

# A NEW OLIGOCENE ASTRAPOTHERE (MAMMALIA, MERIDIUNGULATA) FROM PATAGONIA AND A NEW APPRAISAL OF ASTRAPOTHERE PHYLOGENY

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**SYNOPSIS** The new genus and species *Maddenia lapidaria* from pre-Deseadan (Oligocene) deposits at the southern cliff of Lake Colhue Huapí (Chubut Province, Argentina) is described. This small Oligocene astrapothere represents an adaptive type that is distinct from the usual one proposed for post-Casamayoran (Eocene) forms. Because of its small body size and dental characters, preliminarily interpreted as primitive, this genus was originally considered to be a member of the Albertogaudryinae surviving into the Oligocene and coexisting with more derived species. However, a phylogenetic analysis based on dental and mandibular characters indicates that *Maddenia lapidaria* is, rather, the sister group of the giant Deseadan and later astrapotheriids by sharing with them a well developed upper molar *crista* and *crochet*, P<sub>4</sub> lingual valley, p<sub>2</sub> absent and superficial premolar and molar hypoflexid. *Maddenia lapidaria* has highly molarised upper premolars, representing the top-most expression of the evolutionary trend of increasing premolar complexity in the Astrapotheria. A subsequent evolutionary turnover resulted in a reduction of the size and number of premolars and secondary occlusal simplification, coinciding with an abrupt increase in hypsodonty and body size that characterise the more advanced astrapotheriids. This interpretation challenges the progressive acquisition of astrapotheriid characters traditionally accepted for the group. The moderately deep premolar and molar hypoflexid seen in *Maddenia lapidaria* is interpreted as the ancestral condition for the younger astrapotheres, which, on the one hand, would have evolved into the complete reduction of this structure in the Uruguaytheriinae and, on the other hand, the development of a deep labial vertical cleft in the Astrapotheriinae (*Astrapotherium* and *Astrapothericulus*).

**KEY WORDS** Astrapotheria, Systematics, Sarmiento Formation, Oligocene, Patagonia

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## INTRODUCTION

Astrapotheres are enigmatic South American extinct herbivorous land mammals, characterised by having strongly retracted nasals suggesting the presence of a proboscis, enlarged canines and rhino-like jugal cheek teeth (Ameghino 1894; Scott 1937). The group is recorded from the Palaeocene (Soria & Powell 1981) up to the middle Miocene (Johnson & Madden 1997) and includes the largest species within the Tertiary native faunas. Previous studies on the evolution of these mammals have proposed a gradual development of skeletal and dental specialisations associated with body size increase (Scott 1937; Simpson 1967; Soria 1988). Here, we describe a new and very peculiar astrapothere recovered from Oligocene deposits in the Sarmiento Formation exposed at the Southern Cliffs of Colhue Huapí Lake (Chubut province, Patagonia, Argentina; Fig. 1) (Ameghino 1906), known worldwide as Gran Barranca. The fossil-bearing level outcrops in a very restricted locality termed 'La Cantera', dated to between 30 and 34 Ma (Carlini *et al.* 2005; López *et al.* 2005, Vucetich *et al.* 2005), stratigraphically located approximately 20 m below deposits bearing a mammal association typical of the Deseadan South American Land Mammal Age (late Oligocene) (e.g. *Pyrotherium*, *Parastrapotherium*, *Leontinia*, etc). The new taxon described here stands out from the remaining Oligocene astrapotheres by its very small size and by several dental features preliminarily interpreted as primitive (López *et al.* 2005). Examination of this new astrapothere and comparison with other previously known genera allows a re-evaluation of the main evolutionary trends of these mammals. These new interpretations are also supported by the analyses of new and more complete materials of *Astrapotus* (Mustersan SALMA, Late Eocene) and by the

conclusion of recent studies on Deseadan and Early Miocene astrapotheres (Kramarz & Bond, 2008).

## Institutional abbreviations

MPEF PV = Museo Paleontológico Egidio Feruglio (Chubut Province, Argentina), palaeovertebrate Collection.

MACN = Museo Argentino de Ciencias Naturales Bernardino Rivadavia.

MLP = Museo de La Plata (Argentina).

## SYSTEMATIC PALAEOLOGY

Order **ASTRAPOTHERIA** Lydekker, 1894

Family **ASTRAPOTHERIIDAE** Ameghino, 1887

Genus **MADDENIA** nov.

TYPE AND ONLY SPECIES. *Maddenia lapidaria* sp. nov.

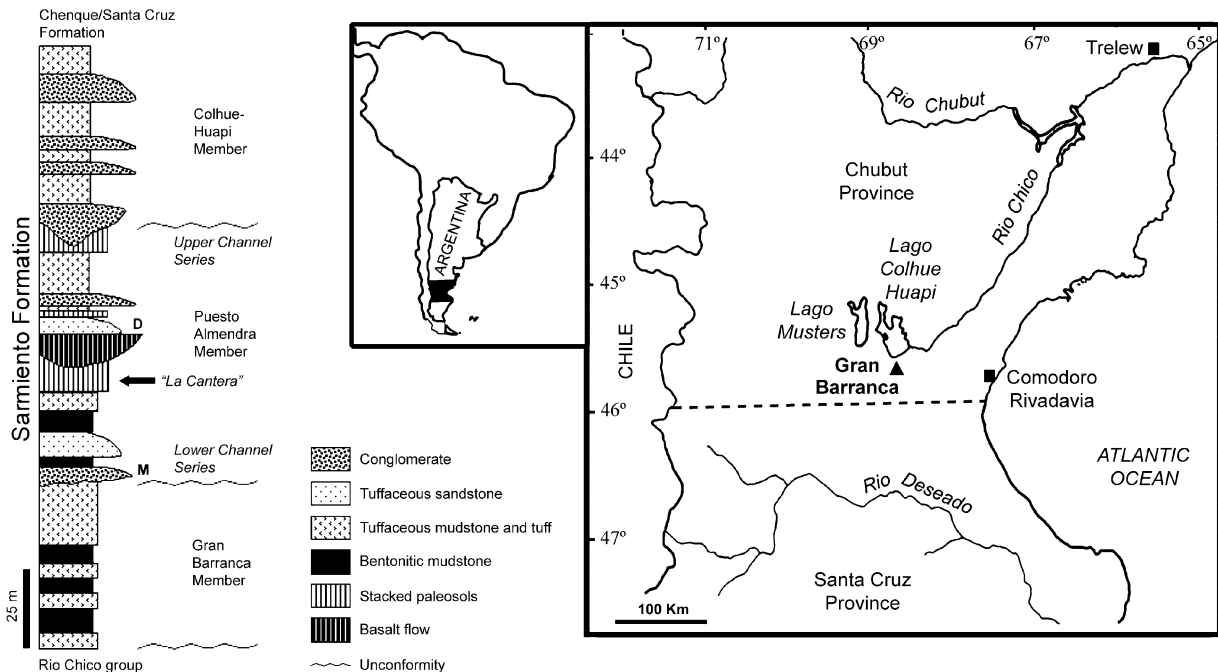
DIAGNOSIS. As for the type species.

ETYMOLOGY. Dedicated to Dr Richard Madden (Duke University, USA), for his contributions to South American palaeontology.

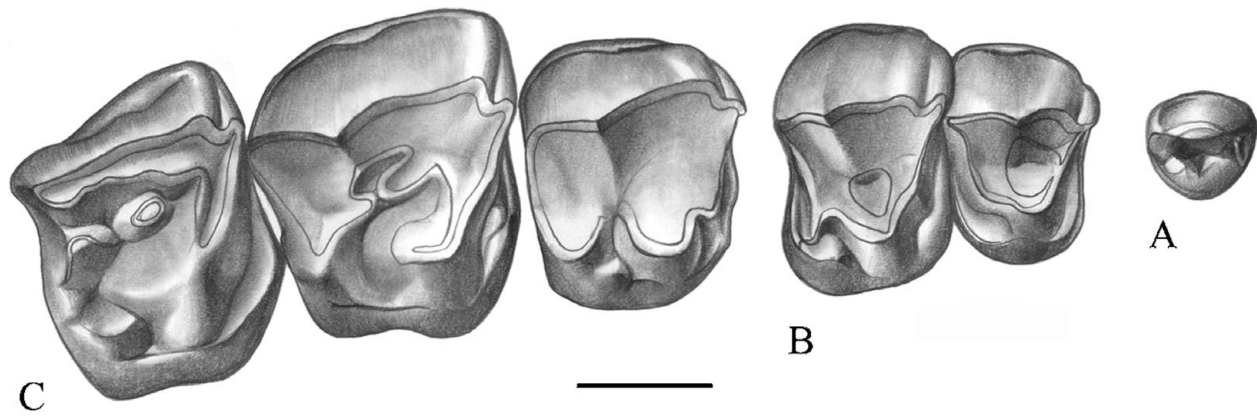
CHRONOLOGICAL AND GEOGRAPHICAL DISTRIBUTION. Early Oligocene, Chubut Province, Argentina.

*Maddenia lapidaria* gen. et sp. nov. Figs 2–6

TYPES. Holotype: MPEF PV 7735, a maxillary fragment with right P3–M3 and left M3, associated right P2 and left



**Figure 1** Stratigraphical and geographical provenance of *Maddenia lapidaria* gen. et sp. nov. **A**, Reconstructed profile of the Sarmiento Formation at the Southern Cliffs of Colhue Huapí Lake (Gran Barranca, Patagonia, Argentina) (modified from Bellosi *et al.* 2002), showing the main lithologies and the stratigraphical position of 'La Cantera' in relation to the levels bearing mammals characteristic of the Deseadan (**D**) and Mustersan (**M**) South American Land Mammal Ages (SALMAS). **B**, Map of central Patagonia, Argentina, showing the location of Gran Barranca.



**Figure 2** Upper cheek teeth of *Maddenia lapidaria* gen. et sp. nov. MPEF PV 7735 (holotype), from 'La Cantera', Sarmiento Formation at Gran Barranca, Patagonia, Argentina. **A**, Right P2, occlusal view. **B**, Right P3-P4, occlusal view. **C**, Right M1-M3, occlusal view. Scale bar = 1 cm.

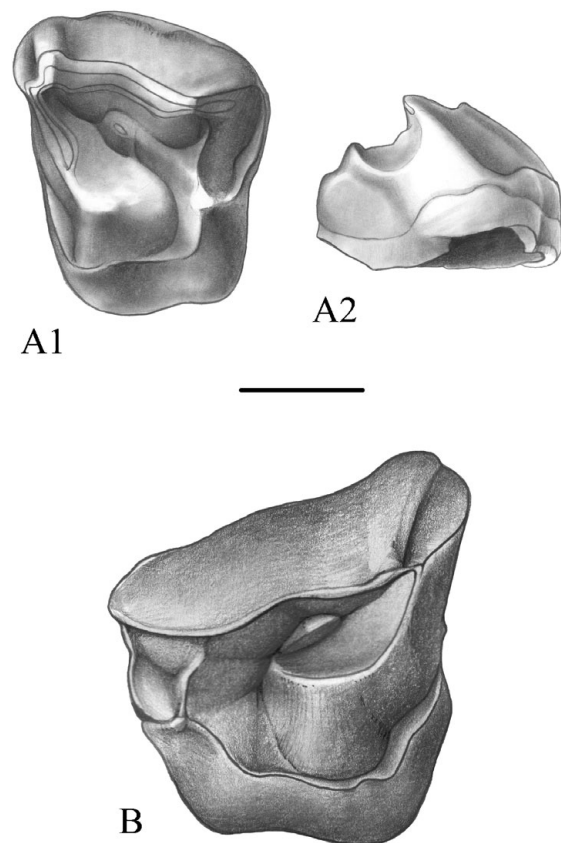
P3, and a probably associated partial upper canine. Paratypes: MPEF PV 6113, incomplete right m1 or m2; MPEF PV 6145, isolated right M3; MPEF PV 6238a, isolated left M3; MPEF PV 6238b, right m1 or m2; MPEF PV 6254, left lower canine; MPEF PV 7013, left M2; MPEF PV 7082, right p3; MPEF PV 7508, right m2?; MPEF PV 7696a, left mandibular fragment with m1-m2, partial m3 and probably associated p4; MPEF PV 7696b, left m1; MPEF PV 7701, left mandibular fragment with p4-m3; MPEF PV 7707, three isolated upper canines; MPEF PV 7709, left mandibular fragment with m2-m3 and preserved condyle, angular, and coronoid regions; MPEF PV 7724, two associated upper canines (crushed); MPEF PV 7725a, left p4; MPEF PV 7727, partial symphysis with left p3; MPEF PV 7732, right mandibular fragment with m1-m3 and the roots for p3 and p4; MPEF PV 7738, left mandibular fragment with p3-m3; MPEF PV 7774, small portion of symphysis with left canine; MPEF PV 7848, right mandibular fragment with m2-m3.

**STRATIGRAPHICAL AND GEOGRAPHICAL PROVENANCE.** Sarmiento Formation, Puesto Almendra Member, 'La Cantera' (Carlini *et al.* 2005; López *et al.* 2005; Vucetich *et al.* 2005). Southern cliff of Lake Colhué Huapi (Gran Barranca), Chubut Province, Argentina (Fig. 1).

**ETYMOLOGY.** From the Latin, *lapidarius* 'of stone'.

**DIAGNOSIS.** Small astrapothere, almost 50% smaller than *Astraponotus assymetrus*. P2 subcircular with central valley, unlike *Trigonostylops wortmani* and *Tetragonostylops apthomasi*. P4 molariform with metaloph, hypocone and hypoflexus more developed than in other astrapotheres; labial fold of metacone reduced as in *Parastrapotherium holmbergi* and Miocene astrapotheriids, unlike all pre-Oligocene astrapotheres. Upper molars with complete metaloph, unlike *Albertogaudrya unica*, well developed *crista*, in opposition to *Scaglia kraglievichorum*, and *crochet*, unlike *A. assymetrus*. p2 absent, unlike all pre-Oligocene astrapotheres. Lower cheek teeth with paralophid less developed than in *A. unica* and *A. assymetrus*. Hypoflexid more superficial than in *A. unica* and *A. assymetrus*, but less than in the uruguaytheriine species.

**DESCRIPTION AND COMPARISONS.** The cheek teeth are brachydont, higher crowned than in *Albertogaudrya*. All upper cheek-teeth (Figs 2, 3A) have marked unilateral hypsodonty



**Figure 3** Comparison of upper molars from **(A)** *Maddenia* gen. nov. from 'La Cantera', Sarmiento Formation (Early Oligocene) at Gran Barranca, Patagonia, Argentina and **(B)** *Astraponotus* sp. from the Sarmiento Formation at Gran Hondonada (Odreman Rivas 1978), Mustersan South American Land Mammal Age (SALMA) (Late Eocene). **A**, MPEF PV 7013, unworn left M2 in occlusal view (**A1**) and posterior view (**A2**). **B**, MPEF PV 1296 A, unworn right M1, occlusal view. Scale bar = 1 cm.

and conspicuous basal cingulum as in *Astraponotus*, *Albertogaudrya* and *Trigonostylops* (Eocene of Patagonia).

The P2 has only one root with a deep labial furrow, so that the root shows a V-shaped cross-section. The crown has a subcircular contour and it has a main labial, elongated

cuspid and at least one accessory lingual cuspid (this part of the tooth is damaged), separated by a narrow central valley (Fig. 2A). The anterior wall has a small basal cingulum that delimits a minute anterior pocket, as in the P3 and P4 of *Parastrapotherium*. The same features are present in the P2 of *Astraponotus*, but in some specimens there is a distinct anterolabial root. In *Trigonostylops* the P2 has two roots, anterior and posterior, the crown is more elongated, with a single central cuspid with a lingual cingulum that in some specimens bears a small cuspidule, but lacking a protocone and therefore also lacking a central valley. In *Tetragonostylops* (Palaeocene of Brazil and Eocene of Patagonia) the P2 is also elongated and has a main cuspid with no trace of a central valley.

In contrast to *Parastrapotherium*, the P3 and P4 (Fig. 2B) are not reduced in size in comparison with the molars. The P3 resembles that of *Albertogaudrya* by having a sub-quadrangular contour, protocone located at the anterolingual corner of the crown and well-developed posterolingual cingulum with a well-insinuated rudimentary hypocone, in contrast to *Trigonostylops*, *Tetragonostylops*, *Parastrapotherium* and all the Miocene astrapotheres. The labial wall shows two folds, less prominent than in *Trigonostylops*, *Albertogaudrya* and *Astraponotus*. The postprotocrista is present, as in *Trigonostylops*, *Tetragonostylops* and *Albertogaudrya*, thus the central valley does not open posteriorly. A vestigial, low postprotocrista is variably present in *Parastrapotherium* and later forms.

The P4 is larger and proportionally wider than the P3. The hypocone is a conspicuous cingular cuspid, much more developed than in *Albertogaudrya* and *Astraponotus*, and it is isolated from the protocone by a lingual valley. The postprotocrista has a lingual projection that reaches the base of the hypocone, forming a rudimentary metaloph. The posterior slope of the metaloph has a well-defined wear facet, indicating that this structure already had a masticatory function, as in the molars. These features give a molar-like appearance to this tooth, in contrast to all the remaining astrapotheres. The labial wall has only one fold corresponding to the paracone, as in *Parastrapotherium* and Miocene genera. The anterior wall of the protocone is slightly concave and it delimits a small basal anterolingual pocket, as in the premolars and molars of *Parastrapotherium* and Miocene genera.

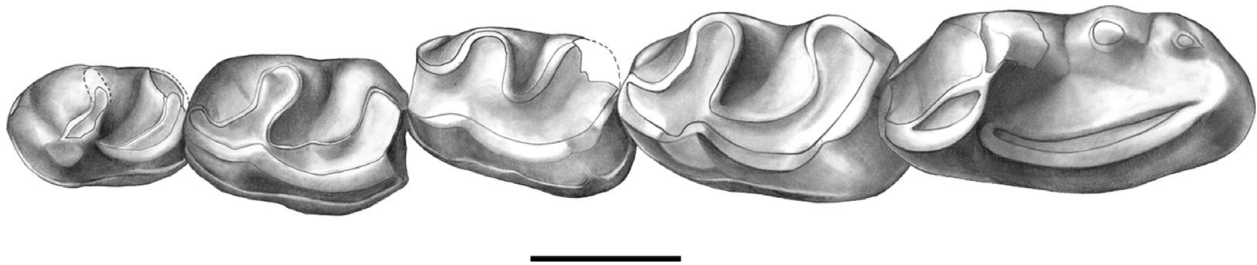
The upper molars (Fig. 2C) have the characteristic astrapotheriid structure: a high ectoloph, protoloph joining the conical protocone and a well developed hypocone separated from the protocone by a deep lingual flexus. The parastyle is moderate and the metastyle reduced, except in M3. The ectoloph has only one labial fold corresponding to the paracone and there is no trace of the labial fold of the metacone, as in *Parastrapotherium* and Miocene forms. By contrast, the labial fold of the metacone is still present in *Trigonostylops* and variably reduced in *Tetragonostylops*, whereas in *Albertogaudrya*, *Scaglia* (Eocene) and *Astraponotus* this structure is insinuated as a slight convex area at the outer wall of the ectoloph. Labial and anterior cingula are well developed. The anterior cingulum continues as a weak lingual cingulum, reaching the base of the hypocone. M1 and M2 have a trapezoidal contour; the former is slightly larger than P4, as in *Astraponotus*, and rather smaller than the M2. The only available M1 belongs to the holotype; it is much worn and few occlusal features are observable. As in the P4, the anterior wall of the protoloph shows a conspicuous anterolingual inflection that becomes more penetrating to the base, forming an anterolingual pocket, as in *Parastrapotherium* and the

Miocene genera. This feature is absent or barely insinuated in older astrapotheres. The lingual cingulum has a small accessory cuspid between protocone and hypocone, absent in M2 and M3. All the occlusal structures are well shown in the isolated and little worn M2 of MPEF 7013 (Fig. 3A). The anterolingual inflection of the protoloph is less marked than in M1. The posterior cingulum is elevated and rises lingually to the apex of the hypocone, enclosing a very ephemeral posterofossette, as in *Astraponotus*. The most noteworthy characters are the presence of a distinct hypocone connected to the metacone by a complete metaloph (with no trace of metaconule), as in *Scaglia* and *Astraponotus*, and the presence of two accessory elements in the central valley, lower than the remaining occlusal structures. The anteriormost is a small cuspidule between the protocone and the ectoloph, topographically equivalent to the *crista*. It has traditionally been interpreted that the *crista* of the upper molar of astrapotheres corresponds to a notoungulate-like enlarged posterolingual spur of the ectoloph (Cifelli 1993), as seen in the rather worn holotype of *Astraponotus holdichi* (Ameghino 1904: fig. 115; Simpson 1967: fig. 41B). However, in the unworn molar of the juvenile specimen of *Astraponotus* (MEF PV 1296: Fig. 3B) the *crista* is not an inner spur derived from the ectoloph, but it is clearly represented by a high, compressed, acute, independent cuspidule, rising from the central valley and connected to the inner wall of the ectoloph only at its base. Thus, the accessory cuspidule of the M2 of *Maddenia lapidaria* is herein interpreted as a well-developed *crista*, as in *Astraponotus*. The posterior accessory element in the central valley is a long, oblique anterior projection of the metaloph that reaches the base of the *crista* and represents a very well developed *crochet*, not observed in either *Astraponotus* or in older astrapotheres. In the more worn M2 of the holotype, the *crista* is connected to the ectoloph and spur-like. The posterior end of the *crista* and the *crochet* are in contact but still independent, and delimit a rudimentary median fossette. Such a fossette is complete and persists even in worn stages in *Parastrapotherium*, whereas it is ephemeral in all Miocene genera.

The M3 has a more quadrangular contour than M1. There is a conspicuous, slightly elongated hypocone attached to the posterolingual base of the protocone, thus the central valley does not open on the lingual side, as in the P4. The same pattern is observed in the M3 of *Albertogaudrya* and *Astraponotus*. The metaloph is incomplete, so that the metaconule is isolated from the hypocone, as in *Albertogaudrya* and *Astraponotus*. The lingual portion of the posterior cingulum is higher than in *Albertogaudrya* and *Astraponotus*, thus the central valley does not open on the posterior side. In the M3 of the holotype the *crista* is represented by an isolated bulky cuspid in the central valley and the *crochet* by an anterior projection of the base of the metaconule shorter than in M2. Both *crista* and *crochet* are absent in the two remaining available M3 (MPEF PV 6238 and 6145), suggesting that the presence of these elements is variable in this locus.

All lower cheek teeth (Fig. 4) have well-developed, continuous labial cingulids, as in *Albertogaudrya* and *Astraponotus*, in contrast with *Trigonostylops*. Lingual cingulids are restricted to the anterolingual portion of the trigonid, in contrast to the Miocene Patagonian *Astrapotherium* and *Astrapothericulus*, which exhibit a continuous lingual cingulid (this feature is variable in *Astraponotus*).

The mandibular fragment MPEF PV 7732 has m1-m3 and the roots for p3 and p4; the preserved portion of the



**Figure 4** Lower cheek teeth of *Maddenia lapidaria* gen. et sp. nov. from 'La Cañera' Sarmiento Formation (Early Oligocene), at Gran Barranca, Patagonia, Argentina. MPEF PV 7738, left p3-m3, occlusal view. Scale bar = 1 cm.

mandible anterior to the p3 has no trace of an alveolus for p2. Similarly, all the available p3 lack a wear facet on the anterior margin, confirming the absence of a p2, in contrast to *Trigonostylops*, *Tetragonostylops*, *Albertogaudrya* and *Astraponotus*. The p3 and p4 (Fig. 4) are similar in shape; p4 is rather larger than p3. In both, the posterior crescent is large but the anterior crescent is rudimentary due to poor development of the paralophid, which is shorter than in *Trigonostylops* and in the p4 of *Tetragonostylops* and *Albertogaudrya*, but longer than in the p3 of *Parastrapotherium holmbergi* (p3 of *P. martiale* has a very well developed paralophid). As in *Albertogaudrya* and *Parastrapotherium*, the entoconid of p3 and p4 is completely integrated into the posterolophid, in contrast with the condition in *Trigonostylops*. The labial flexid (hypoflexid) is absent in p4 and hardly insinuated in p3, as in *Parastrapotherium*.

Similarly to the premolars, the lower molars (Fig. 4) have a large, crescentic talonid and an incipient anterior crescent formed by a very short paralophid, more developed than in *Trigonostylops*, but less than in *Tetragonostylops*, *Albertogaudrya*, *Astraponotus* and much less than in *Parastrapotherium*. The labial cingulid ascends on the anteriormost portion of the trigonid, and continues in a prominent descending anterolingual cingulid, enclosing the trigonid valley, as in *Albertogaudrya* and *Astraponotus*. In some specimens a distinct, short ridge descends from the lingual end of the paralophid contacting the anterolingual cingulid. The hypoflexid is a shallow vertical depression, opposite the metaconid, resembling the condition seen in *Parastrapotherium* and unlike *Tetragonostylops* and *Albertogaudrya*. In some Mustersan specimens referable to *Astraponotus* the hypoflexid shows the same condition as in *Maddenia*, whereas in others this structure is as deep as in *Albertogaudrya*. Unlike in *Trigonostylops*, the entoconid of m1 and m2 is lower than the posterolophid and partially attached to the anterolingual slope of the hypoconulid. In *Astraponotus* the entoconid has the same disposition, but it is comparatively higher than in *Maddenia lapidaria*. However, in *Tetragonostylops* this cusp is as high as the hypoconulid and it is continuous with the lingual end of the posterolophid. All lower molars show an important wear facet on the labial wall of the protoconid, in contrast to all compared astrapotheres.

As in *Albertogaudrya* and *Astraponotus*, the m3 (Fig. 4) has a more elongated talonid and the hypoconid is more lophoid than in *Trigonostylops* and *Tetragonostylops*. The posterolingual cingulid (absent in *Trigonostylops*) is more pronounced than in *Albertogaudrya*. The hypoconulid is evidently represented by the elevated posterior end of the hypolophid and the entoconid corresponds to the bulky lingual cusp behind the metaconid. Therefore, the m3 has a

small accessory cuspid located at the posterolingual corner different from the hypoconulid and the entoconid. This cuspid, not observed in *Astraponotus*, is topographically equivalent to that observed in *Albertogaudrya*, but in this genus this element is connected to the hypoconulid. In *Tetragonostylops* the entoconid and hypoconulid are united through a delicate crest, which very probably involves an intermediate element equivalent to that of *Maddenia lapidaria* and *Albertogaudrya*. *Parastrapotherium* and younger astrapotheriids have a very simplified occlusal morphology and no individual cusp is distinguishable in this portion of the m3.

A central portion of an upper canine, probably associated with the holotype, has a subtriangular cross-section; the anterior face is strongly convex and the lateral walls bear a longitudinal sulcus, more marked on one side, probably the lingual one as in *Parastrapotherium* and *Astrapotherium*. The enamel covers only the lateral sides. Similar features are present in more complete but isolated upper canines (MPEF PV 7707); they are columnar, slightly curved and the tip is strongly bevelled. The enamel extends to the base of the preserved portion, with no trace of a closed crown. In *Albertogaudrya* and especially in *Astraponotus* the canines are less compressed, the anterior face is less convex, and the lateral sulci are less pronounced. In *Astraponotus* the upper canines show evidence of root formation in very adult to senile stages, whereas in *Albertogaudrya* they are not preserved.

There are two lower canines referable to this genus; one isolated (MPEF PV 6254) and the other inserted in a small portion of symphysis (MPEF PV 7774; Fig. 5). The canine is proportionally as large as in *Albertogaudrya*, but smaller than the known canines of *Astraponotus*. In *Parastrapotherium* and some Miocene genera (i.e. *Astrapothericulus*, *Granastrapotherium*) the canines shows substantial intra-specific variation that has been interpreted as sexual dimorphism (Scott 1937; Johnson & Madden 1997), but this condition cannot be evaluated in pre-Desadean astrapotheres which are represented by only a single or very few specimens. The canine is pointed, with the apical end subtriangular in cross section and then becoming sub-circular toward its base. The apex is slightly compressed with a sharp anterior edge; the labial wall is more convex than the lingual one, less than in *Albertogaudrya*. Anteriorly, the enamel is restricted to the tip of the crown; laterally it extends downwards not reaching the base of the tooth. Two delicate lateral cingula start near the base and merge at a point coincident with the limit of the enameled portion of the anterior face. At least the preserved part of the tooth has an open base with no trace of root formation. The base of this tooth would probably close in more adult stages, as seen in other astrapotheriids such as *Parastrapotherium* and *Astraponotus*. The preserved portion of the



**Figure 5** *Maddenia lapidaria* gen. et sp. nov. from 'La Cantera' Sarmiento Formation (Early Oligocene), at Gran Barranca, Patagonia, Argentina. MPEF PV 7774, left symphyseal fragment with canine, in labial view. Scale bar = 1 cm.

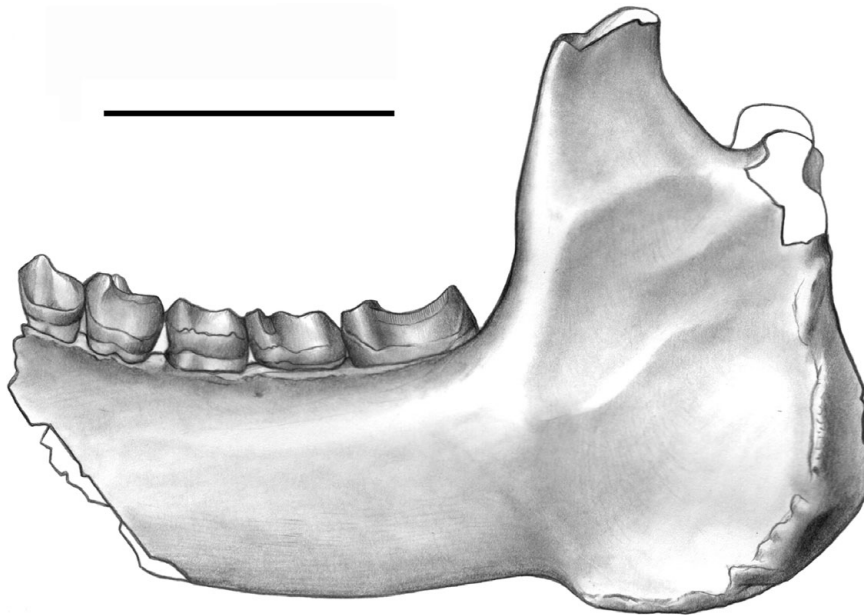
symphysis (Fig. 5) suggests that the canine was implanted slightly extroverted as in *Trigonostylops*, not as much as in *Astraponotus*, *Parastrapotherium* and *Astrapotherium*. The symphysis is cylindrical, with a marked medial groove on the dorsal surface, as in *Trigonostylops*, although it extends to the level of the talonid of p3. A single foramen mentale is located on the lateral surface near the base of the canine.

The horizontal ramus of the mandible (Fig. 6) is higher and more compressed than in *Albertogaudrya*. The ventral surface is concave and shows the characteristic ventral inflection delimiting the anterior margin of the angular region, as in *Trigonostylops*, *Tetragonostylops*, *Albertogaudrya* and *Astraponotus* (unlike *Eoastrapostylops*, *Astrapotherium* and *Granastrapotherium*). However, this feature is retained in juveniles of *Parastrapotherium* and *Astrapothericulus*. The ascending ramus is high, the coronoid process is promin-

ent and the condyle is cylindrical as in *Tetragonostylops*. In specimen MPEF PV 7738 the angular process extends backwards up to the level of the condyle, as in *Parastrapotherium* and Miocene astrapotheres; however, in MPEF PV 7709 the angular process extends backwards slightly posterior to the condyle, resembling the condition in *Eoastrapostylops* and *Tetragonostylops*. The entire posterior and ventral margin of the angular process is markedly thickened, with rugosities on the external side, more pronounced than in *Astrapotherium*. The post-alveolar foramen is absent, unlike the condition in *Albertogaudrya*.

## AFFINITIES OF *MADDENIA LAPIDARIA* AND CONSIDERATIONS ON ASTRAPOTHERIAN PHYLOGENY

The most conspicuous feature of *M. lapidaria* is its much reduced size in comparison with other Oligocene and even Eocene astrapotheres. According to the measurements for the m2 (Appendix 1), *M. lapidaria* is almost 50% smaller than *Astraponotus* and 70% smaller than *Parastrapotherium holmbergi*. The M1 is nearly 20% smaller than in *Scaglia*. Lower molars of *M. lapidaria* have a large and crescentic talonid but very simple trigonid due the poor development of the paralophid. In this respect, *Albertogaudrya* and *Astraponotus* (and even *Tetragonostylops*) are closer to the bicrescentic pattern of *Parastrapotherium* than *M. lapidaria*. Moreover, *M. lapidaria* has slightly extroverted lower canines and, at least, the available upper and lower ones are comparatively delicate, resembling those of *Trigonostylops* and *Albertogaudrya*. At first sight, these characters suggest that *M. lapidaria* belongs to an Eocene radiation of the astrapotheres (the *Albertogaudryinae*) surviving into the Oligocene epoch rather than being related to the giant and very specialised astrapotheriids (López *et al.* 2005).



**Figure 6** *Maddenia lapidaria* gen. et sp. nov. from 'La Cantera' Sarmiento Formation (Early Oligocene), at Gran Barranca, Patagonia, Argentina. MPEF PV 7738, left mandibular fragment with p3-m3, side view. Scale bar = 5 cm.

Simpson (1967) proposed that the dental evolution of astrapotheres was characterised by the increase of (unilateral) hypsodonty and gradual development of the *crista* in the upper molars. Soria (1984) included the development of the hypocone and the metaloph into this trend and extended it back up to the trigonodont pattern of trigonostyloids and *Eoastrapostylops*. Soria (1984) considered that there is a morphological hiatus between 'Albertogaudryinae' (i.e. *Tetragonostylops*, *Albertogaudrya*, *Scaglia* and *Astraponotus*) and his 'Astrapotheriinae' (i.e. *Parastrapotherium*, *Uruguaytherium* and all the Miocene genera). The upper molars of *M. lapidaria* have a large hypocone, a complete metaloph and a well-developed *crista*, as in the more derived 'albertogaudryine' *Astraponotus*, and a well developed *crochet* reaching the *crista*, as in 'Astrapotheriinae'. Except for its small size, *M. lapidaria* fills the morphological hiatus pointed out by Soria (1984) in relation to the evolution of the upper molar morphology. Similarly, the cheek teeth of *M. lapidaria* are nearly as hypsodont as those of *Astraponotus* and *M. lapidaria* shares the absence of p2 with both *Parastrapotherium* and Miocene genera. Moreover, *M. lapidaria* resembles *Parastrapotherium* and the uruguaytheriines in lacking hypoflexids in p3 and p4, and in having very superficial hypoflexids in m1-m3.

However, the upper premolars of *M. lapidaria*, including the P2, show the highest degree of molarisation among astrapotheres. In particular, the P4 strongly resembles the molars due to the presence of metaloph and hypocone, a hypoflexus partially separating protocone from hypocone, an anterolingual basal pocket and the reduction of the labial fold of the metacone. By contrast, the giant astrapotheres possess reduced and non-molarised upper premolars (hypocone and metaloph absent), suggesting that this pattern is directly derived from the trigonodont arrangement observed in *Eoastrapostylops*, *Trigonostylops* and *Tetragonostylops*. *Albertogaudrya* and *Astraponotus* exhibit an intermediate condition, with quadrangular non-reduced P3 and P4, but the hypocone is a rudimentary cingular cusp and the metaloph is absent. The lower premolars of *M. lapidaria* also resemble its own molars, reproducing the pattern observed in the upper dentition in having a very short paralophid, less developed than in *Astraponotus* and than in the p4 of *Albertogaudrya* and *Tetragonostylops*. However, the p3 of *M. lapidaria* resembles that of *Parastrapotherium holmbergi*, in which the paralophid is very small or even reduced to a small cusplule attached to the anterior base of the protoconid.

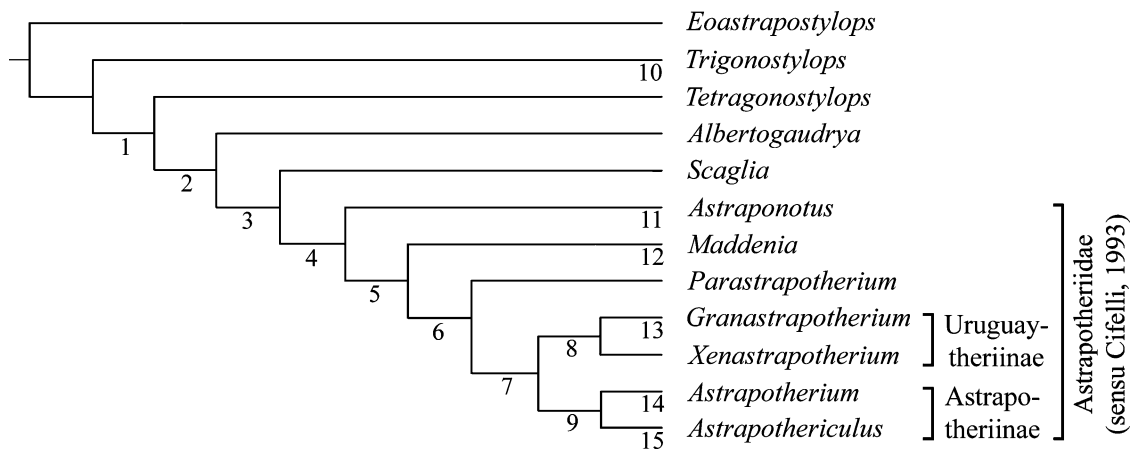
A phylogenetic analysis was performed in order to elucidate the evolutionary significance of these characters and evaluate the relationships of *M. lapidaria* with the other astrapotheres. The criterion of maximum parsimony was followed using the NONA program (Goloboff, 1993). Character polarity was determined by outgroup comparison using *Eoastrapostylops riolorensis* Soria & Powell, 1981 as the outgroup, because of previous hypotheses suggesting that this genus is the most primitive among Astrapotheria (Soria & Powell 1981; Soria 1984, 1988; Cifelli 1993). The taxa used for the analysis include *Tetragonostylops*, as described by Paula Couto (1952, 1963) and additional material from Patagonia described by Soria (1982); *Trigonostylops*, *Albertogaudrya*, *Scaglia* and *Astraponotus*, as described by Simpson (1967) with additional observations on more complete Mustersan *Astraponotus* materials, as yet undescribed,

housed at MPEF; *Parastrapotherium* as described by Scott (1937), with additional observations on type materials from the Ameghino Collection of MACN, described by Kramarz & Bond (2008); *Astrapothericulus*, following Ameghino (1904) and abundant, undescribed material from the Early Miocene Pinturas Formation (Santa Cruz Province) at the MACN; *Astrapotherium*, essentially as in Scott (1928); and the uruguaytheriines *Xenastrapotherium* (including *X. christi* Stehlin and *X. kraglievichi* Cabrera) and *Granastrapotherium* (Laventan SALMA, Middle Miocene), as described by Johnson & Madden (1997). The multi-state characters 1, 2, 7, 18, 21, 23 and 30 (see Appendix 2) were codified as ordered. Size of m2 (character 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* (only known through a juvenile partial skull with C-M1) was inferred by comparison with *Albertogaudrya*. Cranial characters were taken from Johnson & Madden (1997), with only minor modification. Relative size of the canines was not included in the analysis because of the great intraspecific variation due to sexual dimorphism. The data matrix is shown in Appendix 3.

A single most parsimonious tree (MPT) was obtained by exhaustive searching, with tree length = 87, consistency index = 71 and retention index = 76 (Fig. 7). *Maddenia lapidaria* clusters with the clade formed by *Parastrapotherium* and Miocene astrapotheres. This affiliation is strongly supported by six synapomorphies (Appendix 4): a well developed lingual valley in the P4 (character 8), absence of the labial fold of the metacone in P4 (character 9), presence of *crochet* in the M1-M2 (character 15), an anterolingual pocket in M1 (character 18), absence of p2 (character 24), and reduction of the hypoflexid in lower premolars (character 28). The great development of the hypocone in the P4 of *M. lapidaria* is identified as an autapomorphy and the reductions of the paralophid in the p4 and in the molars are herein interpreted as homoplastic.

These results suggest that astrapotheres show a clear trend toward increasing upper premolar complexity, from the Palaeocene to the Early Oligocene. *Maddenia lapidaria* and *Astraponotus* represent the most extreme stages of this process, in which even P2 has a complex occlusal pattern. However, at least since Deseadan times, the astrapotheres show a reversion of this trend, expressed by a drastic reduction in the size and number of premolars and secondary simplification of the remaining upper premolars. Therefore, the simple occlusal pattern of the upper premolars of the giant astrapotheriids is not derived from a primitive trigonodont one. This interpretation is in opposition to the progressive acquisition of astrapotheriid characters traditionally proposed for the Order (Simpson 1967; Soria 1984; Frailey 1987; Cifelli 1993).

The upper molars of *Maddenia* show a more advanced condition of occlusal complexity (well developed *crista* and *crochet*) with respect to *Astraponotus*, which clearly denotes this genus as the nearest structural ancestor of the giant Deseadan and younger astrapotheriids. However, this derived condition coexists with some characters, preliminarily interpreted as primitive and shared with the 'Albertogaudryinae' mentioned above (i.e. small size, slightly extroverted canines and short paralophid). The results of our analysis indicate that at least the poor development of the paralophid



**Figure 7** Single most parsimonious tree obtained by exhaustive searching (NONA; Goloboff 1993). Apomorphies are listed in Appendix 4.

(characters 27 and 29) is an autapomorphic reversion in *M. lapidaria*, probably related to its reduced body size, and would be associated to a habit different from that of the giant astrapotheres.

The relative positions of the remaining taxa in our cladogram (Fig. 7) do not differ significantly from those of previous phylogenetic proposals based upon dental and skeletal characters (Soria 1984; Frailey 1987; Cifelli 1993). Soria (1984: 180) considered *Albertogaudrya* on a collateral branch of the main lineage leading to *Scaglia* and *Astraponotus* and he grouped this genus with *Tetragonostylops* in his cladogram. Our analysis indicates that *Albertogaudrya* is more closely related to *Scaglia* and the astrapotheriids younger than Casamayoran (Casamayoran SALMA, Middle Eocene) by having more hypsodont cheek teeth (character 2) and a rudimentary hypocone in P4 (character 7). In fact, *Albertogaudrya* shows no autapomorphy that would justify separating it from the lineage leading to *Scaglia* and later astrapotheres, in agreement with Ameghino (1901), Pascual & Vucetich (*in* Carabajal *et al.* 1977) and Frailey (1987).

Johnson & Madden (1997) concluded that *Parastrapotherium* is close to *Astrapotherium* and that *Astrapothericulus* is the sister group of this clade plus the Uruguaytheriinae, but noted that this association is weakly supported. In any case, their proposal implies that *Parastrapotherium* (which has two lower premolars) would have derived from an ancestor with only one lower premolar, as in *Astrapothericulus*. Moreover, those authors did not consider that the cheek teeth of *Parastrapotherium* are positively lower crowned than those of *Astrapotherium* and *Astrapothericulus* (Kramarz & Bond, 2008). Our results (Fig. 7) suggest, rather, that *Parastrapotherium* is the sister group of all Miocene astrapotheres, all of them with higher crowned cheek teeth and more reduced dental formula.

Our results also allow a reassessment of the homology of some occlusal structures of the molars in the Astrapotheria. The M3 of *Parastrapotherium* and later astrapotheriids has a characteristic subtriangular outline and lacks a hypocone. Soria (1988) interpreted this condition as being directly derived from a trigonodont pattern as seen in *Eoastrapostylops* (the M3 of *Trigonostylops* also lacks a hypocone and *Tetragonostylops* has a modest posterolingual cingular cusp). Our

analysis indicates that, as in the case of the P4, the absence of a hypocone in the M3 of the 'Astrapotheriinae' (*sensu* Soria 1984) is a secondary reduction from an ancestor with a conspicuous hypocone, as in *Albertogaudrya*, *Astraponotus* and *Maddenia*. In these genera the hypocone is lower than the protocone and attached to its posterolingual slope; both cusps are partially separated by a shallow hypoflexus isolated from the central valley. The hypocone of the 'Astrapotheriinae' could be fused to the base of the protocone, which is typically projected backwards, partially occupying the position of the hypocone in M1 and M2. Some M3 of *Parastrapotherium* show a very superficial vertical groove on the posterolingual face of the protocone, which probably represents a vestigial hypoflexus.

Lower molars of the Uruguaytheriinae have no distinct entoconid. *Parastrapotherium*, *Astrapotherium*, *Astrapothericulus* and one species of *Xenastrapotherium* (Johnson & Madden 1997) have a characteristic small column or 'pillar' attached to the posterior face of the metaconid, which has been interpreted as homologous to the entoconid (Scott 1928, 1937; Paula Couto 1974; Soria 1988). Such an interpretation implies a drastic forward displacement of this cusp. However, *Trigonostylops*, *Albertogaudrya* and *Astraponotus* have a conspicuous entoconid located at the posterolingual corner of the crown and separated from the hypoconulid by a shallow notch. In *M. lapidaria* the entoconid is lower than the posterolophid and partially attached to the anterolingual slope of the hypoconulid. In *Parastrapotherium* there is a small excrescence on the base of the anterolingual slope of the posterolophid, the expected location for the entoconid, which can be interpreted as a remnant of this cusp, more reduced than in *M. lapidaria*. This pattern suggests an evolutionary trend in the pre-Deseadan astrapotheres toward reduction of the entoconid and its fusion to the hypoconulid, instead of a forward displacement of this cusp, and also that the pillar is an accessory element different from the entoconid. The presence of the pillar is not unambiguously distributed in our resulting cladogram, but it was very probably already present in the common ancestor of *Parastrapotherium*, *Uruguaytherium* and the Miocene genera. This pattern, which is observed for both the hypocone of M3 and the entoconid of lower molars, reveals that some occlusal structures



evolved differentially during the increase of hypsodonty and were gradually assimilated into proportionally taller structures.

The Uruguaytheriinae are traditionally typified by an extreme reduction of the lower molar hypoflexid (Kraglievich 1940; Johnson & Madden 1997). However, the hypoflexid of the lower molars of *Parastrapotherium* is moderately deep (Johnson & Madden 1997), as in *M. lapidaria*. This condition is herein interpreted as the ancestral one for *Uruguaytherium* and the Miocene astrapotheriids, from which it would have evolved into a reduction of this structure in the Uruguaytheriinae and, conversely, the development of a deep labial vertical cleft in *Astrapotherium* and *Astrapothericulus*. Thus the Astrapotheriinae–Uruguaytheriinae dichotomy is valid. The monophyly of the Uruguaytheriinae was advanced by Johnson & Madden (1997) and confirmed by our analyses (if *Uruguaytherium* is included, the three uruguaytheriines cluster in an unresolved trichotomy). Astrapotheriinae, as herein defined (*Astrapotherium* plus *Astrapothericulus*), is also a monophyletic group supported by the condition of the hypoflexid of the lower molars (character 30) and the presence of a continuous lingual cingulid (character 33). The p4 of *Astrapothericulus* lacks a hypoflexid (similarly to *Albertogaudrya*, *Maddenian* and *Parastrapotherium*) and this is a primitive condition; the presence of such a structure in *Astrapotherium* is here interpreted as an autapomorphy.

## CONCLUSIONS

The Order Astrapotheria has traditionally been interpreted as a small group of individually large and conservative ungulates (Simpson 1967; Paula Couto 1974; Cifelli 1993). *Maddenian lapidaria* documents the occurrence of a small Oligocene astrapothere representing an adaptive type that is different from that proposed for the post-Casamayoran forms. In spite of its small size, *Maddenian* is structurally intermediate between *Astraponotus* and *Parastrapotherium* in the development of the upper molars *crista* and *crochet*, the reduction of the lower molar entoconid and the reduction of the dental formula. Our analysis of the dentition of *M. lapidaria* and its comparison with that of other astrapotheres provides new information on the evolution of astrapothere dentition. Palaeocene–Eocene astrapotheres evolved toward increasing molar and premolar complexity and the upper dentition of *M. lapidaria* represents an extreme expression of this initial trend. A later evolutionary turnover resulted in a reduction in the size and number of premolars and secondary occlusal simplification. This interpretation challenges the progressive and unidirectional acquisition of astrapotheriid characters traditionally accepted for the Astrapotheria (Simpson 1967; Soria 1984; Frailey 1987; Cifelli 1993). The reduction in the size and number of premolars seems to be coincident, and probably associated with, the acquisition of hypsodonty and the enormous increase of body size, although this requires a more detailed analysis.

The phylogenetic analysis based on dental, mandibular and cranial features suggests that *Albertogaudrya* cannot be separated from the lineage leading to *Scaglia* and *Astraponotus* and that *Albertogaudryinae* is not a natural

group. *Parastrapotherium* is the sister group of the Uruguaytheriinae (*Uruguaytherium*, *Xenastrapotherium* and *Granastrapotherium*) and the Astrapotheriinae (*Astrapotherium* and *Astrapothericulus*) within Astrapotheriidae. Both subfamilies are monophyletic; the former is characterised by the reduction of the lower molar hypoflexid, and the latter by the deepening of this structure. Both extreme conditions evolved from an intermediate one represented by the morphology of *M. lapidaria* and *Parastrapotherium*. This dichotomy represents the terminal, and probably only, radiation of the Astrapotheriidae.

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## APPENDIX 1: DENTAL MEASUREMENTS FOR *MADDENIA LAPIDARIA* GEN. ET SP. NOV. (IN MM):

APD, maximum preserved anteroposterior diameter; TW, maximum preserved transverse diameter

| MPEF     |     | C1   | P2        | P3        | P4        | M1        | M2        | M3        | P3-M3 length        |
|----------|-----|------|-----------|-----------|-----------|-----------|-----------|-----------|---------------------|
| PV 7735  | APD | 15.2 | 7.6       | 11.7      | 13.1      | 15.8      | 18.8      | 17.3      | 72.9                |
|          | TW  | 10.7 | 8.0       | 16.2      | 20.1      | 19.9      | 22.8      | 23.1      |                     |
| PV 7013  | APD |      |           |           |           |           | 18.6      |           |                     |
|          | TW  |      |           |           |           |           | 23.8      |           |                     |
| PV 7707a | APD | 17.6 |           |           |           |           |           |           |                     |
|          | TW  | 11.5 |           |           |           |           |           |           |                     |
| PV 7707a | APD | 18.9 |           |           |           |           |           |           |                     |
|          | TW  | 11.4 |           |           |           |           |           |           |                     |
| PV 7707c | APD | 17.0 |           |           |           |           |           |           |                     |
|          | TW  | 11.9 |           |           |           |           |           |           |                     |
| PV 7724  | APD | 18.2 |           |           |           |           |           |           |                     |
|          | TW  | 17.0 |           |           |           |           |           |           |                     |
| PV 6238a | APD |      |           |           |           |           |           | 16.3      |                     |
|          | TW  |      |           |           |           |           |           | 23.2      |                     |
| PV 6145  | APD |      |           |           |           |           |           | 16.4      |                     |
|          | TW  |      |           |           |           |           |           | 22.3      |                     |
|          |     |      | <b>c1</b> | <b>p3</b> | <b>p4</b> | <b>m1</b> | <b>m2</b> | <b>m3</b> | <b>p3-m3 length</b> |
| PV 7738  | APD |      | 11.1      | 14.5      | 13.3      | 17.6      | 22.6      | 77.7      |                     |
|          | TW  |      | 8.1       | 9.9       | 10.5      | 11.6      | 11.2      |           |                     |
| PV 7774  | APD |      | 12.2      |           |           |           |           |           |                     |
|          | TW  |      | 11.8      |           |           |           |           |           |                     |
| PV 6254  | APD |      | 13.4      |           |           |           |           |           |                     |
|          | TW  |      | 12.8      |           |           |           |           |           |                     |
| PV 7727  | APD |      |           | 10.7      |           |           |           |           |                     |
|          | TW  |      |           | 7.7       |           |           |           |           |                     |
| PV 7082  | APD |      |           | 10.8      |           |           |           |           |                     |
|          | TW  |      |           | 8.3       |           |           |           |           |                     |
| PV 7696a | APD |      |           |           | 13.2      | 14.0      | 17.0      | -         |                     |
|          | TW  |      |           |           | 9.5       | 10.0      | 10.1      | 10.8      |                     |
| PV 7701  | APD |      |           |           | 12.1      | 14.0      | 16.3      | 20.5      |                     |
|          | TW  |      |           |           | 9.6       | 11.1      | 12.3      | 11.6      |                     |
| PV 7709  | APD |      |           |           |           |           | 17.5      | 23.4      |                     |
|          | TW  |      |           |           |           |           | 10.5      | 11.4      |                     |
| PV 6113  | APD |      |           |           |           |           | 16.0      |           |                     |
|          | TW  |      |           |           |           |           | 11.7      |           |                     |
| PV 7732  | APD |      |           |           |           |           | 18.0      | 22.6      |                     |
|          | TW  |      |           |           |           |           | 11.3      | 10.7      |                     |
| PV 7848  | APD |      |           |           |           |           | 17.3      | 21.0      |                     |
|          | TW  |      |           |           |           |           | 11.3      | 11.6      |                     |
| PV 6238b | APD |      |           |           |           |           | 16.9      |           |                     |
|          | TW  |      |           |           |           |           | 10.0      |           |                     |

## APPENDIX 2. 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. M1, anterolingual pocket: 0 = absent; 1 = weakly developed; 2 = well developed.
19. M1-M3, labial fold of the metacone: 0 = absent; 1 = present.
20. M3, hypocone: 0 = absent; 1 = present.
21. Number of lower incisors: 0 = all incisors present; 1 = i1 and i2 present, i3 absent; 2 = all incisors absent.
22. Lower incisors, crown shape: 0 = simple; 1 = bilobed.
23. Lower canine, implantation: 0 = not extroverted 1 = slightly extroverted; 2 = strongly extroverted.
24. p2: 0 = present; 1 = absent.
25. p3: 0 = present; 1 = absent.
26. p3, paralophid: 0 = reduced or absent; 1 = well developed.
27. p4, paralophid: 0 = reduced; 1 = well developed.
28. p4, hypoflexid: 0 = present; 1 = absent.
29. m1-m3, paralophid: 0 = reduced; 1 = well developed.
30. m1-m3, hypoflexid: 0 = deep; 1 = superficial; 2 = absent.
31. Lower molars, entoconid: 0 = present; 1 = absent.
32. m1-m3, pillar: 0 = absent; 1 = present.
33. Lower molars, lingual cingulid: 0 = absent; 1 = present.
34. Ventral inflection of the mandible: 0 = absent; 1 = present.
35. Angular process extending posterior to the condyle: 0 = present; 1 = absent.
36. Frontals: 0 = uninflated, narrow; 1 = broad, slightly domed; 2 = very broad, domed and inflated.
37. Bulla: 0 = attached; 1 = unattached.
38. Nasals: 0 = elongated; 1 = retracted.
39. Choanae: 0 = divided by a median septum of the palate; 1 = undivided.
40. Pterygoid or palatine processes: 0 = alate processes anterior to choanae; 1 = slight tubercles lateral to choanae; 2 = alate processes lateral to choanae, thickened ventrally.
41. Palatal portion of the palatines: 0 = broad, without lateral palatine notch; 1 = broad, with lateral palatine notch; 2 = narrow, elongate, broad, without lateral palatine notch.
42. Lacrimal and lacrimal foramen: 0 = on the orbital rim; 1 = within orbit, orbital rim projecting.
43. Zygomatic arches: 0 = not flaring, dorsoventrally shallow, maxillary root above M1-M2; 1 = not flaring, dorsally curved, dorsoventrally thick, maxillary root above M1-M2; 2 = flare widely, horizontal, dorsoventrally shallow, maxillary root above M2.
44. Sagittal and temporal crests: 0 = sagittal long, temporal crests weak; 1 = sagittal short, temporal crests strongly developed.
45. Infraorbital foramen: 0 = single foramen, positioned anterior to the orbit; 1 = multiple foramina, positioned very anterior to orbit; 2 = single foramen, positioned near the orbit.
46. Supraoccipital: 0 = not constricted; 1 = constricted.
47. Occipito-squamosal contact: 0 = occipital exposure of mastoid; 1 = extensive, no occipital exposure of mastoid.
48. Glenoid fossa: 0 = at the level of or anterior to the basioccipital–basisphenoid suture; 1 = posterior to the basioccipital–basisphenoid suture.
49. Post-tympanic process of the squamosal: 0 = very weak, far removed from paraoccipital process, 1 = weak, closely applied to paraoccipital process, 2 = strong, closely applied to paraoccipital process.

### APPENDIX 3. TAXON-CHARACTER MATRIX

Characters and character definitions are listed in Appendix 2. The taxon-character matrix used to assess the phylogenetic relationships of *Maddenia lapidaria* gen. et sp. nov. with well known astrapothere genera is listed below.

'?' indicates missing or unknown character; '-' indicates non-applicable character; 'a' = 0 or 1.

|                           | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
|---------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Eoastrapostylops</i>   | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | -  | 0  | 0  | 0  | ?  | ?  | 0  | 0  | 0  |
| <i>Trigonostylops</i>     | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 | 1 | 0  | a  | 0  | 0  | 0  | 0  | 0  | -  | 0  | 1  | 0  | 0  | 0  | 1  | 0  | 0  |
| <i>Tetragonostylops</i>   | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 | 1 | 0  | 1  | 1  | 0  | 0  | 0  | a  | -  | 0  | 1  | 1  | 0  | ?  | 0  | 0  | 0  |
| <i>Albertogaudrya</i>     | 1 | 1 | 1 | ? | 0 | 1 | 1 | 0 | 1 | 0  | 1  | 1  | 0  | 0  | 0  | 0  | -  | 0  | 0  | 1  | ?  | 0  | ?  | 0  | 0  |
| <i>Scaglia</i>            | 0 | 1 | ? | ? | ? | ? | ? | ? | ? | ?  | 1  | 1  | 1  | 0  | 0  | 1  | -  | 0  | 0  | ?  | ?  | ?  | ?  | ?  | ?  |
| <i>Astraponotus</i>       | 1 | 1 | 1 | 1 | 0 | ? | 1 | 0 | 1 | 1  | 1  | 1  | 1  | 1  | 0  | 1  | -  | 0  | 0  | 1  | 0  | 1  | 2  | 0  | 0  |
| <i>Maddenia</i>           | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 0  | 1  | ?  | ?  | 1  | 1  | 0  |    |
| <i>Parastrapotherium</i>  | 2 | 2 | 1 | - | 1 | 0 | 0 | 1 | 0 | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 1  | 2  | 1  | 0  |    |
| <i>Astrapotherium</i>     | 2 | 2 | 1 | - | 1 | 0 | 0 | 1 | 0 | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 0  | 1  | 2  | 1  | 1  |    |
| <i>Granastrapotherium</i> | 2 | 2 | 0 | - | 1 | - | 0 | 1 | 0 | 0  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 2  | 0  | 0  | 2  | -  | 0  | 1  | 1  |
| <i>Astrapothericulus</i>  | 1 | 2 | 1 | - | 1 | 0 | 0 | 1 | 0 | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 1  |
| <i>Xenastrapotherium</i>  | 2 | 2 | 0 | - | 1 | 0 | 0 | 1 | 0 | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 2  | 0  | 0  | 1  | 1  | 2  | 1  | 1  |

|                           | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 |
|---------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Eoastrapostylops</i>   | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | ?  | 0  | ?  | ?  | ?  | ?  | ?  | 0  | 0  | ?  | ?  | ?  | ?  |
| <i>Trigonostylops</i>     | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  |
| <i>Tetragonostylops</i>   | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 1  | 0  | ?  | 1  | 0  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |
| <i>Albertogaudrya</i>     | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 1  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |
| <i>Scaglia</i>            | ?  | ?  | ?  | ?  | ?  | ?  | 0  | ?  | ?  | ?  | 1  | ?  | 0  | 1  | 1  | ?  | ?  | ?  | ?  | 0  | ?  | ?  | ?  | ?  |
| <i>Astraponotus</i>       | 1  | 1  | 0  | 1  | a  | 1  | 0  | a  | 1  | 0  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |
| <i>Maddenia</i>           | 0  | 0  | 1  | 0  | 1  | 1  | 0  | 0  | 1  | a  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |
| <i>Parastrapotherium</i>  | a  | 1  | 1  | 1  | 1  | 0  | 1  | 0  | 0  | 1  | ?  | 1  | 1  | 1  | 2  | ?  | ?  | ?  | 1  | ?  | 1  | 1  | 0  | 1  |
| <i>Astrapotherium</i>     | -  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 2  | 1  | 1  | 1  | 2  | 1  | 1  | 1  | 1  | 2  | 1  | 1  | 0  | 1  |
| <i>Granastrapotherium</i> | -  | 1  | 1  | 1  | 2  | 0  | 0  | 0  | 0  | 1  | ?  | 1  | ?  | 1  | ?  | 2  | ?  | 2  | 1  | 2  | ?  | ?  | 1  | 2  |
| <i>Astrapothericulus</i>  | -  | 1  | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 1  | ?  | 1  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |
| <i>Xenastrapotherium</i>  | -  | 1  | 1  | 1  | 2  | 0  | 0  | 0  | 0  | 1  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |

### APPENDIX 4. LIST OF SYNAPOMORPHIES

Appendix 4 gives the list of synapomorphies that support each node of the single most parsimonious tree that was obtained in the analysis of the data matrix shown in Appendix 3, as well as the generic or suprageneric correspondance.

Characters in italics are reversions in relation to the state observed in the outgroup.

**Node 1:** 12(1), 20(1), 29(1); **Node 2:** 2(1), 7(1); **Node 3:** 13(1), 16(1); **Node 4:** (*Astrapotheriidae* sensu Cifelli 1993) 14(1); **Node 5:** 8(1), 9(0), 15(1), 18 (1), 24(1), 28(1); **Node 6:** 1(2), 2(2), 5(1), 7(0), 20(0), 31(1), 34(0); **Node 7:** 17(1), 25(1); **Node 8:** (*Uruguaytheriinae*) 3(0), 10(0), 18(2), 21(1), 30(2); **Node 9:** (*Astrapotheriinae*) 30(0), 33(1); **Node 10:** (*Trigonostylops*) 26(1), 45(1); **Node 11:** (*Astraponotus*) 26(1); **Node 12:** (*Maddenia*) 7(2), 27(0), 29(0); **Node 13:** (*Granastrapotherium*) 11(0), 21(2), 23(0); **Node 14:** (*Astrapotherium*) 28(0), 36(2); **Node 15:** (*Astrapothericulus*) 1(1).