



New Metatherian Mammal from the Early Eocene of Antarctica

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Published online: 20 September 2018

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Abstract

A new Paleogene metatherian from locality IAA 1/90, Marambio (Seymour) Island in the Antarctic Peninsula is described. *Pujatodon ektopos*, gen. et sp. nov., is recognized on the basis of a tiny lower left molar recovered from early Eocene (late Ypresian) levels of the *Cucullaea* I Allomember, La Meseta Formation. The tooth is characterized by its small size, bunoid aspect, short trigonid with closely set paraconid and metaconid, wide and long talonid, the development of an incipient cingulid at the labial base of the crown between the trigonid and talonid, and an expanded posterior cingulid. Body mass estimations for the new taxon range from 83.13 to 153.15 g. Its enamel microstructure shows the earliest evidence among metatherians of aligned prisms, as well as of interprismatic sheets of matrix. The analysis of other parameters, like body mass, molar morphometric index, and wear facets, suggests that the molars of *Pujatodon* were primarily adapted to the processing of fruits, nuts, seeds, and/or hard insects. Several features suggest the allocation of this specimen among basal polydolopimorphians (Prepidolopidae or, more probably, Glasbiidae). The discovery of the specimen MLP 14-I-10-20 could offer new insights on the origins and early diversification of Australidelphian marsupials in southern (and northern?) continents. It also adds significant information on the diversity of Antarctic Paleogene mammals, their evolution, habits, and historical biogeography.

Keywords Antarctic Peninsula · La Meseta Formation · Late Ypresian · Polydolopimorphia · Enamel microstructure · Paleobiology

Introduction

During the greenhouse conditions that predominated from the Late Cretaceous up to the end of the Eocene (Zachos et al.

2001), the Antarctic continent experienced a much warmer climate than today. In this climatic setting, and as heritage of ancient Gondwana, terrestrial connections such as the Tasmania Gateway and the Scotia Arc worked as land corridors, allowing

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biotic dispersal events between South America, West Antarctica, and Australia (Goin et al. 2012, 2016; Reguero et al. 2013). These interchanges can be inferred from the presence of monotremes in the early Paleocene of Patagonia (Pascual et al. 1992), astrapotherian and litoptern ungulates in the Eocene of Antarctica (Bond et al. 2011; Gelfo et al. 2017) and, mostly, by the Paleogene metatherian fossil record (Reguero et al. 2013; Goin et al. 2016). The endemic extant Australian marsupial diversity is one consequence of these tectonic events; for this reason, the Antarctic fossil record is a crucial footprint of metatherian paleobiogeographic history.

The Antarctic land mammal fossil record comes entirely from the Eocene outcrops of the La Meseta and Submeseta formations in Marambio (Seymour) Island, West Antarctica (Reguero et al. 2013). Terrestrial mammals include (1) a dryolestoid (Meridiolestida; Martinelli et al. 2014), originally regarded as an “enigmatic insectivorous mammal” of uncertain affinities (Goin and Reguero 1993) and later referred to the Insectivora (MacPhee et al. 2008); (2) a gondwanatherian closely related to *Sudamerica ameghinoi* (Danian of Patagonia; Goin et al. 2006a), (3) a medium-sized? Tardigrada or? Vermilingua xenarthran (Carlini et al. 1990, 1992), (4) sparnotheriodontid litopterns (Gelfo et al. 2017), (5) astrapotheriids (Bond et al. 2011), and (6) a suite of quite diverse, small-sized ‘opposum-like’ metatherians (see below).

The first extinct mammal from Paleogene levels of the Antarctic Peninsula to be recognized is a metatherian: *Antarctodolops dailyi* (Woodburne and Zinsmeister 1982, 1984). Since then, a series of successive reports have provided accounts of a quite diverse assemblage of “Ameridelphian” and Australidelphian metatherians from the La Meseta Formation levels: derorhynchids, microbiotheriids, prepidolopids, polydolopids, and a few additional taxa of unknown affinities (Candela and Goin 1994; Goin and Carlini 1995; Goin et al. 1994, 1999, 2007; Chornogubsky et al. 2009). Particularly notable of this assemblage is, if the record is not biased, the complete absence of strictly carnivorous metatherians of the Order Sparassodonta.

As it happens with other early Paleogene associations in South America (e.g., that of the early Eocene of Itaboraí, Brazil), the proportion of metatherians in the Antarctic association is larger than that of eutherians (see below). This stands in sharp contrast with the Metatheria/Eutheria ratio of Recent South American mammals. By the early Eocene, metatherians constituted around 70% of the terrestrial mammalian associations in South America; currently they are less than 15% (Goin et al. 2016). This was so because metatherians flourish under warm climates, mainly due to their reproductive physiology (Zimicz 2012 and literature cited therein). Faunal associations representative of the Itaboraian SALMA (South American Land Mammal Age) temporally coincide with the Early Eocene Climatic Optimum (EECO; Woodburne et al. 2014a, b), i.e., the climax of the greenhouse world during

Cenozoic times. It is precisely during this age when the highest rate of metatherians vs. eutherians is recorded in South America.

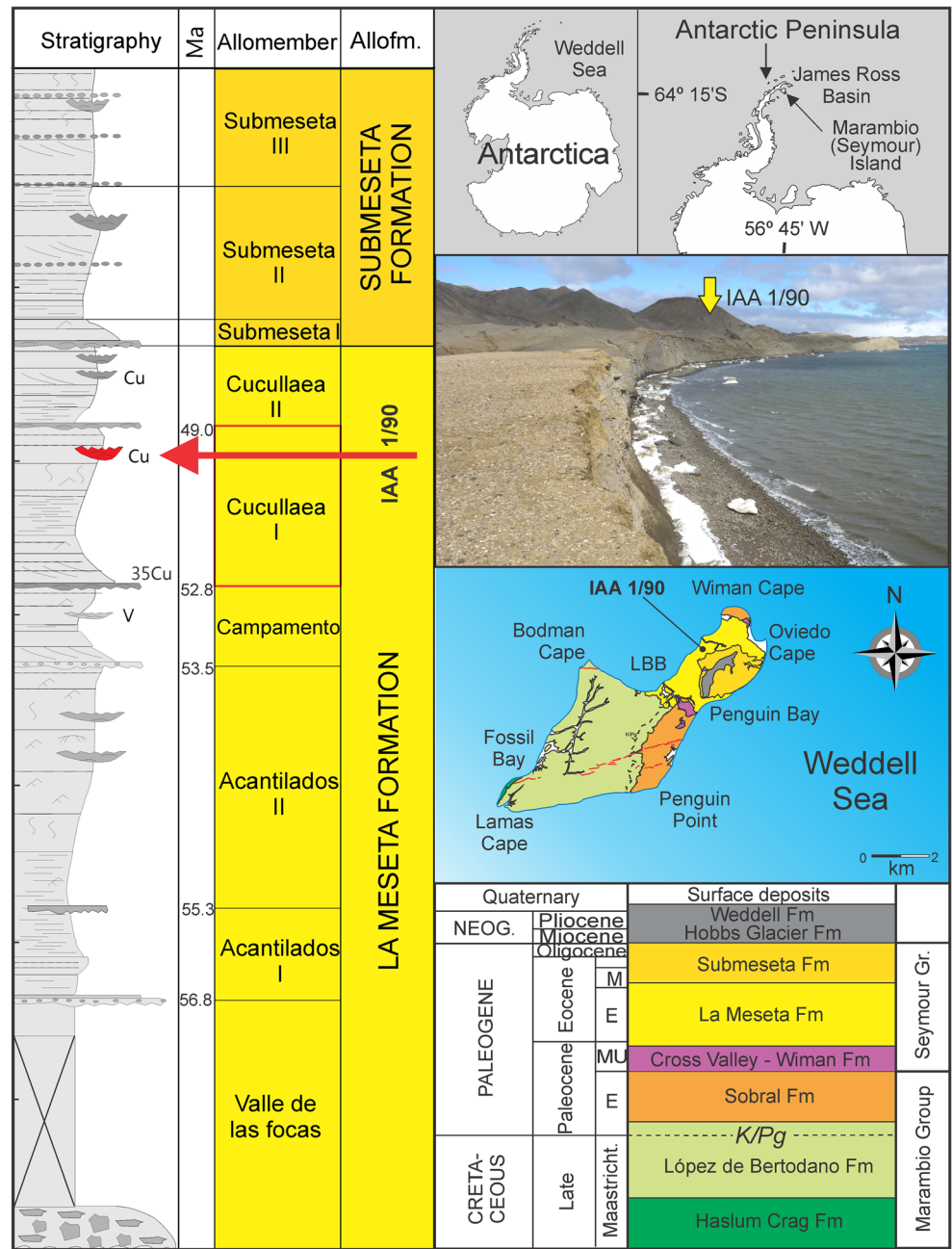
The faunal association recovered from *Cucullaea* I Allomember in the Antarctic Peninsula is slightly younger than the EECO. It has been referred to the Vacan Sub-SALMA (early Lutetian; Reguero et al. 2002); more recently it was correlated with the Paso del Sapo assemblage in Western Patagonia, slightly older in age (Ypresian-Lutetian boundary; Tejedor et al. 2009; see below). This temporal interval is later than the EECO, and correlates with the beginnings of a cooling phase that would continue throughout the middle and late Eocene. It is highly probable that this cooling phase was stronger in Antarctica than, for instance, in South America or Australia. Notwithstanding, even in Antarctica, features characteristic of the last phase of the greenhouse world persisted: ice-free poles, warm-temperate climates, and the persistence of some climatic equability, both daily and seasonal.

As part of the 2013–2014 summer field work organized by the Dirección Nacional del Antártico - Instituto Antártico Argentino (DNA-IAA), a new extinct mammal was discovered (Reguero et al. 2016; Goin et al. 2017). The purpose of this work is to describe the new mammal, a metatherian, which confirms the predominance of this group over eutherians in the southern Paleogene. Not without doubts we opted to refer the new taxon to the Order Polydolopimorphia, its precise family allocation being still uncertain. In spite of its fragmentary nature (an isolated lower molar; Figs. 3, 4, 5, and 6), the new taxon adds information on the diversity and paleoecology of the southernmost metatherians, and opens new questions on its intercontinental affinities and morphological evolution as well.

Geological Setting

The James Ross Basin includes an Early Cretaceous and Paleogene stratigraphic sequence, composed mostly of marine sedimentary rocks that comprise from base to top the Gustav (Aptian - Coniacian), Marambio (Santonian-Danian), and Seymour Island (Selandian-Rupelian) groups (Reguero et al. 2013; Montes et al. 2013). La Meseta Formation of Elliot and Trautman (1982) is part of the Seymour Island Group and crops out mainly in Marambio (Seymour) Island. The unit is composed of sandstones and mudstones with interbedded shell-rich conglomerates. It was divided by Sadler (1988) in seven numbered units (Telm 1 through Telm 7). Later, it was organized into erosional-based internal units (allomembers; Marenssi 1995; Marenssi et al. 1998a, b) while the upper section of the sequence (Telm 7) was recognized as an independent unit: the Submeseta Formation (Montes et al. 2013). From base to top the La Meseta Formation includes the following allomembers (Fig. 1): Valle de Las Focas, Acantilados I, Acantilados II, Campamento, *Cucullaea* I, and *Cucullaea* II

Fig. 1 Geographic and stratigraphic location of the studied specimen, MLP 14-I-10-20 (*Pujatodon ektopos*, gen. et sp. nov.). Left, geological profile of the Palaeogene sequence of La Meseta and Submeseta formations indicating the outcrops at locality IAA 1/90 (arrow). Right: top, Antarctic map and details of the James Ross Basin where Marambio (Seymour) Island is located; middle, photograph of locality IAA 1/90 looking to SW; below, geological profile of Marambio (Seymour) Island (modified from Montes et al. 2013)



(Marenssi 1995; Marenssi et al. 1998a, b, 2002; Montes et al. 2013). These units were deposited during Eocene times under deltaic, estuarine, and shallow marine depositional environments, mostly within a northwest–southeast trending valley (Marenssi 1995).

Although we follow the temporal calibration based on the paleomagnetic information of Montes et al. (2013), it should be noted that there is not a complete agreement about the age of the La Meseta and Submeseta formations. Most inferences constrain their age to the Eocene; however, the age of the allomembers is still uncertain depending on the consideration of biostratigraphy or isotopes (see a review in Ivany et al.

2008). Specimen MLP 14-I-10-20 comes from the naticid bed of *Cucullaea* I allomember of the La Meseta Formation, which is regarded as late early Eocene (late Ypresian) following the stratigraphic framework of Montes et al. (2013) and the magnetostratigraphic dating of the Seymour Island Group by Beamud et al. (2015). This agrees with biochronological correlations previously made between the “Sapোন” mammalian association from Western Patagonia and that of *Cucullaea* I (Tejedor et al. 2009; Reguero et al. 2013). The “Sapোন” assemblage comes from two localities near the town of Paso del Sapo, in northwestern Chubut Province, Argentina. The type locality of Laguna Fría has been dated at 49.51 ± 0.32 Ma

(40Ar/39Ar). Correlative deposits and faunal association of the nearby locality of La Barda overlies the upper member of the Andesitas Huanchache Formation, dated at 47.89 ± 1.21 Ma; in turn, it is overlain by basalts dated at 43 Ma (Tejedor et al. 2009; Woodburne et al. 2014a). Based on these dates, Tejedor et al. (2009) argued that the “Sapoan” association occurs within the interval of 47 to 49 Ma (latest Ypresian-earliest Lutetian, Fig. 2).

Based on ^{206}Pb - ^{238}U analysis for the Kaluel Kaike and middle part of the Las Flores formations of Argentina, a recalibration of some Paleogene SALMAs and faunas was recently suggested (Krause et al. 2017). In this context, the La Barda assemblage of the “Sapoan” was regarded as closer to the Vacan subage of the Casamayoran SALMA and almost equivalent to the lower part of the Riochican SALMA (see Krause et al. 2017: fig. 8). Although the “Sapoan” was considered as formed by two temporally

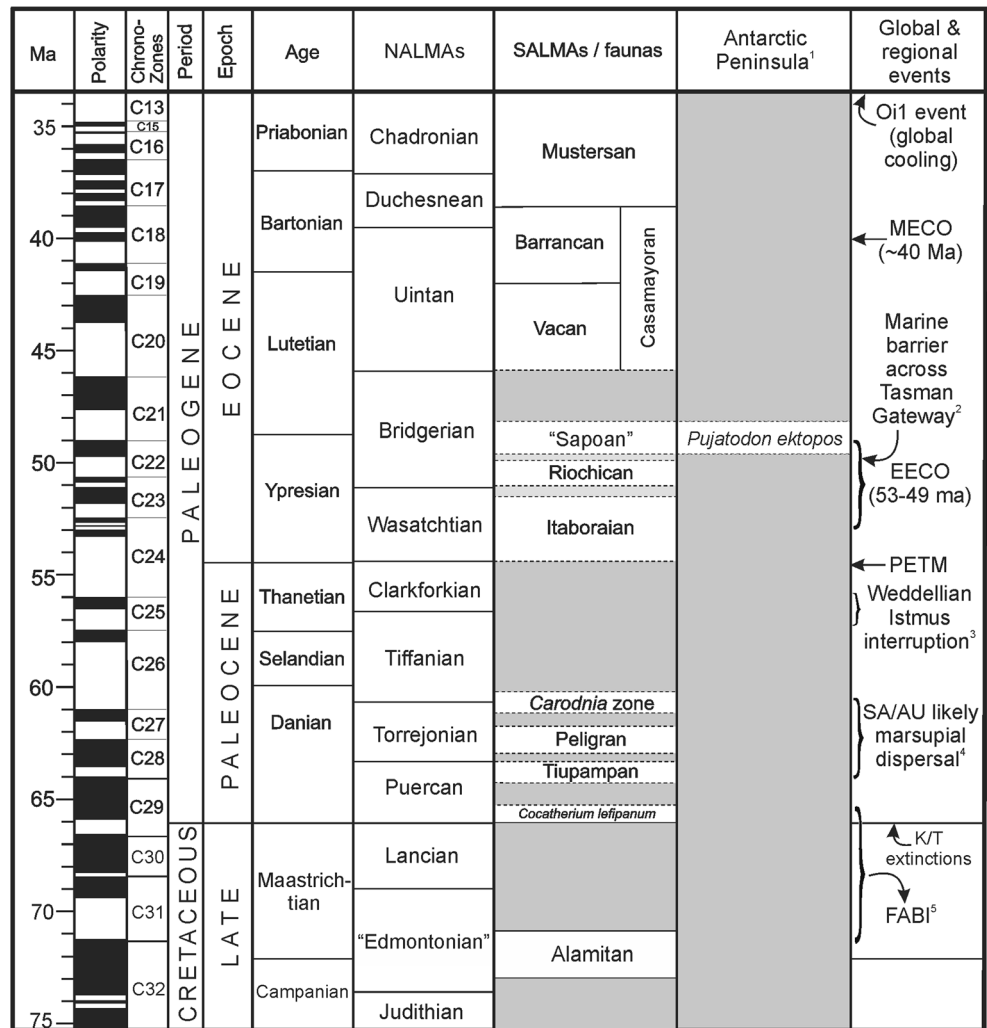
distinct faunas, Krause et al. (2017) failed to explain the taxonomic similarity between Laguna Fría and La Barda associations (Tejedor et al. 2009), and their differences with previously defined SALMAs. Despite the temporal identity of the La Barda fauna, the “Sapoan” in a strict sense is still a well identifiable assemblage using the Laguna Fría fauna.

Material and Methods

Specimen Recovery

Around one ton of sediment from different localities of the La Meseta and Submeseta formations was dry sieved during field work in Marambio (Seymour) Island. The sediment was divided in three size fractions, coarse (>10 mm), medial (>4 mm

Fig. 2 Late Cretaceous-Eocene chronology, biochronology, and global and regional events. Abbreviations: EECO, Early Eocene Climatic Optimum; FABI, First American Biotic Interchange; K/T, Cretaceous-Tertiary; MECO, Middle Eocene Climatic Optimum; NALMA, North American Land-Mammal Age; Oi1, earliest Oligocene oxygen isotope excursion that marks the beginning of the ice sheet coverage in Antarctica; PETM, Paleocene-Eocene Thermal Maximum; SA/AU, South America/Australia; SALMA, South American Land-Mammal Age. Notes: 1, upper naticid bed of *Cucullaea* I Allomember, La Meseta Formation; 2, after Goin et al. (2016); 3, after Reguero et al. (2014); 4, after Goin et al. (2016); (5) after Goin et al. (2012)



<10 mm) and thin (<4 mm), and bagged for transportation. Sediment samples were washed at lab; later, microvertebrates were sorted out using a stereoscopic microscope Leica MS5 at the Museo de La Plata. The specimen studied here (Figs. 3, 4, 5, and 6) was found during this work.

Imaging

Micrographs of the new taxon (Figs. 4 and 6) were made with a scanning electronic microscope (SEM) Jeol JSM 6360 LV at the Museo de La Plata. The enamel microstructure (Fig. 6) was observed directly on the worn cusps (protoconid) of the specimen in order not to damage it (i.e., the cusp was not polished). The enamel surface was treated with 10% HCl.

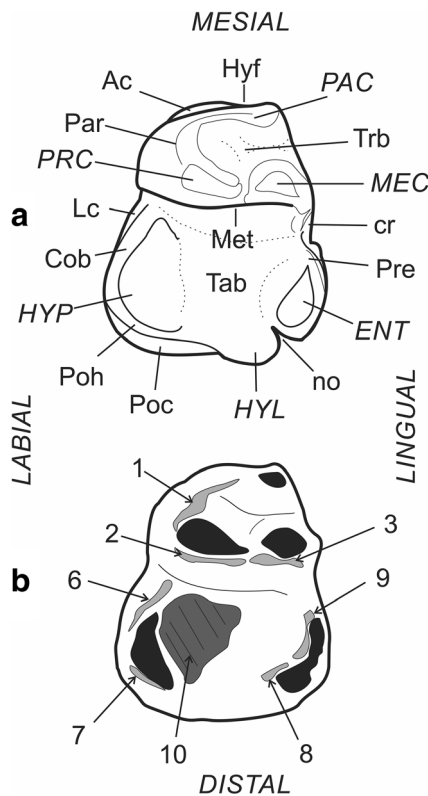


Fig. 3 Schematic drawings of specimen MLP 14-I-10-20 (*Pujatodon ektopos*, gen et sp. nov.; holotype), showing the terminology for cusps and crests of lower metatherian molars (a), as well as the wear facets of the tooth (b). Abbreviations: Ac, anterior (or anterobasal) cingulid; Cob, cristid obliqua; cr, crest; ENT, entoconid; Hyf, hypoconulid fossa (or notch); HYL, hypoconulid; HYP, hypoconid; Lc, labial cingulid; MEC, metaconid; Met, metacristid (postprotocristid + postmetacristid); no, notch; PAC, paraconid; Par, paracristid (postparacristid + preprotocristid); Poc, posterior cingulid; Poh, posthypoconid; PRC, protoconid; Pre, preentocristid; Tab, talonid basin; Trb, trigonid basin. Wear facets: see text

Phylogenetic Analysis

A preliminary phylogenetic analysis based on maximum parsimony was performed adding *Pujatodon ektopos*, gen. et sp. nov., to the data matrix of Chornogubsky and Goin (2015) and using TNT software (Goloboff et al. 2008). The data matrix included 26 taxa and 45 characters. *Alphadon* was considered as the outgroup taxon and all characters were regarded as equally weighted and unordered. Several analyses were performed. First, a traditional search, starting with 50 Wagner trees using random seed, with 1000 replicates, followed by TBR branch-swapping algorithm saving 100 trees per replication. The same analysis was done applying a monophyly constraint to Polydolopimorphia and setting *Pujatodon ektopos*, gen. et sp. nov., as a floating taxon (Fig. 7). Bootstrap and Jackknife resamplings were performed using default options and 1000 replicates with a traditional search.

Ecomorphology

In order to reconstruct the paleoecology of the new taxon, we estimated and integrated information from three sources: body mass, morphometric variables, and molar wear pattern. (1) Body mass was inferred using the equation derived by Gordon (2003) from a large data base of living marsupials. This equation relates body mass with dental variables, such as molar length and molar area. In order to consider the bias introduced in the inference by the logarithmic transformation, we calculated a correction factor (“smearing estimate”; Smith 1993) to apply to the de-transformed result of body mass. Following Van Valkenburgh (1990), we calculated for each equation the prediction error (PE%) and the standard error of the estimate (%SEE) to evaluate the accuracy of the resulting body mass estimate. The best equation is the one with lowest values of PE, SEE, and highest values of the determination coefficient (R²). Body mass is expressed in grams (g). Body mass estimations for *Pujatodon ektopos*, gen. et sp. nov., are shown in Table 1 and Fig. 8. (2) In order to quantify the morphological features related to diet, we calculated several morphometric indexes that roughly characterize distinct feeding categories (see Dewar 2003; Zimicz 2014): (a) crest relative length is an indicator of the shearing capacity of a tooth. The variable results from calculating the ratio between the sum of all crests length and the total length of the tooth. (b) The trigonid-talonid relief is the difference between the height of the tallest cusp of the trigonid and the tallest cusp of the talonid. The trigonid-talonid relief was divided by the length of the m2 of each specimen in order to account for size differences. Insectivores and carnivores have the largest reliefs, contrary to granivores and frugivores, which have low relief values

Table 1 Body mass estimations for *Pujatodon ektopos*, gen. et sp. nov. Abbreviations: PE%, prediction error; %SEE, standard error of the estimate; R2, determination coefficient

Tooth loci	a	b	r ²	%PE	%SEE	ES	Body mass (in g)
m2 length	1,65	3,32	0,95	39,72	37,34	1,20	90,69
m2 area	2,52	1,65	0,95	20,96	37,44	1,72	153,15
m3 length	1,76	3,17	0,97	12,82	39,14	1,11	83,13
m3 area	2,54	1,60	0,93	58,38	43,10	1,12	93,11

(Zimicz 2014:111). (c) The postvallid wall angle describes the angle between the distal wall of the trigonid and the horizontal plane, such that 90° is the highest possible angle. High angles typify insectivores and carnivores, while lower values characterize molars adapted to frugivorous diets (Zimicz 2014:111). (d) The relative area and relative length of the talonid are measurements of the grinding capacity of the tooth. Molars adapted to high compressive and grinding forces have well-developed talonids in both, area and length. Indices were calculated as the ratio between the talonid area or length and the trigonid area or length. Values higher than one indicate an expansion of the talonid at the expense of the trigonid and characterize frugivore and granivore teeth (Zimicz 2014). Morphometric variables and quantitative estimations for *Pujatodon ektopos*, gen. et sp. nov., are shown in Table 2. (3) The wear pattern was analyzed identifying the apical contacts and wear facets corresponding to each stage of the masticatory cycle (Hiimae and Crompton 1985; Hiimae 2000). The facet system adopted here (Fig. 3b) follows Butler (1980, 1985), considering facets 1,2,3, 4, 6, 7, 8, and 9 developed along crests during the Phase I or shearing stage; facets 5 and 10 correspond to the Phase II or grinding stage and are developed on the trigonid and talonid basins, respectively. In order to quantify the relative development of each stage of the masticatory cycle, we measured the area of each wear facet, we grouped the facets corresponding to each phase (I and II) and calculated the percentage of the total wear represented by Phase I and Phase II. This was compared with the average values for each dietary category (Zimicz 2014).

Paleobiological Summary

The diagram of Fig. 9 is a summary of inferred diets, body masses, and dental morphologies in selected Paleogene South American metatherian assemblages: Las Flores (Central Patagonia; early Eocene; black circles; Zimicz 2014), La Cancha (Central Patagonia, early Oligocene; grey circles; Goin et al. 2010), and West Antarctica (late early Eocene, red circles; Reguero et al. 2013). Each circle represents a species. Arrows indicate evolutionary pathways in the development of basic molar morphologies, departing from a generalized insectivorous pattern. I, II refer to the dominant masticatory phases that determine the wear patterns (Hiimae 2000). Body size is expressed

as log₁₀ intervals of body mass (in grams). Of the eight dietary categories shown here, the herbivorous (grazer) one was not exploited by South American metatherians. Figures outside the circle illustrate basic upper right molar designs for each dietary category. Center, top: a deltatheridian (insectivory); then, clockwise: a generalized microbiotherian (omnivory); a caroloameghiniid (frugivory); *Klohnia*, a basal argyrolagoid (granivory); the bonapartherioid *Gashternia* (folivory); an Australian macropodid, *Macropus* (herbivory); counterclockwise: a sparassocynid (faunivory), and an hathliacynid sparassodont (carnivory). Modified from Goin et al. (in press).

Data Availability All data generated during this study are included in this published article. The datasets analyzed during the current study are available in the Journal of Vertebrate Paleontology repository, https://www.tandfonline.com/doi/suppl/10.1080/02724634.2015.983238/suppl_file/ujvp_a_983238_sm5672.pdf (Chornogubsky and Goin 2015, Supplementary data).

Institutional Abbreviations

DNA, Dirección Nacional del Antártico; IAA, Instituto Antártico Argentino; MLP, División Paleontología Vertebrados, Museo de La Plata (Universidad Nacional de La Plata, Argentina).

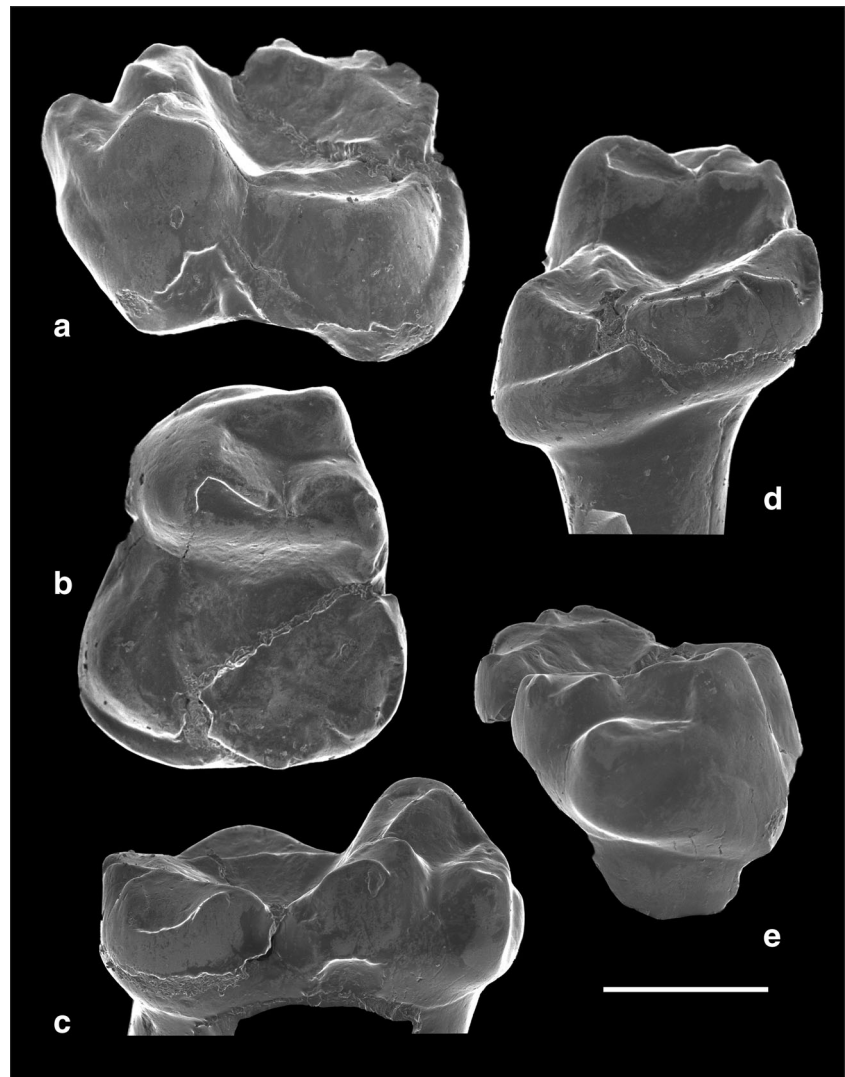
Other Abbreviations

D, dentine; EDJ, enamel-dentine junction; EECO, Early Eocene Climatic Optimum (Tsukui and Clyde 2012); g, grams; HSB, Hunter-Schreger Bands; IPM, interprismatic matrix; IRS, inter-row sheets; kg, kilograms; Ma, Megannum (one million years in the radioisotopic time scale); mm, millimeters; NALMA, North American Land-Mammal Age (Woodburne 2004); OES, outer enamel surface; P, prisms; %PE, prediction error; PLEX, prismless enamel; R2, determination coefficient; SALMA, South American Land-Mammal Age (see e.g., Woodburne et al. 2014a); %SEE, standard error of the estimate; T, tubules; μm, micrometers.

Anatomical Conventions

Lingual, buccal, or internal; labial, vestibular, or external; mesial, anterior; distal, posterior; m1, m2, m3, m4, loci nomenclature for metatherian lower molars. The terminology of cusps and crests follows Goin et al. (2016) and is shown in Fig. 3a. Enamel microstructure definitions and abbreviations follow Koenigswald and Sander (1997). Enamel measurements are in micrometers (μm), molar measurements are in millimeters, while body mass is expressed in grams and kilograms (Figs. 8 and 9).

Fig. 4 *Pujatodon ektopos*, gen. et sp. nov. Scanning electronic micrographs of specimen MLP 14-I-10-20 (holotype), a left lower molar in labial (a), occlusal (b), lingual (c), posterior (d), and anterior (e) views. Scale: 1 mm



Systematic Paleontology

Class Mammalia Linnaeus, 1758.
 Infraclass Metatheria Huxley, 1880.
 Order Polydolopimorphia Archer, 1984.
 Family indet.

Pujatodon ektopos, gen. et sp. nov.

Etymology

The generic name honors General Hernán Pujato (1904–2003), a military officer, diplomat, and explorer who founded the San Martín Antarctic base and the world's first Antarctic Institute, the Instituto Antártico Argentino. The suffix *-odon* comes from the Greek *odontos*, tooth. Gender is masculine. The specific name *ektopos* is Greek, meaning “away, distant,” in allusion to the extreme southern distribution of this marsupial

with respect to other members of the polydolopimorphian lineage.

Type (and Only Known) Specimen

MLP 14-I-10-20 (Figs. 3, 4, 5, and 6), a lower left molar (m2 or m3) partially worn.

Locality, Stratigraphy, and Age

Locality IAA 1/90, Marambio (Seymour) Island, Antarctic Peninsula (Fig. 1). Specimen MLP 14-I-10-20 comes from the naticid bed in *Cucullaea* I Allomember, which is equivalent to the lower half of Telm 5 of Sadler (1988). This level is different from the lower conglomeratic shell bed at the base of the *Cucullaea* I Allomember, which is reworked from the Campamento Allomember and therefore equivalent to

the short span of T_{elm} 4. The age is early Eocene (late Ypresian), probably equivalent in chronology to the “Sapuan” mammal association of Paso del Sapo in Western Patagonia (see above and Tejedor et al. 2009; Reguero et al. 2013; Fig. 2).

Measurements

MLP 14-I-10-20: total length, 2.24 mm; trigonid length, 0.72 mm; trigonid width, 1.11 mm; talonid width, 1.45 mm. Body mass estimations are shown in Table 1, while morphometric variables relative to tooth wear are shown in Table 2.

Species Diagnosis

Differs from other basal polydolopimorphians in the following combination of features in the lower molars: 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; cristid obliqua reaches anteriorly the postero-labial face of the protoconid; enamel type radial with interrow sheets. Diagnosis extends to genus by monotypy.

Description

The molar is very small, brachydont, and bunoid. It has two roots which that are slightly mesio-distally compressed. The labial face is higher than the lingual one. In relation to its size, the enamel layer is thin (see below); however, it is not even along the tooth surface, being thicker on the labial face of the protoconid and the hypoconid, and thinner at the talonid basin. The trigonid is shorter than the talonid and its distal crest, the metacristid (post-protocristid + post-metacristid) is not vertical; instead, it slopes downward towards the talonid basin. Besides being longer, the talonid is evidently wider than the trigonid. All cusps are worn, especially the labial ones (protoconid and hypoconid). The anterior cingulid is short and narrow; lingual to it, the hypoconulid fossa is poorly developed. The posterior cingulid is present, being better developed than the anterior one, and runs downwards from the hypoconulid to the disto-labial corner of the tooth, basally surrounding the hypoconid almost to its labial face. Between the protoconid and the hypoconid, on the labial face and near the base of the crown, there is a slight thickening or flange resembling a (very weak) labial cingulid. Its

true length cannot be estimated because the enamel is broken at the base of the protoconid.

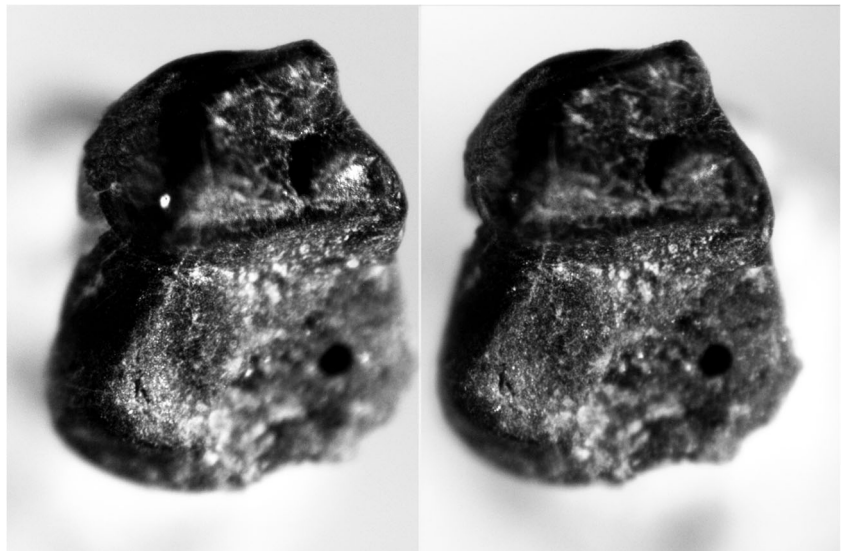
The protoconid is larger and higher than the metaconid. The paraconid is the smallest cusp of the trigonid and is located close to the metaconid; its general aspect is conical, with the mesial face relatively flat. The post-paracristid is almost perpendicular to the dental axis, while the pre-protocristid is parallel to it; in consequence, the paracristid (post-paracristid + pre-protocristid) is not straight; instead, it forms an almost right angle at the joint of both subcristae. The metaconid is placed at the same level than the protoconid and is much larger than the paraconid. At its distolingual corner there is a crest oriented towards the entoconid.

The talonid is longer and wider than the trigonid; both the entoconid and the hypoconid are large cusps, with the entoconid higher. The hypoconid is labially very salient and the cristid obliqua is short, almost parallel to the mesio-distal dental axis. The post-hypocristid is more or less perpendicular to this axis. The entoconid is slightly labio-lingually compressed. Even though broken, the presence of a short pre-entocristid directed towards the very short crest placed at the posterolingual corner of the metaconid can be inferred. Posterior to the entoconid there is a small notch that separates this cusp from the hypoconulid. The hypoconulid is almost twinned to the entoconid and is not distally salient.

Inferred Molar Locus

The molar locus of MLP 14-I-10-20 cannot be unambiguously determined. Notwithstanding, several features suggest that it is neither an m1 nor an m4. (1) In metatherians the paraconid of m1 usually occupies a more mesial (anterior) position and is located not close but far from the metaconid; in MLP 14-I-10-20 the paraconid is placed more posteriorly, close to the metaconid. The paracristid of MLP 14-I-10-20 shows a strong (almost straight) angle at the joint between the postparacristid and the preprotocristid, while in the m1 of most metatherians the paracristid is straighter and obliquely oriented. (2) The talonid of m4 is usually smaller than the trigonid, or, at least, subequal; in turn, the hypoconid is not labially salient. In MLP 14-I-10-20 the talonid is large, wider and longer than the trigonid, owing part of its width to the labially salient hypoconid. For these reasons we refer the type of *Pujatodon ektopos* to an m2 or m3.

Fig. 5 *Pujatodon ektopos*, gen. et sp. nov. Photographic stereopair of specimen MLP 14-I-10-20 (holotype) in occlusal view. Note that part of the talonid basin is lacking. Scale: 1 mm



Enamel Microstructure

Description

The enamel layer is thin (25 to 44 μm). The enamel is prismatic, radial, and lacking an external prismless layer (PLEX). Prisms are small (around 3.5 μm in diameter), lack seams, and are frequently pierced by tubules, sometimes more than one per prism. Prisms appear to have a distinct contour (i.e., the sheath prisms are complete). In occlusal view they are vertically (apically) oriented regarding the horizontal plane. They are organized in rows that are roughly parallel and radially oriented, from the enamel-dentine junction (EDJ) up to the outer enamel surface (OES). The prisms of each row are not strictly aligned with those of contiguous rows (i.e., prism to prism); instead, they are interleaved as bricks in a wall. Decussation of prisms and interprismatic matrix (IPM) are almost at a straight angle. The IPM forms continuous layers between the prism rows: the interrow sheets (IRS), which are clearly thinner than the average diameter of the individual prisms. The layers of IPM frequently bifurcate, anastomose, or display irregularities in such a way that the prism rows are not always aligned and parallel to each other. It can be appreciated that the IPM sheets regularly display narrow bridges of crystals between two adjacent layers of IRS, which separate each individual prism in a row.

Comparisons

The presence of prismatic enamel is a feature common to therian mammals (Wood et al. 1999). Tubules are frequent

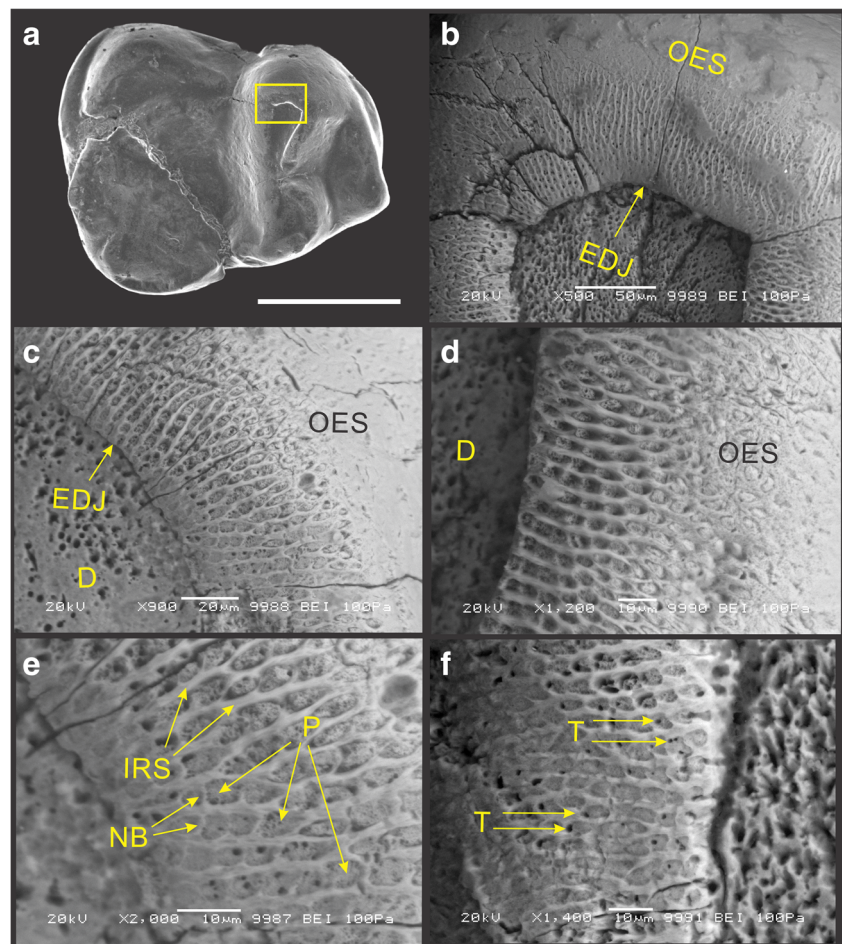
in the enamel of several metatherian lineages. The arrangement of the IPM in interrow-sheets (IRS) is a derived feature and appears independently in various mammal groups; among metatherians it characterizes several marsupials, being absent in more basal lineages. Among South American marsupials, IRS occurs independently in several Didelphimorphia (*Marmosa*, *Philander*, *Didelphis*; Wood et al. 1999), Paucituberculata (several Palaeothentoidea; Koenigswald and Goin 2000), as well as in Polydolopimorphia (*Wamradolops*; von Koenigswald and Goin 2000). Among Australasian marsupials it occurs in Yalkaparidontia (Lester et al. 1988), Peramelemorphia, and Diprotodontia (e.g., Gilkeson 1997). As in *Wamradolops*, IPM sheets of enamel of *Pujatodon* are oriented parallel to each other from the EDJ, occasionally being anastomosed towards the outer enamel surface (OES). Prism diameter of *Pujatodon* (3.5 μm) is relatively small for Metatheria; notwithstanding, even smaller sizes have been recorded for other polydolopimorphians (2 μm ; Groeberiidae, Patagoniidae; Koenigswald and Goin 2000).

Paleocology

Body Mass

Because of the uncertainty about the molar loci of the specimen, body mass was calculated considering the tooth alternatively as an m2 or an m3. Table 1 summarizes the resulting body mass estimations as well as the statistical parameters associated with

Fig. 6 Enamel microstructure of *Pujatodon ektopos*, gen. et sp. nov. (a–f), scanning electron micrographs of specimen MLP 14-I-10-20 (holotype). (a), occlusal view; the square on the protoconid indicates the area detailed in b–f. (b–f), several views of the enamel microstructure of specimen MLP 14-I-10-20. (c–d) the enamel-dentine junction can be observed. (c–e) the anastomosed interrow sheets, especially near the outer enamel surface, are visible. (e–f) there are details of individual prisms and of the tubules that pierce many prisms. Abbreviations: D, dentine; EDJ, enamel-dentine junction; IRS, interrow sheets; NB, narrow bridges of crystals between two adjacent layers of IRS; OES, outer enamel surface; P, prisms; T, tubules. In (a), scale equals 1 mm; in (b–f), scales are represented in microns: b = 50 μ m, c = 20 μ m, d–f = 10 μ m



each equation. The best result from a statistic standpoint is that with the highest value of r^2 , and the lower %PE and %SEE. In this case, best estimations are 83.13 g (m3 length) and 153.15 g (m2 area).

Diet

Living mammals with a body mass in the range of 100 g are insectivores, granivores, frugivores, or a combination of them (McNab 2008). Some optional folivores could be around 100 g but always combining a rich nutrient item in their diets such as insects or fruits; strict folivores are near 1000 g in body mass (McNab 2008). Carnivores (vertebrate consumers) have larger sizes, generally larger than 1000 g (McNab 2008). The inferred body mass for *Pujatodon* suggests that the diet of this (very small) marsupial must have been within the range of insectivores, granivores, or frugivores. Which of these categories, or combination of them, is more plausible, can be suggested from the molar morphology and its pattern of wear facets (see below).

The molar shape of *Pujatodon* is characterized by the large development of basins plus a short extension of shearing blades. The cusps are low with blunt apices and crests. The result of morphometric variables and the quantitative estimations of tooth wear are summarized in Table 2. The small difference in height

of the trigonid and talonid (0.109) is in the range of primary consumers and out of range for insectivores whose lower boundary is 0.2 (Zimicz 2014). The moderate postvallid angle (56.93°) is within the range of granivores and omnivores (Zimicz 2014). The relative crest length is in the range of omnivores while the relative talonid area and length, are in the range of frugivores and granivores (Zimicz 2014). Quantitative analysis of wear facets indicates a predominance of grinding activity, which accounts for 73.33% of the total wear facets. This is evidenced by the large area occupied by grinding facet 10, which occupies most of the talonid basin. Shearing facets 6 and 7 are the most developed along with the cristid obliqua and the post-hypocristid, while the trigonid shearing facets are only slightly developed. In overall dimensions, the quantitative wear is within the range of frugivores in which Phase II/Phase I facets ratio is lower than 1 (Zimicz 2014). Apical wear is evidenced in the lake-like facets developed on the apex of the cusps. This wear is the result of abrasion during the puncture-crushing stage (Dewar 2003), and indicates the processing of hard particles like nuts or seeds.

In summary, the body mass, morphometric index, and wear facet analysis suggest that the molars of *Pujatodon* were primarily adapted to the processing of fruits, nuts, seeds, and/or hard insects, probably being these items the main components of its diet.

Discussion

Affinities of *Pujatodon*

Pujatodon ektopos does not belong to the Sparassodonta. Its small size, relatively wide trigonid, well-developed metaconid, unpiercing paracristid, and wide talonid precludes any further comparison with this group of carnivorous metatherians. Its belonging to the Didelphimorphia (sensu stricto; see Goin et al. 2016) can also be discarded: compared to most didelphimorphians, molars of *Pujatodon* are more bunoid, with a proportionally longer and wider talonid and a larger, much higher entoconid. Compared to the Caroloameghiniidae (here regarded as didelphimorphians) there are also significant differences in the lower molar morphology: *Caroloameghinia* has much larger hypoconulids, the posterior cingulid is absent, the anterior cingulid is better developed, the hypoconid is less salient, and the metacristid is disconnected, i.e., the postprotocristid does not join the postmetacristid; instead, the latter contacts behind the protoconid with a supernumerary cusp (see Goin 2006).

Due to their more generalized tribosphenic condition, most lineages of “Ameridelphia” can also be discarded as allied to *Pujatodon*. The only group that deserves further comparison is the Protodidelphidae, from the early Paleogene of Patagonia and Brazil (Oliveira and Goin 2011). Besides the much larger size of protodidelphids, the trigonid in *Pujatodon* has the paraconid closer to the metaconid, the paracristid is not straight, the talonid is wider, and lacks the very tall, spire-like entoconid that characterizes protodidelphids. Additionally, protodidelphids may have a vestigial posterior cingulid, while in *Pujatodon* it is wide and well-developed towards the posterolabial corner of the tooth.

Three groups of South American metatherians show in their lower molars some or many similarities with *Pujatodon ektopos*: Microbiotheria, Paucituberculata, and Polydolopimorphia. Microbiotherians (see Goin and Abello 2013) differ from *Pujatodon* in the following features: the paraconid is lower and not close to the metaconid, being instead more mesially placed in all molars; the posterior wall of the trigonid (metacristid) is vertical rather than sloped; the entoconid is proportionally smaller; even though the hypoconid in microbiotherians is also labially salient, it is not rounded in occlusal view; instead, its anterior and posterior crests form an acute angle at their joint; finally, especially in m1–2 the microbiotherian hypoconulid is not twinned to the entoconid.

Several features indicate that *Pujatodon* can also be discarded as a Paucituberculata (sensu Abello 2013): even though some advanced palaeothenoids have a similar trigonid/talonid width proportion to that of *Pujatodon*, this latter has more bunoid molars, the hypoconid is more rounded, the entoconid is not labio-lingually compressed and is

more posteriorly placed in the disto-lingual corner of the talonid. In most Paucituberculata the metacristid is subvertical; in most palaeothenoids the hypoconulid is less distinct and frequently wide. Unlike *Pujatodon*, palaeothenoids have their paraconid either far from the metaconid (m1) or completely paired with it (m2–4); their talonid is proportionally narrower; the hypoconulid is not leveled with the talonid basin, but it is placed in a relatively ventral position in the distal face of the molar; finally, the preentocristid is less parallel to the mesio-distal axis of the molar.

Pujatodon ektopos shows more affinities with basal polydolopimorphians (sensu Goin et al. 2016) than to any other South American metatherian lineage; more precisely, with representatives of the plesion Glasbiidae and with some basal members of the Suborder Bonapartheriiformes: the Prepidolopidae. *Pujatodon* shares with *Glasbius* (see Boyd et al. 2017) the following features: small size, bunoid cusps, sloped metacristid, well-developed posterior cingulid, paracristid forming a straight angle (around 90°), wide and labially salient hypoconid, the preentocristid contacting the disto-lingual edge of the metaconid (the latter developing a crest) by means of a notch, the cristid obliqua contacting the protoconid at a point clearly labial to the metacristid notch. It differs from *Glasbius* in that in the m2–4 of the latter the metaconid is more mesially placed than the protoconid, and in having a less developed cingulid complex: *Pujatodon* has a less developed anterior cingulid and lacks a continuous labial cingulid (see, e.g., Boyd et al. 2017: fig. 3) connecting both the anterior and posterior ones. In all these features *Pujatodon* is more generalized than *Glasbius*.

Several additional taxa have been variously referred to the Glasbiidae: *Chulpasia*, from the late Paleocene-early Eocene of Peru (Crochet and Sigé 1993), *Thylacotinga* from the earliest Eocene of Australia (Archer et al. 1993; Sigé et al. 2009), *Palangania* from the early Eocene of Patagonia (Goin et al. 1998), and *Periakros* from the late Eocene-early Oligocene of Patagonia (Goin et al. 2010). No lower molars are known for *Periakros*. Regarding *Chulpasia* and *Thylacotinga*, *Pujatodon* is more bunoid, the paraconid and metaconid are more close to each other, the anterior cingulid is less developed, and its talonid is proportionally wider (at least compared to the specimen CHU2 of *Chulpasia*; see Crochet and Sigé 1993: fig. 1d). Compared to *Palangania*, *Pujatodon* is even more bunoid, the para- and metaconid are closer, the entoconid is more posteriorly placed, and the posterior cingulid is well-developed (absent in *Palangania*).

Another polydolopimorphian lineage with which *Pujatodon* shows affinities is the Prepidolopidae, the basalmost representatives of the Suborder Bonapartheriiformes. *Pujatodon* resembles prepidolopids in its small size, bunoid cusps, wide posterior cingulid, trigonid-talonid overall proportions, and sloped metacristid (see Pascual 1980). An obvious difference between

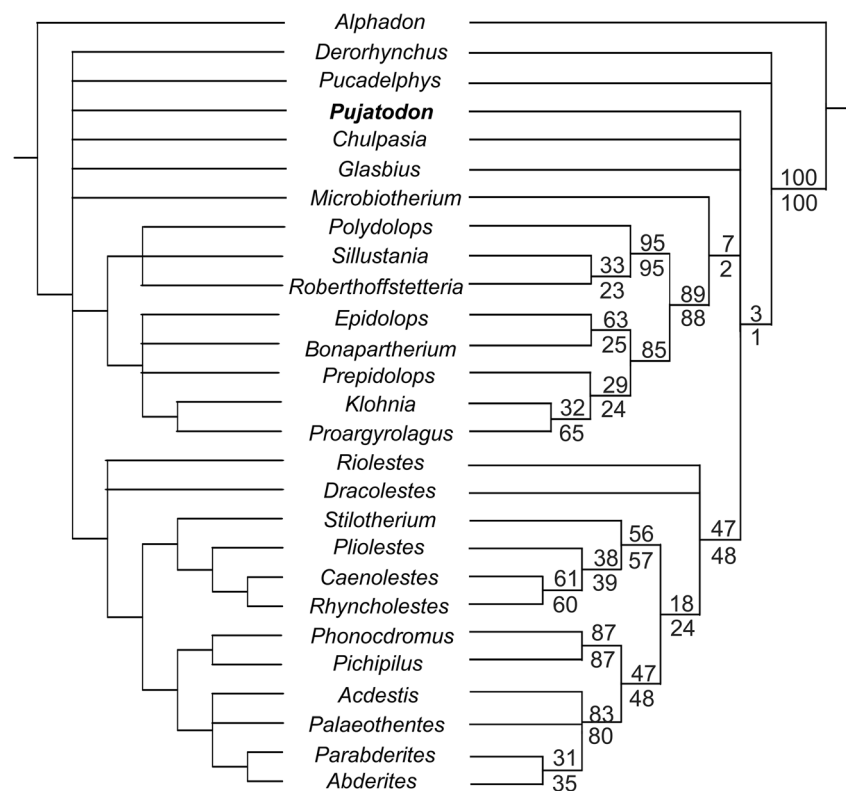
Pujatodon and *Prepidolops* lies in the morphology of the entoconid, which in the latter is proportionally larger and subcircular (not ovoidal) in section. A second difference is that in prepidolopids the paraconid is much more reduced. An extreme example of this feature is shown by *Perrodelpheys coquinense* (Goin et al. 1999), from the same locality and levels than those of *Pujatodon*. *Perrodelpheys* has a minute paraconid which is placed on the very mesiolingual slope of the protoconid (see Goin et al. 1999: fig. 8). In spite of their overall similar dimensions (though *Pujatodon* is smaller), *Perrodelpheys* also differs from *Pujatodon* in that the protoconid is proportionally larger, the talonid is narrower, and the molar lacks anterior, posterior, and labial cingulids.

A few other polydolopimorphians show similar features to those of *Pujatodon*, even though they are less noticeable. For instance, *Cocatherium lefpanum*, from the earliest Paleocene of western Patagonia (Goin et al. 2006b), resembles *Pujatodon* in the proximity of paraconid and metaconid, while they differ in the relative sizes and morphology of the talonid cusps: the talonid is subequal in width to the trigonid, and the entoconid is proportionally larger. *Bobbschaefferia*, from the early Eocene of the Itaboraí Formation in SE Brazil (see Oliveira 1998) shows a less bunoid aspect, trigonid and talonid subequal in width in m3, and paraconid not close but more mesial than the metaconid.

Procaroloameghinia, from the same locality and levels (Oliveira 1998), was referred to the Polydolopimorphia by several authors (but see Goin 2006). It shares with *Pujatodon* the bunoid aspect of molars, but in all other features it displays a more generalized tribosphenic pattern. Finally, *Mirandatherium*, also from the early Eocene of Brazil (tentatively referred to the Microbiotheria or Polydolopimorphia by Goin et al. 2016) shows a few similarities with *Pujatodon*, but differs in major aspects: trigonid longer and subequal in width to the talonid, paraconid and metaconid clearly apart from each other (partly due to the posterior placement of the metaconid relative to the protoconid), and distinct, posteriorly salient hypoconulid.

Summarizing, the overall morphology of *Pujatodon ektopos* resembles more that of basal polydolopimorphians (Glasbiidae, some Prepidolopidae) than that of any other South American or Antarctic metatherian so far known. Two aspects of its enamel microstructure are also present in at least some polydolopimorphians: small-sized prisms that are aligned in incipient rows. For these reasons and in spite of the inconclusive results of our phylogenetic analysis (see below), we tentatively allocate this new Antarctic taxon within the Polydolopimorphia, family indet. Interestingly enough, it resembles more closely –and is more generalized than– species of *Glasbius* from the Late Cretaceous of North America.

Fig. 7 Left, strict consensus of 14 trees of 127 steps with monophyly constraints in Polydolopimorphia; right, values on each node of Standard Bootstrap (above) and Jackknifing (below) using 1000 replications



Phylogenetic Analysis

The maximum parsimony analysis resulted in 28 most parsimonious trees of 127 steps and their strict consensus failed to recover the monophyly of the Polydolopimorphia (Fig. 7). In this last tree *Pujatodon* forms part of an unresolved polytomy. A new analysis leaving *Pujatodon* as a floating taxon and using monophyly constraints for Polydolopimorphia (sensu Chornogubsky and Goin 2015) was performed. The result was partially in agreement with the previous analysis, obtaining 14 trees of 127 steps that were already recovered previously. In the strict consensus, *Pujatodon* is part of a basal polytomy with *Chulpasia*, *Glasbius*, *Microbiotherium*, *Derorhynchus*, *Pucadelphys*, Polydolopimorphia, and Paucituberculata. Probably due to the few characters available, as well as their nature (i.e., relative to the lower molar morphology), the analysis is not confident enough to confirm -or refute- the inclusion of *Pujatodon* within Polydolopimorphia. The main difference with the original result of the matrix analysis presented in Chornogubsky and Goin (2015) rests in the more basal position of the sister group of Paucituberculata (i.e., *Derorhynchus*, *Pucadelphys*).

Paleobiology

The trophic categories represented in the Antarctic metatherian assemblage include insectivores (microbiotherians and derorhynchids), frugivores (microbiotherians, prepidolopids), and frugivore-folivores (polydolopids) (Zimicz 2012). If not due to a sampling bias, it is noteworthy that the carnivorous role was not fulfilled by any metatherian in the Antarctic assemblage, contrasting with continental localities (e.g., La Barda and Laguna Fría) in which the Sparassodonta were conspicuous elements. As a general rule, frugivory and folivory are the dominant trophic categories among mammals in the La Meseta Formation assemblage. Besides metatherians, Antarctic gondwanatherians were probably herbivores (Goin et al. 2006a); xenarthrans were represented by herbivorous lineages (Pilosa: Reguero et al. 2002); and ungulates (sparnotheriodonts and astrapotheres) were probably browsers or folivores (Reguero et al. 2002).

An additional feature of the La Meseta Formation assemblage is the increase in body mass relative to Patagonian counterparts, verified among several groups. Among the Microbiotheria, the species represented in the “Sapooan” association (western Patagonia) were small-sized, while the Antarctic species *Woodburnodon casei* reached a kilogram of weight (Goin et al. 2007). A similar phenomenon occurred among Polydolopidae

(Polydolopimorphia), with the Antarctic genus *Antarctodolops* being larger than their Patagonian counterparts (Zimicz 2012; Chornogubsky et al. 2009). Both the trophic composition and the increased body mass of the species recorded in Antarctica could respond to latitudinal differences in climatic parameters, with the Antarctic ones cooler than the Patagonian counterparts.

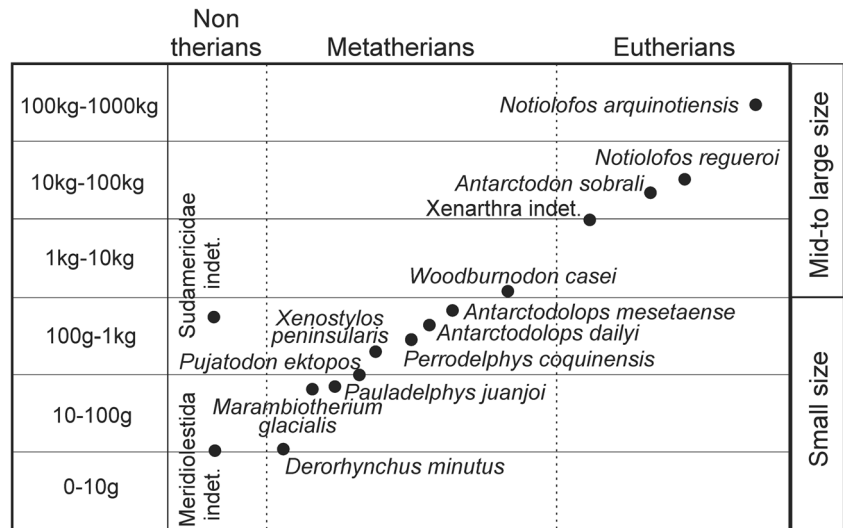
Ungulates seem to be less informative on changes in their body mass related to latitudinal differences. This does not necessarily mean that ungulates were less sensitive to their geographic distribution. A possible explanation rests in the higher body mass range among Antarctic ungulates (see below) in contrast to marsupials (Fig. 8). Antarctic sparnotheriodontids and astrapotherians almost fit in the same range of body mass as several South American fossil ungulates recorded from the early Eocene such as those of Itaboraí (Brasil) and Patagonian localities like Laguna Fría in Paso del Sapo or even in Cañadón Vaca (Gelfo et al. 2017).

Pujatodon ektopos, as well as the rest of the La Meseta metatherians, are part of the smallest-sized mammalian assemblage of the Eocene of West Antarctica. A previous body mass estimation for the metatherian assemblage of this region gave a range of 50 to 300 g (Vizcaíno et al. 1998). Since then, the addition of new taxa, as well as a refinement in the methods used to infer body mass, has expanded this range to 10 g – 1100 g (Zimicz 2012). Within the small-sized category should also be considered the Antarctic meridiolestid (Dryolestida) and the gondwanatherian (Allotheria; Fig. 8). Conversely, the (scarce) diversity of Eocene West Antarctic placentals fits in the category of medium- to large-sized terrestrial mammals. Middle-sized mammals include an indeterminate xenarthran, only known by a phalanx remain from which a body mass of ca. 10 kg was inferred (Vizcaíno et al. 1998), as well as browser ungulates such as the astrapotherian *Antarctodon sobrali* (18.5–38 kg) and the litoptern sparnotheriodontid *Notiolofof regueroi* (25.07–57.86 kg). In turn, the single large-sized species known so far is *Notiolofof arquinoiensis*, with an estimated body mass between 395 and 400 kg (Gelfo et al. 2017).

Enamel Microstructure

The enamel microstructure of MLP 14-I-10-20 represents the earliest evidence of interrow sheets (IRS) among metatherian mammals. In a few other polydolopimorphians, such as the Bonapartheriidae *Epidolops* of the early Eocene of Patagonia and Brazil, some tendency towards the orientation of prisms in parallel rows can be appreciated, even though the interprismatic matrix (IPM) does not form distinct sheets (IRS; Koenigswald and Goin 2000: fig. 12C). The occurrence of IRS at the inner zone of the enamel is reported in *Wamradolops tsulldodon* (referred as a “Polydolopinae indet.”

Fig. 8 Inferred body masses for the mammalian assemblage of the La Meseta Formation. Mammals are arranged in two main categories: small size (less than 1 kg), and mid- to large-size (more than 1 kg)



in Koenigswald and Goin 2000: 159). *Wamradolops* appears in the late Eocene or early Oligocene of intertropical South America (Goin and Candela 2004).

In *Pujatodon*, the IRS are plesiomorphic: even though the IPM forms distinct sheets, these are relatively narrow and there are narrow bridges of IPM between prisms of the same row. A more derived condition shows thicker IRS and absent bridges of IPM (see below). The incipient alignment of prisms by the early Eocene (*Epidolops*) and the presence of plesiomorphic IRS in *Pujatodon*, from the latest early Eocene (Ypresian-Lutetian boundary) suggest that this type of enamel microstructure was developed by this time, at least among South American-Antarctic metatherians. However, it should be noted that even though *Pujatodon* sheds light on the origins of IRS among metatherians, this structure was already present among other mammalian groups. A noticeable example is that of the Gondwanatheria from the Late Cretaceous of India, which at that time had already developed compact IRS and perfectly aligned prisms (Koenigswald and Krause 2014).

Koenigswald (2000: 223) distinguished between the thin plates of IPM called interrow sheets –IRS– by Boyde (1965), which are those that characterize *Pujatodon*, from the thick sheets named “modified radial enamel” by Pfretzschner (1994). Both enamel types constitute derived stages of radial enamel. Among eutherians, modified radial enamel is recorded in several large-sized, high-crowned taxa: Perissodactyla, Artiodactyla, Notoungulata, Typotheria, Pantodonta, Desmostylia, and Embrithopoda (Fortelius 1984; Pfretzschner 1992). Concerning IRS among von

Koenigswald (1997) indicated that there is an incipient structure of this type in a few genera of Soricinae (Lipotyphla), whose age goes back to the early Neogene (Dubey et al. 2007). It should be noted, however, that other complex enamel strengthening structures, as Hunter-Schreger Bands (HBS), have a long history among eutherians, being recorded as far back as the early Paleocene (Koenigswald et al. 1987).

Because of their presence in several independent lineages, these types of structures (as IRS) give no clear phylogenetic signals. The arrangement of prisms in roughly vertical rows separated by interrow sheets of IPM correspond to “Pattern 2” of Boyde (1964, 1989) and is recorded, among living mammals, in Artiodactyla, Perissodactyla, Marsupialia, Lagomorpha, and Rodentia (Hillson 2005). Among marsupials it is present in premolars of Thylacoleonidae, molars of Peramelidae, Diprotodontidae, and Phalangeridae, as well as in molars and incisors of Potoroidae, Macropodidae, Pseudocheiridae, and Petauridae (Koenigswald 2000).

In functional terms, the organization of rows of prisms and IPM in alternate layers represents, as in other decussation structures, a mechanical strengthening against fractures and ulterior crack propagation. It is one of multiple developments of an inherently brittle material, developed in each of the four specific organizational levels of the enamel (Koenigswald and Clemens 1992). Pfretzschner (1988) showed that such structures are effective if they are oriented parallel to the directions of maximum tensile stresses (which are those responsible for most enamel damage due to the breaking apart of adjacent elements).

Table 2 Quantification of wear facets in the lower molar of *Pujatodon ektopos*, gen. et sp. nov.

Trigonid / talonid relief	Relative crest length	Relative talonid length	Relative talonid area	Inclination of the distal trigonid wall	% grinding wear (Phase II)
0.109	1.38	2.11	2.78	56.94 °	73.3%

Several authors (Rensberger and Koenigswald 1980; Fortelius 1985; Pfretzschner 1988; Rensberger 2000) argued that in low-crowned molars, tensional stresses are circumferential and enhance towards the base of the crown. Because of this, it is precisely in this region where most enamel reinforcements are developed (e.g., transversal HSB, perpendicular to the vertical fracture planes). In mammals with high-crowned teeth, in which the chewing direction is strongly horizontal, severe radial stress occurs at the EDJ and near the occlusal surface (due to differences in elasticity between dentine and enamel). These molars show, near the dentine (or EDJ), special types of enamel characterized by vertical decussation planes (e.g., vertical HSB, modified radial enamel; Koenigswald et al. 1987; von Koenigswald and Pfretzschner 1991), which are aligned towards the direction that maximizes the resistance to fractures.

Pujatodon, as well as most metatherians, does not have hypsodont molars; however, as suggested by the masticatory analysis, it does have a strong lateral component (Phase II) in the masticatory movement. Thus, it is reasonable to assume that the interrow sheet structure (IRS) evolved in order to counter the stress at the EDJ due to an increase in horizontal masticatory movements.

Decussation of elements is weakly developed in those taxa that eat soft foods or in molar areas where maximum tensile stresses are low (Rensberger 1993); in turn, it is better developed in those that include hard foods in their diets (Maas 1986). Our paleoecological analysis of *Pujatodon* (body mass, morphometric index, and wear facet analysis) suggests that the molars were primary adapted to the processing of fruits, nuts, seeds, and/or hard insects, with these items probably the main components of its diet. The development of interrow sheets in the enamel microstructure of *Pujatodon* agrees well with this inference.

Significance of *Pujatodon* among the Antarctic metatherian ensemble

Pujatodon ektopos is the seventeenth mammal known so far from the early Eocene *Cucullaea* I Allomember, La Meseta Formation, Antarctic Peninsula. In order to consider the Paleogene land mammal diversity from Antarctica, it should be emphasized that, up to now, all specimens come from Marambio (Seymour) Island and from the marginal marine outcrops of the La Meseta and Submeseta formations. The scarce available data add additional constraints to diversity comparisons with South American Paleogene faunas. As a consequence, paleoecologic, taphonomic, and transport conditions should not be dismissed as possible explanations for the lack of a better representation of land mammals in these levels.

The mammalian assemblage coming from this level (not all of them nominated; see Table 3) includes one gondwanatherian, one meridiolestidan, eleven metatherians, and four eutherians. It is noteworthy that, as it happens in all pre-middle Eocene South American faunas, the Metatheria/Eutheria rate is highly favorable to the former (73.33%). Even if all mammals are considered, metatherians constitute almost two thirds (64.70%) of the whole Antarctic assemblage.

The taxonomic composition of the metatherian assemblage from Antarctica is typical of early Paleogene faunas from Patagonia. It includes various “Ameridelphians” (e.g., derorhynchids), microbiotherians, and polydolopimorphians, including two species of polydolopids (*Antarctodolops dailyi* and

Table 3 Updated list of early Eocene mammals from West Antarctica

ALLOTHERIA
Gondwanatheria
Sudamericidae
Gen. et sp. indet., cf. <i>Sudamerica ameghinoi</i> (Goin et al. 2006a)
DRYOLESTIDA
Meridiolestida
?Brandoniidae
Gen. et sp. indet. (Martinelli et al. 2014)
METATHERIA
“Ameridelphia”
Derorhynchidae
<i>Derorhynchus minutus</i> (Goin et al. 1999)
<i>Pauladelphys juanjoii</i> (Goin et al. 1999)
Derorhynchidae gen. & sp. indet. (Goin et al. 1999)
Family indet.
<i>Xenostylos peninsularis</i> (Goin et al. 1999)*
Australidelphia
Microbiotheria
?Microbiotheriidae
<i>Marambiotherium glacialis</i> (Goin et al. 1999)
Woodburnodontidae
<i>Woodburnodon casei</i> (Goin et al. 2007)
Polydolopimorphia
Family indet.
<i>Pujatodon ektopos</i> gen. & sp. nov.
Prepidolopidae
<i>Perrodelyphs coquinense</i> (Goin et al. 1999)
Polydolopidae
<i>Antarctodolops dailyi</i> (Woodburne and Zinsmeister 1982)
<i>Antarctodolops mesetaense</i> (Chomogubsky et al. 2009)
?Marsupialia
Order, family, gen. & sp. indet.**
EUTHERIA
Epitheria
Xenarthra
?Tardigrada or? Vermilingua indet. (Carlini et al. 1990, 1992)
Panperissodactyla
Litopterna
Sparnotheriodontidae
<i>Notiolofof arquinoiensis</i> (Bond et al. 2009)***
<i>Notiolofof regueroi</i> (Gelfo et al. 2017)
Meridiungulata
Astrapotheria
<i>Antarctodon sobralis</i> (Bond et al. 2011)

(*) *Xenostylos*, not *Xenostylus* (preoccupied; Goin 2007)

(**) See Goin et al. (1999: 356)

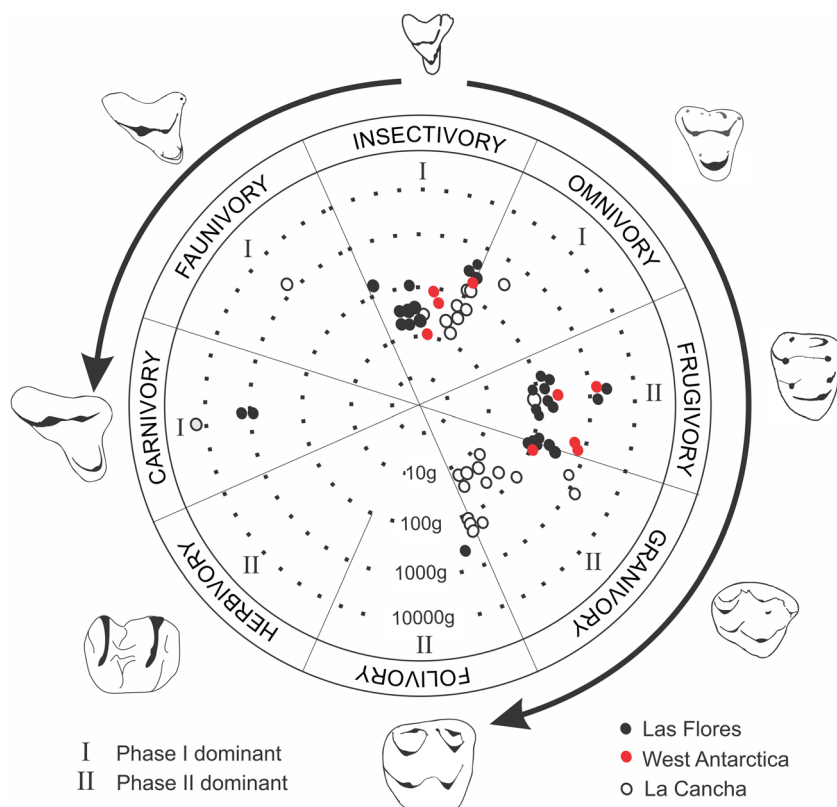
(***) *Notiolofof*, not *Notolophus* (preoccupied; Bond et al. 2009)

A. mesetaense; Chornogubsky et al. 2009). Polydolopids are perhaps the most geographically restricted lineage of South American–Antarctic metatherians because they are not recorded north of Patagonia in Argentina. It is striking, however, that the otherwise ubiquitous metatherian carnivores, the Sparassodonta, are still absent from the Antarctic association. Sparassodontans are usually of medium to large size. As other large-sized specimens have been recorded in the La Meseta Formation (xenarthrans, litopterns, astrapotherians), their absence in the *Cucullaea* I levels cannot be due to a bias related to size. Nevertheless, it should be taken into account that the entire *Cucullaea* I mammalian association includes less than 50 specimens as a whole. Sparassodonts reached far south Patagonia at various times during the Cenozoic, including the early Paleocene (Forasiepi and Rougier 2009, and literature cited therein); it is therefore expected to find these metatherians in Antarctica.

Figure 9 represents a paleobiological summary of the metatherian association of the early Eocene of Antarctica. As a comparative framework, two other Paleogene metatherian associations from central Patagonia are also represented: that of the early Eocene of Las Flores (Itaboraian SALMA; Zimicz 2012), and that of La Cancha (Eocene–Oligocene

boundary, Tinguirirican SALMA; Goin et al. 2010). The Las Flores assemblage occurred at or immediately after the climax of the EECO (Woodburne et al. 2014b). In contrast, the La Cancha association occurred after the global cooling event of the Eocene–Oligocene boundary. Even though less rich in individual species, the Antarctic association resembles that of Las Flores more than that of La Cancha, both in body mass distribution as well as in feeding habits. The La Cancha assemblage, on the contrary, includes several granivorous taxa not recorded in the former two. The La Cancha environments were most probably cooler (Barreda and Palazzesi 2010) and semi-arid (Bellosi and González 2010) compared to those of Las Flores or Antarctica during early Eocene times. Based on paleobotanical evidence, Reguero et al. (2013) summarized the climatic–environmental context of the Antarctic Peninsula during the Paleocene–Eocene transition. Among the families Nothofagaceae, Podocarpaceae, and Cunoniaceae that dominated the vegetation, several subtropical to temperate angiosperms are noteworthy (Lauraceae, Myrtaceae, Malvaceae or Sterculiaceae, Elaeocarpaceae, and Anacardiaceae). Early Eocene floras share many similarities with coeval floras from southernmost South America, confirming the presence of mixed mesophytic forests.

Fig. 9 Summary of paleobiological parameters (body mass, diet, molar morphology, and masticatory phases) of the metatherian assemblage of the La Meseta Formation (Antarctica; see Reguero et al. 2013), compared to two different assemblages from central Patagonia: Las Flores (early Eocene; Itaboraian SALMA; Zimicz 2014) and La Cancha (latest Eocene–early Oligocene; Tinguirirican SALMA; Goin et al. 2010). Note the similarity between the Las Flores and West Antarctic metatherian assemblages in size and diet. Modified from Goin et al. (in press)



Previously, we stated that *Pujatodon* resembles *Glasbius* more than any other known polydolopimorphian. The allocation of *Glasbius* among polydolopimorphians is a recurrent conclusion of several recent phylogenetic analyses (e.g., Williamson et al. 2014). The fact that *Pujatodon* is more generalized than *Glasbius* puts in question the very origins of this latest Cretaceous North American taxon: does *Glasbius* represent an endemic lineage to North America or, in contrast, was it derived from *Pujatodon*-like South American ancestors that migrated northward during the Late Cretaceous-early Paleogene event known as FABI (First American Biotic Interchange; Goin et al. 2012)? Boyd et al. 2017: 14) asked a similar question: "...it is difficult to determine if *Glasbius* was an endemic North American lineage that dispersed into South America during the late Maastrichtian or early Paleocene, or if *Glasbius* was part of a lineage endemic to South America (as the result of an earlier, unrecognized dispersal from North America) that then emigrated back to North America in the late Maastrichtian." In absence of more comprehensive phylogenetic studies of North and South American, Late Cretaceous-Paleogene metatherians, and with Cretaceous metatherians still missing from the South American record, the question remains unanswered.

Finally, we wonder if *Pujatodon* or *Pujatodon*-like ancestors could have had a role in the initial radiation of the (almost exclusively) Australasian Diprotodontia. For Goin et al. (2016) polydolopimorphians are, together with microbiotherians, part of the basal radiation of Australidelphian marsupials (for an alternative view on polydolopimorphian affinities see Beck 2017). Recently Lorente et al. (2016) discussed the existence of non-microbiotherian Australidelphian marsupials, referable to the Order Diprotodontia, in the Eocene of Patagonia (La Barda locality; see Tejedor et al. 2009). Their evidence comes from isolated tarsal bones; therefore the unnamed taxon from Patagonia cannot be unambiguously related to any known lineage of South American australidelphians. However, based on their size, the authors (Lorente et al. 2016: 544) stated that "... there are only four possible candidates for the assignation of the La Barda tarsals, all of them referable to the Polydolopimorphia: one gashterniid (*Gashternia*), one glasbiid (*Palangania*), and two polydolopids (*Polydolops* and *Amphidolops*)." It is interesting to note that the glasbiid from La Barda mentioned by Lorente et al. (2016) was referred by Tejedor et al. (2009) to *Palangania* sp. on the basis of an isolated upper molar; future discoveries of glasbiid lower molars at La Barda may led to the recognition of the generalized (*Pujatodon*-like?) molar pattern of basal diprotodontians.

Our suggestion that *Pujatodon* may represent a basal form within derived australidelphians is not the only possible relationship between South American and Australasian metatherians. In addition to microbiotherians being stem australidelphians, several Antarctic taxa add to a much more complex panorama. Reguero et al. (2013) hypothesized that there are at least three

Antarctic taxa that could prove to be generalized to specific australidelphian lineages: (1) *Xenostylos peninsularis* (basal to the dasyuromorphian radiation; Goin et al. 1994), (2) derorhynchids (basal to the Peramelemorphian radiation; Goin 2003), and (3) some lineages of bonapartheriiform polydolopimorphian marsupials (basal to the vombatiform (Diprotodontia) radiation; see also Lorente et al. 2016). Most probably, these interrelationships were restricted to the Austral biogeographical realm, involving southernmost Patagonia, Antarctica, and Australasia (Goin et al. 2012, 2016).

Woodburne and Case (1996) suggested that metatherian dispersals from South America into and through West Antarctica, and onward to Australia, must have occurred during the Late Cretaceous (Maastrichtian?). This process may have continued some time into the early (Reguero et al. 2013) or middle?-late? Paleocene (Goin et al. 2016), up to the interruption of the Scotia Arc as a land mammal corridor to Antarctica, which began by the end of the Paleocene. According to paleobiogeographic reconstructions, this terrestrial interruption predates in about 25 Ma the deep- water circulation conditions of the Drake Passage (Reguero et al. 2014). The existence of basal stocks of the above mentioned metatherian clades (currently undocumented by fossils in the Late Cretaceous of South America, West Antarctica, or Australia), is suggested by stratigraphically calibrated molecular phylogenies revealing long ghost lineages that extend into the Late Cretaceous (e.g., Meredith et al. 2008).

Acknowledgements Special thanks to staff of the Instituto Antártico Argentino (IAA), Fuerza Aérea Argentina (FAA), and Dirección Nacional del Antártico (DNA) for their logistic support during the field season, particularly to Alejandro "Chuchu" Crivero. To Carolina Acosta Hospitaleche, Guillermo López, and Sergio Santillana, who were part of the summer field team. To Agustín Pérez Moreno (who discovered the specimen MLP 14-I-10-20) and Facundo Irazoqui for their help in the sorting of sediment concentrates. To Patricia Sarmiento for her help with the Scanning Electron Microscope (MEB, MLP). Alfredo Carlini, Mónica Tassara, Estela Martín, and Mariana Adami helped with some of the photos of the type specimen. Marcela Tomeo designed most of the figures that illustrate this work. Cecilia Deschamps helped with the English version. We also thank two anonymous reviewers and the Editor of JME for comments on the manuscript. CONICET (Argentina), Agencia Nacional de Promoción Científica y Tecnológica (Argentina), Universidad Nacional de La Plata (UNLP, Argentina), Instituto Antártico Argentino (IAA), the Alexander von Humboldt Foundation (AvH, Germany) to F. J. G., Universidad Nacional de La Plata (N812-UNLP), and Agencia Nacional de Promoción Científica y Tecnológica, PICT 201-0508 to A. N. Z and L. C. J. N. G. is particularly grateful to Oceanwide Expeditions, Vlissingen (NL) for financial support.

Appendix

Character states for *Pujatodon ektopos*, gen. et sp. nov., based on the matrix of Chornogubsky and Goin (2015: supplementary data).

Pujatodon ektopos

0?????????0?????10,000,000?0?000???????????????

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