

## 12 Colhuehuapian Astrapotheriidae (Mammalia) from Gran Barranca south of Lake Colhue-Huapi

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### Abstract

In this contribution the taxonomic status of the numerous astrapothere species described by Ameghino for his *Colpodon* beds (Colhuehuapian) are revised, and the diversity and distribution of the Colhuehuapian astrapotheres are examined in light of new and more complete material, and with more precise stratigraphic information. The new material discussed here comes from the Lower Fossil Zone of the Colhue-Huapi Member of the Sarmiento Formation; previously described material is known of presumed to have come from this same level and belongs to the Colhuehuapian SALMA, the *Colpodon* beds of Ameghino. The Lower Fossil Zone is dated to early Miocene, about 20 Ma from radiometric and magnetic polarity data (Ré *et al.* Chapter 4, this book).

Our revision reveals the certain presence of three species: *Astrapotherium? ruderarium* (Ameghino 1902), *Parastrapotherium symmetrum* (Ameghino 1902), and *Parastrapotherium martiale* Ameghino 1901 (the latter also known from the older Deseadan SALMA). *Parastrapotherium herculeum* may represent a fourth very large species but the type material of Ameghino (1889), supposed to come from Colhuehuapian beds, cannot be located, and no available specimen can be certainly referred to it. Finally, a single upper canine seems to represent a fifth unnamed species, perhaps a uruguaytheriine astrapothere. Examination of old and new collections suggests that *Astrapothericulus* is not recorded at these levels, although the genus does occur at other Colhuehuapian localities.

The following names are brought into synonymy with *Astrapotherium? ruderarium*:

*Parastrapotherium paucum* Ameghino 1902

*Parastrapotherium crassum* Ameghino 1902 (*partim*)

*Astrapothericulus minusculus* Ameghino 1902

*Astrapothericulus laevisculus* Ameghino 1902

*Astrapotherium triangulidens* Ameghino 1902

*Prochalicotherium patagonicum* Ameghino 1902

*Astrapotherium? ruderarium* is the only recognized species of *Astrapotherium* in the Colhuehuapian Age.

*The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*, eds. R. H. Madden, A. A. Carlini, M. G. Vucetich, and R. F. Kay. Published by Cambridge University Press. © Cambridge University Press 2010.

*Astrapotherium? ruderarium* also is the most abundant astrapothere in Colhuehuapian levels of Gran Barranca.

### Resumen

En esta contribución se revisa el status taxonómico de las numerosas especies de astrapoterios descritos por Ameghino para sus capas con *Colpodon* (Colhuehuapense) y se examina la diversidad y la distribución de los astrapoterios colhuehuapenses a la luz de nuevos y más completos materiales y con información estratigráfica más precisa. El nuevo material discutido aquí proviene de la *Lower Fossil Zone* del Miembro Colhue-Huapi de la Formación Sarmiento; el material descrito previamente se presume como proveniente de este mismo nivel y corresponde a la Edad Colhuehuapense, las Capas con *Colpodon* de Ameghino. La *Lower Fossil Zone* está asignado al Mioceno temprano, aproximadamente 20 Ma. a partir de datos radiométricos y polaridad magnética. Nuestra revisión revela la presencia certera de tres especies: *Astrapotherium? ruderarium* (Ameghino 1902), *Parastrapotherium symmetrum* (Ameghino 1902), y *Parastrapotherium martiale* Ameghino, 1901 (el último también conocido para la inmediatamente más antigua Edad Deseadense). *Parastrapotherium herculeum* puede representar una cuarta especie muy grande, pero el material tipo de Ameghino, supuestamente proveniente de capas colhuehuapenses, no pudo ser localizado, y ningún ejemplar disponible pudo ser referido a ésta con certeza. Finalmente, un canino superior aislado parece representar una quinta especie innominada, tal vez un astrapoterio uruguayterino. El examen de viejas y nuevas colecciones sugiere que *Astrapothericulus* no se registra en estos niveles, aunque el género ocurre en otras localidades colhuehuapenses.

Los siguientes nombres son pasados a sinonimia con *Astrapotherium? ruderarium*:

*Parastrapotherium paucum* Ameghino 1902

*Parastrapotherium crassum* Ameghino 1902 (*partim*)

*Astrapothericulus minusculus* Ameghino 1902

*Astrapothericulus laevisculus* Ameghino 1902

*Astrapotherium triangulidens* Ameghino 1902

*Prochalicotherium patagonicum* Ameghino 1902

*Astrapotherium? ruderarium* es la única especie reconocida de *Astrapotherium* en la Edad Colhuehuapense.

*Astrapotherium? ruderarium* también es el astrapoterio más abundante en los niveles colhuehuapenses de Gran Barranca.

## Introduction

Astrapotheriidae (*sensu* Cifelli 1993) is the most derived family within the Order Astrapotheria, an extinct group of herbivorous South American land mammals (Scott 1937). The family is among the largest and most specialized mammals among the Tertiary native faunas. Their stratigraphic range is from the Mustersan (late Eocene) to the Laventan SALMA (middle Miocene) (Soria 1984; Cifelli 1993; Johnson and Madden 1997). Ameghino (1899, 1902) described eight species for his “couches à *Colpodon*” at the Gran Barranca south of Lake Colhue-Huapi (Colhuehuapian SALMA, early Miocene: Flynn and Swisher 1995; Ré *et al.* Chapter 3, this book), which range in from the size of a living Neotropical peccary to as large as an African rhinoceros. He grouped these species in the genera *Parastrapotherium*, *Astrapotherium*, and *Astrapothericulus*. On this basis, it is traditionally accepted that there are three Oligocene to Miocene Patagonian genera and that they co-occur during the Colhuehuapian Age (Scott 1937; Pascual and Odreman Rivas 1971; Marshall *et al.* 1983; Pascual *et al.* 1996; Johnson and Madden 1997). Unfortunately, most of the Colhuehuapian species described by Ameghino (1902) are based on fragmentary dental remains, which are not directly comparable.

Museo de La Plata – Duke University expeditions to Gran Barranca provide new specimens of Colhuehuapian astrapotheriids. These materials complement the abundant and more complete materials recovered by the Muséum National d’Histoire Naturelle (1899), Field Museum of Natural History (1923–24), and American Museum of Natural History (1930) expeditions to Gran Barranca, as well the specimens collected by A. Bordas (1940–41), and A. Castellanos (1944). In this contribution the astrapotheriids that come from Colhuehuapian levels at Gran Barranca are analyzed, the status of the species previously described for these beds is evaluated, and the diversity of the Colhuehuapian astrapotheres is re-examined.

## Institutional abbreviations

AMNH, American Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”; MLP, Museo de La Plata (Argentina); MPEF, Museo Paleontológico “Egidio Feruglio” (Trelew, Chubut Province, Argentina); MUFYCA, Museo Universitario “Florentino y Carlos Ameghino” (Rosario, Argentina); MNHN, Muséum National d’Histoire Naturelle (Paris, France); FMNH, Field Museum of Natural History (Chicago, USA); YPM PU, Yale Peabody Museum, Princeton University (New Haven, USA).

## List of specimens used for comparisons

- (1) *Parastrapotherium holmbergi* Ameghino: MACN A 52–509, MACN A 52–504, MACN A 52–515, MACN A 52–518 (Syntypes), and additional materials from the Deseadan La Flecha locality, Santa Cruz Province, (MLP 95-III-10–74, 95-III-10–90, and 95-III-10–103; FMNH 13329, 13343, 13354, 13364, 13365, 13369, 13462, 13473, 13491, 13492, and 13579).
- (2) *Parastrapotherium martiale* Ameghino: MACN A 52–604 (Holotype) and additional materials from the Deseadan beds of the Upper Puesto Almendra Member (Sarmiento Formation) at Gran Barranca (MLP 93-XI-18–41, 93-XI-18–45, 93-XI-18–43, 93-XI-18–42, 93-XI-18–9, 93-XI-18–39, 93-XI-18–10, 93-XI-18–14, 93-XI-18–30, 93-XI-18–40, 93-XI-18–7, and 93-XI-18–5; MPEF PV 7129, 7133, 7135, 7128, and 7807; AMNH 29565; FMNH 13427, 13428, and 13529).
- (3) *Astrapothericulus iheringi* Ameghino: MACN A 52–408 to 414, 52–417, 52–419, 52–421, 52–422, and 52–605 (Syntypes) and abundant additional materials from the Pinturas Formation, Santa Cruz Province, at the MACN.
- (4) *Astrapotherium magnum* (Owen): MACN A 3207 (Ameghino 1894, Fig. 20), 3210, 3214, 3216–3220, 3296, 3279–3281, 3295–3298, 8580–8581, 8603, 11250 (Ameghino 1904, Fig. 226); MACN PV 14512; AMNH 9278 (Scott 1928, plates, 13–14); FMNH 13170, 13173, 14251, 14259; YPM PU 15142, 15332 (Scott 1928, plate 14). These materials were referred to this species following interpretations provided by Ameghino (1894).

## Systematic paleontology

Order ASTRAPOTHERIA Lydekker 1894

Family ASTRAPOTHERIIDAE Ameghino 1887

Genus *Parastrapotherium* Ameghino 1895

**Type species** *Parastrapotherium holmbergi* Ameghino 1895

**Distribution** Argentina. Late Oligocene to early Miocene.

***Parastrapotherium symmetrum* (Ameghino 1902) nov. comb.**

Fig. 12.1A, A’.

*Astrapotherium? symmetrum*; Ameghino 1902

**Holotype** MACN A 52–507a, an isolated lower incisor.

**Referred material** MPEF PV 7923, an isolated lower incisor.

**Diagnosis** Similar in size to *Parastrapotherium holmbergi*. Incisors with a prominent medial longitudinal crest on the lingual face.

**Provenance** According to Ameghino (1902), the holotype comes from the “*Colpodon* beds” at the

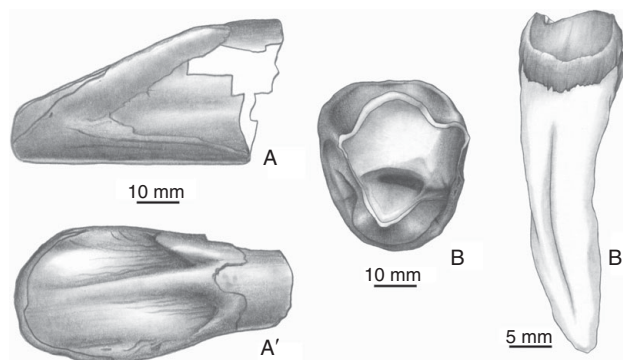


Fig. 12.1. *Parastrapotherium* spp. from Colhuehuapian beds at Gran Barranca. *P. symmetrum* (Ameghino, 1902), MACN A 52–507a, (holotype), incisor in (A) lateral view, (A') lingual view. *?P. herculeum* (Ameghino, 1899), MACN A 52–516a, left P3 in (B) occlusal view, (B') labial view.

Gran Barranca south of Lake Colhue-Huapi, Chubut Province, Argentina. The only referred specimen comes from the Lower Fossil Zone (Gran Barranca Colhuehuapian West locality, Level B), Colhue-Huapi Member of the Sarmiento Formation (Spalletti and Mazzoni 1979; Bellosi this book).

**Comments** The diagnostic character of this incisor (Fig. 12.1), already indicated by Ameghino (1902), is distinct from those of all the remaining astrapotheres and justifies its specific distinction: the wear produces a regular curve around the tip and most of the sides of the crown, unlike the other species. As in *Parastrapotherium holmbergi* and *P. martiale*, the base of the crown of this incisor is bucco-lingually much broader than in the species of *Astrapotherium*, and therefore it is herein transferred to the genus *Parastrapotherium*. Ameghino also assigned to this species an isolated upper premolar (MACN A 52–507b) that he interpreted as a P3, pointing out that the crown have quadrangular contour and fused roots. However, this tooth is a P4, as evidenced by the presence of a wear facet on the anterior face for the P3. This tooth has very prominent labial fold and styles, as typically in the species of *Astrapotherium*, but lacks a cingulum at the base of the labial fold, as in the species of *Parastrapotherium*. Moreover, this tooth is not physically associated to the type material (Ameghino, 1902), and there is no other evidence to refer it to *P. symmetrum*.

*Parastrapotherium herculeum* Ameghino 1899 nov. comb.

Fig. 12.1B, B'.

*Astrapotherium herculeum* Ameghino 1899

*Parastrapotherium herculeum* (Ameghino 1901)

*Astrapotherium herculeum* Ameghino 1901, Ameghino 1902

**Comments** Ameghino (1899) based this species upon a mandibular fragment with p3–m3, a lower canine, and a P4. According to Ameghino (1899), the type materials come from “la Formación Patagónica del interior del Deseado y del Lago Musters” (Colhuehuapian or Astrapothericulan). In 1902 he described new materials as coming from his “couches à *Colpodon*” (but see below), suggesting that the type material comes from the same horizon. The type materials of *Astrapotherium herculeum* are not found in the paleontological collections of MACN, but according to the original description (Ameghino 1899) this species has two permanent lower premolars, thus the more proper generic assignment is to *Parastrapotherium*, a conclusion later arrived at by Ameghino (1901). In his original description, Ameghino (1899) did not indicate any specific diagnostic features of this taxon, other than to note that this is a very large species. Indeed, the measurements given by Ameghino (1899) for the m3 and for the complete p3–m3 length reveal that it is significantly larger than *P. martiale* and *P. superabile* (the largest Deseadan species of *Parastrapotherium*; see Table 12.1). Later, Ameghino (1902) described the P4 included in the type series, pointing out that it differs from other species by having fused tooth roots. However, this condition (also present in the premolars of the types of the Deseadan species *Parastrapotherium holmbergi* and *Traspoatherium convexidens*) could be merely individual variation, as Loomis (1914) contends, and the characters indicated of the crown do not differ from those observed in the P4 of *P. superabile*. Moreover, the size of this P4 is proportionally smaller than the lower teeth of the type series of *P. herculeum*, and they could not be conspecific. In 1902 Ameghino described several isolated incisors (MACN A 25–516b) and an isolated P3 (MACN A 25–516a). The incisors do not differ significantly from those of *P. martiale*; they are herein included in the list of specimens referred to the latter species (see below). We agree that the P3 should be referred to *P. herculeum*. The tooth has fused roots, as does the P4 of the type series (see Fig. 12.1B, B'). The ectoloph shows a conspicuous wear facet on the labial side from occlusion with the p3 (a tooth that is absent in *Astrapotherium*). MACN A 25–516a has a continuous labial cingulum at the base of the labial wall, as in the species of *Astrapotherium*, but the base of the fold is very broad and little prominent, as in *P. holmbergi* and *P. martiale*. This particular combination of characters, not noted by Ameghino (1899, 1902) for the P4 of the type series, is not observed in upper premolars of other known astrapotheriids. Following

Table 12.1. Dental measurements (in cm) for *Parastrapotherium herculeum* (after Ameghino, 1899), from the Gran Barranca south of Lake Colhue-Huapi, Colhuehuapian SALMA, and *Parastrapotherium martiale*, Deseadan and Colhuehuapian? SALMAs

	Parastrapotherium martiale			
	MACN 52–604 (Holotype)	MNHN COL 1 (Colhuehuapian?)	MLP 93-XI-18–14 (Deseadan)	MPEF 6693 (Deseadan)
m3 APL	10	8.1	8.2	–
p3–m3 length	28	23.8	–	–
Lower canine width	10	6.2	7.6	6.9

Note: APL, anteroposterior length.

Ameghino's proposal, this P3 is tentatively referred to *P. herculeum*.

Because it is impossible to compare the type specimens with the other species, we provisionally accept the validity of *Parastrapotherium herculeum* as a species distinct from other *Parastrapotherium*, the only diagnostic feature being its significantly larger size than the remaining species of *Parastrapotherium*. The possibility that the type of *P. herculeum* is an extreme variant of *P. martiale* should continue to be considered.

*Parastrapotherium martiale* Ameghino 1901

**Referred materials from Colhuehuapian levels at Gran Barranca** MACN A 52–516b, seven isolated incisors; MACN Pv 12833, an incomplete P4; MPEF PV 7924, an incomplete incisor and fragment of lower molar (not associated); MPEF PV 7333, an isolated p4; MPEF PV 5500, a maxillary fragment with left P3, M1–3, and right P3; MNHN COL 1, both mandibular rami with canines, roots for p3, p4–m3; MNHN COL unnumbered, an isolated left M3.

**Remarks** *Parastrapotherium martiale* is a typical Deseadan species (Ameghino 1900–02), and it is also well represented at Deseadan levels at Gran Barranca. According to a recent revision of *Parastrapotherium* (Kramarz and Bond, in press) *P. martiale* is the largest Deseadan species of the genus, but neither the type (MACN A 52–604, jaw and palate with an almost complete dentition) nor the referred Deseadan specimens are as large as *P. herculeum*. We herein refer to *P. martiale* those specimens described by Ameghino (1902) as *Astrapotherium herculeum*, but not included in the type series, that match in size with *P. martiale*. Similarly, the MNHN specimens from Gran Barranca (collected by Tournouër) catalogued as *Astrapotherium herculeum*, match in size and morphology with the type of *P. martiale* (see Table 12.1). The stratigraphic level of Ameghino's

specimens from Gran Barranca is unknown. On the contrary, the MNHN specimens almost surely are derived from Colhuehuapian levels (Gaudry 1906). Similarly, the more recently collected MPEF specimens (PV 7924, 7333, and 5500) come positively from the Lower Fossil Zone, Colhue-Huapi Member of the Sarmiento Formation. The survival of this species into the Colhuehuapian is also documented in levels of equivalent age of the Cerro Bandera Formation at Neuquén Province (Kramarz et al. 2005).

Genus *Astrapotherium* Burmeister 1879

**Type species** *Astrapotherium magnum* (Owen 1853)

**Distribution** Argentina and Chile. Early to middle Miocene.

*Astrapotherium?* *ruđerarium* (Ameghino 1902)

Fig. 12.2.

*Parastrapotherium ruđerarium* Ameghino 1902

*Parastrapotherium paucum* Ameghino 1902

*Parastrapotherium crassum* Ameghino 1902 (*partim*)

*Astrapothericulus minusculus* Ameghino 1902

*Astrapothericulus laevisculus* Ameghino 1902

*Astrapotherium triangulidens* Ameghino 1902

*Prochalicotherium patagonicum*; Ameghino 1902

**Lectotype** MACN A 52–524, a right mandibular fragment with dp3–dp4, the posterior portion of m1, a complete m2, and erupting m3 (Fig. 12.2).

**Types in synonymy** MACN A 52–525 (syntype of *Parastrapotherium paucum*), three incisors and two isolated cheek teeth; MACN A 52–512 (holotype of *Astrapothericulus laevisculus*), probably associated dp4, four deciduous incisors, a fragment of a lower canine, and a fragment of an upper canine; MACN A 52–511 (holotype of *Astrapothericulus minusculus*), probably associated DP3, two deciduous incisors, a fragment of a lower canine and a fragment of dp3; MACN A 52–521 (syntype of *Parastrapotherium crassum*), a right mandibular ramus with erupting

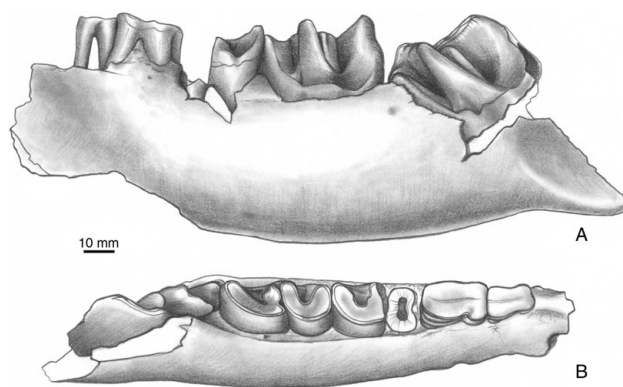


Fig. 12.2. *Astrapotherium? ruderarium* (Ameghino, 1902) MACN A 52-524, lectotype, right mandibular fragment with dp3-m3 in (A) lingual view, (B) occlusal view.

p4 and m1, an associated lower canine; an m2, two P4s, and one M2 of different individuals; MACN A 52-523 (type of *Astrapotherium triangulidens*), two probably associated fragments of upper canines; MACN A 52-337 (lectotype of *Prochalicotherium patagonicum*), an isolated right P4.

**Remarks** Although all the species here are referred to *Astrapotherium? ruderarium* were described in the same contribution (Ameghino 1902), we consider *Parastrapotherium ruderarium* the senior synonym because it is the species based on more complete materials and with verifiable diagnostic characters.

**Referred material** MACN A 52-513 (syntype of *P. ruderarium*), a P4 and two incisors; MACN A 52-522 (syntype of *P. ruderarium*), a fragment of an upper canine, p4, m1, m2, three incisors, a fragment of a lower juvenile canine, an M1, an M2, an M3, and an astragalus; MACN A 52-514d, an isolated m2; MACN A 52-520, a right mandibular ramus with dp4-m2 and alveoli for dp2?, dp3, and m3; MACN A 52-519a, two isolated p4s, two P4s and a lower molar; MACN Pv 11244, one lower molar and three fragments of upper molars; MACN Pv 12830a, two fragments of upper canines and three fragments of lower canines; MACN Pv 12829b, five isolated incisors; MACN Pv 12831a, an isolated m2; MACN Pv 14543, a right mandibular ramus with m2, three fragments of upper molars, three incisors, two fragments of lower canines, and one fragment of an upper canine; FMNH 13307, both mandibular rami with p4-m3; FMNH P13426, mandible with a complete dentition; FMNH P13429, a partial skull with C, P3, DP4, M1-2, and erupting M3; AMNH 29716, a juvenile mandible with c1, dp3-dp4, m1-2, and encrypted p4 and m3; AMNH 29717, an associated left mandibular ramus with m1-3 and right mandibular ramus with

m2-3; AMNH 29720, a left maxillary fragment with M1-3; AMNH 29723, a right maxillary with P4-M1, a left maxillary with P3-M2, and an upper canine; AMNH 29724, a palate with right P3-M3, left P3, M2-3 and a canine; MPEF PV 1134, an isolated lower canine; MPEF PV 1135, isolated upper canine; MPEF PV 1276, isolated M2; MPEF PV 5656, three isolated incisors; MPEF PV 7915, both maxillaries with a complete dentition and both mandibular rami with, c, p4-m3, and two incisors; MPEF PV 7918, an associated incisor, two lower molars, and one incomplete upper molar; MPEF PV 7919, an associated left M1 and M2; MPEF PV 7920, two fragments of upper canines, two fragments of lower canines, three incisors, a DP4, a P4, an incomplete upper molar, and an incomplete lower molar; MPEF PV 7921, a left maxillary fragment with DP4, M1, M2, P3, and an erupting P4; MPEF PV 7922, an associated right and left DP3, left DP4, two deciduous incisors, right dp3-dp4, left dp2-dp4, and several fragments of skull; MPEF PV 5635, an isolated ?m1; MLP 93-XI-18-4, a left lower molar; MLP 93-XI-18-23, an isolated left P4; MLP 93-XI-18-35, an incomplete left upper molar; MUFYCA 803, both mandibular rami with m1-3.

**Diagnosis** An astrapotheriid slightly larger than *Astrapothericulus iheringi*, nearly 25% smaller than *Astrapotherium magnum* and *Parastrapotherium holmbergi*. Permanent dental formula as in the species of *Astrapotherium* and *Astrapothericulus*. Cheek teeth comparatively lower crowned than in *Astrapotherium magnum*, but higher than in *Parastrapotherium holmbergi*. Basal cingula of all cheek teeth less prominent than in *Astrapothericulus iheringi*. Upper premolars with labial fold more prominent and with a narrower base than in *Parastrapotherium holmbergi*, and with cingulum present at the base of this fold, as in *Astrapotherium magnum* and *Astrapothericulus iheringi*. Upper molars with an anterolingual pocket less marked than in *Astrapothericulus iheringi*. Incisors broader and with more robust roots than in *Astrapothericulus iheringi*. The p4 with a labial flexid, thought not as penetrating as in *Astrapotherium magnum*. Lower molars with well-developed hypoflexids and lingual cingula present at the bases of the metaconids, as in *Astrapotherium magnum* and *Astrapothericulus iheringi*. The ever-growing upper canines have smooth enamel covering the lateral walls up to the base of the tooth. The lower canines are more robust than in *Astrapothericulus iheringi* and with more convex lingual wall than in other Astrapotheriidae.

**Geographic and stratigraphic provenance** According to Ameghino (1902) all the MACN

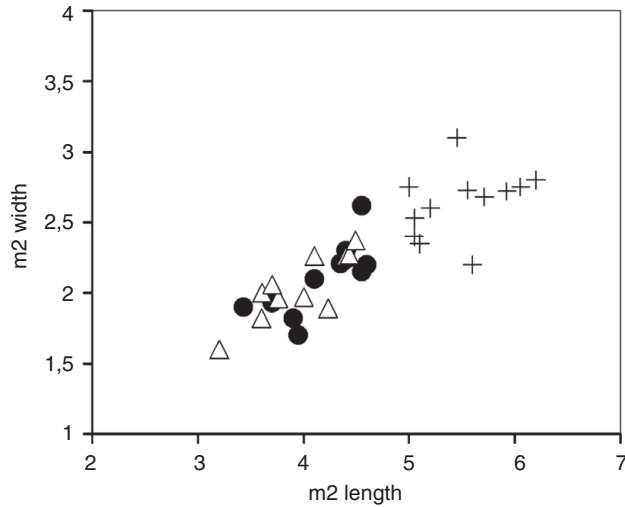


Fig. 12.3. Bivariate plot of m2 crown length and width (in cm) for *Astrapotherium? ruderarium* (circles), from the Gran Barranca south of Lake Colhue-Huapi (Colhuehuapian SALMA), *Astrapothericulus iheringi* (triangles), and *Astrapotherium magnum* (plus signs). Measured specimens of *Astrapotherium? ruderarium*: MACN A 52–514, 52–520, 52–521, 52–522, 54–524, MACN Pv 12831a, 14543, MUFYCA 803a, MPEF PV 7915, FMNH P13426, AMNH 29717. Measurements for *Astrapothericulus iheringi* taken from MACN specimens; for *Astrapotherium magnum* taken from FMNH, AMNH, YPM PU, and MACN specimens.

A specimens are from the “*Colpodon* beds” at the Gran Barranca south of Lake Colhue-Huapi. The MLP specimens, MPEF PV specimens, AMNH 29716, 29717, 29720, and FMNH 13426, 13429 come from the Colhue-Huapi Member, Lower Fossil Zone (Colhuehuapian) at Gran Barranca. MACN Pv 14543, 11244, 12830a, 12829b, 12831a, AMNH 29724, 29723, FMNH 13307, and MUFYCA 803 also come from Gran Barranca, but their exact position in the stratigraphic position is uncertain.

**Description and comparisons** The cheek teeth are slightly larger (nearly 6%) than those of *Astrapothericulus iheringi* (Ameghino 1899) from the “Astrapothericulan beds” (Ameghino 1900–02, 1906), assigned to the late early Miocene (Fleagle *et al.* 1995). However, the cheek teeth show a wide range of size, with variation of nearly 25% in m2 measurements. The measured specimens cluster in two groups (Fig. 12.3). The absence of other relevant morphological differences suggests that these two groups could represent males and females of a single species. A similar dispersion is also observed for the measurements of the m2 of *Astrapothericulus iheringi* (Fig. 12.3).

The height of the crowns nearly agrees with that of *Astrapothericulus iheringi*, which is intermediate

between that of *Parastrapotherium holmbergi* and *Astrapotherium magnum* (Santacrucian). However, *Astrapotherium? ruderarium* clearly differs from *Astrapothericulus iheringi* by having all cheek teeth with much more delicate basal cingula, as in *Astrapotherium magnum*, whereas *Astrapothericulus iheringi* have much more prominent and crenulated basal cingula, which is the most characteristic feature of this species (Ameghino 1902). Moreover, the upper molars (Fig. 12.4A) differ from those of *Astrapothericulus iheringi* by having less penetrating fold of the anterior wall of the protocone; thus the anterolingual pocket is less conspicuous. As distinct from the species of *Parastrapotherium*, P3 and P4 (Fig. 12.4B) have a continuous cingulum at the base of the labial fold. This is a resemblance to *Astrapothericulus iheringi* and *Astrapotherium magnum*, although the fold is more prominent and with a narrower base. As in *Astrapotherium magnum*, the upper canines are ever-growing, and completely columnar in adults, with a subtriangular cross-section, the anterior face lacks enamel and it is flat in juvenile stages or it has a longitudinal furrow in adults (Fig. 12.4C), and the enamel extends up to near the base of the lateral walls. However, the enamel is comparatively smoother than in other astrapotheriids. Upper canines of *Astrapothericulus iheringi* are rooted and proportionally smaller.

The incisors (Fig. 12.4D, D') are larger and comparatively broader and the base is more robust than in *Astrapothericulus iheringi*, resembling those of the species of *Parastrapotherium*. The lower canines (Fig. 12.4E, E') are more robust than in *Astrapothericulus iheringi*, strongly extroverted, as in *Astrapotherium magnum* and the species of *Parastrapotherium*. In adult stages the canines are rooted, as in *Astrapothericulus iheringi* and the species of *Parastrapotherium* (but probably the same condition is present in *Astrapotherium magnum*). The lingual face is more convex than in those species. The p3 is absent. The p4 (Fig. 12.4F) is typically bicrescentic and has a conspicuous labial flexid as in *Astrapotherium magnum* but, unlike *Astrapothericulus iheringi* and the species of *Parastrapotherium*, but the flexid is not as penetrating as in *Astrapotherium magnum*. Unlike the species of *Parastrapotherium* but as in *Astrapotherium magnum* and *Astrapothericulus iheringi*, the lower molars have a well-developed and deep labial flexid, and lingual cingulids are present at the bases of the metaconids (Figs. 12.2, 12.4G). All lower molars have a conspicuous column attached to posterior wall of the metalophid (“pillar” after Scott

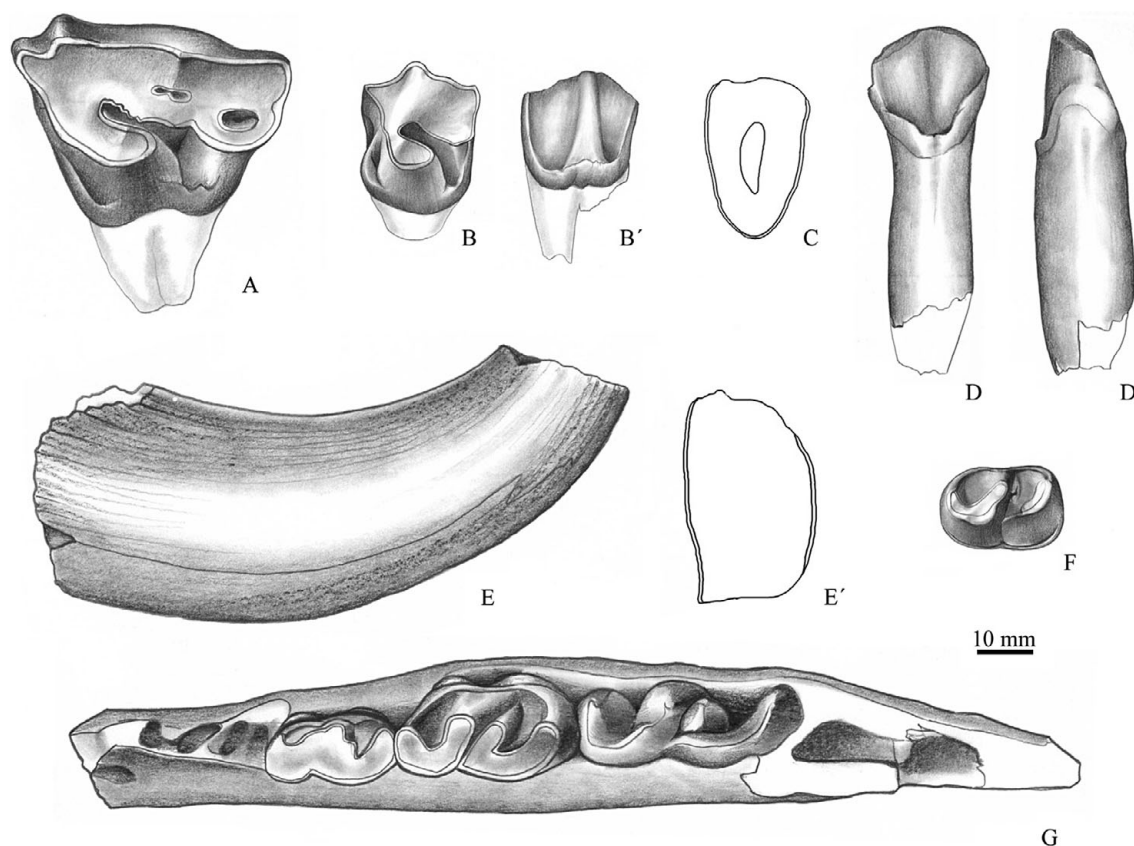


Fig. 12.4. *Astrapotherium? ruderarium* (Ameghino 1902). (A) MACN A 52–522, upper molar in occlusal view; (B) MACN A 52–513, P4 in occlusal view, (B') in labial view; (C) MACN A 52–523 (holotype of *Astrapotherium triangulidens* Ameghino 1902), upper canine in schematic cross-section; (D) MACN A 52–522, incisor in lingual view, (D') in lateral view; (E) MACN A 52–521 (syntype of *Parastrapotherium crassum* Ameghino 1902), lower canine in labial view, (E') schematic cross-section; (F) MACN A 52–522, p4 in occlusal view; (G) MACN A 52–520, left mandibular fragment with dp4, m1, and m2 and alveoli for dp2, dp3, and m3.

1928, 1937), as in the species of *Parastrapotherium* and *Astrapothericulus iheringi*, but it has more bunoid appearance than in *Astrapotherium magnum*.

MPEF PV 7922 has associated DP3 and DP4. Both are molariform and the former lacks the anterolingual projection characteristic of an anteriormost deciduous premolar, suggesting that this specimen had at least another anterior deciduous premolar (DP2), as in *Parastrapotherium holmbergi*, *Astrapotherium magnum*, and *Astrapothericulus iheringi*. The juvenile mandibular fragment herein designed lectotype (MACN A 52–524) has five cheek teeth, the posteriormost is evidently the m3 in eruption (Fig. 12.2). The two anteriormost teeth are very worn dp3 and dp4. A diastema anterior to the dp3 shows no trace of an alveolus for another deciduous premolar. Deep inside the dentary there is an unerupted tooth below the dp4, but there is not a corresponding tooth for replacement below the dp3. Another juvenile mandibular fragment in the MACN Ameghino collection

(MACN A 52–520, Fig. 12.4G), also referable to *Astrapotherium? ruderarium*, is a slightly younger juvenile than the lectotype; it shows two small alveoli before the alveoli for the dp3, corresponding to a minute dp2. These two juvenile specimens reveal that *Astrapotherium? ruderarium* has only one lower permanent premolar, as in *Astrapotherium magnum* and *Astrapothericulus iheringi*, but the lower deciduous formula agrees with that of *Parastrapotherium*, though with a more ephemeral dp2. All deciduous premolars are similar in structure to that of *Astrapothericulus iheringi*, but differ in having more delicate basal cingula, as in the molars.

The mandible is partially preserved in the adult MPEF PV 7915; it is much more robust and the diastema is much longer than in *Astrapothericulus iheringi*, and proportionally slightly longer than in *A. magnum* and *P. martiale*. The strongly extroverted implantation of the canines and other features of the dentary bear no significant differences with *A. magnum*.

The juvenile skull FMNH P13429 (with erupting P3 and M3) was previously referred to *Astrapothericulus* by Johnson and Madden (1997). However, the molars differ from those of the species of *Astrapothericulus* and match with *Astrapotherium?* *ruđerarium* in having delicate basal cingula and poorly developed anterolingual pocket. The canines have smooth enamel, as in other specimens referred to *Astrapotherium?* *ruđerarium*. The preserved portions of the skull, which is partially restored, show that the frontals are proportionally narrower, the skull roof is somewhat more curved anteroposteriorly, and the zygomatic arches are less flared than in a skull of *Astrapotherium magnum* in similar ontogenetic stage (MLP 38-X-30-1). These differences are also observed in adult skulls of *Astrapotherium magnum*. Moreover, the occipital region (not preserved in the MLP 38-X-30-1) is lower than in adults of *Astrapotherium magnum*. Because of the ontogenetic variations of the skull in the *Astrapotheria* are very poorly known, the taxonomic significance of these cranial features remains uncertain.

**Comments** Ameghino's (1902) description of *Parastrapotherium ruđerarium* is based upon a juvenile mandibular fragment with five teeth (MACN A 52-524), herein designed the lectotype (Fig. 12.2), and two lots of teeth (MACN A 52-522 and MACN A 52-513) corresponding to more than one individual. All the cheek teeth and incisors included in these lots are coherent in morphology and size with the lectotype. However, the upper canine described by Ameghino (1902) included in the lot MACN A 52-522 is significantly different from other canines that are positively associated with molars referable to this species. This canine is treated as a separate taxon in a section below.

Ameghino (1902) concluded that the juvenile mandibular fragment herein designed lectotype has four deciduous premolars, of which only two were replaced. As we mentioned above, this specimen has preserved three molars and only two deciduous premolars (dp3-dp4) but only the dp4 is replaced.

According to Ameghino (1902), the incisors of this species are characterized by being nearly similar in shape and size. Actually, the incisors he interpreted as i1 and i2 (MACN A 52-522) very probably are right and left to i2s.

Ameghino (1902) based *Parastrapotherium paucum* on two very worn cheek teeth and three isolated incisors (MACN A 52-525), and concluded that it was a separate species even smaller than *Parastrapotherium ruđerarium*. However, the cheek teeth are in fact barely smaller than those described as

*Parastrapotherium ruđerarium*, and equal in size to other specimens herein referred to this species, and they are not distinct morphologically. One of the incisors described as *Parastrapotherium paucum* is very similar in size and morphology to the i2 included in the original type series of *Parastrapotherium ruđerarium*, but more worn. Another incisor is smaller is probably the i1. The remaining incisor is much more slender and smaller and could be a deciduous tooth.

*Astrapothericulus minusculus* and *Astrapothericulus laevisculus* Ameghino 1902 are based on several deciduous teeth. The premolars of both types do not differ from those of the lectotype of *Astrapotherium?* *ruđerarium*.

Ameghino (1902) based *Astrapotherium triangulidens* on an isolated fragment of an upper canine (MACN A 52-523), noting that it has smooth enamel, triangular cross section and unlimited growth. These same features also occur in the specimen MACN Pv 14543, associated with molars and incisors clearly assigned to *Astrapotherium?* *ruđerarium*.

According to Ameghino (1902), *Parastrapotherium?* *crassum* is a giant species, as large as *Astrapotherium giganteum* (Santacrucian SALMA), although he included in the original description a small lower canine (MACN A 52-521) that he interpreted as belonging to a juvenile individual. This canine (Fig. 12.4E) is associated with a mandibular fragment with p4-m1 and other cheek teeth referable to *Astrapotherium?* *ruđerarium*.

Ameghino (1902) described *Prochalicotherium patagonicum* as a member of Homalodotheriidae (Notoungulata), and mentioned that this species is identifiable from features of the upper molars, but unfortunately he only described two upper premolars, a canine, and an incisor. Ameghino noted that the most characteristic element is the upper premolar MACN A 52-337 (Ameghino 1904, Fig. 391) that he understood to be a left P3. We find that this tooth, herein designed lectotype of *Prochalicotherium patagonicum*, has vertically banded enamel and corresponds to a right P4 of an *astrapotheriid* (Patterson 1952) very similar in shape and size to others here assigned to *Astrapotherium?* *ruđerarium*, differing only in having a slightly less prominent labial fold and no lingual cingulum at the base of the protocone, features we consider to be merely variation at the population level. The remaining teeth described by Ameghino (1902) as *Prochalicotherium patagonicum* (MACN A 52-339, 52-534, and 52-550) have uncertain affinities, but they surely do not belong to an *astrapothere*.

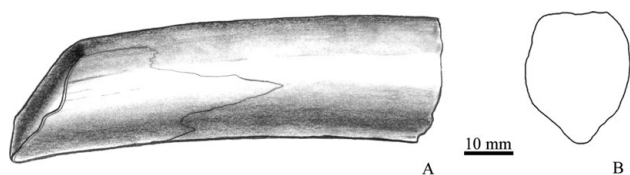


Fig. 12.5. *Astrapotheriidae* gen. et sp. nov., MACN A 52–522 (syntype of *Parastrapotherium ruderarium* Ameghino, 1902). (A) upper canine in lateral view, (B) schematic cross-section.

#### Affinities of *Astrapotherium? ruderarium*

Ameghino (1902) referred *Astrapotherium? ruderarium* to *Parastrapotherium* based on the erroneous assumption that the specimen herein designed lectotype has two lower permanent premolars. The dentition of this species does in fact share with *Parastrapotherium holmbergi* the presence of three lower deciduous premolars and the robust incisors with broader bases than in other astrapotheriids. On the other hand, *Astrapotherium? ruderarium* differs in significant ways from *Parastrapotherium holmbergi*, for example by having a cingulum at the base of the labial fold in all the upper premolars and at the lingual base of the metaconid in the lower molars, in lacking a p3 and in having more hypsodont teeth. *Astrapotherium magnum* and *Astrapothericulus iheringi* share the presence of a “pillar” in all the lower cheek teeth, the reduced lower premolar formula, the higher degree of hypsodonty of the cheek teeth; some or all these features are derived characters. Therefore, we conclude that the original assignation of *Astrapotherium? ruderarium* to *Parastrapotherium* is not justified. Indeed, in some ways *Astrapotherium? ruderarium* is more derived than *Astrapothericulus iheringi*: it shares with *Astrapotherium magnum* upper ever-growing canines and the derived presence of a labial flexid in p4, both features being absent in *Astrapothericulus iheringi*. Based on these characters we provisionally refer this species to the genus *Astrapotherium*.

*Astrapotheriidae* gen. et sp. nov.

**Referred material** MACN A 52–522b, an isolated upper canine (syntype of *Parastrapotherium ruderarium*).

**Provenance** According to Ameghino (1902), it comes from the “*Colpodon* beds” at the Gran Barranca south of Lake Colhue-Huapi, Colhuehuapian SALMA (early Miocene; Flynn and Swisher 1995; Ré *et al.* Chapter 4, this book), Chubut Province, Argentina.

**Comments** This canine (Fig. 12.5), described by Ameghino (1902) as belonging to *Parastrapotherium*

*ruderarium*, differs from all canines positively associated to molars of this species because it is much less curved and compressed, the cross section is nearly subcircular, and the enamel does not extend up to the preserved base of the tooth. This tooth resembles an upper canine (associated with upper cheek teeth) more recently collected from Colhuehuapian sediments of the Cerro Bandera Formation, northwest Patagonia (Leanza and Hugo 1997; Kramarz *et al.* 2005). The associated cheek teeth have characters that suggest uruguaytheriine affinities (Kramarz and Bond 2005).

#### *Parastrapotherium crassum* (Ameghino 1902)

*Parastrapotherium crassum* was described by Ameghino (1902) as being from his “*Colpodon* beds” (Colhuehuapian). This species is based on several isolated specimens that clearly belong to different species. The type specimens have black, polished enamel and dark dentine. This kind of preservation is typical of the fossils teeth from the Deseadan levels at the Gran Barranca, and different from the characteristic brown and light-coloured teeth from Colhuehuapian levels at the Barranca. The remaining specimens referred by Ameghino to *P. crassum*, which preservation agrees with those more recently recovered at the Colhue-Huapi Member, are herein referred to *Astrapotherium? ruderarium*. Therefore, *P. crassum* should not be listed among the Colhuehuapian species.

## Conclusions

The revision of astrapotheres from Colhuehuapian levels at Gran Barranca south of Lake Colhue-Huapi reveals the certain presence of three species: *Astrapotherium? ruderarium* (Ameghino 1902), *Parastrapotherium symmetrum* (Ameghino 1902), and *Parastrapotherium martiale* Ameghino 1901 (the latter also known from the Deseadan SALMA). *Parastrapotherium herculeum* may represent a fourth very large species but the type material of Ameghino (1889), supposed to come from Colhuehuapian beds, cannot be located, and no available specimen can be certainly referred to it. Finally, a single upper canine (part of the original syntype of *Parastrapotherium ruderarium*) seems to represent a fifth unnamed species, perhaps a uruguaytheriine. The number of species, then, is significantly less than the 12 originally proposed by Ameghino (1902). Six of Ameghino’s species have been brought into synonymy with the remaining five. The seventh species, *Parastrapotherium crassum*, is valid taxon from the Deseadan, but is not known in the Colhuehuapian.

The dentition of *Astrapotherium? ruderarium* shows a confusing combination of characters, in part transitional

between *Parastrapotherium holmbergi* on one hand, and *Astrapotherium magnum* and *Astrapothericulus iheringi* on the other hand. We assign this species to *Astrapotherium* until further evidence is known.

Both Colhuehuapian species of *Astrapothericulus* described by Ameghino (1902) are here considered synonyms of *Astrapotherium? ruderarium*. Although some specimens (e.g. AMNH 29687, FMNH 15049) resemble *Astrapothericulus iheringi* in having lower molars with basal cingula somewhat more developed than in the lectotype of *Astrapotherium? ruderarium*, no examined specimen from Colhuehuapian levels at Gran Barranca is positively referable to *Astrapothericulus*. However, the record of *Astrapothericulus* is well documented in levels of equivalent age of the Cerro Bandera Formation in Neuquén Province (Kramarz and Bond 2005; Kramarz et al. 2005).

The record of *Astrapotherium* in Colhuehuapian beds is revised. In our revision *Astrapotherium triangulidens* is made a junior synonym of *Astrapotherium? ruderarium*. *Astrapotherium? symmetrum* and *Astrapotherium herculeum* are transferred to *Parastrapotherium*. This leaves only *Astrapotherium? ruderarium*.

*Astrapotherium? ruderarium*, the smallest astrapotheriid recorded at Colhuehuapian levels at Gran Barranca, is also the most abundantly represented. *Parastrapotherium symmetrum* is identified only through two isolated incisors; this is a middle-sized species equivalent in size to *Astrapotherium magnum*. The largest astrapotheres are *Parastrapotherium martiale* and *Parastrapotherium herculeum*, supposedly the largest astrapotheres known so far.

#### ACKNOWLEDGEMENTS

The authors thank R. Madden (Duke University) and G. Vucetich (MLP) for allowing us to study material obtained during the MLP – Duke University expeditions to Gran Barranca. The authors are grateful to E. Ruigómez (MEF), M. Reguero (MLP), J. Flynn (AMNH), and P. Makovicky (FMNH) for access to materials under their care, and to C. de Muizon and G. Billet (MNHN) for providing casts of specimens in the Tournouër collection. The critical comments of P. O. Antoine (Université Paul Sabatier, Toulouse, France) and an anonymous reviewer improved this paper considerably. Drawings were made by the artist Jorge González. This work was supported by PICT 32344 awarded to Dr. Viviana Barreda (MACN) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Field research was supported by US National Science Foundation grants EAR-0087636, BCS-0090255, and DEB-9907985 to Richard F. Kay and Richard H. Madden.

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