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ABSTRACT
Hitherto, only the Proterotheriidae Ameghino, 1887 litopterns from the Cerro Azul Formation (Chasicoan-Huayquerian Stages/Ages; Late Miocene-Early Pliocene) in La Pampa Province had been studied, recognizing Proterotheriidae indet. at Cerro La Bota, *Diplasiotherium pampa* Soria, 2001 at several localities,

Eoauchenia primitiva Ameghino, 1887 at El Guanaco, and cf. *Brachytherium cuspidatum* Ameghino, 1883 at Salinas Grandes de Hidalgo, which added to *Epecuenia thoatherioides* Cabrera, 1939 from Laguna Epecuén in Buenos Aires Province; this locality also yielded the Macraucheniidae Gervais, 1855 *Huayqueriana cristata* (Rovereto, 1914). Now, we enlarge the study to both litoptern families and to the outcrops of the Cerro Azul Formation in Buenos Aires Province. Concerning Macraucheniidae, we recognize: *Scalabrinitherium bravardi* Ameghino, 1883 at Salinas Grandes de Hidalgo, Telén, and Guatraché (La Pampa), and Laguna Epecuén (Buenos Aires); *Paranauchenia denticulata* Ameghino, 1891, *Promacrauchenia* sp., and *Cullinia* sp. at Salinas Grandes de Hidalgo and Laguna Chillhué (La Pampa); cf. *Oxyodontherium zeballosi* Ameghino, 1883b at Laguna del Monte (Buenos Aires); and *Promacrauchenia* sp. at Cantera Relleno Sanitario (Buenos Aires). Referring to Proterotheriidae, new results reveal the first record of *Diplasiotherium pampa* in Buenos Aires (Arroyo El Venado) and *Neobrachytherium* sp. at Laguna Epecuén and Laguna La Paraguaya (Buenos Aires). The litoptern diversity is close to that from the Lower Member of the Ituzaingó Formation, Late Miocene, Entre Ríos Province. The litoptern record does not provide confident data to support or reject the established relative biostratigraphic succession of localities of the Cerro Azul Formation, which is mainly based on some rodent lineages.

KEY WORDS
Macraucheniidae,
Proterotheriidae,
Cerro Azul Formation,
Late Miocene,
Early Pliocene,
central Argentina.

RÉSUMÉ
Mise à jour des Litopterna du Huayquerien (Miocène Supérieur) du centre-est de l'Argentine.
Jusqu'à présent, seuls les litopternes Proterotheriidae Ameghino, 1887 de la formation Cerro Azul (étages/âges Chasicoen-Huayquerien; Miocène supérieur-Pliocène inférieur) dans la province de La Pampa ont été étudiés, en identifiant : Proterotheriidae indet. à Cerro La Bota, *Diplasiotherium pampa* Soria, 2001 dans plusieurs localités, *Eoauchenia primitiva* Ameghino, 1887 à El Guanaco et cf. *Brachytherium cuspidatum* Ameghino, 1883 à Salinas Grandes de Hidalgo, en plus d'*Epecuenia thoatherioides* Cabrera, 1939 à Laguna Epecuén dans la province de Buenos Aires; cette localité a aussi livré le Macraucheniidae Gervais, 1855 *Huayqueriana cristata* (Rovereto, 1914). Cette contribution élargit l'étude aux deux familles de litopternes, ainsi qu'aux affleurements de la formation dans la province de Buenos Aires. En ce qui concerne les Macraucheniidae, nous avons identifié : *Scalabrinitherium bravardi* Ameghino, 1883 à Salinas Grandes de Hidalgo, Telén et Guatraché (La Pampa), et Laguna Epecuén (Buenos Aires); *Paranauchenia denticulata* Ameghino, 1891, *Promacrauchenia* sp. et *Cullinia* sp. à Salinas Grandes de Hidalgo et Laguna Chillhué (La Pampa); cf. *Oxyodontherium zeballosi* Ameghino, 1883b à Laguna del Monte (Buenos Aires) et *Promacrauchenia* sp. à Cantera Relleno Sanitario (Buenos Aires). Concernant les Proterotheriidae : *Diplasiotherium pampa* Soria, 2001 est identifié pour la première fois dans la province de Buenos Aires (Arroyo El Venado) et *Neobrachytherium* sp. est trouvé à Laguna Epecuén et Laguna La Paraguaya (Buenos Aires). La diversité de litopternes identifiés est proche de celle du membre inférieur de la formation Ituzaingó, Miocène supérieur, province d'Entre Ríos. Les litopternes ne fournissent pas de données précises pour la séquence biostratigraphique des localités de la Formation Cerro Azul, principalement basée sur quelques lignées de rongeurs.

MOTS CLÉS
Macraucheniidae,
Proterotheriidae,
formation Cerro Azul,
Miocène supérieur,
Pliocène inférieur,
Argentine centrale.

INTRODUCTION

Litopterna is one of the orders included in the so-called South American native ungulates. They were common elements in the Cenozoic faunas since the Paleocene of Argentina and Brazil up to the Late Pleistocene/Early Holocene of several South American localities (Bonaparte & Morales 1997; Bond *et al.* 2006, 2009; Bergqvist 2008; Gelfo *et al.* 2009, 2017; Dozo & Vera 2010; Schmidt & Ferrero 2014; Billet *et al.* 2015; Welker *et al.* 2015; Gelfo 2016; Forasiepi *et al.* 2016; López Mendoza *et al.* 2018).

Two families of litopterns, Macraucheniidae Gervais, 1855 and Proterotheriidae Ameghino, 1887, are recognized in Late Miocene levels of central-east Argentina (La Pampa and Buenos Aires provinces) and other areas such as Entre Ríos, Catamarca, San Luis, La Rioja, and Mendoza provinces (Rovereto 1914; Cabrera 1939; Delupi de Bianchini & Bianchini 1971; Zetti 1972; Bondesio *et al.* 1980; Soria 1986, 2001; Cione *et al.* 2000; Cerdeño 2003; Montalvo *et al.* 2005; Verzi & Montalvo 2008; Cerdeño *et al.* 2008; Reguero & Candela 2011; Brandoni *et al.* 2012, 2019; Brandoni 2013; Schmidt 2013, 2015; Schmidt & Cerdeño 2013; Bonini 2014; Deschamps & Tomassini 2016; Forasiepi *et al.* 2016; Bonini *et al.* 2017; Schmidt *et al.* 2018, 2020). Late Miocene litopterns are also known in Venezuela (Urumaco Formation), Brazil (Acre Region, Solimões Formation), and Uruguay (Camacho Formation) (Carlini *et al.* 2006; Latrubesse *et al.* 2010; Corona *et al.* 2020).

Macraucheniids include large to very large, cursorial animals with long neck and limbs, tridactyl autopodium, continuous dental series, and retracted nares, reaching a dorsal position in the skull (especially in the Pleistocene genus *Macrauchenia* Owen, 1838), with browser-grazer or mostly grazer feeding

habits (Bond *et al.* 1995; Bond 1999; Cassini *et al.* 2012; Schmidt 2013). They have complete dental formula; upper molars with two labial concavities, enamel fossettes and other secondary structures on the occlusal face; I/i1-P/p1 generally imbricated; prohypsodont P4-M3/p4-m3 in Macraucheniinae, with well-developed fossettes in M1-3 and the hypocone displaced towards the protocone, also observable in the Cramaucheniinae Ameghino, 1902 *Theosodon* Ameghino, 1887 (Soria 1981). The ml-3 usually present entolophid, although it can be absent in some taxa (e.g. *Macrauchenia patachonica* Owen, 1838 or *Cramauchenia normalis* Ameghino, 1902; see Paula Couto 1979; Soria 2001).

Proterotheriids were medium to large-sized, cursorial herbivores, mostly browser, characterized by the reduction of lateral digits (II and IV), becoming functionally monodactyl, comparable to equids (Soria 2001; Ubilla *et al.* 2011; Cassini *et al.* 2012; Schmidt 2013). They present incomplete dental formula (1/2; 0/1; 4/4; 3/3), with P/p3-4 molarized; P3-M3 with three labial styles, paraconule connected to protocone by a weak protoloph, and variable position and shape of metaconule; hypocone present in P3-4 of Neogene taxa; M3 usually without hypocone and reduced metastyle; cl-p2 reduced and subequal; p4-m3 without paraconid and paralophid in Oligocene forms; hypoconulid of m3 tending to form a third lobe, entoconid – when present – connected to hypoconulid or free (Soria 2001).

Concerning the Late Miocene litopterns from the Cerro Azul Formation in La Pampa Province, Proterotheriidae recovered from levels of Chasicoan and Huayquerian Stages/Ages (see Material and methods about the followed biostratigraphic scheme) have been recently studied (Schmidt *et al.* 2018). The aim of the present contribution is to extend the considered area to the Huayquerian levels of the same formation cropping out in Buenos Aires Province (according to Folguera & Zárate 2009), updating data on proterotheriids and completing the knowledge of the diversity of this order with the inclusion of Macraucheniidae.

GEOLOGICAL SETTING AND FOSSILIFEROUS LOCALITIES

The fossils of Litopterna studied herein were recovered from levels of the Cerro Azul Formation assigned to the Late Miocene-Early Pliocene Huayquerian Stage/Age, cropping out at different localities of La Pampa and Buenos Aires provinces (Folguera & Zárate 2009).

This formation was described by Linares *et al.* (1980) to encompass the Neogene sediments in the center and east of La Pampa Province. Later, Folguera & Zárate (2009) extended the areal distribution of this unit to the south-west of Buenos Aires Province, including Late Miocene deposits, with Chasicoan and Huayquerian faunas, previously assigned to other formations (e.g. Epecuén, Saldungaray, and Arroyo Chasicó). Based on a sedimentological analysis of the outcrops in La Pampa Province, Visconti *et al.* (2010) interpreted the levels of the Cerro Azul Formation as eolian deposits with intercalated paleosols. Folguera & Zárate (2018) reinterpreted these deposits and recognized both eolian (loess) and fluvial (reworked sandy silts) facies. More descriptions on the stratigraphy and sedimentology of this formation can be found, for instance, in Linares *et al.* (1980), Goin *et al.* (2000), Folguera & Zárate (2009, 2018), and Visconti *et al.* (2010).

The localities including Huayquerian levels that yielded the studied litopterns are: Bajo Giuliani (36°42'40.39"S, 64°16'59.89"W), El Guanaco (36°17'S, 64°16'W), Telén (36°15'11.81"S, 65°30'46.98"W), Loventué (36°20'0.96"S, 65°16'50.51"W), Laguna Chillhué (37°17'S, 64°9'W), Salinas Grandes de Hidalgo (37°13'04.83"S, 63°36'04.71"W), Guatraché (34°46'S, 69°33'W) and Caleufú (35°41'S, 64°40'W), in La Pampa Province, and Laguna Epecuén – Carhué (37°07'53"S, 62°48'36"W), Laguna del Monte – Guaminí (37°02'06"S, 62°29'15"W), Laguna La Paraguaya (37°05'53.57"S, 62°47'34.98"W), Arroyo El Venado (36°59'30"S, 62°41'51.45"W), and Cantera Relleno Sanitario (38°46'24"S, 62°09'25"W) in Buenos Aires Province (Fig. 1).

The relative age and biochronology of the Cerro Azul Formation in La Pampa and Buenos Aires provinces were established through schemes proposed and recently improved for fossil-bearing localities, based on octodontoid rodents and notoungulates (Verzi 1999; Verzi *et al.* 2008; Sostillo *et al.* 2014, 2019; Montalvo *et al.* 2019; Piñero *et al.* 2021). Two numerical dates were obtained for levels of this formation. One of them (5.28 ± 0.04 Ma) corresponds to the Cantera Vialidad locality (Buenos Aires Province; referred to as "exposures near Bahía Blanca"; Schultz *et al.* 2004, 2006; Folguera & Zárate 2009), where the record of the rodent *Xenodontomys ellipticus* Kraglievich, 1927 allows biostratigraphic correlations with other localities with levels assigned to the late Huayquerian (Deschamps & Tomassini 2016). The other date (9.23 ± 0.09 Ma) corresponds to the Arroyo Chasicó site, type locality of the Chasicoan (Zárate *et al.* 2007). In this sense, the fossiliferous levels of the Cerro Azul Formation include faunal assemblages assigned to Chasicoan (e.g. Arroyo Chasicó, Cerro Patagua – without litopterns – and Cerro La Bota localities; Pascual 1965; Pascual *et al.* 1965; Verzi 1999; Montalvo *et al.* 2019), early Huayquerian (e.g. Laguna Chillhué, Loventué, Telén, and Salinas Grandes de Hidalgo localities), and late Huayquerian (e.g. Bajo Giuliani, El Guanaco, Guatraché, and Cantera Relleno Sanitario localities) (Verzi 1999; Verzi *et al.* 2008; Sostillo *et al.* 2014, 2019; Montalvo *et al.* 2019; Piñero *et al.* 2021). Finally, Caleufú is now considered Early Pliocene, based on the presence of several Octodontoidea rodents, but within the late Huayquerian (Piñero *et al.* 2021: fig. 9).

The localities from western Buenos Aires Province in Las Encadenadas area (Laguna Epecuén, Laguna del Monte, Laguna La Paraguaya, and Arroyo El Venado) (Cabrera 1939; Pascual 1961, 1965; Pascual & Bochino 1963; Zetti 1972; Tonni *et al.* 1992; Goin *et al.* 2000) have not provided, at the moment, taxa with biostratigraphic and/or biochronological value (Bonini *et al.* 2017), but the assemblages suggest a Huayquerian *s.l.* An accurate adjustement of the age of these faunal assemblages of the Cerro Azul Formation in western Buenos Aires is still needed.

MATERIALS AND METHODS

The studied specimens are housed in different institutions of La Pampa and Buenos Aires provinces, Argentina (see Abbreviations and acronyms). Morphometric descriptions and comparisons are included, following usual terminology in litoptern systematics (e.g. Soria 1981, 2001; Soria & Hoffstetter 1985; Schmidt 2015; Souza Lobo *et al.* 2017; Corona *et al.* 2020). Measurements were taken using a digital caliper (0.01 mm) and a Nikon d3100 camera was used to take photographs. The material for comparison mainly consists of specimens from the Lower Member of the Ituzaingó Formation (traditionally known as "Mesopotamian", Late Miocene; De Alba 1953; Brunetto *et al.* 2013), Entre Ríos Province, analyzed and illustrated by G. I. Schmidt (2013) in her Ph.D. Thesis. Other material mentioned along the text corresponds to national and foreign collections and bibliographic data.

From a biostratigraphic viewpoint, we follow the scheme of Stages/Ages proposed by Cione & Tonni (2005) for the late Cenozoic of Pampean Region of Argentina. We also considered the modifications suggested by other authors (e.g. Verzi *et al.* 2008; Tomassini *et al.* 2013; Piñero *et al.* 2021) particularly for the Late Miocene-Early Pliocene of La Pampa and Buenos Aires provinces.

Abbreviations and acronyms

Institutions

FCP-V-M	Fundación Casa del Pueblo, Museo de Paleontología, Mineralogía y Arqueología, Firmat;
FMNH P	Field Museum of Natural History, Chicago;
GHUNLPam	Colección Paleontológica, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa;
IANIGLA-PV	Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Paleontología de Vertebrados, Mendoza;
MACN Pv	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Paleontología de Vertebrados, Buenos Aires;
MAS PALEO-VERT	Museo de Ciencias Naturales y Antropológicas "Profesor Antonio Serrano", Paraná;
MHG-P	Museo Histórico Regional de Guaminí "Coronel Marcelino E. Freyre", Guaminí;
MHIN-UNSL-GEO-V	Museo de Historia Natural, Departamento de Geología, Universidad Nacional de San Luis, San Luis;
MLP	Museo de La Plata, La Plata;
MMH-MCH	Museo Municipal de Ciencias Naturales "Vicente Di Martino", Colección Macachín, Monte Hermoso;
MMP-M	Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia", Mar del Plata;
PV-UNS	Departamento de Geología, Universidad Nacional del Sur, Paleontología de Vertebrados, Bahía Blanca;
PVL	Fundación Miguel Lillo, Colección Paleontología de Vertebrados, San Miguel de Tucumán.

Other abbreviations

C/c	upper/lower canine;
DI/di	upper/lower deciduous incisors;
DP/dp	upper/lower deciduous premolars;
I/i	upper/lower incisors;
M/m	upper/lower molars;
P/p	upper/lower premolars.

SYSTEMATIC PALEONTOLOGY

Order LITOPTERNA Ameghino, 1889
Suborder LOPHOLIPTERNA Cifelli, 1983
Family Macraucheniidae Gervais, 1855
Subfamily Macraucheniinae Gervais, 1855

Genus *Scalabrinitherium* Ameghino, 1883

Type species. — *Scalabrinitherium bravardi* Ameghino, 1883.

Type locality, stratigraphic horizon and age. — Paraná river cliffs (Entre Ríos Province); Lower Member of the Ituzaingó Formation; Late Miocene.

Scalabrinitherium bravardi Ameghino, 1883
(Fig. 2A-R)

Scalabrinitherium bravardi Ameghino, 1883a: 108.

Referred material. — GHUNLPam 6765, associated left P2 and fragments of right M1?, GHUNLPam 8146, right M1, GHUNLPam 6110, left mandibular fragment with incomplete m2 and complete m3, and GHUNLPam 6207, incomplete lower molar, from Salinas Grandes de Hidalgo (early Huayquerian); GHUNLPam 8233, right M3, from Telén (early Huayquerian); GHUNLPam 5138, left partial maxilla with M1 (incomplete)-M3, and GHUNLPam 5139, right trigonid of a lower molar, from Guatraché (late Huayquerian); and MMP-M 2000, left mandibular fragment with p3-m1, from Laguna Epecuén (Huayquerian *s.l.*).

Description

The P2 GHUNLPam 6765 (Fig. 2A) is a worn tooth, labially convex. It is triangular in occlusal view, compressed anteriorly and wider and rounded posterolingually. There is a long anterolingual fossette, limited by a basal cingulum, and a tiny fossette posterolingually placed. The associated molar fragment (M1? Fig. 2B) preserves a large, tear-shaped posterolingual fossette, a notably smaller, laterally compressed mediolingual fossette, and a partially preserved, roughly compressed anterolingual one.

GHUNLPam 8146 (Fig. 2C, D) is an incomplete, worn M1, with four fossettes. The posterior one is tear-shaped as in the molar of GHUNLPam 6765; the anterior fossette is a little smaller, quadrangular, and slightly more lingually placed; the other two fossettes are placed in between. The most lingual of the latter is smaller, but similar to the anterior one and separates protocone and hypocone with similar development, while the most labial one is centrally placed, subcircular and much smaller. The labial styles (Fig. 2C) are poorly developed; the interstylar concavities are shallow, longer the anterior one.

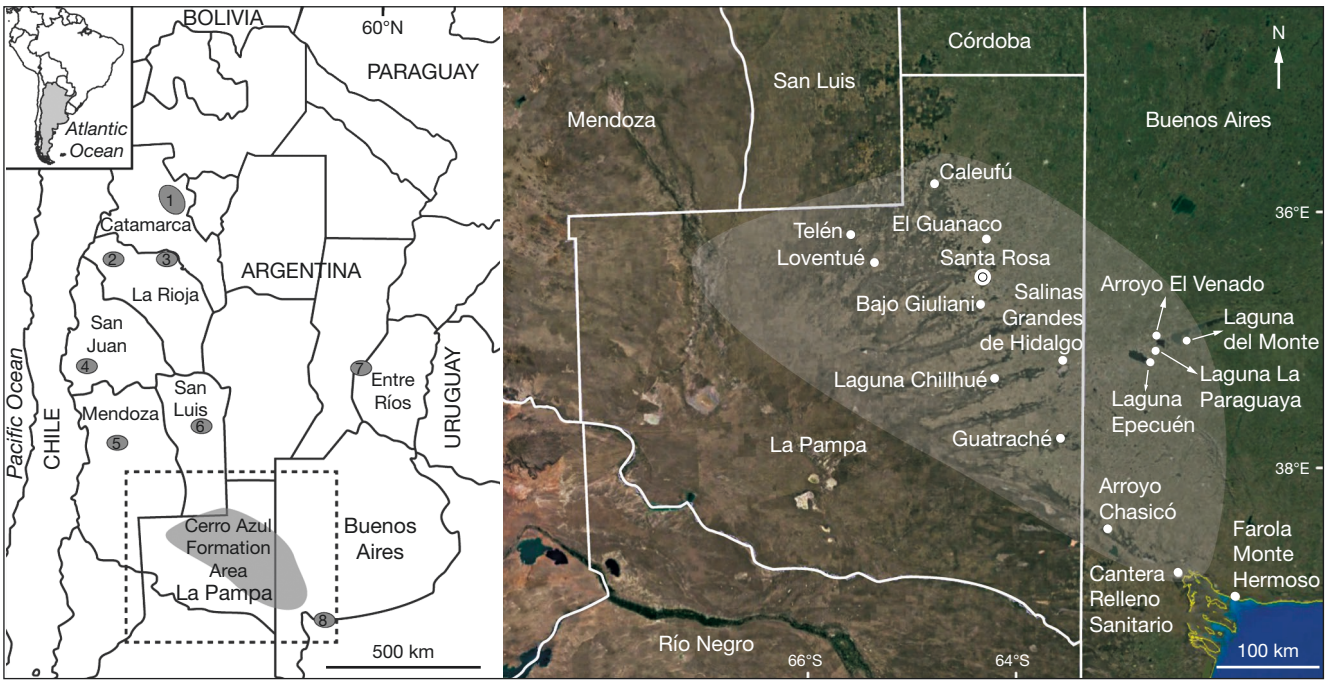

FIG. 1. — Geographic location of the Late Miocene-Early Pliocene deposits of the Cerro Azul Formation, with remains of Litopterna, in La Pampa and Buenos Aires provinces, Argentina, and other compared Late Miocene-Pliocene formations. **1**, Andalhuala and Corral Quemado formations, Catamarca; **2**, Toro Negro Formation, La Rioja; **3**, Salicas Formation, La Rioja; **4**, Loma de Las Tapias Formation, San Juan; **5**, Huayquerías Formation, Mendoza; **6**, Río Quinto Formation, San Luis; **7**, Ituzaingó Formation (Lower Member), Entre Ríos; **8**, Monte Hermoso Formation, Buenos Aires.

The labial cingulum descends slightly from the posterior to the anterior region.

In GHUNLPam 5138 (Fig. 2E), the posterior fossette of the incomplete M1 is oval, differing from that described above. The M2 shows the protoloph wider than the metaloph; preserves the four fossettes and the lingual ones show a low lingual border (also observed in M3); labially, the styles and the interstylar concavities are pronounced, and the distance between parastyle and mesostyle is greater than that between mesostyle and metastyle (Fig. 2F). The M3 is labiolingually compressed, with all fossettes well developed, except the small mediolingual one; the hypocone is less extended lingually than the protocone, and both are shorter than in M2 due to the trapezoidal outline of M3; the labial concavity between parastyle and mesostyle is shallow, and there is an incipient metacone fold between mesostyle and metastyle. All these teeth present traces of cementum on the labial face and inside the fossettes.

The unworn M3 GHUNLPam 8233 (Fig. 2G-I) shows the four fossettes well delimited and a fifth one opposite to the paracone (mesiolabial fossette *in* Souza Lobo *et al.* 2017). The anterior half of the crown is higher than the posterior one (Fig. 2H) as usually happens in unworn teeth. The protoloph is wider than the metaloph, and protocone and hypocone are poorly developed. There is a smooth labial cingulum. In contrast to GHUNLPam 5138, the parastyle and mesostyle are very projected labially, with a very deep concavity in between, but both specimens share the incipient metacone fold. The metastyle is much less developed than the other styles and somewhat more reduced than in GHUNLPam 5138.

The mandibular fragment MMP-M 2000 (Fig. 2J-L) presents an abnormal labial concavity at the p4 level (Fig. 2J), probably due to distortion produced by lithostatic load. The p3 is labiolingually flattened, with the paralophid lingually oriented; the labial face is triangular (Fig. 2K), its profile slightly convex anteriorly and straighter posteriorly; the labial cingulum is limited to the base of the crown, better developed posteriorly; the lingual cingulum is developed at the base of the valleys (Fig. 2L). The p4 is molariform with a wide and deep ectoflexid; the talonid is labially more acute than the trigonid; the paralophid is longer than the hypolophulid; labial and lingual cingula cannot be observed because of the presence of sedimentary matrix. In the m1, the trigonid is more labially rounded than the talonid; paralophid and hypolophulid have similar length; the entoconid is notorious; the labial cingulum is only observed on the anterior region; and the lingual cingular area is covered by sediment.

In GHUNLPam 6110 (Fig. 2M-O), the talonid of m2 is labially rounded. The m3 presents a labially rounded trigonid and an acute talonid (Fig. 2N); the hypolophulid is shorter than the paralophid; the entoconid forms a well-developed central pillar that does not reach the lingual level of the metaconid, which is high and massive; the ectoflexid is wide and deep; the lingual cingulum is conspicuous, weaker at the base of the metaconid; and there are cementum remains on the labial wall and in the talonid valley (Fig. 2O).

The fragmentary lower molar GHUNLPam 5139 (Fig. 2P-R) shows the trigonid with rounded labial surface and a deep metaflexid; the preserved part of the metaconid is massive and higher than the acuminated paraconid; there are cementum remains, and the preserved root is massive.

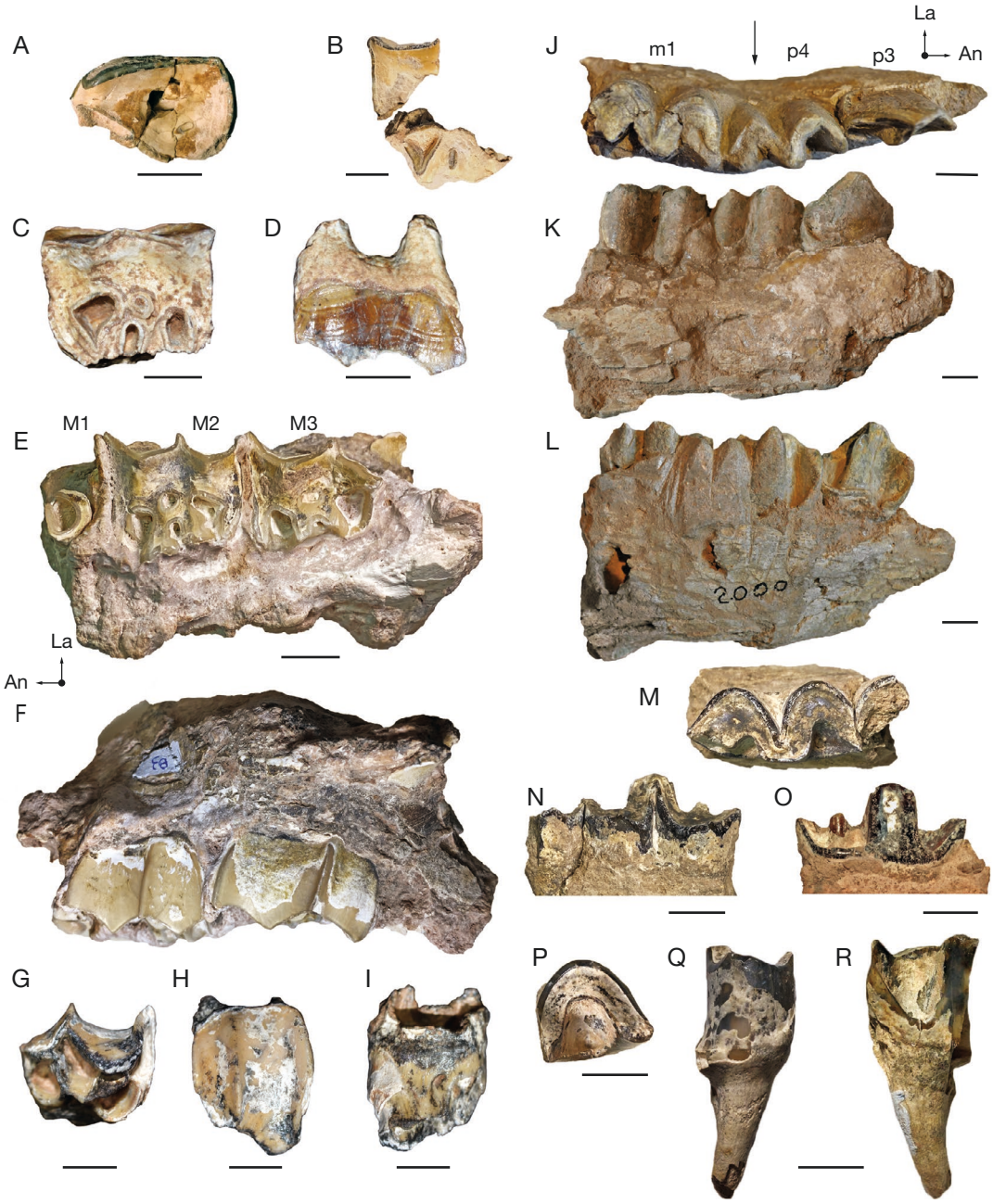

Fig. 2. — *Scalabrinitherium bravardi* Ameghino, 1883: **A**, **B**, GHUNLPam 6765, associated left P2 and fragments of right M1? (occlusal view); **C**, **D**, GHUNLPam 8146, right M1 (occlusal and labial views); **E**, **F**, GHUNLPam 5138, left partial maxilla with M1 (incomplete) – M3 (occlusal and labial views); **G**-**I**, GHUNLPam 8233, right M3 (occlusal, labial, and lingual views); **J**-**L**, MMP-M 2000, left mandibular fragment with p3-m1 (occlusal, labial, and lingual views); the arrow indicates the abnormal labial concavity; **M**-**O**, GHUNLPam 6110, left mandibular fragment with incomplete m2 and m3 (occlusal, labial, and lingual views); **P**-**R**, GHUNLPam 5139, right trigonid of a lower molar (occlusal, labial, and lingual views). Abbreviations: **An**, anterior; **La**, labial. Scale bars: 10 mm.

GHUNLPam 6207 is a poorly preserved lower tooth, without enamel preserved, with deep ectoflexid and remains of cementum on the labial cingulum.

Comments

The M2 of GHUNLPam 5138 is similar to the syntype MACN Pv 4414 (calcotype, original lost) of *Scalabrinitherium bravardi* from the Lower Member of Ituzaingó Formation (Ameghino 1883a, 1889; Schmidt 2013: fig. 3, pl. 9; Brunetto *et al.* 2013), with slight differences in fossette morphology due to a more advanced wear; they share protoloph wider than metaloph, marked interstylar concavities, distance between parastyle and mesostyle greater than that between mesostyle and metastyle, presence of cementum, and comparable size (Appendix 1). These features are also present in other specimens from the Lower Member of Ituzaingó Formation (Schmidt 2013); particularly, the M1 GHUNLPam 8146 is similar to MACN A 1443 and MACN Pv 4430; the M3 of GHUNLPam 5138 resembles the isolated specimens MACN Pv 3754, MACN Pv 4425, and MACN Pv 6606; the M3 GHUNLPam 8233 is

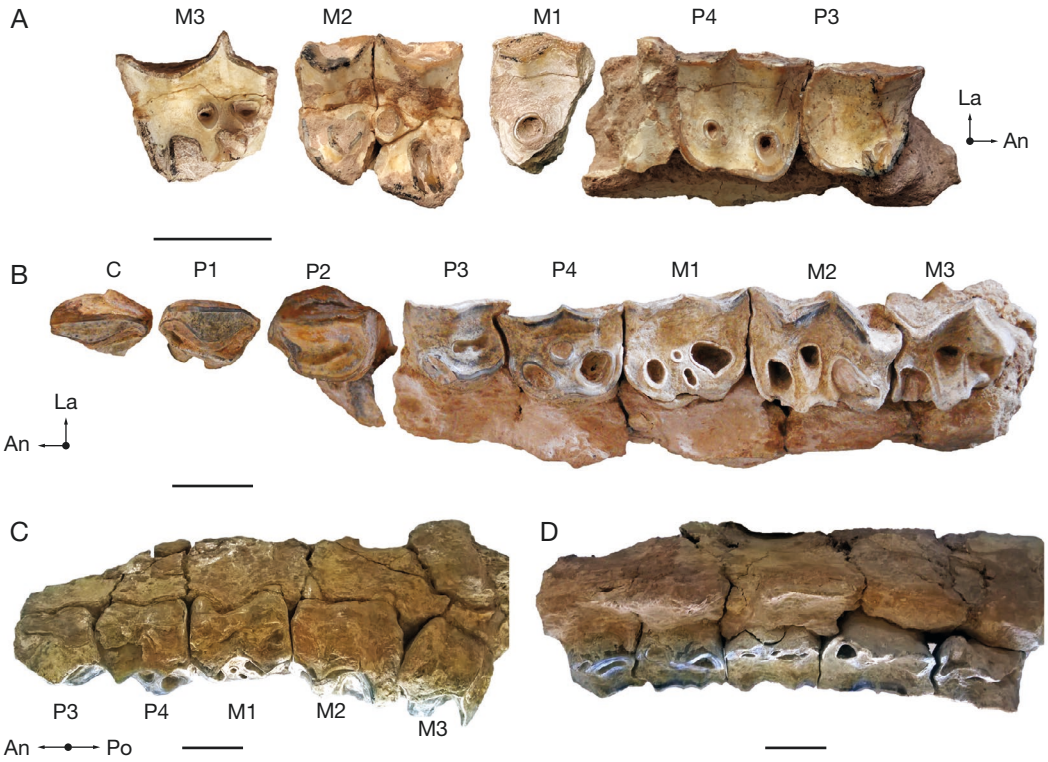

FIG. 3. — *Paranauchenia denticulata* (Ameghino, 1891): **A**, GHUNLPam 18805, incomplete right maxilla with P3-4, fragment of M1, M2, and associated left M3 (reversed) (occlusal view); cf. *Oxyodontherium zeballosi* Ameghino, 1883: **B-D**, MHG-P 126-20, left maxillary fragment with P3-M3, and associated left C-P1 and right P2 (reversed) (occlusal, labial, and lingual views). Abbreviations: **An**, anterior; **La**, labial; **Po**, posterior. Scale bars: 20 mm.

closer to the unworn teeth MLP 52-X-1-71b and MACN Pv 4385, although the latter is smaller (Appendix 1; this molar was interpreted as belonging to a female by Schmidt 2013). In turn, the P2 GHUNLPam 6765 is similar in morphology and size to MACN Pv 2487, MLP 52-X-1-71a, and MAS PALEO-VERT 415 also assigned to *S. bravardi* (Schmidt 2013).

Concerning lower teeth, the m3 of GHUNLPam 6110 and the molar fragments GHUNLPam 5139 and GHUNLPam 6207 are comparable to the syntype of *S. bravardi* MLP 69-XII-2-1 (mandibular fragment with m2-3) and the specimen MACN Pv 3744, although GHUNLPam 5139 has a deeper metaflexid and GHUNLPam 6110 presents a well-developed entoconid, a cusp that disappears to the base of the entoflexid in MLP 69-XII-2-1 (Schmidt 2013: fig. 21, pl. 10). The p3-m1 of MMP-M 2000 are particularly similar to the homologous teeth in MLP 69-XII-2-12 of *S. bravardi* (Schmidt 2013: fig. 19, pl. 10), the latter showing the paralophid of p4 more anteriorly extended. The m1 is also similar to MACN Pv 1060, MACN Pv 2589, MACN Pv 4086, and MACN Pv 13168 (Schmidt 2013).

In summary, protoloph wider than metaloph, interstylar concavities well-marked, parastyle and mesostyle more separated than mesostyle and metastyle in upper teeth, together with p4-m2 with trigonid more rounded labially than talonid, m1-2 with metaconid massive, entoconid well developed, and paralophid longer than hypolophulid in lower teeth, support the ascription of the described specimens to *S. bravardi*.

Genus *Paranauchenia* Ameghino, 1904

TYPE SPECIES. — *Paranauchenia denticulata* (Ameghino, 1891).

TYPE LOCALITY, STRATIGRAPHIC HORIZON AND AGE. — Paraná river cliffs (Entre Ríos Province); Lower Member of the Ituzaingó Formation; Late Miocene.

Paranauchenia denticulata (Ameghino, 1891) (Fig. 3A)

Paranauchenia denticulata (Ameghino, 1891): 136.

REFERRED MATERIAL. — GHUNLPam 18805, incomplete right maxilla with P3-4, fragment of M1, M2, and associated left M3, from Laguna Chillhué (early Huayquerian).

DESCRIPTION

GHUNLPam 18805 shows brachyodont, highly worn teeth (Fig. 3A), corresponding to an old individual. The P3 is subsquare; its labial surface is flat, with a notorious parastyle; it presents two small anterolingual fossettes, not fully formed, as they appear separated by a long fold and lingually open at the occlusal level. The posterior face is convex and continues lingually without a marked angle. The P4 is subsquare, a little longer labially than lingually; the parastyle is well developed and the mesostyle is thin and acute (Fig. 3A); two circular lingual fossettes are still present, the anterior is larger and more lingually placed than the posterior. P3-4 present well-developed

labial cingula, and smooth lingual ones. The incomplete M1 preserves a rounded posterior fossette and the mesostyle is wider than in P4. The M2 is trapezoidal, with the protoloph wider and more extended lingually than the metaloph, and thus the posterolingual fossette is more labially placed than the anterolingual one; the elliptical central fossette is close to the anterolabial corner of the posterior fossette and opposite to a badly preserved mediolingual fossette; labial and lingual cingula are poorly developed; protocone, hypocone and lingual fossettes are anteroposteriorly compressed. The M3 is also trapezoidal, narrower posteriorly; the anterolingual and mediolingual fossettes are wider and labiolingually shorter than in M2. The M2-3 present acute and well-developed mesostyle, but shallow interstylar concavities (Fig. 3A).

Comments

GHUNLPam 18805 shares with *Paranauchenia denticulata* the following features: brachyodont teeth, subsquare P4, with two lingual fossettes, M2 with compressed lingual cusps and fossettes, and trapezoidal M3. Particularly, GHUNLPam 18805 is morphologically similar to specimens MACN Pv 3747, MACN Pv 4444 (Schmidt 2013: figs 1, 3, pl. 12), MACN Pv 4396, and MLP 41-XII-13-308 assigned to *P. denticulata* by Schmidt (2013) and Schmidt & Ferrero (2014). The only difference is the less marked interstylar concavities and its larger size (Appendix 1); however, we consider that these differences fall in the expected intraspecific variability. On the other hand, this specimen differs from *Paranauchenia hystata* (Cabrera & Kraglievich 1931), from Chasicoan levels outcropping at Arroyo Chasicó locality (Buenos Aires Province), in the absence of a metastyle labially oriented and the lack of a small fossette opposite to the paracone in the M3 (Schmidt & Ferrero 2014). The recognition of GHUNLPam 18805 as *P. denticulata* implies the first description of P3 for this species.

Genus *Oxyodontherium* Ameghino, 1883

Type species. — *Oxyodontherium zeballosi* Ameghino, 1883.

Type locality, stratigraphic horizon and age. — Paraná river cliffs (Entre Ríos Province); Lower Member of the Ituzaingó Formation; Late Miocene.

cf. ***Oxyodontherium zeballosi*** Ameghino, 1883 (Fig. 3B-D)

Oxyodontherium zeballosi Ameghino, 1883b: 284.

Referred material. — MHG-P 126-20, left maxillary fragment with P3-M3 and isolated, but associated left C-P1 and right P2, from Laguna del Monte (Huayquerian *s.l.*), Buenos Aires Province.

Description

The canine is incisiform, with a single root; in occlusal view (Fig. 3B), the tooth is more worn posteriorly than anteriorly; it is smoothly labially convex, with the paracone displaced forward; a short basal lingual cingulum divides the tooth into two shallow fossettes. The P1 is similar to the C, but with more developed lingual fossettes (Fig. 3B), two roots, and greater size. The P2 is slightly labially convex, with the paracone anteriorly displaced; parastyle and metastyle are barely developed; the labial cingulum is observable on the posterior region and the lingual cingulum delimits an anterior basal fossette; in occlusal view, there is a central shallow fossette anteroposteriorly elongated (Fig. 3B); the posterolingual region is rounded. The P3 is roughly similar to P2, with the paracone in a central position; the parastyle directs labially whereas the metastyle is well projected posteriorly, greatly overlapping the parastyle of P4 (Fig. 3B, D). The P4 is molariform, roughly square; the three labial styles are well developed; occlusally, there are three rounded-oval fossettes, more elliptical the anterior one that is more lingually placed and anterolingually oriented; the central fossette is the most labially placed; the posterolingual fossette is placed behind the protocone; there is a shallow lingual groove at the protocone level. M1-2 have a wide lingual median groove; M2 is more trapezoidal and larger than M1 (Fig. 3B-D; Appendix 1); both molars present four fossettes, larger in M2 due to its lesser wear degree; protocone and hypocone are labiolingually long and anteroposteriorly compressed; paracone and metacone are opposite to the anterolingual and posterolingual fossettes, respectively; the labial concavities between the styles are more pronounced in M2 than in M1; the metastyle of M2 is overlapped by the parastyle of M3 (opposite condition to that between P3-4). The M3 is trapezoidal, shorter than M2, with metastyle little developed and a reduced posterolingual area; it shows three fossettes, the anterolingual is the largest and the most lingually placed; protocone and hypocone are very compressed. Cement deposits are observed in all these protohypsodont teeth (Fig. 3C).

Comments

The series P3-M3 of MHG-P 126-20 was figured and preliminarily identified as aff. *Huayqueriana cristata* (Rovereto, 1914) by Bonini *et al.* (2017), who did not include the associated C-P2. In contrast to this identification, the present analysis allows establishing that MHG-P 126-20 differs from *H. cristata* (MLP 41-IV-29-4, IANIGLA-PV 29; Soria 1986; Forasiepi *et al.* 2016) by longer and narrower protocone and hypocone of M2-3, hardly developed mediolingual fossette of M2, larger and posteriorly extended posterolingual fossette of M2, and overlapped P3-4 and M2-3. Instead, MHG-P 126-20 shares several features with other Late Miocene taxa, particularly with the remains of *Oxyodontherium zeballosi* from the Lower Member of the Ituzaingó Formation (Ameghino 1883b; Schmidt 2013) and the Río Quinto Formation (San Luis Province; Cerdeño *et al.* 2008 and references therein). Tooth measurements of MHG-P 126-20 (Appendix 1) roughly coincide with the larger specimens of the former sample (e.g. MACN Pv 13671, MACN Pv 3287; Schmidt 2013: figs 1; 4, pl. 11), in which size differences were attributed

to sexual dimorphism (Schmidt 2013). Similarities with *O. zeballosi* are also evident in the morphology of P1-2, the lingual contour of M1 and the long and compressed protocone and hypocone of M2 (e.g. MACN Pv 4441; Schmidt 2013: fig. 6, pl. 11), and the degree of hypsodonty (protohypsodont). Some of these features are also observed in specimens of *Paranauchenia* (morphology of M1-2) or *Promacrauchenia calchaquiorum* Rovereto, 1914 (morphology of P1-2) from Catamarca Province, but these two taxa differ from MHG-P 126-20 by their degree of hypsodonty (brachyodont and hypsodont, respectively) (Schmidt 2013; Schmidt & Ferrero 2014).

The most distinctive feature of MHG-P 126-20 is the described overlapping between P3-4 and M2-3. A little imbrication between M2-3 is observed in *O. zeballosi* (MACN Pv 13671 and MACN Pv 17745; Schmidt 2013: fig. 5, pl. 11) and *S. bravardi* (MLP 12-1480, MACN Pv 17744, MACN Pv 8903; Schmidt 2013: fig. 2, pl. 9), whereas a marked, but opposite imbrication of premolars (P4 overlaps P3) is observed in the specimen MLP 28-X-11-31 of *Cullinia levis* Cabrera & Kraglievich, 1931 (Bond & López 1995) from levels assigned to the Chasicoan at Arroyo Chasicó locality.

In conclusion, MHG-P 126-20 presents more similarities with *O. zeballosi* than with the other mentioned species, but commented differences prevent an accurate identification, even though they could be interpreted as a possible intraspecific variation.

Genus *Promacrauchenia* Ameghino, 1904

TYPE SPECIES. — *Promacrauchenia antiquua* (Ameghino, 1887).

TYPE LOCALITY, STRATIGRAPHIC HORIZON AND AGE. — Farola Monte Hermoso locality (Buenos Aires Province); Monte Hermoso Formation; Early Pliocene (Montehermosan).

Promacrauchenia sp.
(Fig. 4A-K)

REFERRED MATERIAL. — MMP-M 996, left maxillary fragment with DP3-4; MMH-MCH 87-9-58, associated right I1-3 and m3; and MMH-MCH 85-7-43, left mandibular fragment with m1 or m2, from Salinas Grandes de Hidalgo (early Huayquerian); and PV-UNS-8014, rostral fragment with right I1-M1 and left I1-3, P2-M1, from Cantera Relleno Sanitario (late Huayquerian).

DESCRIPTION

The DP3 of MMP-M 996 (Fig. 4A-C) is a rectangular tooth, barely narrower anteriorly; parastyle and mesostyle are well developed; the latter is anteriorly placed forming a short anterior concavity; the posterior interstylar area is much longer and slightly concave-convex; a little paracone is near the anterolabial angle whereas the metacone tip occupies a central position (Fig. 4A). A smooth lingual groove divides the tooth in two subequal lobes, wider the posterior one. There are three fossettes, one anteriorly placed and two posteriorly. DP4 is trapezoidal, longer labially than lingually and wider anteriorly (Fig. 4A). Labial styles are well labially projected, with a strong centered mesostyle. There are five fossettes, a central one extended lingually, another in front of the paracone, and other three lingually placed (the median one smaller). Protocone and hypocone are hardly developed (Fig. 4A, C). Both DP3 and DP4 present a well-developed labial cingulum (Fig. 4B).

The rostral fragment PV-UNS-8014 (Fig. 4D, E) preserves fragments of premaxillae and maxillae, as well as the suture between them on the right side. The palate is long and narrow; it is too cracked to show any groove or foramen. The incisors are laterally flattened and labially convex, with the paracone anteriorly displaced and a smooth labial cingulum. Length increases from I1 to I3; they are more worn posteriorly. The canine is similar to incisors, but larger (Appendix 1) and obliquely implanted. Both incisors and canines show a main central lingual cusp (protocone?) and a basal sinuous cingulum delimiting two fossettes, the posterior deeper. The P1 is more convex labially and wider posteriorly than I-C. The P2 is elliptical, with a large anterior fossette and a smaller posterior one; the paracone is anteriorly placed. The P3 is shorter and wider than P2 (Appendix 1), posterolingually convex, with a rounded anterolingual fossette; the paracone is centrally placed and the parastyle projects anterolabially. The P4 is molariform, with a centered lingual groove; it shows two large lingual fossettes and a little central one (it seems labially displaced due to the breakage effect); the three labial styles are well developed and the interstylar concavities are marked. All premolars have a well-developed labial cingulum and cementum remains. The M1 preserves the posterolingual rounded fossette; the labial cingulum descends from the posterior to the anterior region (Fig. 4E).

The lower molar (m1 or m2) in MMH-MCH 85-7-43 (Fig. 4F-H) has labially rounded lobes; the ectoflexid is deep and narrow, basally limited by a labial cingulum; the metaconid is wide and there is an entoconid; all lingual cusps are at the same level and a cingulum is at the base of the valleys; the metaflexid is deeper than the entoflexid. There are cement deposits on walls and valleys. The m3 of the specimen MMH-MCH 87-9-58 (Fig. 4I-K) presents a deeper and wider ectoflexid than the molar MMH-MCH 85-7-43; the paralophid is longer than the hypolophulid; there are not observable entoconid or entolophid; and cingula are present at the base of the valleys. The incisors of MMH-MCH 87-9-58 are comparable to those in PV-UNS-8014; the I3 is longer and narrower than I1-2 (Appendix 1).

COMMENTS

The tooth morphology of PV-UNS-8014 was briefly recognized as coincident with the species of *Promacrauchenia* in previous papers (Deschamps 2003; Deschamps & Tomassini 2016). We now confirm this ascription for the three referred specimens after comparing them with different species of

this genus (Schmidt 2013, personal data). The labial cingulum trajectory in DP4 and M1 is comparable to that in *P. calchaquiorum* (MACN Pv 5528), *P. antiquua* (MACN Pv 7986, FMNH P 14490, and FMNH P 14448), and *Promacrauchenia* sp. (FMNH P 14517); the incisors are close to those of *P. antiquua* (MACN Pv 7986). P3 shorter than P2, with more developed parastyle, lingual groove in P4, and labial cingulum in M1 are features observed in *Promacrauchenia* spp.; the lingual position of P2 with respect to P1 is present in *P. antiquua* (MACN Pv 7986 and FMNH P 14490) and *P. calchaquiorum* (MACN Pv 5528); the lower molars are comparable to those of *P. antiquua* (MLP 69-XII-2-10, MACN Pv 13201, MACN Pv 2591, MLP 12-1455, MACN A-1189, MACN Pv 7986, FMNH P 14448, FMNH P 14490) and *P. chapadmalense* Ameghino, 1908 (MACN A-11643, holotype), although the latter presents a little fossettid in the talonid of m1-2, and the former does not show the paralophid longer than the hypolophulid (except FMNH P 14490) in m3, and the entolophid is perceptible in little worn molars (MACN Pv 2591, MACN Pv 7986).

Some similarities are also evident with *Scalabrinitherium bravardi* (e.g. Schmidt 2013: figs 6, 9, pl. 9), but this species differs by the better-developed labial cingulum of incisors, DP4 square, m1-2 with labially angled talonid and well-developed and continuous labial cingulum, and m3 with entoconid as a narrower column.

According to the previous paragraphs, the described specimens are similar to the species of *Promacrauchenia*. However, a more precise determination is not possible due to the incompleteness of the preserved material.

Genus *Cullinia* Cabrera & Kraglievich, 1931

TYPE SPECIES. — *Cullinia levis* Cabrera & Kraglievich, 1931.

TYPE LOCALITY, STRATIGRAPHIC HORIZON AND AGE. — Arroyo Chasicó locality (Buenos Aires Province); Arroyo Chasicó Formation; Late Miocene (Chasicoan).

Cullinia sp.
(Fig. 4L-M)

REFERRED MATERIAL. — MMH-MCH 87-9-4, mandibular fragment with right i1-m1 and left i1-p3, from Salinas Grandes de Hidalgo (early Huayquerian).

DESCRIPTION
The i1 is a simple tooth, labiolingually flattened; i2-3 are also compressed, but more conical (Fig. 4L). The i3 and the c are well acuminated, resembling arrowheads. The single-rooted p1 is more lingually implanted, with a subtle cingulum surrounding the base of the crown. The p2 is labially convex with an incipient metaconid. All these teeth present short diastemata between them (Fig. 4L, M). The p3-4 are subtriangular, as the anterior teeth; the trigonid is longer than the talonid, with acute labial border and deep metaflexid; the paralophid is notably longer than the hypolophulid; the ectoflexid is shallow and the metaconid is the main lingual cusp. Cingula become better developed from p1 to m1, the lingual ones are at the base of the valleys. The incomplete m1 presents both lobes labially rounded, deep ectoflexid, prominent metaconid, slightly lingually extended, and short entoconid joined through an entolophid to a long and oblique hypolophid; a well-developed cingulum surrounds the crown. All teeth present a thick layer of cement.

COMMENTS
MMH-MCH 87-9-4 shares with *Cullinia levis* (MLP 29-IX-1-78, holotype), from levels assigned to the Chasicoan at Arroyo Chasicó locality, Buenos Aires Province, the triangular labial outline of p2-4 and the ectoflexid of p3-4 (incipient in p3 and better developed in p4). The m2 of *C. levis* (m1 unknown) and several specimens assigned to *Cullinia* sp. from Arroyo Chasicó locality (MLP 28-X-11-36 and MLP 29-IX-1-77) and Entre Ríos Province (MLP 52-X-3-69 and MACN Pv 4087; Schmidt 2013: figs 1, 2, pl. 15) show the entoconid joined to a long hypolophid similar to the described m1 of MMH-MCH 87-9-4. MMH-MCH 87-9-4 also coincides with *C. levis* in the presence of p1. Even though several authors (Cabrera & Kraglievich 1931; Bond & López 1995; Schmidt 2013) had considered the absence of p1 in *C. levis* as a diagnostic feature, its holotype MLP 29-IX-1-78 shows a single root between c and p2, which implies an error in the original diagnosis.

Despite these similarities, MMH-MCH 87-9-4 differs from *C. levis* in having ectoflexid of p3 better developed, hypolophulid of p3-4 shorter, and m1 with deeper and compressed ectoflexid, narrower entoconid, and lingually extended metaconid; besides, it is larger in size (Appendix 1). At the same time, the m1 of MMH-MCH 87-9-4 shares some features with other taxa: the long and oblique hypolophid is similar to that of *Oxyodontherium zeballosi* (MACN Pv 12260a, MACN Pv 3175, Schmidt 2013: figs 9-10, pl. 11), but this species differs in the larger p4, with deep and wide ectoflexid; also, the lingually extended metaconid is similar to that in *Paranauchenia hystata* (MLP 29-IX-1-75, Schmidt & Ferrero 2014: fig. 1D-F), but the latter differs in the shorter talonid of p4, with less developed hypolophulid. In general, MMH-MCH 87-9-4 is closer to *C. levis* than to any other taxon, but the expressed differences could be representing a different species of *Cullinia*.

MACRAUCHENIINAE indet.

COMMENTS
There are numerous specimens (detailed in Appendix 2) whose incomplete condition does not allow reaching a precise determination, but they contribute to complete the distribution of macraucheniines in the studied localities. This is the case of Laguna Chillhué, Loventué, Telén, and Salinas Grandes

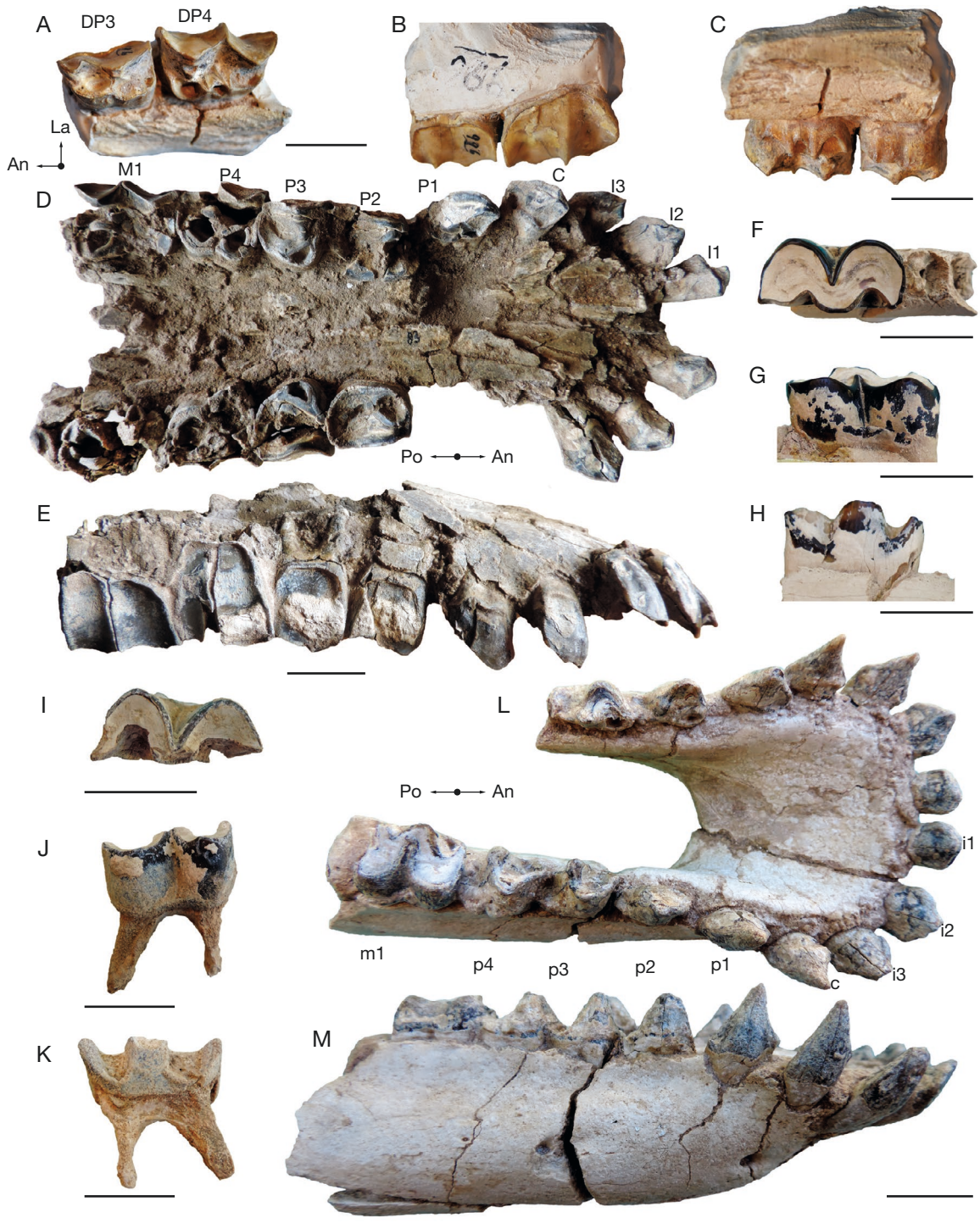

FIG. 4. — *Promacrauchenia* sp.: **A**-**C**, MMP-M 996, left maxillary fragment with DP3-4 (occlusal, labial, and lingual views); **D**, **E**, PV-UNS-8014, rostral fragment with right I1-M1, and left I1-3, P2-M1 (occlusal and right labial views); **F**-**H**, MMH-MCH 85-7-43, left mandibular fragment with m1 or m2 (occlusal, labial, and lingual views); **I**-**K**, MMH-MCH 87-9-58, right m3 (occlusal, labial, and lingual views). *Cullinia* sp.: **L**, **M**, MMH-MCH 87-9-4, mandibular fragment with right i1-m1 and left i1-p3 (occlusal and right labial views). Abbreviations: **An**, anterior; **La**, labial; **Po**, posterior. Scale bars: 20 mm.

de Hidalgo (early Huayquerian) in La Pampa, and Laguna La Paraguaya and Laguna Epecuén (both Huayquerian *s.l.*) in Buenos Aires. Among these specimens, we can mention some incisors such as GHUNLPam 14191 (Telén) and GHUNLPam 18876 (Laguna Chillhué), with crenulated borders and roughly undulated lingual surfaces, which are considered deciduous teeth; they present similarities with some taxa (e.g. *Oxyodontherium*), but not enough to get a confident determination. The same happens with the astragalus MMP-M 435 from Laguna Epecuén, which presents a macraucheniine morphology, but cannot be confidently ascribed to any species.

Family Proterotheriidae Ameghino, 1887
Subfamily Proterotheriinae Ameghino, 1887

Genus *Diplasiotherium* Rovereto, 1914

Type species. — *Diplasiotherium robustum* Rovereto, 1914.

Type locality, stratigraphic horizon, and age. — Farola Monte Hermoso locality (Buenos Aires Province); Monte Hermoso Formation; Early Pliocene (Montehermosan).

Diplasiotherium pampa Soria, 2001
(Fig. 5A-L)

Diplasiotherium pampa Soria, 2001: 97.

Type locality, stratigraphic horizon and age. — Salinas Grandes de Hidalgo (La Pampa Province); Cerro Azul Formation; Late Miocene (early Huayquerian).

Referred material. — MMH-MCH 87-9-23, isolated right M3, and MMH-MCH 87-9-56, associated mandibular fragments with right p2-m3 and left p4-m3 (broken at p4-m1 level), from Salinas Grandes de Hidalgo (early Huayquerian); GHUNLPam 21589, associated left maxillary fragment with P4-M2 and left mandibular fragment with incomplete p4-m1 from Caleufú (late Huayquerian; Schmidt *et al.* 2018); and MHG-P 126-22, isolated left m3, from Arroyo El Venado (Huayquerian *s.l.*; Bonini *et al.* 2017). These specimens add to those previously described by Schmidt *et al.* (2018).

Description
MMH-MCH 87-9-56 (Fig. 5A-F) shows the p2 labiolingually compressed. Anteriorly, it presents a bifurcation formed by a short parastylid and a long paraconid (Fig. 5A). The metaconid is posteriorly directed, what makes the anterior lingual valley longer than the posterior one. Labially, the ectoflexid is barely insinuated. The p3-4 are similar to each other, both having the trigonid labially rounded and the talonid acuminated; the p3 has a tiny anterior bifurcation and the trigonid longer and narrower than the talonid (Fig. 5A); the p4 has the entoflexid shorter than the metaflexid, and the ectoflexid is deep; entoconid and hypoconulid are joined, but the former is larger and more lingually placed. The m1 is shorter than the m2 (Appendix 1), with narrower ectoflexid. The m2 has the trigonid smaller than the talonid, the paralophid is shorter than the hypolophulid, and entoconid and hypoconulid have a similar development (Fig. 5A, D). Both m3 are hardly worn, the trigonid is wider and higher than the talonid (Fig. 5B, E); the entoconid is a short and low crest posterolabially oriented, which appears triangular in lingual view (Fig. 5F); it is separated from the hypoconulid by a valley. All teeth have thick enamel and developed lingual cingula, the labial ones cannot be observed (Fig. 5B, E).

The worn m3 MHG-P 126-22 (Fig. 5G) has the trigonid wider and shorter than the talonid. The paralophid is shorter than the hypolophulid. Bunoid entoconid and hypoconulid have similar development and are joined by a surface of wear, but separated by a valley at its base. The entoflexid is deeper than the metaflexid. The enamel is thick and the lingual cingula are better developed than the labial ones.

MMH-MCH 87-9-23 is a worn M3 (Fig. 5H). The anterior region is wider than the posterior, the latter barely concave. Labially, the styles are well developed, the parastyle being more projected; the mesostyle is anteriorly placed, not centered in the ectoloph. The metacone fold is well developed. In the occlusal face, there is a large, irregular central fossette and a smaller posterior one, labiolingually extended, and the metaconule is placed in between. The anterolingual cingulum reaches the base of the protocone; it is well developed and forms a deep fossette. The lingual wall is vertical, with a smooth concavity separating protocone and hypocone on the posterolingual surface. The posterior wall is gently concave. The enamel is thick.

Comments
Among the remains from La Pampa Province, GHUNLPam 21589 (Fig. 5I-L) was previously described and recognized as Proterotheriidae indet. (Schmidt *et al.* 2018), but is now taxonomically reassessed as *Diplasiotherium pampa*, adding to the other specimens from Laguna Chillhué, Salinas Grandes de Hidalgo, Bajo Giuliani, and Caleufú described by Schmidt *et al.* (2018). The same happens with the m3 MHG-P 126-22 from Arroyo El Venado, Buenos Aires Province, previously illustrated and identified as Proterotheriidae indet. by Bonini *et al.* (2017); this specimen constitutes the first record of *D. pampa* outside La Pampa Province.

The mandibular fragment MMH-MCH 87-9-56 presents important morphological and metrical similarities with the holotype of *D. pampa* (MLP 57-X-10-13), MHG-P 126-22, and other specimens referred to this species (GHUNLPam 18601 and GHUNLPam 5621; Schmidt *et al.* 2018). All of them share thick enamel, developed cingula, and similar crown height. However, they differ in the morphology of the entoconid of m3: forming a short crest in MMH-MCH 87-9-56 and bunoid in MHG-P 126-22, GHUNLPam 18601, and GHUNLPam 5621. A similar variation of the entoconid in m3 is registered in *Neobrachytherium intermedium* (Moreno & Mercerat, 1891) (Schmidt 2015; Schmidt *et al.* 2018). The m3 MHG-P 126-22 is more worn than MMH-MCH 87-9-56, GHUNLPam 18601, and GHUNLPam 5621, but maintains the same general tooth morphology. The p2 is described for the first time for *D. pampa*, and differs from that of *D. robustum* Rovereto, 1914 (holotype MACN Pv 7985 from Farola Monte Hermoso, Early Pliocene, Montehermosan) in being slender, with shorter paralophid and wider and deeper metaflexid.

Although the M3 MMH-MCH 87-9-23 cannot be accurately compared with *D. pampa*, as this is based on lower teeth, the thick enamel, labial folds, posterior wall hardly concave, hypocone well developed, and shallow posterolingual groove allow discarding other taxa such as *Brachytherium cuspidatum* Ameghino, 1883b and *Pseudobrachytherium breve* Corona, Badín, Perea, Ubilla & Schmidt, 2020 (lacking hypocone), *Neobrachytherium* spp. (with anterolingual cingulum less developed), *Thoatheriopsis mendocensis* Soria, 2001 (having a deep groove between

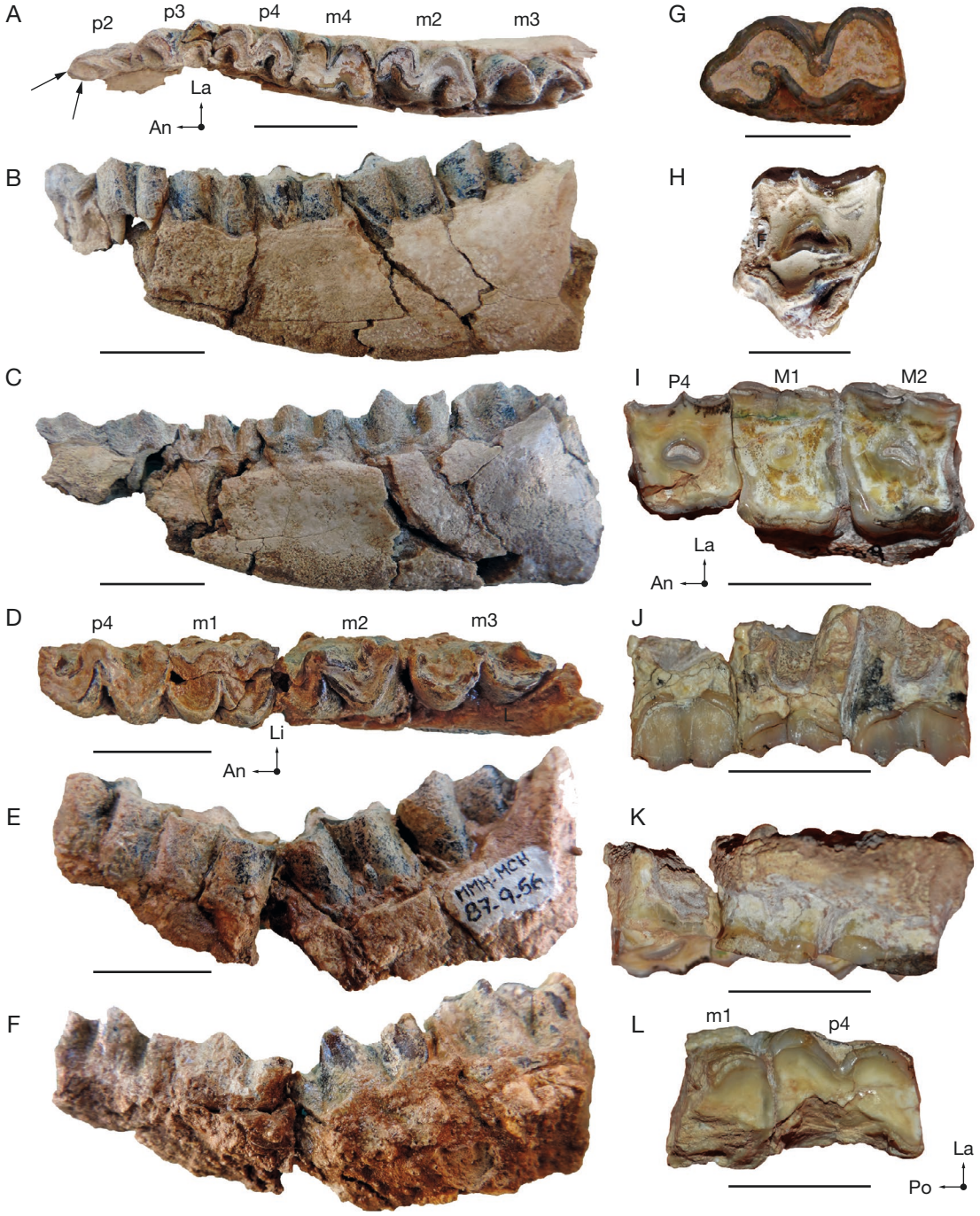

FIG. 5. — *Diplasiotherium pampa* Soria, 2001: **A-F**, MMH-MCH 87-9-56, associated right p2-m3 and left p4-m3 (broken at p4-m1 level) (occlusal, labial, and lingual views of each fragment); arrows in A indicate parastylid (labial) and paraconid (lingual); **G**, MHG-P 126-22, left m3 (occlusal view); **H**, MMH-MCH 87-9-23, right M3 (occlusal view); **I-L**, GHUNLPam 21589, associated left maxillary fragment with P4-M2 (occlusal, labial, and lingual views) and left mandibular fragment with incomplete p4-m1 (occlusal view). Abbreviations: **An**, anterior; **La**, labial; **Li**, lingual; **Po**, posterior. Scale bars: A-F, I-K, 20 mm; G-H, L, 10 mm.

paracone and hypocone), and *Epitherium laternarium* Ameghino, 1888 (with a lophoid metaconule), all of them with thinner enamel than MMH-MCH 87-9-23. The latter shares, in turn, some features with the M2 of the specimen GHUNLPam 21589 (upper and lower teeth) from Caleufú, previously determined as Proterotheriidae indet. (Schmidt *et al.* 2018). Besides, the partial p4 of GHUNLPam 21589 (Fig. 5L) is similar to the p4 of the holotype of *D. pampa* (MLP 57-X-10-13). Subsequently, we propose that both MMH-MCH 87-9-23 and GHUNLPam 21589 represent the upper dentition of *D. pampa*.

Genus *Neobrachytherium* Soria, 2001

TYPE SPECIES. — *Licaphrium intermedium* Moreno & Mercerat, 1891.

TYPE LOCALITY, STRATIGRAPHIC HORIZON AND AGE. — Andalhuala (Catamarca Province); Corral Quemado Formation; Late Pliocene.

Neobrachytherium sp.
(Fig. 6A-F)

REFERRED MATERIAL. — MMP-M 4657, incomplete skull with right P3 (broken), P4-M3 and left P4 (broken), M1-3; MMP-M 1236, incomplete skull with left M1 (badly preserved), M2 complete, and M3 erupting, from Laguna Epecuén (Huayquerian *s.l.*); and MHG-P 126-35, associated right p4, m1, m2 and m3, more or less incomplete, from Laguna La Paraguaya (Huayquerian *s.l.*). These specimens add to those previously described by Schmidt *et al.* (2018).

DESCRIPTION

The skull fragments are covered by sediment agglutinated with a varnish that greatly hides their morphology. MMP-M 4657 (Fig. 6A-C) preserves part of a long sagittal crest, the left closed orbit, the supraorbital foramen posterolaterally placed and obtruded by varnish (Fig. 6A, B), and the thin zygomatic arch, rather horizontal; the occipital projects posterodorsally (Fig. 6B). Ventrally (Fig. 6C), the pterygoids, basisphenoid, and basioccipital are poorly preserved. The fragment MMP-M 1236 is too badly preserved to be described; only the M2 (Fig. 6D) is comparable to that of MMP-M 4657 (see below), but smaller.

In the dentition of MMP-M 4657, the incomplete P3 shows protocone, hypocone, and metacone well developed. The P4 lacks an accessory lingual cuspule and is a bit smaller than the M1 (Appendix 1), both having the bunoid metaconule opposite to the metacone, interrupting the posterolingual groove, and connected to the hypocone due to wear. In the less worn M2, the posterolingual groove is not interrupted by the bunoid metaconule, which is closer to the protocone. The M3 is smaller and trapezoidal, wider anteriorly; the paraconule is reduced, placed in the middle of a crest that starts in the protocone and runs anterolabially; the protocone is well developed and separated from a low hypocone by a groove; the metaconule is small and bunoid. The anterolingual cingulum is narrow, except in M2-3 where it develops a concavity. Labial styles are well developed and only M3 has a subtle paracone fold. The lingual walls are labially inclined and the enamel is thin.

The p4 fragment of MHG-P 126-35 preserves a wide metaconid, deep entoflexid, and the entoconid closer to the hypoconulid, but more lingually placed; the m1 fragment presents the hypolophid joined to the metalophid. The m2 and m3 are robust (Fig. 6E, F), the trigonid is shorter than the talonid, and the paralophid ends in the paraconid that is oriented to the metaflexid. In the incomplete m2 (Fig. 6E), the hypolophid ends in the metalophid; the metaconid is slightly more lingually placed than the paraconid; the entoconid is more lingual than the hypoconulid, and both are separated by a valley. The m3 (Fig. 6F) shows the entoconid more separated from the hypoconulid, and a low crest extends from the entoconid to the hypolophulid. The paralophid is longer than the hypolophulid.

COMMENTS

Neobrachytherium is also recognized in other Late Miocene-Early Pliocene levels of Argentina and Uruguay (Soria 2001; Cerdeño 2003; Schmidt 2015; Schmidt *et al.* 2018; Corona *et al.* 2020). Materials assigned to this genus from several localities of La Pampa Province (Telén, Salinas Grandes de Hidalgo, and Bajo Giuliani) were described by Schmidt *et al.* (2018). According to Soria (2001), the nomenclatural steadiness of this genus depended on the better comprehension of *Epecuenia* Cabrera, 1939. The new specimens MMP-M 4657 and MMP-M 1236 share the same geographic and stratigraphic origin as the holotype of *Epecuenia thoatherioides* Cabrera, 1939 (MLP 37-III-7-12, postcranial remains) and *Eoauchenia cingulata* Cabrera, 1939 (MLP 37-III-7-4, left p3 and astragalus), the latter synonymized with the former by Soria (2001). Due to the absence of homologous elements for comparison with *Epecuenia* (postcranial remains similar to those of *N. intermedium*; Soria 2001), we only compare the remains under study with *Neobrachytherium* spp.

MMP-M 4657 shares with *Neobrachytherium* the square upper teeth, parastyle and mesostyle more developed than metastyle, comparable crown height (similar to *Brachytherium* and *Thoatheriopsis*, more hypsodont than *Proterotherium* Ameghino, 1883, but less than *Epitherium* Ameghino, 1888 and *Eoauchenia* Ameghino, 1887), and deep anteroposterior groove (Schmidt 2015). However, MMP-M 4657 differs from *N. intermedium* because the latter has a lophoid metaconule; *N. ullumense* Soria, 2001 lacks this cusp in M3; *N. morenoi* (Rovereto, 1914) has the labial concavities of M1-2 less marked than MMP-M 4657 (the M3 is unknown in *N. morenoi*) and presents an accessory lingual cuspule in the P4 (lacking in MMP-M 4657); instead, MMP-M 4657 shares with *N. morenoi* the lingual walls labially inclined. Finally, MMP-M 4657 differs from *N. ameghinoi* Soria, 2001 by the well-developed metaconule in M1-2, instead of being a little cusp joined to the conjunction of protocone and hypocone (Soria 2001; Schmidt 2015).

The dimensions of MMP-M 4657 exceed those of other contemporaneous taxa such as *Thoatheriopsis mendocensis*, *Brachytherium cuspidatum*, *Pseudobrachytherium breve*, and *Neobrachytherium* spp. (Appendix 1). The M2 of MMP-M 1236 surpasses the width of *N. intermedium* and *B. cuspidatum* (e.g. FMNH P 14483 and FCP-V-M-053, respectively), despite being slightly shorter (Appendix 1).

The fragments of p4 and m1 of MHG-P 126-35 are similar to *N. morenoi* from the Corral Quemado Formation (Catamarca Province; Soria 2001) (e.g. MACN Pv 8431, holotype of "*Proterotherium simplicidens*" Rovereto, 1914 and PVL 3196); the m2 also shares some features (trigonid shorter than the talonid, paraconid oriented towards the metaflexid, and hypolophid closing on the metalophid) with *N. ullumense* from the Loma de las Tapias Formation (San Juan Province) and Arroyo Chasicó locality (Buenos Aires Province) (Soria 2001; Cerdeño 2003), with which also shares the lingual position of the metaconid; the m3 differs from all species of *Neobrachytherium* (unknown for *N. morenoi*): entoconid more separated from the hypoconulid

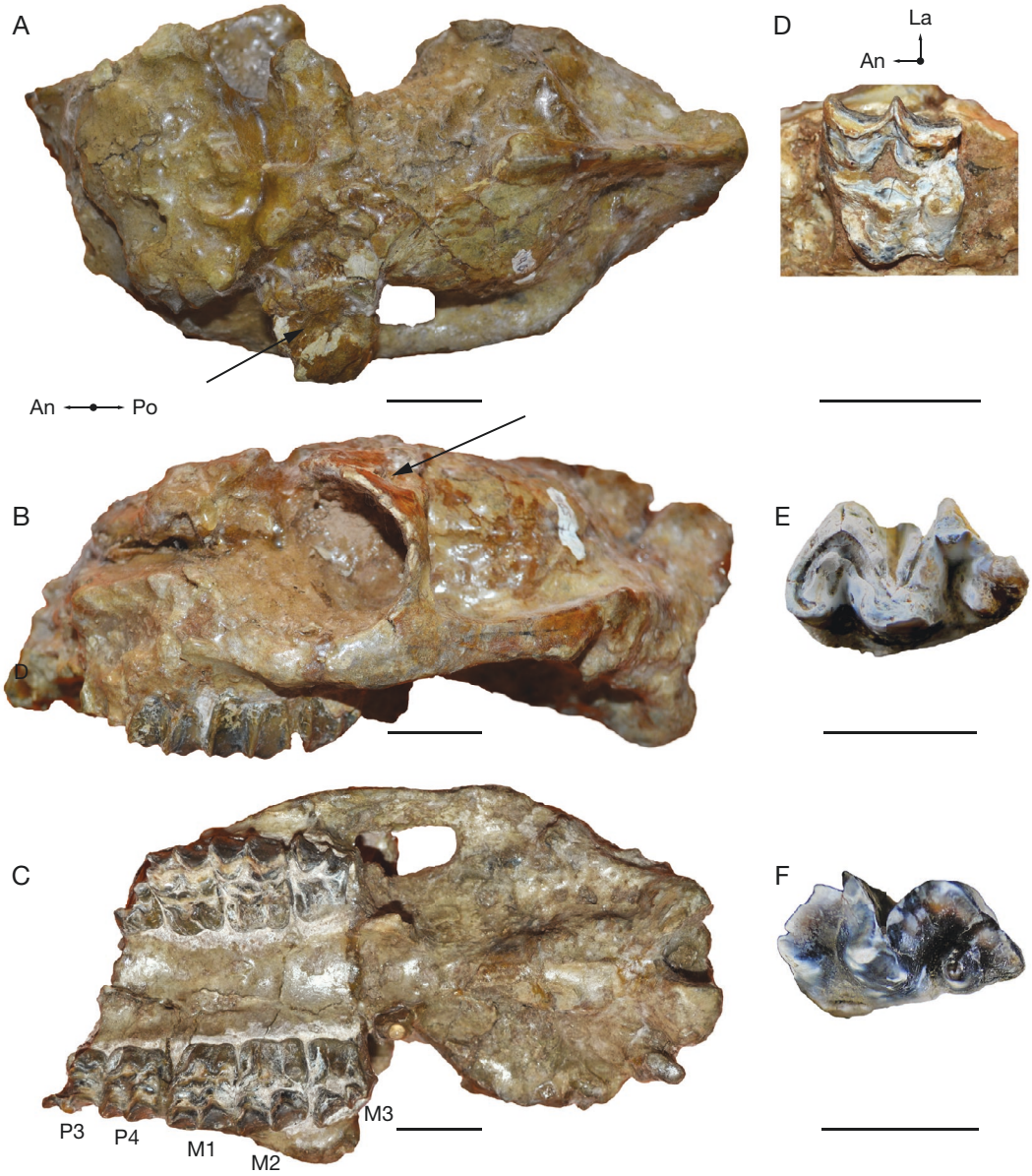

FIG. 6. — *Neobrachytherium* sp.: **A**-**C**, MMP-M 4657, incomplete skull with right P3 (incomplete)–M3 and left P4 (incomplete)-M3 (dorsal, lateral, and ventral views); **arrows** in **A** and **B** indicate the supraorbital foramen position; **D**, MMP-M 1236, detail of the M2 preserved in a distorted skull fragment, in which there is also a fragment of M1 and M3 erupting; **E**, **F**, MHG-P 126-35, associated right m2 and m3 (occlusal views). Abbreviations: **An**, anterior; **La**, labial; **Po**, posterior. Scale bars: A-D, 20 mm; E, F, 10 mm.

than in *N. ullumense*, paraconid not posteriorly oriented in *N. intermedium*, and entoconid free in the middle of the entoflexid in *N. ameghinoi*.

Proterotheriinae indet.

REFERRED MATERIAL. — MHG-P 126-38, right M3; MMP-M 541, mandibular fragment with incomplete right p2, p3, and m1, and roots of left anterior teeth, from Arroyo El Venado (Huayquerian *s.l.*), and MMP-M 1669, associated right mandibular fragment with dp1-4 (and the left m1 wrongly restored as right) and incomplete left dp2-4, from Laguna Epecuén (Huayquerian *s.l.*).

DESCRIPTION

The M3 MHG-P 126-38 lacks the hypocone and has a strong parastyle and mesostyle (Fig. 7A), with a deep concavity in between. The protocone is more developed than the paraconule, and the metaconule is lophoid. The metaconule separates a central fossette from a posterior one. The latter is posteriorly limited by a thick and curved enamel edge from the protocone to the metastyle. The anterolingual cingulum is low and barely developed.

The incomplete p2 and the p3 of MMP-M 541 (Fig. 7B) have paraconid, parastylid (longer in p2), and well-developed labial and lingual cingula. The p2 is narrower and lower than the p3 and the ectoflexid is insinuated; the trigonid of p3 is

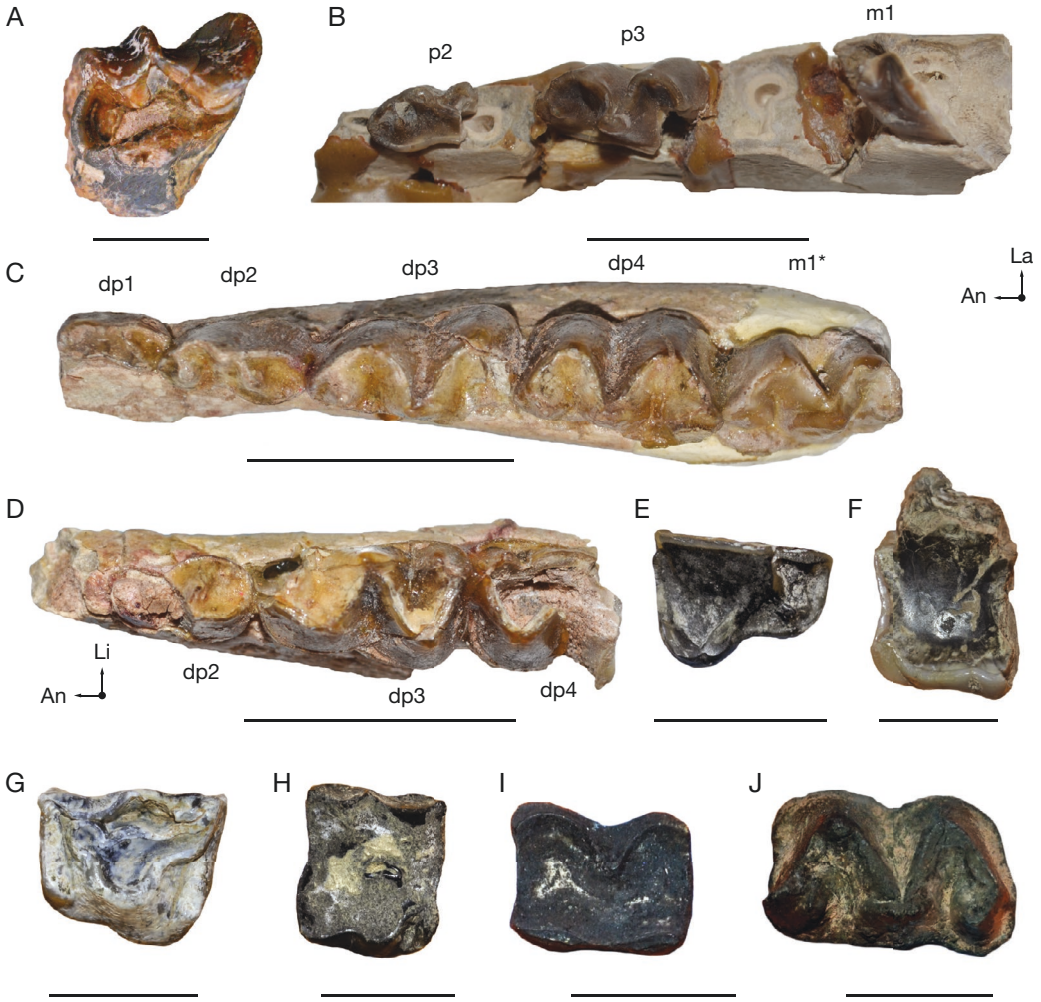

Fig. 7. — Proterotheriinae indet.: **A**, MHG-P 126-38, right M3; **B**, MMP-M 541, mandibular fragment with incomplete right p2, p3, and m1; **C**, **D**, MMP-M 1669, associated right mandibular fragment with dp1-4 and the left m1* wrongly located as right, and left fragment with dp2-4 (badly preserved); **E**, GHUNLPam 22676, right P1; **F**, GHUNLPam 21536, incomplete, left upper molar (M1?); **G**, GHUNLPam 9569, incomplete right upper molar (M3?); **H**, GHUNLPam 14535, right upper molar (M1?); **I**, GHUNLPam 9040, left lower molar (m1 or m2); **J**, GHUNLPam 8864, left dp4. All specimens in occlusal view. Abbreviations: **An**, anterior; **La**, labial; **Li**, lingual. Scale bars: A, E-J, 10 mm; B-D, 20 mm.

longer and narrower than the talonid, and the ectoflexid is deep. The m1 only preserves a hardly worn paraconid. All have thin enamel.

In the juvenile MMP-M 1669, dp1 and dp2 mainly differ by the smaller size of the former and the slightly more evident ectoflexid of the latter (Fig. 7C). In both teeth, the paralophid bifurcates anteriorly in paraconid and parastylid, and a mediolingual concavity subdivides the tooth; in the posterior area, a short lophid (buttress) is posterolingually projected. The dp3-4 are molariform, with a deep and wide ectoflexid; both preserve the anterior bifurcation, but the parastylid is shorter in dp4; the entoconid is an incipient cusp in the dp3, while it is better developed in dp4. The enamel is thin. The left dp2-dp4 are more worn than the right series (Fig. 7D). In the m1 (wrongly placed as right, Fig. 7C), the paraconid is posteriorly oriented, the paralophid is shorter than the hypolophulid, the metaconid has a wide base, and the entoconid is joined basally to the hypoconulid.

Comments

MHG-P 126-38 differs from other Proterotheriinae in the great development of the parastyle, only similar to that of the unpublished remain MMH-FMH 86-4-1 from the Monte Hermoso Formation (Farola Monte Hermoso, Early Pliocene, Montehermosan), inventoried as *Eoauchenia primitiva* Ameghino, 1887 (Schmidt, pers. obs.; see comments on this species in Biostratigraphic and Paleobigeographic Remarks section); however, this specimen differs from MHG-P 126-38 by the absence of anterolingual cingulum, paraconule more developed, and lesser size (length = 11.7 mm *vs* 17 mm in MHG-P 126-38; width = 15.07 mm *vs*. 18.4 mm). *Epitherium laternarium* (MACN Pv 8001), also from the Monte Hermoso Formation, and *N. intermedium* (FMNH P 14500), from the Andalhuala Formation (Catamarca Province), have lophoid metaconule and anterolingual cingulum as MHG-P 126-38, but differ by the presence of hypocone.

TABLE 1. — Stratigraphic chart of the Late Miocene and Early Pliocene localities of central Argentina with Macraucheniidae Gervais, 1855 and Proterotheriidae Ameghino, 1887 taxa. The relative biostratigraphic succession of localities follows Verzi *et al.* (2008), Sostillo *et al.* (2014), Deschamps & Tomassini (2016), and Piñero *et al.* (2021). Abbreviations: **BA**, Buenos Aires Province; **LP**, La Pampa Province.

Epoch	South American Stages/Ages	Localities	*Scalabrinitherium bravardi*	*Paranauchenia denticulata*	*Paranauchenia hystata*	cf. *Oxyodontherium zeballosi*	*Promacrauchenia* sp.	*Promacrauchenia antiquua*	*Cullinia* sp.	*Cullinia levis*	*Huayqueriana cristata*	Macraucheniinae indet.	*Diplasiotherium pampa*	*Diplasiotherium robustum*	*Eoauchenia primitiva*	cf. *Brachytherium cuspidatum*	*Neobrachytherium* sp.	*Neobrachytherium ullumense*	*Epecuenia thoatherioides*	Proterotheriinae indet.
Pliocene	Montehermosan	Farola M. Hermoso (BA)	–	–	–	–	–	x	–	–	–	–	–	x	x	–	–	–	–	–
		Caleufú (LP)	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	x
Late Miocene	late Huayquerian	Cantera Rell. Sanitario (BA)	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–
		Guatraché (LP)	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		El Guanaco (LP)	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–
		Bajo Giuliani (LP)	–	–	–	–	–	–	–	–	–	–	x	–	–	–	x	–	–	x
	early Huayquerian	Salinas G. de Hildalgo (LP)	x	–	–	–	x	–	x	–	–	x	x	–	–	x	x	–	–	–
		Telén (LP)	x	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	x
		Loventué (LP)	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–
		Laguna Chillhué (LP)	–	x	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	–
	Chasicoan	Arroyo Chasicó (BA)	–	–	x	–	–	–	–	x	–	–	–	–	–	–	–	x	–	–
		Cerro La Bota (LP)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x
	Huayquerian *s.l.*	Laguna Epecuén (BA)	x	–	–	–	–	–	–	–	x	x	–	–	–	–	x	–	x	x
		Laguna del Monte (BA)	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		Laguna La Paraguya (BA)	–	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	–
		Arroyo El Venado (BA)	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	x

The p3 of MMP-M 541 differs from *B. cuspidatum* (e.g. MLP 12-103a, MACN Pv 13187, MAS PALEO-VERT 402; Schmidt 2015) and *N. morenoi* (MACN Pv 8431), because it is less robust and the cingula are better developed, similar to *Ep. thoatherioides* (MLP 37-III-7-4, holotype of *Eo. cingulata*). However, the latter has the talonid slightly more acute than in MMP-M 541 and *B. cuspidatum*.

MMP-M 1669 is similar to the holotype of *B. cuspidatum* (MLP 69-XII-2-4), but the teeth are slenderer (Appendix 1) and with higher crown, the mandibular fragment is lower, and the ectoflexid of the m1 is wider.

According to the previous lines, the differences indicated prevent an accurate taxonomic assignation of the described specimens beyond the subfamily level. They add to those from La Pampa Province determined as Proterotheriidae indet. by Schmidt *et al.* (2018; as original figures lack scale bars, occlusal views are herein reproduced as scaled new photographs in Figure 7E-J).

OTHER LITOPTERN TAXA PREVIOUSLY IDENTIFIED BUT NOT REVISED

Aside to the revised taxa described above, other three litoptern species had been previously described for the levels now assigned to the Cerro Azul Formation. As no new remains are herein added, we just mention them here to provide a summary on the total litoptern diversity that is commented in the following section.

Huayqueriana cristata is a macraucheniid originally described for the Huayquerías Formation (Late Miocene, Huayquerian, Mendoza Province) (Rovereto 1914; Soria 1986; Forasiepi *et al.* 2016), which was also recognized at Laguna Epecuén locality (Buenos Aires Province) from the remains previously described as *Macrauchenidia latidens* Cabrera, 1939. In this locality, the proterotheriid *Epecuenia thoatherioides* (including as synonymous *Eoauchenia cingulata*; see comments on *Neobrachytherium* sp.) was also recognized. Another proterotheriid, *Eoauchenia primitiva*, originally recognized at the Monte Hermoso Formation (Farola Monte Hermoso, Early Pliocene, Monthermosan), was recorded at El Guanaco (La Pampa Province; Cabrera 1939; Schmidt *et al.* 2018).

BIOSTRATIGRAPHIC AND PALEOBIOGEOGRAPHIC REMARKS

Litopterna recorded from the Cerro Azul Formation in La Pampa and Buenos Aires provinces include both Macraucheniidae and Proterotheriidae taxa (Table 1; see also Schmidt *et al.* 2018). Our study adds five Macraucheniidae taxa to the three previously recognized and some remains only identified at subfamily level (Table 1). Regarding the temporal representation within the previous schemes proposed for this unit in La Pampa Province, most taxa were recovered from levels assigned to the early Huayquerian; just *Scalabrinith-*

erium bravardi is present in both early and late Huayquerian levels. Macraucheniids are absent from the Chasicoan levels of the Cerro Azul Formation in La Pampa Province (i.e., Cerro La Bota locality), but they are present in Buenos Aires Province, at Arroyo Chasicó locality, with *Paranauchenia hystata* and *Cullinia levis* (Table 1).

The Proterotheriidae are represented by six taxa from levels assigned to Chasicoan and early and late Huayquerian (Table 1); one taxon, *Neobrachytherium* sp. from localities in Buenos Aires Province, adds to the previously recognized proterotheriids in La Pampa (Schmidt *et al.* 2018), and one of the latter (*Diplasiotherium pampa*) is identified at Arroyo El Venado in Buenos Aires, implying its first record outside La Pampa. In addition, remains identified at the subfamily level come from Cerro La Bota (Chasicoan) and several localities with levels assigned to the early and late Huayquerian: Arroyo El Venado, Laguna Epecuén, Telén, Bajo Giuliani, and Caleufú. *Neobrachytherium ullumense* is present in Chasicoan levels at Arroyo Chasicó locality, but the Huayquerian remains from Telén, Salinas Grandes de Hidalgo, Bajo Giuliani, Laguna Epecuén, and Laguna La Paraguaya can just be determined at generic level.

Based on the entire sample of Litopterna from the Cerro Azul Formation, the highest diversity appears at Salinas Grandes de Hidalgo (early Huayquerian), followed by Laguna Epecuén (Huayquerian *s.l.*). The proterotheriids *Diplasiotherium pampa* and *Neobrachytherium* sp. are the best represented taxa, being recorded in five localities throughout the Huayquerian, followed by the macraucheniid *Scalabrinitherium bravardi*, in four localities of early and late Huayquerian (Table 1).

The results indicate that the Litopterna remains from different localities of La Pampa and Buenos Aires provinces where the Cerro Azul Formation crops out do not provide relevant information to better adjust the biochronological and biostratigraphic schemes proposed for this unit. The macraucheniid *Cullinia levis* was described from Arroyo Chasicó, type locality of the Chasicoan (Cabrera & Kraglievich 1931; Bond & López 1995), but early Huayquerian remains from Salinas Grandes de Hidalgo cannot be identified with this species and could represent a new representative of the genus (see Systematic Paleontology section); so, we can only confirm the temporal extension of the genus in the Pampean region, agreeing with its presence in the Lower Member (Late Miocene) of the Ituzaingó Formation. *Cullinia levis* was also mentioned in the Barranca de los Loros Formation (Middle-Late Miocene, Río Negro Province; Pascual *et al.* 1984; Rodríguez *et al.* 2007).

Among the identified species, *Scalabrinitherium bravardi*, *Paranauchenia denticulata*, and *Oxyodontherium zeballosi* were originally described from the Lower Member (Late Miocene) of the Ituzaingó Formation (Ameghino 1883a, b, 1904; Brunetto *et al.* 2013). *Oxyodontherium zeballosi* was also recognized in the Late Miocene levels of the Río Quinto Formation (San Luis Province; Cerdeño *et al.* 2008). Instead, the presence of this species in the Mio-Pliocene beds of Uruguay (Kraglievich 1932) is very doubtful, because it is based on a metapodial (Schmidt 2013). The mention of *O. zeballosi* in the Arenas Blancas locality (Buenos Aires Province; Oliva *et al.* 2011) needs to be confirmed, as well as the Huayquerian age of the bearing-levels.

Concerning *Promacrauchenia*, remains from the Cerro Azul Formation cannot be confidently assigned to any of the known species that are distributed from Late Miocene to Late Pliocene. The type species, *P. antiquua*, comes from the Early Pliocene levels (Montehermosan) of the Monte Hermoso Formation at Farola Monte Hermoso locality (Table 1), and Schmidt (2013) recognized it in the Lower Member of the Ituzaingó Formation. In turn, *P. calchaquiorum* is recorded in the Late Miocene Andalhuala Formation (Rovereto 1914), while *P. chapadmalense* is known in the Late Pliocene levels of the Chapadmalal Formation (Chapadmalalense; Buenos Aires Province; Ameghino 1908; Schultz *et al.* 1998).

The proterotheriid *Diplasiotherium pampa*, originally known from Salinas Grandes de Hidalgo (early Huayquerian; Soria 2001), was later recorded at Laguna Chillhué (early Huayquerian), Bajo Giuliani, and Caleufú (late Huayquerian; Schmidt *et al.* 2018). Here, we report new remains from Salinas Grandes de Hidalgo and Caleufú, as well as the first remains from Buenos Aires Province at Arroyo El Venado (Huayquerian *s.l.*; Table 1); a second, younger species of the genus, *D. robustum*, has a single record in the Early Pliocene (Montehermosan) levels of the Monte Hermoso Formation at Farola Monte Hermoso locality (Rovereto 1914). In turn, the proterotheriid *Eoauchenia primitiva* at El Guanaco (late Huayquerian) supports the relative younger age of this locality in the context of the Cerro Azul Formation, as this taxon is well represented in the Monte Hermoso Formation at Farola Monte Hermoso, but the accompanying fauna from El Guanaco does not support a Montehermosan age. El Guanaco was considered within the biozone of *Xenodontomys simpsoni* Kraglievich, 1961, but younger than Barrancas Coloradas, the type area of this biozone (Verzi *et al.* 2008).

The identified Macraucheniidae and Proterotheriidae from the Cerro Azul Formation reveal affinities with other Neogene faunas from different areas of Argentina [Northwestern (NOA), Northeastern (NEA), and Cuyo region] (Schmidt *et al.* 2018, 2020), but considering both families altogether, the higher similarity appears with the assemblage from the Lower Member of the Ituzaingó Formation, Entre Ríos Province, with which it shares seven of the 13 recognized genera (Table 2). Two of these genera (*Scalabrinitherium* and *Neobrachytherium*) are registered throughout the Huayquerian (early and late, or even *s.l.*); one (*Brachytherium*) only in the early Huayquerian, and cf. *Oxyodontherium zeballosi* comes from levels assigned to the Huayquerian *s.l.* Cione *et al.* (2000) stated that the "Mesopotamian" (Lower Member of the Ituzaingó Formation) and its fauna should be referred to the Huayquerian (Late Miocene). However, Brandoni (2013) and, more recently, Schmidt *et al.* (2020) concluded that an accurate age cannot be established for this level from its faunal assemblage, because it encloses a mixture of Chasicoan and Huayquerian taxa whose remains accumulated during the lapse late Tortonian-early Messinian. In this sense, the detailed analysis performed in this work also locates the litopterns from the Cerro Azul Formation in the Chasicoan-Huayquerian lapse (Late Miocene-Early Pliocene), with a better chronological order.

CONCLUSIONS

The litoptern material herein revised adds six taxa to the previous known diversity for the Late Miocene-Early Pliocene levels (Huayquerian) of the Cerro Azul Formation. It allows increasing the knowledge of Macraucheniidae from both La Pampa and Buenos Aires provinces, as well as the Proterotheriidae from localities in Buenos Aires Province.

The macraucheniids *Scalabrinitherium bravardi* and *Paranauchenia denticulata* had been previously recorded only in the Lower Member of the Ituzaingó Formation in Entre Ríos Province. Based on the new records, *S. bravardi* is also identified at Salinas Grandes de Hidalgo, Guatraché, Telén (La Pampa Province), and Laguna Epecuén (Buenos Aires Province). *P. denticulata* is recognized at Laguna Chillhué (La Pampa Province). Cf. *Oxyodontherium zeballosi* from Laguna del Monte (Buenos Aires Province) enlarges the geographical distribution of the species, previously known in Entre Ríos and San Luis provinces. The new remains of *Promacrauchenia* sp. from Salinas Grandes de Hidalgo (La Pampa Province) extend the geographical distribution of the genus, originally known at Farola Monte Hermoso and also now at Cantera Relleno Sanitario in Buenos Aires Province, as well as in Entre Ríos and Catamarca provinces. Similarly, the presence of *Cullinia* sp. at Salinas Grandes de Hidalgo expands the generic geographical distribution, originally described for Arroyo Chasicó in Buenos Aires Province, and also documented in Río Negro and Entre Ríos provinces.

Regarding proterotheriids, the presence of *Diplasiotherium pampa* at Arroyo El Venado (Buenos Aires Province) constitutes the first record outside La Pampa Province; in addition, the p2 and P4-M3 (specimens from Caleufú and Salinas Grandes de Hidalgo) are described for the first time for this species. The new specimens from Buenos Aires Province assigned to *Neobrachytherium* sp. add to those previously recognized in La Pampa Province and other localities from Late Miocene-Early Pliocene levels in Argentina and Uruguay.

The whole sample of Litopterna recovered from Huayquerian levels of the Cerro Azul Formation in localities of La Pampa and Buenos Aires provinces allows the recognition of eight taxa of Macraucheniidae and six of Proterotheriidae (and several specimens determined just at subfamily level). Salinas Grandes de Hidalgo (La Pampa Province) and Laguna Epecuén (Buenos Aires Province) are the localities with the highest litoptern diversity. The identified taxa show a manifest affinity with the assemblage from the Late Miocene levels of the Lower Member of the Ituzaingó Formation in Entre Ríos Province.

TABLE 2. — Genera of Macraucheniidae Gervais, 1855 and Proterotheriidae Ameghino, 1887 from the Cerro Azul Formation (La Pampa and Buenos Aires provinces) compared with other Late Miocene-Early Pliocene Argentinean assemblages. Abbreviations: **BA**, Buenos Aires; **CA Fm.**, Cerro Azul Formation; **Cat**, Catamarca; **ER**, Entre Ríos; **Fm.**, Formation; **LP**, La Pampa; **LR**, La Rioja; **Mza**, Mendoza; **SJ**, San Juan; **SL**, San Luis.

	Macraucheniidae						**Proterotheriidae**						
Geological formations	*Scalabrinitherium*	*Paranauchenia*	*Oxyodontherium*	*Promacrauchenia*	*Cullinia*	*Huayqueriana*	*Diplasiotherium*	*Eoauchenia*	*Brachytherium*	*Neobrachytherium*	*Diadiaphorus*	*Proterotherium*	*Epecuenia*
CA Fm., early Huayquerian (LP)	x	x	–	x	x	–	x	–	x	x	–	–	–
CA Fm., late Huayquerian (LP)	x	–	–	x	–	–	x	x	–	x	–	–	–
CA Fm., Huayquerian *s.l.* (BA)	x	–	x	–	–	x	x	–	–	x	–	–	x
CA Fm., Chasicoan (BA, LP)	–	x	–	–	x	–	–	–	–	x	–	–	–
Ituzaingó Fm. (ER)	x	x	x	x	x	–	–	–	x	x	x	x	–
Huayquerías Fm. (Mza)	–	–	–	–	–	x	–	–	–	–	–	–	–
Andalhuala Fm. (Cat)	–	–	–	–	–	–	–	–	–	x	–	–	–
Corral Quemado Fm. (Cat)	–	–	–	–	–	–	–	–	–	x	–	–	–
Loma de las Tapias Fm. (SJ)	–	–	–	–	–	–	–	–	–	x	–	–	–
Toro Negro Fm. (LR)	–	–	–	–	–	–	–	x	–	–	–	–	–
Salicas Fm. (LR)	–	–	–	–	–	–	–	–	–	x	–	–	–
Río Quinto Fm. (SL)	–	–	x	–	–	–	–	–	–	–	–	–	–
Monte Hermoso Fm. (BA)	–	–	–	x	–	–	x	x	–	–	–	–	–

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REFERENCES

AMEGHINO F. 1883a. — Sobre una colección de mamíferos fósiles recogidos por el profesor Pedro Scalabrini en las barrancas del río Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* 5: 101-116.

AMEGHINO F. 1883b. — Sobre una nueva colección de mamíferos fósiles recogidos por el profesor Pedro Scalabrini en las barrancas del río Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* 5: 257-306.

AMEGHINO F. 1889. — Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de la República Argentina en Córdoba* 6: 1-1027. https://www.biodiversitylibrary.org/page/51769581

AMEGHINO F. 1891. — Caracteres diagnósticos de cincuenta especies nuevas de mamíferos fósiles argentinos. *Revista Argentina de Historia Natural* 1: 129-167.

AMEGHINO F. 1904. — Recherches de morphologie phylogénétique sur les molaires supérieures des ongulés. *Anales del Museo Nacional de Buenos Aires* 9: 1-541. https://www.biodiversitylibrary.org/page/15536266

AMEGHINO F. 1908. — Las formaciones sedimentarias de la región litoral de Mar del Plata y Chapadmalán. *Anales del Museo Nacional de Historia Natural* 10: 343-428.

BERGQVIST L. P. 2008. — Postcranial skeleton of the Upper Paleocene (Itaboraian) 'Condylarthra' (Mammalia) of Itaboraí Basin, Brazil, *in* SARGIS E. J. & DAGOSTO M. (eds), *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay*. Springer (coll. Vertebrate Paleobiology and Paleoanthropology Series), New York: 107-133. https://doi.org/10.1007/978-1-4020-6997-0_6

BILLET G., MUIZON C. DE, SCHELLHORN R., RUF I., LADEVÈZE S. & BERGQVIST L. 2015. — Petrosal and inner ear anatomy and allometry amongst specimens referred to Litopterna (Placentalia). *Zoological Journal of the Linnean Society* 173 (4): 956-987. https://doi.org/10.1111/zoj.12219

BONAPARTE J. F. & MORALES J. 1997. — Un primitivo Notonychopidae (Litopterna) del Paleoceno Inferior de Punta Peligro, Chubut, Argentina. *Estudios Geologicos* 53: 263-274. https://doi.org/10.3989/egeol.97535-6232

BOND M. 1999. — Quaternary native ungulates of Southern South America. A synthesis, *in* TONNI E. P. & CIONE A. L. (eds), *Quaternary Vertebrate Paleontology in South America. Quaternary of South America and Antarctic Peninsula* Special Volume 12: 177-205.

BOND M. & LÓPEZ G. M. 1995. — Los Macraucheniidae (Mammalia, Litopterna) de la Formación Arroyo Chasicó (Partido de Villarino, Provincia de Buenos Aires). *IV Jornadas Geológicas y Geofísicas Bonaerenses, Junín, 15-17 de noviembre, 1995.* Vol. 1. Universidad Nacional de la Plata: 23-27.

BOND M., CERDEÑO E. & LÓPEZ G. M. 1995. — Los ungulados nativos de América del Sur, *in* ALBERDI M. T., LEONE G. & TONNI E. P. (eds), *Evolución Biológica y Climática de la Región Pampeana durante los Últimos Cinco Millones de Años. Un Ensayo de Correlación con el Mediterráneo Occidental*. CSIC (coll. Monografías del MNCN), Madrid: 257-276.

BOND M., REGUERO M. A., VIZCAÍNO S. F. & MARENSSI S. A. 2006. — *A new "South American Ungulate" (Mammalia, Litopterna) from the Eocene of the Antarctic Peninsula*. Geological Society (coll. Special Publications; 258), London: 163-176. https://doi.org/10.1144/GSL.SP.2006.258.01.12

BOND M., REGUERO M. A., VIZCAÍNO S. F., MARENSSI S. A. & ORTIZ JAUREGUIZAR E. 2009. — *Notiolofos*, a replacement name for *Notolophus* Bond, Reguero, Vizcaíno & Marenssi, 2006, a preoccupied name. *Journal of Vertebrate Paleontology* 29 (3): 979. https://doi.org/10.1671/039.029.0321

BONDESIO P., LAZA J. H., SCILLATO-YANÉ G. J., TONNI E. P. & VUCETICH M. G. 1980. — Estado actual del conocimiento de los vertebrados de la Formación Arroyo Chasicó (Plioceno temprano) de la provincia de Buenos Aires. *Actas del Segundo Congreso Argentino de Paleontología y Bioestratigrafía y Primer Congreso latinoamericano de Paleontología, Buenos Aires, Argentina, 2-6 de abril, 1978. Asociación Paleontológica Argentina, Buenos Aires:* 101-127.

BONINI R. A. 2014. — *Bioestratigrafía y diversidad de los mamíferos del Neógeno de San Fernando y Puerta de Corral Quemado (Catamarca, Argentina)*. Ph.D. Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 366 p.

BONINI R. A., SCANFERLA A. C., CANDELA A. M., RASIA L. L. & SCHMIDT G. I. 2017. — Estudio preliminar de una nueva fauna de mamíferos del Neógeno de las Lagunas Encadenadas del oeste de la Provincia de Buenos Aires, *in* NASIF N. & ORTIZ P. (eds), *XX Congreso Geológico Argentino. Simposio 1: IV Simposio Mioceno-Pleistoceno del centro-norte de Argentina, San Miguel de Tucumán, Tucumán, 7-11 de agosto, 2017*. Asociación Geológica Argentina, Buenos Aires: 19-24.

BRANDONI D. 2013. — Los mamíferos continentales del "Mesopotamiense" (Mioceno Tardío) de Entre Ríos, Argentina. Diversidad, edad y paleobiogeografía, *in* BRANDONI D. & NORIEGA J. I. (eds), *El Neógeno de la Mesopotamia argentina*. Asociación Paleontologica Argentina (coll. Publicación Especial; 14), Buenos Aires: 179-191.

BRANDONI D., SCHMIDT G. I., CANDELA A. M., NORIEGA J. I., BRUNETTO E. & FIORELLI L. E. 2012. — Mammals from the Salicas Formation (Late Miocene), La Rioja Province, Northwestern Argentina: paleobiogeography, age, and paleoenvironment. *Ameghiniana* 49 (3): 375-387. https://doi.org/10.5710/AMGH.v49i3(467)

BRANDONI D., BREA M., BRUNETTO E., DIEDERLE J. M., FRANCO M. J., GOIS F., LUTZ A., NORIEGA J. I., PEREZ L. M., SCHMIDT G. I. & ZUCOL A. F. 2019. — Paleontología del Mioceno tardío de la región Noreste de Argentina, *in* NASIF N., ESTEBAN G., CHIESA J., ZURITA A. & GEORGIEFF S. (eds), *Mioceno al Pleistoceno del centro y norte de Argentina*. Fundación Miguel Lillo (coll. Ópera lilloana; 52), Tucumán: 131-162.

BRUNETTO E., NORIEGA J. I. & BRANDONI D. 2013. — Sedimentología, estratigrafía y edad de la Formación Ituzaingó en la provincia de Entre Ríos, Argentina, *in* BRANDONI D. & NORIEGA J. I. (eds), *El Neógeno de la Mesopotamia argentina*. Asociación Paleontológica Argentina (coll. Publicación Especial; 14), Buenos Aires: 13-27.

CABRERA A. 1939. — Sobre vertebrados fósiles del Plioceno de Adolfo Alsina. *Revista del Museo de La Plata* 2: 1-35.

CABRERA A. & KRAGLIEVICH L. 1931. — Diagnosis previas de los ungulados fósiles de la Formación Arroyo Chasicó. *Notas del Museo La Plata* 1: 107-113.

CARLINI A. A., GELFO J. N. & SÁNCHEZ R. 2006. — A new Megadolodinae (Mammalia, Litopterna, Proterotheriidae) from the Urumaco Formation (Late Miocene) of Venezuela. *Journal of Systematic Palaeontology* 4 (3): 279-284. https://doi.org/10.1017/S1477201906001830

CASSINI G. H., CERDEÑO E., VILLAFAÑE A. L. & MUÑOZ N. A. 2012. — Paleobiology of Santacrucian native ungulates (Meridiungulata: Astrapotheria, Litopterna, and Notoungulata), *in* VIZCAÍNO S. F., KAY R. F. & BARGO M. S. (eds), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge: 243-286. https://doi.org/10.1017/CBO9780511667381.015

CERDEÑO E. 2003. — Neobrachytherium ullumense (Proterotheriidae, Litopterna) en el Mioceno Superior de la Provincia de Buenos Aires (Argentina). *Ameghiniana* 40 (3): 505-508.

CERDEÑO E., CHIESA J. & OJEDA G. 2008. — Presence of *Oxyodontherium* (Macraucheniidae, Litopterna) in the Río Quinto Formation, San Luis (Argentina). *Journal of South American Earth Sciences* 25 (2): 217-226. https://doi.org/10.1016/j.jsames.2007.06.004

CIONE A. L. & TONNI E. P. 2005. — Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina, *in* Congreso Geológico Argentino no. 16. *Geología y Recursos Minerales de la Provincia de Buenos Aires* 11: 183-200.

CIONE A. L., AZPELICUETA M. M., BOND M., CARLINI A. A., CASCIOTTA J. R., COZZUOL M. A., DE LA FUENTE M., GASPARINI Z., GOIN F. J., NORIEGA J., SCILLATO-YANE G. J., SOIBELZON L., TONNI E. P., VERZI D. & VUCETICH M. G. 2000. — Miocene vertebrates from Entre Ríos Province, eastern Argentina, *in* ACEÑOLAZA F. G. & HERBST R. (eds), *El Neógeno de Argentina. Serie Correlación Geológica* 14: 191-237.

CORONA A., BADÍN A. C., PEREA D., UBILLA M. & SCHMIDT G. I. 2020. — A new genus and species and additional reports of South American native ungulates Proterotheriidae (Mammalia, Litopterna) in the Late Miocene of Uruguay. *Journal of South American Earth Sciences* 102: 102646. https://doi.org/10.1016/j.jsames.2020.102646

DE ALBA E. 1953. — Geología del Alto Paraná en relación con los trabajos de derrocamiento entre Ituzaingó y Posadas. *Revista de la Asociación Geológica Argentina* 8: 129-161.

DELUPI DE BIANCHINI L. H. & BIANCHINI J. J. 1971. — Revisión de los Proterotheriinae (Mammalia, Litopterna) del Mesopotamiense. *Ameghiniana* 8: 1-24.

DESCHAMPS C. M. 2003. — *Estratigrafía y paleoambientes del Cenozoico en el sur de la Provincia de Buenos Aires. El aporte de los vertebrados*. Ph.D. Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 317 p.

DESCHAMPS C. M. & TOMASSINI R. L. 2016. — Late Cenozoic vertebrates from the southern Pampean Region: systematic and bio-chronostratigraphic update, *in* MARTÍNEZ M. & OLIVERA D. (eds), Palinología del Meso-Cenozoico. *Publicación Electrónica de la Asociación Paleontológica Argentina* 16: 202-225.

DOZO M. T. & VERA B. 2010. — First skull and associated postcranial bones of Macraucheniidae (Mammalia, Litopterna) from the Deseadan SALMA (late Oligocene) of Cabeza Blanca (Chubut, Argentina). *Journal of Vertebrate Paleontology* 30 (6): 1818-1826. https://doi.org/10.1080/02724634.2010.521534

FOLGUERA A. & ZÁRATE M. 2009. — La sedimentación neógena continental en el sector extrandino de Argentina central. *Revista de la Asociación Geológica Argentina* 64: 692-712.

FOLGUERA A. & ZÁRATE M. 2018. — La estructuración miocena tardía del Bloque de La Pampa Central. *Revista de la Asociación Geológica Argentina* 75: 115-133.

FORASIEPI A. M., MACPHEE R. D. E., HERNÁNDEZ DEL PINO S., SCHMIDT G. I., AMSON E. & GROHÉ C. 2016. — Exceptional skull of *Huayqueriana* (Mammalia, Litopterna, Macraucheniidae) from the Late Miocene of Argentina: anatomy, systematics, and paleobiological implications. *Bulletin of the American Museum of Natural History* 404: 1-77. https://doi.org/10.1206/0003-0090-404.1.1

GELFO J. N. 2016. — Considerations about the evolutionary stasis of *Notiolofos arquinotiensis* (Mammalia: Sparnotheriodontidae), Eocene of Seymour Island, Antarctica. *Ameghiniana* 53: 316-332. https://doi.org/10.5710/AMGH.14.09.2015.2934

GELFO J. N., GOIN F. J., WOODBURNE M. O. & MUIZON C. DE 2009. — Biochronological relationships of the earliest South American Paleogene mammalian faunas. *Palaeontology* 52 (1): 251-269. https://doi.org/10.1111/j.1475-4983.2008.00835.x

GELFO J. N., LÓPEZ G. M. & SANTILLANA S. N. 2017. — Eocene ungulate mammals from West Antarctica: implications from their fossil record and a new species. *Antarctic Science* 29 (5): 445-455. https://doi.org/10.1017/S0954102017000244

GOIN F., MONTALVO C. I. & VISCONTI G. 2000. — Los Marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (provincia de La Pampa, Argentina). *Estudios Geológicos* 56: 101-126. https://doi.org/10.3989/egeol.00561-2158

KRAGLIEVICH L. 1932. — Nuevos apuntes para la geología y paleontología uruguayas. *Anales del Museo de Historia Natural de Montevideo* 3: 1-65.

LATRUBESSE E. M., COZZUOL M., SILVA-CAMINHA S. A. F. DA, RIGSBY C. A., ABSY M. L. & JARAMILLO C. 2010. — The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth-Science Reviews* 99 (3-4): 99-124. https://doi.org/10.1016/j.earscirev.2010.02.005

LINARES E., LLAMBÍAS E. J. & LATORRE C. O. 1980. — Geología de la provincia de La Pampa y geocronología de sus rocas metamórficas y eruptivas. *Revista de la Asociación Geológica Argentina* 35: 87-146.

LÓPEZ MENDOZA P., ROJAS MONDACA O., FLORES-AQUEVEQUE V., LOYOLA MUÑOZ R., MARTÍNEZ RIVERA I. & CARTAJENA FASTING I. 2018. — *El Pleistoceno de la cuenca de Calama. Evidencias paleontológicas y arquelológicas*. Museo de Historia Natural y Cultural del Desierto (coll. Monografías; 1), Atacama: 1-226.

MONTALVO C. I., CERDEÑO E. & ALCALÁ L. 2005. — Análisis tafonómico de los macromamíferos del Mioceno superior de Caleufú (La Pampa, Argentina). *Geogaceta* 38: 15-18.

MONTALVO C. I., TOMASSINI R. L., SOSTILLO R., CERDEÑO E., VERZI D. H., VISCONTI G., FOLGUERA A. & SCHMIDT G. I. 2019. — A Chasicoan (Late Miocene) vertebrate assemblage from Cerro Azul Formation, central Argentina. Geomorphological and biochronological considerations. *Journal of South American Earth Sciences* 95: 102218. https://doi.org/10.1016/j.jsames.2019.102218

OLIVA C., DI MARTINO V. & RETAMOZO M. 2011. — Nuevos aportes al conocimiento del Piso/Edad Huayqueriense (Mioceno tardío) del curso inferior del Arroyo Chasicó, provincia de Buenos Aires, Argentina, *in* MARTÍNEZ R. N. (ed.), *IV Congreso Latinoamericano de Paleontología de Vertebrados, San Juan, Argentina, 21-24 de septiembre, 2011* [Digital abstracts].

PASCUAL R. 1961. — Un nuevo Cardiomynae (Rodentia, Caviidae) de la Formación Arroyo Chasicó (Plioceno inferior) de la Provincia de Buenos Aires. *Ameghiniana* 2 (4): 61-71.

PASCUAL R. 1965. — Los Toxodontidae (Toxodonta, Notoungulata) de la Formación Arroyo Chasicó (Plioceno inferior) de la provincia de Buenos Aires. Características geológicas. *Ameghiniana* 4 (4): 101-132.

PASCUAL R. & BOCHINO A. 1963. — Un nuevo Borhyaeninae (Marsupialia) del Plioceno medio de Hidalgo (La Pampa). *Ameghiniana* 3 (4): 97-107.

PASCUAL R., PISANO J. & ORTEGA E. 1965. — Un nuevo Octodontidae (Rodentia, Caviomorpha) de la Formación Epecuén (Plioceno medio) de Hidalgo (Provincia de La Pampa). *Ameghiniana* 4 (1):19-30.

PASCUAL R., BONDESIO P., VUCETICH M. G., SCILLATO YANÉ G. J., BOND M. & TONNI E. P. 1984. — Vertebrados fósiles cenozoicos. *Relatorio IX Congreso Geológico Argentino, Buenos Aires* 2: 439-461.

PAULA COUTO J. C. 1979. — *Tratado de Paleomastozoología*. Academia Brasileira de Ciencias, Río de Janeiro, 590 p.

PIÑERO P., VERZI D. H., OLIVARES A. I., MONTALVO C. I., TOMASSINI R. L. & FERNÁNDEZ-VILLOLDO A. 2021. — Evolutionary pattern of *Metacaremys* gen. nov. (Octodontidae, Rodentia) and its biochronological implications for the Late Miocene-Early Pliocene of southern South America. *Papers in Palaeontology* 7 (4): 1895-1917. https://doi.org/10.1002/spp2.1368

REGUERO M. A. & CANDELA A. M. 2011. — Late Cenozoic mammals from the Northwest of Argentina, *in* SALFITY J. A. & MARQUILLAS R. A. (eds), *Cenozoic Geology of the Central Andes of Argentina*. INCE (Instituto del Cenozoico), Salta: 411-426.

RODRÍGUEZ M. F., LEANZA H. A. & SALVARREDY ARANGUREN M. 2007. — Programa Nacional de Cartas Geológicas de la República Argentina 1:250.000: Hoja Geológica 3969-II, Neuquén, provincias del Neuquén, Río Negro y La Pampa. *Servicio Geológico Minero Argentino, Instituto de Geología y Recursos Minerales, Boletín* 370: 1-165.

ROVERETO C. 1914. — Los estratos araucanos y sus fósiles. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 25: 1-250.

SCHMIDT G. I. 2013. — *Litopterna y Notoungulata (Mammalia) de la Formación Ituzaingó (Mioceno Tardío-Plioceno) de la Provincia de Entre Ríos: sistemática, bioestratigrafía y paleobiogeografía*. Ph.D. Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 423 p.

SCHMIDT G. I. 2015. — Actualización sistemática y filogenia de los Proterotheriidae (Mammalia, Litopterna) del "Mesopotamiense" (Mioceno tardío) de Entre Ríos, Argentina. *Revista Brasileira de Paleontologia* 18 (3): 521-546. https://doi.org/10.4072/rbp.2015.3.14

SCHMIDT G. I. & CERDEÑO E. 2013. — Los ungulados nativos (Litopterna y Notoungulata: Mammalia) del "Mesopotamiense" (Mioceno Tardío) de Entre Ríos, *in* BRANDONI D. & NORIEGA J. I. (eds), *El Neógeno de la Mesopotamia argentina*. Asociación Paleontológica Argentina (coll. Publicación Especial; 14), Buenos Aires: 145-152.

SCHMIDT G. I. & FERRERO B. S. 2014. — Taxonomic reinterpretation of *Theosodon hystatus* Cabrera & Kraglievich, 1931 (Litopterna, Macraucheniidae) and phylogenetic relationships of the family. *Journal of Vertebrate Paleontology* 34 (5): 1231-1238. https://doi.org/10.1080/02724634.2014.837393

SCHMIDT G. I., SOSTILLO R., MONTALVO C. I. & CERDEÑO E. 2018. — Proterotheriidae (Litopterna) from the Cerro Azul Formation (Late Miocene), La Pampa Province, Argentina. *Journal of South American Earth Sciences* 83: 168-177. https://doi.org/10.1016/j.jsames.2018.02.009

Schmidt G. I., Diederle J. M., Vallone E. R., Góis F. Tarquini J., Fernández Osuna M. A., Gottardi M. G. & Brandoni D. 2020. — New vertebrates from the Late Miocene of Entre Ríos Province, Argentina: diversity, age, and paleoenvironment. *Journal of South American Earth Sciences* 101: 102618. https://doi.org/10.1016/j.jsames.2020.102618

Schultz P. H., Zárate M. A., Hames W., Camilión C. & King J. 1998. — A 3.3-Ma impact in Argentina and possible consequences. *Science* 282 (5396): 2061-2063. https://doi.org/10.1126/science.282.5396.2061

Schultz P. H., Zárate M. A., Hames W., Koeberl C., Bunch T., Storzer D., Renne P. R. & Wittke J. 2004. — The Quaternary impact record from the Pampas, Argentina. *Earth and Planetary Science Letters* 219 (3-4): 221-238. https://doi.org/10.1016/S0012-821X(04)00010-X

Schultz P. H., Zárate M. A., Hames W., Koeberl C., Bunch T., Harris R. S., Renne P. R. & Wittke J. 2006. — The record of Miocene impacts in the Argentine Pampas. *Meteoritics and Planetary Science* 41 (5): 749-771. https://doi.org/10.1111/j.1945-5100.2006.tb00990.x

Soria M. F. 1981. — Los Litopterna del Colhuehuapense (Oligoceno tardío) de la Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Serie Paleontología* 3 (1): 1-54.

Soria M. F. 1986. — *Huayqueriana* Kraglievich, 1934: género de Macraucheniidae (Litopterna) de edad Huayqueriense (Mioceno tardío). Aspectos evolutivos vinculados, *in* Leanza H. (ed.), *Actas: IV Congreso Argentino de Paleontología y Bioestratigrafía. Simposio Temas libres "Icnofósiles. Invertebrados. Vertebrados", Mendoza, 23-27 de noviembre, 1986*. El Congreso, Mendoza: 157-164.

Soria M. F. 2001. — Los Proterotheriidae (Litopterna, Mammalia), sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales* 1: 1-167.

Soria M. F. & Hoffstetter R. 1985. — *Pternoconius tournoueri*, nueva especie de Macraucheniidae (Mammalia; Litopterna) de Edad Colhuehuapense (Oligoceno tardío); Pcia del Chubut, República Argentina. *Ameghininana* 22 (3-4): 149-158.

Sostillo R., Montalvo C. I. & Verzi D. H. 2014. — A new species of *Reigechimys* (Rodentia, Echimyidae) from the Late Miocene of Central Argentina and the evolutionary pattern of the lineage. *Ameghiniana* 51: 284-294. https://doi.org/10.5710/AMGH.24.04.2014.2718

Sostillo R., Montalvo C. I., Cerdeño E., Schmidt G. I., Folguera A. & Cardonatto M. C. 2019. — Updated knowledge on the Notoungulata (Mammalia) from the Late Miocene Cerro Azul Formation, La Pampa Province, Argentina. *Historical Biology* 33 (8). https://doi.org/10.1080/08912963.2019.1689239

Souza Lobo L., Lessa G., Cartelle C. & Romano P. S. R. 2017. — Dental eruption sequence and hypsodonty index of a Pleistocene macraucheniid from Brazilian Intertropical Region. *Journal of Paleontology* 91 (5): 1083-1090. https://doi.org/10.1017/jpa.2017.54

Tomassini R. L., Montalvo C. I., Deschamps C. & Manera T. 2013.— Biostratigraphy and biochronology of the Monte Hermoso Formation (early Pliocene) at its type locality, Buenos Aires Province, Argentina. *Journal of South American Earth Sciences* 48: 31-42. https://doi.org/10.1016/j.jsames.2013.08.002

Tonni E., Prado J., Fidalgo F. & Laza J. 1992. — El Piso/Edad Montehermosense (Plioceno) y sus mamíferos. *Actas del III Jornadas Geológicas Bonaerenses, La Plata, 9-13 de marzo, 1992*. Asociación Geológica Argentina, Buenos Aires: 113-118.

Ubilla M., Perea D., Bond M. & Rinderknecht A. 2011. — The first cranial remains of the Pleistocene proterotheriid *Neolicaphrium recens* Frenguelli, 1921 (Mammalia, Litopterna): a comparative approach. *Journal of Vertebrate Paleontology* 31 (1): 193-201. https://doi.org/10.1080/02724634.2011.539647

Verzi D. H. 1999. — The dental evidence on the differentiation of the ctenomyine rodents (Caviomorpha, Octodontidae, Ctenomyinae). *Acta Theriologica* 44 (3): 263-282. https://doi.org/10.4098/AT.arch.99-25

Verzi D. H. & Montalvo C. I. 2008. — The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): Late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange. *Palaeogeography, Palaeoclimatology, Palaeoecology* 267 (3-4): 284-291. https://doi.org/10.1016/j.palaeo.2008.07.003

Verzi D. H., Montalvo C. I. & Deschamps C. M. 2008. — Biostratigraphy and biochronology of the Late Miocene of central Argentina: evidence from rodents and taphonomy. *Geobios* 41 (1): 145-155. https://doi.org/10.1016/j.geobios.2006.09.005

Visconti G., Melchor R. N., Montalvo C. I., Umazano A. M. & de Elorriaga E. E. 2010. — Análisis litoestratigráfico de la Formación Cerro Azul (Mioceno Superior) en la provincia de La Pampa, Argentina. *Revista de la Asociación Geológica Argentina* 67 (2): 257-265.

Welker F., Collins M. J., Thomas J.A., Wadsley M., Brace S., Cappellini E., Turvey S. T., Reguero M., Gelfo J. N., Kramarz A., Burger J., Thomas-Oates J., Ashford D. A., Ashton P., Rowsell K., Porter D. M., Kessler B., Fisher R., Baessmann C., Kaspar S., Olsen J., Kiley P., Elliott J. A., Kelstrup C., Mullin V., Hofreiter M., Willerslev E., Hublin J. J., Orlando L., Barnes I. & MacPhee R. D. E. 2015. — Ancient proteins resolve the evolutionary history of Darwin's South American ungulates. *Nature* 522: 81-84. https://doi.org/10.1038/nature14249

Zárate M., Schultz P., Blasi A., Heil C., King J., & Hames W. 2007. — Geology and geochronology of type Chasicoan (Late Miocene) mammal-bearing deposits of Buenos Aires Province (Argentina). *Journal of South American Earth Sciences* 23 (1): 81-90. https://doi.org/10.1016/j.jsames.2006.09.018

Zetti J. 1972. — *Los mamíferos fósiles de Edad Huayqueriense (Plioceno medio) de la región pampeana*. Ph.D. Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata, 122 p.

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APPENDICES

APPENDIX 1. — Dental measurements of Litopterna from the Huayquerian of La Pampa and Buenos Aires provinces and specimens used for comparisons. *****, approximate; right/left; **L**, length; **W**, width. Available at the following address: https://doi.org/10.5852/cr-palevol2022v21a32_s1

APPENDIX 2. — Undetermined specimens of Macraucheniinae from the Cerro Azul Formation in La Pampa and Buenos Aires provinces.

Collection number	Description	Locality	South American Stage/Age	Province
GHUNLPam 14191	deciduous incisor	Telén	early Huayquerian	La Pampa
GHUNLPam 18876	deciduous incisor	Laguna Chillhué	early Huayquerian	La Pampa
GHUNLPam 18602	I1?	Salinas Grandes de Hidalgo	early Huayquerian	La Pampa
GHUNLPam 6961	third upper incisor (I3)	Laguna Chillhué	early Huayquerian	La Pampa
GHUNLPam 9279	incomplete left upper molar (M1?)	Loventué	early Huayquerian	La Pampa
GHUNLPam 5647	incomplete upper molar	Laguna Chillhué	early Huayquerian	La Pampa
GHUNLPam 14365	labial enamel of an upper molar	Salinas Grandes de Hidalgo	early Huayquerian	La Pampa
GHUNLPam 14479	labial enamel of an upper molar	Salinas Grandes de Hidalgo	early Huayquerian	La Pampa
GHUNLPam 6394	left mandible poorly preserved with i1-m2	Laguna Chillhué	early Huayquerian	La Pampa
GHUNLPam 27060	right p2	Salinas Grandes de Hidalgo	early Huayquerian	La Pampa
GHUNLPam 12825	right p3	Salinas Grandes de Hidalgo	early Huayquerian	La Pampa
GHUNLPam 6228	fragment of a lower molar	Salinas Grandes de Hidalgo	early Huayquerian	La Pampa
GHUNLPam 6479	incomplete lower molar	Telén	early Huayquerian	La Pampa
GHUNLPam 8760	enamel of premolar	Laguna Chillhué	early Huayquerian	La Pampa
GHUNLPam 21741	fragment of a lower molar	Laguna Chillhué	early Huayquerian	La Pampa
MHG-P 126-34	left? I1	Laguna La Paraguaya	Huayquerian *s.l.*	Buenos Aires
MHG-P 126-36	incomplete upper molar	Laguna La Paraguaya	Huayquerian *s.l.*	Buenos Aires
MMP-M 435	upper incisor(?), lower premolar fragments, astragalus	Laguna Epecuén	Huayquerian *s.l.*	Buenos Aires