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Original article

On the status of *Isolophodon* Roth, 1903 (Mammalia, Astrapotheria) and other little-known Paleogene astrapotheres from central Patagonia[☆]

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ARTICLE INFO

Article history:

Received 22 June 2012

Accepted 31 October 2012

Available online 16 April 2013

Keywords:

Astrapotheria

Isolophodon

Scaglia

Systematics

Paleogene

Patagonia

Abbreviations:

MLP, Museo de La Plata, Argentina

MPEF, Museo Paleontológico Egidio

Feruglio, Trelew, Argentina

P/p, upper/lower premolar

M/m, upper/lower molar

SALMA, South American Land Mammal Age

ABSTRACT

Most of the 16 currently recognized astrapothere genera are well known through numerous specimens preserving at least almost complete dentition. One of the exceptions is the enigmatic genus *Isolophodon* Roth, 1903, based on very scant and fragmentary materials from Paleogene levels of central Patagonia. This taxon was ruled out from almost all taxonomic lists, although its validity has not been discussed by subsequent authors. We herein re-describe and discuss the taxonomic status of the species of *Isolophodon*. The type species, *I. cingulosus* Roth, 1903, is characterized by having lower cheek teeth with a much reduced hypoflexid, resembling derived uruguaytheriines, but lower-crowned and with three lower premolars, as in the species of *Astrapotheria* Ameghino, 1901. This is the only astrapothere nominal species attributable to the Tinguirirican South American Land Mammal Age (SALMA, Early Oligocene). *Isolophodon aplanatus* Roth, 1903 (Casamayoran and Mustersan SALMAs, middle Late Eocene) has proportionally more elongated lower molars and a less developed paraflexid than the type species. *Isolophodon* would represent an early diverging lineage of astrapotheriids, in which some dental features evolved convergently with the more derived uruguaytheriines. Additionally, we describe other fragmentary but very significant specimens from Paleogene localities in central Patagonia (Argentina) attributable to the following taxa: cf. *Scaglia kraglievichorum* (Barrancan? subage), based on a partial upper molar nearly 60% larger than the type of *Scaglia kraglievichorum* Simpson, 1957; Astrapotheriidae gen. et sp. 1 (Barrancan? Subage, Middle Eocene), based on an isolated upper molar larger than any other Eocene astrapothere; Astrapotheriidae gen. et sp. 2, based on five isolated upper cheek teeth from “La Cantera” (Gran Barranca, Early Oligocene), characterized by a large, isolated hypocone and accessory cusps on P3–P4. These taxa enlarge the known diversity of Paleogene astrapotheres and document novel evolutionary patterns for these mammals.

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1. Introduction

Astrapotheres are some of the most characteristic and representative mammals of the South American Tertiary native faunas. These mammals are recorded from the Paleocene (Soria and Powell, 1981) up to the Middle Miocene (Johnson and Madden, 1997; Goillot et al., 2011); at least 34 species grouped in 16 genera are currently recognized. Their diversity and temporal distribution have been intensively studied by previous authors (Table 1). Most of these taxa are well known through numerous specimens preserving skulls and jaws with complete or almost complete dentition. However, some few taxa are known through very scant and fragmentary materials and their status is still enigmatic. This is particularly the case of the species of *Isolophodon* described by Roth (1903), which were ignored

by subsequent authors and ruled out from almost all comprehensive taxonomic lists (e.g., Soria, 1984; Pascual et al., 1996) and phylogenetic analyses (e.g., Kramarz and Bond, 2009).

In this contribution, we re-describe the type specimens of the species of *Isolophodon* and report new materials; we discuss the taxonomic status of these taxa, with some preliminary comments about their relationships and evolutionary significance. Additionally, we describe other fragmentary but very significant specimens found during the last sixty years in several Eocene and Oligocene localities in central Patagonia, attributable to other taxa. These remains enlarge the knowledge on Paleogene diversity and distribution of these mammals, and provide new insights into their early evolution and diversification.

2. Geographical, geological, and paleontological settings

The fossil specimens studied herein come from five Paleogene localities from the Chubut Province, central Patagonia: Aguada

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Table 1
Temporal distribution of the pre-Deseadan (Paleocene? to Early Oligocene) astrapothere species. Chronological intervals (columns) are SALMAs, ranging upward from left to right.

	Itaboraian	Riochican	Casamayoran	Mustersan	Tinguirirican	“La Cantera”
<i>Eoastrapostylops</i>		<i>E. riolorensis</i>				
<i>Trigonostylops</i>		<i>Trigonostylops</i> sp.	<i>T. wortmani</i>	<i>T. gegenbauri</i>		
<i>Tetragonsotylops</i>	<i>T. apthomasi</i>		cf. <i>T. apthomasi</i>			
<i>Shecenia</i>			<i>S. ctirneru</i>			
<i>Albertogaudrya</i>			<i>A. unica</i>			
<i>Scaglia</i>			A? <i>carahuasensis</i>			
			<i>S. kraglievichorum</i>			
			cf. <i>S. kraglievichorum</i>			
<i>Antarctodon</i>			<i>A. sobrali</i>			
Astrapotheriidae gen. et sp. 1			X			
<i>Astraponotus</i>				<i>A. assymetrus</i>		
				<i>A. hodichi</i>		
				<i>A. dicksoni</i>		
				<i>A. thompsoni</i>		
				<i>A. dilatus</i>		
<i>Isolophodon</i>			cf. <i>I. cingulosus</i>	<i>I. aplanatus</i>	<i>I. cingulosus</i>	
			<i>I. aplanatus</i>			
<i>Maddenia</i>						<i>M. lapidaria</i>
Astrapotheriidae gen. et sp. 2						X

Based on Simpson (1935, 1957, 1967), Paula Couto, 1963, Carabajal et al. (1977), Soria (1982), Kramarz and Bond (2009), and Bond et al. (2011).

Taxa in bold face are described and discussed in this paper.

Batistín, Cañadón Blanco, Cerro del Humo, and the Gran Barranca South of Colhue Huapi Lake, the latter with two different stratigraphic/faunistic units (La Cantera and Simpson’s “Bed Y”) (Fig. 1). The stratigraphy and paleontology of some of them have been intensively studied over the last decades, whereas those of others have not been re-visited for almost one century, and little information is currently available. Here, we summarize the most relevant geological and geo/biochronological data published for each locality.

2.1. Aguada Batistín

It is located nearly 10 km southeast of Laguna de la Bombilla, Paso de Indios Department, Chubut Province (Pascual, 1965; Fig. 1). The concerned fossils come from pink tuffs and bentonites with abundant siliceous concretions, overlying light cineritic tuffs. The limit between these two units is marked by a regionally continuous bed with abundant scaraboid nests (Pascual, 1965). According to Pascual (1965), both units bear fossil mammals attributable to the Casamayoran SALMA (middle

Late Eocene; Gelfo et al., 2008), but the mammal assemblage from the pink tuffs would represent an evolutionary stage more advanced than the typical Casamayoran one, and would be assigned to an “upper Casamayoran” age (*sensu* Pascual, 1965; see also Marshall, 1982). A revision of all available mammal remains from the pink tuffs exposed at Aguada Batistín (housed at MLP) revealed the occurrence of *Plexotemnus complicatissimus* Ameghino, 1904 (Notoungulata) and *Didolodus multicuspis* Ameghino, 1897 (Condylarthra), previously known as restricted to the Barrancan subage of the Casamayoran SALMA (Gelfo, 2010). The rest of the fauna is composed of taxa previously recorded in both Vacan and Barrancan faunas (e.g., *Amphidolops serrula* Ameghino, 1902a, *Eudolops caroliameghinoi* (Ameghino, 1903), *Didolodus minor* Simpson, 1948, *Notostylops murinus* Ameghino, 1897, *Pleurostylyodon* sp. *Thomashuxleya* sp., *Albertogaudrya* sp.), and one known for Casamayoran and Mustersan faunas (*Poydolops thomasi* Ameghino, 1897). We tentatively attribute the mammal assemblage from the pink tuffs to the Barrancan subage until more geo/biochronological evidences are available.

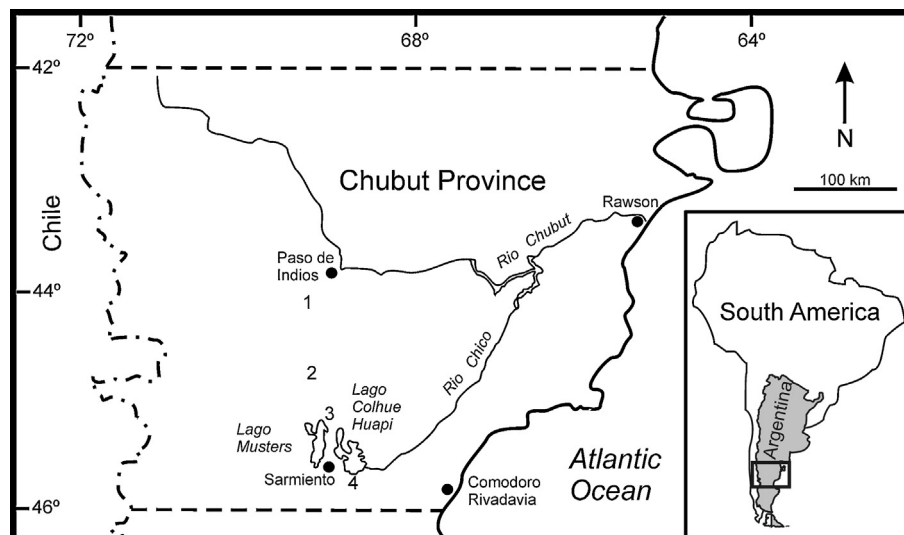


Fig. 1. Location map showing the localities mentioned in the text. 1. Aguada Batistín; 2. Cañadón Blanco (tentative position); 3. Cerro del Humo; 4. Gran Barranca South of Colhue Huapi Lake (“La Cantera” and Simpson’s “Bed Y”).

2.2. Cañadón Blanco

Paleogene mammals from this locality were first reported by Roth (1901, 1903), but precise geographic or geological data were not provided. Reguero (1999: p. 43) deduced that Cañadón Blanco could be located NW of Laguna Palacios in the Paso de los Indios Department, Chubut Province (Fig. 1). The Cañadón Blanco mammal assemblage is temporally equivalent to the Tinguiririca Fauna, and thus attributable to the Early Oligocene (Wyss et al., 1994; see also Reguero, 1993; Hitz et al., 2000).

2.3. Cerro del Humo

Located about 45 km north of Colonia Sarmiento, north of the lakes Colhue Huapi and Musters, Sarmiento Department, Chubut Province (Simpson, 1936; Bond and Deschamps, 2010; Fig. 1). The fossil mammals occur in the lower part of a whitish to greenish gray bentonite bed, overlying a light green tuff and covered by a basaltic bed (Bordas, 1943: fig. 9). Although the top of the Paleogene sequence at Cerro del Humo provided a few mammals assigned to the Deseadan SALMA (e.g., *Helicolophodon giganteus* Roth, 1903), Simpson (1936) assigned the bulk of the fossil-bearing deposits to the Mustersan SALMA (Late Eocene; Ré et al., 2010).

2.4. “La Cantera” (GBV-19)

Located at the west end of Gran Barranca South of Colhue Huapi Lake, Sarmiento Department, Chubut Province (Fig. 1). The fossil-bearing horizon is a 6 m-thick unit of yellowish clay and tuff above a massive, gray tuff and below a thin, hard, orange channel bed within the Puesto Almendra Member of the Sarmiento Formation (Vucetich et al., 2010). The age of these deposits (31.1–29.5 Ma; Ré et al., 2010) as well as their biochronological correlations and stratigraphic position, strongly suggest a post-Tinguirirican–pre-Deseadan age (Madden et al., 2010).

2.5. Simpson’s “Bed Y”

This bed is exposed at the Gran Barranca South of Colhue Huapi Lake, Sarmiento Department, Chubut Province (Fig. 1). This unit is a massive volcanic ash bed included in the Gran Barranca Member of the Sarmiento Formation; it is a continuously-marked bed extending the entire length of Gran Barranca (Simpson, 1941; Ré et al., 2010). It is dated as 40.2–39.4 Ma (Ré et al., 2010). The mammal assemblage of this unit and other fossil-bearing levels of the Gran Barranca Member forms the basis for the recognition of the Barrancan subage of the Casamayoran SALMA (Cifelli, 1985).

3. Systematic paleontology

Order ASTRAPOTHERIA Lydekker, 1894

Family ASTRAPOTHERIIDAE Ameghino, 1887

Genus *Isolophodon* Roth, 1903

Type species: *Isolophodon cingulosus* Roth, 1903

Occurrence: Late Eocene–Early Oligocene, Chubut Province, Argentina.

Diagnosis: lower cheek teeth with a much-reduced hypoflexid, resembling the uruguaytheriines, which are diverging later within Astrapotheriidae (Johnson and Madden, 1997; Kramarz and Bond, 2009). As in *Astraponotus* Ameghino, 1901, cheek teeth with labial and lingual cingulids, higher crowned than in *Albertogaudrya* Ameghino, 1901, but lower than in *Parastrapotherium* Ameghino, 1895 and all the Miocene astrapotheres.

Remarks: this genus erected by Roth (1903) is a very enigmatic taxon, whose validity has not been discussed by subsequent

authors. The general pattern of the known cheek teeth resembles those of the partially coeval *Astraponotus*. The type series of *Astraponotus assymetrus* and of the species of *Notamynus* Roth, 1903, later referred to as *Astraponotus* by Simpson (1967), do not include lower cheek teeth, which impedes making any direct comparison. Nevertheless, *Isolophodon cingulosus* and *Isolophodon aplanatus* differ from all specimens referred to *Astraponotus* preserving lower cheek teeth (Kramarz et al., 2010) in having a more reduced hypoflexid. This striking feature, already noticed by Roth (1903), is the one that typifies the uruguaytheriine astrapotheres (Kraglievich, 1928); it is a synapomorphy of this clade (Johnson and Madden, 1997; Kramarz and Bond, 2009), although no uruguaytheriine had been described at Roth’s times. However, *Isolophodon* lacks all the synapomorphies shared by the uruguaytheriines, astrapotheriines and *Parastrapotherium* (i.e., higher crowned cheek teeth, premolars much more reduced in size and number). Additionally, in most uruguaytheriines the lower cheek teeth lack cingulids (except in the putative uruguaytheriine *Xenastrapotherium aequatorialis* Johnson and Madden, 1997). Moreover, the reduction of the lower premolar hypoflexid also occurs in non-uruguaytheriine astrapotheres (i.e., *Maddenia* Kramarz and Bond, 2009, *Parastrapotherium*, and *Astrapothericulus* Ameghino, 1902b); accordingly, the particular resemblance between *Isolophodon* and the uruguaytheriines is limited to the lower molars. Based on this systematic context, we interpret herein the species of *Isolophodon* as representing an early diverging astrapotheriid lineage in which the reduction of the lower molar hypoflexid developed convergently and much earlier than in the uruguaytheriines. The analysis of the affinities of *Isolophodon* with the remaining astrapotheres is pending on the discovery of more complete and informative materials.

Isolophodon cingulosus Roth, 1903

Fig. 2(A–D)

Syntype: MLP 12-1510, partially restored right mandibular fragment with p3-p4; MLP 12-3163, two right m1 or m2, a portion of an upper canine and a portion of a lower canine (not associated).

Occurrence: Cañadón Blanco, Chubut Province, Argentina; Tinguirirican SALMA (Early Oligocene).

Diagnosis: large-sized astrapotheriid, nearly 30% larger than *Astraponotus assymetrus* Ameghino, 1901; about 15% smaller than *Astrapotherium magnum* (Owen, 1853). p3 and p4 not reduced in size, fully molariform. Lower molars with moderately-developed paralophid; talonid of m1-m2 not elongated.

Description: *Isolophodon cingulosus* was described by Roth (1903) based upon a mandibular fragment with two cheek teeth, an additional mandibular portion (presumably edentulous, at present lost in the MLP Collections) and four isolated teeth. The mandibular fragment bearing two cheek teeth (MLP 12-1510, Fig. 2(A–C)) has preserved the posteriormost portion of the symphysis and a conspicuous mental foramen, both located below the anterior tooth. Available mandibular fragments of *Astraponotus* from Mustersan levels (e.g., MLP 67-II-27-28, MLP 82-V-7-2) bear these features either below or slightly in front the p3. Consequently, the cheek teeth preserved in MLP 12-1510 correspond to p3 and p4. A small portion of the alveolus for p2 is preserved in front of p3, thus the mandible had at least three premolars, in agreement with Roth’s original interpretation. The preserved premolars are subequal, massive, bicrescentic, fully molariform in appearance, with conspicuous labial and lingual cingulids. In both teeth there is a very slight vertical depression on the labial wall between the trigonid and the talonid, representing a vestigial hypoflexid (*sensu* Van Valen, 1966). The only significant difference is the lesser thickness of the trigonid on p3. The premolars of the MLP 12-1510 are structurally similar to those of the Mustersan specimens of *Astraponotus* recently described by Kramarz et al.

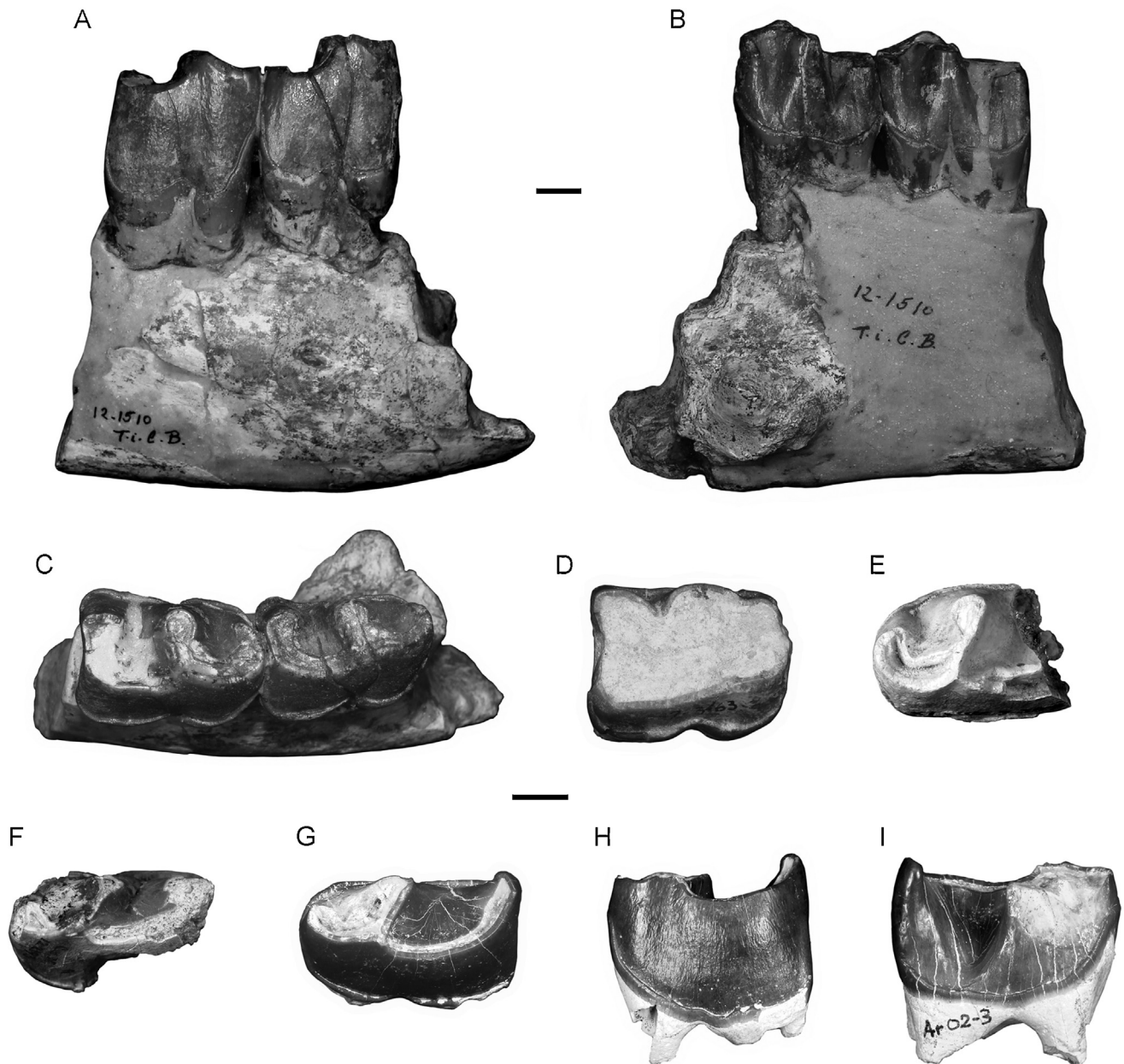


Fig. 2. *Isolophodon* spp. A–C. MLP 12-1510, syntype of *Isolophodon cingulosus* Roth, 1903: partially restored right mandibular fragment with p3-p4 in labial (A), lingual (B), and occlusal (C) views; Cañadón Blanco, Tinguirirican SALMA (Early Oligocene). D. MLP 12-3163, syntype of *Isolophodon cingulosus* Roth, 1903: isolated right m1 or m2; Cañadón Blanco. E. MLP 61-VIII-3-387, cf. *Isolophodon cingulosus*: partial left lower cheek tooth; Aguada Batistin, Casamayoran SALMA (Barrancan? subage). F. MLP 12-2139, Holotype of *Isolophodon aplanatus* Roth, 1903: incomplete left lower molar; Cerro del Humo, Mustersan SALMA. G–I. MPEF PV 7475, *Isolophodon aplanatus* Roth, 1903: left m1 or m2 in occlusal (G), labial (H), and lingual (I) views; Simpson's "Bed Y", Gran Barranca South of Colhue Huapi Lake (Barrancan subage). Scale bars: 1 cm.

(2010), and differ only by being larger and by having a more reduced hypoflexid.

The isolated cheek teeth of the syntype (MLP 12-3163; Fig. 2(D)) were interpreted by Roth (1903) as m1, probably by being slightly larger than the p4 of the MLP 12-1510 (Table 2). These teeth are much more worn than the premolars, and the only preserved occlusal features are a vestigial paraflexid, revealing a moderately-developed paralophid, and a superficial remnant of the metaflexid. They are massive as the premolars, with marked lingual and labial cingulids, and the hypoflexid is strongly reduced, at least in the preserved portion of the labial wall. Except for their size, these teeth are essentially what is expected for the p4 of MLP 12-1510 in a more advanced stage of wear. As for the premolars, the putative molars closely resemble the worn m1 of the

Mustersan specimens of *Astraponotus*, except by being larger and by lacking a hypoflexid. The partial canines of the syntype do not differ from those of the Mustersan specimens either.

Remarks: the available evidences support the assignment of all the teeth included in the syntype to the same species, and the designation of a lectotype seems unnecessary.

cf. *Isolophodon cingulosus* Roth, 1903

Fig. 2(E)

Material: MLP 61-VIII-3-387, a partial left lower cheek tooth.

Occurrence: Aguada Batistin, Casamayoran SALMA (Barrancan? subage).

Description: this tooth preserves the entire trigonid and the anterior portion of the talonid. The preserved part is structurally

Table 2

Compared dental measurements (in cm) for the astrapothere specimens described in the text.

Taxon	Specimen	Locus	MPL	MPW
<i>Isolophodon cingulosus</i>	MLP 12-1510 (Syntype)	p3	3.28	2.29
		p4	3.34	2.46
	MLP 12-3163 (Syntype)	m1 or m2	3.73	2.81
		m1 or m2	3.69	2.79
cf. <i>Isolophodon cingulosus</i>	MLP 61-VIII-3-387	m?	–	2.44
<i>Isolophodon aplanatus</i>	MLP 12-2139 (Holotype)	m1 or m2	4.13	2.47
	MLP 59-II-28-115	m3	5.30	2.47
	MPEF PV 7475	m1 or m2	4.16	2.23
cf. <i>Scaglia kraglievichorum</i>	MLP 59-II-28-37	M1 or M2	–	3.62
Astrapotheriidae gen. et sp. 1	MLP 66-V-4-50	M1 or M2	5.10	4.92
Astrapotheriidae gen. et sp. 2	MPEF PV 6124 MPEF PV 6148 MPEF PV 7694 MPEF PV 7695 MPEF PV 7761	P4?	2.91	4.87
		P4?	3.42	4.97
		P4?	3.50	5.11
		P3?	3.04	4.71
		M1 or M2	4.02	5.04

MPL: maximum preserved length; MPW: maximum preserved width.

similar to the premolars of *I. cingulosus* but larger (Table 2; when complete even longer than the putative molars), lower-crowned, and with a more conical metaconid. These differences suggest that it could belong to a distinct species.

Isolophodon aplanatus Roth, 1903

Fig. 2(F–I)

Holotype: MLP 12-2139, an incomplete left m1 or m2.

Material: MLP 59-II-28-115, an isolated right m3; MPEF PV 7475, an isolated left m1 or m2.

Occurrence: the holotype comes from “Cretácico Superior del Lago Musters” (= Simpson’s (1936) Cerro del Humo Locality), Mustersan SALMA. MLP 59-II-28-115 comes from Aguada Batistín, Casamayoran SALMA (Barrancan? subage); MPEF PV 7475 comes from Simpson’s “Bed Y”, at Gran Barranca South of Colhue Huapi Lake (Barrancan subage), Chubut, Argentina.

Diagnosis: middle-sized astrapotheriid, similar to *Astraponotus asymmetrus* Ameghino, 1901, and about 35% smaller than *Astrapotherium magnum* (Owen). Lower molars with talonid proportionally much more elongated than in *Isolophodon cingulosus* and other astrapotheres. Paralophid reduced, paraflexid absent, unlike *Isolophodon cingulosus*.

Description: this species is based on an isolated partial lower cheek tooth (Fig. 2(F)) interpreted by Roth (1903) as an m3, probably because it has the talonid much more elongated than the trigonid. However, the posterior wall of the teeth is incomplete and the existence of a wear facet for a posterior tooth is uncertain. Here, we assign to *Isolophodon aplanatus* two additional, much better preserved isolated lower cheek teeth. MPEF PV 7475 (Fig. 2(G–I)) is structurally identical to the holotype (talonid much more elongated than the trigonid, paralophid very reduced, hypoflexid absent) and very similar in size (Table 2) and crown height. This tooth shows a small wear facet on the posterior wall for a subsequent tooth, indicating that it does not correspond to an m3. MLP 59-II-28-115 also agrees with the holotype, but the crown is longer (Table 2) and somewhat more massive, the talonid is even more elongated, lacking a wear facet for a posterior tooth, and the posterior root has a small posterior lobe, indicating that it positively corresponds to an m3. Thus, in this species, at least in m2 the talonid is markedly elongated in relation to the trigonid, like the m3 of other species and unlike the m1 or m2 of *Isolophodon cingulosus*. Both in the holotype and in the referred specimens, the paralophid is very short, resembling the condition in *Trigonostylops* Ameghino, 1897, but the metaconid has a very inflated anterolabial base occupying most of the trigonid basin, thus the paraflexid is

entirely obliterated, as in the p3 of *Albertogaudrya*. Contrarily, in the much worn molars of the holotype of *Isolophodon cingulosus* there is still a vestige of the paraflexid, indicating that this valley was not obliterated when less worn. Neither the lower molars of *Trigonostylops* nor those of other known astrapotheriids show the very unusual features observed in *Isolophodon aplanatus*.

Genus *Scaglia* Simpson, 1957

Type species: *Scaglia kraglievichorum* Simpson, 1957.

Occurrence: Middle and Late(?) Eocene (Casamayoran SALMA), Chubut Province, Argentina.

cf. *Scaglia kraglievichorum*

Fig. 3

Material: MLP 59-II-28-37, isolated partial left M1 or M2.

Occurrence: Aguada Batistín, Casamayoran SALMA (Barrancan? subage).

Description: this tooth preserves the entire crown except the parastyle, the posterolabial portion of the ectoloph and the postcingulum. It matches with the M1 of *Scaglia kraglievichorum* in being low-crowned (lower than in *Astraponotus*), in having a

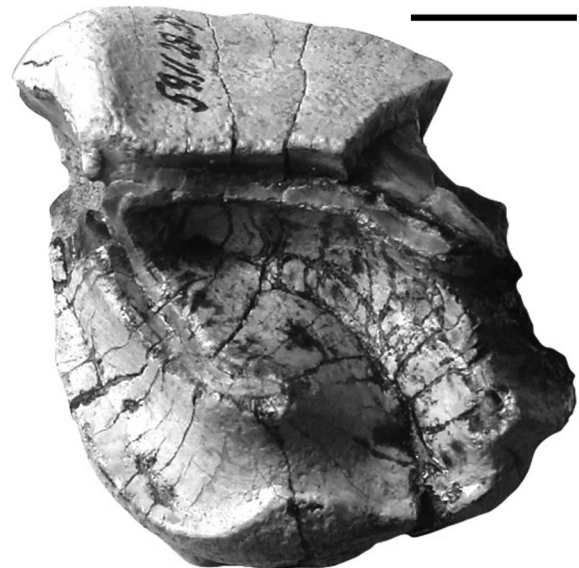


Fig. 3. MLP 59-II-28-37, cf. *Scaglia kraglievichorum* Simpson, 1957: partial left M1 or M2; Aguada Batistín, Casamayoran SALMA (Barrancan? subage). Scale bar: 1 cm.

complete metaloph (unlike *Tetragonostylops* Paula Couto, 1963), and in lacking any trace of accessory crests (i.e., *crista* and *crochet*); it differs in being almost 60% larger (Table 2). Additionally, the labial fold of the paracone is more prominent, the labial cingulum is absent, and the anterolingual cingulum is broader, forming a conspicuous basal shelf in front of the base of the protocone. Besides the size, these subtle differences suggest that this tooth could represent a distinct taxon. This tooth is proportionally smaller than all lower molars here described as *Isolophodon*.

Astrapotheriidae gen. et sp. 1

Fig. 4

Material: MLP 66-V-4-50, isolated left M1 or M2.

Occurrence: Aguada Batistín, Casamayoran SALMA (Barrancan? subage).

Description: the tooth is highly worn; only the base of the crown is preserved and almost all occlusal features are worn away. The width measured at the base of the crown (Table 2) is similar to that of the highly-worn M1 of *Astrapotherium magnum*, and thus larger than any other Eocene astrapothere. The posterior margin is badly preserved and the presence of a wear facet for a posterior tooth is doubtful, although judging by its preserved occlusal contour, it is more likely an M1 or M2 than an M3. At this stage of wear the crown is longer than wide. In contrast, the highly-worn M1 and M2 of all known astrapotheres are wider than long. The crown is trapezoidal in outline; the anterolabial corner of the crown is projected anteriorly due to the presence of the bases of the parastyle and the labial fold of the paracone. The labial cingulum is moderately marked. A very low and broad anterolingual cingulum forms a prominent anterolingual shelf; the extension of this cingulum on the lingual base is not preserved. A remnant of the lingual entrance of the central valley is indicated by a slight inflection of the lingual enamel border. Such lingual inflection is located at the posterior quarter of the lingual wall, more posteriorly than in M1 and M2 of other astrapotheriids, indicating that at least the base of the protocone is much larger than the hypocone.

This tooth is much larger (Table 2) and proportionally much longer than the upper molar MLP 59-II-28-37 from the same locality and level described above as cf. *Scaglia kraglievichorum*. Moreover, it has a conspicuous labial cingulum (absent in the MLP 59-II-28-37) and the anterolingual cingulum is lower.



Fig. 4. MLP 66-V-4-50, Astrapotheriidae gen. et sp. 1: left M1 or M2; Aguada Batistín, Casamayoran SALMA (Barrancan? subage). Scale bar: 1 cm.

Astrapotheriidae gen. et sp. 2

Fig. 5

Material: MPEF PV 7694, right P4?; MPEF PV 7695, incomplete left P3?; MPEF PV 6124, right P4?; MPEF PV 6148, left P4?; MPEF PV 7761, right M1 or M2.

Occurrence: all the specimens come from the Sarmiento Formation, Puesto Almendra Member, “La Cantera” Locality (GBV-19; see Madden et al., 2010 and references therein), Southern cliff of Lake Colhué Huapi (Gran Barranca), Chubut Province, Argentina.

Description: although all these cheek teeth are isolated, they are sub-quadrangular to trapezoidal, low-crowned, three-rooted, wider than long, and similar in size (Table 2), suggesting that all belong to the same taxon. All show wear facets on the anterior and posterior walls, indicating they correspond neither to M3 nor to anterior premolars.

The best preserved and less worn tooth (MPEF PV 7694; Fig. 5(A)) is barely trapezoidal, the parastyle and the paracone fold are well marked, the metacone fold is hardly insinuated, and the metastyle is reduced. A continuous, well-defined labial cingulum rises anteriorly to the base of the parastyle, and posteriorly to the base of the metastyle, passing below the base of the paracone fold. The protoloph is very oblique and short, ending far from the lingual margin of the tooth. The lingual end of the protoloph is slightly forked; the anterior branch is projected anterolingually and probably corresponds to the protocone. A slight anterior inflection is defined between the protoloph and the protocone; this groove becomes deeper to the base, originating a shallow anterolingual

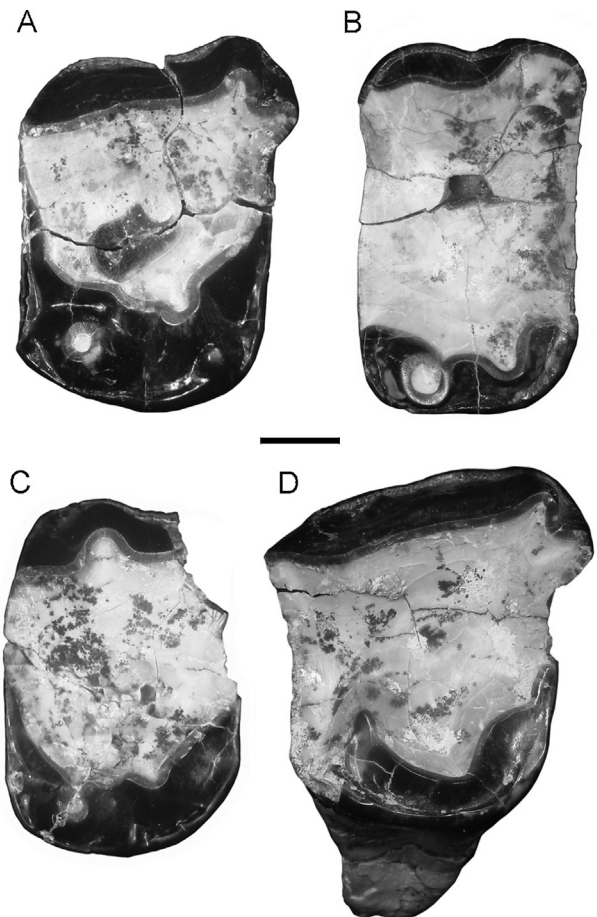


Fig. 5. Astrapotheriidae gen. et sp. 2. **A.** MPEF PV 7694: right P4? **B.** MPEF PV 6124: right P4? **C.** MPEF PV 7695: reversed left P3? **D.** MPEF PV 7761: right M1 or M2. All specimens from “La Cantera” Locality (GBV-19), Sarmiento Formation, Puesto Almendra Member, Gran Barranca South of Colhué Huapi Lake, post-Tinguirirican-pre-Deseadan age. Scale bar: 1 cm.

pocket. A posterior transverse crest (metaloph) departs from the posterior portion of the ectoloph and ends more labial than the protoloph. The end of the metaloph bears an anterolingual projection connecting the posterior branch of the protoloph, probably representing a vestigial postprotocrista, isolating the central valley from the lingual wall. A low, bunoid cusp is located on the posterolingual corner of the tooth, likely corresponding to the hypocone. This cusp is entirely isolated from the metaloph and from the protoloph. A marked continuous cingulum surrounds the anterior, lingual, and posterior base of the crown, running lingually and posteriorly to the base of the hypocone. This cingulum bears a low accessory cusplule located at the anterolingual base of the protocone and a small notch between the protocone and the hypocone. On the posterior wall the cingulum is very low and does not enclose a postfossette.

MPEF PV 6124 and MPEF PV 6148 are more worn than MPEF PV 7694, and, concordantly, the crowns are proportionally shorter (Table 2). MPEF PV 6124 (Fig. 5(B)) preserves the base of the anterior branch of the protoloph and the still isolated hypocone. However, it differs in lacking the accessory cusplule and the notch on the lingual cingulum. Moreover, the lingual cingulum ends at the base of the hypocone, and the posterior cingulum rises to the posterolingual slope of the hypocone, separated from the lingual cingulum. MPEF PV 6148 is similar, but proportionally slightly longer (Table 2); the base of the hypocone is represented by a conspicuous posterolabial fold of the preserved enamel border; the cusp was probably isolated when less worn. In both teeth, the base of the paracone fold is represented by a marked labial emargination of the anterolabial corner; a less prominent fold of the posterior portion of the labial wall likely represents the base of the metacone fold.

MPEF PV 7695 is shown reversed in Fig. 5(C) for better comparisons with the remaining teeth. This tooth is somewhat smaller than the remaining ones (Table 2), and the lingual corners are more rounded. The orientation of this tooth is problematic because the crown is incomplete and both lingual corners bear marginal pockets (only an anterolingual pocket is the usual condition in upper cheek teeth of astrapotheres). The labialmost cusp (at the left lower angle of the crown in Fig. 5(C)) can be interpreted as the hypocone. Alternatively, this cusp could be equivalent to the accessory cusplule at the anterolingual base of the protocone of MPEF PV 7694 (Fig. 5(A)), but much enlarged. However, this latter interpretation is less likely to us. Additionally, a very prominent fold is located near the center of the labial wall, separated from the only preserved labial corner (left upper corner in Fig. 5(C)). This corner shows no trace of a labial style. This disposition suggests that this corner is the posterior one, and that the fold corresponds to the metacone. Following these interpretations, the MPEF PV 7695 is a left upper tooth (shown as right in Fig. 5(C)). The hypocone is hardly isolated from the metaloph in this stage of wear. A moderate folding of the preserved anterolingual enamel margin represents the lingual slope of the protocone (probably equivalent to the anterior branch of the protoloph of MPEF PV 7694). The central valley is entirely worn away. A short enamel wall connects the protocone with the point uniting the hypocone and the metaloph, indicating that the central valley was isolated from the lingual wall, as in MPEF PV 7694. There is a continuous anterolingual-posterolingual cingulum, only interrupted by a superficial notch between the protocone and the hypocone. The cingulum encloses a deep pocket at the anterolingual base of the protoloph (although there is no anterolingual inflection of this crest) and a smaller, posterolingual pocket between the hypocone and the metaloph.

MPEF PV 7761 (Fig. 5(D)) is highly worn and almost all occlusal features are missing. However, it differs from the teeth described

above in having a more trapezoidal contour, more developed metastyle, and much more reduced labial fold of the metacone. Additionally, the preserved lingual enamel margin shows a conspicuous, transverse unfolding penetrating almost one third of the width of the occlusal surface. This structure clearly corresponds to the hypoflexus, much more penetrating than in the remaining teeth, and suggests that the central valley opened on the lingual wall. The hypoflexus is located much closer to the posterior than to the anterior margin, indicating that the hypocone is smaller than in the other teeth. The area of the hypocone is extremely worn, making impossible to determine whether the cusp was isolated. The cingula are well marked; the labial is as in MPEF PV 7694, the anterolingual is somewhat broader and lacks the lingual notch and accessory cusps. The anterolingual inflection of the protoloph is less marked and the anterolingual pocket is much shallower.

Remarks: Assuming that all these isolated cheek teeth belong to a single species, their position in the tooth row can be interpreted by comparison with other basal astrapotheriids. MPEF PV 7761, with well-developed metastyle and hypoflexus, is very probably a molar, and shows no significant differences with the worn M2 of *Astrapotonotus* described by Kramarz et al. (2010). It only differs from it because it is slightly larger and the cingula are more elevated and broader. MPEF PV 7694, with a reduced metastyle and isolated central valley, is likely to be a posterior premolar. MPEF PV 6124 and 6148 are probably posterior premolars as well. At least the former partially resembles the P4 of *Maddenia* (Kramarz and Bond, 2009), but in the latter genus the hypocone is less bunoid, entirely integrated to the posterior cingulum, and connected to the metaloph. Moreover, *Maddenia* lacks the additional anterolingual cusplule and the cingula are less marked. In *Albertogaudrya*, P4 is even less molariform, the hypocone is represented by a moderate elevation of the posterolingual cingulum, and the metacone fold is much more conspicuous. The only known P4 referred to *Astrapotonotus* (Kramarz et al., 2010: fig. 4) is as worn as MPEF PV 6148, and all the occlusal features are worn away; nevertheless, the preserved enamel margin shows no evidence of an enlarged hypocone, or at least not as much as in MPEF PV 6148. The P4 of other astrapotheres is not molariform and lacks a hypocone. MPEF PV 7695, with more rounded outline and more developed metacone fold, resembles the P3 of *Astrapotonotus* and *Maddenia*, but differs in the same characters mentioned for P4.

4. Discussion and conclusions

4.1. The status and significance of *Isolophodon*

The species of *Isolophodon* described by Roth (1903) were ignored by subsequent authors and excluded from most taxonomic lists, except for that of Flynn et al. (2003). Here, we consider that both *I. cingulosus* and *I. aplanatus* are valid species and that they may represent an early diverging lineage within Astrapotheriid, already represented in Barrancan beds, which evolved convergently with the more derived uruguaytheriines. The syntypes and known specimens of *I. cingulosus* all come from Paleogene beds at Cañadón Blanco, Central Patagonia – the inclusion of *I. aplanatus* within the Cañadón Blanco faunal list by Flynn et al. (2003: table 2) is clearly a mistake. The Cañadón Blanco mammal assemblage is biochronologically equivalent to the Tinguiririca Fauna (Wyss et al., 1994; see also Reguero, 1993; Hitz et al., 2000), where no astrapotheres remain had been reported yet. Therefore, *I. cingulosus* is the only known astrapothere attributable to the Tinguirirican SALMA, which accordingly fills the Early Oligocene gap of the record of the Order Astrapotheria.

4.2. On *Scaglia-like* *astrapotheres*

Other remains here examined enlarge the known diversity of Paleogene *astrapotheres*. The isolated upper molar MLP 59-II-28-37 described above as cf. *Scaglia kraglievichorum* shows the same general pattern as the type of *Scaglia kraglievichorum*. Nevertheless, it exhibits sufficient differences to be included in a separate species, although the formal nomination is pending on the availability of more complete material. Simpson (1957, 1967) described *S. kraglievichorum* as a basal *astrapotheriid* and interpreted the molar pattern of this species as structurally ancestral to *Astrapotonus* and all the later *astrapotheres*. The species represented by MLP 59-II-28-37 reveals that *astrapotheriids* with a primitive molar pattern experienced at least a moderate diversification apart from evolving to forms with a more derived molar pattern.

4.3. The age of *Astrapotheriidae* gen. et sp. 2

The dental loci of the isolated cheek teeth described herein as *Astrapotheriidae* gen. et sp. 2 are doubtful, but whatever their proper allocations, they show sufficient distinct features from all other known *astrapotheres* to be interpreted as a new taxon. Madden et al. (2010: p. 430) mentioned these specimens as belonging to “*Astrapotheriinae* comparable to *Parastrapotherium*”; although these authors reported this taxon for “La Cantera” locality, they suggest that these remains could have derived from younger mammal-bearing levels (i.e., Deseadan and Colhuehuapian) also exposed at Gran Barranca. We interpret that the cheek teeth of *Astrapotheriidae* gen. et sp. 2 differ radically from those of all the *astrapotheres* reported from Deseadan and Colhuehuapian levels (*Parastrapotherium*, *Astrapotherium*, and *Comahuetherium* Kramarz and Bond, 2011), and only resemble the more derived *astrapotheriids* by their comparatively large size. Additionally, the kind of preservation of these teeth is identical to that of the type of *Maddenian lapidaria* Kramarz and Bond, 2009 (recovered *in situ* at GBV-19), and very different from those of all *astrapotheres* from Deseadan and Colhuehuapian beds at Gran Barranca. Consequently, *Astrapotheriidae* gen. et sp. 2 positively derives from “La Cantera” locality at Gran Barranca and belongs to a pre-Deseadan Age.

4.4. The biggest Eocene South American mammal?

The isolated upper molar MLP 66-V-4-50 (*Astrapotheriidae* gen. et sp. 1) from putative Barrancan levels belongs to a large *astrapothere*, probably as large as the Santacrucian *Astrapotherium magnum*, whose estimate body mass ranges between 921 kg (Cassini et al., 2012) and 2094 kg (Kramarz and Bond, 2011). The partial lower cheek tooth MLP 61-VIII-3-387, described above as cf. *Isolophodon cingulosus*, is from the same locality and level, and probably equivalent in size. Their assignment to the same taxon is highly speculative, and we preferred describing them separately. In any case, these specimens document the occurrence of very large *astrapotheres* during the Middle Eocene in Patagonia, and probably the largest Eocene South American mammals known so far.

Acknowledgements

We thank M. G. Vucetich (MLP) and R. Madden (Duke University) for allowing us to study the material collected during the MLP – Duke University expeditions to Patagonia funded by the US National Science Foundation and Consejo Nacional de Investigaciones Científicas y Técnicas (Argentina). We also thank M. Reguero (MLP) and E. Ruigómez (MPEF) for access to collections under their care, and E. Bellosi (MACN) for valuable information on

the Gran Barranca stratigraphy. We acknowledge the reviewers E. Cerdeño and P.O. Antoine for their useful suggestions to improve the manuscript.

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