



A new early Miocene astrapotheriid (Mammalia, Astrapotheria) from Northern Patagonia, Argentina

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With 3 figures and 3 tables

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Abstract: In this contribution we describe the astrapotheriid *Comahuetherium coccaorum* gen. nov. sp. nov. from Colhuehuapian (early Miocene) sediments of the Cerro Bandera Formation in Neuquén Province, Northern Patagonia, Argentina, also recorded in levels of equivalent age at the Gran Barranca south of Lake Colhué Huapi, in Chubut Province, central Patagonia, Argentina. *Comahuetherium coccaorum* is a small species with generalized astrapotheriid characters, but it shows some derived dental features (i.e. absence of P3, straight upper canines, and lingual cingulum enclosing the central valley on M3), which were preliminarily interpreted as indicating affinities with the uruguaytheriine astrapotheres. However, the result of a phylogenetic analysis indicates that the new taxon is part of the stem group of the clade formed by Uruguaytheriinae plus Astrapotheriinae, and that the abovementioned dental specializations were acquired independently, an evolutionary pattern not previously reported among these mammals. The body mass estimations for *Comahuetherium* and other late Oligocene – Miocene astrapotheriids reveal a wide range of body size, suggesting that these mammals played diverse ecological roles.

Key words: Astrapotheria, *Comahuetherium*, Systematics, body weight, Cerro Bandera Formation, Miocene, Patagonia.

1. Introduction

The Astrapotheriidae (*sensu* CIFELLI 1993) are the most specialized group within the Order Astrapotheria, and they include the largest and most bizarre terrestrial mammals among the native Tertiary South American faunas. The most advanced astrapotheriids are characterized by the reduction of the size and number of premolars and the enlargement of the molars, features not present in pre-Deseadan South American Land Mammal Age (SALMA, pre-late Oligocene) astrapotheres (KRAMARZ & BOND 2009). They are traditionally classified in subfamilies: the Astrapotheriinae, restricted to the Patagonian region, and the Uruguaytheriinae, of extra-Patagonian distribution (Kraglievich 1928; JOHNSON & MADDEN

1997). Recent phylogenetic analyses have concluded that both groups are monophyletic (JOHNSON & MADDEN 1997; KRAMARZ & BOND 2009).

KRAMARZ et al. (2005) reported the presence of a new, small sized astrapotheriid in the Miocene Cerro Bandera Formation at Neuquén Province, Northern Patagonia, Argentina (Fig. 1). KRAMARZ & BOND (2010) assigned to this new taxon an isolated tooth from Colhuehuapian levels at the Gran Barranca south of Lake Colhué Huapi (central Patagonia), and in a preliminary non-cladistic analysis interpreted some dental features of this new astrapotherid as suggesting uruguaytheriine affinities. This interpretation implies the coexistence of an uruguaytheriine with the astrapotheriids traditionally regarded as astrapotheriines (i.e. *Parastrapotherium*, *Astrapotherium*, and *Astra-*

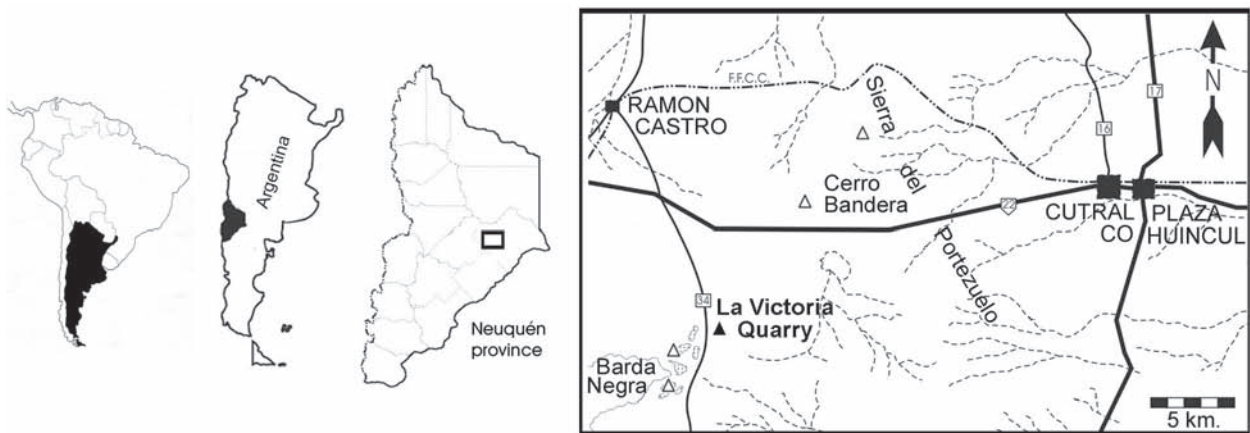


Fig. 1. Sketch map showing the location of the site bearing the holotype of *Comahuetherium coccaorum* gen. et sp. nov. (black triangle) and other fossil localities (white triangles) of the Cerro Bandera Formation (modified from KRAMARZ et al. 2005), north-western Patagonia, Argentina.

pothericulus) in Patagonia during the early Miocene, which contrasts with the traditional view of the biogeographic segregation between both groups. In this contribution this new astrapotheriid is described and compared with other known astrapotheriids, and its phylogenetic relationships with other members of the family are analyzed within a cladistic framework. Additionally, here we estimate the body mass for this new astrapotheriid using regression equations based on dental measurements proposed by DAMUTH (1990), we compare it with other Oligocene-Miocene astrapotheriids, and provide new considerations about the evolutionary interpretation of the size and the dental features of these mammals.

Institutional abbreviations: AMNH, American Museum of Natural History (USA); FMNH, Field Museum of Natural History (USA); MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; MNHN, Muséum National d'Histoire Naturelle (France); MLP, Museo de La Plata (Argentina); MOZ, Museo "Prof. Juan Olsacher", Zapala (Argentina); MPEF PV, Museo Paleontológico Egidio Feruglio (Chubut Province, Argentina), paleovertebrate collection; UCMP, University of California Museum of Paleontology (Berkeley, USA); YPM PU, Yale Peabody Museum, Princeton University Collection (New Haven, USA).

List of astrapotheriid specimens used for comparisons:

Astrapotherium AMEGHINO: MACNA 10971 (type of *A. asymmetricus* AMEGHINO), MLP 12-1471 [type of *A. holdichi* (ROTH)], MLP 12-2217 [type of *A. dicksoni* (ROTH)], additional materials described by SIMPSON (1967) at AMNH, and undescribed additional materials at MLP and MPEF.

Maddenia Lapidaria KRAMARZ & BOND: MPEF PV 7735 (holotype) and referred materials described by KRAMARZ & BOND (2009).

Parastrapotherium holmbergi AMEGHINO: MACNA 52-509, MACNA 52-504, MACNA 52-515, MACNA 52-518 (syn-types), and additional materials from the Deseadan La Flecha locality, Santa Cruz Province, (MLP 95-III-10-74, 95-III-10-90, and 95-III-10-103; FMNH 13329, 13343, 13354, 13364, 13365, 13369, 13462, 13473, 13491, 13492, and 13579).

Parastrapotherium martiale AMEGHINO: MACNA 52-604 (holotype) and additional materials from the Deseadan beds of the Puesto Almendra Member (Sarmiento Formation) at Gran Barranca. (MLP 93-XI-18-41, 93-XI-18-45, 93-XI-18-43, 93-XI-18-42, 93-XI-18-9, 93-XI-18-39, 93-XI-18-10, 93-XI-18-14, 93-XI-18-30, 93-XI-18-40, 93-XI-18-7, and 93-XI-18-5; MPEF PV 7129, 7133, 7135, 7128, and 7807; AMNH 29565; FMNH 13427, 13428, and 13529).

Astrapothericulus iheringi AMEGHINO: MACNA 52-408 to 414, 52-417, 52-419, 52-421, 52-422, and 52-605 (syn-types) and abundant additional materials from the Pinturas Formation at the MACN.

Astrapotherium magnum (OWEN): MACNA 3207 (figured in AMEGHINO 1894: fig. 20), 3210, 3214, 3216-3220, 3296, 3279-3281, 3295-3298, 8580-8581, 8603, 11250 (figured in AMEGHINO 1904: fig. 226); MACNA Pv 14512; AMNH 9278 (figured in SCOTT 1928: pls. 13-14); FMNH 13170, 13173, 14251, 14259; YPM PU 15142, 15332 (figured in SCOTT 1928: pl. 14). These materials were referred to this species following interpretations provided by AMEGHINO (1894).

Xenastrapotherium kraglievichi CABRERA: MLP 12-96 (holotype) and referred materials described by JOHNSON & MADDEN (1997) at YPM PU.

Granastrapotherium snorki JOHNSON & MADDEN: UCMP 40358 (holotype) and referred materials described by JOHNSON & MADDEN (1997) at YPM PU.

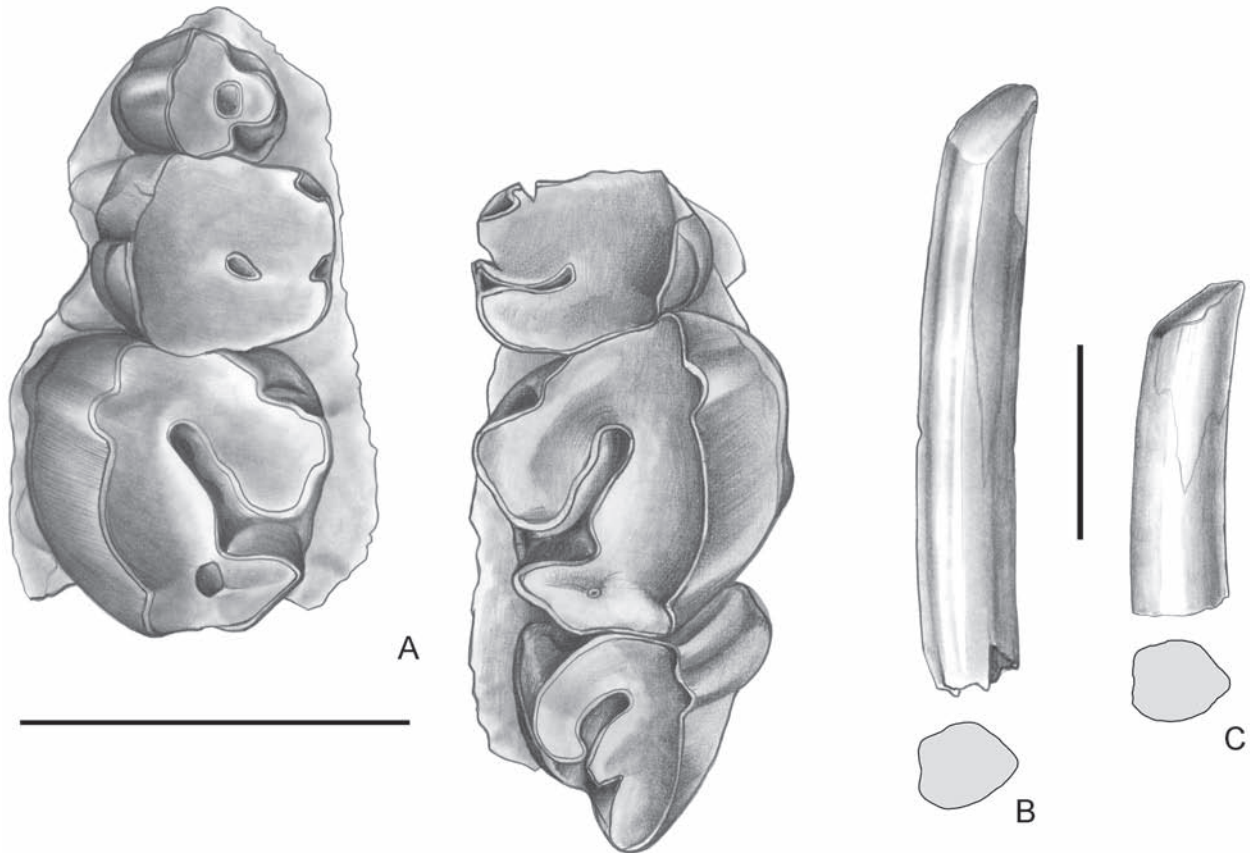


Fig. 2. *Comahuetherium coccaorum* gen. et sp. nov.: A – MOZ PV 4082 (Holotype), right maxillary fragment with P4-M2 and left maxillary fragment with M1-M3 in occlusal view, B – idem, left upper canine in lingual view and schematic cross section, C – MACN A 52-522b (syntype of *Parastrapotherium ruderarium* AMEGHINO, 1902), right upper canine in lingual view and schematic cross section (shown as left, modified from KRAMARZ & BOND 2010). Scale bar = 5cm.

2. Systematic paleontology

Order Astrapotheria LYDEKKER, 1894
Family Astrapotheriidae AMEGHINO, 1887

Genus *Comahuetherium* nov.

Type species: *Comahuetherium coccaorum* sp. nov.

Etymology: From “*Comahue*” (Araucanian), a sub-region of Patagonia (Argentina) including the Neuquén Province, where the holotype was found, and “*therios*” (Greek) = beast.

Geographic and chronological distribution: Colhuehupian SALMA (early Miocene), northern and central Patagonia, Argentina.

Diagnosis: As for the type and only species.

Comahuetherium coccaorum sp. nov.

Fig. 2

1902 *Parastrapotherium ruderarium* AMEGHINO, p. 98-100, descriptions and measurements (partim)

Etymology: Dedicated to SERGIO and RAFAEL COCCA, previously in charge of the Museo Juan Olsacher (Zapala), who provided the holotype and other fossil mammals for our studies.

Holotype: MOZ PV 4082, associated right maxillary fragment with P4 – M2, left maxillary fragment with M1 – M3, and left upper canine.

Hypodigm: The holotype and MACN A 52-522b, an isolated upper canine (syntype of *Parastrapotherium ruderarium* AMEGHINO, 1902).

Remarks. – AMEGHINO’s (1902) description of *Parastrapotherium ruderarium* is based upon a juvenile mandibular

fragment with five teeth (MACN A 52–524) and two lots of teeth (MACN A 52–513 and MACN A 52–522a-b) corresponding to more than one individual. KRAMARZ & BOND (2010) concluded that the canine MACN A 52-522b is not co-specific with the remaining syntypes, designated the MACN A 52–524 as the lectotype, and transferred the species to the genus *Astrapotherium*.

Stratigraphic provenance and locality: The holotype comes from the basal bentonitic levels of the Cerro Bandera Formation (LEANZA & HUGO 1997; KRAMARZ 2005; KRAMARZ et al. 2005), La Victoria quarry, Zapala Department, Neuquén Province, Argentina (Fig. 1). This unit comprises a series of isolated outcrops that represent the relicts of an old alluvial filling developed on small local valleys excavated on late Cretaceous and Paleocene deposits. It is composed by a succession of reworked pyroclastic deposits alternating with primary pyroclastic and scant sandstone levels (LEANZA & HUGO 1997; KRAMARZ et al. 2005). Based upon its faunal content, the fossil bearing levels of the Cerro Bandera Formation was assigned to the Colhuehuapian SALMA (early Miocene) (KRAMARZ et al. 2005). The MACN A 52-522b comes from the “*Colpodon* beds” of the Sarmiento Formation at the Gran Barranca south of Lake Colhué Huapi (AMEGHINO 1902, 1906; KRAMARZ & BOND 2010), Chubut Province, Argentina.

Diagnosis: Small astrapotheriid, M1-M3 length about 15 % smaller than in *Astrapothericulus*. Basal cingula much less developed than in *Astrapothericulus*. P3 absent, as in *Granastrapotherium*. P4 with paracone labial fold in central position; much developed postprotocrista closing posteriorly the trigon basin. M2 with hypocone lingually pointed, as in *Parastrapotherium*. Upper canines nearly sub-cylindrical in cross section, less curved than in *Astrapotherium* and *Astrapothericulus*.

Description and comparisons. – The upper cheek teeth (Fig. 2A) are brachyodont, higher crowned on the labial than on the lingual side (unilateral hypsodonty). According to the linear dental measurements (Table 1), this species is smaller than *Astrapothericulus iheringi* AMEGHINO and *Xenastrapotherium kraglievichi* CABRERA, and much smaller than *Astrapotherium magnum* (OWEN), *Granastrapotherium snorki* JOHNSON & MADDEN, and the species referred to *Parastrapotherium* AMEGHINO (KRAMARZ & BOND 2008).

The anteriormost cheek tooth preserved is the P4. The preserved portion of the maxillary anterior to this tooth shows no evidence of the alveolus for the P3; moreover, the P4 has no interdental wear facet on its anterior wall. These features indicate that this specimen lacked P3, a condition only observed so far in *Granastrapotherium snorki* (Laventan SALMA, middle Miocene of Colombia; JOHNSON & MADDEN 1997). As an alternative interpretation, the presence of a diastema between P4 and P3 appears as highly unlikely since such a condition does not occur in other known astrapotheres. The possibility that P3 be lost at earlier ontogenetic stages (not recognized in better known astrapotheriids) would be explored when ontogenetic series of this species were available.

The P4 is sub-rectangular, much smaller than the molars. The labial roots are almost parallel, less divergent than in *Astrapotherium* and *Astrapothericulus*. Only the paracone and the protocone are developed. The parastyle is very weak, as in *Xenastrapotherium kraglievichi* (Laventan SALMA, middle Miocene), and *Granastrapotherium* (JOHNSON & MADDEN 1997). The labial fold of the paracone is located in the middle of the ectoloph, opposed to the protocone, unlike other astrapotheriids. The protocone is columnar and limited by well defined antero and posterolingual grooves. There is a continuous anterolingual-posterolingual cingulum surrounding the base of the protocone, and enclosing a small but well defined anterolingual pocket and a somewhat larger and deeper posterolingual pocket. The postprotocrista is high and at this stage of wear closes posteriorly the trigon basin. Because of this pattern, the premolar presents a nearly symmetrical appearance (the anterior half of the tooth is a mirror image of the posterior half). On the contrary, in all other late Oligocene – Miocene astrapotheriids the labial fold is more anterior and the post-protocrista is absent or much more reduced; consequently the central valley opens posteriorly even in more advanced stages of wear. The labial cingulum is delicate and continuous, with a slight V-shaped inflection (in labial view), concave to the apex of the tooth, at the base of the labial fold of the ectoloph, as in some specimens of *Astrapotherium* (e.g. MACN A 3217, 3221, YPM PU 15261). In *Astrapothericulus* this cingulum is inverted (concave to the base) (KRAMARZ 2009); in *Parastrapotherium* (late Oligocene – early Miocene of Patagonia (SCOTT 1937; KRAMARZ & BOND 2008, 2009) the cingulum is interrupted at the base of the labial fold (KRAMARZ & BOND 2008), whereas *Xenastrapotherium* and *Granastrapotherium* have no labial cingula (JOHNSON & MADDEN 1997).

The M1 is almost completely worn, especially the anterolabial corner, and only preserves vestiges of the central valley and the anterolingual pocket. A minute remain of the lingual cingulum is preserved at the base of the protocone – hypocone junction. At least at this stage of wear, the base of the crown is significantly smaller (about 50 %) than the base of the M2 (see Table 1), whereas in other astrapotheriids the base of M1 is 30–40 % smaller than the base of M2. The M2 has a trapezoidal outline. As in *Parastrapotherium*, the crown tapers markedly towards the base, especially on the labial side, and the parastyle and the labial fold of the paracone are strongly convergent, more than in *Astrapothericulus* and *Astrapotherium*. These features suggest that, as in *Parastrapotherium*, the molars of *Comahuetherium* are lower crowned than those of *Astrapothericulus* and *Astrapotherium* (KRAMARZ & BOND 2008). As in the remaining Patagonian astrapotheriids, the parastyle and the labial fold of the paracone are well developed (SCOTT 1937; KRAMARZ & BOND 2008; KRAMARZ 2009); on the contrary, in *Xenastrapotherium kraglievichi* the parastyle is less conspicuous, and in *Granastrapotherium* the labial fold of the paracone is also reduced (JOHNSON & MADDEN 1997). The lingual wall of the ectoloph is markedly convex, more than in *Astrapothericulus* and *Astrapotherium*, and much more than in *Xenastrapotherium*. The anterolingual pocket is present, but is less penetrating than in both La Venta species. As in *Parastrapotherium* and *Xenastrapotherium*, the hypo-

Table 1. Dental measurements for *Comahuetherium coccaorum* gen. et sp. nov. (in cm) compared with *Astrapothericulus iheringi* (AMEGHINO). APL, maximum preserved anteroposterior length; TW, maximum preserved transverse width.

			C	P4	M1	M2	M3	M1-M3 length	
<i>C. coccaorum</i> gen. et sp. nov.	PV 4082 MOZ	right	APL	2.40	-	2.57	4.14	3.82	9.51
			TW	1.96	-	3.21	4.08	3.71	
		left	APL	-	1.58	2.60	3.95	-	-
			TW	-	2.35	3.17	4.05	-	-
	MACN A 52-522b		APL	2.58	-	-	-	-	-
			TW	2.20	-	-	-	-	-
<i>A. iheringi</i> (AMEGHINO)	MACN A 52-419 (syntype)		APL	-	1.94	3.71	4.51	3.70	11.43
			TW	-	2.31	3.81	4.22	3.95	

cone is lingually sharp, not rounded as in other astrapotheriids, with a somewhat lophoid appearance resembling the condition observed in the late Eocene astrapotheriid *Astraponotus*. There is a small vestige of the posterofosse, which is worn away in similar stages, or even less worn M2 of *Astrapothericulus* and *Astrapotherium*. The labial and lingual cingula are present, but not as prominent as in *Astrapothericulus* (AMEGHINO 1902; KRAMARZ 2009).

The M3 is nearly triangular in occlusal outline. The protocone is lophoid, with a strong posterior projection almost closing the central valley, which is anterolabially more penetrating than in *Astrapothericulus* at a similar stage of wear. The hypocone is absent. The crista is comparatively shorter than in *Astrapotherium* and *Astrapothericulus*. The lingual cingulum extends posteriorly connecting the bases of the protocone and metacone, partially closing the central valley, resembling the condition described by JOHNSON & MADDEN (1997) in *Xenastrapotherium*.

The upper canine (Fig. 2B) is an almost straight columnar tusk with a nearly heart-shaped cross section. The preserved portion of the base does not show indication of root formation, suggesting it was an evergrowing tooth. The enamel covers the apical portion of the lateral walls, and is gradually reduced toward the base. The dentine is exposed on the entire anterior wall, which bears a slight longitudinal groove. An accessory, less conspicuous, longitudinal groove is present on the anterior half of the lingual wall. The beveled anterior wear facet is nearly 45° in relation to the axis of the canine. An accessory, irregular, wear facet is present on the tip of the posterior face. This canine differs from those of *Parastrapotherium*, *Astrapotherium*, *Astrapothericulus*, and *Xenastrapotherium* by being less compressed and much less curved. In *Granastrapotherium* the upper canines are also almost straight, but are comparatively more robust, the labial wall is more convex than the lingual one and lacks the anterior longitudinal groove (JOHNSON & MADDEN 1997). The partial upper canine MACN A 52-522b (syntype of *Parastrapotherium ruderarium* AMEGHINO) (Fig. 2C) from the Colhuehuapian beds of Gran Barranca (AMEGHINO 1902; KRAMARZ & BOND 2010), strongly resembles the

holotype of *C. coccaorum*, and it is herein referred to this species.

Affinities. – The more conspicuous dental feature of *Comahuetherium* is the absence of P3. This condition is shared only with the advanced uruguaytheriine *Granastrapotherium snorki*, and represents the most extreme reduction of the dental formula among Astrapotheria (JOHNSON & MADDEN 1997). Concordantly, the upper canines of *Comahuetherium* are almost straight as in *Granastrapotherium*, and not curved as in other astrapotheres (SCOTT 1937; JOHNSON & MADDEN 1997; KRAMARZ & BOND 2008; KRAMARZ 2009); this feature suggests that the upper tusks were horizontally implanted as in the *G. snorki* (JOHNSON & MADDEN 1997). Additionally, *Comahuetherium* shares with *Xenastrapotherium* the presence of a lingual cingulum connecting the bases of the protoloph and metaloph, enclosing the central valley. This character was interpreted by JOHNSON & MADDEN (1997) as a synapomorphy for the uruguaytheriines, although it is absent in *Granastrapotherium*. On this basis, KRAMARZ & BOND (2010) interpreted that *Comahuetherium* would be closely related to the Uruguaytheriinae. This interpretation implies the occurrence of an uruguaytheriine coexisting with the astrapotheriids classified as astrapotheriines (i.e. *Astrapotherium*, and *Astrapothericulus*) in Patagonia during the early Miocene, and opposes to the traditional posture of the biogeographic segregation between both groups. However, the upper dentition of *Comahuetherium* does not exhibit the remaining characters interpreted by JOHNSON & MADDEN (1997) as synapomorphies for the uruguaytheriines (i.e. extreme developed anteroligual pocket in upper molars, reduced upper molar parastyle). Moreover, *Comahuetherium* differs from the uruguaytheriines in having both lingual and labial cingula, and from all known astrapotheriines and uruguaytherines by having lower crowned cheek teeth.

To assess the affinities of *Comahuetherium*, a phylogenetic analysis was performed based primarily on the 33 dental characters from the data matrix of KRAMARZ & BOND (2009) with the addition of two characters (18 and 43)

Table 2. Distribution of character states for 44 characters among 13 ingroup terminal taxa and 1 outgroup taxon (*Eoastrapostylops*) used for assessing phylogenetic relationships of *Comahuetherium coccaorum* gen. et sp. nov. Characters and character definitions are listed in Appendix 1. “A” = 0 or 1; “B” = 0 or 2; “C” = 1 or 2. “?” indicates missing or unknown character. “-” indicates non-applicable character.

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

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
<i>Eoastrapostylops</i>	?	?	?	?	0	?	0	0	0	0	0	0	0	0	-	0	0	0	0	-	0	
<i>Trigonostylops</i>	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	0	-	0
<i>Tetragonostylops</i>	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	-	0	
<i>Albertogaudrya</i>	?	?	?	0	?	0	0	0	0	1	0	0	1	0	0	1	0	0	0	-	0	
<i>Scaglia</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Astraponotus</i>	0	0	0	1	2	0	0	0	0	1	1	0	B	1	A	0	C	0	A	0	-	0
<i>Maddenia</i>	?	?	?	?	1	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	-	0
<i>Parastrapotherium</i>	0	0	0	1	2	1	1	1	0	0	1	1	0	1	1	0	0	1	0	0	0	0
<i>Astrapotherium</i>	0	0	0	1	2	1	1	1	1	-	1	0	0	1	0	0	0	2	1	0	0	0
<i>Granastrapotherium</i>	1	1	1	-	0	0	1	1	1	-	1	1	0	1	2	1	0	0	0	1	0	1
<i>Astrapothericulus</i>	0	0	0	1	1	1	A	1	1	-	1	1	0	1	0	0	0	1	1	0	0	0
<i>Xenastrapotherium</i>	0	0	1	1	2	1	1	1	1	-	1	1	0	1	2	1	0	0	0	0	1	0
<i>Uruguaytherium</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	0	?	0	0	?	?	?
<i>Comahuetherium</i>	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1

modified from JOHNSON & MADDEN (1997) and seven new characters (21, 28, 29, 35, 38, 42, and 44). The multistate character 21 of KRAMARZ & BOND (2009) (number of lower incisors) was herein split into three binary characters (23-25), in order to avoid the inclusion of an “a priori” phylogenetic hypothesis. The complete list of characters and character states is presented in Appendix 1. The multi-state characters 35, 39, and 40 are unordered. Character were polarized using the Paleocene *Eoastrapostylops riolorensis* SORIA & POWELL, 1981 as the outgroup, because of previous hypotheses suggesting that this genus is the most primitive among Astrapotheria (SORIA 1984, 1988; CIFELLI 1993).

The data matrix is shown in Table 2. Exhaustive searching by maximum parsimony using the NONA program (GOLOBOFF 1993) showed a single most parsimonious tree, with length = 81 steps, CI = 0.62 and RI = 0.74 (Fig. 3). The result of the analysis indicates that *Comahuetherium* has no particularly close relationships with the uruguaytheriines.

On the contrary, this new taxon resulted as the sister group of the clade formed by *Parastrapotherium* plus the uruguaytheriines [*Uruguaytherium* [*Granastrapotherium*, *Xenastrapotherium*]] and the astrapotheriines [*Astrapotherium*, *Astrapothericulus*]. This location is substantiated by five unambiguous synapomorphies (Node 6, Fig. 3): slightly hypsodont cheek teeth [character 2(2)], reduced premolars [character 5(1)] P4 hypocone reduced to a low posterolingual cingulum [character 7(0)], hypocone absent on M3 [character 22(0)], and upper canines with anterior groove [character 28(0)]. Consequently, the derived dental features of *Comahuetherium* (i. e. absence of P3, straight upper canines, and M3 lingual cingulum enclosing the central valley) previously proposed by KRAMARZ & BOND (2010) as indicating uruguaytheriine affinities, are here interpreted as autapomorphies acquired independently from the uruguaytheriines.

The uruguaytheriine clade (Node 9, Fig. 3) is supported by the absence of labial cingulum on molars [character

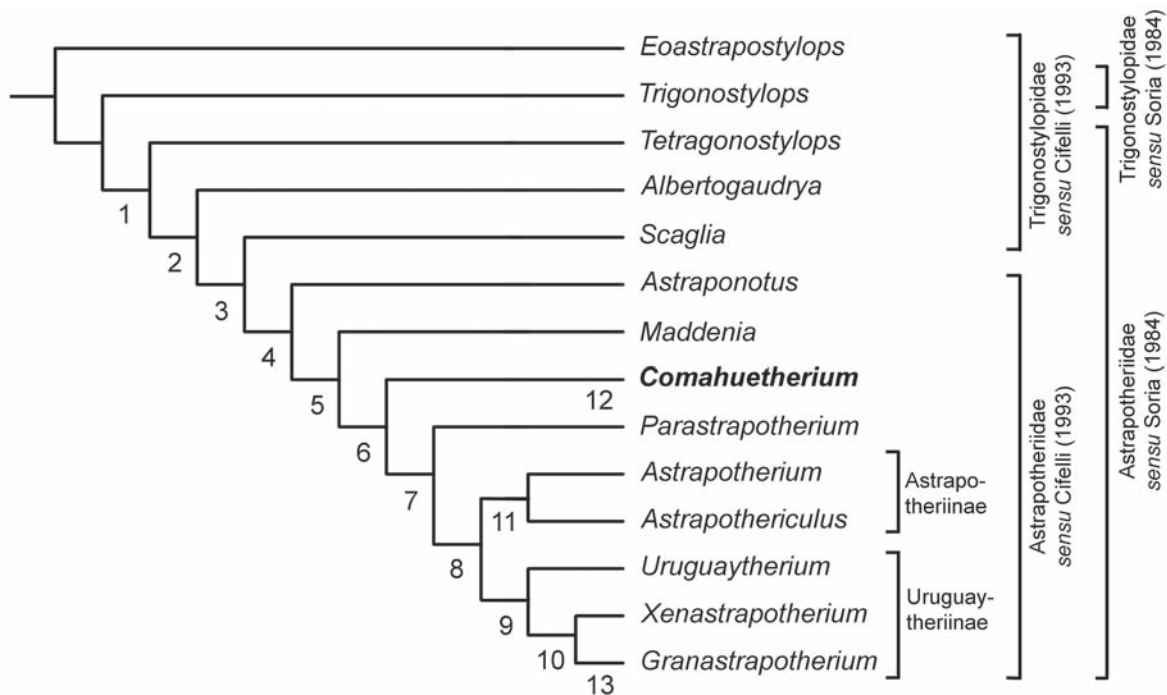


Fig. 3. Single most parsimonious tree (length = 82 steps, CI = 0.61 and RI = 0.74) obtained by exhaustive searching analysis (NONA, GOLOBOFF 1993) of the data matrix containing 44 dental characters coded in 13 astrapothere genera (using *Eoastropostylops* as the outgroup) shown in Table 2. List of synapomorphies: Node 1: 12(1), 22(1), 36(1); Node 2: 2(1), 7(1), 33(1); Node 3: 13(1), 16(1), 21(1); Node 4: 14(1); Node 5: 9(0), 15(1), 19(1), 29(1), 30(1), 34(1); Node 6: 2(2), 5(1), 7(0), 22(0), 28(1); Node 7: 1(2); Node 8: 17(1); 31(1); Node 9: 3(0), 37(2); Node 10: 18(1), 38(1); Node 11: 37(0), 41(1); Node 12 (autapomorphies of *Comahuetherium*): 42(1), 44(1); Node 13 (autapomorphies of *Granastrapotherium*): 11(0), 23(1), 24(1), 27(0), 28(0), 42(1), 44(1).

3(0)], unlike in *Comahuetherium*, and by the extreme reduction of the lower molar hypoflexid [character 37(2)]. As advanced by JOHNSON & MADDEN (1997) and KRAMARZ & BOND (2009), the latter is a synapomorphy of the Uruguaytheriinae, and the most conspicuous dental feature on which this group was defined (KRAGLIEVICH 1928). At present, this character in *Comahuetherium* is uncertain since the taxon is only known through upper teeth. However, in those uruguaytheriines with known upper and lower dentition (i. e. *Granastrapotherium* and *Xenastrapotherium*) the extreme reduction of the lower molar hypoflexid is associated with a reduction of the upper molar parastyle (character 18), which would be its occlusal antagonist in other astrapotheres. The upper molars of *Comahuetherium* have a “normally” developed parastyle, suggesting a moderate development of the lower molar hypoflexid as in *Maddenia* (early? Oligocene) and *Parastrapotherium* (KRAMARZ & BOND 2008, 2009).

3. Body mass

Length and volume (or weight) are measures of size, and are commonly used to describe and to compare organisms (GINGERICH & SMITH 1985). Dental length increases proportionally to the linear dimensions, but

body weight (being proportionally to volume), increases to relation of the cube of a linear dimension, assuming geometric similarity is maintained (GINGERICH & SMITH 1982). Thus, body mass is preferable over linear dimensions to express body size because mass explains more variability than linear dimensions (CALDER 1996).

The only previous study on body weight estimates in astrapotheriids was made by JOHNSON & MADDEN (1997), who used the regression equations proposed by DAMUTH (1990) and JANIS (1990) for ungulates. However, these equations are based on lower dental, mandibular, and cranial measurements, which are still unknown in *Comahuetherium*. In order to estimate and compare the body mass for *Comahuetherium coccaorum*, we calculated the body mass of other Oligocene – Miocene astrapotheriids using the non-selenodont ungulate regression equation based on lower molar series length $Mo = 3.03 \text{Log}(m1-m3 \text{ length}) - 0.39$ (DAMUTH 1990) (Table 3). This equation certainly overestimates the body weight of the species

Table 3. Compared dental measurements and estimates of body weight for late Oligocene – middle Miocene astrapotheriids. The body mass for *Comahuetherium coccaorum* was calculated from the geometric similarity equation $Mc = (Lc/Lo)^3 \times Mo$, where Lc is the M1-M3 length for *Comahuetherium coccaorum* (= 95.10 mm), and Lo and Mo are the M1-M3 length and the body mass for each other astrapotheriid specimen. The equation was applied only for those specimens with positively associated upper and lower dentition. Mo was calculated using the nonselenodont ungulate regression equation based on lower molar series length $3.03\text{Log}(m1-m3 \text{ length})-0.39$ (DAMUTH 1990).

Taxon	specimen	Lo	Mo	Mc	<i>Comahuetherium</i> body mass (kg)
		M1-M3 length (mm)	m1-m3 length (mm)	Body mass (kg)	
<i>Astrapothericulus iheringi</i>	MACN A 52-605 (syntype)	-	126.5	955.82	-
<i>Astrapotherium ruderarium</i>	MPEF PV 7915	135	137	1214.12	424.43
	AMNH 29717	-	131	1060.06	-
<i>Xenastrapotherium kraglievichi</i>	MLP 12-96 (holotype)	-	141	1324.75	-
<i>Astrapotherium magnum</i>	MACN A 3208-3211	156.5	164	2094.00	469.87
	AMNH 9278	152	151	1630.42	399.31
	YPM PU 15117	167	160	1943.05	358.82
	YPM PU 14259	144	151	1630.42	469.63
<i>Parastrapotherium holmbergi</i>	FMNH 13364	-	160	1943.05	-
	FMNH 13365	-	131	1060.06	-
	FMNH 13354	-	163	2055.55	-
	FMNH 13462	-	176	2593.60	-
	FMNH 13343	-	163.5	2074.72	-
<i>Granastrapotherium snorki</i>	from JOHNSON & MADDEN, 1997	-	187.5	3141.91	-
<i>Parastrapotherium martiale</i>	MACN A 52-604 (holotype)	210	194	3483.69	323.54
<i>Astrapotherium giganteum</i>	MACN A 3274-78 (holotype)	183	196	3593.65	504.34
<i>Parastrapotherium herculeum?</i>	Cast of MNHN COL 1	-	205	4117.32	-

herein analyzed because all have very enlarged molars in comparison to the complete cheek tooth series. Consequently, this estimate provides values for reasonable relative comparisons among these species, but not for comparison with others with typical ungulate dental pattern. We discarded the regression equations based on m1 length and m1 area proposed by DAMUTH (1990) as the size of this tooth shows strong individual variation and does not provide an adequate indication of the differences in body mass among other astrapotheriids (e.g. *Xenastrapotherium* and *Granastrapotherium* have similar m1 dimensions but very different m1-m3 length, JOHNSON & MADDEN 1997). We calculated the body mass of 17 Oligo-Miocene astrapotheriid specimens representing all the species interpreted as valid in recent taxonomic revisions (JOHNSON & MADDEN 1997; KRAMARZ & BOND 2008, 2010) (Table 3). Dental measurements for *Xenastrapotherium kraglievichi*, *Astrapotherium giganteum*, *Parastrapotherium martiale*, and *Astrapo-*

thericulus iheringi were taken from the respective type specimens. Dental measurement for *Astrapotherium magnum* (whose type specimen is an upper molar fragment) and *Parastrapotherium holmbergi* (the syntypes are isolated teeth) were taken from specimens referred to the concerned taxa by SCOTT (1937). For *Astrapotherium ruderarium* (the lectotype is a juvenile mandible with erupting m3), measurements were taken from specimens referred by KRAMARZ & BOND (2010). The measurement for *Granastrapotherium snorki* was taken from JOHNSON & MADDEN (1997). We also included a cast of the giant specimen MNHN COL 1 (from the Gran Barranca south of Lake Colhué Huapi, supposedly from Colhuehuapian levels) labeled as *Parastrapotherium herculeum* AMEGHINO (the type is presumably lost), although it does not differ significantly from the type of *Parastrapotherium martiale* except by being somewhat larger (KRAMARZ & BOND 2010). The minute Colhuehuapian species *Parastrapotherium*

paucum AMEGHINO, 1902, *Astrapothericulus minusculus* AMEGHINO, 1902, *Astrapothericulus laevisculus* AMEGHINO, 1902, and *Astrapotherium triangulidens* AMEGHINO, 1902 were not considered since they are junior synonyms of *Astrapotherium ruderarium* (KRAMARZ & BOND 2010). Similarly, *Astrapotherium nanum* AMEGHINO (Santacrucian SALMA) and *Astrapotherium ephelicum* AMEGHINO (Deseadan SALMA) were excluded as they are based on deciduous cheek teeth of some undetermined large sized species (KRAMARZ & BOND 2008).

The body mass for *Comahuetherium coccaorum* (*Mc*) was calculated assuming geometric similarity from the equation $Mc/Mo = (Lc/Lo)^3$ (MACMAHON & BONNER 1983), being *Mo* and *Lo* the body mass and the M1-M3 length for other astrapotheriid specimen, and *Lc* is the M1-M3 length for *Comahuetherium coccaorum* (= 95.10 mm). This equation was applied for seven astrapotheriid specimen with positively associated upper and lower dentition. The seven obtained results of the body mass for *Comahuetherium coccaorum* range from ca. 324 to ca. 504 kg (mean = ca. 421 kg) (Table 3). Even considering the maximum estimated body weight value for *Comahuetherium coccaorum*, the mass of this new species is about 50% lesser than that of the second smallest astrapotheriid species (*Astrapothericulus iheringi*) and 90% smaller than the largest studied specimen (“*Parastrapotherium herculeum*”?) (Table 3).

4. Conclusions

The astrapotheres have been traditionally interpreted as a small group of large ungulates (SIMPSON 1967; PAULA COUTO 1974; CIFELLI 1993). Particularly, the late Oligocene – Miocene astrapotheriids were considered as typically conservative, giant mammals, being the middle sized *Astrapothericulus* an exception to that concept (SORIA 1984). The record of *Comahuetherium coccaorum* described here increases the known diversity of this group, and documents the occurrence of a small species in Patagonia during the early Miocene Colhuehuapian SALMA, in addition to other previously known non-giant astrapotheres (i.e. *Astrapotherium ruderarium* and an undetermined species of *Astrapothericulus*, see KRAMARZ 2009; KRAMARZ & BOND 2010). This wide body size range (ca. 400 – 4000 kg) suggests that astrapotheriids were not only mega-herbivores but played diverse ecological roles, although further studies are needed to understand the still obscure paleobiology of these mammals.

The middle Miocene *Granastrapotherium snorki* is one of the largest astrapotheres known so far, and concordantly the species with most reduced dental formula within the Astrapotheria (JOHNSON & MADDEN 1997). These combined features supported previous proposals about that in these mammals the reduction of the dental formula would be associated to an increase of body size (KRAMARZ & BOND 2009). The dental formula of *Comahuetherium* is as reduced as that of *Granastrapotherium*, but the former is much smaller (almost 80 % according to the body weight estimate), indicating that the body size and dental formula are not necessarily correlated.

A preliminary analysis (KRAMARZ & BOND 2010) suggested that *Comahuetherium* could be allied to the uruguaytheriine astrapotheres by sharing putative synapomorphies with *Granastrapotherium* and *Xenastropotherium*, thus challenging the traditional hypothesis of biogeographical segregation between Uruguaytheriinae and Astrapotheriinae. The results of our phylogenetic analysis do not support the alleged uruguaytheriine affinities of *Comahuetherium*. Consequently, there are no evidences of the occurrence of uruguaytheriine astrapotheres in Patagonia, but the occurrence of non-uruguaytheriines astrapotheres in northern latitudes still needs to be explored.

The phylogenetic analysis shows that dental specializations (e.g. extreme reduction of the dental formula) occurred convergently within Astrapotheria. This case, as well as others reported by KRAMARZ & BOND (2009), demonstrates that the evolution of these mammals was not a mere progressive acquisition of astrapotheriid characters as proposed by previous authors (SIMPSON 1967; SORIA 1984; FRAILEY 1987; CIFELLI 1993), but that it was much more complex and involved diverse evolutionary processes.

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Appendix 1. List and definition of characters used in the phylogenetic analysis. Except characters 18 and 43 (modified from JOHNSON & MADDEN 1997), the characters were taken from KRAMARZ & BOND (2009), with the addition of the new characters 21, 28, 29, 35, 38, 42, and 44.

1. Length of m2, 0 = less than 20 mm; 1 = between 20 and 40 mm; 2 = more than 40 mm
2. Cheek teeth, crown height 0 = bunolophodont, very low crowned; 1 = lophodont, high crowned (crown height lesser than anteroposterior diameter); 2 = lophodont, slightly hypsodont (crown height greater than anteroposterior diameter)
3. Molars, labial cingulum. 0 = absent; 1 = present
4. P2, central valley. 0 = absent; 1 = present
5. Posterior upper premolars. 0 = P2 present, size of P3-P4 not reduced in relation to molars; 1 = P2 absent, P3-P4 reduced.
6. P3, hypocone. 0 = absent; 1 = present
7. P4, posterolingual cingulum. 0 = low posterolingual cingulum; 1 = broaden, elevated posterolingual cingulum, hypocone insinuated; 2 = inflated posterolingual cingulum forming a well defined hypocone
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 (post-protocrista absent)
14. M1-M2, *crista*. 0 = absent; 1 = present
15. M1-M2, *crochet*. 0 = absent; 1 = present
16. M1-M2, metaloph. 0 = absent or incomplete (hypocone isolated); 1 = complete
17. Upper molar median fossette 0 = persistent in worn stages; 1 = ephemeral
18. Upper molar parastyle. 0 = well developed; 1 = reduced
19. M1, anterolingual pocket. 0 = absent; 1 = superficial; 2 = very penetrating, protocone anteriorly constricted
20. M1-M3, labial fold of the metacone. 0 = absent; 1 = present
21. M1-M3 hypocone; 0 = rounded; 1 = lophoid, lingually sharp
22. M3, hypocone; 0 = absent; 1 = present
23. i1. 0 = present; 1 = absent
24. i2. 0 = present; 1 = absent
25. i3. 0 = present; 1 = absent
26. Lower incisors, crown shape. 0 = simple; 1 = bilobed
27. Lower canine, implantation. 0 = not extroverted 1 = slightly extroverted; 2 = strongly extroverted
28. Upper canines, anterior groove. 0 = absent; 1 = present
29. Upper canines. 0 = rooted 1 = rootless
30. p2. 0 = present; 1 = absent
31. p3. 0 = present; 1 = absent
32. p3, paralophid. 0 = reduced or absent; 1 = well developed
33. p4, paralophid: 0 = reduced; 1 = well developed
34. p4, hypoflexid. 0 = present; 1 = absent
35. p4 entoconid. 0 = included into the posterolophid; 1 = bunoid, isolated; 2 = forming a distinct lophid (unordered)
36. m1-m3, paralophid. 0 = reduced; 1 = well developed
37. m1-m3, hypoflexid. 0 = deep; 1 = superficial; 2 = absent
38. m1-m3, paraflexid; 0 = transverse, very penetrating; 1 = oblique, superficial
39. Lower molars, entoconid. 0 = included into the posterolophid; 1 = bunoid, isolated; 2 = forming a distinct lophid (unordered)
40. m1-m3, pillar. 0 = absent; 1 = present, as a column; 2 = present, lophoid, enclosing with the metalophid a minute fossetid (unordered)
41. Lower molars, lingual cingulid. 0 = absent; 1 = present
42. Upper canines. 0 = strongly curved; 1 = nearly straight
43. M3, central valley. 0 = open lingually; 1 = enclosed by a posterolingual cingulum
44. P3. 0 = present; 1 = absent