



Protheroetheriidae (Mammalia, Litopterna) from the Cerro Azul Formation (late Miocene), La Pampa Province, Argentina



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ABSTRACT

Remains of Protheroetheriidae (Litopterna) recovered from different localities in La Pampa Province, Argentina, are described. The fossiliferous levels in these localities correspond to the Cerro Azul Formation (late Miocene), where Chasicuan and Huayquerian faunal associations are known. The specimens of Protheroetheriidae herein studied are assigned to *Diplasiotherium pampa*, *Eoauchenia primitiva*, cf. *Brachytherium cuspidatum*, *Neobrachytherium* sp. and Protheroetheriidae indet. Although the holotype of *D. pampa* (left mandibular fragment with p3-m2) was defined in a previous paper, it is figured and fully described here, and its m3 is now known among the new collected specimens. *Eoauchenia*, *Brachytherium* and *Neobrachytherium* are registered in La Pampa Province for the first time, and the record of *E. primitiva* extends back to late Miocene its temporal distribution. Protheroetheriids from the Cerro Azul Formation gather exclusive elements and others related to taxa represented in different Argentinean geological units corresponding to late Miocene-early Pliocene period.

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1. Introduction

The order Litopterna includes South American native ungulates widely spread from late Eocene to late Pleistocene/early Holocene (Cifelli, 1983; Cifelli and Guerrero, 1997; Cifelli and Villarreal, 1997; Carlini et al., 2006; Dozo and Vera, 2010; Schmidt and Ferrero, 2014; Forasiepi et al., 2016), also registered in the early Eocene-early Oligocene from West Antarctica (Bond et al., 2006, 2009; Gelfo, 2016; Gelfo et al., 2017). Litopterns were common elements of the Cenozoic faunal assemblages, but became extinct to the end of Pleistocene/early Holocene. Two families of Litopterna, Protheroetheriidae and Macraucheniiidae, have been recorded from the Cerro Azul Formation (late Miocene), La Pampa Province, Argentina (Zetti, 1972; Cione et al., 2000; Soria, 2001; Montalvo et al., 2005; Verzi and Montalvo, 2008; Brandoni, 2013; Schmidt, 2013). Up to now, protheroetheriids from the Cerro Azul Formation were only

known from the holotype of *Diplasiotherium pampa* Soria, 2001, from Salinas Grandes de Hidalgo, and a specimen identified as Protheroetheriidae indet. from Caleufú (Montalvo et al., 2005; Verzi and Montalvo, 2008). In this contribution, we study new Protheroetheriidae remains from the Cerro Azul Formation, which allows the recognition of other taxa together with additional material of *D. pampa*, and comments on their geographical and temporal distribution.

Protheroetheriidae include small to medium-sized cursorial herbivores, with brachyodont, mesodont or protohyssodont dentition (sensu Mones, 1982), and reduced lateral digits (II and IV) (Bond et al., 2001; Villafañe et al., 2006, 2012; Ubilla et al., 2011; Schmidt, 2015; Morosi and Ubilla, 2017). They occupied forested to open habitats of South America (Argentina, Brazil, Bolivia, Chile, Colombia, Venezuela, and Uruguay; Carlini et al., 2006; Scherer et al., 2009 and references therein) and show two peaks of maximum diversity in the early and late Miocene, that is in Santacrucian and Huayquerian South American Land Mammal Ages—SALMAs—, respectively (see comments on SALMAs or Stages/Ages in section 3), with 13 species in the former and 10 in the latter (Villafañe et al., 2006; Ubilla et al., 2011). During the Pleistocene, the protheroetheriid diversity decreased to a single

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species, *Neolicaphrium recens* Frenguelli 1921, registered in Argentina, Brazil, and Uruguay (Villafañe et al., 2006; Scherer et al., 2009; Ubilla et al., 2011; Morosi and Ubilla, 2017).

2. Geological setting and fossiliferous localities

Late Miocene deposits in La Pampa Province are very extensive and grouped into the Cerro Azul Formation (Linares et al., 1980; Folguera and Zárate, 2009), including the “Epecuén Formation” in west of Buenos Aires Province (sensu Pascual, 1961, Goin et al., 2000). They outcrop from the northernmost sector to the Colorado River at the south, and from the western margin of the Central Block of La Pampa to the Bonaerian High (Positivo Bonaerense) in Buenos Aires (Fig. 1). This formation is predominantly composed of brown silts and sandy silts primarily of eolian origin (loess deposits), which have been reworked by aqueous agents (loess-like deposits). Palaeosols are common throughout the sequence. A detailed description of the geology and stratigraphy can be consulted in Linares et al. (1980), Goin et al. (2000), Folguera and Zárate (2009) and Visconti et al. (2010).

In this study, the following exposures of the Cerro Azul Formation are included: Cerro La Bota ($37^{\circ}22'S-65^{\circ}28'W$), Laguna Chillhué ($37^{\circ}24'18''S-64^{\circ}13'01''W$), Telén ($36^{\circ}15'S-65^{\circ}30'W$), Salinas Grandes de Hidalgo ($37^{\circ}13'S-63^{\circ}36'W$), Bajo Giuliani ($36^{\circ}42'40.39''S-64^{\circ}16'59.89''W$), El Guanaco ($36^{\circ}17'S-64^{\circ}16'W$), and Caleufú ($35^{\circ}41'S-64^{\circ}40'W$) (Fig. 1). Levels of Cerro Azul Formation at Cerro La Bota represent an ephemeral fluvial event (Goin et al., 2000; Verzi et al., 2008). Deposits at Telén, Bajo Giuliani, El Guanaco and Caleufú were interpreted as loess-like deposits with immature palaeosols and little diagenetic alteration (Montalvo et al., 2008, 2016; Verzi et al., 2008). At Laguna Chillhué and Salinas Grandes de Hidalgo, fluvial and eolian deposits are intercalated (Deschamps et al., 2013; Mehl and Zárate, 2014). Lithological homogeneity and reduced areal extension do not allow the correlation of different outcrops based on lithological criteria. Instead, five

proposed biozones, based on the anagenetic change pattern of Ctenomyidae and Echimyidae rodents, allow establishing chronological differences among localities according to the recorded species, covering from Chasicooan to late Huayquerian SALMAS (Verzi et al., 2008, 2011; Sostillo et al., 2014). According with the proposed scheme, the studied Proterotheriidae come from assemblages assigned to the Chasicooan (Cerro La Bota) and Huayquerian (from the oldest to the most modern locality: Laguna Chillhué, Telén, Salinas Grandes de Hidalgo, Bajo Giuliani, El Guanaco and Caleufú) (Fig. 2).

3. Materials and methods

The material under study consists of specimens (mainly isolated molars) of Proterotheriidae (Litopterna) stored at the Paleontological Collection of the Facultad de Ciencias Exactas y Naturales of the Universidad Nacional de La Pampa (GHUNLPam), Argentina. The sample comprises a total of 17 specimens from different localities where the Cerro Azul Formation crops out in La Pampa Province (see above and Fig. 1). All of them are detailed by the number of collection and the corresponding locality in Appendix A.

Descriptive morphology of Proterotheriidae follows Delupi de Bianchini and Bianchini (1971), Soria (2001), Kramarz and Bond (2005), Villafañe et al. (2012), and Schmidt (2015).

We conduct a comparative morphometric study to determine the systematic approach of the specimens from La Pampa Province and establish the similarities and differences with other taxa from Argentina of similar age (Mio-Pliocene) stored at different institutions. Data from the literature complete the direct study of specimens. Measurements of the compared material are presented in Supplementary material.

Concerning the biostratigraphic scheme, we follow the broadly used term of SALMA; some authors prefer Stage/Age for late Cenozoic subdivisions after Cione and Tonni (1995), but with an equivalent meaning (e.g., Deschamps et al., 2013: abstract, 145).

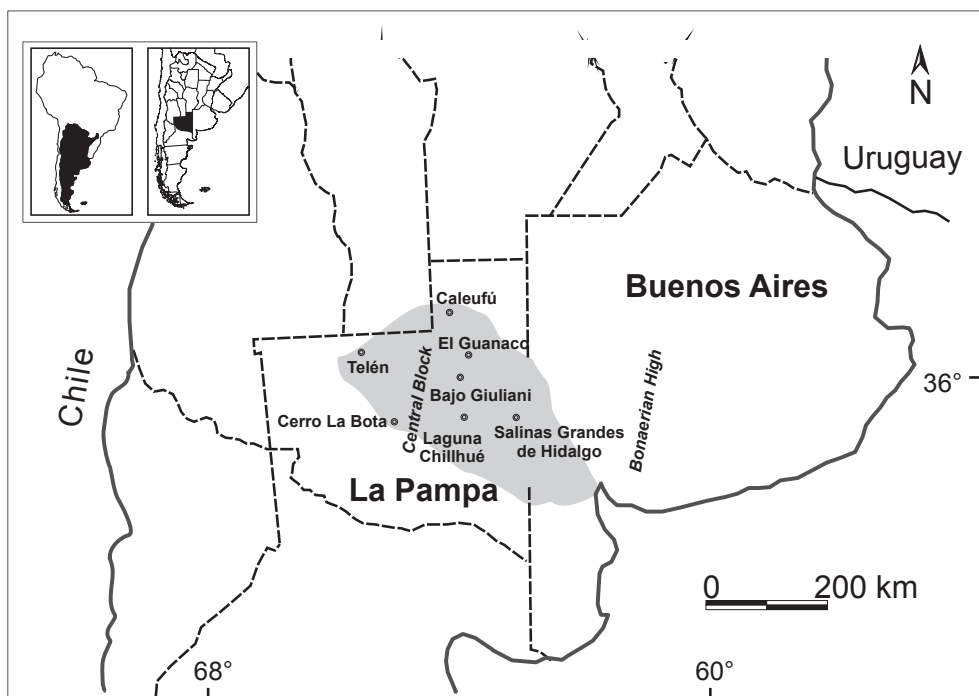


Fig. 1. Geographic location of the late Miocene deposits of Cerro Azul Formation (grey area, without considering the Quaternary cover) and localities with Proterotheriidae in La Pampa Province, Argentina.

Ma	Epoch	SALMA	Litho-stratigraphic Unit	La Pampa localities	Biozones	Proterotheriidae
5	late Miocene	Huayquerian	Cerro Azul Formation	Caleufú	<i>Xenodontomys elongatus</i>	Proterotheriidae indet. <i>Diplasiotherium pampa</i> <i>Eoarchenia primitiva</i> <i>Neobrachytherium</i> sp. <i>Brachytherium</i> cf. <i>B. cuspidatum</i>
6				El Guanaco	<i>Xenodontomys simpsoni</i>	
				Bajo Giuliani	<i>Chasichimys</i> morphotype a	
7				Salinas Grandes de Hidalgo		
				Telén		
8				Laguna Chillhué	<i>Chasichimys scagliai</i>	
	Cerro La Bota	<i>Chasichimys bonaerense</i>				
		Chasicosan				

Fig. 2. Stratigraphic distribution of octodontoid biozones and Proterotheriidae recovered from Cerro Azul Formation (late Miocene) in La Pampa Province, Argentina. Modified from Verzi et al. (2008), Deschamps et al. (2013) and Sostillo et al. (2014).

Absolute time intervals for Chasicosan, Huayquerian and Montehermosan SALMAs are not definitive (Brandoni, 2013), but for the purpose of this paper we follow previous schemes for the Cerro Azul Formation (Verzi et al., 2008; Deschamps et al., 2013; Sostillo et al., 2014).

Institutional abbreviations. CRILAR Pv, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Vertebrate Paleontology Collection, Anillaco, Argentina; GHUNLPam, Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de La Pampa, Argentina; FMNH, Field Museum of Natural History, Chicago, USA; MACN A/PV, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ameghino Collection/Vertebrate Paleontology Collection, Buenos Aires, Argentina; MCNAM-PV, Museo de Ciencias Naturales y Antropológicas “J. C. Moyano”, Vertebrate Paleontology Collection, Mendoza, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMH-FMH, Museo Monte Hermoso, Farola Monte Hermoso Collection, Monte Hermoso, Argentina; PVSJ, Museo de la Universidad de San Juan, San Juan, Argentina.

Anatomical abbreviations. DP/dp, deciduous upper/lower premolar; M/m, upper/lower molar; P/p, upper/lower premolar.

4. Results

Systematic Paleontology

Litopterna Ameghino, 1889.

Proterotheriidae Ameghino, 1887a.

Proterotheriinae Ameghino, 1887a.

Diplasiotherium Rovereto, 1914

Type species. *Diplasiotherium robustum* Rovereto, 1914.

Extended diagnosis (after Rovereto, 1914 and Soria, 2001). Proterotheriidae with p3-m3 higher-crowned than *Neobrachytherium* spp. and *Brachytherium cuspidatum*, similar to *Epitherium laterarium* and *Eoarchenia primitiva*. The p3 with or without anterior divergence (between paraconid and parastylid). Lower premolars and molars with paralophid shorter or similar in length to the hypolophulid. The m3 with entoconid well developed

or reduced, separated from the hypoconulid by a valley.

Diplasiotherium pampa Soria, 2001.

Fig. 3 A–F – Table 1

Holotype. MLP 57-X-10-13, left mandibular fragment with p3-p4, fragment of m1, and complete m2 moderately worn. Salinas Grandes de Hidalgo, La Pampa Province, Argentina.

Extended diagnosis (after Soria, 2001). Lower premolars and molars with paralophid slightly shorter than the hypolophulid. The p3 with an incipient anterior divergence between paraconid and parastylid, in contrast to *Diplasiotherium robustum* (absent) and less marked than in *Brachytherium cuspidatum*. Hypoconulid reduced in p4. The m2 with trigonid and talonid of similar size; entoconid and hypoconulid joined and more developed than in p4; ectoflexid more open than in p4 and stronger cingula. The m3 with trigonid shorter and higher than talonid, with bunoid and well-developed entoconid, differing from *D. robustum* (reduced entoconid), and separated from the hypoconulid by a valley in contrast to *Neobrachytherium ameghinoi*, *N. ullumense* and *N. intermedium*. All teeth with thick enamel and smaller than *D. robustum*.

Referred Material. GHUNLPam 5646, left m1?; GHUNLPam 19826, right mandibular fragment with m2-m3 (heavily worn); GHUNLPam 18601, left m3; GHUNLPam 18806, right m1?; GHUNLPam 5621, left m3 (unworn).

Distribution. Cerro Azul Formation, Huayquerian SALMA, late Miocene, La Pampa Province, Argentina; Laguna Chillhué, type locality of *Chasichimys scagliai* Zone; Salinas Grandes de Hidalgo; Bajo Giuliani, type locality of *Chasichimys* morphotype a Zone; and Caleufú, type locality of *Xenodontomys elongatus* Zone (Fig. 2).

Description. *Diplasiotherium pampa* was defined upon a left mandibular fragment (MLP 57-X-10-13) with p3-p4, fragment of m1, and complete m2 moderately worn from Salinas Grandes de Hidalgo (Soria, 2001). Although the author included a specific diagnosis and a schematic drawing of the specimen, he did not provide a full description, which is presented here along with original photographs (Fig. 3A).

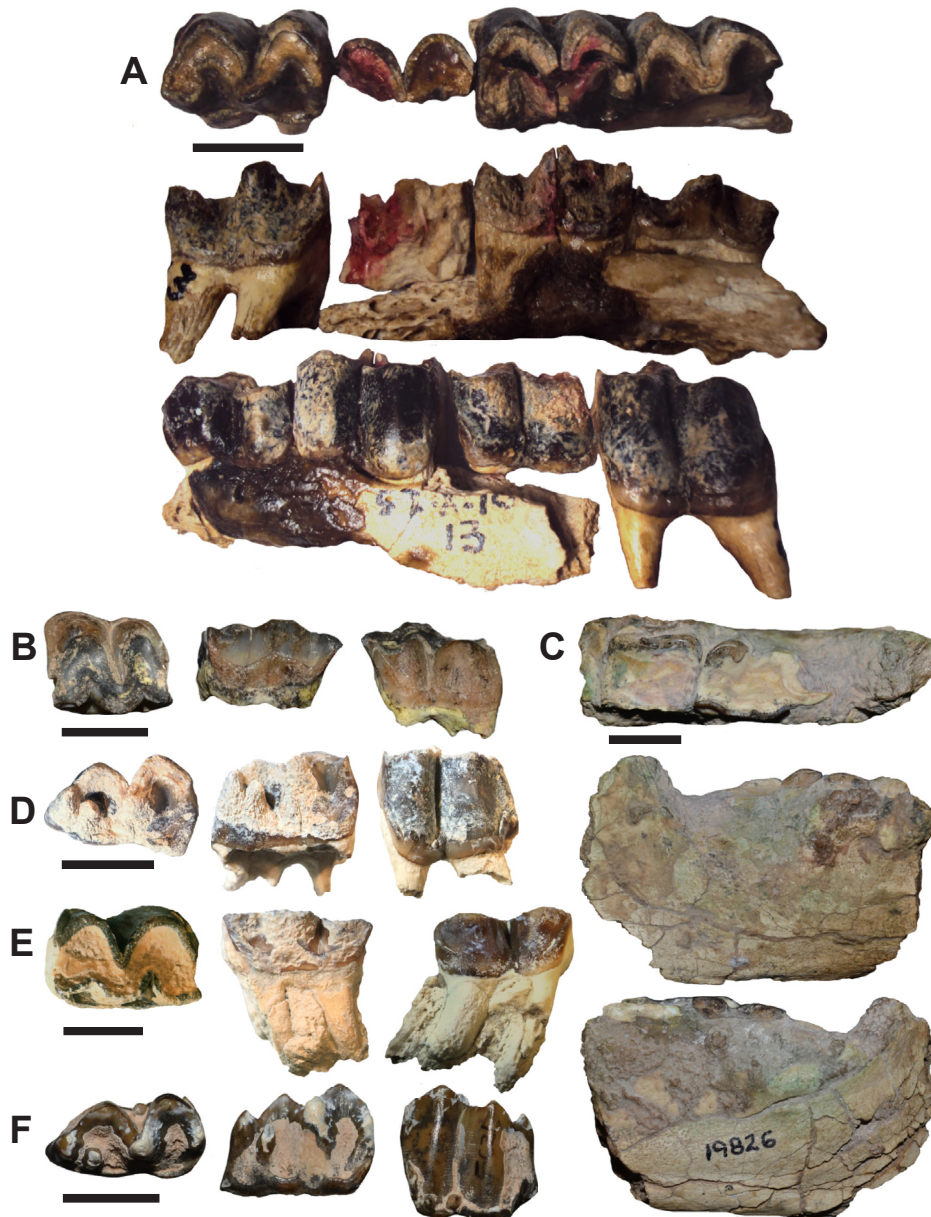


Fig. 3. *Diplasiotherium pampa*, **A.** MLP 57-X-10-13 (holotype) left p3-m2. **B.** GHUNLPam 5646, left m1?. **C.** GHUNLPam 19826, right mandibular fragment with m2-m3. **D.** GHUNLPam 18601, left m3. **E.** GHUNLPam 18806, right m1?. **F.** GHUNLPam 5621, left m3. **A** and **C**, from top to bottom: occlusal, lingual and labial views. **B**, **D-F**, from left to right: occlusal, lingual and labial views. Scale bar: 10 mm.

The p3 of MLP 57-X-10-13 has the trigonid longer and narrower than the talonid, and there is an incipient anterior divergence between the paraconid and the parastylid, less developed than it appears in [Soria's \(2001\)](#) scheme. In labial view, the talonid is lower than the trigonid. The labial cingulum is more developed at the base of the trigonid whereas the lingual cingulum is well developed along the entire tooth and tends to fade at the base of the metaconid. The p4 is split in the middle and the lingual side is poorly preserved. It is molariform and higher than the p3. Trigonid and talonid show a similar development. The entoflexid is shorter than the metaflexid, and the ectoflexid is deep. The entoconid is joined to a small hypoconulid. Cingula are developed as in p3. The labial side of the fragmented m1 is similar to p4 and m2, although it is more worn. The m2 is the highest tooth, with trigonid and talonid of similar size. The entoconid and the hypoconulid are joined and more developed than in p4. The ectoflexid is more open than in p4

and the cingula are stronger. All teeth present thick enamel.

New material adds data on lower molars, particularly on m3, which was not previously described. The molars identified as m1, GHUNLPam 5646 and GHUNLPam 18806, are very similar to each other; they share thick enamel (with respect to other taxa; see [Soria, 2001](#): 140) and conspicuous cingula on labial and lingual sides ([Fig. 3B](#) and [E](#)). Moreover, the labial cingulum is developed at the base of the tooth but raises both anteriorly and posteriorly to the occlusal level. The lingual cingulum is weak at the base of the metaconid.

The mandibular fragment GHUNLPam 19826 ([Fig. 3C](#)) was previously recognized as Proterotheriidae indet. by [Montalvo et al. \(2005\)](#); it is heavily worn, but also show thick enamel and conspicuous labial and lingual cingula in the trigonid of m3. The m3s GHUNLPam 18601 ([Fig. 3D](#)) and GHUNLPam 5621 ([Fig. 3F](#)) coincide with m1-m2 in the thick enamel and the development of the

Table 1

Dental measurements of studied Proterotheriidae from the Cerro Azul Formation; L, length; W, width.

Upper dentition		DP4	P1	P2	P3	P4	M1	M2	M3
<i>Eoauchenia primitiva</i>									
GHUNLPam 6379	L							16.15	
	W							19.50	
cf. <i>Brachytherium cuspidatum</i>									
GHUNLPam 168	L						15.10		
	W						~16.50		
<i>Neobrachytherium</i> sp.									
GHUNLPam 22712	L						15.26		
	W						16.20		
GHUNLPam 8260	L	15.40							
	W	17.05							
GHUNLPam 2277	L						~11.10		
	W						14.70		
Proterotheriidae indet.									
GHUNLPam 22676	L		10.40						
	W		7.35						
GHUNLPam 14535	L						11.27		
	W						13.40		
GHUNLPam 9569	L								12.10
	W								–
GHUNLPam 21589	L					13.96	14.25	15.82	
	W					17.00	19.50	20.20	
GHUNLPam 21536	L						~12.25		
	W						~19.00		
Lower dentition		dp4	p1	p2	p3	p4	m1	m2	m3
<i>Diplasiotherium pampa</i>									
MLP 57-X-10-13 (holotype)	L				14.60	14.00		16.60	
	W				9.50	11.70		11.90	
GHUNLPam 5646	L						14.30		
	W						11.35		
GHUNLPam 19826	L							14.90	20.90
	W							12.10	11.85
GHUNLPam 18601	L								17.80
	W								12.10
GHUNLPam 18806	L						14.60		
	W						9.60		
GHUNLPam 5621	L								17.10
	W								9.40
Proterotheriidae indet.									
GHUNLPam 9040	L						11.25		
	W						9.15		
GHUNLPam 21589	L					14.40			
	W					11.41			
GHUNLPam 8864	L	17.60							
	W	12.36							

cingula. The trigonid is shorter and higher than the talonid. The parolophid is shorter than the hypolophulid. The entoconid is bunoid, well developed, and separated from the hypoconulid by a valley. A feature observed in GHUNLPam 18601 and GHUNLPam 5621 is that the hypolophulid presents a V-shaped depression between the hypoconid and the hypoconulid (more evident in GHUNLPam 5621, Fig. 3F), which is not observed in GHUNLPam 19826 due to its extreme wear. The least worn teeth, GHUNLPam 18601 and GHUNLPam 5621, evidence a relatively high crown, corresponding to protohypodont teeth, which is the condition stated by Soria (2001) for the species of *Diplasiotherium*.

Comments. GHUNLPam 5646 and GHUNLPam 18806 are morphologically comparable to the m2 of MLP 57-X-10-13. They share the thick enamel and well-developed cingula, but the new specimens are smaller (Table 1 and Suppl. mat.) and more worn, differences that lead us to interpret them as m1. Even though GHUNLPam 19826 is heavily worn, its m2 presents the same general morphology as GHUNLPam 5646, GHUNLPam 18806, and MLP 57-X-10-13, and its dimensions are close to the latter (Table 1 and

Suppl. mat.). However, taking into account the level of wear, GHUNLPam 19826 is assigned to *D. pampa* with some reserves.

With respect to the m3, the isolated entoconid is similar to the condition in *Neobrachytherium* Soria, 2001. In GHUNLPam 18601 and GHUNLPam 5621, the entoconid of m3 is barely displaced to the hypolophulid whereas that cusp occupies the center of the valley in *N. ameghinoi* Soria, 2001 (MACN PV 14308, holotype from “Mesopotamian”, lower levels of Ituzaingó Formation, Entre Ríos Province; Soria, 2001; Schmidt, 2015); in *N. ullumense* Soria, 2001, it is placed next to the hypolophulid as an independent cusp (MCNAM-PV 3223, Arroyo Chasicó Formation, Buenos Aires Province; Cerdeño, 2003) or in the center of the talonid (PVSJ 135 from Ullum Valley, San Juan Province, Soria, 2001: Fig. 23b) similar to *N. ameghinoi*; and is joined to the hypoconulid by a lingual crest (MLP 12–316, Soria, 2001: Fig. 21b) or separated from the hypolophulid, occupying a more lingual position (FMNH P 14500 and MACN PV 8434, Schmidt, 2015) in *N. intermedium* (Moreno and Mercerat, 1891) from Corral Quemado Formation, Catamarca Province (Soria, 2001). It is important to note that the V-shaped depression

observed in the talonid of the m3s GHUNLPam 18601 and GHUNLPam 5621 is also present in MACN PV 8434 of *N. intermedium*. Probably, this characteristic is common to unworn teeth.

The attribution of GHUNLPam 18601 and GHUNLPam 5621 to *Diplasiotherium pampa* is based on the similarities in size and general morphology with the m2 MLP 57-X-10-13, especially by the thick enamel and the development of the cingula.

Currently, *Diplasiotherium* includes two species: *D. robustum* Rovereto, 1914 (MACN PV 7985 from Farola Monte Hermoso, Buenos Aires Province, Montehermosan SALMA) and *D. pampa*. In the generic diagnosis, Soria (2001) stated that the m3 (based on *D. robustum*) is similar to that of *Diadiaphorus* from Santacrucian SALMA in Santa Cruz Province. Although the m3s present an evident general resemblance, *Diplasiotherium* differs from *Diadiaphorus* because the latter lacks entoconid. Within *Diplasiotherium*, a trend in the development of the entoconid can be established as it is well developed and separated from the hypophulid in the oldest species *D. pampa* (GHUNLPam, 18601 and GHUNLPam 5621) whereas it is lower and reduced in the youngest *D. robustum*.

Up to now, *Diplasiotherium* is only known by the lower dentition and it can be thought that it could correspond to other species known by upper teeth, such it was the case of *Eoauchenia*. Nevertheless, features of upper and lower molars of *E. primitiva* were preliminarily described by Schmidt et al. (2010) and no such a correspondence is observed among the material from Cerro Azul Formation; in fact, only one upper molar is recognized as *E. primitiva* (see below); the lower teeth of the latter are different, with rounded lobes, narrower molars, talonid of m3 relatively longer, and trigonid of p4 shorter than talonid (G. Schmidt's personal data). The only possibility is that the specimen GHUNLPam 21589, with associated upper and lower dentition, could belong to *D. pampa*, as the lower teeth present some similarities with the holotype of this species; however, the teeth of GHUNLPam 21589 are too worn to reach a confident comparison and determination, and this is why we prefer to consider it as Proterotheriidae indet. (see below).

Eoauchenia Ameghino, 1887b

Eoauchenia primitiva Ameghino, 1887b.

Fig. 4A–Table 1

Referred Material. GHUNLPam 6379, right M2.

Distribution. El Guanaco locality, Cerro Azul Formation, late Huayquerian SALMA, late Miocene, La Pampa Province, Argentina (Fig. 2).

Description. GHUNLPam 6379 is a protohipsidont upper molar. The protoloph is convex and the anterolingual cingulum is absent; there is a large, deep central fossette and a smaller, shallower posterior one, labiolingually elongated and slightly lingually displaced. There is a smooth posterolingual groove between protocone and hypocone. On the labial side, the parastyle is the most developed style, and the paracone and metacone folds are absent.

Comments. The specimen from El Guanaco (GHUNLPam 6379) shows strong similarities with those recognized as *Eoauchenia primitiva* from the classical Monte Hermoso locality now named Farola Monte Hermoso (MACN PV 8002, MACN PV 8004, MMH-FMH 86-4-1 and MMH-FMH 86-4-6) in Buenos Aires Province (Ameghino, 1904; Rovereto, 1914; Schmidt et al., 2010).

GHUNLPam 6379 shares with the M2 of MACN PV 8002, MMH-FMH 86-4-1, and MMH-FMH-86-4-6 the convex protoloph, absence of anterolingual cingulum, similar morphology of central and posterolingual fossettes (the latter are absent in MACN PV 8002 probably due to extreme wear) and the labial concavity between

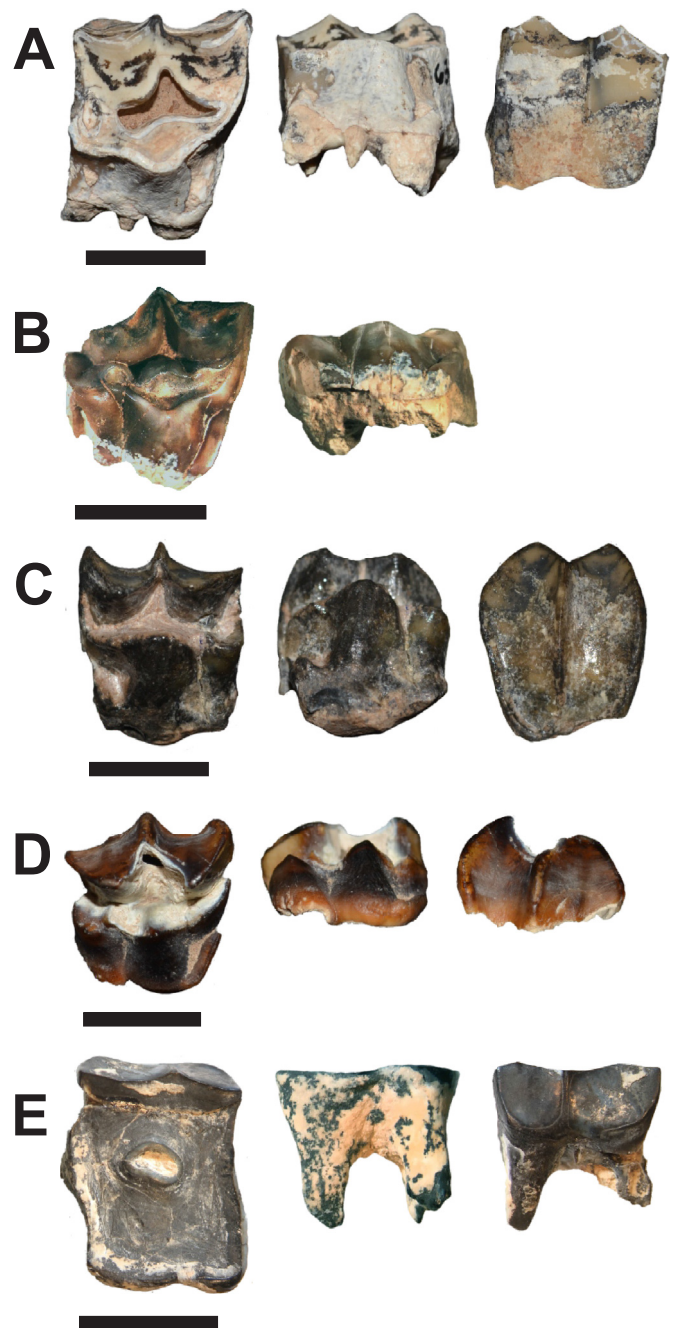


Fig. 4. *Eoauchenia primitiva*, A. GHUNLPam 6379, right M2. *Brachytherium* cf. *B. cuspidatum*, B. GHUNLPam 168, fragmentary M1 or M2. *Neobrachytherium* sp., C. GHUNLPam 22712, left M1 or M2. D. GHUNLPam 8260, right DP4?. E. GHUNLPam 2277, left M1?. From left to right: occlusal, lingual and labial views. Scale bar: 10 mm.

parastyle and mesostyle more marked than that between mesostyle and metastyle. Although MACN PV 8004 lacks M2, the morphology of P4 and M1 (incomplete) is comparable to GHUNLPam 6379 and the other mentioned specimens. With respect to size, GHUNLPam 6379 is a bit larger than MACN PV 8002 and MACN PV 8004, and closer to MMH-FMH 86-4-1 and MMH-FMH-86-4-6 (Table 1 and Suppl. mat.).

The holotype of *Eoauchenia primitiva* (MLP 12–2401; Ameghino, 1887b) consists of postcranial remains, but Ameghino (1904) also assigned to the species a fragment of skull with some teeth (MACN PV 8004), to which Rovereto (1914) added another skull (MACN PV

8002), apparently associated to a third metatarsal according to Soria (2001). The validity of the name *E. primitiva* has been controversial, but it would be supported by the similar metapodials of the holotype MLP 12–2401 and the specimen MACN PV 8002 (Soria, 2001); in both cases, bones are more gracile than those assigned to *Epitherium laterarium* Ameghino, 1888, another species recorded in Farola Monte Hermoso. The knowledge of *E. primitiva* was recently increased with the two maxillaries mentioned above, together with some mandibular and postcranial remains, from Farola Monte Hermoso (Schmidt et al., 2010).

Brachytherium Ameghino, 1883

cf. *Brachytherium cuspidatum* Ameghino, 1883.

Fig. 4B–Table 1

Referred Material. GHUNLPam 168, fragmentary right upper molar (M1 or M2).

Distribution. Salinas Grandes de Hidalgo, Cerro Azul Formation, Huayquerian SALMA, late Miocene, La Pampa Province, Argentina (Fig. 2).

Description. GHUNLPam 168 is labially broken. In occlusal view, the protocone is conspicuous and joined to the paraconule. The metaconule is bunoid, isolated, but close to the protocone. The anteroposterior groove is slightly interrupted by the metaconule. The hypocone is robust and separated from the protocone by a posterolingual groove. The anterolingual cingulum is thin and long and almost reaches the base of the protocone.

Comments. GHUNLPam 168 shows evident similarities with upper molars (particularly M2) from “Mesopotamian”, Entre Ríos Province, assigned to *Brachytherium cuspidatum* (MACN PV 14303 and MLP 69–XII-2-11; Schmidt, 2015). They share the position and morphology of the metaconule, the lingually acute protocone, the robust hypocone separated from the protocone by the posterolingual groove, and its anteroposterior length fall between the values of the “Mesopotamian” specimens (Table 1 and Suppl. mat.). However, the anterolingual cingulum differs, as it is a bit longer than in MACN PV 14303, and longer but less developed than in MLP 69–XII-2-11.

GHUNLPam 168 shares with *Neobrachytherium intermedium*, *Thoatheriopsis mendocensis* Soria, 2001 and *Epitherium laterarium* the posterolingual groove that separates hypocone from protocone. However, it differs from *N. intermedium* and *E. laterarium* because these species have a lophoid metaconule. In *T. mendocensis*, the metaconule is similar to GHUNLPam 168, but the anterolingual cingulum is shorter and presents a thick crenulated surface at the base of the crown on the lingual side. GHUNLPam 168 is also different from *Neobrachytherium ameghinoi* (MACN A 1401), because the metaconule in this species is reduced and joined to the protocone-hypocone conjunction. The isolated metaconule of GHUNLPam 168 discards its assignment to *N. ullumense* and *N. morenoi* (Rovereto, 1914). In *N. ullumense*, the metaconule is joined to the wall between protocone and hypocone (as in *N. ameghinoi*), and in *N. morenoi* it is joined to the hypocone (Schmidt, 2015).

Despite the similarities with *Brachytherium cuspidatum* and the differences with other Argentinean taxa (species of *Neobrachytherium*, *Thoatheriopsis mendocensis* and *Epitherium laterarium*), we prefer to consider GHUNLPam 168 as cf. *Brachytherium cuspidatum* due to the partial condition of the specimen.

Neobrachytherium Soria, 2001.

Neobrachytherium sp.

Fig. 4C–E – Table 1

Referred Material. GHUNLPam 22712, left M1 or M2 (unworn);

GHUNLPam 8260, right crown of DP4? (unworn); GHUNLPam 2277, left M1? (heavily worn).

Distribution. Cerro Azul Formation, Huayquerian SALMA, late Miocene, La Pampa Province, Argentina: Telén, Salinas Grandes de Hidalgo, and Bajo Giuliani. The latter is the type locality of *Chasichimys* morphotype a Zone (Fig. 2).

Description. GHUNLPam 22712 (Fig. 4C) is an unworn, square tooth. The styles and labial cusps are higher than the lingual ones. Labial styles are well marked, but parastyle and mesostyle are more developed than metastyle. Labial folds of paracone and metacone are absent. Protocone, paracone and metacone are more developed than paraconule and metaconule. The hypocone is separated from the protocone by the posterolingual groove. The paraconule is reduced and takes part of the crest (preprotocrista?) that joins protocone to the anterior border. The metaconule is very reduced and somewhat displaced to the hypocone (Fig. 4C). The anteroposterior groove is deep and divides the tooth. The anterolingual cingulum does not reach the base of the protocone and forms a small anterior fossette. The roots are not preserved.

GHUNLPam 8260 only preserves the crown without wear (Fig. 4D). It is very similar to GHUNLPam 22712, but metaconule and paraconule are a bit more developed, the anterolingual cingulum is extended almost to the base of the protocone, and the labial folds of the paracone and metacone are barely marked. It is difficult to decide whether it corresponds to a deciduous tooth (DP4) or to the germ of a permanent one (M1 or M2). However, GHUNLPam 8260 presents some characteristics coincident with deciduous teeth such as rugose surface of the crown (particularly on lingual cusps) and thinner and whiter enamel (Ungar, 2010: 11).

GHUNLPam 2277 is an upper molar heavily worn, wider than long (Fig. 4E; Table 1 and Suppl. mat.). The styles are hardly marked and the most pronounced is the mesostyle. In occlusal view, there is a little central fossette (remnant of the anteroposterior groove) and the posterolingual groove is hardly marked.

Comments. GHUNLPam 22712 share several features with the species of *Neobrachytherium*, such as the square outline, parastyle and mesostyle more developed than metastyle, deep anteroposterior groove, and upper molars with metaconule less developed than in *Brachytherium* (Entre Ríos Province, late Miocene). However, GHUNLPam 22712 also shows differences that make it difficult to assign it to any of the species of *Neobrachytherium* (Schmidt, 2015). The position of the metaconule near the hypocone in GHUNLPam 22712 is similar to that observed in *N. intermedium* and *N. morenoi*, while this cusp is joined to protocone-hypocone conjunction in *N. ameghinoi* and *N. ullumense*. The paracone is less developed than in all species of *Neobrachytherium*. The anterolingual cingulum is short and defines a fossette similar to *N. morenoi*, *N. ameghinoi* and *N. ullumense*, while it forms a flat edge in *N. intermedium*. As *N. ameghinoi*, GHUNLPam 22712 does not present labial folds, which are barely marked in *N. intermedium*, *N. morenoi* and *N. ullumense*. GHUNLPam 22712 also differs from *N. ameghinoi* and *Neobrachytherium* sp. from Salicas Formation, La Rioja Province (CRILAR Pv 429; Brandoni et al., 2012) because its lingual wall is inclined toward the labial side, instead of being straight; in addition, the posterolingual groove in GHUNLPam 22712 is shallower than in CRILAR Pv 429. With respect to the size, GHUNLPam 22712 is similar to *Neobrachytherium*, except CRILAR Pv 429, which is smaller (Table 1 and Suppl. mat.).

The morphological features mentioned above for GHUNLPam 8260 make us consider it as a deciduous tooth, probably a DP4. None species of *Neobrachytherium* has known upper deciduous teeth and so the comparison is not possible. For the late Miocene, only *Brachytherium cuspidatum* has known deciduous teeth (MACN A 11000a and MLP 81–XI-29-8), which differs from GHUNLPam 8260 in the position of the metaconule (near the protocone in

MACN A 11000a), the shallower anteroposterior groove, the deeper posterolingual groove, the labial styles and concavities less developed, and the smaller size (Suppl. mat.).

GHUNLPam 2277 resembles some worn specimens assigned to *N. ameghinoi* (MACN PV 13212 and MACN PV 9150; Soria, 2001; Schmidt, 2015). They share the absence of labial folds, parastyle more developed and more separated from the mesostyle and metastyle, and a central fossette (larger in GHUNLPam 2277). In MACN PV 13212 and MACN PV 9150 there is a little posterior fossette, which would have disappeared with wear in GHUNLPam 2277 together with the anterolingual cingulum. Concerning size, GHUNLPam 2277 is smaller than *N. ameghinoi* (Table 1 and Suppl. mat.).

The preceding comparisons reveal that GHUNLPam 22712, GHUNLPam 8260 and GHUNLPam 2277 share the general morphology and characteristics with upper teeth of *Neobrachytherium*, but they also present evident differences that do not allow a confident determination at the species level. Despite this, they constitute the first record of *Neobrachytherium* for the Cerro Azul Formation (La Pampa Province).

Proterotheriidae indet.

Fig. 5A–G - Table 1

Referred Material. GHUNLPam 22676, right P1; GHUNLPam 21589, left maxillary fragment with P4–M2 and left mandibular fragment with p4–m1 (broken); GHUNLPam 21536, left upper molar (M1?, heavily worn); GHUNLPam 9569, fragmentary right upper molar (M3?); GHUNLPam 14535, right M1? (heavily worn); GHUNLPam 9040, left lower molar (m1 or m2), heavily worn; GHUNLPam 8864, left crown of dp4.

Distribution. Cerro Azul Formation, late Miocene, La Pampa Province, Argentina: Cerro La Bota, Type locality of *Chasichimys scagliai* Zone, Chasicoan SALMA; Telén; Bajo Giuliani, Type locality of *Chasichimys* morphotype a Zone, and Calefú, Type locality of *Xenodontomys elongatus* Zone, Huayquerian SALMA (Fig. 2).

Description and comments. GHUNLPam 22676 is a triangular upper premolar with flat labial side and cingulum barely marked. In occlusal view, it is wider posteriorly than anteriorly, separated by a middle constriction. The lingual cingulum delimits a posterior fossette and becomes thinner from the middle constriction

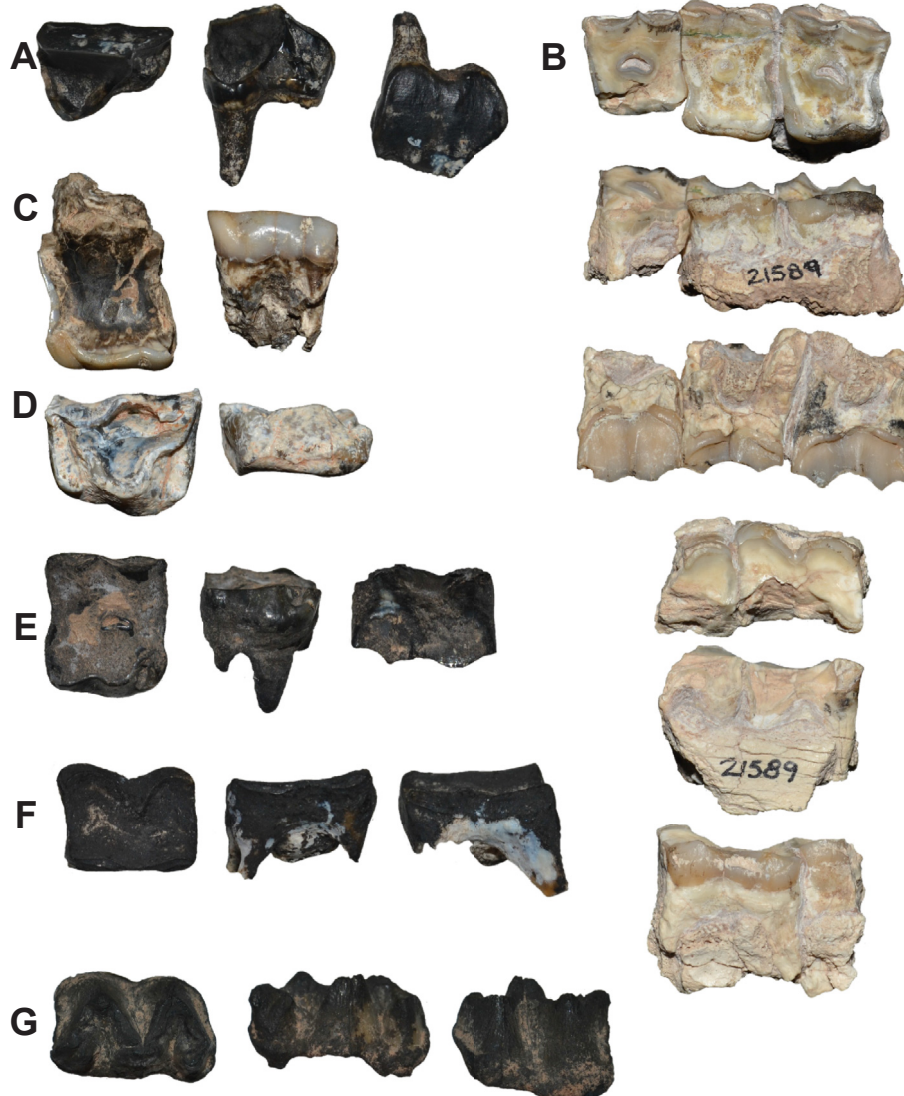


Fig. 5. Proterotheriidae indet. **A.** GHUNLPam 22676, right P1. **B.** GHUNLPam 21589, left maxillary fragment with P4–M2 and left mandibular fragment with p4–m1. **C.** GHUNLPam 21536, left upper molar (M1?). **D.** GHUNLPam 9569, fragmentary right upper molar (M3?). **E.** GHUNLPam 14535, right M1?. **F.** GHUNLPam 9040, left m1 or m2. **G.** GHUNLPam 8864, left dp4. **A, C–G,** from left to right: occlusal, lingual and labial views. **B,** from top to bottom: occlusal, lingual and labial views. Scale bar: 10 mm.

forward. Anterolingually, there is a low and short ridge. This tooth preserves one of the two roots (Fig. 5A).

GHUNLPam 22676 shows similarities and differences with late Miocene-Pliocene taxa registered in Argentina. It shares with *Neobrachytherium intermedium* (MACN PV 8429 and FMNH P 14500) and *Epitherium laternarium* (MACN PV 8001) its narrow anterior portion, the labial cusp (paracone?) displaced anteriorly, and the lingual constriction separating the fossettes (the anterior fossette less evident in GHUNLPam 22676). The mesostyle is less pronounced than in *N. intermedium* and *E. laternarium*. The anterior fossette is shallower than in *N. intermedium* (MACN PV 8429), and both fossettes are more developed in *E. laternarium*. GHUNLPam 22676 is similar to *Eoauchenia primitiva* (MACN PV 8002 and MACN PV 8004), but the P1 of the latter is anteriorly wider and the mesostyle is marked. Also, GHUNLPam 22676 is different from *Thoatheriopsis mendocensis* (MLP 81-XI-28-1), because the latter lacks lingual constriction and fossettes, and presents a very developed lingual cingulum extended from the mesial to the distal region. The size of GHUNLPam 22676 is close to *N. intermedium* and *E. laternarium*, and larger than *E. primitiva* and *T. mendocensis* (Table 1 and Suppl. mat.).

GHUNLPam 21589 has upper and lower teeth associated, although they are poorly preserved and show advanced dental wear (Fig. 5B). The upper teeth present conspicuous cingula, the labial styles are similarly developed, the paracone and metacone folds are evident, and the anterolingual cingulum in M1-M2 does not reach the base of the protocone. In M2, a smooth posterolingual groove separates the protocone from the hypocone. These teeth are rectangular, shorter than wide (Table 1). The anteroposterior groove is reduced to a central fossette, almost absent in M1. The p4 (lingually broken) presents thick enamel, labial cingulum, and labially extended talonid. The m1 only shows a fragment of the trigonid with labial cingulum.

The upper teeth of GHUNLPam 21589 differ from GHUNLPam 22712 and GHUNLPam 8260 (assigned here to *Neobrachytherium* sp.) in having: more developed labial cingulum, shallower interstylar concavities, labial folds, and larger size. Despite the advanced wear, the general morphology of GHUNLPam 21589 resembles *Epitherium laternarium*, even though the M1 is wider and the M2 is shorter and narrower (Suppl. mat.). GHUNLPam 21589 share with *Brachytherium cuspidatum* the presence of labial folds (e.g. MLP 69-XII-2-11) and the size (Table 1 and Suppl. mat.). The comparison with *Diplasiotherium pampa* is not possible as its upper molars are presently unknown. The lower teeth of GHUNLPam 21589 are very worn and poorly preserved to compare them with the holotype of *Diplasiotherium pampa* (MLP 57-X-10-13) and the remains assigned in this contribution (GHUNLPam 5646, 19826, 18601, 18806 and 5621). We can only indicate that some features observed in p4 (thick enamel, labial cingulum, and talonid labially extended) are similar to MLP 57-X-10-13. Both upper and lower teeth are not significant enough to reach a confident taxonomic determination of GHUNLPam 21589.

GHUNLPam 21536 is a heavily worn, incomplete tooth (Fig. 5C). The only observable features are the short anterolingual cingulum and the shallow posterolingual groove. The anterior side presents a shallow depression. The comparison of this tooth is very limited and we can just state that it shares with GHUNLPam 21589 the anterior side depressed, the short anterolingual cingulum and the smooth posterolingual groove. Both teeth could belong to the same taxon.

GHUNLPam 9569 is a fragmentary upper molar, probably an M3 as it is wider anteriorly (Fig. 5D). The labial side is broken. The protocone is robust and it is joined to paracone and metacone

in a continuous surface of wear. The anteroposterior groove is interrupted posteriorly by the bunoid metacone. The anterolingual cingulum is developed, but does not reach the base of the protocone. There is a thick posterior cingulum. The hypocone is not well differentiated. GHUNLPam 9569 presents great similarities with *Neobrachytherium* and *Brachytherium*. The morphology and development of the metacone are similar to those in the M3 of *N. ameghinoi* (MACN PV 4413). In contrast, the presence of metacone discards its assignment to *N. ullumense* (MCNAM PV-3222) and its bunoid morphology separates GHUNLPam 9569 from *N. intermedium* (PVL 3152, FMNH P 14500 and MACN PV 8430) and *Epitherium laternarium* (MACN PV 8001), in which this cusp is lophoid. The M3 of *N. morenoi* is unknown. The absence of a well-developed hypocone in GHUNLPam 9569 coincides with *Brachytherium cuspidatum* (MACN PV 14303 and MACN PV 9250), as well as the size of the preserved portion (Table 1).

GHUNLPam 14535 is an isolated square upper molar, probably an M1 (Fig. 5E). In occlusal view we can observe the central fossette, the short anterolingual cingulum and a shallow posterolingual groove. The distance between parastyle and mesostyle is longer than between mesostyle and metastyle. The labial folds of paracone and metacone are absent. The outline of GHUNLPam 14535 is comparable to that of the M1 of *Neobrachytherium ameghinoi* (MACN A 1401) and also resembles the P4 of *Neobrachytherium* sp. CRILAR Pv 429 (Brandoni et al., 2012). The anterolingual cingulum in GHUNLPam 14535 is also similar to MACN A 1401 and more developed than in CRILAR Pv 429, but the labial concavities are less pronounced and the size is notably smaller than in these specimens (Table 1 and Suppl. mat.). For the late Miocene, only *Proterotherium cervioides* Ameghino, 1883 (MLP 69-XII-2-9, holotype, from “Mesopotamian”, Entre Ríos Province; Soria, 2001; Schmidt, 2015) presents similar dimensions to GHUNLPam 14535 (Table 1 and Suppl. mat.), but its morphology is clearly different as it presents labial folds of paracone and metacone and the protoloph is oblique, not straight as in GHUNLPam 14535.

GHUNLPam 9040 is a heavily worn lower molar with no distinguishable features (Fig. 5F). It is a very small tooth with similar features to those of GHUNLPam 14535 from the same site (Telén, Appendix A) and both teeth could correspond to the same taxon. The small dimensions of GHUNLPam 9040 (Table 1) are below the smallest specimens of *B. cuspidatum* (Suppl. mat.). It cannot be compared with the small *Proterotherium cervioides* because this has no known lower dentition (except one dp4; Soria, 2001; Schmidt, 2015).

GHUNLPam 8864 is a partial dp4 with the trigonid shorter than the talonid (Fig. 5G). The paraconid is oriented to the metaflexid and lacks parastyloid. The metaconid is the highest lingual cusp. The entoconid is joined to the hypoconulid at the base. The labial and lingual cingula are present and the surface of the tooth is rugose. GHUNLPam 8864 is similar to the dp4 of *Brachytherium cuspidatum* (MLP 69-XII-2-4 and MACN PV 13172) as they share the orientation of the paraconid and the rugose surface. However, GHUNLPam 8864 is larger and the lophids are straighter, which do not allow an accurate identification; besides, the deciduous dentition of other coeval species is still unknown and comparisons are not possible.

In summary, the characteristics mentioned for each of these specimens prevent their confident identification with the genera and species previously recognized in La Pampa Province or in other late Miocene-Pliocene localities of Argentina. In this sense, we maintain them as *Proterotheriidae* indet., waiting that new discoveries allow a precise assignment.

5. Biochronologic and paleobiogeographic comments

Argentinean Mio-Pliocene continental sedimentary units are well-known both in faunal content and absolute chronology, particularly those corresponding to late Miocene (Contreras and Baraldo, 2011; Brandoni, 2013; Esteban et al., 2014): Arroyo Chasicó Formation (Buenos Aires Province), Loma de las Tapias Formation (San Juan Province), base of the Ituzaingó Formation ("Mesopotamian", Entre Ríos Province), Chiquimil and Andalhuala formations (Catamarca Province), and Cerro Azul Formation (La Pampa and Buenos Aires provinces). Andalhuala Formation was traditionally considered as late Miocene, but recently Bonini and Brandoni (2015) stated that part of this formation reaches the early Pliocene. In turn, Corral Quemado Formation (Catamarca Province), Toro Negro Formation (La Rioja Province), and Monte Hermoso Formation (Buenos Aires Province) correspond to early Pliocene (Schmidt et al., 2010; Brandoni, 2013; Tomassini et al., 2013; Esteban et al., 2014). At least one taxon of Litopterna is recorded from each one of these formations.

Concerning Proterotheriidae, identified taxa distribute as follows: 1) Arroyo Chasicó Formation: *Neobrachytherium* (Cerdeño, 2003; Brandoni, 2013; Schmidt, 2013); 2) Ullum, Loma de las Tapias Formation: *Neobrachytherium* (Soria, 2001); 3) "Mesopotamian": *Proterotherium*, *Neobrachytherium*, *Brachytherium*, and

Diadiaphorus (Brandoni, 2013; Schmidt and Cerdeño, 2013; Schmidt, 2015); 4) Chiquimil Formation: *Diadiaphorus* (Reguero and Candela, 2011; Brandoni, 2013); 5) Andalhuala Formation: *Neobrachytherium* (Brandoni, 2013); 6) Corral Quemado Formation: *Neobrachytherium* (Soria, 2001; Brandoni, 2013; Schmidt, 2013, 2015); 7) Toro Negro Formation: *Eoauchenia* (Brandoni, 2013); 8) Monte Hermoso Formation: *Eoauchenia*, *Diplasiotherium*, *Epi-therium* (Bond et al., 1995; Soria, 2001; Schmidt et al., 2010). The material herein described adds the presence of Proterotheriidae in the Cerro Azul Formation in central Argentina (Fig. 6).

The taxa recognized in different localities of La Pampa Province are common to some of the other mentioned units, but they do not constitute an association exactly comparable to any other locality (Figs. 2 and 6).

Diplasiotherium pampa is endemic in the Cerro Azul Formation, and is present in the faunal assemblages from the earliest (Laguna Chillhué) to the latest (Caleufú) Huayquerian. A different species, *D. robustum*, is present in the early Pliocene of Farola Monte Hermoso.

Eoauchenia primitiva is known in the early Pliocene Toro Negro and Monte Hermoso formations, so its presence in Cerro Azul Formation implies the first record of this species in the late Miocene, extending back its temporal distribution. At the same time, this record supports that El Guanaco assemblage is more

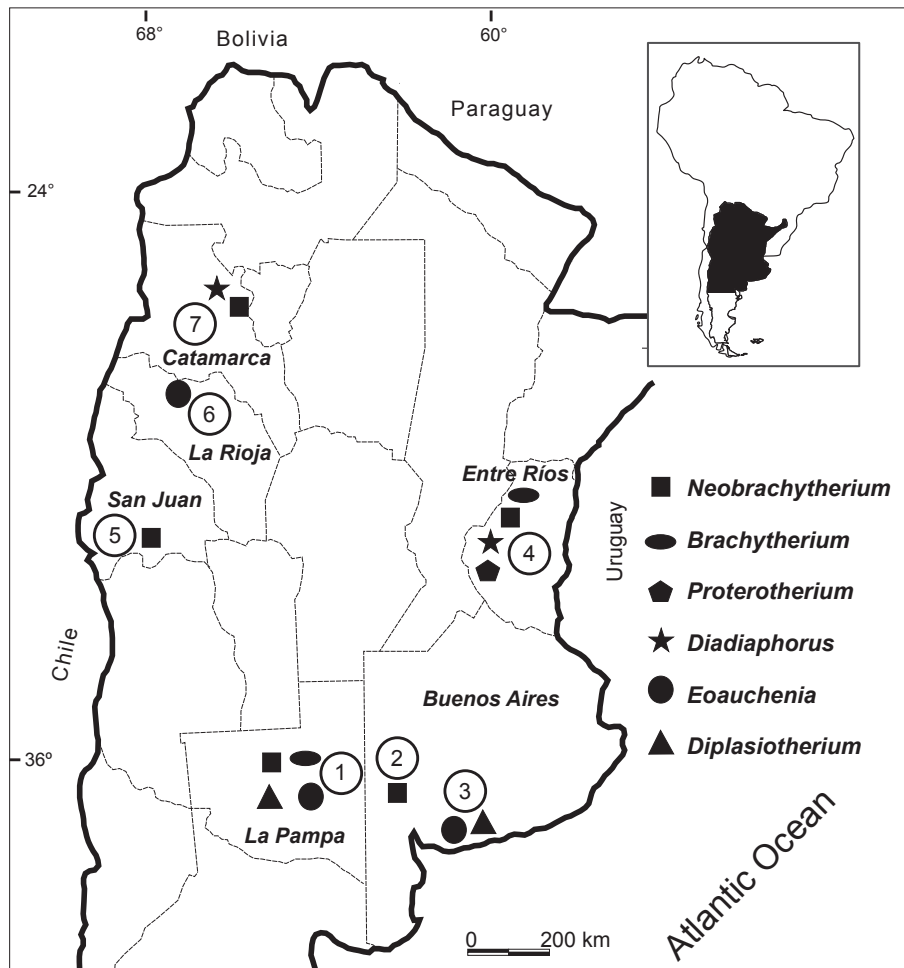


Fig. 6. Geographical distribution of Proterotheriidae from the late Miocene-early Pliocene. 1) Cerro Azul Formation; 2) Arroyo Chasicó Formation; 3) Monte Hermoso Formation; 4) lower levels of Ituzaingó Formation, "Mesopotamian"; 5) Loma de las Tapias Formation; 6) Toro Negro Formation; 7) Chiquimil, Andalhuala and Corral Quemado formations.

recent than most localities in the biostratigraphic scheme proposed for the late Miocene Cerro Azul Formation (Verzi et al., 2008; Sostillo et al., 2014; see Fig. 2).

The attribution of a partial molar from Salinas Grandes de Hidalgo to cf. *Brachytherium cuspidatum* establishes some similarities with the Ituzaingó Formation, the only unit where this species is known. This taxon adds to the other shared litopterna, the macraucheniid *Promacrauchenia*, as well as to other common mammals among marsupials, rodents, xenarthrans and carnivores (Brandoni, 2013).

Regarding *Neobrachytherium*, the lack of a precise identification of the three specimens assigned to this genus, from Telén, Salinas Grandes de Hidalgo, and Bajo Giuliani, prevents an accurate correlation with the localities where different species are recorded (*N. ameghinoi* in Entre Ríos Province, *N. intermedium* and *N. morenoi* in Catamarca Province, and *N. ullumense* in San Juan—Loma de las Tapias Formation— and Buenos Aires provinces).

In summary, Proterotheriidae from Cerro Azul Formation gather exclusive elements and others related to late Miocene or early Pliocene species. They do not contradict the temporal sequence of the respective faunal assemblages/localities previously established based on octodontoid rodents (Verzi et al., 2008; Sostillo et al., 2014). Even though the studied sample of Proterotheriidae is still scarce and insufficiently diagnostic, it could be indicating a sort of turnover from the oldest to the youngest localities, for instance, by the presence of *Eoauchenia primitiva* only at one of the youngest localities, El Guanaco (Fig. 2). In addition, the identified taxa reveal geographic affinities with coeval faunas from Buenos Aires, Entre Ríos, Catamarca, and La Rioja provinces (Fig. 6).

6. Conclusions

The detailed study of the Proterotheriidae from different outcrops of the Cerro Azul Formation (late Miocene) in La Pampa Province allow the recognition of new specimens of *Diplasiotherium pampa*, and the presence of *Eoauchenia primitiva*, *Brachytherium* cf. *B. cuspidatum*, *Neobrachytherium* sp., and Proterotheriidae indet.

Among the materials assigned to *D. pampa*, its m3 is described for the first time; besides, the description of its holotype (MLP 57-X-10-13; Soria, 2001) is herein completed with photographs of this

specimen. The identification of *E. primitiva* in La Pampa adds a new record of the species outside Buenos Aires Province and implies the extension of its biochron to the late Miocene. The incomplete molar considered as cf. *Brachytherium cuspidatum* extends the geographic distribution of the species, so far known in Entre Ríos Province. *Neobrachytherium* is also recognized in La Pampa Province for the first time. Several dental remains are not diagnostic enough to get a taxonomic identification beyond the family level.

The sample of Pampean proterotheriids gathers an endemic element (*D. pampa*) with others already known from different areas of Argentina: *Brachytherium* (Entre Ríos Province), *Neobrachytherium* (Entre Ríos, Catamarca, La Rioja, San Juan and Buenos Aires provinces) and *Eoauchenia* (La Rioja and Buenos Aires provinces).

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Supplementary materials

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jsames.2018.02.009>.

Dental measurements of different Proterotheriidae used for comparisons. * approximate; ** both correspond to the same specimen (casts), deposited in different collections; left/right; L, length; W, width.

Appendix A. List of specimens of Proterotheriidae from the Cerro Azul Formation, La Pampa Province

Proterotheriidae	Description	Locality	Department
<i>Diplasiotherium pampa</i>			
GHUNLPam 18601	left m3	Salinas Grandes de Hidalgo	Atreucó
GHUNLPam 18806	right m1 or m2	Salinas Grandes de Hidalgo	Atreucó
GHUNLPam 19826	right m2-m3 (heavily worn)	Caleufú	Rancul
GHUNLPam 5646	left m1 or m2	Laguna Chillhué	Guatraché
GHUNLPam 5621	left m3 (unworn)	Bajo Giuliani	Capital
<i>Eoauchenia primitiva</i>			
GHUNLPam 6379	right M2	El Guanaco	Capital
cf. <i>Brachytherium cuspidatum</i>			
GHUNLPam 168	right M1 or M2 (broken)	Salinas Grandes de Hidalgo	Atreucó
<i>Neobrachytherium</i> sp.			
GHUNLPam 22712	left M1 or M2 (unworn)	Telén	Loventué
GHUNLPam 8260	right crown of DP4?	Macachín	Atreucó
GHUNLPam 2277	left M1? (heavily worn)	Bajo Giuliani	Capital
Proterotheriidae indet.			
GHUNLPam 22676	right P1	Bajo Giuliani	Capital
GHUNLPam 21589	left P4-M2 and p4-m1 (broken)	Caleufú	Rancul
GHUNLPam 21536	M1? (heavily worn)	Caleufú	Rancul
GHUNLPam 14535	right M1?	Telén	Loventué
GHUNLPam 9569	right M3? (broken)	Cerro La Bota	Utracán
GHUNLPam 9040	left m1 or m2 (heavily worn)	Telén	Loventué
GHUNLPam 8864	left dp4	Telén	Loventué

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