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TAXONOMIC REINTERPRETATION OF *THEOSODON HYSTATUS* CABRERA AND KRAGLIEVICH, 1931 (LITOPTERNA, MACRAUCHENIIDAE) AND PHYLOGENETIC RELATIONSHIPS OF THE FAMILY

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ABSTRACT—Associated fragments of a maxilla and mandible of *Theosodon hystatus* Cabrera and Kraglievich (Macraucheniidae, Litopterna) from the late Miocene Arroyo Chasicó locality (Buenos Aires Province, Argentina) are described and taxonomically reinterpreted. The systematic arrangement is supported by the first phylogenetic analysis of the family. The holotype (MLP 29-IX-1-75) of *T. hystatus* was originally poorly described and its generic assignment was not fully justified. The comparison of MLP 29-IX-1-75 with *Paranauchenia denticulata* Ameghino from the ‘Mesopotamiense’ (lower member of the Ituzaingó Formation, Entre Ríos Province; late Miocene) shows significant morphological similarities that lead us to propose that *T. hystatus* belongs to the genus *Paranauchenia* Ameghino, resulting in the new combination *Paranauchenia hystata*. The phylogenetic analysis of Macraucheniidae supports this proposal because both taxa form a monophyletic clade, sharing one synapomorphy: metaconid of m2 lingually placed. This new taxonomic interpretation implies the geographic extension of *Paranauchenia* to Buenos Aires Province. The obtained phylogeny also corroborates the monophyly of Macraucheniidae, but not that of the currently considered subfamilies, because Cramaucheniinae is paraphyletic.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The geographic isolation of South America during most part of Cenozoic originated a fauna dominated by native terrestrial groups. Within these groups, the so-called South American extinct native ungulates included some families of Condylarthra and the orders Litopterna, Notoungulata, Astrapotheria (with Trigonostylopoidea), Xenungulata, Pyrotheria, and Notopterna (Bond et al., 1995; Vucetich et al., 2007). Within Litopterna, the family Macraucheniidae includes taxa from late Eocene (Dozo and Vera, 2010) to late Pleistocene–early Holocene (Tonni, 1990; Bond, 1999).

Macraucheniids were large- to very-large-sized herbivores with long necks and limbs, and three digits. They constituted cursorial forms, with a browser-grazer or mostly grazer diet (Bond et al., 1995; Bond, 1999). They are characterized by a complete dentition without diastema; uniformly sharp-pointed incisors and canines; nares reaching the frontal level in derivate taxa (*Macrauchenia* Owen, 1838); and the canal of the vertebral artery passing through the neural arch in most cervical vertebrae (Scott, 1912; Cassini et al., 2012).

Macraucheniidae originally included the subfamilies Cramaucheniinae, Theosodontiinae, and Macraucheniinae, represented by *Cramauchenia* Ameghino, 1902, *Theosodon* Ameghino, 1887a, and *Macrauchenia*, respectively (Ameghino, 1902; Dozo and Vera, 2010). However, other authors (Soria, 1981; Cifelli and Soria, 1983) considered only Cramaucheniinae (including Theosodontiinae) and Macraucheniinae. Although the systematics of the family is still controversial, the latter classification is the most currently accepted.

The oldest record of a macraucheniid is *Polymorphis* Roth, 1899, from Mustersan (late Eocene), Patagonia, Argentina (Cifelli, 1993; Dozo and Vera, 2010). Cramaucheniinae includes some Oligocene and early Miocene primitive forms: *Coniopternium* Ameghino, 1895, *Cramauchenia*, *Phoenixauchenia* Ameghino, 1904a, *Pternoconius* Cifelli and Soria, 1983, and *Theosodon*. Macraucheniinae is represented from the late Miocene to late Pleistocene–early Holocene and comprises *Macrauchenia*, *Scalabrinitherium* Ameghino, 1883a, *Oxydontherium* Ameghino, 1883b, *Paranauchenia* Ameghino, 1904a, *Promacrauchenia* Ameghino, 1904a, *Cullinia* Cabrera and Kraglievich, 1931, *Huayqueriana* Kraglievich, 1934, *Macrauchenioopsis* Paula Couto, 1945, *Xenorhinotherium* Cartelle and Lessa, 1988, and *Windhausenia* Kraglievich, 1930 (Soria, 1981; Cartelle and Lessa, 1988; Schmidt, 2013). Some of these taxa need a full taxonomic revision, particularly *Theosodon* (Cassini et al., 2012). This genus comprises seven species originally described for the Santa Cruz Formation (early Miocene): *Theosodon lydekkeri* Ameghino, 1887a, *T. lallemanti* Mercerat, 1891, *T. garretorum* Scott, 1910, *T. fontanae* Ameghino, 1891a, *T. gracilis* Ameghino, 1891a, *T. patagonicum* Ameghino, 1891a, and *T. karaiakensis* Ameghino, 1904b (Scott, 1910); and one species from the Arroyo Chasicó Formation (late Miocene), *T. hystatus* Cabrera and Kraglievich, 1931, poorly described by Cabrera and Kraglievich (1931). Recently, Croft et al. (2004) recognized *Theosodon* sp. in the early Miocene Chucal Formation, north of Chile.

The generic assignment of the holotype of *Theosodon hystatus* (MLP 29-IX-1-75) was already questioned by Bond and López (1995), considering it as a Macraucheniinae of an imprecise generic status (*T. hystatus*), and established some similarities with *Oxydontherium* from the ‘Mesopotamiense’, an informal stage recently recognized as the lower member of the

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Ituzaingó Formation, Entre Ríos Province, Argentina (Brunetto et al., 2013, and references therein).

In this contribution, we provide a detailed taxonomic revision of the holotype and only known specimen of *Theosodon hystatus* and discuss its phylogenetic relationships in the first cladistic analysis of Macraucheniidae.

MATERIALS AND METHODS

The holotype of *Theosodon hystatus* (MLP 29-IX-1-75) includes associated fragments of a right maxilla and mandible. The specimen belongs to the vertebrate paleontological collection of the Museo de la Plata (Buenos Aires, Argentina). The study was performed through morphometric description and comparisons with other Macraucheniidae stored at the MLP and MACN collections (Tables S1, S2 in Supplementary Data). Bibliographic data mainly come from Scott (1910), Soria (1981, 1986), Cifelli (1983), Cifelli and Soria (1983), Cartelle and Lessa (1988), and Bond and López (1995).

In order to evaluate the phylogenetic affinities of *T. hystatus*, we performed a cladistic analysis of Macraucheniidae with the TNT program (Goloboff et al., 2008), using equal weight and unordered states for all characters. We conducted an exact search (implicit enumeration).

Institutional Abbreviations—MACN Pv, Colección Paleontología Vertebrados del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

Anatomical Abbreviations—L, length of dental elements; l, left; M/m, upper/lower molar; P/p, upper/lower premolar; r, right; W, width of dental elements.

SYSTEMATIC PALEONTOLOGY

LITOPTERNA Ameghino, 1889

MACRAUCHENIIDAE Gervais, 1855

PARANAUCHENIA Ameghino, 1904a

PARANAUCHENIA HYSTATA (Cabrera and Kraglievich, 1931), nov. comb.
(Fig. 1, Table 1)

Theosodon hystatus Cabrera and Kraglievich, 1931:112–113 (original description).

Holotype—MLP 29-IX-1-75, a partial right maxilla with roots of P2–M1, M2 incomplete, and M3; an almost complete associated mandible with incisor roots, right p3–m2 and left p1–p2 (roots), talonid of p4, and m1–m2.

Geographic and Stratigraphic Distributions—MLP 29-IX-1-75 comes from the Arroyo Chasicó Formation that crops out in the distal area of the Chasicó stream basin and along the cliffs of the Laguna Chasicó, Villarino Department, south of Buenos Aires Province, Argentina (Pascual, 1965) (Fig. 2). The Arroyo Chasicó Formation was assigned to the late Miocene (Marshall et al., 1983; Zárate et al., 2007) and traditionally subdivided into the lower Vivero Member and the upper Las Barrancas Member (Bondesio et al., 1980; Marshall et al., 1983; Bond and López, 1995), although recent studies do not support this differentiation (Zárate et al., 2007).

Emended Diagnosis—Upper molars quadrangular in outline and brachyodont as in *Paranauchenia denticulata*. M2–M3 with lingual posterior fossette laterally compressed and hypocone long and slender, similar to *Oxydontherium*. M2 with hypocone more lingually projected than the protocone. M3 trapezoidal, with well-marked interstylar concavities, small, rounded fossette opposite to paracone, and central fossette lingually extended as in *P. denticulata*. Metastyle labially curved, enhancing a large concavity with the mesostyle, deeper than in other Macraucheniidae. Mandible low, similar to *Oxydontherium*. The c–p2 series placed

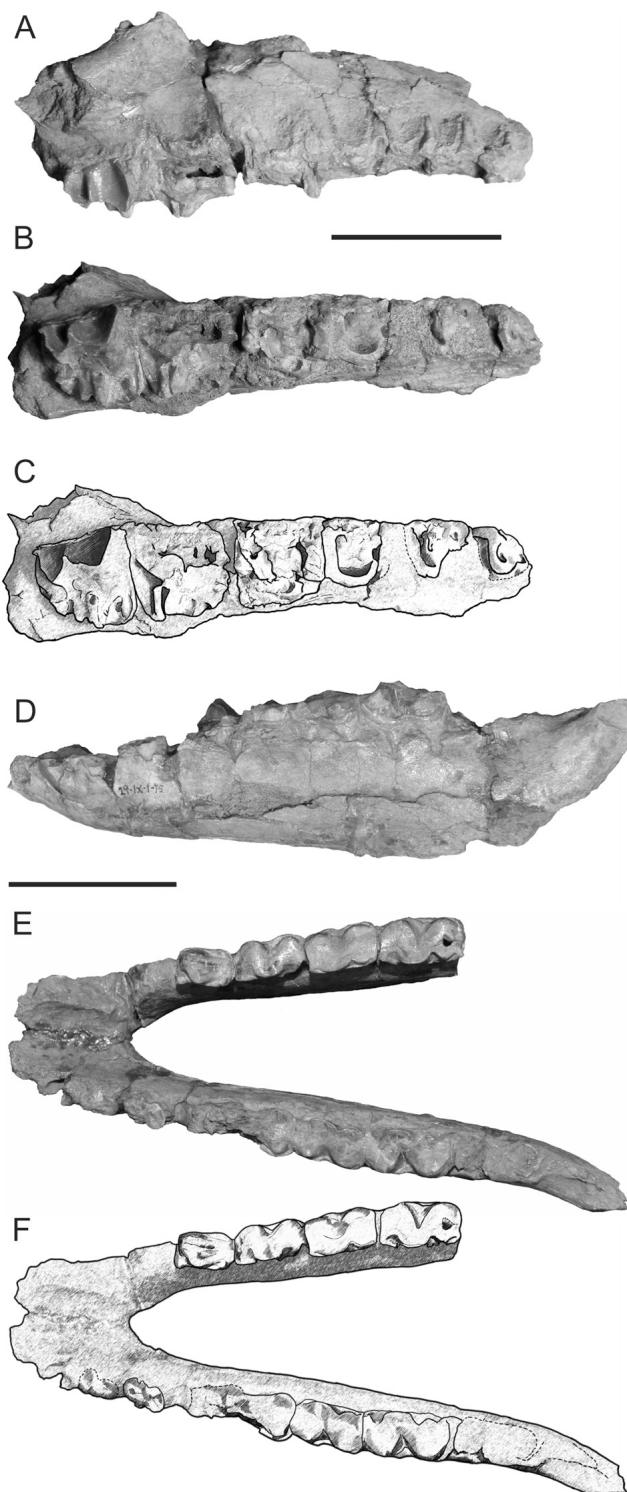


FIGURE 1. MLP 29-IX-1-75, holotype of *Paranauchenia hystata* (Cabrera and Kraglievich, 1931), nov. comb. Photographs and drawings. **A–C**, partial maxilla (**A**) in lateral view; (**B**) in occlusal view; (**C**) drawing in occlusal view; **D–F**, mandible (**D**) in lateral view; (**E**) in occlusal view; (**F**) drawing in occlusal view. Both scale bars equal 5 cm.

parallel to mandibular edge as in *Theosodon* and *Pternoconius*. The p3–m2 series with rounded labial edges, and well-marked cingula as in *P. denticulata*. The p4 without entoconid, resembling most of the Macraucheniidae except *Xenorhinotherium*.

TABLE 1. Dental dimensions (in mm) of *Paranauchenia hystata* (Cabrera and Kraglievich, 1931), nov. comb., and *P. denticulata* (Ameghino, 1891b).

Taxon/Specimen	Dimension	P4	M1	M2	M3	p3	p4	m1	m2
<i>Paranauchenia hystata</i>									
MLP 29-IX-1-75	L	(16.50)	(22.60)	(23.50)	22.60	19.70	22.30	21.50(r)/21.40(l)	25.30(r)/25.40(l)
	W	(20.70)	(20.50)	(22.60)	23.80	11.80	12.50	14.20(r)/13.80(l)	14.30(r)/15.50(l)
		P4	M1	M2	M3	m2	m3		
<i>Paranauchenia denticulata</i>									
MACN PV 4396	L	19.30	—	—	—	—	—		
	W	19.40	—	—	—	—	—		
MACN PV 4444	L	18.90	20.80	23.70	22.50	—	—		
	W	19.90	21.90	23.90	20.60	—	—		
MACN PV 1052	L	—	21.00	—	—	—	—		
	W	—	21.15	—	—	—	—		
MACN PV 6604	L	—	24.80	—	—	—	—		
	W	—	23.70	—	—	—	—		
MACN PV 12263c	L	—	21.65	—	—	—	—		
	W	—	21.60	—	—	—	—		
MACN PV 13179	L	—	28.00	—	—	—	—		
	W	—	25.50	—	—	—	—		
MLP 81-XI-29-7	L	—	26.40	—	—	—	—		
	W	—	23.50	—	—	—	—		
MACN A-1578	L	—	25.06	—	—	—	—		
	W	—	25.10	—	—	—	—		
MACN PV 13177	L	—	30.00	—	—	—	—		
	W	—	26.50	—	—	—	—		
MACN PV 3734	L	—	19.70	—	—	—	—		
	W	—	19.75	—	—	—	—		
MACN PV 4405	L	—	30.10	—	—	—	—		
	W	—	29.20	—	—	—	—		
MACN PV 3747	L	—	—	20.90	—	—	—		
	W	—	—	21.10	—	—	—		
MACN PV 13178	L	—	—	26.50	—	—	—		
	W	—	—	24.20	—	—	—		
MACN PV 4384	L	—	—	—	20.40	—	—		
	W	—	—	—	18.30	—	—		
MLP 41-XII-13-308	L	—	—	—	25.35	—	—		
	W	—	—	—	21.15	—	—		
MACN PV 4428	L	—	—	—	—	29.10	—		
	W	—	—	—	—	15.35	—		
MACN PV 9148	L	—	—	—	—	30.45	—		
	W	—	—	—	—	15.05	—		
MACN PV 8880	L	—	—	—	—	—	31.90		
	W	—	—	—	—	—	17.16		

Measurements in parentheses are approximate values.

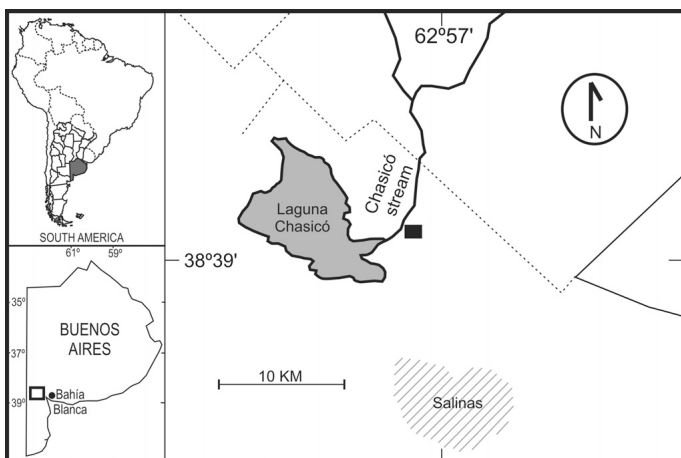


FIGURE 2. Geographic provenance of MLP 29-IX-1-75 from Buenos Aires Province, Argentina, South America. The black square shows the locality.

Presence of entolophid in m1–m2, different from *Macrauchenia* and *Macrauchenioipsis*. Entoconid weak in m1–m2 as in *P. denticulata*. Metaconid of m2 less lingually placed than in *P. denticulata*; entoconid robust and lophids broader than in *Oxydontherium*.

Description

The specimen MLP 29-IX-1-75 corresponds to an adult individual with advanced dental wear. The preserved upper teeth (Fig. 1, Table 1) show a quadrangular outline in occlusal view. The lingual posterior fossette in M2 and M3 is laterally compressed and shallow; the hypocone is slender and long (particularly in M2). The outline of M3 is trapezoidal, with the protoloph broader than the metaloph. On the labial side, three stylar cusps and a thin cingulum are developed. The concavities between the stylar cusps are well marked. The metastyle is labially curved, developing a large concavity with the mesostyle. A small, rounded fossette is opposite to paracone and a lingual central fossette opens to the lingual side. An edge extends from the metacone to the trigon, forming a valley posteriorly.

The mandible is poorly preserved and incomplete. The posterior edge of the symphysis reaches the level of the p1. The horizontal rami are low.

The p3–m2 series (Fig. 1, Table 1) exhibits low crowns, with rounded labial edges and well-developed cingula surrounding the crown completely. The p3 is labially convex and the talonid is broader than the trigonid. The labial cingulum projects posteriorly surrounding a shallow fossetid with the tooth wall. The p4 is molariform, without the entoconid; this cusp is instead well developed in m1 and m2.

The metaconid is broad in all teeth and extends more lingually than the other three lingual cusps in m1 and m2. The lingual cingulum is semicircular in m2.

Comparison

The comparative study of MLP 29-IX-1-75 and *Paranauchenia denticulata* (Ameghino, 1891b) (the holotype and other specimens referred) from the ‘Mesopotamiense’ of Entre Ríos Province highlights important similarities between them: quadrangular upper molars in occlusal outline; M2 with long, slender hypocone, and more lingually placed than protocone; lingual posterior fossette laterally compressed; anterior and posterior fossettes shallow; M3 with well-marked interstylar concavities and the central fossette opening to the lingual side; M3 with a smaller fifth fossette opposite to paracone; and m1 and m2 with well-marked cingulum and entolophid.

At the same time, MLP 29-IX-1-75 and *P. denticulata* show some morphological differences: the M3 of MLP 29-IX-1-75 has a metastyle labially curved, developing a large concavity with the mesostyle; in lower teeth, the metaconid is less lingually placed than the other cusps.

On the other hand, MLP 29-IX-1-75 differs from *Theosodon* in the deeper concavity between styles in M1–M3 (character 10), the location of the hypocone in M2 (character 12), and the presence of entoconid in m1 and m2 (character 17).

Phylogenetic Analysis

The analyzed data matrix (Appendix 1) comprises a total of 18 terminal taxa and 25 (7 cranial and 18 dental) characters (Appendix 2). Outgroups include two of the most complete and best-known genera of litopterns Adiantidae from the late Oligocene: *Proadiantus* Ameghino, 1897, and *Tricoelodus* Ameghino, 1897 (Cifelli and Soria, 1983). The ingroup includes the specimen MLP 29-IX-1-75 and 15 genera of Macrauchenidae: *Polymorphis*, *Cramauchenia*, *Coniopternium*, *Pternoconius*, *Theosodon*, *Cullinia*, *Huayqueriana*, *Scalabrinitherium*, *Oxyodontherium*, *Paranauchenia*, *Promacrauchenia*, *Xenorhinotherium*, *Macrauchenia*, *Macrauchenioptis*, and *Windhausenina*. *Phoenixauchenia* is excluded from the analysis because it is based on one astragalus.

Taxa were considered at the generic level. Most of them are monospecific, with the exception of *Pternoconius* (*P. polymorphoides* Cifelli and Soria, 1983, and *P. tournoueri* Soria and Hoffstetter, 1985), *Coniopternium* (*C. andinum* Ameghino, 1895, and *C. primitivum* Cifelli and Soria, 1983), *Promacrauchenia* [*P. antiqua* (Ameghino, 1887b); *P. calchaquiorum* Roverto, 1914; *P. chapalmalense* Ameghino, 1908, and *P. (Pseudomacrauchenia) yepesi* Kraglievich, 1930], and *Theosodon*. The number of species of *Theosodon* varies among different authors, being 10 (Croft et al., 2004) or 7 (Cassini et al., 2012); this diversity is probably overestimated and this genus needs a full taxonomic revision, which exceeds the scope of our contribution.

With respect to character coding, some comments are needed. The specimens of *Huayqueriana cristata* (Rovereto, 1914)

(MACN PV 8463 and MLP 41-IV-29-4) show a poor state of preservation of their orbits. However, the orbit shape (character 3) was coded as closed (3⁰), taking into account the description and figures in Rovereto (1914:212, pl. 29, fig. 4): “[...] la apófisis orbitaria baja perpendicularmente hasta juntarse con la apófisis cigomática del temporal [...]”. Concerning *Scalabrinitherium*, Cerdeño et al. (2008:223) mentioned that it has open orbits. Nevertheless, we did not see any specimen with a complete orbital region, so we considered this character as missing data.

An unpublished adult specimen of *Oxyodontherium* (MACN PV 13671) allowed us to recognize that hipsodonty (character 7) is similar to that of adult specimens of *Scalabrinitherium*, being both prohypodonts.

In the specimens of *Coniopternium primitivum*, the interstylar concavity in M1–M3 is poorly marked. They were used to code character 10 (10⁰) for *Coniopternium*.

The analysis provided three most parsimonious topologies of 55 steps, with a consistency index (CI) of 0.63 and a retention index (RI) of 0.75. The strict consensus tree (Fig. 3) indicates that the monophyly of the family Macrauchenidae is supported by two synapomorphies (node 2): hypolophid in p4 shorter than the paralophid (14⁰) and similar development of valleys in p4 (22¹). *Polymorphis* appears as the most basal taxon.

The cladogram shows a polytomy (node 3) with *Pternoconius*, *Coniopternium*, and *Cramauchenia* included.

Node 4 is supported by two synapomorphies: paralophid developed in m1 and m2, terminating on the lingual side (18⁰) and lower molars (m2) of medium size (24¹). In this clade, *Theosodon* appears as the sister group of the remaining taxa with more derived characters, which traditionally represented the subfamily Macraucheninae (node 5), and share five synapomorphies: nasal opening in a medial position (1¹), palate narrowed at P2 and P3 level (2¹), prohypodont dentition (7¹), P3 and P4 with parastyle labially projected (9⁰), and M1–M3 with well-marked interstylar concavities (10¹). In this clade, *Scalabrinitherium* is placed in a basal position. The next node (node 6) is defined by the absence of diastema between I3 and C (8¹), and shows *Oxyodontherium* as the sister group of taxa included in the node 7. This node, where *Huayqueriana* is the sister group of the remaining taxa, is supported by the palate narrowed at P3 level (2²) and with a smoothly lingual precingulum in M1 and M2 or precingulum at the level of the posterolingual cingulum (13¹).

Node 8 unites two clades supported by brachyodont dentition (7⁰). One of them is composed of *Paranauchenia* and MLP 29-IX-1-75 (node 9), which share the metaconid placed lingually in m2 (20¹). The other clade (node 10) is defined by two synapomorphies: incipient entoconid on hypolophid in m3 (19¹) and c–p2 obliquely implanted (21⁰). *Cullinia* is the sister taxon of the remaining taxa. In node 11, *Promacrauchenia* is the sister taxon of the Plio-Pleistocene taxa and is supported by three synapomorphies: hypsodont teeth (7²), hypocone labially placed in M2 (12⁰), and hypolophid similar in size to paralophid (14¹). Node 12 is defined by three synapomorphies: nasal opening placed posteriorly (1²), concavities or depressions on frontals (6¹), and specimens with large molars (m2) (24²). At this node, the relationships between *Windhausenina* and the Pleistocene taxa are unresolved, probably due to missing data for *Windhausenina*.

Node 13 shows a clade with *Macrauchenioptis* and *Macrauchenia* supported by three synapomorphies: diastema between I3 and C (8⁰), hypocone opposite to metacone in M1 and M2 (11⁰), and absence of entolophid in m1 and m2 (15¹).

DISCUSSION

Cabrera and Kraglievich (1931) briefly described a new species of macraucheniid from Arroyo Chasicó Formation (Buenos Aires, Argentina), naming it *Theosodon hystatus*. Bond

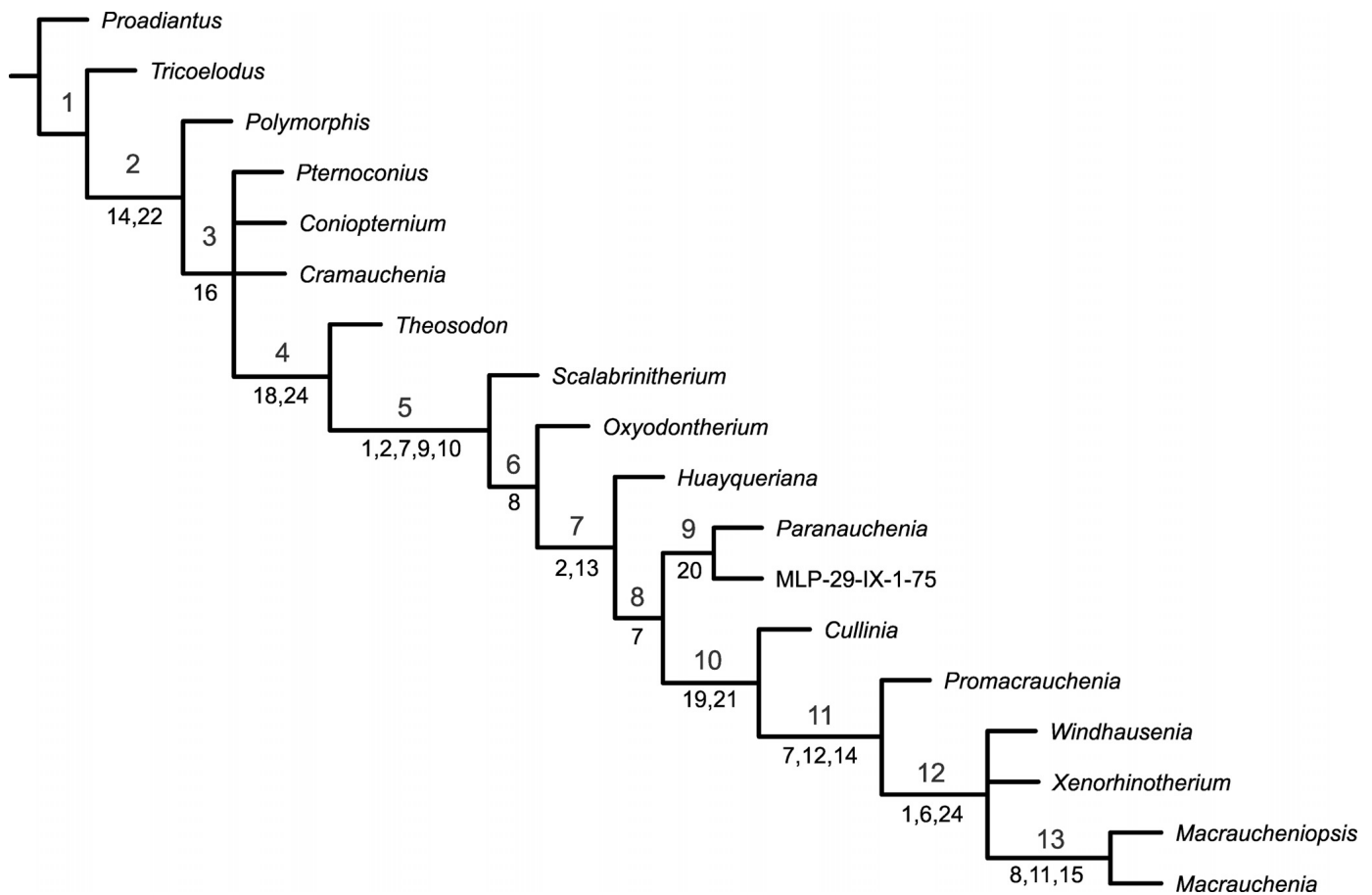


FIGURE 3. Consensus tree of the phylogenetic relationships of Macraucheniidae. Numbers above branches indicate nodes. Numbers below branches indicate synapomorphies.

and López (1995) questioned this assignment, pointing out its morphological similarities with *Oxydontherium* from the 'Mesopotamiense' of Ituzingó Formation (Entre Ríos Province, Argentina). However, from the comparison between MLP 29-IX-1-75 and *Oxydontherium*, we noticed that upper teeth of *Oxydontherium* have labial concavities less marked and do not present a quadrangular outline. The lower molars of *Oxydontherium* show a long, oblique hypolophid, slender entoconid with acute labial borders, and lingual cingula restricted to valleys. These features are absent in MLP 29-IX-1-75, whose m1 and m2 have rounded labial borders, robust entoconid, and well-developed cingula.

MLP 29-IX-1-75 presents brachyodont teeth as in *Cullinia*, *Theosodon*, *Polymorphis*, *Pternoconius*, *Coniopternium*, and *Cramauchenia*. The hypocone in M2 is more lingually projected than the protocone, differing from *Theosodon*, *Promacrauchenia*, *Xenorhinotherium*, and *Macraucheniopsis*.

The c-p2 series is placed parallel to the mandibular edge as in *Polymorphis*, *Theosodon*, and *Pternoconius*. The hypolophid in p4 is shorter than paralophid, different from *Promacrauchenia*, *Xenorhinotherium*, *Macrauchenia*, *Macraucheniopsis*, and *Windhausenien*. Also, the absence of entoconid resembles most of the Macraucheniidae except *Xenorhinotherium*.

MLP 29-IX-1-75 presents an entolophid in m1 and m2, different from *Macrauchenia* and *Macraucheniopsis*, and different from *Polymorphis*, *Cramauchenia*, *Coniopternium*, and *Pter-*

noconius by having a paralophid well developed and terminating lingually in these teeth.

Regarding size of the dentition, MLP 29-IX-1-75 is larger than *Polymorphis*, *Cramauchenia*, *Coniopternium*, and *Pternoconius*, overlapping with the size range of *Theosodon*, *Paranauchenia denticulata*, *Scalabrinitherium*, and *Oxydontherium* (Tables 1, S1, S2).

The morphological differences between MLP 29-IX-1-75 and the taxa mentioned above, and its similarities with *Paranauchenia* (see Comparison), allow us to establish it as belonging to this genus. This conclusion is further supported by the phylogenetic analysis.

Concerning the phylogenetic relationships of Macraucheniidae, our phylogeny does not support the two established subfamilies of Macraucheniidae, Cramaucheniinae and Macraucheniinae (Soria, 1981; Cifelli and Soria, 1983). In the obtained topology, there is a monophyletic group (Fig. 3, node 5) supported by five synapomorphies, which is representative of Macraucheniinae. Instead, Cramaucheniinae appears as a paraphyletic group in which *Polymorphis*, *Cramauchenia*, *Pternoconius*, *Coniopternium*, and *Theosodon* are successively placed in a basal position showing more primitive characters than Macraucheniinae.

Within this group, *Huayqueriana* is more related to *Scalabrinitherium* and *Oxydontherium* than to *Theosodon*, which does not support the hypothesis of Soria (1986) that

Huayqueriana is derived from one of the species of *Theosodon* or a related genus.

Different authors have used the body size to recognize species and evolutionary grades (Ameghino, 1893; Scott, 1910; Soria, 1986). In this regard, our character 24, length of m2, is a measurable parameter of the size of the specimens, and we observed that taxa with short m2 (small forms) occupy a more basal position than those with longer molars (larger forms).

Concerning cranial morphology, Soria (1986) proposed that *Scalabrinitherium* and *Promacrauchenia* would be more derived than *Huayqueriana*. The results of our analysis, in contrast, show that *Scalabrinitherium* has more primitive characters than *Huayqueriana*.

Neither does our analysis support the two evolutionary lineages proposed by Soria (1986): *Promacrauchenia antiqua* and *Macrauchenia patachonica* Owen, 1838, respectively. In addition, both species were found to be more derived than *Huayqueriana cristata*.

Marshall et al. (1984) regarded *Windhausenina* as a synonym of *Macrauchenia*. However, Soria (1986) and Cartelle and Lessa (1988) considered these taxa as different evolutionary lineages. Our phylogenetic analysis shows *Windhausenina* closer to *Xenorhinotherium* than to *Macrauchenia*.

Our results do not support the proposal of Guérin and Faure (2004) that *Xenorhinotherium bahiense* Cartelle and Lessa, 1988, is a synonym of *Macrauchenia patachonica* because the former is positioned as the sister taxon of *Macrauchenia* and *Macrauchenia*.

Although Bond and López (1995) did not perform a phylogenetic analysis, they mentioned that '*Theosodon*' *hystatus* showed some more derived characters than *Theosodon* and *Cramaucheniinae* in general. One of these characters was the hypocone more lingually extended in M2 and M3, a character that in our phylogenetic analysis is plesiomorphic (12¹) in both MLP-29-IX-1-75 and the rest of 'cramaucheniines'.

According to our analysis, '*Theosodon*' *hystatus* (MLP 29-IX-1-75) is placed in macraucheniines and not associated with *Theosodon*. The allocation of MLP-29-IX-1-75 with *Paranauchenia* (based on *Paranauchenia denticulata* from Entre Ríos Province) supports our taxonomic proposal of being related to this genus instead of to *Theosodon*, and the new combination *Paranauchenia hystata*.

CONCLUSIONS

The specimen MLP 29-IX-1-75 from Arroyo Chasicó (Buenos Aires Province, Late Miocene), originally identified as *Theosodon hystatus*, shares with *Paranauchenia denticulata* from 'Mesopotamiense' (lower member of Ituzaingó Formation, Entre Ríos Province) brachyodont teeth; M1–M3 with interstylar concavities well marked; M3 with a small, rounded fossette opposite to paracone, and central fossette lingually extended; lower teeth with well-marked cingula; and m1 and m2 with weak entoconid and paralophid developed, terminating on the lingual side. However, the M3 of MLP 29-IX-1-75 has a metastyle labially curved and the metaconid of lower teeth more lingually placed than the other three cusps. Therefore, *Theosodon hystatus* is reassigned to the genus *Paranauchenia* as *P. hystata*, nov. comb. The phylogenetic analysis supports this view because both taxa form a monophyletic clade supported by one synapomorphy: metaconid lingually placed in m2 (20¹). The analysis also corroborates the monophyly of *Macraucheniidae* and the subfamily *Macraucheniinae*, but genera traditionally included in *Cramaucheniinae* appear as a paraphyletic group.

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[illegible]

- (0) Development of nasals: developed (0); reduced (1); vestigial (2).
- (1) Nasal opening position: anterior (0); medial (1); posterior (2).
- (2) Anterior palatal shape: without narrowing (0); with narrowing to P2–P3 level (1); with narrowing to P3 level (2).
- (3) Orbit shape: close (0); open (1).
- (4) In palatal view, anterior edge of premaxilla: straight (0); sharpened (1); rounded (2).
- (5) Anterior rostral edge in lateral view: curved ventrally (0); not curved (1).
- (6) Frontal concavities: absent (0); present (1).
- (7) Hypsodonty level: brachyodont (0); prohypsodont (1); hypsodont (2).
- (8) Diastema between I3 and C: present (0); absent (1).
- (9) Parastyle in P3–P4: labially projected (0); not labially projected (1).
- (10) Concavity between styles in M1–M3: slightly marked (0); well marked (1).
- (11) Hypocone in M1–M2: opposite to metacone (0); near to protocone (1).
- (12) Location of hypocone in M2: more labial than protocone (0); more lingual than protocone (1).

- (13) Anterolingual cingulum (precingulum) in M1–M2: noticeably more lingual than posterolingual cingulum (0); slightly lingual or at the same level of posterolingual cingulum (1).
- (14) Hypolophulid in p4: shorter than the paralophid (0); similar to paralophid (1).
- (15) Entolophid in m1–m2: present (0); absent (1).
- (16) Hypoconulid in m3: expanded, forming a third lobe (0); not expanded (1).
- (17) Entoconid in m1–m2: weak (0); developed (1); absent (2).
- (18) Paralophid in m1–m2: developed, terminating on the lingual side (0); less developed, terminating in an anterior medial position (1).
- (19) Entoconid in m3: developed and joined to hypolophid (0); incipient on the hypolophid (1); joined to hypoconulid (2); absent (3).
- (20) Metaconid in m2: not linguallly displaced (0); linguallly displaced (1).
- (21) Implantation of c–p2: oblique (0); parallel to mandibular edge (1).
- (22) Trigonid valley in p4: more developed than the talonid valley (0); with similar development to the talonid valley (1).
- (23) Entoconid in p4: present (0); absent (1).
- (24) Length of m2: 5–20 mm [small tooth] (0); 21–35 mm [medium tooth] (1); 36–45 mm [large tooth] (2); more than 45 mm [very large tooth] (3).