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RESEARCH PAPER

New remains of *Astraponotus* (Mammalia, Astrapotheria) and considerations on Astrapothere cranial evolution

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Abstract *Astraponotus* Ameghino, 1901, the only valid Mustersan (late Eocene) astrapothere, typifies the Ameghino's "*Capas Astraponotenses*". This taxon is traditionally interpreted as structurally ancestral to all the Oligocene–Miocene astrapotheriids. However, it was imperfectly known: only isolated teeth and very partial mandibles have hitherto been described. In this contribution we provide the first description of the skull, mandible, and complete dentition of *Astraponotus* based on new materials from the Gran Hondonada and other Mustersan localities in central Patagonia, Argentina. The features observed in the dentition of *Astraponotus* are intermediate between the Casamayoran (middle Eocene) and the Oligocene–Miocene astrapotheres in the degree of hypsodonty, reduction of the dental formula, and development of accessory occlusal elements. Concordantly, the skull retains some plesiomorphies, also observed in *Trigonostylops*, whereas the auditory region and the basicranium are much closer to those of *Parastrapotherium*, *Astrapotherium*, and *Granastrapotherium*. On the other hand, the skull of *Astraponotus* differs from all known astrapotheres by the disproportioned height and narrowness of the braincase, the extreme reduction of the nasals and the premaxillaries, the absence of anteorbital rim, and the reduction of the frontal region. Some of these features represent cranial specializations exactly opposite to that of *Astrapotherium*. These characters look astonishingly derived for an Eocene astrapothere, suggesting that extreme cranial specializations occurred independently during the evolution of the order, and that *Astraponotus* represents a distinctive lineage from that of *Astrapotherium* and other Miocene forms.

Keywords *Astraponotus* · *Astrapotherium* · *Trigonostylops* · Eocene · Patagonia

Kurzfassung *Astraponotus* Ameghino, 1901, der einzige valide Astrapothere aus dem Mustersan (spätes Eozän), diagnostiziert die "Capas Astraponotenses" von Ameghino. Dieses Taxon wurde traditionell als strukturell ursprünglich im Vergleich zu allen Oligozänen-Miozänen Astrapotheriiden angesehen. Allerdings war es nur unzulänglich bekannt: nur isolierte Zähne und teilweise erhaltene Dentalia wurden bisher beschrieben. Hier beschreiben wir zum ersten Mal den Schädel, Unterkiefer und die gesamte Bezahnung von *Astraponotus* auf der Basis von neuen Materialien aus der Gran Hondonada und anderen Mustersanen Lokalitäten im zentralen Patagonien. Die in der Bezahnung beobachteten Merkmale von *Astraponotus* sind intermediär zwischen Astrapotheren des Casamayor (mittleres Eozän) und des Oligozän-Miozän in Hinsicht auf Hypsodontie, Reduktion der Zahnformel und der Entwicklung zusätzlicher Okklusionsstrukturen.

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Zusätzlich behält der Schädel einige Plesiomorphien bei, wie sie auch bei *Trigonostylops* vorkommen, während die Gehör-Region und die Schädelbasis bereits jenen von *Parastrapotherium*, *Astrapotherium* und *Granastrapotherium* deutlich ähnlicher sind. Auf der anderen Seite unterscheidet sich der Schädel von *Astraponotus* von jenen aller anderen Astrapotheren durch den ungewöhnlich hohen und schmalen Hirnschädel, die extreme Reduktion der Nasalia und Prämaxillaria, das Fehlen eines anteorbitalen Randes und die Reduktion der Frontal-Region. Diese Merkmale erscheinen erstaunlich fortschrittlich für einen eozänen Astrapotheren und deuten darauf hin, dass extreme Spezialisierungen des Schädels unabhängig in der Evolution der Ordnung entstanden sind und dass *Astraponotus* eine eigene Entwicklungslinie, getrennt von jener von Astrapotherium und anderer Miozäner Formen, darstellt.

Schlüsselwörter *Astraponotus* · *Astrapotherium* · *Trigonostylops* · Eozän · Patagonien

Introduction

Astrapotheria is one of the most enigmatic, specialized groups of South American native ungulates, and it includes the largest species within the Cenozoic native faunas. These mammals have recently been hypothesized to be the sister taxa of notoungulates + pyrotheres (Billet 2010), although this hypothesis needs to be substantiated in a broader taxonomic context. Astrapotheres are characterized by having strongly retracted nasals suggesting the presence of a proboscis (at least in the later forms), enlarged canines, and rhino-like cheek teeth, among other features (Ameghino 1894; Scott 1937). The best known genus is *Astrapotherium*, which is abundant in Santacrucian (early Miocene) strata, known through a nearly complete skeleton, and several almost complete skulls and jaws with dentition (Scott 1928, 1937). Cranial and mandibular remains and the complete dentition are known for most of the remaining astrapotheres (Ameghino 1904; Gaudry 1904; Simpson 1933, 1957, 1967b; Scott 1937; Paula Couto 1952, 1963; Soria and Powell 1981; Soria 1984, 1987; Soria and Bond 1984; Frailey 1987; Johnson and Madden 1997; Kramarz 2009; Kramarz and Bond 2008, 2009); the postcranial skeleton is represented by mostly isolated parts and only for few of the remaining taxa.

By the late Eocene (Mustersan SALMA), the only valid genus currently recognized is *Astraponotus* Ameghino 1901. This taxon was traditionally interpreted as structurally ancestral to all the post-Eocene astrapotheriids (Scott 1937; Soria 1984; Cifelli 1993). *Astraponotus* was, by now, very imperfectly known; only isolated teeth (Ameghino 1901; Simpson 1967b) and fragmentary mandibles (Simpson 1967b; Carabajal et al. 1977) were hitherto referred to this taxon. Ameghino (1906) selected this genus to typify his "*Capas Astraponotenses*"; nevertheless, this taxon is one of the rarest in these beds (Simpson 1967b).

Odreman Rivas (1978) reported the discovery of an unusual Mustersan fossil concentration at the Gran Hondonada locality (El Pozón site), in central Patagonia, Argentina (Fig. 1). A later party from the Museo Paleontológico Egidio Feruglio (Trelew) recovered a large amount of vertebrate remains, that included three partial skulls of *Astraponotus*, besides reptiles, birds, and a broad diversity of mammals (i.e., metatherians, xenarthrans, condylarths, litopterns, and notoungulates; Cladera et al. 2004). The fossils were disarticulated and chaotically accumulated in fluvial channels, with little evidence of transportation (Cladera et al. 2004), leading to an excellent preservation. In this contribution, we provide the first description of the skull and upper dentition of *Astraponotus*, based on new material collected from the Gran Hondonada locality, and compare them primarily with

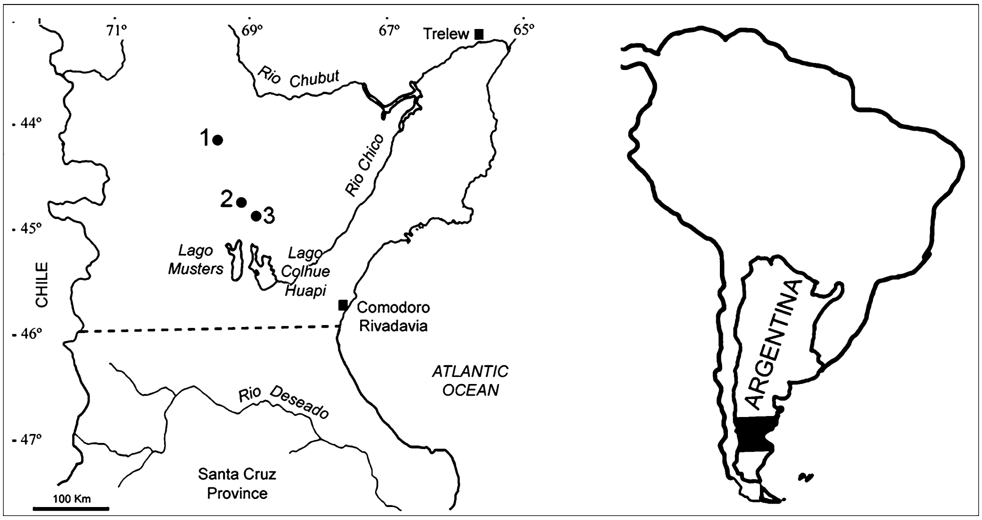

Fig. 1 Location map showing the Mustersan (late Eocene) localities (Chubut Province, Argentina) bearing the *Astraponotus* material studied here. *1* Gran Hondonada; *2* Cerro del Humo; *3* Cerro Talquino

Astrapotherium (as described by Scott 1928, 1937), *Trigonostylops* (middle-late Eocene; as described by Simpson 1933, 1967b) and other known astrapotheres. Additionally, we complete the description of *Astraponotus* with more complete mandibles with dentition collected from Gran Hondonada and other Mustersan localities of central Patagonia. The specimens used for comparisons are listed in Appendix 1 of electronic supplementary material. The described materials provide new and relevant anatomical data for a preliminary discussion about the cranial and dental character evolution within the Order Astrapotheria. Phylogenetic comments are based on recent results obtained by Kramarz and Bond (2009) and Billet (2010). A more exhaustive analysis will be performed in further works.

Abbreviations

AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; MLP, Museo de La Plata; MMMP, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata; MPEF-PV Museo Paleontológico "Egidio Feruglio", Colección Paleontología Vertebrados, Trelew; YPM PU, Yale Peabody Museum, Princeton University Collection (New Haven). I/i, incisive, C/c, canine, P/p, premolar, and M/m, molar (capital and lower case letters refer to upper and lower teeth, respectively). SALMA, South American Land Mammal Age.

Systematic palaeontology

Order Astrapotheria (Lydekker 1894)

Family Astrapotheriidae Ameghino 1887

Astraponotus Ameghino 1901

Type species. Astraponotus assymmetrus Ameghino 1901

Referred species (after Simpson 1967b). *Astraponotus holdichi* (Roth 1903), *Astraponotus dicksoni* (Roth 1903), *Astraponotus thompsoni* (Roth 1903), and *Astraponotus dilatus* (Roth 1903).

Distribution. Mustersan SALMA (late Eocene). Chubut Province, Argentina.

Astraponotus sp.

Materials

MPEF PV 1084, partial skull with almost complete basicranium and occiput, right side of the braincase and zygoma, base of the right canine, and right and left P2–M3. MPEF PV 1279, left half of the skull with almost complete rostrum, left P2–P3, and M3 and alveoli for P4–M2; MPEF PV 1296, right maxillary fragment with erupting canine and DP2–M1, and left maxillary fragment with erupting canine and DP2–DP4, very probably belonging to a single individual; MLP 67-II-27-28, right mandibular fragment with p2–m3; MLP 67-II-27-379, almost complete lower jaw with partial dentition; MLP 67-II-27-167, partial symphysis with right canine and left p2; MLP 83-III-3-1, incomplete right lower jaw with, c-m3, MLP 82-V-7-2, incomplete lower jaw with almost complete dentition; MLP 69-III-24-295, subadult right mandibular fragment with c, p4–m2.

Provenance

MPEF PV 1084, 1279, 1296, MLP 67-II-27-28, 67-II-27-379, 67-II-27-167, and 69-III-24-295 come from the Sarmiento Formation at the Gran Hondonada locality, S 44°20′49″, W 69°46′57″ (Cladera et al. 2004; el Pozón site after Odreman Rivas 1978), Department of Tehuelches, Chubut Province. MLP 83-III-3-1 comes from Mustersan levels of the Sarmiento Formation at Cerro del Humo locality (Bordas 1945; Simpson 1967a), Department of Sarmiento, Chubut Province. MLP 82-V-7-2 comes from Mustersan levels of the Sarmiento Formation at the eastern slope of Cerro Talquino (Bordas 1945; Simpson 1967b), Department of Sarmiento, Chubut Province, Argentina.

Description and comparisons

Skull

The available skulls are very high, with the braincase extremely narrow (Fig. 2a–b). The observed proportions could be emphasized by *post mortem* compression. However, both skulls have similar proportions, with only minor evidence of crushing on bones and overlapping. Moreover, the zygomatic arches, which are usually the parts of the skull most susceptible to deformation, are completely free from distortion in both skulls. Therefore, our interpretation is that the current aspect of the skull was not very different from the original. Cranial measurements are shown in Table 1.

In lateral view (Fig. 2a), the upper profile of the skull describes a marked convex line, interrupted solely by the free anterior margin of the nasals. The rostrum is clearly different from that of *Astrapotherium.* Its lateral margins are shallowly concave, not constricted in front of the orbits. The facial process of the maxilla is higher, especially below the nasals. The facial process bears a shallow but extended rostral fossa anterior to the orbit, such as in *Trigonostylops,* which is here interpreted as corresponding to muscular attachments. In the adult specimen MPEF PV

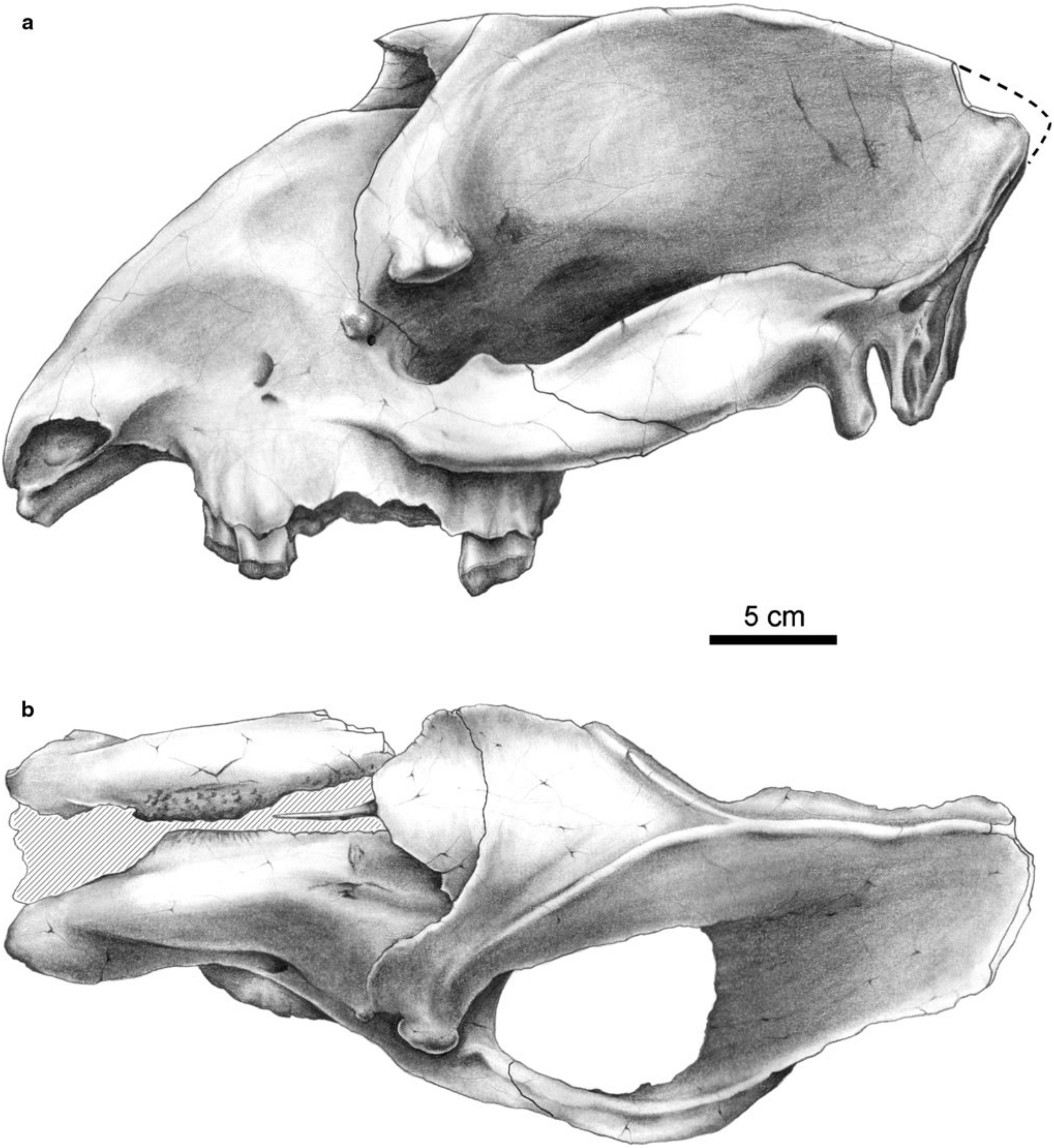

Fig. 2 *Astraponotus* sp. MPEF PV 1279 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Partial skull in lateral (**a**) and dorsal (**b**) views

1279, there are two infraorbital foramina located at the lower portion of the rostral fossa, above P4, far from the orbit; the larger foramen is set dorsally and slightly more anterior than the second aperture. In the juvenile specimen MPEF PV 1296 there are at least three preserved infraorbital foramina above the DP2. In *Trigonostylops* (only known through adult skulls, Simpson 1933, 1967b; Soria and Bond 1984), there are at least five infraorbital foramina also located far from the orbit. Adult specimens of *Astrapotherium*, *Astrapothericulus*, and *Granastrapotherium* (Laventan SALMA, middle Miocene) have a single foramen, but a juvenile specimen referred to *Astrapotherium*

Table 1 Cranial measurements of *Astraponotus* sp. (in cm) from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene)

	MPEF PV 1084	MPEF PV 1279
Maximum preserved cranial length (without premaxillaries)	–	40.4
Palatal width between canines	–	6.76
Palatal width between P4s	3.84	–
Palatal width between M3s	5.67	–
Basicranium width between postglenoid processes	8.49	
Cranial height at orbital level	–	20.1
Occipital height (including condyles)	16.3	–
Occipital width	13.85	–
Inter-zygomatic width (estimated)	23.7	–
Orbital height	–	3.58

(MLP 38-X-30-1) has three foramina, all located on the orbital rim, more posterior than in *Astraponotus*.

The alveolar sheaths for the canines are strongly curved, less divergent, and longer than in *Astrapotherium,* extending up from a point above the orbits to nearly the palatal level. The canine alveolus opens more lateral than in *Astrapotherium*. The alveolar sheaths are dorsally exposed because of the extreme reduction of the nasals. The nasal channel is, therefore, well exposed, long and deep between the maxillae. The nasals are extremely short, far removed from the maxillaries. These bones are located at the level of the orbits, even more retracted than in *Astrapotherium*. The free anterior portion of the nasals overhangs the posteriormost part of the nasal channel, such as in *Astrapotherium*. In anterior view, the nasals are convex, forming part of the domed forehead. In contrast to *Astrapotherium*, the nasals in *Astraponotus* are not upturned; they are more laterally extended, and are not interposed in a deep notch of the frontals. As seen in anterior view, the external nasal aperture is wide and low, limited laterally by the frontals, dorsally by the nasals, and ventrally by the maxillae. Both sides of the nasal cavity are separated by a thin median septum, which descends towards the nasal channel.

In dorsal view (Fig. 2b), the frontals are retracted and form a small triangular portion of the skull roof. These bones are transversely narrow and convex, more so than in *Astrapotherium*, and do not form a broad roof over the orbits. The postorbital process is represented by a prominent and blunt projection of the frontals. There is a notch at the anterior base of the postorbital process, which may be homologous to the supraorbital foramen, such as that seen in living ungulates, for the supraorbital nerve and vessels (Sisson 1965). In *Astrapotherium*, instead of a notch, there is a large foramen perforating the robust postorbital process (Scott 1928, 1937). In the skull of *Astraponotus*, the temporal crests are subtly defined above the orbits, becoming more prominent backward. They are posteriorly concave and shorter than in *Astrapotherium*. The temporal region of the skull is broad, bearing numerous scars, suggesting that the temporal musculature was robust. The postorbital portion of the frontals, which forms part of the temporal region, is very high and slightly convex. Similar to *Astrapotherium*, there is no postorbital constriction, differing thus from other generalized forms, for example *Trigonostylops* (Simpson 1933, 1967b).

The orbits are very small and located nearly at the same height as the external acoustic meatus, comparatively lower than in *Astrapotherium* and *Trigonostylops*. The anteorbital rim is not prominent; consequently, the orbits are very shallow and partially visible in anterior view. The lachrymal foramen is very small and exposed laterally. In the specimen MPEF PV 1279, there is a small, rough area on the anterior border of the orbit, anterior and dorsal to the lachrymal foramen. Although no suture is evident in the material, this area is interpreted here as corresponding to the lachrymal bone, according to that observed in *Trigonostylops* (Simpson 1933). In *Astrapotherium*, there is a very prominent anteorbital rim, thus the orbits face completely laterally and the lachrymal foramen and the lachrymal bone are intraorbital (Simpson 1933). In *Astraponotus,* the portion of the maxilla forming the floor of the orbit, or orbital platform, is very short and wide. In posterior view, the maxilla forms an extremely high vertical wall behind the roots of M3. In the specimen MPEF PV 1084, a foramen is located on the medial part of this wall, very close to the orbital portion of the frontal (Fig. 3). This aperture is interpreted here as the maxillary foramen. A second and smaller foramen, which would correspond to the sphenopalatine foramen, is located more ventral to the former, near (and probably involving) the palatine bone. There are, in addition, two tiny foramina: one is located between the maxillary and sphenopalatine foramina; the other is ventral to the sphenopalatine foramen. Because of the proximity, with the apertures related to the passage of the maxillary division of the trigeminal nerve (i.e., maxillary foramen and sphenopalatine foramen), it is probable that these tiny foramina would transmit some of its branches. If so, they would correspond to

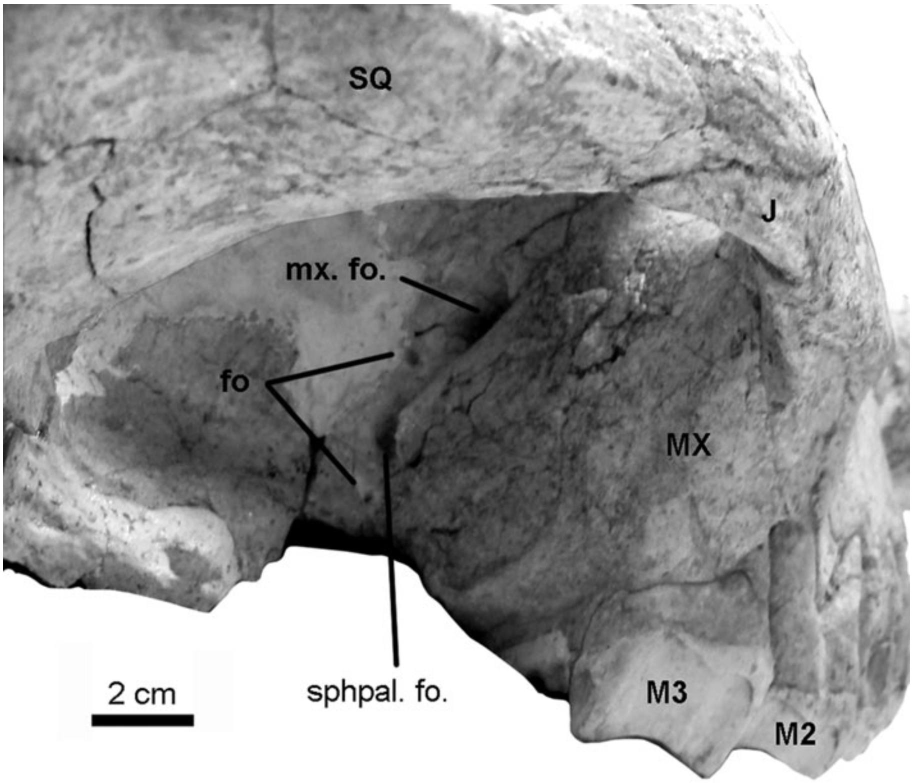

Fig. 3 *Astraponotus* sp. MPEF PV 1084 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Ventral part of the right orbital cavity, in posterior view. *Abbreviations fo.* alveolar foramina and/or caudal palatine foramen?, *J* jugal bone, *MX* maxillary bone, *mx. fo.* maxillary foramen, *sphpal. fo.* sphenopalatine foramen, *SQ* squamosal bone

alveolar foramina and/or the caudal palatine foramen. All these foramina are roughly aligned and seen only in posterior view. In contrast, in *Astrapotherium* the sphenopalatine foramen is much larger, and the maxillary foramen opens more anterior. In both available skulls of *Astraponotus*, the ventro-lateral wall of the cranium is extremely crushed and no particular structure is distinguishable. The only preserved features are a set of shallow grooves for vasculature, radiating upward and forward from the presumed position of the optic and sphenorbital fissure, similar to *Astrapotherium.*

The zygomatic arch is slender, in comparison with *Astrapotherium* and *Granastrapotherium,* with a backward sigmoid profile, not as straight as in the latter genera. The anterior root of the zygoma is located above the posterior part of the M2 and M3, as in *Granastrapotherium*, more posterior and less laterally projected than in *Astrapotherium* and *Trigonostylops*, and closely appressed to the suborbital portion of the maxilla. The jugal is short, high, and even taller at the level of the frontal process. Ventrally, the jugal extends backwards, almost reaching the glenoid cavity, as in *Astrapotherium*. In lateral view, the zygomatic process of the squamosal is higher and longer than the jugal, contributing to most of the length of the zygoma. Similar to *Astrapotherium*, the postglenoid process of *Astraponotus* is robust, as high as wide, restricted to the medial portion of the glenoid cavity, but it is slightly more concave anteriorly than in the former genus. The glenoid cavity is narrower, with the main axis more transverse, and located at the level of the basioccipital—basisphenoid suture, as in *Granastrapotherium* and more posterior than in *Astrapotherium.*

The fronto-parietal suture is hardly distinguishable on the lateral wall of the braincase. Only a small portion is observed, slightly anterior to the origin of the sagittal crest. The parietals are long, extremely high, mostly vertical, and becoming gradually concave to the back. The sagittal crest is robust and prominent, and it extends over most of the length of the cranial roof, being much longer than in *Astrapotherium.* The posterior portion of the parietals bear a variable number of emissary foramina irregularly distributed, such as in *Trigonostylops* and *Astrapotherium.* Some of them are aligned to the fronto-squamosal suture, similar to *Trigonostylops*. The squamous portion of the squamosal is almost excluded from the side-wall of the braincase. It forms a long, laterally expanded, and concave plate above the glenoid cavity and the external auditory meatus, rising posteriorly. Accordingly, there is a continuous lateral crest that extends from the zygoma to the occipital nuchal crest. This morphology is more similar to that of *Trigonostylops* than *Astrapotherium*, in which the squamosal is narrower and shorter, with a strong constriction between the dorsal rim of the zygoma and the nuchal crest.

In the available skulls of *Astraponotus*, all the elements of the occiput are tightly fused. The occiput differs from that of *Astrapotherium* in being wider, more oblique,

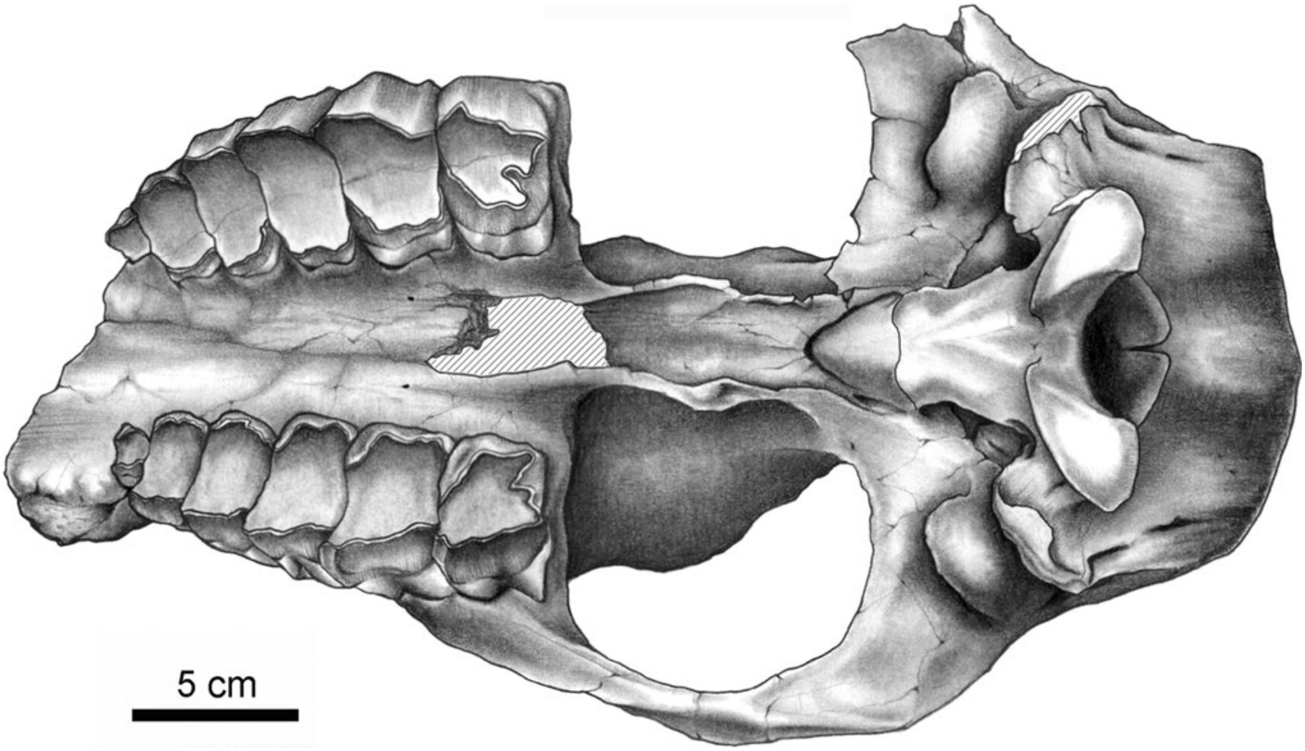

Fig. 4 *Astraponotus* sp. MPEF PV 1084 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Partial skull with almost complete dentition, in ventral view

poorly sculptured, and not constricted. The foramen magnum in *Astraponotus* is wider than it is higher. Consequently, the condyles are more separated than in *Astrapotherium*. The dorsal margin of the foramen magnum has a conspicuous median notch that is better defined than in *Trigonostylops* and much more than in *Astrapotherium.* The condyles are proportionally smaller, less protruding, and with the main axis more oblique than in *Astrapotherium*. In the specimen MPEF PV 1084, there is a small condylar foramen placed at the base of the right condyle. This aperture is absent in the other side of the skull, and for that reason we interpret it as being for a vein.

The palate (Fig. 4) is formed by the maxilla anteriorly and palatine posteriorly. The premaxillae are not preserved in any of the available specimens, but a very small anterior triangular slit between both maxillae suggests the projection of a very short wedge of premaxillae, extending backwards up to the anterior margin of the canine alveolus. In *Astrapotherium,* the premaxillae lie in a long triangular notch that extends backwards to the level of the posterior margin of the canine alveolus (Scott 1928, 1937). The anterior part of the palatine plates of the maxilla is strongly convex, extending forward ahead of the canine alveoli. The anterior rim of the maxilla is thick and bears a very conspicuous notch that faces anteriorly on each side of the skull. This notch is herein interpreted as the posterior border of the incisive foramen, which would be closed anteriorly by the now missing premaxilla. According to this disposition, the foramen would open anteroventrally, similar to what occurs in *Astrapotherium.* The palate is long, slightly constricted in front of the P2, and transversely concave. The feeble observable portions of the palatine sutures suggest that the palatine extends forward at least to a point between the M2s. There is no ridge along the median suture, differing from the morphology in *Astrapotherium.* One pair of small palatal foramina is located between the M2s; these probably represent the major palatine foramina, following the ungulate architecture (Sisson 1965). In the specimen MPEF PV 1279 (Fig. 4), a small portion of the border of the choanes is preserved. It is located at the level of the M2 (more anterior than in *Trigonostylops*, *Astrapotherium* and *Granastrapotherium*). There are no lateral palatine notches, differing from what occurs in *Astrapotherium* and *Granastrapotherium.* None of the available skulls has the posterior portion of the palate completely preserved. Therefore, the presence of a median septum of the choanes, as is present in *Trigonostylops* (Simpson 1933, 1967b), or other median palatal structures is uncertain. The roof of the nasopharyngeal passage is formed by two medially expanded bones sutured at the midline that are herein interpreted as corresponding to the pterygoids. If so, the presphenoid and the anterior portion of the basisphenoid lay hidden above the pterygoids, such as in some living artiodactyls. In contrast, in *Trigonostylops*, *Astrapotherium*, and other

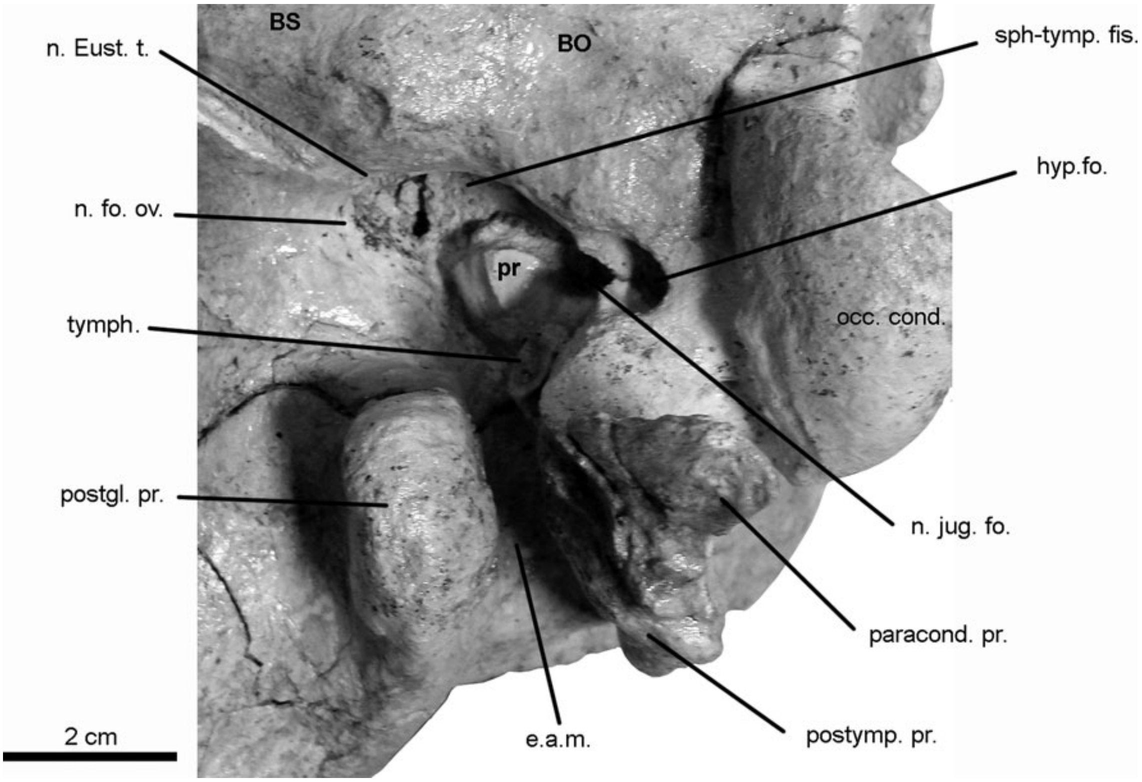

Fig. 5 *Astraponotus* sp. MPEF PV 1084 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Right auditory region, in ventral view. *Abbreviations BO* basioccipital, *BS* basisphenoid, *hyp. fo.* hypoglossal foramen, *e. a. m.* external acoustic meatus, *n. Eust. t.* notch for Eustachian tube, *n. fo. ov.* notch for foramen ovale, *n. jug. fo.* notch for jugular foramen, *paracond. pr.* paracondylar process, *postgl. pr.* postglenoid process, *postymp. pr.* postympanic process, *pr.* promontorium, *occ. cond.* right occipital condyle, *sph-tymp. fis.* sphenotympanic fissure, *tymph.* tympanohyal

Miocene astrapotheriids, the presphenoid is exposed in ventral view.

The general morphology of the basicranium and the auditory region (Figs. 4, 5) closely resembles that of *Astrapotherium*, *Parastrapotherium* (late Oligocene–early Miocene), and *Granastrapotherium*. The basicranium is wide and short, reaching nearly one third the total length of the skull. The postglenoid and the post-tympanic processes of the squamosal are long, close to each other, and enclosing a very deep external acoustic meatus. There is no exposure of the mastoid in posterior view, in contrast with the condition observed in *Trigonostylops* (Simpson 1933). None of the elements of the auditory bulla has been preserved, and there is no border suggesting the area of attachment for the tympanic. This bone was probably loosely attached to the skull, as suggested for *Astrapotherium* by Scott (1928, 1937). The tympanic cavity is deeply excavated and well-exposed in ventral view (Fig. 5). The petrosal is located dorsal to the horizontal plane of the skull defined by the basisphenoid. The only portion of the petrosal clearly seen is the promontorium, which is globular, teardrop-shaped, bearing a crest-like ventral process. In the specimen MPEF-PV 1084, the right tympanohyal has been preserved. This is a short, vertical bone attached to the petrosal and closely appressed to the base of the paracondylar process. The base of the tympanohyal is wider than the rest of the bone and oval in cross section. In ventral view, a round foramen opens on the mid-lateral part of the process that directs vertically. The hypoglossal foramen opens in a deep depression of the exoccipital separated from the depression into which the jugular foramen opens. There is a large gap between the petrosal, basisphenoid, and alisphenoid, which is interpreted here as the sphenotympanic fissure following Gabbert (2004), which is located ventral to the position of the piriform fenestra if the bulla were present. Similar to *Astrapotherium*, there are two notches at the anterior border of the fissure, defined by the alisphenoid. The lateral and largest notch is interpreted as the anterior border of the foramen ovale, thus the foramen is not individualized, whereas the most medial one is interpreted as the notch for the passage of the Eustachian tube. In contrast, in *Trigonostylops* there are two close foramina separated by a septum of the alisphenoid. A separate aperture for the carotid foramen

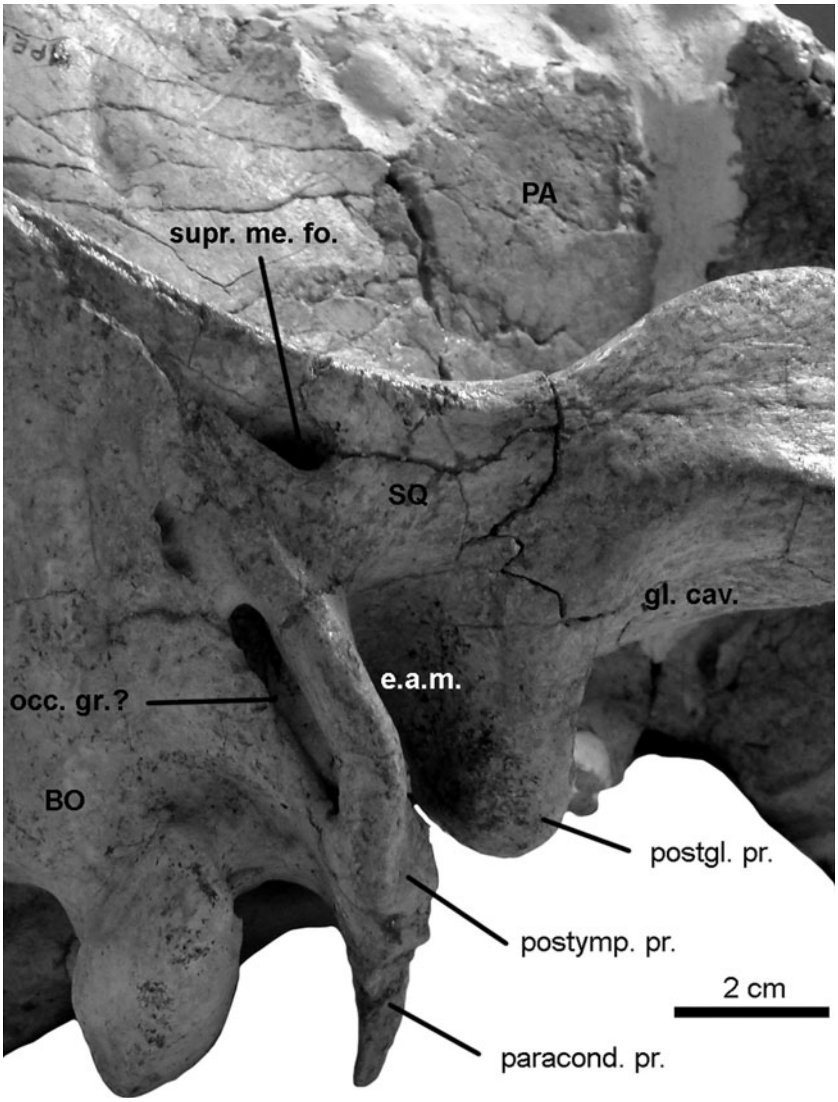

Fig. 6 *Astraponotus* sp. MPEF PV 1084 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Occipital and auditory region, in postero-lateral view. *Abbreviations BO* basioccipital, *e. a. m.* external acoustic meatus, *gl. cav*. glenoid cavity, *occ. gr.?* occipital groove? (or mastoid foramen; see text for discussion), *PA* parietal bone, *paracond. pr.* paracondylar process, *postymp. pr.* postympanic process; *SQ* squamosal bone, *supr. me. fo.* suprameatal foramen

could not be identified; neither could the aperture of the vidian foramen. Therefore, our interpretation is that the large sphenotympanic fissure housed, in life, the passage for the internal carotid artery, the nerves of the pterygoid canal, the mandibular branch of the trigeminal nerve, and the Eustachian tube as mentioned above. A similar construction was described for notoungulates and pyrotheres (Gabbert 2004; Billet 2010). In posterior view, the post-tympanic process and the paracondylar process of the exoccipital enclose a deep, narrow fissure, which bears two openings, one above the other (Fig. 6). Because the associated intracranial grooves could not be followed in the specimens of *Astraponotus*, the homology of this aperture is uncertain. If the opening connects to a component of the stapedial system, then this structure was for arterial passage and the fissure could be interpreted as the occipital groove and the openings as the post-temporal canal, following the architecture of basal mammals (Wible 1987; Wible and Gaudin 2004). In contrast, if the opening connects to the transverse or sigmoid sinus, it was for venous passage and the aperture would correspond to the mastoid foramen, as interpreted for notoungulates and pyrotheres (Gabbert 2004; Billet 2010), although the published data (Roth 1903; Patterson 1932; Gabbert 2004; Billet 2010) give no special reasons for this interpretation.

Despite major architectural resemblances with *Astrapotherium* and other Miocene astrapotheres in the basicranium, several subtle differences with this genus can be remarked. The basioccipital has a median keel and lateral grooves that are less evident than in *Astrapotherium*, although more than in *Trigonostylops*. The junction between the basioccipital and the basisphenoid is angled and has blunt basilar tubercles. This angle at the bone junction is even more evident than in *Astrapotherium* and *Trigonostylops*. In *Astrapotherium* there is a deep notch at the anterior base of the paracondylar process, between the

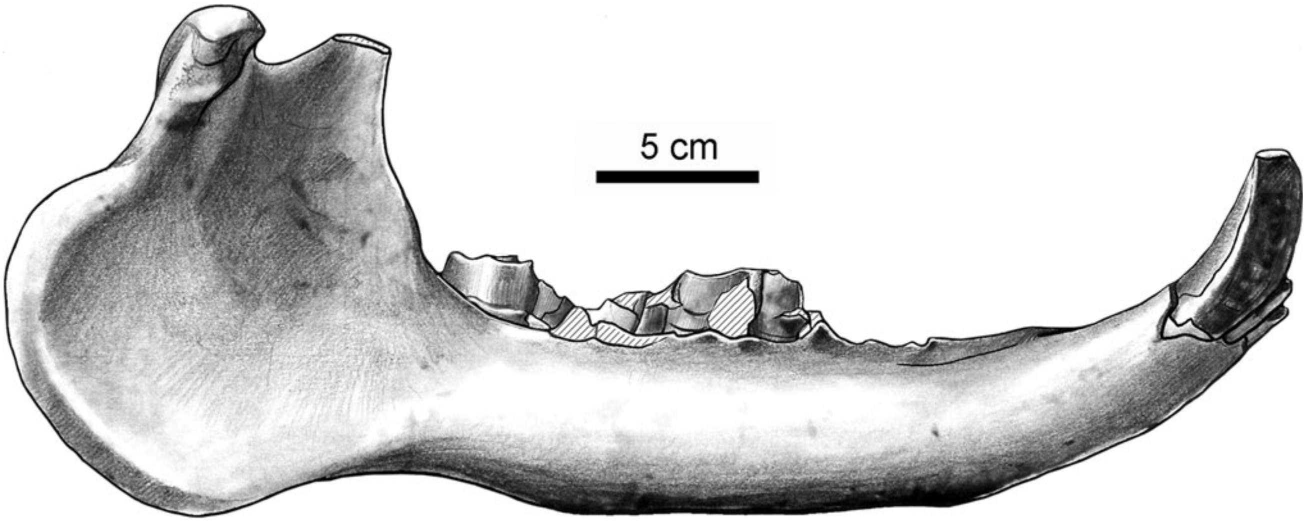

Fig. 7 *Astraponotus* sp. MLP 67-II-27-379 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Right dentary with partial dentition, in lateral view

petrosal and the exoccipital. This notch corresponds to the posterior border of the jugular foramen, and is much less pronounced in *Astraponotus*. The hypoglossal foramen is close to the notch of the jugular foramen (Fig. 5), as in *Trigonostylops*, but separated by a thin, laminar bone, whereas in *Astrapotherium* the posterior border of the hypoglossal foramen is thicker. Unlike *Astrapotherium*, the hypoglossal and condylar foramina are exposed in ventral view, not hidden by the overhanging posterior margin of the condyle. The postglenoid and the post-tympanic processes are closer in *Astraponotus*, thus the gap for the external acoustic meatus is narrower than in *Astrapotherium*. The paracondylar process is proportionally longer (vertically), with its distal end laminar and slightly concave posteriorly and medially, not blunt as in *Astrapotherium*. The fissure between the post-tympanic and the paracondylar processes extends more ventrally than in the Santacrucian genus. There is a suprameatal foramen at the base of the post-tympanic process, dorsal and slightly posterior to the external acoustic meatus, and ventral to the suprameatal bridge (Fig. 6); this foramen was not recognized in *Astrapotherium* or in *Trigonostylops*. The postglenoid foramen was not observed in any of the specimens of *Astraponotus* at hand; in contrast, *Astrapotherium* has a very large postglenoid foramen located at the level of the medial border of the postglenoid process. The notch on the alisphenoid for the passage of the Eustachian tube is less evident than in *Astrapotherium*.

Dentary

A partial mandibular symphysis with canines (AMNH 2930) was described by Simpson (1967b). Carabajal et al. (1977) illustrated, but did not describe, a mandibular fragment with p3–m3 (MLP 67-II-27-28). Additional almost complete adult jaws with dentition and a subadult right mandible complete our knowledge of the dentary and lower dentition. As described by Simpson (1967b) the symphysis is long, wide, and strongly procumbent; the incisors are implanted nearly horizontal and the canines are very extroverted, as in *Astrapotherium*, but there is no ventrolateral tuberosity for the base of the canines and the symphysis is more constricted behind the canines. However, in the subadult MLP 69-III-24-295 (with un-erupted m3) the symphysis is comparatively narrower, shorter, less procumbent, and the canine is implanted nearly horizontally. Similar ontogenetic differences are observed in *Parastrapotherium* and *Astrapotherium*. The diastema is comparatively shorter than in the latter genus, because of the presence of two additional anterior premolars (i.e., p2–p3), and slightly more concave anteroposteriorly. The horizontal ramus is narrow and low; ventrally it is somewhat convex in the adult specimens (Fig. 7), similar to the early Miocene *Astrapothericulus*, but strongly convex in the subadult MLP 69-III-24-295, as in *Albertogaudrya* (Casamayoran SALMA, middle Eocene). In contrast, the ventral border is almost completely straight in adults of *Parastrapotherium* and of all the remaining Miocene astrapotheres. The vertical ramus is high, but not as high as in *Astrapotherium*, the coronoid process is more recurved, and the sigmoid notch is longer than in the latter genus. The condyles are cylindrical, proportionally wider than in *Astrapotherium*. The angle is slightly deflected laterally, extended ventrally beyond the ventral level of the horizontal ramus, forming a marked ventral inflection, and posteriorly beyond the condyle, as in *Maddenia* (early Oligocene) and all the Paleocene and

Table 2 Dental measurements of *Astraponotus* sp. (in cm) from Gran Hondonada, Cerro del Humo, and Cerro Talquino localities, Chubut Province, Argentina; Mustersan SALMA (late Eocene)

		C1	DP2	DP3	DP4	P2	P3	P4	M1	M2	M3	P2–M3 length	DP2–M1 length
MPEF PV 1084	MPL	–	–	–	–	–	2.08	2.25	2.51	3.21	3.18	13.47	–
	MPW	–	–	–	–	1.68	3.29	3.93	4.32	4.63	4.37		
MPEF PV 1279	MPL	–	–	–	–	1.61	2.00	–	–	–	2.77	13.08	–
	MPW	–	–	–	–	1.87	3.23	–	–	–	4.19		
MPEF PV 1296	MPL	2.46	2.02	2.03	2.71	–	–	–	3.15	–	–	–	8.87
	MPW	–	1.84	2.22	2.96	–	–	–	–	–	–		

		c1	p2	p3	p4	m1	m2	m3	p2–m3 length
MLP 67-II-27-28	MPL	–	1.97	–	2.74	2.97	3.28	4.38	18.20
	MPW	–	1.45	2.00	2.30	2.33	2.34	2.19	
MLP 67-II-27-379	MPL	–	–	–	2.48	2.74	3.24	4.31	–
	MPW	–	–	–	1.66	1.85	2.02	2.22	
MLP 67-II-27-167	MPL	–	1.63	–	–	–	–	–	–
	MPW	–	1.19	–	–	–	–	–	
MLP 83-III-3-1	MPL	2.7	1.58	2.06	2.78	–	2.89	3.91	14.24
	MPW	2.88	1.12	1.48	1.54	–	1.69	1.63	
MLP 82-V-7-2	MPL	2.65	1.41	1.96	2.37	2.24	2.81	–	–
	MPW	2.78	1.08	1.52	1.75	1.72	1.97	–	
MLP 69-III-24-295	MPL	2.23	–	–	2.94	2.66	3.00	–	–
	MPW	1.85	–	–	1.71	1.76	2.40	–	

MPL maximum preserved length, *MPW* maximum preserved width

Eocene astrapotheres. Consequently, the masseteric fossa is much more defined than in *Parastrapotherium* and the Miocene forms. The posterior margin of the angle is rounded, slightly thickened and rough.

Dentition

Scott (1913) wrote that *Astraponotus* had complete premolar series. Schlosser (1923) interpreted that the dental formula was apparently complete. Simpson (1967b) pointed out that these are assumptions that lacked evidence and rather improbable. As interpreted above, the premaxillaries of *Astraponotus* were extremely reduced, and consequently they should not bear incisors. There is no evidence of an intermediate tooth either between the alveolus for the canine and the P2 of the adult specimen or between the erupting canine and the DP2 of the juvenile specimen. Therefore, the interpreted dental formula is 0I, 1C, 3P, 3M, in agreement with Simpson's (1967b) assumption. In both available adult skulls the cheek teeth are deeply worn, and except the M3 none has preserved the unworn occlusal morphology. Therefore, some observations made at this wear stage may not be valid at other wear stages. The complete cheek teeth series is preserved in the MPEF PV 1084 (Fig. 4). The P2 is a very small (Table 2), three-rooted tooth. The crown has a subtriangular outline, but the anterolabial corner projects forward as a distinct lobe, which partially resembles the DP2 of *Scaglia* (Casamayoran SALMA) and *Parastrapotherium*. The main wear facet is located at the center of the crown and at the anterolabial lobe. The labial wall has a weak basal cingulum; the lingual one is not preserved. All the following cheek teeth have a well defined labial cingulum, slightly elevated between the bases of paracone and metacone, and rising anteriorly to the base of the labial fold of the paracone, and posteriorly to the base of the metastyle, as in the lectotype of *Astraponotus holdichi* (MPL 12-1471). The P3 is nearly rectangular in outline, wider than longer. The labial wall bears the folds of the paracone and metacone and a conspicuous parastyle. A broad and very low anterior cingulum delimits an anterolingual basin, much shallower than the corresponding anterolingual pocket in *Astrapotherium* and *Parastrapotherium*. The preserved enamel border forms a slight labial inflection, suggesting the presence of a rudimentary hypocone. The P4 is slightly larger (especially bucco-lingually) (Table 2) and the labial fold of the metacone is much less prominent; there is no preserved evidence of the hypocone.

The molars are proportionally smaller than in *Astrapotherium*. The M1 (Fig. 4) is transversally larger than P4

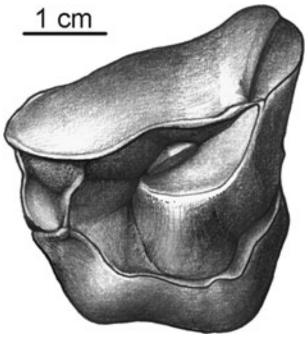

Fig. 8 *Astraponotus* sp. MPEF PV 1296 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Erupting right M1 in occlusal view (modified from Kramarz and Bond 2009)

(Table 2), wider anteriorly than posteriorly, insinuating a trapezoidal contour. The labial margin shows no trace of the labial fold of the metacone; the parastyle and the labial fold of the paracone are not preserved. The enamel border forms a distinct posterolabial spur corresponding to the base of the hypocone. The M2 is similar to M1 but larger (Table 2) and with a more marked trapezoidal contour. The parastyle and the labial fold of the paracone are hardly insinuated and the labial fold of the metacone is lacking. The anterolingual cingulum reaches the lingual base of the protocone; it is low and broad and there is no basal inflection of the anterolingual wall of the protoloph; consequently there is no anterolingual pocket. The size and outline of this tooth nearly agree with that expected for the M2 lectotype of *A. holdichi* (MLP 12-1471) in a more advanced stage of wear. The M3 is transversally smaller than the preceding molar (Table 2). The parastyle and the labial fold of the paracone are well marked, and the metastyle is very prominent. The enamel border has a very faint lingual inflection and a deep one on the posterior wall, suggesting that the hypocone was close to, or probably attached to, the protocone and isolated from the metacone-metaconule crest, as in the M3 of *Albertogaudrya* and *Maddenia*.

The erupting canines are preserved in the juvenile MPEF PV 1296. They are sharp pointed, very compressed, and faintly curved. The crown becomes gradually columnar to the base; the lingual and the anterior faces turn flat. The enamel is faintly grooved on the lingual face, and gradually reduced to the base on the anterior one. At least the preserved part of the canines show no sign of a root, and the teeth would have continued to grow in length and thickness. This ontogenetic series is very similar to that of *Parastrapotherium* and *Astrapotherium*. The well preserved diastema between the canine and the DP2 show no trace of an intermediate tooth. The DP2 is nearly triangular because of the strong anterior development of the parastyle region, which forms a distinct anterior lobe. This feature is also observed in the DP2 of *Scaglia* and of all post-Eocene astrapotheriids. Labial folds of the paracone and metacone are prominent. There is a vestigial hypoflexus represented by lingual folding of the preserved enamel border, separating the lingual bases of the protocone and hypocone; the former is located somewhat more labial than the latter. A conspicuous anterolingual cingulum descends from the enlarged parastyle region and continues around the labial base of the protocone. A shallow anterolingual groove is defined between the cingulum and the anterior wall of the protoloph. A very thin, transverse enamel lake is located very close and parallel to the posterior margin of the tooth, which suggests the presence of a metaloph. The DP3 is less triangular, because of the normal development of the parastyle. The labial fold of the metacone is weaker, the anterolingual groove is shorter, and the posterior enamel lake is vestigial. The DP4 is rather larger, more trapezoidal, and completely molariform in structure. The protocone is well separated from the hypocone by a deep hypoflexus, which is continuous with the oblique and very compressed central valley. The hypocone is anteroposteriorly compressed and connected with the metacone through somewhat oblique, short metaloph. A posterior cingulum descends from the hypocone and rises to the base of the moderate metastyle, enclosing a rather shallow posterofossette. The anterolingual cingulum is prominent, and reaches the anterolingual base of the protocone, enclosing an anterior groove, which is deeper than in the preceding premolars. The M1 (Fig. 8) is completely unworn and shows, essentially, the structures that would be present in the DP4 when recently erupted, but all the cingula are higher and, consequently the anterolingual groove and the posterofossette are deeper. The anterior cingulum extends posteriorly around the base of the protocone and reaches the anterior base of the hypocone, closing the opening of the hypoflexus. This feature, which cannot be verified in the much worn molars of the skulls described above, is variably present in M1 and M2 of *Parastrapotherium* and *Astrapothericulus*, and resembles the condition described for the M3 of the middle Miocene *Xenastrapotherum* (Johnson and Madden 1997). The more remarkable difference with the M1 of *Scaglia* is the presence of an accessory cuspule rising from the base of the central valley between the protocone and the ectoloph, connected to the inner wall of the ectoloph only at its base. This cuspule is sharp pointed, compressed, with the main axis oblique following the orientation of the central valley. This element is a less worn equivalent to the posterolingual spur of the ectoloph observed in the lectotype of *A. holdichi* (Kramarz and Bond 2009), interpreted by Simpson (1967b) as a notoungulate-like *crista* derived from an enlarged posterolingual spur of the ectoloph. Besides the presence of this

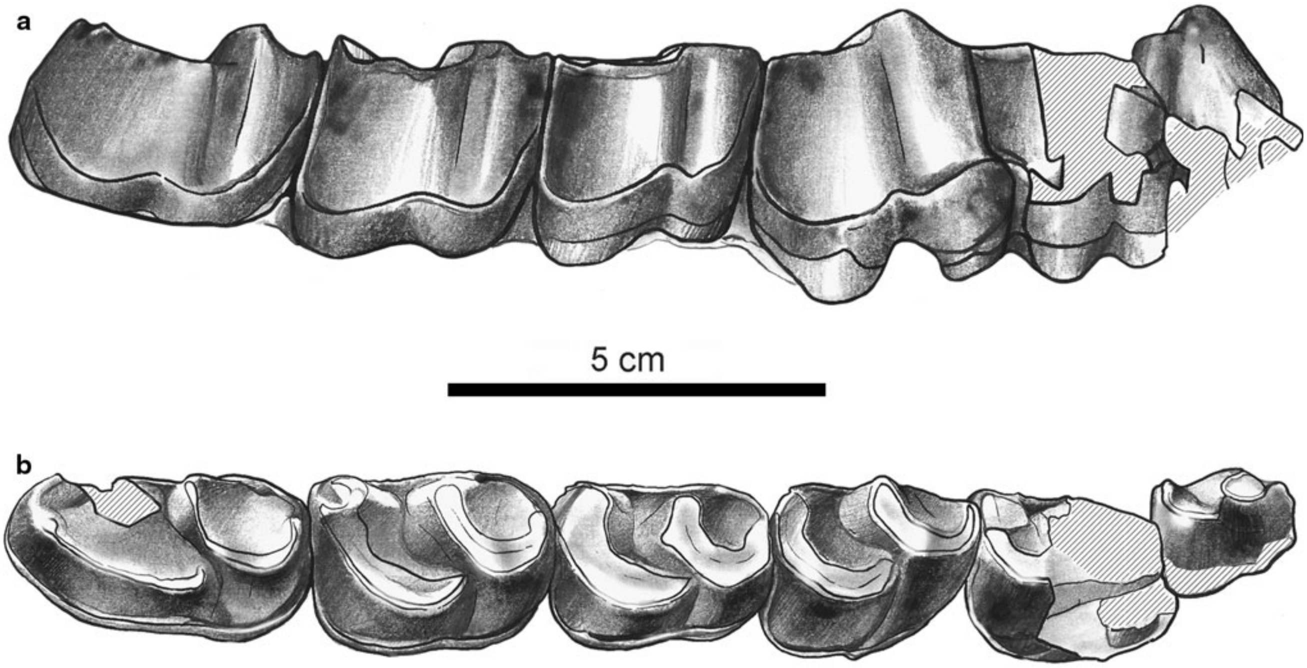

Fig. 9 *Astraponotus* sp. MLP 67-II-27-28 from Gran Hondonada locality, Chubut Province, Argentina; Mustersan SALMA (late Eocene). Right p2–m3, in labial (*a*) and occlusal (*b*) views

cuspule, this tooth differs from the M1 of *Scaglia* by being higher crowned, with a higher metaloph, by bearing a small elevation between the hypocone and the metacone, which could correspond to a vestigial metaconule, and by having less prominent metastyle and more developed basal cingula.

Simpson (1967b) described the lower dentition of *Astraponotus* on the basis of isolated teeth housed in AMNH and MLP. Currently described new and more complete materials complement Simpson's (1967b) description and essentially confirm locus assignment of the isolated cheek teeth. Measurements of lower teeth are shown in Table 2. Lower incisors and canines are as described by Simpson (1967b: 204). The almost complete cheek teeth series is preserved in MLP 67-II-27-28 (Fig. 9). The p2 (not represented in the AMNH sample) is a small, single-rooted tooth, with a main anterior, somewhat compressed cusp and a small posterior crescent, which ends in a tiny posterolingual cusp. This tooth strongly resembles the p2 of *Albertogaudrya*, but it is comparatively smaller and the posterior crescent is longer and higher. The p3 and p4 are fully molariform, only differentiable from m1 by having a comparatively narrower trigonid, a shorter talonid, and more superficial paraflexid and hypoflexid, especially the p3. The m1 and m2 are bicrescentic, but the anterior crescent is much shorter, because of the poor development of the paralophid, as in *Albertogaudrya*. Both teeth bear a conspicuous entoconid very close to the hypoconulid; in some specimens this cusp is connected with the hypolophid through a notoungulate-like entocristid, whereas in others the entoconid is isolated, as in *Trigonostylops* and *Maddenia*. In the subadult MLP 69-III-24-295 (with slightly worn p4 and m2) the entocristid is present in the p4 and absent in m2, suggesting that this could be a mere individual variation. In both cases, with wear the entoconid merges with the hypolophid and forms the characteristic entoconid spur, separated from the hypoconulid by a shallow posterolingual notch, as seen in the m2 of MLP 67-II-27-28 (Fig. 9). The m3 (not represented in the AMNH sample) has a much more elongated talonid and larger, conical entoconid isolated from the hypolophid and the hypoconulid. There is no accessory posterolingual cusp between the entoconid and hypoconulid, in contrast with the m3 of *Albertogaudrya* and *Maddenia*. All lower cheek teeth have wider lingual valleys than in *Albertogaudrya* and well developed labial and lingual cingulids, even at the base of the metaconid, as in *Astrapotherium*. In contrast, *Albertogaudrya*, *Maddenia*, and *Parastrapotherium* have no lingual cingulid at the base of the metaconid, and the uruguaytheriines (*Uruguaytherium*, *Xenastrapotherium*, and *Granastrapotherium*) lack lingual and labial cingulids. Most available p3s–m3s have a rather superficial hypoflexid, resembling *Maddenia* and *Parastrapotherium*, whereas in others (e.g., MLP 69-III-24-295 and some isolated cheek teeth at AMNH) the hypoflexid is as penetrating as in *Albertogaudrya*; the taxonomic significance of these differences is still uncertain. Simpson (1967b) described a small swelling on the inner side of the hypoconid crescent in an un-catalogued tooth in the Roth collection (MLP), and interpreted this structure as a rudimentary “pillar”. However, none of the examined specimens shows such a structure.

Discussion and conclusions

Simpson (1967b) recognized four species as probably valid referable to the genus *Astraponotus*, but the taxonomic status of the species described by Roth (1903) is still uncertain. The specimens described here do not provide new evidence enabling resolution of this matter, and consequently they are not identified at specific level.

Based upon the scarce dental remains previously described, *Astraponotus* was traditionally interpreted as structurally ancestral to all the post-Eocene astrapotheriids (Scott 1937; Soria 1984; Cifelli 1993). The more complete remains herein described support the idea that the dentition of *Astraponotus* is structurally intermediate in degree of hypsodonty, reduction of the dental formula, and development of accessory occlusal elements (i.e., crista of upper molars and paralophid in the lowers) between the Casamayoran astrapotheriids (i.e., *Albertogaudrya* and *Scaglia*) and the Oligocene–Miocene genera.

Unlike the dentition, examination of the skull of *Astraponotus* reveals many specialized and unique features, for example the remarkable height and narrowness of the forehead, the extreme shortness and lateral expansion of the nasals, the length of the maxillary sheaths of the canines, the retraction of the frontals, and the low position of the orbits. In addition, the posterior telescoping of the dorsal facial region is even more pronounced than in later astrapotheres. At first sight, these characters look astonishingly derived for an Eocene astrapothere. In particular, the reduction of the frontal bones and the absence of the anteorbital rim in *Astraponotus* represent cranial specializations which are exactly the opposite of those of *Astrapotherium*, suggesting that the different cranial specializations occurred separately during the evolution of the order. In addition, and based on the phylogenetic results obtained by Kramarz and Bond (2009), *Astraponotus* can be regarded as a member of an early diverging lineage of specialized, large-sized astrapothere, independent from the lineage leading to the better known later astrapotheres, for example *Astrapotherium*, *Parastrapotherium*, *Granastrapotherium*, and other closer relatives.

Besides the derived features mentioned above, *Astraponotus* shares with *Trigonostylops* and *Astrapotherium* the absence of a truly individualized foramen ovale. This feature was interpreted by Billet (2010) as a synapomorphy uniting astrapotheres, notoungulates, and pyrotheres, and consequently this is a primitive feature for the astrapotheres. Other characters resemble *Trigonostylops* instead of *Astrapotherium*. These include the rostral and temporal regions (not shortened), frontals not expanded forming a broad roof over the orbit, infraorbital foramina far anterior from the orbit, absence of lateral palatine notches, and occiput not constricted. In addition, adults of *Astraponotus* have two infraorbital foramina; this appears as an intermediate condition between *Trigonostylops* (with multiple, probably five foramina) and *Astrapotherium* (with a single foramen). Although most of these features were not explicitly treated by Billet (2010), they also occur in basal notoungulates, and can be initially interpreted as primitive characters.

Billet (2010) concluded that both in *Trigonostylops* and *Astrapotherium* the hypoglossal foramen opens in a common depression with the posterior lacerate (jugular) foramen, and that this condition is a synapomorphy of astrapotheres. However, in the *Astrapotherium* specimens we examined the hypoglossal foramen opens in a depression separated from the jugular foramen, which is in accordance with that observed by Simpson (1933: 21). In *Astraponotus* the condition is closer to that of *Astrapotherium* than to that of *Trigonostylops*, and consequently the phylogenetic meaning of this feature should be re-discussed. Similarly, most of the remaining characters of the auditory region and the basicranium observed in *Astraponotus* are closer to those of *Parastrapotherium*, *Astrapotherium*, and *Granastrapotherium*, than to *Trigonostylops*, evidence that the characteristic general pattern of the astrapotheriid basicranium was established within the group at least in the common ancestor of the two lineages and as early as the late Eocene. Unfortunately, the skull of most of the pre-Mustersan astrapotheriids is very imperfectly known. *Scaglia* is only known through a very badly preserved juvenile specimen in which the adult specialized cranial features have probably still not developed (Simpson, 1957, 1967b). Cranial features of *Tetragonostylops* are mostly unknown, and the skull of *Albertogaudrya* is completely unknown. *Eoastrapostylops* (late Paleocene?) is the sister taxon of all the remaining astrapotheres (Soria 1984; Kramarz and Bond 2009), but the skull has no astrapotheriid features, being morphologically closer to that of *Trigonostylops* (Soria 1987). *Trigonostylops* is known from Casamayoran and Mustersan beds of Patagonia (Simpson 1933, 1967b; Cladera et al. 2004). Considering that *Tetragonostylops* is from the Itaboraian age (?early Eocene), *Trigonostylops* would have diverged at least in the Itaboraian, persisting late until the Eocene and retaining most of the primitive cranial character of the Order. Consequently, there are no elements to determine if the typical astrapotheriid cranial specializations were acquired before the Mustersan SALMA.

Future findings would probably help to solve this controversy.

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References

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1894. Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias en Córdoba* 13: 259–455.

Ameghino, F. 1901. Notices préliminaires sur des ongulés nouveaux des terrains Crétacés de Patagonie. *Boletín de la Academia de Ciencias en Córdoba* 16: 349–426.

Ameghino, F. 1904. Recherches de morphologie phylogénétique sur les molaires supérieures des ongulés. *Anales del Museo Nacional de Buenos Aires* 3(3): 1–541.

Ameghino, F. 1906. Les Formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie. *Anales del Museo Nacional de Buenos Aires* 8(3): 1–358.

Billet, G. 2010. New observations on the skull of Pyrotherium (Pyrotheria, Mammalia) and new phylogenetic hypotheses on South American ungulates. *Journal of Mammalian Evolution* 17(1): 21–59.

Bordas, A.F. 1945. Geología estratigráfica de algunas zonas de Patagonia. *Anales del Museo de la Patagonia* 1: 139–184.

Carabajal, E., R. Pascual, R. Pinedo, J. Salfity, and M.G. Vucetich. 1977. Un nuevo mamífero de la Formación Lumbrera (Grupo Salta) de la comarca de Carahuasi (Salta, Argentina). Edad y correlaciones. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata "Galileo Scaglia"* 2(7): 148–163.

Cifelli, R.L. 1993. The phylogeny of the native South American ungulates. In *Mammal Phylogeny*, ed. F.S. Szalay, M.J. Novacek, and M.C. McKenna, 195–216. New York: Springer.

Cladera, G., E. Ruigómez, E. Ortiz Jaureguizar, M. Bond, and G. Lopez. 2004. Tafonomía de la Gran Hondonada (Formación Sarmiento, Edad—Mamífero Mustersense, Eoceno Medio) Chubut, Argentina. *Ameghiniana* 41(3): 315–330.

de Paula Couto, C. 1952. Fossil mammals from the beginning of the Cenozoic in Brazil. *Bulletin of the American Museum of Natural History* 99(6): 359–394.

de Paula Couto, C. 1963. Um Trigonostylopidae do Paleoceno de Brazil. *Anais Academia Brasileira de Ciências* 35(3): 339–351.

Frailey, C.D. 1987. The Miocene vertebrates of Quebrada Honda, Bolivia. Part I. Astrapotheria. *Occasional Papers of the Museum of Natural History, the University of Kansas* 122: 1–15.

Gabbert, S.L. 2004. The basicranial and posterior cranial anatomy of the families of the Toxodontia, Chapter 14. *Bulletin of the American Museum of Natural History* 285: 177–190.

Gaudry, A. 1904. Fossiles de Patagonie. Dentition de quelques mammifères. *Mémoires de la Société Géologique de France. Paléontologie* 12: 5–43.

Johnson, S.C., and R.H. Madden. 1997. Uruguaytheriine Astrapotheres of Tropical South America. In *Vertebrate Paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*, ed. R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn, 355–381. Washington, DC: Smithsonian Institution Press.

Kramarz, A.G. 2009. Adiciones al conocimiento de *Astrapothericulus* (Mammalia, Astrapotheria): anatomía cráneo-dentaria, diversidad y distribución. *Revista Brasileira de Paleontología* 12(1): 55–66.

Kramarz, A.G., and M. Bond. 2008. Revision of *Parastrapotherium* (Mammalia, Astrapotheria) and other Deseadan astrapotheres of Patagonia. *Ameghiniana* 45(3): 537–551.

Kramarz, A.G., and M. Bond. 2009. A new Oligocene astrapothere (Mammalia, Meridiungulata) from Patagonia and a new appraisal of astrapothere phylogeny. *Journal of Systematic Palaeontology* 7(1): 117–128.

Lydekker, R. 1894. Contribution to the knowledge of the fossil vertebrates of Argentina. 3. A study of extinct Argentine ungulates. *Anales del Museo de La Plata. Paleontología Argentina* 2: 1–91. pls. 1–32.

Odreman Rivas, E.O. 1978. Sobre la presencia de Polydolopidae (Mammalia, Marsupialia) en capas de edad Mustersense (Eoceno Medio) de Patagonia. *Obra del Centenario del Museo de La Plata* 5: 29–38.

Patterson, B. 1932. The auditory region of the Toxodontia. Field Museum of Natural History, Geological Series 6:1-27.

Roth, S. 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretáceo superior y Terciario inferior de la Patagonia. *Revista del Museo de La Plata* 11: 135–158.

Schlosser, M. 1923. Mammalia. In *Grundzuege der Palaeontologie. II. Abteilung: Vertebrata*, 4th ed, ed. K.A. von Zittel, 402–689. Munich: Oldenburg press.

Scott, W.B. 1913. *A history of land mammals in the Western Hemisphere,* xiv + 1–693. New York: Macmillan co.

Scott, W.B. 1928. Astrapotheria. In *Reports of the Princeton University Expeditions to Patagonia, 1896–1899, Volume IV, Paleontology. Mammalia of the Santa Cruz beds. Part IV*, ed. W.B. Scott, 301–351. Stuttgart: E. Schweizerbart'sche Verlagshandlung (E. Nägele).

Scott, W.B. 1937. The Astrapotheria. *Proceedings of the American Philosophical Society* 77(3): 309–393, pls. 1–9.

Simpson, G.G. 1933. Structure and affinities of *Trigonostylops*. *American Museum Novitates* 608: 1–28.

Simpson, G.G. 1957. A new Casamayoran astrapothere. *Revista del Museo de Ciencias Naturales y tradicionales de Mar del Plata* 1(3): 149–173.

Simpson, G.G. 1967a. The Ameghino's localities for early Cenozoic mammals in Patagonia. *Bulletin of the Museum of Comparative Zoology* 136(4): 63–76.

Simpson, G.G. 1967b. The beginning of the age of mammals in South America. Part 2. *Bulletin of the American Museum of Natural History* 137: 1–259. pls. 1–46.

Sisson, S. 1965. *Anatomía de los Animales Domésticos (4° edición).* Barcelona: Salvat.

Soria, M.F. 1984. Eoastrapostylopidae: diagnosis e implicaciones en la sistemática y evolución de los Astrapotheria preoligocénicos. Actas 2° Congreso Argentino de Paleontología y Bioestratigrafía, 175–182.

Soria, M.F. 1987. Estudio sobre los Astrapotheria (Mammalia) del Paleoceno y Eoceno. Parte I: Descripción de Eoastrapostylops riolorense Soria y Powell, 1982. *Ameghiniana* 24(1–2): 43–51.

Soria, M.F., and M. Bond. 1984. Adiciones al conocimiento de *Trigonostylops* Ameghino, 1897 (Mammalia, Astrapotheria, Trigonostylopidae). *Ameghiniana* 21(1): 43–51.

Soria, M.F., and J.E. Powell. 1981. Un primitivo Astrapotheria (Mammalia) y la Edad de la Formación Río Loro, provincia de Tucumán, República Argentina. *Ameghiniana* 18(3–4): 155–168.

Wible, J.R. 1987. The eutherian stapedial artery: character analysis and implications for superordinal relationships. *Zoological Journal of the Linnean Society* 91: 107–135.

Wible, J.R., and T.J. Gaudin. 2004. On the cranial osteology of the yellow armadillo *Euphractus sexcinctus* (Dasypodidae, Xenarthra, Placentalia). *Annals of Carnegie Museum* 73: 117–196.