

Contributions to the knowledge of *Antarctodon sobrali* (Mammalia: Astrapotheria) from the Eocene of Antarctica

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Received 28 November 2023; accepted 27 February 2024; published online 30 March 2024

Abstract The Astrapotheria constitutes one of the five orders of extinct South American native ungulates, with a fossil record that also extends to the Eocene of the Antarctic Peninsula. In contrast to the abundant specimens known for lioptern Sparnotheriodontidae and metatherians, astrapotheres are represented by scant remains assigned to the endemic *Antarctodon sobrali* and indeterminate astrapotheres, restricted to levels 35Cu₀ and 35n of the *Cucullaea* I Allomember of the La Meseta Formation. The discovery of a lower molar assignable to this species in the Eocene levels of Seymour (Marambio) Island, enables a revision of the diagnosis and the homologies of the dental characters used to describe this taxon. A reanalysis of its phylogenetic relationships reveals the nearly simultaneous presence of basal astrapotheres in the early Eocene of Itaborai (Brazil), Patagonia, and West Antarctica. These taxa are characterized by lacking dental specializations usually associated with more abrasive diets like terminal forms of Uruguaytheriinae and Astrapotheriinae. *Antarctodon* appears to have thrived on the Antarctic continent during the Early Eocene Climatic Optimum within the paleoclimatic context of a hot-house world. Unlike present conditions in Antarctica where no terrestrial mammals inhabit, the early Eocene climate was characterized by warmer temperatures and a biologically diverse environment rich in primary producers, dominated by *Nothofagus* forests, encompassing both deciduous and evergreen forests, which supported a diverse assemblage of continental vertebrates.

Keywords Astrapotheria, *Antarctodon*, Eocene, Seymour Island, La Meseta Formation

Citation: Gelfo J N. Contributions to the knowledge of *Antarctodon sobrali* (Mammalia: Astrapotheria) from the Eocene of Antarctica. Adv Polar Sci, 2024, 35(1): 48-62, doi: 10.12429/j.advps.2023.0031

1 Introduction

Currently, the absence of autochthonous terrestrial vertebrates on Antarctica is related to the availability of liquid water and a biome whose primary productivity is insufficient to meet the energy demands of these diverse communities (Convey et al., 2014). This biome largely corresponds to an ice desert, also considered tundra-like due

to the presence of lichens, bryophytes, algae, fungi, but only two vascular plant species, the Antarctic hair grass (*Deschampsia antarctica*) and the Antarctic pearlwort (*Colobanthus quitensis*). In contrast, the interaction of various factors such as the presence of warmer climates during the Late Cretaceous and early Eocene, the terrestrial connection of the Antarctic Peninsula to South America and Australia, and the development of significant vegetation cover, facilitated the development of diverse communities of terrestrial birds and mammals (Reguero et al., 2002, 2013). Within this context, significant assemblages of

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terrestrial vertebrates have been recovered from the Paleogene levels of the La Meseta and Submeseta formations on Seymour (Marambio) Island in the James Ross Basin (Acosta Hospitaleche et al., 2019; Gelfo et al., 2019). The presence of these Paleogene mammals and their close relationships with those from the southern part of South America were the consequence of a paleobiogeographic unit defined as the West Weddellian Biogeographic Province (WWBP) (Reguero and Goin, 2021). This unit was composed by an assemblage of the southern part of South America (Patagonia) and the crustal block of West Antarctica, including the Antarctic Peninsula and possibly Thurston Island; spanning from the Late Cretaceous (Campanian) through the early Paleogene (Reguero and Goin, 2021) probably up to the early Eocene. At present, there are no records of Mesozoic land-mammals in Antarctica, although they could be expected from paleobiogeographic inferences, at least since the Jurassic (Gelfo et al., 2019). The fossil record from the Eocene of La Meseta and Submeseta formations seems to depict the ultimate manifestation of the WWBP in Antarctica, occurring before the complete extinction of the terrestrial vertebrates on that continent. The disappearance of land-mammals is likely a result of the widespread deterioration of terrestrial ecosystems, probably triggered by climate changes associated with tectonic events. These involve the decline in global temperatures from the Eocene–Oligocene boundary and the subsequent Antarctic glaciations (McKay et al., 2022). Additionally, the evolution of the Antarctica–South America–Scotia Plate System (Eagles and Jokat, 2014; Eagles and König, 2008; Eagles et al., 2006) led to the final Gondwana break-up, and the opening of the Drake Passage. This event began around 50 Ma or even earlier (Hutchinson et al., 2021) and initiated a progressive transformation from a shallow sea to a broader and deeper seaway. Subsequently, with the disappearance of the multiple ridges that obstructed the deep Circumpolar Antarctic Current by the Middle Miocene Climatic Optimum (MMCO), Antarctica experienced its complete isolation (Barker and Thomas, 2004; Dalziel et al., 2013). Despite this, paleontological proxies suggest that Antarctic and South American land-masses became disconnected before the early Eocene (Reguero and Goin, 2021; Reguero et al., 2014) or, at least, the full interruption of terrestrial mammal dispersal between both continents.

Paleogene West Antarctic land-mammals are well-represented and include a diverse array of metatherian groups, such as Polydolopimorphia (Chornogubsky et al., 2009; Goin et al., 2020; Woodburne and Zinsmeister, 1984); Microbiotheria (Goin and Carlini, 1995); and didelphimorphians (Goin et al., 1999). To a lesser extent, other taxa include Gondwanatheria (Goin et al., 2006), Dryolestida? (Gelfo et al., 2019), Xenarthra (Vizcaíno and Scillato-Yané, 1995), and South American native ungulates (SANus) represented by Litopterna Sparnotheriodontidae (Bond et al., 2006; Gelfo et al., 2017), as well as

Astrapotheria (Bond et al., 2011). The SANus exhibit close affinities with Eocene taxa from South America, including those from Patagonia (Argentina) and Itaboraí (Brazil). They represent the largest-bodied herbivores (exceeding 10 kg) known from Antarctica with suggested browser specializations, likely associated with the presence of dense *Nothofagus* type forests as inferred from the botanical fossil record of *Cucullaea* I Allomember of the La Meseta Formation (Reguero et al., 2002).

The presence of astrapotheres in the La Meseta Formation is scarce and by now confined to the basal coquina of the *Cucullaea* I Allomember. They were reported by Bond et al. (1990) and Marenssi et al. (1994) in the locality DPV 2/84, and by Hooker (1992) in BAS-DJ 154, but this last specimen was later considered to belong to litoptern Sparnotheriodontidae (Bond et al., 2011). Although all these specimens were tentatively associated with the Trigonostylopidae, when Bond et al. (2011) named, *Antarctodon sobrali* was not assigned to any family. All the mentioned specimens are represented by isolated teeth, but also postcranial remains from La Meseta Formation, were compared with astrapotheres. Davis et al. (2020) described a mammalian metacarpal, also from *Cucullaea* I Allomember, but astrapotheres affinities were discarded in favor of xenarthran ones. This assignment seems to be correct, but it is important to note that no skeleton of basal astrapotheres is known, and comparisons done with Miocene astrapotheres (e.g., Scott, 1937) could be too derived respect to an Eocene counterpart. In addition to the mentioned metacarpal, an intermediate phalanx referred as *Eutheria incertae sedis* was described for Acantilados II Allomember (Figure 1), where only the sparnotherodontid litoptern *Notiolofofos* was recorded (Gelfo et al., 2015).

In the present contribution, a new specimen from Seymour (Marambio) Island is described and assigned to *A. sobrali*, adding new dental features to the knowledge of this Antarctic endemic species. Their phylogenetic relationships are reanalyzed and discussed, along with the implications of the presence of this group from an environmental and paleobiogeographic perspective.

2 Material and methods

2.1 Geological and stratigraphic context

The geological description and stratigraphic interpretation follow the synthesis of Montes et al. (2013, 2019) plus personal observations. The specimen here studied was found at locality DPV 2/84 in the *Cucullaea* I Allomember of the La Meseta Formation, identified as unit 35 in Montes et al. (2019). This allomember is positioned above the Campamento Allomember through an erosive, irregular, and mappable surface that outcrops around the La Meseta reliefs, except for a short segment on the southeastern slope of the Weddell Sea at Penguin Bay (Figure 1a). This erosive surface is well-defined along

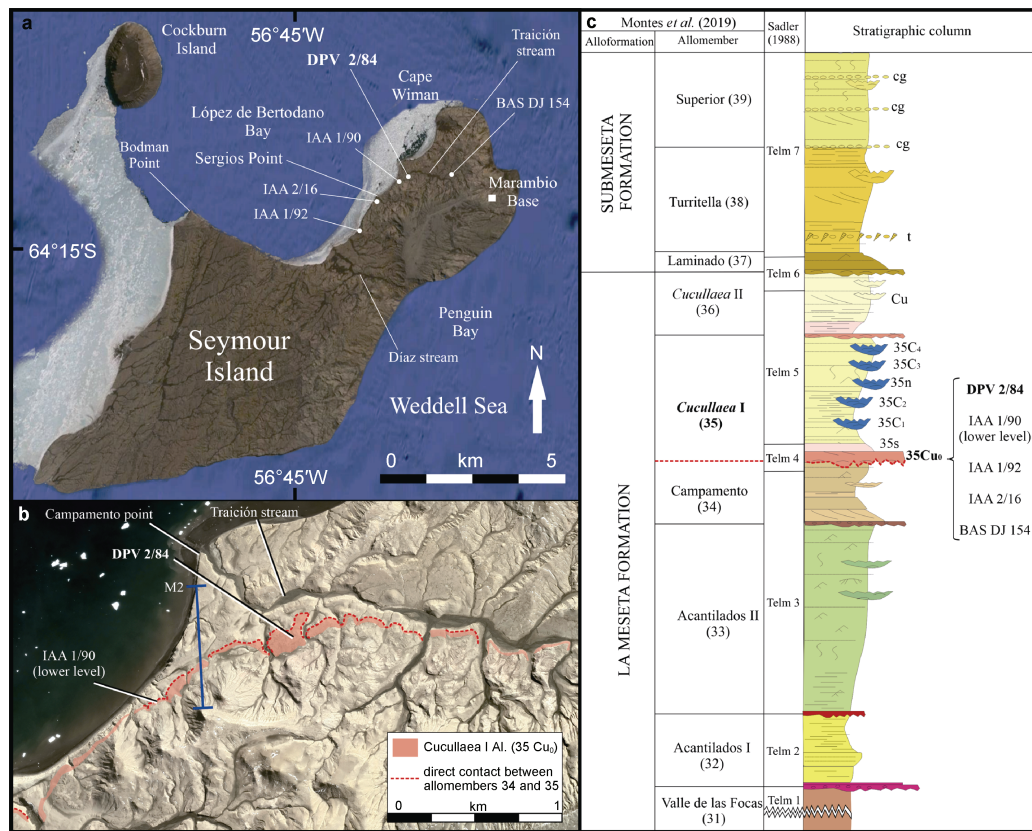


Figure 1 a, Geographical location of the main localities at Seymour (Marambio) Island, Antarctic Peninsula; b, details of the relief and exposure zones of level 35Cu₀ of the *Cucullaea* I Allomember in the vicinity of DPV 2/84 locality, stratigraphic section considered by Montes *et al.* (2019) in a blue segment (M2); c, stratigraphic column of La Meseta and Submeseta formations, detailing the levels of the *Cucullaea* I Allomember and the land-mammals localities corresponding to the 35Cu₀ level (modified from Montes *et al.*, 2019 and Gelfo *et al.*, 2019).

almost its entire extent, as it is covered by coquinas of the bivalve *Cucullaea* spp., which stand out noticeably on the terrain. The maximum extent of the unit is in the central area of the plateau reliefs along the López de Bertodano Bay, inland from the island between Sergios Point and Campamento Point (Figure 1a). A small outcrop also appears towards the southeast on the cliffs south of the plateau towards Penguin Bay. Montes *et al.* (2019) have recorded a thickness of 140 m in its M2 column (Figure 1b). Overall, both to the south and north, the thickness decreases, resulting in a lenticular morphology for the entire unit, correlative with the entire Telm 4 and the lower part of the Telm 5 of Sadler (1988).

The base of *Cucullaea* I Allomember consists of an irregular channel-shaped erosive surface associated with a coquina along with conglomerates and sandstones identified by Montes *et al.* (2019) as 35Cu₀. This level, from which the specimen here studied was found as well as the holotype of *Antarctodon*, consists of approximately 4 m of accumulation of large and robust shells of *Cucullaea* sp., with both intact and/or fragmented valves and gastropods (Sadler, 1988). The largest surface extension of 35Cu₀ belongs to two localities: DPV 2/84, where the materials of *Antarctodon* were found; and the outcrops near Sergios Point of IAA

2/16, where the litopter *Notiolofof regueroi* was recorded (Gelfo *et al.*, 2017, 2019). The basal coquina of *Cucullaea* I Allomember (i.e., 35Cu₀) is organized into individual channel-shaped packages, displaying frequent erosive landforms that shape metric-scale basins, each with a thickness of 1 m. The packages often amalgamate and juxtapose, resulting in a tabular morphology along the entire unit. When the packages are not massive, they show cross-bedding stratification with troughs containing basins between 1 and 2 m in length and 0.5 m in thickness. The matrix between the bivalve shells is coarse sandstone, and rounded dark-colored volcanic gravel. The presence of pelitic intraclasts and other bioclasts such as selachian teeth, brachiopods, and terrestrial mammal remains represented by teeth and, to a lesser extent, bone elements, is also common. Laterally, unit 35Cu₀ wedges are decreasing in thickness along its cartographic extent and giving a general paleochannel geometry with maximum depth and sediment thickness approximately at the trace of the M2 stratigraphic section (Figure 1b). At their top, the coquinas are transitionally replaced by medium to fine sands and greenish-gray to light gray mudstones. This corresponds to the unit 35s with a thickness ranging from 2 to 10 m.

2.2 Dental homologies and phylogenetic analysis

The nomenclature of dental characters employed in Astrapotheria has not always adhered to names that facilitate the establishment of homologies with more primitive dental structures from which they originate. This has hindered the accurate construction of matrices for phylogenetic studies comparing at the ordinal level within the SANus. Indeed, at the dental level, primary homologies largely depend on topographic identification with common names for the observed characters. Therefore, the use of different names for structures with undeniable homology should be avoided. This is particularly relevant to the formation of crests, cristids, and lophids. In the present study, the terms “anterolophid” and “posterolophid” (Thenius, 1989), used respectively for the complete structure of the trigonid and the talonid among Astrapotheria and Trigonostylopoidea, are dismissed since they do not facilitate the establishment of homologies. The term “posterolophid” partially overlaps with the term “hypolophid” used here, representing a simplification of the connection of the talonid structures, which could include the cristid obliqua, hypoconid, postmetacristid, hypoconulid, distocristid, and sometimes the entoconid. If these individual terms can be identified, they are preferred in the current description. For the structure that runs or descends mesiolingually from the protoconid, the use of “crest” (Paula Couto, 1952; Simpson, 1967) “anterolingual crescent” or “anterior crescent” (Bond et al., 2011) is here replaced by “paralophid” (Stirton, 1941). This is homologous to the “paracristid” (Van Valen, 1966) in a more primitive tribosphenic tooth and should represent the topographical homology. The term “protolophid” is preferred for the lophid that connects the protoconid and metaconid (Van Valen, 1966), and is used here to avoid the term “metalophid” (Osborn, 1907), which is used for different structures in several mammal groups. The transverse entoconid in the form of a lophid of *Antarctodon*, which contacts the mesial face of the hypoconulid, has been compared to a notoungulate-like “entolophid” (Bond et al., 2011). However, the direction and related structures do not seem to be the same as in Notoungulata, and, in contrast, this appears to be a more accurate interpretation of Hershkovitz (1971) description of the postentocristid. Given that the structure of *Antarctodon* more closely resembles a lophid than a cristid, the fitting designation would be “postentolophid”. This term had been employed previously by Soria and Hoffstetter (1985) in describing the Macraucheniiidae litoptern, albeit without a distinct acknowledgment of homologies with the structure proposed by Hershkovitz (1971). In this study, postentolophid is utilized to denote the lophid formed by the entoconid and its orientation. The wear facet nomenclature follows Schultz et al. (2018).

The new specimen (IAA-Pv 826) of *Antarctodon* was employed to reassess the phylogenetic matrix proposed by

Bond et al. (2011). The matrix was adjusted to include three dental characters that were previously omitted from the analysis conducted by Kramarz and Bond (2009). These characters involve the number of lower incisors (character 21), p3 paralophid (character 26), and lower molar lingual cingulid (character 33). Also, the taxa *Astrapothericulus* and *Xenastrapotherium*, both previously excluded from the phylogenetic analysis, were added. Multistate characters that were coded as polymorphic for some taxa in Bond et al. (2011) were divided into binary (presence/absence) characters for each of those states to modify the polymorphism coding. This include their character 31 which was subdivided in p4 entoconid included in the hypolophid, p4 entoconid bunoid and isolated, and p4 entoconid forming a distinct lophid. Similarly, their character 33 was divided into m1–m3 hypoflexid deep and m1–m3 hypoflexid superficial. The “absent” state was omitted, as it is encompassed by the presence/absence in the other characters. In *Astraponotus*, the state of entoconid was considered as polymorphic in Bond et al. (2011) and coded as part of the hypolophid (0) and forming a distinct lophid (2), as in *Antarctodon*. This polymorphism could not be corroborated here, so the entoconid of *Astraponotus* was only coded as part of the hypolophid.

The phylogenetic analysis was performed with the data matrix of 13 taxa and 43 characters (Supplementary Table) constructed on Mesquite version 3.70 (Maddison and Maddison, 2021). The cladistic analysis was conducted on TNT version 1.5 (Goloboff and Catalano, 2016) using implicit enumeration option. Different analyses were carried out. The first was performed with characters ordered following the approach of Bond et al. (2011). The other analysis was done using unordered and equally weighted characters. To encode *Antarctodon* and considering the similitudes between p4 and m1 in *Trigonostylops*, characters were coded for both p4 and m1, despite that it is important to note that there is not a clear consensus about the loci of the type specimen. *Eoastrapostylops* was employed as an outgroup, although its position as the most basal Astrapotheria has been questioned in favor of its status as a basal SANu lineage that diverged prior to the differentiation of the astrapotheres, pyrotheres, and notoungulates (Kramarz et al., 2017).

The temporal calibration of astrapotheres in the phylogenetic analysis were extrapolated from the fossil record described for South American Land Mammals Ages. For those biochronological units without available isotopic dates, a consensus of their age was not always achieved, so variations could be expected from the present calibration.

3 Systematic paleontology

Class Mammalia Linnaeus, 1758
 Order Astrapotheria Lydekker, 1894
Antarctodon sobrali Bond et al., 2011

3.1 Emended diagnosis

Astrapothere is similar to *Trigonostylops* but slightly larger. Holotype (p4 or m1) with protoconid and metaconid well differentiated, long and transverse protolophid and shorter paralophid, but proportionally larger than those in *Trigonostylops* and *Tetragonostylops*. Hypolophid lingually retracted, compose of a small hypoconulid, cristid obliqua projected to the lingual base of the protoconid, and a distal part forming a sharp cristid reaching a distally located hypoconulid. Entoconid differentiated and forming part of a postentocristid contacting the mesiolingual base of the hypoconulid. Strong postcingulid.

3.2 Geographic and stratigraphic distribution

All specimens were found in the locality DPV 2/84, Seymour (Marambio) Island, Antarctic Peninsula, West Antarctica. Early Eocene (Ypresian) from La Meseta Formation, lower coquina level (35Cu₀) from the *Cucullaea* I Allomember (Marensi et al., 1998; Montes et al., 2019).

3.3 Assigned material

IAA-Pv 826: fragment of right m1 or m2, including trigonid and mesiolabial part of the talonid and a small

portion of the distal part of the talonid with a portion of the postcingulid.

3.4 Description and comments

IAA-Pv 826 preserves part of the trigonid and the mesiolabial part of the talonid, of a brachyodont tooth (Figures 2a–2e). Additionally, a broken portion of a tooth, was found less than 50 mm away and was interpreted as associated part. This piece is interpreted as a slice of the distal wall of the talonid, which is broken distal to the hypoconulid, exposing mostly the dentine and preserving a portion of the postcingulid. Other broken sections at the base of the postcingulum and on the labial portion can be mistaken for wear facets, but they are placed over the dentine tissue (Figure 3). The fragment does not appear to correspond to the edge of a labial or lingual cingulid due to the exceptionally straight segment preserved.

However, an objection to interpreting this tooth fragment as the distal wall of the talonid lies in its labiolingual length (12.58 mm), slightly longer than that of the trigonid of IAA-Pv 826. In fact, in other astrapotheres, the differences in labiolingual length between the trigonid and talonid are much smaller, especially for an m2 (see Table 1 and Figure 4).

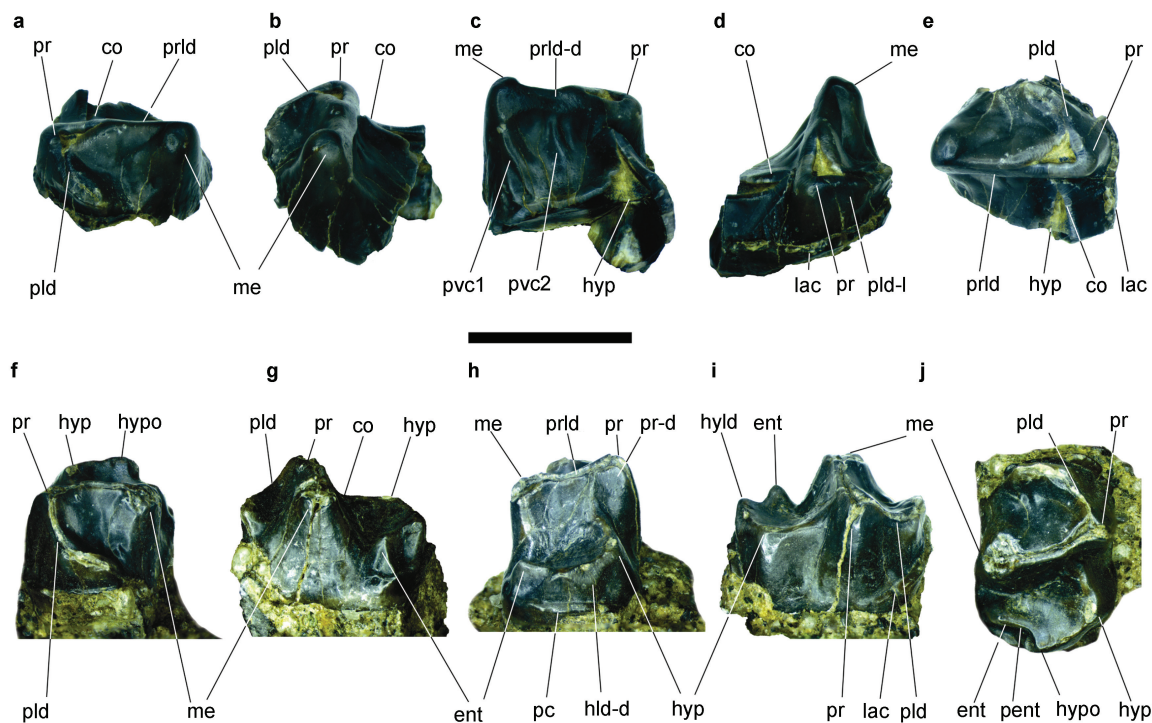


Figure 2 IAA-Pv 826 right lower molar fragment (a–e) and MLP-PV 08-XI-30-1, the holotype of *Antarctodon sobrali* (f–j), shown in mesial (a and f), lingual (b and g), distal (c and h), labial (d and i), and occlusal (e and j) views. Abbreviations: co, cristid obliqua; ent, entoconid; hyp, hypoconid; hypo, hypoconulid; hld-d, hypoconulid distal wear facet; lac, labial cingulid; me, metaconid; pa, paraconid; pc, postcingulid; pent, postentolophid; pld, paralophid; pld-l, paralophid lingual wear facet; pr, protoconid; pr-d, protoconid distal wear facet; prld, protolophid; prld-d, protolophid distal wear facet; pvc1, postvallid column 1; pvc2, postvallid column 2. Approximately scale 10 mm.

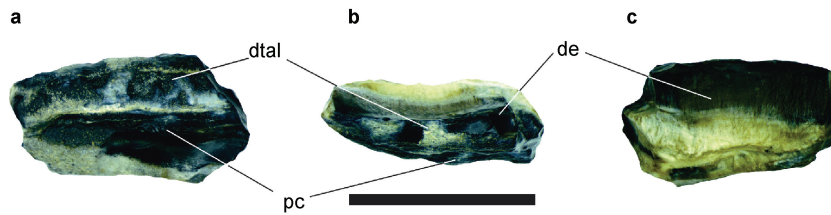


Figure 3 IAA-Pv 826 distal fragment of the talonid of the right lower molar of Figure 2 in distal (a), occlusal (b), and inner views (c). Abbreviations: de, dentine; dtal, distal wall of the taloned; pc, postcingulid. Approximately scale 10 mm.

In the more complete remain of IAA-Pv 826 the nearly intact trigonid is higher than the talonid, except for the absence of the mesiolingual side. Its overall configuration closely resembles that of the holotype of *Antarctodon*; however, it distinguishes itself by being a larger tooth, and approximately 23% wider labiolingually. This difference in size (Table 1) aligns with the observed disparity between the trigonid width of the p4 respect to the m2 in *Trigonostylops gengenbauri* (Figure 4). This difference better supports its assignment to the former locus, rather than the m1. Nevertheless, these measurements should be approached with caution, given the limited number of specimens attributed to *Antarctodon* and their fragmentary nature. Furthermore, comparisons with measurements of lower teeth in more derived astrapotheres, such as *Albertogaudrya unica* (MACN A 12001), reveal a smaller difference in the transverse width of the trigonid between p4 and m1-3 (Table 1).

In addition to size differences attributable to distinct loci, the specimen described here exhibits a metaconid that is clearly less worn and taller than the holotype, where this cusp is broken. The increased height of the metaconid in IAA-Pv 826 results solely from the pronounced wear of the protoconid, which seems to be the higher cusp. This is

evident in the triangular-shaped dentine island, which extends in the occlusal view towards the protoconid and, to a lesser extent, towards the paralophid. Furthermore, the protolophid exhibits a prominent wear facet (Figure 2c: prld-d). Despite the partial breakage of the protolophid structure in the holotype of *Antarctodon sobrali*, there is a distal wear facet, located distal to the protocone (Figure 2h: pr-d). This facet corresponds to the labial remnant of the distal aspect of the original protolophid, as observed in IAA-Pv 826. The base of the metaconid expands much more mesially, forming an inflection with an angle close to 90° between the inner wall of this cusp and the protolophid. While the presence of a metacristid is not evident, the lingual edge of the metaconid is considerably more pronounced, particularly in occlusal view (Figure 2e). The trigonid basin appears to be open mesiolingually similar to the holotype of *Antarctodon*, though the paralophid is more labially positioned, resulting in greater mesial aperture of the trigonid. This corresponds to the observed condition between the premolars and molars of *Trigonostylops* (Figure 4) and to a lesser extent in *Tetragonostylops*, where the paralophid has a more mesiodistal orientation. The protoconid is clearly the most voluminous cusp, with a

Table 1 Measurements of the studied materials expressed in millimeters. The mesiolabial length of the portion of IAA-Pv 826 interpreted as the distal part of the talonid is not included since it may not correspond to the maximum width of the talonid

Taxon	Loci	Mesiodistal/mm	Labiolingual/mm	
			Trigonid	Talonid
<i>Antarctodon sobrali</i> (MLP-PV 8-XI-30-1)	right p4 or m1	13.39	8.70	9.10
<i>Antarctodon sobrali</i> (IAA-Pv 826)	right m2?	13.44	11.40	-
	left p4	10.5	6.93	7.46
<i>Trigonostylops gengenbauri</i> (MLP-PV 121736)	left m1	12.21	7.21	8.22
	left m2	13.78	9.07	9.50
	left m3	16.28	9.41	9.65
	right p4	19.79	14.02	14.86
	right m1	21.10	14.49	14.13
	right m2	24.38	17.05	17.32
<i>Albertogaudrya unica</i> (MACN A 12001)	right m3	34.65	17.19	18.50
	left p4	20.46	14.96	15.72
	left m1	20.47	14.98	15.55
	left m2	24.63	17.39	17.84
	left m3	34.53	17.98	18.16

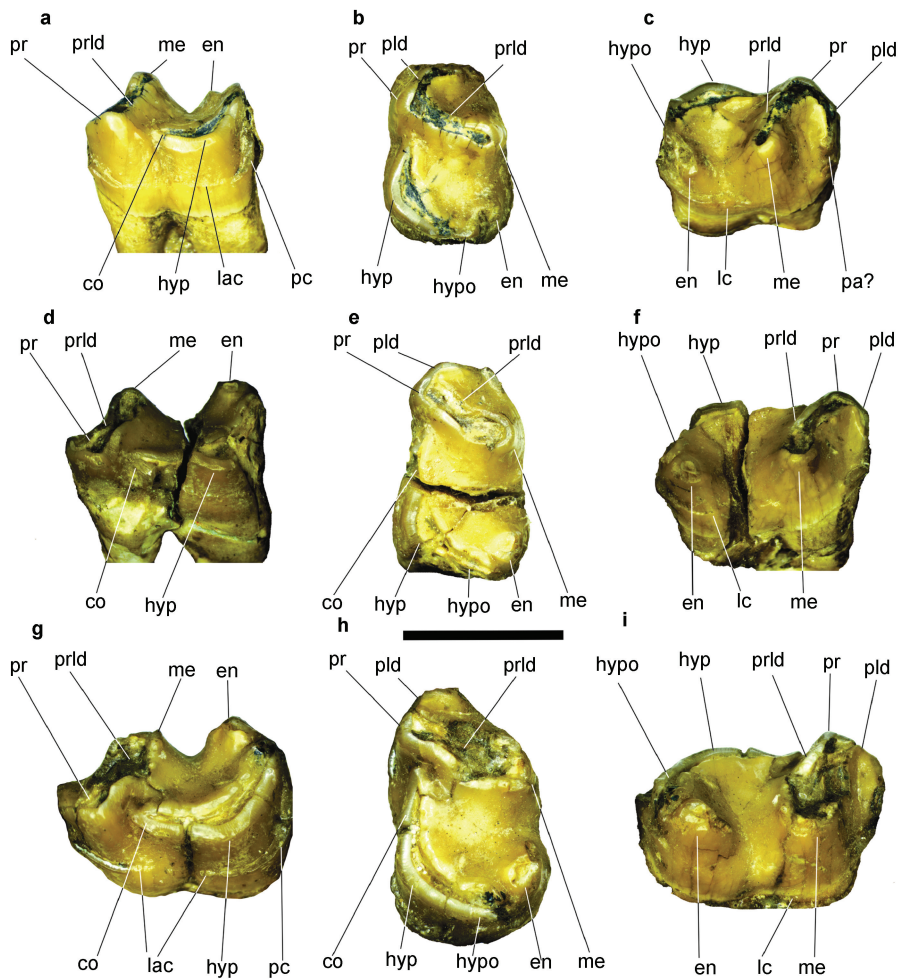


Figure 4 Dental details of *Trigonostylops gengenbauri* (MLP-PV 121736) left p4 in labial (a), occlusal (b), lingual (c); left m1 in labial (d), occlusal (e), lingual (f); and left m2 in labial (g), occlusal (h), lingual (i). Abbreviations: co, cristid obliqua; ent, entoconid; hyp, hypoconid; hypo, hypoconulid; lac, labial cingulid; lc, lingual cingulid; me, metaconid; pa, paraconid; pld, paralophid; pr, protoconid; prld, protolophid; pc, postcingulid. Approximately scale 10 mm.

broad base that invades a significant portion of the trigonid basin. It appears to have been the tallest cusp prior to wear. A shorter but strongest paralophid extends mesiolabially, exhibiting a significant wear facet on its labial face (Figure 2d: pld-l), which extends towards the more mesial part of the protoconid. In occlusal view, the paralophid in its mesial end gives the appearance of a small paraconid erased by wear (Figure 2e). Anyway, neither a clear wear facet, nor an inflation in its base, allows to undoubtedly identify this structure as a cusp, rather than a broken part of the lophid. An anterior cuspule was mentioned for MLP-PV 08-XI-30-1 just before the end of the paralophid (Bond et al., 2011) but not identified it as a paraconid. This probably follows Soria (1988) interpretation of the primitive state for Astrapotheria as lacking the paraconid, and interpreted for Astrapotheriinae, the presence of a new cusp in the paralophid (i.e. neoparaconid). If the described structures in *Antarctodon* could be identified as cusp, this would align with Simpson (1967) observations concerning the presence of a paraconid? in some specimens of *Trigonostylops*

(Figure 4c). In this case, the primary homology (i.e. topographic) should be followed when identifying them as a true paraconid, and their evolutionary change through the Astrapotheria phylogeny must be reevaluated.

The labial cingulid in IAA-Pv 826 is more robust than that of the *Antarctodon* holotype and appears to extend mesially into an anterior cingulid, the continuity of which cannot be confirmed due to damage to this portion of the tooth. No inferences could be done about the mesial cingulid presence since the lingual side of the trigonid is broken, but less than the holotype.

Below the wear facet of the protolophid, the postvallid features a gently undulating wall, owing to the presence of two rounded crest or pillars (Figure 2c: pvc1 and pvc2). While the postvallid of the p4-m2 in all *Trigonostylops* specimen studied here is somewhat deteriorated, such structures are not observed, nor are they inferred from other observations (Figure 4). The first of these pillars (i.e. pvc1) descends somewhat labially from the metaconid, tapering and fading at the base of the talonid. The second crest on

the postvallid is less pronounced and descends from the middle portion of the protolophid, widening and fading towards the talonid. A similar crest descending from the metaconid is partially comparable to that in the holotype of *Antarctodon*, although in this case, it appears to correspond more to the ridge defining the cusp rather than a crest on the postvallid. These structures perpendicular to the direction of the protolophid may potentially be associated with an increase in the tooth's structural strength during mastication, particularly considering the prld-d wear facet.

The talonid is mostly fragmented, with only the more mesial portion of the hypoconid and the cristid obliqua, as part of the hypolophid, being preserved. In this regard, it exhibits more extensive wear than the holotype, additionally revealing a dentine island demarcated by a thick layer of enamel. The labial face of the hypolophid and the protolophid appears to form an angle closer to 90°, whereas in the holotype of *Antarctodon*, this angle appears to be slightly more acute.

4 Discussion

4.1 Phylogenetic relationships of *Antarctodon*

The few teeth fragments previously assigned to astrapotheres were all discovered in the *Cucullaea* I Allomember of the La Meseta Formation and tentatively attributed to the Trigonostylopidae based on their similar features to the genus *Trigonostylops* (Bond et al., 1990; Hooker, 1992; Marensi et al., 1994). However, with the definition of *Antarctodon sobrali*, which incorporated some of these specimens (Bond et al., 2011; Gelfo et al., 2019), their taxonomic placement within the families became contentious. Traditionally, their position has been considered as basal among Astrapotheria and linked to the Trigonostylopidae. Nevertheless, the paraphyly of this family in various phylogenetic analyses (e.g. Bond et al., 2011; Cifelli, 1993; Kramarz and Bond, 2009; Vallejo-Pareja et al., 2015) suggests that this family represents the stem group of the remaining astrapotheres. But the complete scope of Astrapotheriidae remains a subject of debate. Soria (1984) divided the family into Albetogaudryinae (*Scaglia*, *Albertogaudrya*, *Tetragonostylops*, and *Astraponotus*) and Astrapotheriinae (*Astrapotherium*, *Parastrapotherium*, *Astrapothericulus*, *Uruguaytherium*, *Xenastrapotherium*, and *Synastrapotherium*), and led *Trigonostylops* in the Trigonostylopidae. But Cifelli (1993), restricted the Astrapotheriidae and arbitrarily defined them as the monophyletic group including the common ancestor of *Astraponotus* and later astrapotheres, defined by a complete metaloph and by the presence of a spur, extending distolingually from the ectolph. So, *Scaglia*, *Albertogaudrya*, *Tetragonostylops*, *Trigonostylops*, and even *Eoastrapostylops*, considered in its own family Eoastrapostylopidae by Soria (1984), were regarded as part of the paraphyletic Trigonostylopidae. Later, despite the inclusion of *Scaglia*

and *Albertogaudrya* (McKenna and Bell, 1997) or even *Antarctodon* (Gelfo et al., 2019) among Astrapotheriidae by some researchers, the restricted definition of Cifelli (1993) has commonly been adopted by subsequent authors with few additions of genera and the definition of the monophyletic clades Uruguaytheriinae (Johnson and Madden, 1997) and Astrapotheriinae (Kramarz and Bond, 2009).

In Bond et al. (2011) work, two phylogenetic analyses were conducted, considering the holotype (MLP-PV 8-XI-30-1) of *Antarctodon sobrali* coded either as a p4 or as an m1. The analysis involved the dental characters from Kramarz and Bond (2009), with the addition of new characters: 18 (upper molar parastyle), 21 (M1–M2 hypocone), 25 (upper canines anterior groove), 26 (upper canines), and 31 (p4 entoconid). However, three dental characters were omitted from the original matrix: 21 (number of lower incisors), 26 (p3, paralophid), and 33 (lower molars, lingual cingulid). Bond et al. (2011) indicated that multistate characters 31, 34, and 35 were coded as unordered but did not specify which characters were considered as ordered or not in the matrix of Kramarz and Bond (2009) (characters 2, 7, 18, 21, 23, and 30). As a result of their analysis, they reported a single Most Parsimonious Tree (MPT) (L=65). In this tree, whether considering the holotype as a p4 or an m1, *Antarctodon* was recovered as more derived than *Tetragonostylops* and *Trigonostylops*, and as the sister group to all other Astrapotheria. The review of these analyses done here, considering MLP-PV 08-XI-30-1 as a p4 and conducting an exhaustive search, resulted in the retrieval of the same MPT with both ordered and unordered characters, albeit with a notably shorter length (L=62). This suggests that considering these characters as ordered/unordered is irrelevant in the analysis of this matrix. However, the analysis considering MLP-PV 08-XI-30-1 as an m1 did not yield the same MPT as presented in Bond et al. (2011) using an exhaustive search. Instead, *Antarctodon* was recovered as part of a polytomy along with *Tetragonostylops* and a clade leading to the remaining Astrapotheria. The differences with previous results could be explained by the lack of support of the node containing the polytomy of *Antarctodon*, which could not be collapsed in the analysis of Bond et al. (2011).

The analysis conducted here utilizing the expanded and modified matrix, has yielded a single MPT (L=83) with no significant differences between the use of ordered or unordered characters (Figure 5). *Eoastrapostylops* was used as an outgroup, but its role as the most primitive Astrapotheria has recently been challenged in favor of considering it as an early SANu lineage that split off before the divergence of astrapotheres, pyrotheres, and notoungulates (Kramarz et al., 2017). Nevertheless, these data should be reevaluated within a broader context, considering not only the position of *Carodnia* but also that of other Xenungulata like *Rodcania kakan*, also from the Río Loro locality (Gelfo et al., 2020). Morphologically,

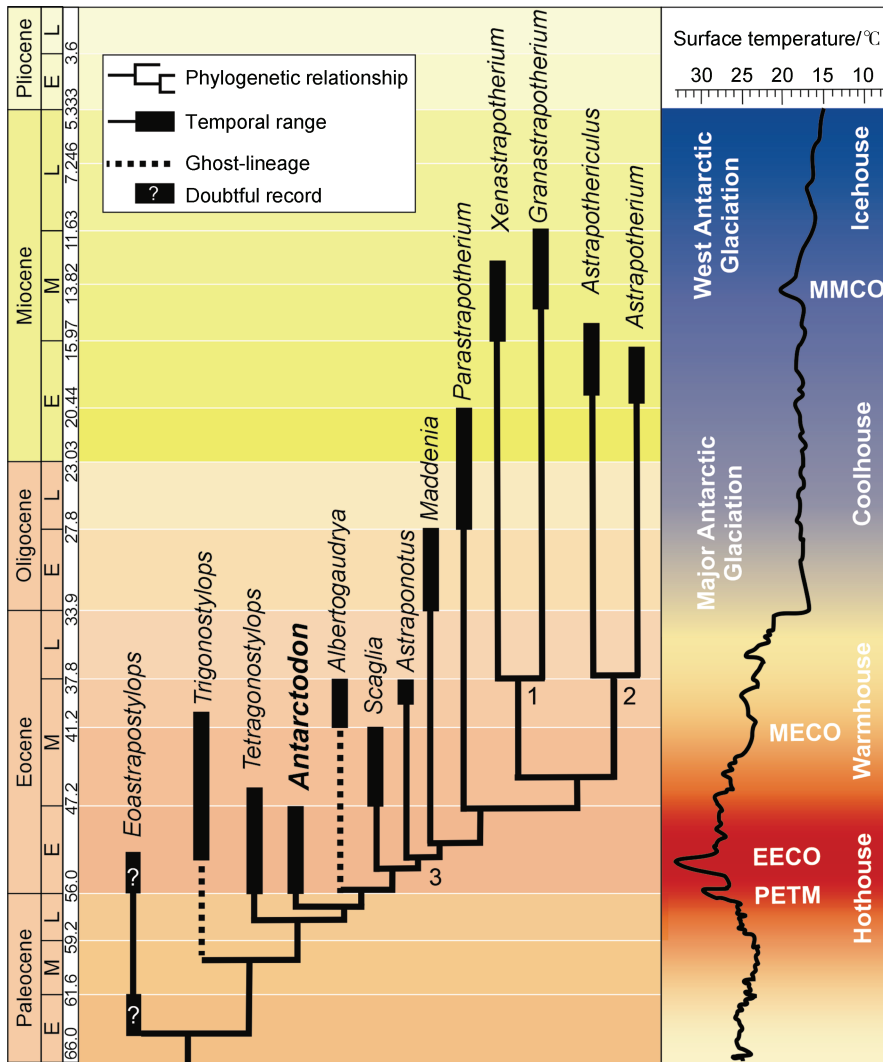


Figure 5 Temporal calibration of the single MPT (L=83) obtained from the phylogenetic analysis and surface temperature, estimated from the benthic $\delta^{18}\text{O}$ modified from the synthesis of Hönisch et al. (2023) and Rae et al. (2021). PETM, Paleocene-Eocene thermal maximum; EECO, Early Eocene Climatic Optimum; MECO, Middle Eocene Climatic Optimum; MMCO, Middle Miocene Climatic Optimum.

Eoastropostylops appears to be a suitable outgroup for rooting and polarize characters in the current analysis. The results obtained here were aligned with previous findings regarding the position of *Antarctodon* as more derived than *Trigonostylops* and *Tetragnostylops* and as the sister group of *Albertogaudrya*. The character that fundamentally distinguishes *Antarctodon* from *Tetragnostylops* and *Trigonostylops* is related to the greater development of the parolophid on the p4 (character 31). This character state is subsequently reversed in the p4 of *Maddenia lapidaria* (MPEF PV 7738), where it is found to be poorly developed, and this state is similar to the condition observed in their molars. However, it is worth noting that the development of the parolophid as a character, probably requires better encoding to express a greater variation than previously considered within the group. This is evident in the specimen described and assigned here to *Antarctodon*

sobrali (Figures 2a–2e). Although the parolophid is developed in comparison to what is observed in the molars of *Trigonostylops*, it appears to be thicker and shorter in its extent than that in other Astrapotheria.

Antarctodon belongs to a paraphyletic group that appears to have closer affinities with the “Trigonostylopidae” than with more derived groups within Astrapotheriidae *sensu* Cifelli (1993). Also, the Uruguaytheriinae and Astrapotheriinae were recovered as monophyletic. *Antarctodon* is defined by three synapomorphic characters, namely, the absence in the p4 of entoconid integrated to the hypolophid (33) and their presence as a distinct postentolophid (35), and the presence of postentolophid in the molars (41). All of these characters are equal to the only multistate character identified by Bond et al. (2011) regarding the entoconid development, previously considered when the holotype was considered alternatively either as p4 or m1. However, in the present

analysis, these features were treated as separate characters for methodological purpose and therefore, this do not truly represent a difference in their synapomorphies. These characters indicate a differentiated entoconid that forms part of a postentolophid, and contact the mesiolingual base of the hypoconulid. This feature particularly differs from the transverse entoconid of notoungulates which is more closely associated with the hypoconid. The development and overall structure of the talonid in *Antarctodon* also differ from those of macraucheniiids where a comparable structure in the entoconid has been described also as a postentolophid (Soria and Hoffstetter, 1985).

4.2 Biostratigraphy, paleoclimate, and paleobiogeography

The *Cucullaea* I Allomember of the La Meseta Formation constitutes the richest unit in terms of the quantity of land-mammals in West Antarctica (Gelfo et al., 2019). The stratigraphic details of the allomember allow the identification of distinct levels in relation to these findings. From bottom to top, various levels of coquinas with *Cucullaea* sp. (35C) and a level dominated by *Natica* sp. (35n) are recognized. In particular, 35Cu₀, from where IAA-Pv 826 came, represents a reworked level, and its boundary with the Campamento Allomember can be traced in Figure 1b. Montes et al. (2019) identify at least two levels of 35C (35C₁ and 35C₂) that can be recognized prior to the 35n level (Figure 1c). The level with *Natica* (35n) is particularly important at the localities IAA 1/95, IAA 2/95, IAA 3/95, and IAA 1/90. The latter is informally known as the “Ungulate site” besides the 35n, and the 35Cu₀ is also exposed at its base (Figure 1b: IAA 1/90 lower level). While there is no undeniable record of *Antarctodon* in the 35n level of IAA 1/90, some dental fragments have been tentatively assigned to it (Gelfo et al., 2019), and others have been attributed to *Astrapotheria* indet. There are also no assignable records for the upper levels 35C₃ and 35C₄ (Figure 1c). Therefore, by now, *Antarctodon* is restricted to 35Cu₀, with uncertainties regarding its extension to 35n.

The age of the strata bearing *Antarctodon* in the *Cucullaea* I Allomember, as well as the entire La Meseta Formation, remains a subject of debate. Dutton et al. (2002) conducted strontium isotope (⁸⁷Sr/⁸⁶Sr) analyses on selected *Cucullaea* bivalve specimens from Telm 2 (Acantilados I Allomember), Telm 5 (parts of *Cucullaea* I and *Cucullaea* II Allomembers), and Telm 7 (Submeseta Formation), and results suggest that the deposition of this unit occurred during the early to late Eocene. Ivany et al. (2008) analyzed the ⁸⁷Sr/⁸⁶Sr ratios in bivalve shells from Telms 2 to 7, indicating that the La Meseta and Submeseta formations spanned nearly the entire Eocene. However, these dating results were challenged by Douglas et al. (2014), who proposed that the lower part of the La Meseta Formation is no older than the base of the middle Eocene. These findings are also consistent with dinoflagellate cysts inferences (Amenábar et al., 2020, 2022). Nonetheless, land mammals

from the La Meseta and Submeseta formations (Gelfo et al., 2019) are similar to those from the better-dated faunas from the early Eocene of Patagonia (but see Bond et al., 2011 for a different opinion). This comparison aligns more closely with the age inferences made by Montes et al. (2019) who proposed an age range from the upper Thanetian (~58.4 Ma) to the lower Lutetian (~45.8 Ma), based on magnetostratigraphy, isotopic (⁸⁷Sr/⁸⁶Sr) data, and lithostratigraphy. Particularly, the basal coquina (35Cu₀) of the *Cucullaea* I Allomember, also known as Telm 4 (Sadler, 1988), contains fossils of reworked shells. This could potentially explain the similarity of their ratios to values from the lower Telm 3 or Campamento Allomember. While the sedimentology of the *Antarctodon*-bearing level suggests a hiatus of some duration in the stratigraphic sequence, strontium isotope ratios indicate that no more than approximately ~2 Ma of the section may be missing (Ivany et al., 2008). The updated ages for this level based on the isotope seawater curve of McArthur et al. (2020) suggest minimum values of two samples 47.6 and 52.6 Ma (Supplementary Material S3 La Meseta recalculated Sr in Amenábar et al., 2022), indicating a likely correlation between the Ypresian and the Lutetian. However, since its reworked origin, this level has been sparsely sampled for geochemistry in comparison to the upper and lower sections, which collectively seem to suggest more modern ages. Here, following the similitude of the land mammal assemblage with those of Patagonia and the analysis of Montes et al. (2019), a late Ypresian age for the base of *Cucullaea* I Allomember is preferred.

The fitting of the MPT to the known fossil record, following the temporal correlations with the highest current consensus, reveals the abrupt appearance of *Astrapotheria sensu stricto* starting from the early Eocene in various localities from Patagonia, São José de Itaboraí in Brazil, and Seymour (Marambio) Island in West Antarctica (Figure 5). Although *Eoastrapostylops* could serve as a suitable morphological ancestor at the dental level, its exact age is not entirely clear, as it has been considered as both, a probable early Paleocene or early Eocene. In the absence of isotopic dates, these estimations were based in faunistic comparisons of different taxa. Indeed, *Eoastrapostylops* is part of an endemic faunistic assemblage here defined as “Rioloroan fauna”, which also includes the litopterns or notopterns Notonychopidae *Notonychops powelli* (Soria, 1989a) and Indaleciidae *Indalecia* sp. (Saade et al., 2023), the alleged notoungulate *Satshatemnus bonapartei* (Soria, 1989b), turtles assigned to “*Podocnemis*” cf. *P. argentinensis* (de Broin and de la Fuente, 1993), and the crocodile *Lorosuchus nodosus* (Pol and Powell, 2011). The high degree of endemism of the Rioloroan fauna hinders direct comparisons at the genus or even family level with other South American localities. Nevertheless, this exclusive taxon representation requires confirmation through independent evidence, in order to discard other possible explanations such as the possibility that the Rioloroan represents a different chronological span. If

Eoastrapostylops and the Rioloroan fauna are assigned as the early Paleocene (see discussion in Gelfo et al., 2020), it remains challenging to explain the absence of “Trigonostylopidae” in Patagonia, particularly in the Danian levels with Notonychopidae and Didolodontidae of the Banco Negro Inferior (Lower Black Bank) of the Salamanca Formation, or in the Paleocene levels of the Río Chico Group where Xenungulates are frequently found. If, on the contrary, the Rioloroan fauna were of early Eocene origin, the rapid appearance of the first indisputable Astrapotheria and *Eoastrapostylops*, as possible morphological ancestors, would have occurred simultaneously in the regions of Río Loro, Itaboraí, Patagonia, and West Antarctica.

In this latter scenario, the paleobiogeographical distribution of Notoungulata considering the most recent biochronological frameworks, presents a noteworthy puzzle. Although notoungulates have their earliest record in the early Paleocene (Danian) of Tiupampa, Bolivia (de Muizon, 1991), their appearance in Patagonia occurs in strata assigned to the early Eocene, which is similar with the Astrapotheria. The main difference between them lies in the complete lack of notoungulates in Antarctica. If this absence is not a due to a sampling bias, it could be indicative of a delayed entry of notoungulates into Patagonia, after the late Paleocene, when the land connectivity that facilitated migrations between South America and Antarctica was probably interrupted (Reguero et al., 2014). So, in the case of Astrapotheria, considering the hypothesis of a dispersal event from South America to Antarctica, the existence of a Patagonian Paleocene record could have been anticipated, and their actual absence should be considered due to a potential sample bias.

The presence of *Antarctodon* in West Antarctica, as well as the general appearance of the “Trigonostylopidae” in South America during the Eocene, occurs between the Paleocene-Eocene Thermal Maximum (PETM) and the Early Eocene Climatic Optimum (EECO) within the context of warmer environmental conditions (Figure 4). In this sense, the paleobiogeographical distribution of the earliest astrapotheres, found in West Antarctica (*Antarctodon*), Patagonia (*Trigonostylops*), and Itaboraí Brazil (*Tetragonostylops*), is striking. This distribution, particularly with the latter taxon, seems to extend beyond the boundaries of the West Weddellian Biogeographic Province (Reguero and Goin, 2021). Unlike the globally warm conditions in which the basal forms of astrapotheres developed, the latest diversification took place during the Early-Middle Miocene, within a global icehouse world. This event is probably linked to the MMCO, which, notably, still featured cooler conditions compared to the PETM or EECO (Figure 5). This event marked by several evolutionary features, includes a remarkable increase in body size among astrapotheres, tooth loss, the development of hypsodont cheek teeth, and the repositioning of the nasal

aperture towards the cranial apex.

5 Conclusions

The significance of the described remains lies in the limited representation of native ungulate specimens, particularly Astrapotheria, in West Antarctica. In this regard, *Antarctodon* appears to be restricted to the basal coquina levels (35Cu₀) of the *Cucullaea* I Allomember of the La Meseta Formation. Despite this record, indeterminate Astrapotheria were also found at 35n in IAA 1/90 upper level (Figure 1). Additionally, other terrestrial mammals have been previously identified in this unit, such as the litoptern sparnotheriodontids *Notiolofofos arquinotiensis* and *N. regueroi*, as well as xenarthrans. However, in contrast to the diversity of these species in the upper naticid level of the same allomember, only one marsupial, *Antarctodolops dailyi*, is known (Gelfo et al., 2019).

Discrepancies in the ages of this unit, obtained through different methods, suggest that these levels may not only represent the end of the Ypresian but may extend into the Lutetian. However, it is worth noting that in both cases, the diversification of ungulates in West Antarctica is associated with warmer environments of the Eocene linked to the EECO during a global Warmhouse event.

Antarctodon inhabited an ice-free, vegetated Antarctica. Evidence of this is recorded in the marine sediments of the La Meseta Formation, particularly at the base *Cucullaea* I Allomember (Marensi et al., 1998; Montes et al., 2019), where allochthonous continental specimens, including those of terrestrial mammals, appear to have been transported from nearby continental regions. The paleoflora records within this unit reveal a predominance of *Nothofagus*, podocarps, and araucarian conifers, indicative of both deciduous and evergreen forests during the Eocene (Reguero et al., 2002). Furthermore, the presence of extensive wetland and freshwater ecosystems can be inferred from the discovery of endemic water lilies, *Notonuphar* sp. (Friis et al., 2017) and frogs belonging to the Australobatrachia anuran clade (Mörs et al., 2020).

Abbreviations

BAS-DJ: British Antarctic Survey, United Kingdom.

DPV: División Paleontología Vertebrados, Argentina.

IAA Pv: Repositorio Antártico de Colecciones Paleontológicas y Geológicas, Instituto Antártico Argentino, Colección Paleovertebrados, Argentina.

MACN A: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Col. Ameghino, Argentina.

MLP-PV: División Paleontología de Vertebrados, Museo de La Plata, Argentina.

MPEF: Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

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).

Acknowledgements To Daniel García López and Facundo Irazoqui for their participation and support in the fieldwork on Marambio Island during 2022. The successful execution of the fieldwork was made possible by the Dirección Nacional del Antártico-Instituto Antártico Argentino (DNA-IAA), and the logistical support from the Comando Conjunto Antártico and particularly Fuerza Aérea Argentina. The fieldwork that led to this study would have been impossible without the entire staff from Marambio Base and the logistic team from DNA-IAA. Special thanks are extended to the personnel overseeing the consulted collections, including Susana Bargo and Martín de Los Reyes from MLP, and Cecilia Amenabar from the IAA. I particularly thank Guillermo López, Enrique Bostelmann and an anonymous reviewer for the constructive comments that allowed to improve this manuscript. Special thanks are given to Editorial Office of the journal *Advances in Polar Science*, particularly to Sai Zhang and Caro Acosta Hospitaleche, and to Marcelo Reguero for the opportunities provided within the framework of the Antarctic projects PICT 0607-2018 and UNLP 11N812.

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Supplementary Table and File

Table S1 Data matrix of 13 taxa and 43 characters for phylogenetic analysis

Taxa	Character																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Eoastrapostylops</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0
<i>Trigonostylops</i>	0	0	0&1	0	0	0	0	0	1	0	0&1	0	0	0	0	0	?	0	0	1	?	0
<i>Tetragonostylops</i>	0	0	0&1	0	0	0	0	0	1	0	1	1	0	0	0	0&1	?	0	0	1	0	1
<i>Albertogaudrya</i>	1	1	1	?	0	1	1	0	1	0	1	1	0	0	0	0	?	0	0	0	0	1
<i>Scaglia</i>	0	1	?	?	?	?	?	?	?	?	1	1	1	0	0	1	?	0	0	0	1	?
<i>Astraponotus</i>	1	1	1	1	0	?	1	0	1	1	1	1	1	1	0	1	?	0	0	0	1	1
<i>Maddenia</i>	0	1	1	1	0	1	2	1	0	1	1	1	1	1	1	1	0	1	1	0	1	1
<i>Parastrapotherium</i>	2	2	1	?	1	0	0	1	0	1	1	1	1	1	1	1	0	0	1	0	1	0
<i>Astrapotherium</i>	2	2	1	?	1	0	0	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0
<i>Granastrapotherium</i>	2	2	0	?	1	?	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0
<i>Antarctodon</i>	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Astrapothericulus</i>	1	2	1	?	1	0	0	1	0	1	1	1	1	1	1	1	1	?	1	0	?	0
<i>Xenastrapotherium</i>	2	2	0	-	1	0	0	1	0	0	1	1	1	1	1	1	1	?	2	0	?	0

Taxa	Character																					
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	
<i>Eoastrapostylops</i>	?	0	?	0	?	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	
<i>Trigonostylops</i>	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	1	0	0	
<i>Tetragonostylops</i>	?	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	
<i>Albertogaudrya</i>	0	?	0	0	?	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	
<i>Scaglia</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	
<i>Astraponotus</i>	1	2	0	0	0	0	0	1	1	0	0	1	0	1	0	0	1	0	0	0	0&1	
<i>Maddenia</i>	?	1	0	1	?	1	0	0	0	1	0	1	1	0	1	0	1	0	1	0	0	
<i>Parastrapotherium</i>	1	2	1	1	0	1	0	0&1	1	1	0	1	1	1	1	0	0	1	1	1	0	
<i>Astrapotherium</i>	1	2	1	1	0	1	1	-	1	0	0	1	1	1	0	1	0	1	1	2	1	
<i>Granastrapotherium</i>	?	0	0	1	2	1	1	-	1	1	0	1	1	1	1	1	0	1	1	0	0	
<i>Antarctodon</i>	?	?	?	?	?	?	0	?	1	0	1	1	0	1	0	1	1	1	0	0	?	
<i>Astrapothericulus</i>	1	1	?	?	0	1	1	-	1	1	?	?	?	1	0	?	0	?	?	1	1	
<i>Xenastrapotherium</i>	2	1	?	?	1	1	1	-	1	1	?	?	?	1	2	?	0	?	?	0	0	

Notes: Characters names and states as followed.

1. Size of m2: 0 less than 20 mm long; 1 between 20–40 mm long; 2 more than 40 mm long.

2. Cheek teeth, crown height: 0 very low crowned; 1 high crowned; 2 slightly hypsodont.

3. Molar, labial cingula: 0 absent; 1 present.

4. P2, central valley: 0 absent; 1 present.

5. P3–P4, size relative to molars: 0 not reduced; 1 reduced.

6. P3, hypocone: 0 absent; 1 present.

7. P4, hypocone: 0 absent; 1 present.

8. P4, lingual valley: 0 absent; 1 present.

9. P4, labial fold of the metacone: 0 absent; 1 present.

10. P4, anterolingual pocket: 0 absent; 1 present.

11. Upper molars, lingual cingulum: 0 absent; 1 present.

12. M1–M2, hypocone/hypoflexus: 0 absent; 1 present.

13. M1–M2, central valley: 0 isolated (vestigial postprotocrista present); 1 communicated with the hypoflexus (postprotocrista absent).

14. M1–M2, crista: 0 absent; 1 present.

15. M1–M2, crochet: 0 absent; 1 present.

16. M1–M2, metaloph: 0 absent or incomplete (hypocone isolated); 1 complete.

17. Upper molar median fossette: 0 persistent in worm stages; 1 ephemeral.

18. Upper molar parastyle: 0 well developed; 1 reduced.

19. M1, anterolingual pocket: 0 absent; 1 weakly developed; 2 well developed.

20. M1–M3, labial fold of the metacone: 0 absent; 1 present.

21. M1–2 hypocone: 0 rounded; 1 lophoid, lingually pointed.

22. M3, hypocone: 0 absent; 1 present.

23. Lower incisors, crown shape: 0 simple; 1 bilobed.

24. Lower canine, implantation: 0 not extroverted; 1 slightly extroverted; 2 strongly extroverted.

25. Upper canines, anterior groove: 0 absent; 1 present.

26. Upper canines: 0 with root; 1 without root.

27. Number of lower incisors: 0 all incisors present; 1 i1 and i2 present, i3 absent; 2 all incisors absent.

28. p2: 0 present; 1 absent.

29. p3: 0 present; 1 absent.

30. p3 paralophid: 0 reduced or absent; 1 well developed.

31. p4 paralophid: 0 reduced; 1 well developed.

32. p4, hypoflexid: 0 present; 1 absent.

33. p4 entoconid included in hypolophid: 0 present; 1 absent.

34. p4 entoconid bunoid: 0 present; 1 absent.

35. p4 postentolophid: 0 present; 1 absent.

36. m1–m3, paralophid: 0 reduced; 1 well developed.

37. m1–3 hypoflexid deep: 0 present; 1 absent.

38. m1–3 hypoflexid superficial: 0 present; 1 absent.

39. m1–3 entoconid included in hypolophid: 0 present; 1 absent.

40. m1–3 entoconid isolated and bunoid: 0 present; 1 absent.

41. m1–3 entoconid as postentolophid: 0 present; 1 absent.

42. m1–m3, pillar: 0 absent; 1 present, bunoid; 2 present, lophoid, enclosing a small fossettid posterior to the protolophid.

43. lower molar lingual cingulid: 0 absent; 1 present.

File S1 Data matrix for phylogenetic analysis

The file is provided in both Nexus format and TNT format, which is available online at <https://aps.chinare.org.cn/EN/10.12429/j.advps.2023.0031>.