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A new astrapothere (Mammalia, Meridiungulata) from La Meseta Formation, Seymour (Marambio) Island, and a reassessment of previous records of Antarctic astrapotheres

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ABSTRACT

During the past quarter century, the uplifted nearshore sediments comprising the Eocene La Meseta Formation (LMF) of Seymour (Marambio) Island have produced a diverse assemblage of terrestrial mammals that closely, but not exactly, resembles late Early Eocene faunas from southern Patagonia. This assemblage includes the only astrapothere and litoptern fossils known from outside South America. The occurrence of astrapotheres in LMF was originally indicated by fragmentary dental remains tentatively referred to family Trigonostylopidae on the basis of their general resemblance to the Patagonian genus *Trigonostylops* Ameghino. In this contribution we describe a new astrapothere specimen from LMF; unlike specimens collected previously, this one is a complete and excellently preserved lower cheek tooth, providing a basis for a review of all previous records of Astrapotheria from this formation. This tooth (probably p4 rather than m1) is sufficiently distinct from all other known astrapothere cheek teeth to warrant assignment to a new genus and species, *Antarctodon sobrali*. It has a transversally elongated entoconid, resembling that observed in at least one specimen of the Mustersan genus *Astraponotus*, but the tooth as a whole is much lower crowned and less lophodont than in the

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latter. Phylogenetic analysis suggests that *Antarctodon* is closer to genera classified by previous authors as astrapotheriids (e.g., *Albertogaudrya* and *Tetragonostylops*) than it is to *Trigonostylops*. Reexamination of other LMF specimens previously referred to Trigonostylopidae reveals that some specimens are attributable to this new taxon and others either are not astrapotheres at all or lack distinctive features. Consequently, at present the record of order Astrapotheria in Antarctica should be considered as restricted to non-trigonostylopids.

INTRODUCTION

Ancient Antarctic land mammals have so far been recovered only in uplifted, nearshore sediments of Eocene La Meseta Formation (LMF) of Seymour (Marambio) Island (Chornogubsky et al., 2009, and references therein; fig. 1). During the past quarter century, this formation has produced single taxonomic representatives of Gondwanatheria, Litopterna, and Astrapotheria,⁴ as well as an impressive array of polydolopid (Woodburne and Zinsmeister, 1984, Case et al., 1988, Bond et al., 1990), microbiotherian (Carlini et al., 1990), and didelphimorphian (Goin et al., 1999, 2006, 2007, Chornogubsky et al., 2009) marsupials. The James Ross Basin, in which Seymour Island is located, was part of the West Antarctic continental shelf when these fossils were deposited in Eocene time from fluvial sources debouching eastward from what is now the Antarctic Peninsula, some 100 km to the west. Biogeographically, the Seymour assemblage has been interpreted as closely resembling late Early Eocene faunas known from southern Patagonia (e.g., Paso del Sapo fauna; Tejedor et al., 2009), although several groups are completely unrepresented (e.g., cingulates) in the La Meseta fauna, perhaps because of inadequate fossil recovery, and there are other differences that suggest development of a certain degree of endemism (e.g., presence of gondwanatheres, not known to have survived into the Patagonian Eocene).

The occurrence of astrapotheres in LMF was first reported by Bond et al. (1990); Marenssi et al. (1994) noted additional fragmentary material from the same locality. Hooker (1992) described a tooth fragment from an unrelocated locality in northern Seymour Island as probably belonging to an astrapothere. All these specimens have been tentatively referred to the family Trigonostylopidae on the basis of their general resemblance to the Patagonian genus *Trigonostylops* Ameghino. Trigonostylopidae was originally conceived as a group including species of *Trigonostylops* and possibly related taxa of questionable identity (Ameghino, 1901). Subsequent authors have proposed differing interpretations of the proper content of Trigonostylopidae (Simpson, 1933, 1967; Paula Couto, 1963; Carabajal et al., 1977; Soria, 1982, 1984; Cifelli, 1993), and at present there is no real consensus concerning the phylogenetic limits of this group.

In this contribution we describe a new astrapothere taxon from LMF. This taxon is based on a single specimen previously reported as a new astrapothere by Bond et al. (2008a) but listed

⁴Although usually listed as part of the Seymour mammal fauna, the presence of xenarthrans in La Meseta sediments is uncertain. The identification of the fragmentary tooth (MLP 94-III-15-14) described by Vizcaíno and Scillato-Yané (1995) as that of a tardigradan has recently been challenged by MacPhee and Reguero (2010). A distal phalanx (MLP 88-I-1-95), attributed to a second possible xenarthran of vermilinguan or tardigradan affinity (Marenssi et al., 1994), cannot now be located in the MLP collections and is therefore unavailable for restudy.

as *Trigonostylops*, sp. nov., by Reguero and Marenssi (2010). Unlike previous La Meseta specimens, this one is almost complete and excellently preserved, and thus provides a basis for a review of all previous records of Astrapotheria from this formation and a reassessment of their systematic position.

INSTITUTIONAL ABBREVIATIONS

BMNH, Natural History Museum, London, UK; DGM, Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil; LIEB, Laboratorio de Investigaciones en Evolución y Biodiversidad, Facultad de Ciencias Naturales, Sede Esquel, Universidad Nacional de la Patagonia “San Juan Bosco,” Chubut Province, Argentina; MPEF PV, Museo Paleontológico Egidio Feruglio, Chubut Province, Argentina; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; MLP, Museo de La Plata, Argentina.

STRATIGRAPHICAL SETTING AND AGE

The Paleogene La Meseta Formation (Elliot and Trautman 1982; Marenssi et al. 1998) crops out in the northern third of Seymour (Marambio) Island and nearby Cockburn Island. This thick (710 m) clastic unit records sedimentation in an environment that is best described as deltaic/estuarine, although with significant variation in the section both laterally and vertically. Localities DPV 2/84 and IAA 1/90, which are of special interest here, occur within the distinctive first *Cucullaea*-dominated shell bed in the middle part of LMF. This is the *Cucullaea* I allomember of Marenssi et al. (1998), and is equivalent to Unit I1 of Elliot and Trautman (1982) and TELM 4 + 5 of Sadler (1988).

Cucullaea I is composed of thick shelly conglomerates, well-sorted sands, and interlaminated sand/mud channel fills with thin shelly conglomeratic intervals. The thanatocoenose is heterogenous: the bioclastic fraction consists of bivalves (*Cucullaea*), gastropods (naticids), and a variety of other marine invertebrates together with the occasional marine or land vertebrate fossil mixed in (Marenssi et al., 1998). This allomember has also provided the largest collection of leaves of Eocene age from Antarctica (locality C/88, Gandolfo et al., 1998), as well as most of the fossil woods collected from LMF (Torres et al., 1994; Brea, 1998).

The age of the middle part of LMF (*Cucullaea* I and *Cucullaea* II allomembers) is unsettled. Based on her study of palynofloras, Askin (1977) considered this interval to be Middle Eocene, which corresponds reasonably well with $^{87}\text{Sr}/^{86}\text{Sr}$ ages reported by Dutton et al. (2002) for TELM 5 (*Cucullaea* I/*Cucullaea* II equivalent) and other evidence, such as the faunal age estimate of Reguero and Marenssi (2010) based on marine and terrestrial vertebrates. However, as Ivany et al. (2008) note, single measured $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of putative Eocene age do not have unique chronometric solutions because the global marine seawater curve varied little during this epoch. On the basis of new strontium-ratio samples from Seymour, the latter authors suggest that Telms 2–5 may actually be several million years older than previously thought (thus possibly Early rather than Middle Eocene in age).

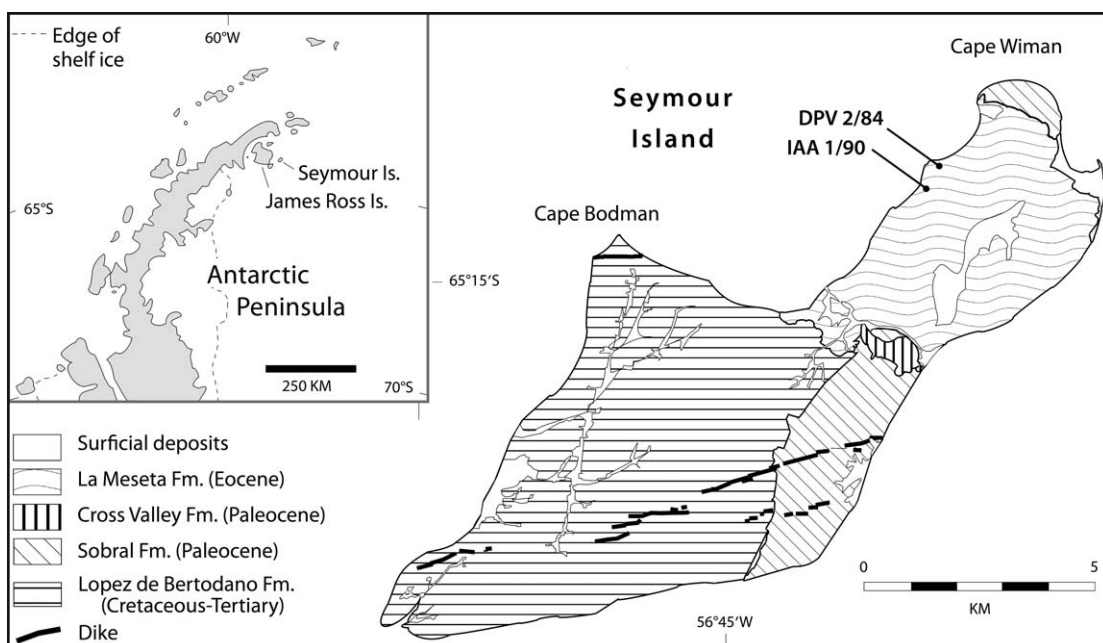


FIG. 1. Geological map of Seymour (Marambio) Island (Antarctic Peninsula) showing the two land mammal bearing localities mentioned in the text. Modified from Reguero et al. (2002).

SYSTEMATIC PALEONTOLOGY
ORDER ASTRAPOTHERIA LYDEKKER, 1894

Antarctodon, new genus

TYPE AND ONLY SPECIES: *Antarctodon sobrali*, new species.

DIAGNOSIS: As for the type species.

ETYMOLOGY: *Antarct-*, from “Antarctica”; and *odon-*, from the Greek “tooth.”

CHRONOLOGICAL AND GEOGRAPHIC DISTRIBUTION: Early Eocene; West Antarctica.

Antarctodon sobrali, new species

Figure 2

Trigonostylops, sp. nov. (Reguero and Marenssi, 2010).

HOLOTYPE: MLP 08-XI-30-1, an isolated right p4 or m1.

HYPODIGM: The holotype only.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE: Seymour (Marambio) Island, Antarctic Peninsula. La Meseta Formation, Cucullaea I Allomember (Marenssi et al., 1998). The holotype comes from locality DPV 2/84, TELM 4 of Sadler (1988) (Marenssi et al., 1994).

ETYMOLOGY: Dedicated to José María Sobral, Argentine navy lieutenant and geologist, participant in the Antarctic expedition led by O. Nordenskjöld (1901–1904).

DIAGNOSIS: Small astrapothere, slightly larger than *Trigonostylops*. Holotype represents p4 (or possibly m1) with long anterolingual crescent, longer than in *Trigonostylops*. Small hypoconulid, lingually retracted hypolophid. Lophoid, transversally elongated entoconid, forming an “entocristid” reaching anterior slope of hypoconulid.

DESCRIPTION AND COMPARISONS

The cheek tooth (fig. 2A–E) is brachyodont, low crowned as in *Trigonostylops* and lower than in *Albertogaudrya*. Its size (1.23 cm long, 1.02 cm wide) is somewhat larger than the m1 of *T. wortmani*, but much smaller than any cheek tooth of *Albertogaudrya*. The base of the tooth is nearly rectangular, although the lingual margin shows a slight inflection at the base of the metaconid, opposing the more marked labial inflection between protoconid and hypoconid. These inflections impart a somewhat hourglass-shaped contour to the tooth (fig. 2A). This configuration is observed in posterior premolars of *Trigonostylops*, but in the latter’s molars the lingual basal inflection is located between the bases of the metaconid and entoconid, more posterior than the labial inflection. The metaconid is massive; the lingual wall is somewhat flattened and positioned more labial than the lingual base of the tooth (fig. 2B). The protoconid is also very large, projecting slightly posterolabially. The protoconid and the metaconid are connected by a broad metalophid, less oblique than in *Trigonostylops*. The anterior crescent departs from the anterior face of the protoconid; it is high, oblique, and falls gradually. It intersects a sizeable anterior cuspule, continuing somewhat lingually beyond this structure, abruptly descending basally thereafter (fig. 2C). The crescent forms almost two-thirds of the anterior face of the trigonid. A set of interstitial wear facets on the anterior face of the anterior crescent indicates the existence of another tooth in front. The trigonid basin is shallow, but well defined by the combined V-shaped metalophid–anterior crescent; the basin opens lingually via a narrow notch between the anterior cuspule and the metaconid (fig. 2D). In *Trigonostylops* the anterior crescent (in both molars and posterior premolars) is much shorter and the trigonid basin is widely open anterolingually. In *Tetragonostylops* the molars have a long, more anteroposteriorly oriented anterior crescent, and the trigonid basin is also widely open on the lingual side. In the p4 of the paratype of *Tetragonostylops aphtomasi* the trigonid is essentially as in *Trigonostylops* (see Paula Couto, 1952, 1963), but in some referred specimens (e.g., DGM 355-M) the trigonid has an anterior crescent that is as long as in the molars. On the p4 and molars of *Albertogaudrya* and *Astraponotus*, the trigonid basin is enclosed by a long, partially transverse anterior crescent, but in these taxa the basin is deeper because of the greater height of the surrounding crests.

The talonid is markedly lower than the trigonid (fig. 2D, E), and it is strikingly shorter than the molar talonids of other astrapotheres. The posterior crescent is also V-shaped, with the conspicuous hypoconid situated on the labial side of the slightly acute vertex. This configuration clearly differs from that of the molars and premolars of all other astrapotheres to which comparisons have been made. The anterior arm of the hypoconid crescent joins the posterior face of the metalophid near the midpoint between protoconid and metaconid; consequently the labial flexid is very penetrating, much more than in *Trigonostylops*, *Tetragonostylops*, and *Albertogaudrya*. The

posterior arm of the hypoconid crescent ends abruptly in an almost indistinguishable hypoconulid, and there is no extension of this crest beyond this point (fig. 2A–B). The entoconid is small and transversally lophoid, not conical, located somewhat anterior to the posterolingual corner of the crown. This transverse element reaches the anterior slope of the hypoconulid, forming a notoungulate-like “entolophid.” This feature is unique among accepted astrapotheres, comparable only to that observed in a few specimens referable to *Astraponotus*. In an isolated, little worn molar of this genus in the Roth collection (MLP 67-II-27-168), the entoconid is bunoid, but has an oblique labial projection that connects to the hypoconulid; the same condition occurs in the p4 of MLP 69-III-24-295, but not in its associated molars. In all remaining astrapotheres with a distinguishable entoconid, this cusp is isolated (e.g., *Trigonostylops*, *Albertogaudrya*) or directly attached to the hypoconulid (e.g., *Tetragonostylops*). As in the trigonid, the talonid basin is shallow and closed, except for the deep lingual trench between the metaconid and the entoconid (fig. 2D).

The anterior cingulid departs from the base of the protoconid and becomes abruptly prominent on the anterolingual corner of the crown. It surrounds the anterior base of the crown, and does not rise upward at the base of the anterior cuspule. The posterior cingulid is also prominent, and forms a conspicuous basal shelf between the entoconid and the hypoconulid (fig. 2A–B). A couple of small protuberances between the bases of the protoconid and hypoconid suggest a rudimentary labial cingulid (fig. 2E). There is no trace of a lingual cingulid.

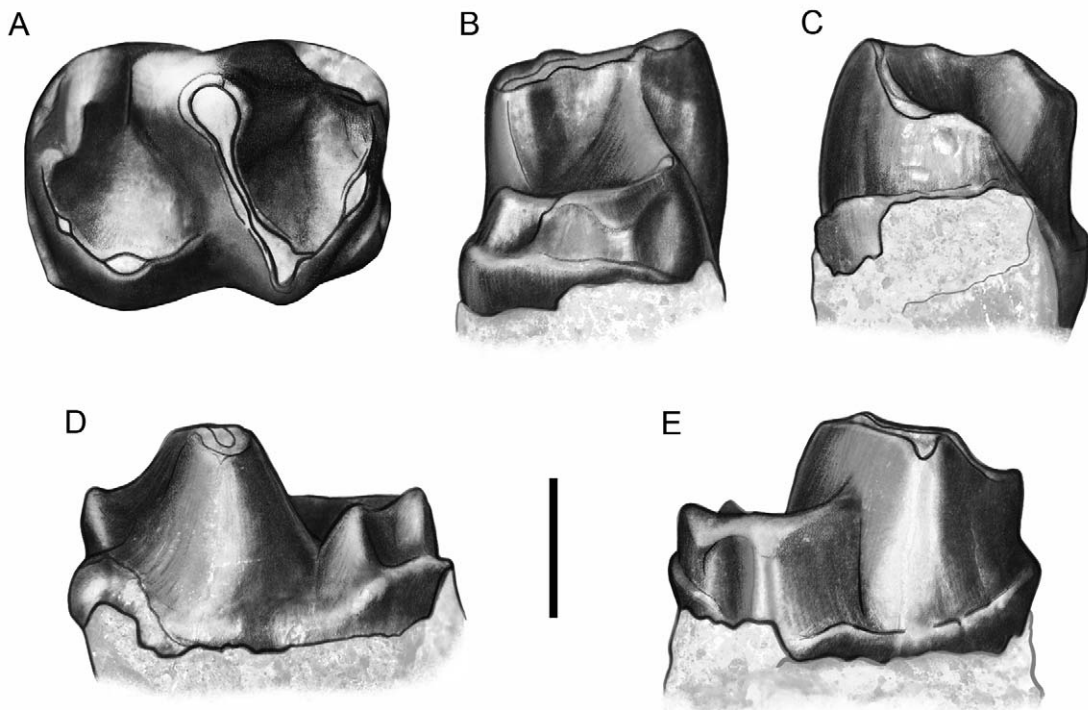


FIG. 2. MLP 08-XI-30-1, right p4 or m1, holotype of *Antarctodon sobrali*, gen. et sp. nov., in A, occlusal; B, posterior; C, anterior; D, lingual; and E, labial views. Scale bar = 5 mm.

The LMF astrapothere fossil previously reported by Bond et al. (1990) is the anterolingual portion of a right upper cheek tooth, MLP 90-I-20-2 (Marensi et al., 1994: fig. 6d), from IAA 1/90, TELM 5 of Sadler (1988). It comprises a partial protocone, complete protoloph, and anterior cingulum of a small, low-crowned species. The cingulum is broad, rather expanded anteriorly, and forms a basal shelf more conspicuous than that of *Trigonostylops*. The preserved parts of the protocone and protoloph are essentially the same as in the Patagonian genus, but the main wear facet is on the apex and posterior slope of the protocone (facet 9, lingual phase of Butler, 1952), whereas in *Trigonostylops*, *Tetragonostylops*, and other astrapotheres with cuspidate molars the wear is consistently more intense on the protoloph. An additional tooth fragment of an astrapothere (MLP 90-I-20-6) reported by Marensi et al. (1994: fig. 6c) as a portion of an upper molar of an astrapothere is highly incomplete and shows no distinctive features.

DISCUSSION

The dental locus of the isolated cheek tooth described herein is uncertain. We can say with confidence that it is neither an anterior premolar nor an m3, but certainty beyond that is not possible. The complex morphology of the talonid might be taken to suggest that it is a molar: having the entoconid located anterior to the hypoconulid is a feature of the molars in other astrapotheres, while the premolar entoconid is usually at the posterolingual corner of the crown, directly lingual to the hypoconulid (except in the p4 of the *Astraponotus* specimen mentioned above). On the other hand, the very short talonid and the presence of an inflection at the base of the metaconid are more premolarlike. In addition, the new fossil has a very short hypolophid, as in the premolars of *Trigonostylops*, whereas in the molars of the latter genus this crest is longer, forming more than half of the posterior margin of the tooth.

If this cheek tooth is interpreted as p4, other dental features of *Antarctodon* can be inferred by comparison with those of other astrapotheres. In none of the known astrapotheres is the p4 more molarized than the true molars. Consequently, the hypoflexid on m1–m3 would be as deep as or deeper than on p4, with the anterior crescent as developed as or even more developed than that on p4. Additionally, a well-developed anterior crescent on m1–m3 corresponds to the presence of a functional hypocone on upper molars (i.e., in tetragonodont molars, in contrast to the trigonodont molars of *Trigonostylops*). Likewise, the well-developed p4 anterior crescent suggests the presence of a hypocone on P3, and consequently also on P4 (unlike *Trigonostylops* and *Tetragonostylops*). However, such morphological relationships are not interchangeable: well-developed anterior crescents in lower molars do not necessarily imply the same condition in p4 (e.g., *Astrapothericulus*) and a hypocone on upper molars does not necessarily imply well-developed anterior crescents on lower molars (e.g., *Maddenia*).

The fragmentary upper cheek tooth MLP 90-I-20-2 differs from those of other astrapotheres in having the main wear facet on the apex and posterior slope of the protocone instead of on the protoloph. This unusual wear pattern would result from having a specialized entoconid structure on the talonid of the antagonist lower cheek tooth, which is the cusp that occludes with the posterior slope of the protocone. This occlusal relationship, in addition to

congruence in size and hypsodonty, suggests that MLP 90-I-20-2 could represent an upper cheek tooth of *Antarctodon*.

Hooker (1992) reported the recovery of the posterior portion of an ectoloph of a first or second upper molar (BMNH BAS M2584) from a locality that he took to be within TELM 4 (sensu Sadler, 1988). After a preliminary analysis, he discarded lioptern and notoungulate affinities for the fossil because it exhibited vertically decussating Hunter-Schreger enamel bands. At that time this decussation pattern was known to occur only in pyrotheres and astrapotheres among endemic South American ungulates (Fortelius, 1985). Pyrotheres could be easily ruled out because of their highly derived cheektooth morphology, and Hooker (1992) concluded that the tooth thus belonged to an astrapothere. In two features—similar orientation of the postmetaconule crista (directed toward the metastyle) and crown height—the fossil appeared to agree adequately enough with the trigonostyloid *Trigonostylops*. However, because of the fossil's greater size and the slightly concave buccal ectoloph wall (flat or gently convex in *Trigonostylops*), Hooker tentatively referred it to Trigonostylopidae indet.

In M1 and M2 of *Trigonostylops* the postmetaconule crista is transverse, oriented toward the metacone; only in some M3s of *Trigonostylops* is this feature oriented toward the metastyle instead. Moreover, even in the latter case it markedly descends toward the postcingulum, rather than paralleling it as in BMNH BAS M2584. By contrast, there is much greater similarity between the latter specimen and upper molars of the Antarctic sparnotheriodontid lioptern *Notiolofo*s (nec *Notolophus*, preoccupied; cf. Bond et al. [2008b]) *arquino*tiensis also recorded from TELM 4 (Bond et al., 2006; see also Marensi et al., 1994). Correspondences include: estimated similar size, similar crown height, concave labial wall of the ectoloph, and postmetaconule crista similarly directed toward the metastyle, not converging with the postcingulum. Of particular note is the fact that vertically decussating Hunter-Schreger enamel bands also occur in *N. arquino*tiensis, as in other sparnotheriodontids (Reguero et al., 2002; Peres Line and Bergqvist, 2005; Bond et al., 2006). In light of this evidence, we propose that BMNH BAS M2584 is much more likely to represent a sparnotheriodontid than an astrapothere.

RELATIONSHIPS

All the astrapothere specimens previously reported from LMF were tentatively referred to family Trigonostylopidae because of their general resemblance to the Patagonian genus *Trigonostylops* Ameghino, (i.e., small size, low-crowned teeth, and other probably primitive features) (Bond et al., 1990; Hooker, 1992; Marensi et al., 1994). Trigonostylopidae is a group originally conceived to include the species of *Trigonostylops* and others of uncertain pertinency (Ameghino, 1901). Simpson (1933) originally interpreted *Trigonostylops* and its allies (i.e., *Albertogaudrya* and *Shecenia*) as members of a group of archaic ungulates (Trigonostylopoidea) doubtfully referable to Astrapotheria, but later (1967) removed them to a distinct order. Carabajal et al. (1977) transferred *Albertogaudrya* to the Astrapotheriidae. Soria and Powell (1981) and Cifelli (1983) concluded that Trigonostylopoidea cannot be separated from Astrapotheria. Soria (1982, 1984) went on to transfer *Tetragonostylops*, originally described as a trigonostyloid (Paula

Couto, 1952, 1963), to Astrapotheriidae and concluded that Trigonostylopidae (*Trigonostylops* and probably *Shecenia*) was a basal collateral branch within Astrapotheria. Finally, Cifelli (1993) concluded that “Trigonostylopidae” (family as conceived by Simpson [1933], with the addition of Eoastrapostylopidae of Soria and Powell [1981]) was the stem group of Astrapotheriidae. Consequently, at present there is really no consensus concerning the systematic content of Trigonostylopidae, and assignment of the Antarctic astrapothere to this family or to Astrapotheriidae requires a comprehensive evaluation.

In order to evaluate the relationships of *Antarctodon* to other astrapotheres, a phylogenetic analysis using the maximum parsimony criterion was performed using NONA (Goloboff, 1993). Character polarity was determined by comparison with conditions in *Eoastrapostylops riolorensis* Soria and Powell (1981), hypothesized to be the most primitive of known astrapotheres (Soria and Powell, 1981; Soria, 1984, 1988; Cifelli, 1993). The taxa used for analysis include: *Tetragonostylops*, as described by Paula Couto (1952, 1963) with additional material from Patagonia described by Soria (1982); *Trigonostylops*, *Albertogaudrya*, *Scaglia*, and *Astraponotus*, as described by Simpson (1967) and Kramarz et al. (2010); the ?early Oligocene *Madden* (Kramarz and Bond, 2009); *Parastrapotherium* as described by Scott (1937), with additional observations on type materials from the Ameghino Collection of MACN, described by Kramarz and Bond (2008); *Astrapotherium*, essentially as in Scott (1928); and *Granastrapotherium* (Laventan SALMA, Middle Miocene), as described by Johnson and Madden (1997).

The list and definition of characters used in the phylogenetic analysis is shown in appendix 1. Analysis was restricted to dental characters. Characters were taken from Kramarz and Bond (2009) except for characters 18, 21, 25, 26, and 31. The multistate characters 31, 34, and 35 were codified as unordered. Size of m2 (char. 1) was coded as a discrete character using three arbitrary states (m2 length < 20 mm, 20 mm < m2 length < 40 mm, m2 length > 40 mm). Length of m2 for *Scaglia* (known only through a juvenile partial skull with C–M1) was inferred by comparison with *Albertogaudrya*. Assuming MLP 08-XI-30-1 is a p4, only characters 29, 30, and 31 could be scored by direct observation. The size of m2 (char. 1) was estimated by comparison with *Trigonostylops*, *Albertogaudrya*, and *Tetragonostylops*. Presence of p3 (char. 28) was deduced from the occurrence of a wear facet on the anterior margin of the supposed p4. The data matrix is shown in table 1.

A single most parsimonious tree was obtained by exhaustive searching, with length = 65, CI = 64 and RI = 70 (fig. 3). *Antarctodon* appears as the sister group of the clade, which includes *Albertogaudrya*, *Scaglia*, and all post-Casamayoran astrapotheres. This arrangement is supported by one synapomorphy: presence of a well-developed p4 anterior crescent (char. 29). It is worth noting that the presence of a hypocone on M1–M2 (char. 12) and on M3 (char. 22), and well-developed anterior crescent on m1–m3 (char. 32) are synapomorphies defining the next most inclusive clade (*Tetragonostylops* + all other astrapotheres except *Trigonostylops* and *Eoastrapostylops*). Although none of these characters can be scored in *Antarctodon* by direct observation, the parsimony analysis predicts that they are the most probable states of these characters in this taxon. These predictions are entirely consistent with the inferences mentioned above based on comparison with other astrapotheres.

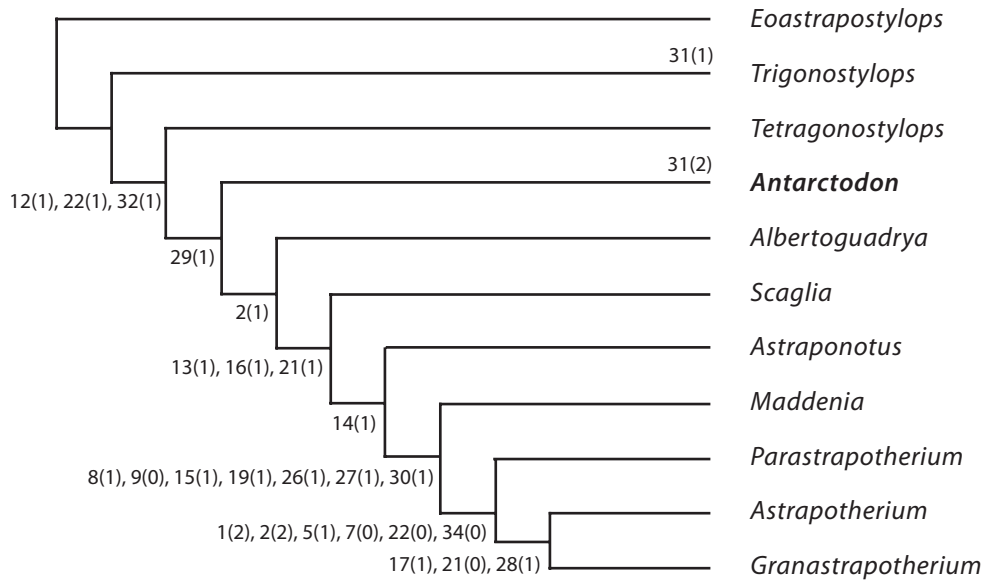


FIG. 3. Single most parsimonious tree (length = 65, CI = 64 and RI = 70) generated by an exhaustive search in NONA (Goloboff, 1993) employing 35 dental characters (table 1) coded for 11 astrapotheriid genera (using *Eoastrapostylops* as the outgroup), under the assumption that the holotype of *Antarctodon sobrali* (MLP 08-XI-30-1) is a p4.

An additional phylogenetic analysis was performed based on the alternative interpretation that the MLP 08-XI-30-1 is an m1. In this case, only characters 2, 32, 33, 34, and 35 could be scored by direct observation. The size of m2 (char. 1) was also estimated by comparison with *Trigonostylops*, *Albertogaudrya*, and *Tetragonostylops*. The result obtained by exhaustive searching is a single most parsimonious tree with topology and length identical to the one obtained in the previous analysis.

CONCLUSIONS

The record of Astrapotheria in what is now West Antarctica is confirmed and significantly enlarged by the isolated lower cheek tooth described here. This tooth is probably a p4 rather than an m1, but whatever its proper allocation, it shows sufficient distinctiveness from species of *Trigonostylops* and all other known astrapotheres to be interpreted as a new taxon, *Antarctodon sobrali*. The very peculiar condition of the entoconid can be said to loosely resemble that observed in at least one specimen of *Astraponotus*, but the tooth is much lower crowned and less lophodont than in the Mustersan genus. Regardless of whether this tooth is interpreted as a p4 or an m1, phylogenetic analysis suggests that *Antarctodon* is closer to genera classified as astrapotheriids by previous authors (e.g., *Albertogaudrya* and *Tetragonostylops*) than it is to *Trigonostylops*. These affinities indicate that the new Antarctic species should not be placed within Trigonostylopidae. As argued here, previous referrals of material from Seymour to

TABLE 1. Taxon-character matrix used for assessing phylogenetic relationships of *Antarctodon*, gen. nov., and other astrapotheres.

Taxon	Character state ^a		
	1	2	3
<i>Eoastrapostylops</i>	0000000000000000	-000-0?0?0000000000	
<i>Trigonostylops</i>	00A0000010A00000	-001-00100000010010	
<i>Tetragonostylops</i>	00A000001011000A	-00101?000000001000	
<i>Albertogaudrya</i>	111?011010110000	-000010?00001001010	
<i>Scaglia</i>	01????????111001	-0001?????????????0	
<i>Astraponotus</i>	11110?1011111101	-0001112000010B1AC0	
<i>Maddenia</i>	011101210111111011011?101100100110		
<i>Parastrapotherium</i>	221-1001011111110010101211101101101		
<i>Astrapotherium</i>	221-100101111111010001211111001002		
<i>Granastrapotherium</i>	220-1-010001111111000-001111101200		
<i>Antarctodon</i> (p4)	00????????????????????????????0102????		
<i>Antarctodon</i> (m1)	00????????????????????????????????1020		

^aCharacters and character definitions are listed in appendix 1. *Antarctodon* was scored under two different assumptions: holotype is a p4 (penultimate line), or, alternatively, it is an m1 (last line). Polymorphic conditions: A = 0,1; B = 0,2; C = 1,2. "?" indicates missing or unknown character. "-" indicates non-applicable character.

Trigonostylopidae (Bond et al., 1990; Hooker, 1992; Marensi et al., 1994) include specimens that are either not astrapotheres at all or lack distinctive features. Consequently, at present the record of order Astrapotheria in Antarctica should be considered as limited to astrapotheres not proximally related to *Trigonostylops*.

Based upon the cooccurrence of mammalian taxa other than astrapotheres, Tejedor et al. (2009) proposed that the Paso del Sapo fauna of west-central Patagonia was putatively coeval with and biogeographically related to the LMF fauna. The only available astrapothere cheek tooth from Paso del Sapo (LIEB-PV 1623) was originally interpreted as being indistinguishable from comparable teeth of *Trigonostylops* and *Tetragonostylops* (Tejedor et al., 2009). Reexamination reveals that this tooth strongly resembles the m1 of *Trigonostylops wortmani*, but with a less marked cingulid and shallower talonid basin, and differs from *Tetragonostylops aptomasi* in having a less pronounced paralophid and distinct entoconid. Additionally, it differs from the type of *Antarctodon sobrali* in being much smaller, more delicate, and lower crowned; the entoconid is not transversally lophoid and the paralophid is less developed. Therefore, the Early

Eocene Patagonian record of Astrapotheria in Paso del Sapo should be limited to *Trigonostylops* or some closely allied form not closely related to *Antarctodon*.

Similarly, the relationship between the Paso del Sapo and LMF sparnotheriodontid litopterns is not conclusive. The sparnotheriodontids from Paso del Sapo are represented by two taxa. One is more closely related to ?*Victorlemoinea longidens* (from Cañadón Vaca) than to *Notiolofo*s (from La Meseta). The other one, represented by MLP 66-V-12-2, has an uncertain taxonomic position (gen. et sp. indet. G of Tejedor et al., 2009); it shares some characters with another sparnotheriodontid from Cañadón Vaca referred to *Victorlemoinea* by Simpson (1948) that could indicate some relationship with *Notiolofo*s *arquino*tiensis (Bond et al., 2006). For this last reason, MLP 66-V-12-2 was considered by Tejedor et al. (2009) as strengthening the case for a biogeographical relationship between LMF and Paso del Sapo faunas. Notwithstanding this, the MLP 66-V-12-2 differs from *N. arquino*tiensis in some diagnostic characters (e.g., protostyle not connected to the protoloph), and its relationship with that species is therefore not clear. Consequently, the referral of MLP 66-V-12-2 to a new species of *Notiolofo*s as proposed by Reguero and Marensi (2010) appears unjustified. Corporately, the ungulate (i.e., astrapothere and litoptern) evidence provides no direct support for an extremely close biogeographic relationship between LMF and Paso del Sapo faunas.

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APPENDIX 1

List and Definition of Characters Used in the Phylogenetic Analysis

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 (m2 crown height larger than anteroposterior diameter).
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 as a cingular cusp; 2 = well developed.
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 worn 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–M2 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 = rooted; 1 = rootless.
27. p2: 0 = present; 1 = absent.
28. p3: 0 = present; 1 = absent.
29. p4: anterior crescent: 0 = reduced; 1 = well developed.
30. p4, hypoflexid: 0 = present; 1 = absent.
31. p4, entoconid: 0 = included in the hypolophid; 1 = bunoid, isolated; 2 = forming a distinct lophid (nonadditive).
32. m1–m3, anterior crescent: 0 = reduced; 1 = well developed.
33. m1–m3, hypoflexid: 0 = deep; 1 = superficial; 2 = absent.
34. Lower molars, entoconid: 0 = included in the posterolophid; 1 = isolated, bunoid; 2 = lophoid, connected to the hypoconulid as distinct crest (nonadditive).
35. m1–m3, pillar: 0 = absent; 1 = present, bunoid; 2 = present, lophoid, enclosing a small fossettid posterior to the metalophid (nonadditive).

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