90 sector "B" was mentioned by Goin et al. (1999) and probably belongs to the thinner section of sand beds of the upper level of the locality, near the informally known "Col Victor" at 64°14'09" S, 56°39'55.1" W (Santillana, pers. com.).

IAA 1/95 is about 500 m from Sergios Point at the coast of López de Bertodano, at 64°14'28.55" S, 56°40'18.59" W at 51 m.a.s.l. (Vizcaíno et al., 1997 and Figure 1). The level outcropping here is the continuity of the upper level in IAA 1/90, which is the naticid conglomerate bank that is also present in IAA 2/95.

IAA 2/95 is roughly 1000 m from the coast at 64°13'57.67" S, 56° 39'5.87" W, 41.46 m.a.s.l. (Vizcaíno et al., 1997; Figure 1).

IAA 1/96, as well as IAA 3/96, are two localities mentioned in Bargo and Reguero (1998). No coordinates were given but they were mapped in a small canyon which flows to the left margin of the last third of Traición stream (Figure 1) and is considered as equivalent to Telm 5. The position of both localities indicates that the levels belong to *Cucullaea* I Allomember, identified as 35 in Montes et al. (2013). Only a couple of mammalian teeth were found in MLP collections that are reported from these localities (Gelfo, 2016).

RV-8200: This was the first locality where fossil land mammals were found in Antarctica (Woodburne and Zinsmeister, 1984) and is probably the most worked area on Seymour Island. The locality is also known in as RV-8200 or DPV 6/84 (Bargo and Reguero, 1998) and is located at 64°14'21.782" S, 56°39'44.840" W, at 45.07 m (Figure 1). This level is placed in the upper third of *Cucullaea* I Allomember, over the upper bed outcropping in IAA 1/90.
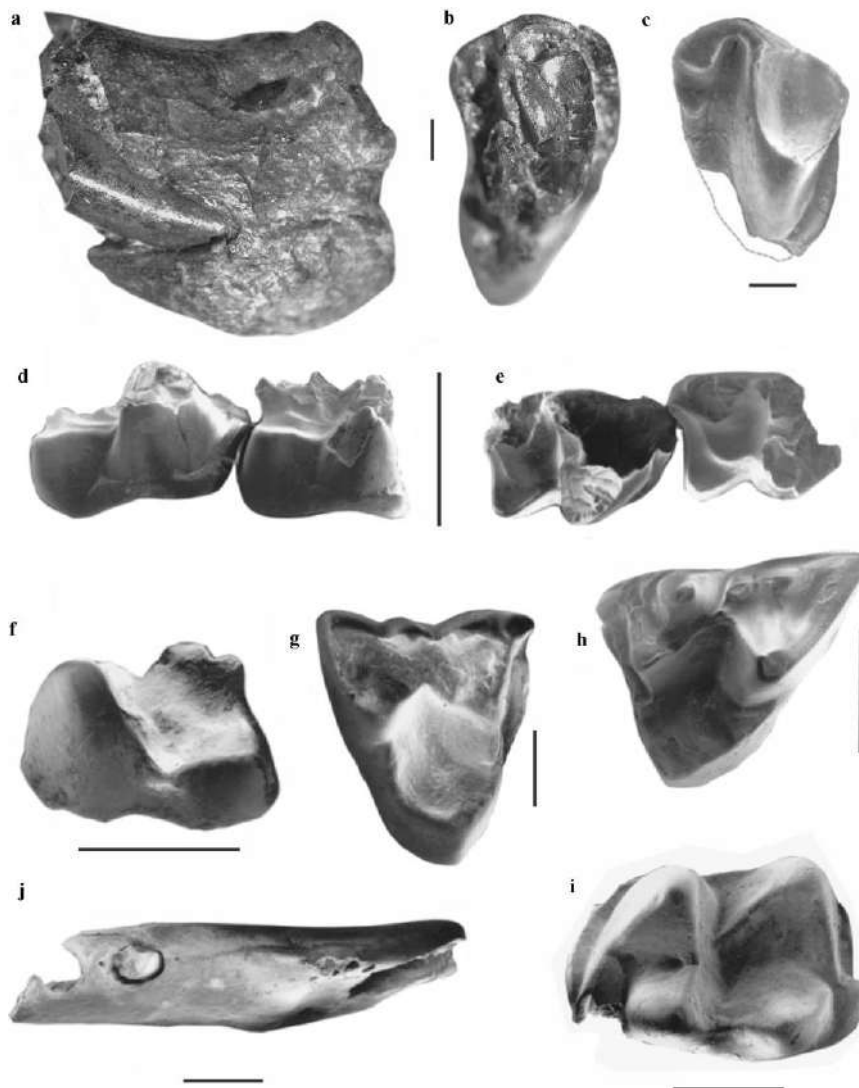
Figure 3 Non therian and metatherian mammals from the early-mid Eocene of Antarctica. **a–b**, Allotheria, Gondwanatheria, Sudamericidae cf. *Sudamerica ameghinoi*; specimen MLP 95-I-10-5, an anterior portion of a left dentary showing the enlarged, rodent-like incisor partially preserved in lateral (**a**), and frontal (**b**) views. **c**, Dryolestida, Meridiolestida, ?Brandoniidae gen. et sp. indet.; specimen MLP-91-II-4-3, a right ?lower molar in occlusal view. **d–i**, Metatheria, "Ameridelphia". **d–e**, *Derorhynchus minutus* (Derorhynchidae); specimen MLP 96-I-5-44 (holotype), a right dentary with partially broken m2-m3 in obliquely labial (**d**), and occlusal (**e**) views. **f**, Derorhynchidae, gen. et sp. indet.; specimen MLP 94-III-15-11, an isolated left lower molar in dorsolabial view. **g**, *Xenostylos peninsularis* (family indet.); specimen MLP 94-III-15-10 (holotype), an isolated right upper molar in occlusal view. **h–i**, *Pauladelphys juanjoi* (Derorhynchidae); specimens MLP 95-I-10-2 (holotype), an isolated right lower molar in occlusal view (**h**), and MLP 96-I-5-45, a left M?1 in occlusal view (**i**). **j**, ?Marsupialia, family, genus and species indet.; specimen MLP 92-II-1-5, a fragment of left dentary with the alveolus and root of the last molar in occlusal view. Scale: 1 mm. Photos are modified from Goin et al. (2006; **a–b**), Reguero et al. (2013; **c**), and Goin et al. (1999; **d–j**).

2.4 Submeseta Formation, Submeseta III Allomember

DPV 16/84 is around 200 m from the landing track of Marambio Base at 64°14' 30.501" S, 56°38' 44.571" W, at 189.53 m.a.s.l. (Figure 1). This part of the section is composed of thick cross-bedded sand, thin sheet-like pebbles beds and clay laminae, with a fauna of veneroid pelecypods, gastropods and brachiopods, bony fishes, penguins, and whales (Vizcaíno et al., 1997).

3 Systematic paleontology

ALLOTHERIA
Gondwanatheria
Sudamericidae
Gen. et sp. indet., cf. *Sudamerica ameghinoi*

Referred material: MLP 95-I-10-5 (Figures 3a–3b), anterior part of a left dentary with the rodent-like incisor partially preserved; specimen MLP 96-I-5-47, a ?left upper incisor broken at its proximal end, is tentatively referred to the same taxon.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90, upper level.

Comments: A preliminary description of these remains was made by Reguero et al. (2002) and a complete analysis is in Goin et al. (2006). Although superficially similar, the jaw does not belong to a polydolopine marsupial, the most abundant mammal in the La Meseta Formation; instead, it can be confidently referred to the Sudamericidae (Gondwanatheria). Based on the similarity of the spatial distribution of enamel types or Schemelzmuster and the absence of Hunter-Schreger bands, the Antarctic taxon seems more closely allied to the early Paleocene *Sudamerica ameghinoi* (Peligran SALMA) than to any other gondwanatherian or therian mammal (Goin et al., 2006). This specimen (MLP 95-I-10-5) and *S. ameghinoi* share lower incisor characteristics of a low inclination of the enamel prisms, the position of the neutral area, two layers of tangential enamel, a specific prism orientation in each layer, the straight orientation of the crystallites of the IPM and the disappearance of prisms in the outer layer, which led to the prevalence of the IPM. In contrast, in the isolated upper incisor, the enamel is thinner (20 µm) and the schmelzmuster consists only of one layer of radial enamel (Goin et al., 2006), a difference that is usually present between incisors of other mammal-like rodents. Even though no upper incisor was assigned to *Sudamerica ameghinoi*, MLP 96-I-5-47 was regarded as a Gondwanatheria. Based on its similarity to other gondwanatherians incisors, such as *Ferugliotherium windhauseni* (Krause et al., 1992), it was tentatively referred to the same taxon as MLP 95-I-10-5.

The few differences between the Antarctic specimen and *Sudamerica ameghinoi* (i.e. more pronounced angle between the inner and outer tangential enamel layers, better definition of the prisms), were considered as derived features in the former (Goin et al., 2006).

DRYOLESTIDA?
Meridiolestida
?Brandoniidae
Gen. et sp. indet.

Referred material: MLP-91-II-4-3, fragment of a left lower molar.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Comments: The specimen MLP-91-II-4-3 (Figure 3c) was lost before a formal description could be made. The small fragment of tooth with only one prominent cusp and a V-shaped crest, was initially compared to the last upper molar of some Chiroptera (e.g. Phyllostomatidae), but without any conclusive affinities. Other possible relationships considered, both with other insectivorous eutherians and with necrolestids, were not discarded (Goin and Reguero, 1993). Later, based on SEM photographs, MacPhee et al. (2008) discarded any possible relationship with extant bats and reinterpreted the specimen as a probable zalambdodont premolar. Although it does not closely resemble any other therian, they found similarities to certain tenrecids, *Necrolestes*, and *Oligoryctes*. The specimen was considered as a Mammalia *incertae sedis* (Reguero et al., 2013), and later, reevaluated as part of a right lower molar of a dryolestoid mammal probably related to, or member of the clade Meridiolestida (Martinelli et al., 2014). This new interpretation considered the trigonid formed by three cusps and a distolingual talonid cusp. The protoconid is flanked mesially by the paracristid and distally by the metacristid, which reach the paraconid and metaconid, respectively. The para- and metacristid form an acute angle without notch at mid-way. The labial wall of the protoconid is convex while the lingual face is slightly concave. The paraconid is worn out, and lower than the other cusps. The flexid is notorious and forms a "v" shaped notch between paraconid and metaconid. The metaconid and protoconid are similar in height. The metaconid connects the talonid by means of a crest. The talonid has a hook-like, disto-lingual projection with a large cusp. The morphology closely resembles that of the meridiolestidans *Barberenia* and *Brandonia* from the Late Cretaceous of Patagonia. If proven correct, this interpretation reinforces previous inferred scenarios that show West Antarctic faunas as more closely related to those of the Paleogene of Patagonia than to any other mammalian fauna from the Southern Hemisphere.

During the Late Cretaceous, dryolestoid mammals experienced an important radiation in South America and, in contrast to the Cretaceous–Paleogene extinctions in the North Hemisphere, survived with specifics lineages recorded during the early Paleocene (Gelfo and Pascual, 2001) and Miocene (Rougier et al., 2012). Although the presence of Eocene meridiolestidans in Antarctica needs to be confirmed by new findings, the presence of the Weddellian Isthmus, acting as a land bridge between South America and Antarctica (Reguero et al., 2013) presents a good paleobiogeographical explanation for their presence in La Meseta Formation. Considering these previous statements and the high diversity of Dryolestoidea and Gondwanatheia in the Late Cretaceous of South America, finding representatives of these groups in Mesozoic outcrops of the James Ross Basin should be expected.

METATHERIA
"Ameridelphia"
Derorhynchidae
Derorhynchus minutus Goin et al. (1999)

Referred material: MLP 96-I-5-44 (only the type; Figure 3d–3e), a fragment of right dentary with m2-3.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Original description and discussion: see Goin et al. (1999).

Comments: *Derorhynchus minutus* is the smallest known species of this genus, and one of the smallest mammals so far known from the Paleogene of Antarctica. The genus had a wide latitudinal distribution. Comparable species, such as *D. singularis* are known from the early Eocene of São José de Itaboraí, Brazil (Oliveira and Goin, 2011). In the early Eocene Patagonian locality Laguna Fría, in Paso del Sapo, eight specimens of almost the same size as those of IAA 1-90, were assigned to *Derorhynchus* cf. *D. minutus* (Tejedor et al., 2009). All these forms share in their lower molars common features such as a small paraconid, relatively short talonid, and high spire-like entoconids.

Derorhynchidae were considered as representative of insectivorous feeding habits and probably constrained to feed on invertebrate resources (Goin et al., 2016).

Pauladelphys juanjoi Goin et al. (1999)

Referred material: MLP 95-I-10-2 (holotype; Figure 3h), an isolated lower molar; MLP 96-I-5-45 (Figure 3i), an upper left molar (M1?).

Stratigraphic and geographic provenance: All the specimens came from the *Cucullaea* I Allomember of La Meseta Formation, from the conglomerate level of naticid. The holotype comes from locality IAA 2/95 while the specimen MLP 96-I-5-45 was recovered from IAA 1/90, sector "B" (Figure 2).

Original description and discussion: see Goin et al. (1999).

Comments: Even though some features of *Paulaldephys juanjoi* resemble those of protodidelphid didelphoids, most other agrees well with its allocation within derorhynchid "ameridelphians". Its size, the comparatively wide trigon basin, and somewhat longer talonid, suggest insectivorous-omnivorous feeding habits rather than strictly insectivorous as in the case of *Derorhynchus minutus.*

Another species of the genera, *Pauladelphys* sp. nov., were reported from early Eocene of Paso del Sapo and is represented by isolated dentition, maxillae, and mandibles mostly from Laguna Fría and a few remains from La Barda localities. In contrast to *Pauladelphys juanjoi* this new species differs in having lower molars with a cristid obliqua more parallel to the dental axis; paraconid less reduced and mesiodistaly compressed; mesiobasal cingulum narrower, and an almost flat labial slope of the entoconid. These features suggest that the Patagonian one was a more generalized taxon than *P. juanjoi* (Tejedor et al., 2009).

Derorhynchidae gen. et sp. indet.

Referred material: MLP 94-III-15-11 (Figure 3f), an isolated lower left molar.

Original description and discussion: see Goin et al. (1999).

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Comments: The whole specimen is heavily worn and the mesiolingual side is broken so the paraconid side is missing. The general morphology of the talonid is not that of a last molar; indeed, it is more reminiscent in proportions and cusp morphology to m2 or m3 of *Derorhynchus singularis* from the early Eocene of São José de Itaboraí, Brazil (Oliveira and Goin, 2011).

Family indet.
Xenostylos peninsularis Goin et al. (1999)

Referred material: MLP 94-III-15-10 (Figure 3g), an isolated upper right molar.

Original description and discussion: see Goin et al. (1999).

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Comments: *Xenostylos* (not *Xenostylus*; preoccupied genera, see Goin, 2007) was originally referred to the Derorhynchidae by Goin et al. (1999). The most distinctive features of *Xenostylos peninsularis* are its low crown height, very wide trigon basin, deep V-shaped centrocrista, para- and metaconule almost merged at the base of the para- and metacone, a unique notch that divides the postparacrista, and the anterior "shifting" of StD in relation to most "ameridelphian" marsupials (some herpetotheriids being an exception). *Xenostylos peninsularis* differs strikingly from Antarctic derorhynchids, microbiotheriids, protodidelphids, and polydolopines, all of which seem to have more direct affinities with known South American taxa.
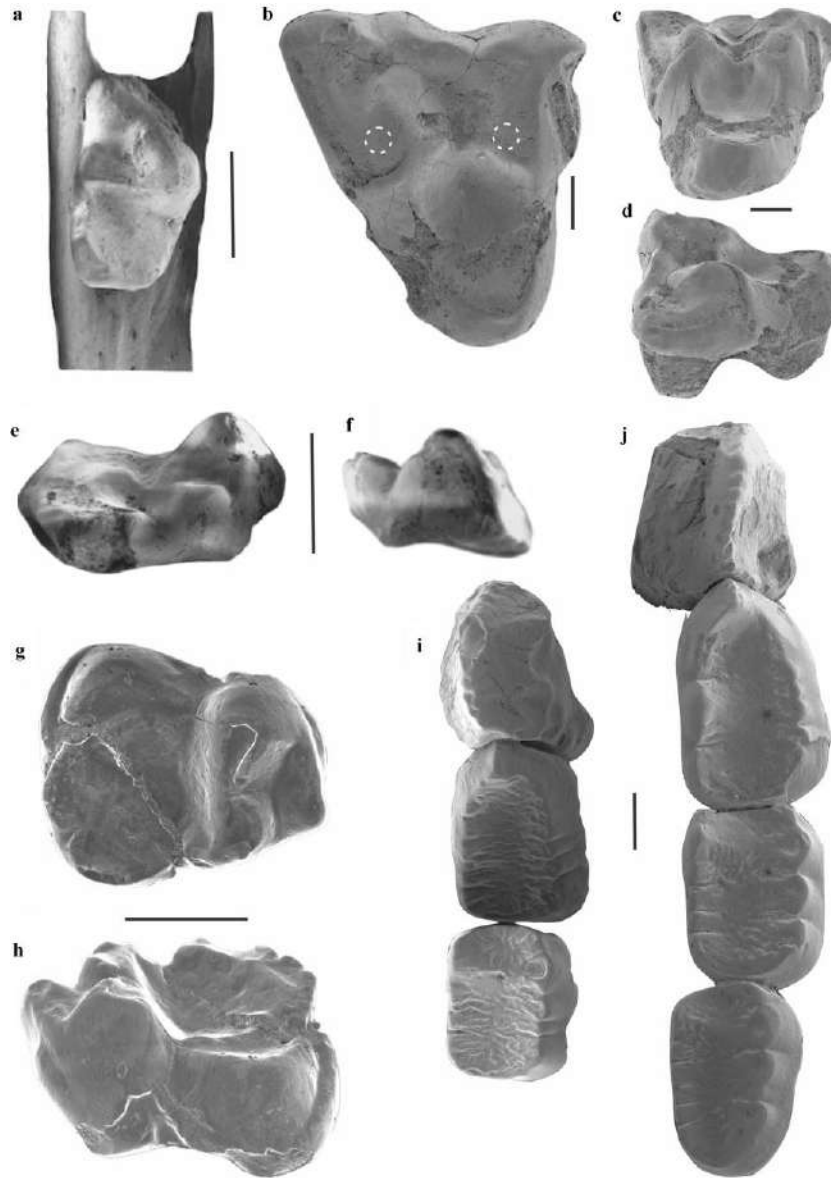
Australidelphia
Microbiotheria
?Microbiotheriidae
Marambiotherium glacialis Goin and Carlini (1995)

Referred material: MLP 95-I-10-1 (holotype; Figure 4a), a fragment of a right mandibular ramus with a complete m4 and the posterior alveolus of m3; MLP 88-1-1-1, an edentulous left mandibular ramus with the alveoli for p3-m4.

Stratigraphic and geographic provenance: All specimens came from La Meseta Formation, *Cucullaea* I Allomember. The type specimen came from IAA 1/90 upper level, while the specimen MLP 88-1-1-1 was collected at RV-8200 (Figure 2).

Original description and discussion: Goin and Carlini

Figure 4 Australidelphian marsupials (Microbiotheria [**a–d**] and Polydolopimorphia [**e–j**]) from the early–mid Eocene of Antarctica. **a**, *Marambiotherium glacialis* (Microbiotheriidae); specimen MLP 95-I-10-1 (holotype), a fragmentary right dentary with m4 in occlusal view. **b–d**, *Woodburnodon casei* (Woodburnodontidae); specimen MLP 04-III-1-2 (holotype), an isolated upper right molar (M2 or M3) in occlusal (**b**), lingual (**c**), and posterior (**d**) views; in **b**, striped circles indicate the position of the metacone (left) and the paracone (right) cusps. **e–f**, *Perrodelphys coquinense* (Prepidolopidae); specimen MLP 96-I-5-11 (holotype), an isolated left lower molar (m?1) in lingual (**e**) and anterior (**f**) views. **g–h**, *Pujatodon ektopos* (family indet); specimen MLP 14-I-10-20 (holotype), a left lower molar in occlusal (**g**), and dorso-labial (**h**) views. **i**, *Antarctodolops dailyi* (Polydolopidae); specimen MLP 94-III-15-254, a right dentary with p3-m2 in occlusal view. **j**, *Antarctodolops mesetaense* (Polydolopidae); specimen MLP 96-I-5-12 (holotype), a right dentary with p3-m3 in occlusal view. Scale: 1 mm. Photos are modified from Goin et al. (1999; **a**, **e–f**), Goin et al. (2007; **b–d**), Goin et al. (2018; **g–h**), and Chornogubsky et al. (2009; **i–j**).

(1995); see also Goin et al. (1999).

Comments: Most observable features of the type specimen suggest the allocation of *Marambiotherium glacialis* within microbiotheriids: reduced m4 relative to m3, reduced hypoconulid, and small hypoconid relative to the entoconid, with its crest forming a sharp angle.

Woodburnodontidae

Woodburnodon casei Goin et al. (2007)

Referred material: MLP 04-III-1-2 (holotype; Figures 4b–4d), an isolated, worn upper right molar (M2 or M3).

Stratigraphic and geographic provenance: The type, and only known specimen, comes from from La Meseta Formation, *Cucullaea* I Allomember, IAA 1/95 (Figure 2).

Original description and discussion: Goin et al. (2007).

Comments: Diagnostic features of *Woodburnodon* (and of Woodburnodontidae as well) are the relatively large size, metacone proportionally larger; preparacrista comparatively longer and more perpendicularly oriented in relation to the molar axis, and a labial notch present between stylar cusps C and D. *Woodburnodon casei* had an estimated body mass between 900 and 1300 g, and represents the largest known microbiothere, living or extinct. Almost all its morphological characters are plesiomorphic when compared with South American microbiotheriids, even with respect to the oldest representatives of this family. According to Goin et al. (2007) this suggests a quite ancient and southern origin for *Woodburnodon* and its ancestors; the origins and initial radiation of the Microbiotheria may have occurred from a generalized peradectoid; representatives of this order evolved within a common, Andean-Patagonian-Antarctic biogeographic region, already present since the Late Cretaceous.

Polydolopimorphia
Family indet.
Pujatodon ektopos Goin et al. (2018)

Referred material: MLP 14-I-10-20 (type; Figures 4g–4h), a lower left molar (m2 or m3) partially worn.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Original description and discussion: see Goin et al. (2018).

Comments: Some of the most distinctive features of *Pujatodon ektopos* include: paraconid and metaconid close to each other due to a posterior position of the paraconid, metaconid with a posterolingual crest, well-developed postcingulid, talonid wider and longer than the trigonid, the cristid obliqua reaches anteriorly the postero-labial face of the protoconid, finally, its enamel microstructure is basically radial with incipient interrow sheets. Summarizing, its overall morphology resembles more that of basal polydolopimorphians (Glasbiidae, some Prepidolopidae) than that of any other South American or Antarctic metatherian so far known. The fact that *Pujatodon* is more generalized than the Late Cretaceous, North American *Glasbius* suggests that North American glasbiids were derived from *Pujatodon*-like South American ancestors that migrated northward during the Late Cretaceous–early Paleogene event known as FABI (Goin et al., 2012)

Prepidolopidae
Perrodelphys coquinense Goin et al. (1999)

Referred material: MLP 96-I-5-11 (holotype; Figures 4e–4f), an isolated left lower molar (m1?).

Stratigraphic and geographic provenance: La Meseta

Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Original description and discussion: see Goin et al. (1999).

Comments: As stated by Goin et al. (1999), the type, and only known, specimen of *Perrodelphys coquinense* is so derived in some aspects of its trigonid morphology that its intergeneric relationships remain unclear. While the talonid is relatively generalized, the trigonid displays some uniquely derived features, all of them a result of the extreme reduction and posterolabial "displacement" of the paraconid. Such a trigonid morphology could have derived from the condition seen in *Prepidolops* or *Punadolops* from Northwestern Argentina (Goin et al., 1998). In the m1 of *Prepidolops* the paraconid is posteriorly shifted and reduced due to the very large size of the p3, which overlaps the most mesial part of the trigonid. This condition seems to be more emphasized in *Perrodelphys* inferring that the p3 should be proportionally larger than in *Prepidolops*.

Polydolopidae
Antarctodolops Woodburne and Zinsmeister (1982)

Comments: *Antarctodolops* is a well-known Antarctic genus of polydolopines. The general morphology of this taxon resembles those of the genus *Polydolops* but with some differences in the molar structure, such as the lack of the p2 and the more mesio-distally elongated molars (Woodburne and Zinsmeister, 1982). The species of this genus share several features such as a m1 with more than four labial cusps, a large lingual cusp at the mesial end of the talonid and, between one and up to three vertical furrows that bound the talonid cusps (Chornogubsky et al., 2009).

Goin and Candela (1995) argued against the assignment of the Antarctic polydolopines to an endemic genera, stressing that the molar differences with other species of *Polydolops* were not enough to separate them. A later review by Chornogubsky et al. (2009) led to the following conclusions: (1) revalidate *Antarctodolops* for the Antarctic polydolopids, (2) regard *Eurydolops seymouriensis* as a junior synonym of *Antarctodolops dailyi*, and (3) recognize a new species of this same genus: *A. mesetaense*. Chornogubsky et al. (2009) considered that *Antarctodolops* is not a generalized polydolopid, and the origin of polydolopids should be traced back to early Palaeocene or even Late Cretaceous times (see also Woodburne and Case, 1996). They also argued that the polydolopid radiation should be regarded, as a whole, as an Austral Kingdom event. Similar conclusions were advanced by Goin et al. (2007) on the origins and radiation of the Microbiotheria.

Antarctodolops dailyi Woodburne and Zinsmeister (1982)

Referred material: UCR 20910 (holotype), UCR 22355,

an isolated left P3 (type of *Eurydolops seymourensis*), a left dentary with p3-m2; UCR 20911, a right dentary with p3-m1; MLP 89-III-2-1, a right m2; MLP 94-III-15-254 (Figure 4i), a right dentary with p3-m2; MLP 95-I-10-3, an isolated left p3; MLP 96-I-5-1, a right m2; MLP 96-I-5-2, a right m3; MLP 96-I-5-3, a right dentary with p3, MLP 88-I-1-2, a left dentary with a broken m2; UCR 20912, an isolated left M1; MLP 87-II-1-1, a right maxilla with P2-M1; MLP 88-I-1-4, an isolated right M1.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember (Figure 2). IAA 2/95 (MLP 94-III-15-254, MLP 95-I-10-3, MLP 96-I-5-1, MLP 96-I-5-2, MLP 96-I-5-3, MLP 96-I-5-4), DPV 2/84 (MLP 89-III-2-1), RV-8200 (MLP 87-II-1-1, MLP 88-I-1-4, MLP 88-I-1-2, UCR 22355, UCR 20910, UCR 20911, UCR 20912).

Original description and discussion: Woodburne and Zinsmeister (1982, 1984); see also Goin and Candela (1998), and Chornogubsky et al. (2009).

Comments: This polydolopid was the first land fossil mammal described for the Antarctic continent (Woodburne and Zinsmeister, 1982, 1984). *A. dailyi* differs from *A. mesetaense* in its smaller size; the anteriormost talonid cusp of the m1 divided by a deep groove; labially, the m1 has up to three labial grooves that run vertically, from almost the crown base up to the occlusal surface; m2 with the central labial cusp divided by a deep groove; the lingual cusps are more bulbous; and narrower p3 with a rounded apex (Chornogubsky et al., 2009).

Antarctodolops mesetaense Chornogubsky et al. (2009)

Referred material: MLP 96-I-5-12 (Figure 4j), a right dentary with p3-m3; MLP 88-I-1-3, a right dentary with m2; MLP 92-II-2-1, an isolated left m2; MLP 94-III-15-13a, an isolated left m1; MLP 94-III-15-13b, an isolated left m3; MLP 96-I-5-46, an isolated right m3; MLP 95-I-10-4, an isolated left M1; MLP 90-I-20-4 (tentatively referred specimen), an isolated P3.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember (Figure 2). IAA 1/90 upper level (MLP 90-I-20-4, MLP 92-II-2-1, MLP 94-III-15-13a and b, MLP 95-I-10-4, MLP 96-I-5-12, MLP 96-I-5- 46, MLP 96-I-5-46) and RV-8200 (MLP 88-I-1-3).

Original description and discussion: Chornogubsky et al. (2009).

Comments: The largest species of the genus. The lower dentition differs from *A. dailyi* for the undivided first talonid cusp of the m1; the lingual cusps of the m2 labiolingually compressed, forming a serrated margin; and p3 relatively longer and with a more quadrangular outline in lateral view (Chornogubsky et al., 2009).

?Marsupialia
Order, family, gen. and sp. indet.

Referred material: MLP 92-II-2-2, a fragment of left mandibular ramus with the alveolus and root of the last

molar and part of its anterior alveolus (Figure 3j).

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Original description and discussion: See Goin et al. (1999).

Comments: This tiny dentary is so fragmentary as to preclude any attempt to determine its affinities. Many Paleogene South American microbiotheriid and didelphimorphian marsupials would fit in its size.

EUTHERIA
Xenarthra?

Referred material: MLP 88-I-1-95 (Figure 5b), ungual phalanx. MLP 94-III-15-14 isolated tooth.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. The phalanx came from RV-8200, while the tooth from DPV locality 2/84 (Figure 2).

Comments: The Antarctic record of xenarthrans is composed of very limited and questionable evidence, and their presence needs to be confirmed by new findings. The phalanx was the first terrestrial placental mammal described from Antarctica (Carlini et al., 1990). It was originally identified as a megatherioid (Tardigrada) but more detailed comparisons with early Miocene specimens from Patagonia led to the uncertainty about their possible Tardigrada or even Vermilingua affinities. This is a small-sized mammal (ca. 10 kg) which was considered to have been semi-arboreal and mainly with a folivorous diet (Vizcaíno et al., 1998). Unfortunately, the specimen is lost and only the previous descriptions are available for comparisons.

The isolated and incomplete tooth is composed entirely of dentine, without evidence for the prior presence of enamel. Although the specimen was interpreted as an upper caniniform of a Tardigrada lacking its base (Vizcaíno and Scillato-Yané, 1995), it was later regarded as a Mammalia *incertae sedis*, based on histological criteria (MacPhee and Reguero, 2010).
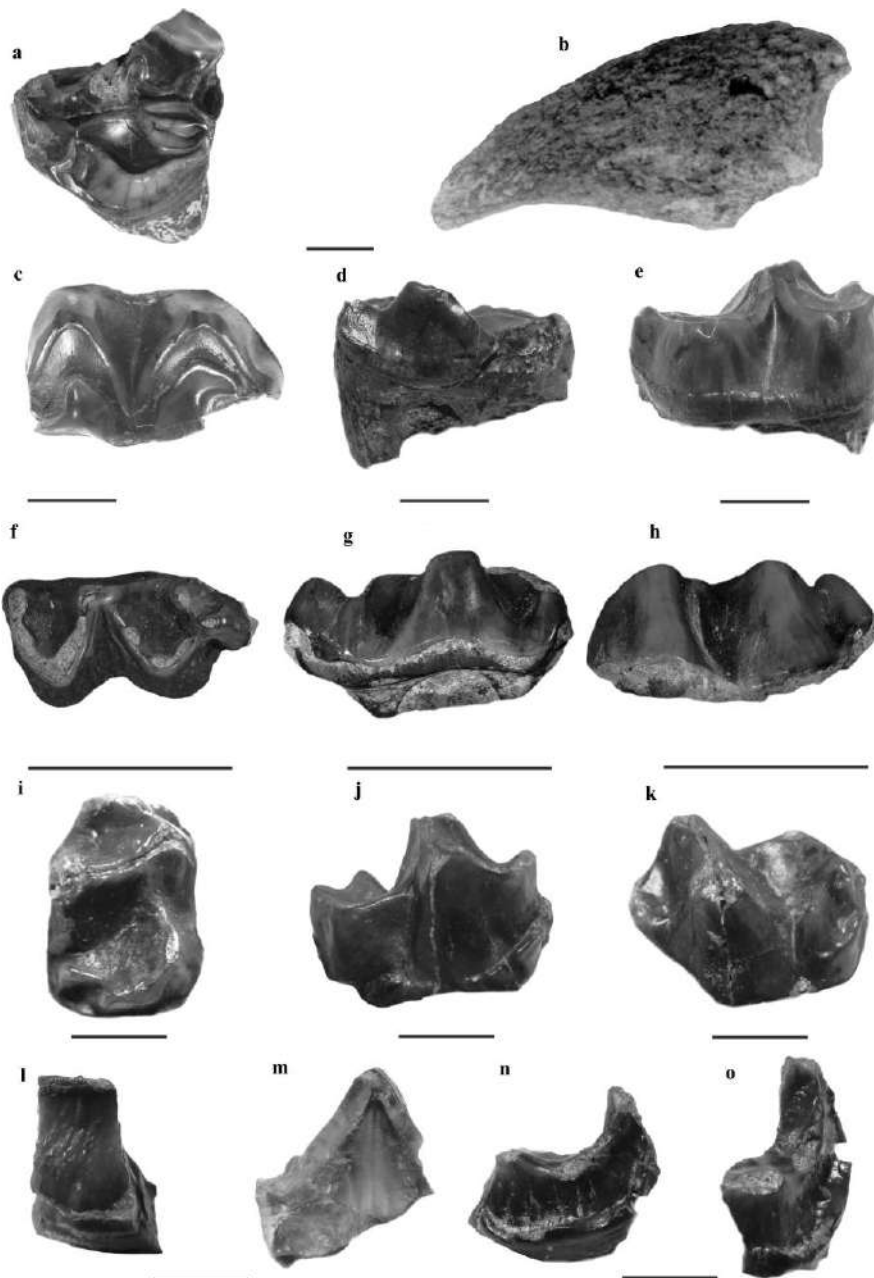
Astrapotheria
Astrapotheriidae
Antarctodon sobrali Bond et al. (2011)

Referred material: MLP 08-XI-30-1 (holotype; Figures 5i–5k) isolated right p4 or m1. Tentatively assigned specimens include MLP 90-I-20-2 a fragmentary upper cheek tooth (Figures 5n–5o).

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. DPV 2/84 (holotype) and the other specimens came from IAA 1/90 upper level (Figure 2).

Original description and discussion: Bond et al. (2011)

Comments: *Antarctodon sobrali* is a small astrapotheriid, slightly larger than the trigonostylopid *Trigonostylops*. Its enamel shows vertically decussating

Figure 5 Eutherian mammals (Litopterna [**a** and **c–h**], Xenarthra [**b**] and Astrapotheria [**j–o**]) from the early-mid Eocene of Antarctica. **a**, *Notiolofos arquinotiensis* (Sparnotheriodontidae); specimen MLP 95-I-10-6 (holotype), isolated fragment of left M3. **b**, Xenarthra?; specimen MLP 88-I-1-95, ungual phalanx. **c–e**, *N. arquinotiensis*; specimen MLP 92-II-2–135, isolated right m3 in occlusal (**c**), lingual (**d**) and labial (**e**) view. **f–h**, *Notiolofos regueroi*; specimen IAA-PV 173, isolated left m3 in occlusal (**f**), lingual (**g**) and labial (**h**) view. **i–k**, *Antarctodon sobrali* (Astrapotheriidae); specimen MLP 08-XI-30-1 (holotype), isolated right p4 or m1 in occlusal (**i**), labial (**j**) and lingual (**k**) view. **l–m**, ?Astrapotheria gen. et sp. indet.; specimen MLP 90-I-20-6, portion of an incomplete upper molar. **n–o**, *Antarctodon cf. sobrali*; specimen MLP 90-I-20-2, portion of a right upper cheek tooth in labial (**n**) and occlusal (**o**) view. Scale 20 mm.

Hunter-Schreger bands. The only assigned tooth has a long protolophid (mentioned as metalophid in Bond et al., 2011) which joins together protoconid and metaconid. The postvallid is high, flat and vertical, only interrupted by the cristid obliqua, which runs up to the lingual base of the protoconid. The cristid obliqua, hypoconid and hypoconulid form a lophid in the talonid, but with the cusps well

identified. The entoconid is elongated and forms an entocristid reaching the anterior slope of hypoconulid.

Specimen MLP 90-I-20-2 (Figures 5n–5o) was regarded as astrapotherian trygonostylopid tooth in previous publications (Marenssi et al., 1994); it consists of a mesiolingual portion of a right upper cheek tooth with part of the protocone, complete protolph and the anterior

cingulum. The analysis of the wear facet suggested that it is more likely to have been made by a lower cheek-tooth like those of *Antarctodon* than that of other astrapotherian. This occlusal relationship, in addition to sizes consideration led Bond et al. (2011) to suggest that MLP 90-I-20-2 could be part of the hypodigm of *Antarctodon sobrali*. By now the evidence is too scarce to allow a certain characterization of the upper dentition of *Antarctodon*.

?Astrapotheria
gen et sp. indet.

Referred material: MLP 90-I-20-6 (Figures 5l–5m) portion of an incomplete upper molar.

Stratigraphic and geographic provenance: La Meseta Formation, *Cucullaea* I Allomember. IAA 1/90 upper level (Figure 2).

Comments: This tooth fragment was mentioned by Marenssi et al. (1994) as a fragment of an upper molar belonging to Astrapotheria; however it is highly incomplete and shows no distinctive features to allow a family assignation. The specimen is a small portion of a lophid structure, with the external wall of enamel and part of a faint cingulum, with a small protuberance on it. The enamel shows a wrinkled surface, and the cut portion exhibit a very thick enamel layer (1.45 mm) which is almost twice the enamel width of the other Antarctic remain (MLP 90-I-20-2). These particular features raises doubt about its taxonomic assignation.

Panperissodactyla
Litopterna
Sparnotheriodontidae
Notiolofos Bond et al. (2009)

Comments: *Notiolofos*, the best known ungulate genus from Antarctica, is represented by two species *N. arquinotiensis* and *N. regueroi* (Gelfo et al., 2015, 2017). The remains assigned to it were originally described as closely related to the sparnotheriodontids (Bond et al., 1990) and then considered as a new species of *Victorlemoinea* (Marenssi et al., 1994; Vizcaíno et al., 1997), a well-known genus recorded in the lower Eocene of South America and represented by *V. labyrinthica* in localities of Patagonia, Argentina, and *V. prototypica* in São José de Itaboraí, Brazil. Later the specimens were considered as endemic genera (Bond, pers. comm. in: Reguero et al., 1998) and described as a single species *Notolophus arquinotensis* (Bond et al., 2006). The generic name was preoccupied and later replaced by *Notiolofos* (Bond et al., 2009).

Notiolofos arquinotiensis Bond et al. (2006)

Referred material: MLP 95-I-10-6, left M3 (holotype, Figure 5a); MLP 94-III-15-3, i2; MLP 96-I-5-9, left i3; MLP 12-XI-1-11, right p3; MLP 08-XI-30-43, left p4; MLP 04-III-3-1, right p4; MLP 91-II-4-1, right m1; MLP 13-I-25-1, right m1 or m2; MLP 92-II-2–135 (Figures 5c–5e), m3; MLP 01-I-1-1, right m3; MLP 15-I-10-1, right jaw fragment with remains of m1-3; MLP 96-I-5-5, I1?; MLP 90-I-20-3, right I3; MLP 96-I-5-10, I3; MLP 91-II-4-5, right P1; MLP 90-I-20-5, P3; MLP 90-I-20-1, M1; MLP 95-I-10-7, an upper molar fragment.

Tentatively referred material: BMNH BAS M2584, distal portion of an ectoloph with the metacone portion broken, belonging to a first or second upper molar.

Stratigraphic and geographic provenance: La Meseta (Acantilados II, Campamento, *Cucullaea* I allomembers) and Submeseta formations (Figure 2). Specimens came from localities: DPV 16/84 (MLP 95-I-10-6), IAA 1/13 (MLP 13-I-25-1), IAA 1/94 (MLP 92-II-2–135, which was mentioned in Bond et al. (2006) and Gelfo (2016) as found in IAA 1/92), DPV 2/84 (MLP 91-II-4-1), BAS DJ 154 (BMNH BAS M2584), IAA 1/90 (MLP 94-III-15-3, MLP 12-XI-1-11, MLP 01-I-1-1, MLP 90-I-20-3, MLP 91-II-4-5, MLP 90-I-20-5, MLP 90-I-20-1), IAA 1-96 (MLP 95-I-10-7), IAA 3/96 (MLP 96-I-5-9), IAA 2/95 (MLP 08-XI-30-43, MLP 96-I-5-5), IAA 1/95 (MLP 04-III-3-1), IAA 1/96 (MLP 96-I-5-10), IAA 2/15 (MLP 15-I-10-1).

Original description and discussion: Bond et al. (2006) and Gelfo (2016).

Comments: *Notiolofos arquinotiensis* is a sparnotheriodontid of large size nearly equal to *Sparnotheriodon epsilonoides* from the Eocene of Patagonia, Argentina. In contrast to other sparnotheriodontids the protocone is projected mesially by a short paraloph connected to a protostyle. There is a mesial and distal rim in the enamel described as a low, extra cingulum forming a 'double-cingulum' (Bond et al., 2006). This feature is also present in other sparnotheriodontid specimens (e.g. MLP 66-V-12-2) as well as in Anisolambdidae litopterns, but it is too thin to work during occlusion as a real cingulum. The metaconule lophid is mesiodistally extended, and no hypocone seems to be present in M3. The lower molars are characteristic of those of other members of the family, with a double V-shaped lophid one in the trigonid and the other in the talonid. The m3 shows a well-developed, bunoid entoconid, and the hypoconulid is distally projected.

Specimen BMNH BAS M2584 was first described by Hooker (1992) as a distal half of a metacone plus postmetacrista of a left upper molar, assigned to a Trygonostylopidae indet. Astrapotheria. The specimen was later considered as probably belonging to the sparnotheriodontid litoptern *Notiolofos arquinotiensis* based on the estimated similar size, crown height, concave labial wall of the ectoloph, and postmetaconule crista similarly directed towards the metastyle (Bond et al., 2011).

Notiolofos arquinotiensis, the most abundant land placental mammal in the Paleogene of Antarctica, was recorded through most of the La Meseta and Submeseta formations, suggesting a continuous fossil record of at least 17.5 Ma. This morphological stasis event, also recorded

among fossil penguins in the same units (Acosta Hospitaleche, 2006), was related to an evolutionary model that related morphological stasis and punctuated equilibrium as the usual responses to widely fluctuating physical environments such as those characteristic of temperate regions and shallow waters (Gelfo, 2016).

Notiolofos regueroi Gelfo et al. (2017)

Referred material: IAA-PV 173: Isolated complete left m3 (Figures 5f–5h).

Stratigraphic and geographic provenance: La Meseta Formation, lower coquina bed of *Cucullaea* I Allomember. The only specimen assigned comes from IAA 2/16 (Figure 2).

Original description and discussion: Gelfo et al. (2017)

Comments: *N. regueroi* is the second species of the genus and represents a sparnotheriodontid of medium size. The estimated body mass of *N. regueroi* is between 25 to 58 kg (Gelfo et al., 2017), indicating a clear difference with *N. arquinotiensis*, with estimations between 395–400 kg (Vizcaíno et al., 1998). It differs from all known members of the family in the absence of mesial and labial cingulids, larger paraconid in the paracristid, wider talonid basin, hypoconulid more distally projected and isolated from the rest of the talonid as a third lobe, more lingual entoconid, short, low and well-developed postcristid, and in the presence of a centroconid over the cristid obliqua. The enamel in *N. regueroi* presents vertically oriented HSBs as in *N. arquinotiensis* but, in contrast to it, the enamel surface is smooth in contrast to wrinkled, except for the lingual area limited by the hypoconulid, entoconid, postcristid, and the remnant of the lingual cingulid.

In contrast to the wide fossil record of *N. arquinotiensis*, this species was only found in a particular level of the La Meseta Formation and restricted to the lower coquina bed of *Cucullaea* I Allomember. This level recorded the widest ungulate diversity in Antarctica.

4　The quest for Antarctic Mesozoic mammals

There are no Mesozoic mammalian fossil records in Antarctica. Nevertheless, it is very probable that the austral continent played a key role during that time frame as an origin centre of fauna or as a main paleobiogeographic connector among Gondwana continents (Gelfo, 2015). Among Mesozoic lineages, Monotremata and Ausktribosphenida, which compose the Australosphenida, have an exclusive Gondwanan distribution. Phylogenetic relationships among them were long discussed (e.g. Woodburne et al., 2003; Kielan-Jaworowska et al., 2004) but a common origin for both in the Southern Hemisphere seems to be the more plausible explanation.

Monotremes are represented by the extant platypus *Ornithorhynchus* and the short-beaked echidna *Tachyglossus* with a fossil record mainly restricted to Australia, which includes the best preserved and less questioned taxa *Steropodon* and *Teinolophos* from the Late Cretaceous and several species of the Miocene genera *Obdurodon* (Bino et al., 2019). The only non-australian representative of the group is *Monotrematum sudamericanum* from the early Paleocene of the Argentinian Patagonia (Pascual et al., 1992). The disjunct distribution of the monotreme fossil record is currently explained by an australian origin of the group and a later dispersal event through West Antarctica to South America, in order to explain their early Paleocene presence in Patagonia. Thus, the presence of monotremes in Cretaceous or Paleogene sediments of Antarctica should be expected.

The fossil record of extinct Ausktribosphenida comprise the genus *Ambondro* (Flynn et al., 1999) from the Middle Jurassic of Madagascar, *Asfaltomylos* (Rauhut et al., 2002) and *Henosferus* (Rougier et al., 2007) from the Late Jurassic of Patagonia, Argentina, an undescribed taxon from the Early/Middle Jurassic from India, represented by an isolated lower molar characterized by the presence of a trigonid and a talonid basin (Prasad et al., 2015), and the records of the Early Cretaceous of Australia: *Ausktribosphenos* (Rich et al., 1997) and *Bishops* (Rich et al., 2001). The above mentioned fossil record suggests that West and East Antarctica should have functioned as an area of connection for Australosphenida. A common origin of the group during the Jurassic and their distribution in Patagonia, Madagascar, and India, suggest at least the presence of Ausktribosphenida in the Jurassic outcrops from Antarctica.

Although the fossil content of the Jurassic outcrops in Antarctica had been very diverse, none of them allowed the recovery of a fossil land mammals. Late Jurassic marine sediments are exposed at a few locations in the northeastern part of the Antarctic Peninsula at localities as James Ross Island (Richter and Thomson, 1989), Longing Cape, and Behrendt and Hauberg mountains (Arratia and Hikuroa, 2010). In these places the Ameghino (= Nordenskjöld) Formation outcrops as a mudstone sedimentary sequence corresponding to the basal infill of the James Ross Basin (Farquharson, 1982). The fossil remains at Ameghino Formation are represented by invertebrates such as ammonoids, nautiloids, bivalves, and radiolarians (e.g. Medina and Ramos, 1983; Whitham and Doyle, 1989; Kiessling and Scasso, 1996; Kiessling et al., 1999) and, among vertebrates, there is a predominance of marine fauna such as osteichthyan and plesiosaurs. At the south-eastern Antarctic Peninsula in the region of Cape Framnes locality, in the Jason Peninsula, the sediments of the Latady Formation are assigned to the Middle–Late Jurassic. In addition to the marine invertebrates (e.g. ammonites, belemnites, oxytomid, trigoniid and astartid bivalves) the fossils of Latady Formation are also represented by bennettitalean fronds and fructifications, which are indicative of an important contribution of terrestrial

material (Riley et al., 1997) but as of yet, no land vertebrates have been found there. Other localities with terrestrial outcrops are located in Hope Bay and Botany Bay at the Antarctic Peninsula. The Early Jurassic Mount Flora Formation is represented by a diverse flora composed of liverworts, horsetails, ferns, seed ferns, cycads, bennettitales and conifers (Ociepa, 2007 and literature therein) but as in Latady Formation, no terrestrial vertebrates have been found. An interesting exception to these Jurassic localities at the Antarctic Peninsula is Mount Kirkpatrick, in the Beardmore Glacier region of the Central Transantarctic Mountains, where outcrops of a Mesozoic sequence with several important vertebrate land faunas have been recognized. These units are represented by the Early and Middle Triassic Fremow Formation, the Late Triassic Falla Formation, and Early Jurassic Hanson Formation (Elliot, 1996; Smith and Pol, 2007 and literature there in). In the Jurassic sediments mentioned above, vertebrates are represented by a sauropodomorpha *Glacialisaurus hammeri* (Smith and Pol, 2007), the theropod *Crylophosaurus ellioti* (Smith et al., 2007), a tritylodont cynodont (Hammer and Smith, 2008) and a pterosaur (Hammer et al., 2004). Ausktribosphenidan mammals could have been part of these terrestrial communities and their presence in the Hanson Formation should be expected if there is not an ecological or sampling bias. In South America for example, the Jurassic Cañadón Asfalto Formation in Patagonia, already recorded a faunistic assemblage of dinosaurs, pterosaurs, turtles, frogs, and mammals, represented by the eutriconodonts *Argentoconodon fariasorum* and *Condorodon spanios* (Gaetano and Rougier, 2011; Gaetano et al., 2013) and the australosphenids *Asfaltomylos patagonicus* and *Henosferus molus* (Rauhut et al., 2002; Rougier et al., 2007).

Since the 1980s the use of novel paleontological prospecting and collection techniques (e.g. screen-washing of sediments), in search of vertebrates as microfossils in the Southern Hemisphere and particularly in Australia and South America, opened a new window to the evolutionary history of mammals with the discovery of the existence of Gondwanan lineages (Pascual and Ortiz Jaureguizar, 2007). Paleobiogeographic evidence indicates that the role of Antarctica during Mesozoic times, and specifically in the Jurassic in the case of the Australosphenida, was central in mammalian evolution.

5 A paleobiological glimpse to the terrestrial mammals in Antarctica

Since the Late Cretaceous and early Paleogene, two main land connections to Antarctica allowed a terrestrial continuity between South America and Australia. The Antarctic Peninsula and Southern South America were united through the Scotia Isthmus (Shen, 1998) or the Weddellian Isthmus (Reguero et al., 2014), and the

Tasmanian Gateway linked East Antarctica and Australia (Bijl et al., 2013; see Chapter 3 in Goin et al., 2016). In addition to the tectonic and geologic evidence, several palaeobiogeographic models support the land connections between Antarctica and the other Southern continents to explain the Paleogene and even extant biotic distribution (Reguero et al., 2014 and literature therein). From the Late Cretaceous up to late Eocene, mostly greenhouse conditions prevailed in Antarctica, and warm water and low latitude-derived currents were thought to have covered the shores of the Antarctic continent (Exon et al., 2004). These particular settings were the environmental context of an intensive mammalian exchange through Southern continents. Monotremes were recorded in the early Paleocene of Patagonia (Pascual et al., 1992), the metatherian radiation spread through South America, Antarctica, and Australia generating a profuse fossil record in Paleogene outcrops (Goin et al., 2016), and astrapotherians and sparnotheriodontids ungulates arrived in Antarctica (Bond et al., 2006, 2011; Gelfo et al., 2017).

A series of interrelated events, such as the progressive drop in global temperatures at the Eocene–Oligocene transition (Zachos et al., 2001), the final and complete break-up of Gondwanaland (Reguero et al., 2014), with the opening of the Drake and Tasman passages, the appearance of the cold Antarctic Circumpolar Current (Bijl et al., 2013), and the presence of a major ice sheet (Birkenmajer et al., 2005); shifted the paleogeographic and paleoclimatic conditions that had previously allowed the flourishing of terrestrial mammals in Antarctica, and probably were responsible for their total extinction.

The Antarctic land mammals, constrained by now to those recorded in La Meseta and Submeseta formations, indicate a representation of just selected dietary niches (Figure 6), specially compared to those in the equivalent time frame in South America. Herbivorous groups were the most abundant and are represented by mammals with a wide range of body size. The largest mammals (> 10 kg) are the only herbivorous which seems to have developed a browser specialization; the sparnotheriodontids *Notiolofos arquinotiensis* with a body mass estimated between 395–400 kg (Vizcaíno et al., 1998), *Notiolofos regueroi* with an estimated range between 25–58 kg (Gelfo et al., 2017) and the astrapotherian *Antarctodon sobrali*, with a range between 18.5–38 kg (Vizcaíno et al., 1998). The dental structure of these taxa share comparable features with the development of lophs, brachyodont teeth, and a vertical orientation of HSBs in the enamel, which are more appropriate for feeding on plant leaves, bark, and green stems, but with fewer abrasive elements than those for feeding on grass, fruits or seeds. Based on these arguments, they were interpreted as ungulates adapted to forested habitats, such as the closed forests dominated by *Nothofagus* inferred for *Cucullaea* I Allomember (Reguero et al., 1998). A comparison between *Antarctodon* and both species of *Notiolofos* indicates that they differ in their dental
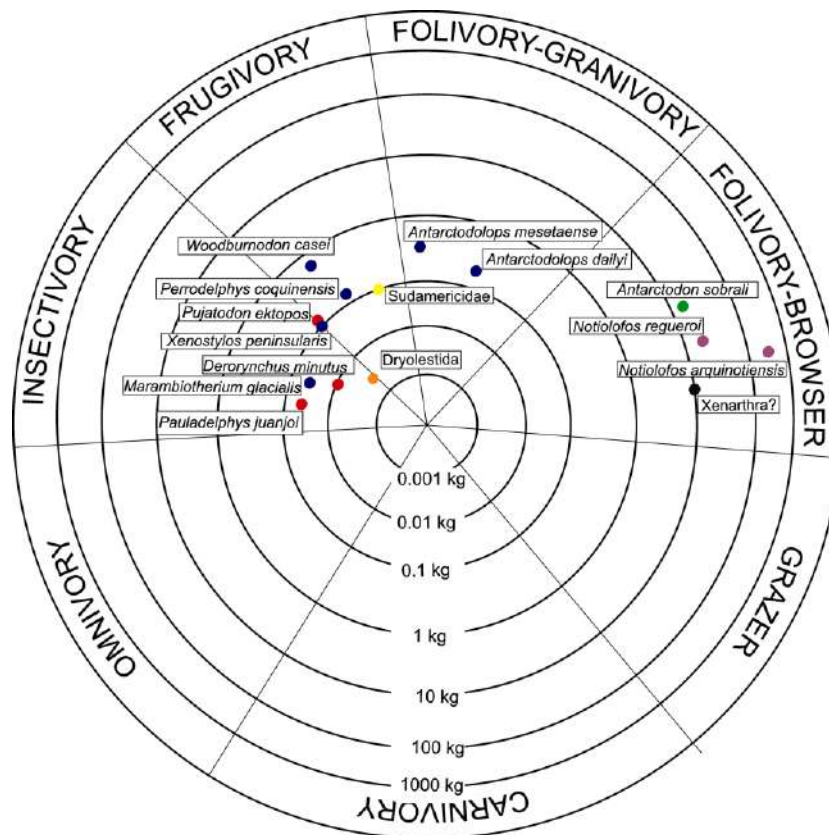
Figure 6 Estimated body mass and dietary types of the land mammals from La Meseta and Submeseta formations. Yellow: Gondwanatheria; orange: Dryolestida?; red: "Ameridelphia"; blue: Australidelphia; black: Xenarthra; green: Astrapotheria; purple: Litopterna.

wear facets, the trigonid and talonid height, and the lophid development. All these features are indicative of distinctive chewing movement and probably a difference in the kind of plant resources they processed. In contrast, the distinction between *N. arquinotiensis* and *N. regueroi* seems to be more related to their great differences in body mass than to their dental structure (Gelfo et al., 2017). The alleged antarctic xenarthran, with a body mass of ca. 10 kg was considered to have been semi-arboreal and could be the only mammal with a completely folivorous diet (Vizcaíno et al., 1998).

The rest of the mammals identified in the Antarctic fossil record do not surpass 1 kg of body weight. Probably the largest of them were gondwanatherians which are represented by incomplete specimens that do not allow a definite inference on their dietary habits. The left dentary with the rodent-like hypsodont incisor, has no other teeth preserved. The Patagonian *Sudamerica ameghinoi* from the early Paleocene shows not only the same feature in the ever growing incisor, but molars with euhypsodonty (Pascual et al., 1999). Although the Antarctic specimen was comparable to *S. ameghinoi* in the few preserved elements, it is not possible to relate the hypsodonty only to grazing habits since it also occurs in burrowing and semi-aquatic mammals (Goin et al., 2006).

If the dryolestoid assignment is confirmed with the discovery of new remains, probably this group would fill part of the insectivore dietary specialization of small mammals, with a body mass of 0.03 to 0.5 kg. Compared with dryolestoids from Patagonia, the lost tooth fragment more resembles the meridiolestidan *Barberenia* from the Late Cretaceous (Martinelli et al., 2015) than the bunodont and large dental structure of *Peligrotherium* from the early Paleocene (Gelfo and Pascual, 2001).

All other land mammals represented in the Eocene of Antarctica belong to small marsupials of a range between 0.03 to around 1 kg. Their diet categories among them are almost equally represented among the strictly insectivorous, and those with a mix of insectivory + frugivory, and frugivory + folivory (Zimickz, 2014, Goin et al., 2018). The derorhynchids *Pauladelphys juanjoi* and *Derorhynchus minutus,* as well as the microbiotheria *Marambiotherium glacialis* represent a strict insectivory dietary type according to their wear facets and the inferred body mass (Goin et al., 1999). The insectivorous habits were complemented in some taxa with a frugivorous component of the diet, for example in *Xenostylos peninsularis* (Goin et al., 1999). The Polydolopimorphia *Pujatodon ektopos* with a body mass between 83 to 153 g probably also mix insectivory and frugivory diets. Wear facet analysis suggest

that the molars of *Pujatodon* were primarily adapted to the processing of fruits, nuts, seeds, and/or hard insects (Goin et al., 2018). These marsupials were presumably well adapted for the consumption of somewhat hard food items, such as seeds, some fruits, and insects with a hard exoskeleton. Other marsupials better fit in an exclusively frugivorous type such as *Woodburnodon casei* and *Perrodelphys coquinensis* which have a mixture of generalized (talonid) and derived (trigonid) features. In contrast, for both species of *Antarctodolops*, more folivorous habits were suggested based on enamel crenulations, indicative of chewing on fibrous and resistant materials such as dicotyledons leafs (Zimicz, 2014).

Despite the sampling bias due to the allochthony of land mammals in the marine sediments of La Meseta and Submeseta formations, it is noteworthy that there is no mammalian representation of species between 1 to 10 kg (Figure 6). Also, the carnivorous role was not represented by any metatherian or in any other mammal in the Antarctic assemblage (Case, 2006). In contrast, at the same times, the Eocene Patagonian localities, such as those at Paso del Sapo (Tejedor et al., 2009), had a good representation of carnivorous Sparassodonta metatherians. Omnivores and grazers are also missing in this faunistic context; in contrast they were well represented in the Eocene communities from Patagonia (Pascual and Ortiz Jaureguizar, 2007).

6   Conclusions

Knowledge of fossil mammals in Antarctica is heavily shaped by the nature and age of the depositional environment. There is a clear bias in the land mammal diversity, which is constrained to the Cenozoic and particularly Eocene outcrops of La Meseta and Submeseta formations. It is clear that not all the possible ecological dietary types or available body sizes are present (Figure 6) and probably, they are constrained to fauna with only a few biotopes available. Despite these limitations, the most parsimonious paleobiogeographic interpretations indicate that Antarctica played a key role for the evolution of different groups during the Mesozoic (i.e. Ausktribosphenida) and the Paleogene (e.g. Monotremata, Metatheria). To test these hypotheses, there is a need to move from inferences to the factual evidence of the fossil record. Units like the Early Jurassic Hanson Formation in the Transantarctic Mountains, could be a good starting point for a new mammalian search since the similarity of this Antarctic continental vertebrates paleocommunity with those of a similar age already known from Patagonia. But other Jurassic units in the Antarctic Peninsula, with a more marine influence, should not be discarded from an intensive survey. In fact, all the lithological units where terrestrial mammals have been found, indicate a paralic and shallow marine environments, where the specimens have been transported and concentrated.

Even when no terrestrial facies are known from Seymour Island, the presence of leaves, tree trunks, and a flower indicate that a forested terrain had to be present nearby the west. The simplest explanation is that the Antarctic Peninsula was by then a highland, with a mountainous terrain characterized by volcanoes which had been sporadically active since the Mesozoic (Reguero et al., 2002). Cockburn Island, 5 km north of Bodman Point, is in the direction where the continental sediments should have generated, it is a high isle with prominent slopes and a small area of around 4 km^2 (Figure 1). The sediments there are from the Late Cretaceous Snow Hill Island Formation, some levels which range between the Miocene? up to the Pleistocene, which belong to the James Ross Island Volcanic Group, the Cockburn Island Formation and, of particular interest, the Eocene La Meseta Formation. This last unit is represented in Cockburn Island, at least by Valle de Las Focas (Telm 1) and Acantilados I (Telm 2) allomembers (Stilwell, 2002). New surveys on Cockburn Island, using sieve techniques similar to those that gave very good results in the mammalian search on Seymour Island, could help to provide a more realistic picture of the faunal composition during the Eocene.

Abbreviations

FABI–First American Biotic Interchange
HSBs–Hunter-Schreger bands
IPM–Interprismatic matrix
Ma–Million years
SALMA–South American Land Mammal Age
SEM–Scanning electron microscope

Uppercase letter indicates a tooth in the maxillary series, and a lowercase letter indicates a tooth in the dentary series. "P" and "p" were used for premolars, and "M" and "m" for molars. The number following the tooth abbreviation indicates locus position (e.g., M1 is a first upper molar, p2 a second lower premolar).

Institutional abbreviations

BAS–British Antarctic Survey, United Kingdom
BMNH–British Museum of Natural History, London, United Kingdom
DPV–División Paleontología de Vertebrados, Museo de La Plata
IAA–Instituto Antártico Argentino
MLP–Museo de La Plata, Argentina
UCR–Department of Earth Sciences, University of California, Riverside, United States

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