



# Small-sized mesotheriines (Mesotheriidae, Notoungulata) from Northwestern Argentina: Systematic, chronological, and paleobiogeographic implications

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## ABSTRACT

The Neogene outcrops in Northwestern Argentina have provided many fossil mammals, particularly notoungulates. However, the fossil record of the early stages of the late Miocene is scarce. The present study describes two mesotheriine specimens from Las Arcas Formation (underlying the Chiquimil Formation dated at  $9.14 \pm 0.09$  Ma; Catamarca Province) and Saladillo Formation (dated at  $10 \pm 0.3$  Ma; Tucumán Province), represented by a left maxillary fragment with complete M1–3 and a right isolated M3, respectively. The main feature of these pieces is their small size, significantly smaller than that of the Miocene genera *Eutypotherium*, *Typotheriopsis*, and *Pseudotypotherium*, recorded in Argentina. In contrast, these mesotheriines are closer to specimens known from Bolivia. The comparative analysis allows us to refer the material herein described to *Plesiotypotherium* aff. *P. achirensis* and Mesotheriinae indet., with all cautions inherent to the incompleteness of the material. In turn, the paleobiogeographic implication of these new records is approached. A relationship concerning phylogenetic aspects, size, temporal range, and distribution pattern is proposed, taking into account the small size of the studied material in a temporal context of medium to large-sized mesotheriines.

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## 1. Introduction

During the Cenozoic South American isolation, an endemic fauna developed, many of its components sharing similarities with Holarctic taxa, which have been considered as cases of convergence (Scott, 1937; Patterson and Pascual, 1968; Simpson, 1980; Pascual and Ortiz Jaureguizar, 1990; Cerdeño and Bond, 1998; Flynn and Wyss, 1998; Croft, 2016). One of the most diverse and widely spread groups is the so-called South American native ungulates (Cifelli, 1985; Bond et al., 1995; Croft, 1999; Cassini et al., 2012; Bond, 1986). They include five orders that were joined as Meridiungulata (McKenna, 1975; McKenna and Bell, 1997); however, the monophyletic condition of this group was not supported by some phylogenetic analyses (Muizon and Cifelli, 2002; O'Leary et al.,

2013) whereas recent analyses based on molecular data recovered the monophyly (Buckley, 2015; Welker et al., 2015; Westbury et al., 2017). The native ungulates reached their greatest diversity throughout the Paleogene, declining progressively along Neogene, until their extinction at the late Pleistocene (Bond, 1986; Bond et al., 1995; López, 2007). Among them, the Order Notoungulata is the most diverse and successful clade (Cerdeño and Bond, 1998). Within Notoungulata, typotheriines developed very marked rodent-like adaptations (Scott, 1937; Bond et al., 1995; Cerdeño and Bond, 1998), especially remarkable in the Hegetotheriidae and Mesotheriidae.

Mesotheriidae is a clade of small to medium-sized notoungulates (see Croft et al., 2004; Macrini et al., 2013; Croft, 2016) that radiated from the early Oligocene (Tinguirirican South American Land Mammal Ages—SALMA) to the early–middle Pleistocene (Ensenadan SALMA) (Bond, 1986; Bond et al., 1995; Cerdeño and Montalvo, 2001; Croft et al., 2004, 2008; Billet et al., 2008; Cerdeño et al., 2012; Cerdeño, 2014; Shockey et al., 2016).

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Throughout the Neogene, this group is represented in several South American localities, becoming very abundant in the Miocene, displaying a high diversity in size and cranial morphology (e.g., Francis, 1965; Villarroel, 1974a, b; Reguero and Castro, 2004; Croft et al., 2004; Cerdeño, 2007; Cerdeño et al., 2012).

Several researchers postulated different relationship hypotheses for the taxa included in Mesotheriidae. Traditionally, two sub-families were recognized: Trachytheriinae and Mesotheriinae (Simpson, 1945). Nevertheless, recent phylogenetic analyses indicated that Trachytheriinae is a paraphyletic assemblage of basal mesotheriids, but supported the monophyly of Mesotheriinae (Cerdeño and Montalvo, 2001; Croft et al., 2004; Reguero and Castro, 2004; Billet et al., 2008; Billet, 2011; Shockey et al., 2016). The latter group is characterized by the loss of I2–P2/i3–p3 (but see Cerdeño and Schmidt, 2013 about specimens with P2/p3, and Gomes Rodrigues et al., 2017b) and the presence of persistently trilobed upper molars, among other features (see Francis, 1965; Villarroel, 1974a; Cerdeño and Montalvo, 2001; Flynn et al., 2005; Billet et al., 2008; Townsend and Croft, 2010; Cerdeño et al., 2012).

Authors mentioned that the Mesotheriinae clade is in great need of systematic revision (Cerdeño and Montalvo, 2001; Flynn et al., 2002; Croft et al., 2003; Townsend and Croft, 2010; Cerdeño, 2018). In this context, new studies are enlarging the knowledge of this group in different South American areas (e.g., Townsend and Croft, 2010; Cerdeño and Schmidt, 2013; Cerdeño et al., 2012).

Regarding Argentina, mesotheriines are mostly known from late Miocene to Pleistocene outcrops in the Northwest and Central (Cuyo and Pampean) regions (see Cerdeño, 2018 for a summary). Among the best studied genera, *Pseudotypotherium* Ameghino 1904, *Typotheriopsis* Cabrera and Kraglievich 1931, and *Mesotherium* Serres 1867 (Rovereto, 1914; Reig, 1957; Tonni, 1970; Cerdeño and Montalvo, 2001; Tauber, 2005; Tomassini and Montalvo, 2013) are abundant and characterized by being large-sized and phylogenetically more derivate mesotheriines (Croft et al., 2003; Billet et al., 2008). On the other hand, small-sized mesotheriines are only represented by scarce remains recovered from early Miocene levels in Mendoza, San Juan and Río Negro provinces (Cerdeño et al., 2006; Cerdeño, 2007; López et al., 2011; Paz et al., 2011). These forms present morphological and temporal similarities to other mid-latitudes mesotheriine faunas, such as those from Chile (Croft et al., 2004), and Bolivia (Villarroel, 1974a, b).

Mesotheriines from northwestern Argentina (NWA) are known mainly by *Pseudotypotherium* and *Typotheriopsis* (Moreno and Mercerat, 1891; Cabrera, 1937; Riggs and Patterson, 1939; Marshall and Patterson, 1981). Their remains come from upper late Miocene-early Pliocene levels from Santa María Valley and Puerta de Corral Quemado locality in Catamarca Province (Marshall and Patterson, 1981) (Fig. 1). Beyond these mentions, during several decades, the mesotheriine fauna from NWA received little attention until Powell and González (1997) and Nasif et al. (2010) communicated new interesting mesotheriines for the region, but these contributions did not present a detailed description or illustration of the specimens, which is the aim of this paper. We deepen the study of the remains from Cerro Pampa, Las Arcas Formation (Catamarca Province), and Cerro Castillo de Las Brujas, Saladillo Formation (Tucumán Province) (Fig. 1), and their taxonomic assignments provide new information about the mesotheriid diversity in NWA. Additionally, we present biogeographic and chronological approaches of the mesotheriines in South America.

## 2. Geographic and geological context

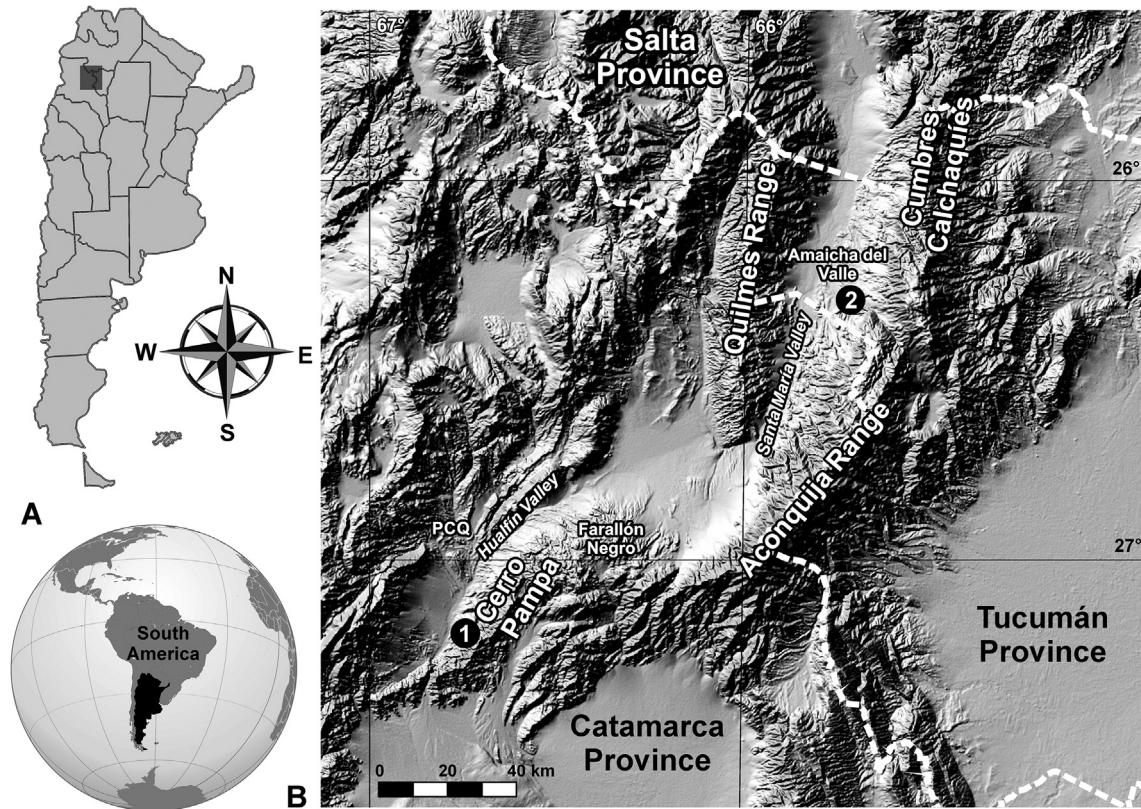
Neogene sediments in the Catamarca and Tucumán provinces (Northwest of Argentina) are very extensive and thick, and since

the end of the 19th century have provided a large amount of continental vertebrates remains, mainly mammals, birds and reptiles (Ameghino, 1906; Rovereto, 1914; Kraglievich, 1932, 1934; Riggs and Patterson, 1939; Peirano, 1943, 1946; Marshall and Patterson, 1981; Marshall et al., 1983; Nasif, 1988; Esteban and Abdala, 1993; Esteban and Nasif, 1996; Nasif et al., 1997, 2000; Powell et al., 1998; Herbst et al., 2000; Roger and Esteban, 2000; Reguero and Candela, 2011; Esteban et al., 2014; and many others). The outcrops are mainly located to the west of Calchaquí and Aconquija ranges and exposed in the intermontane tectonic valleys, originated in different basins or deposit centers (Fig. 1B; Georgieff et al., 2012, 2014). The deposition of these Neogene sediments began about 11 Ma ago and its sedimentary development would not have occurred synchronously nor had the same intensity of sediment accumulation in all areas (Bonini, 2014; Georgieff et al., 2014, 2016, 2017; Herrera and Esteban, 2017).

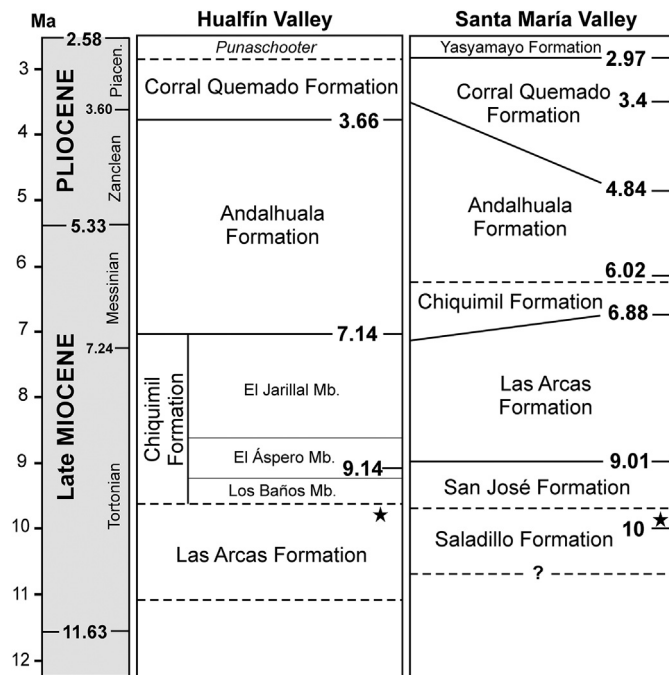
The mesotheriines described below come from two localities within the NWA Neogene sediments: Cerro Pampa and Cerro Castillo de Las Brujas (Fig. 1B). Cerro Pampa is located at the southern end of the Hualfín Valley, Catamarca Province. The fossiliferous levels at the western slope of the Cerro Pampa correspond to the Las Arcas Formation, which contacts in discordance with the igneous and metamorphic rocks of the basement. The Las Arcas Formation is part of the Santa María Group (Galván and Ruíz Huidobro, 1965; Bossi and Palma, 1982; Bossi et al., 1998, 1999, 2001; Georgieff et al., 2014) (Fig. 2). These levels are characterized by fine to medium sandstones, irregularly coherent, reddish brown with boulders and layers of sabulites that pass upward to massive siltstones. In the Hualfín Valley, Las Arcas Formation is located below the volcanic conglomerate El Áspero (middle member of the Chiquimil Formation) that, based on a radiometric  $^{40}\text{Ar}/^{39}\text{Ar}$  date of  $9.14 \pm 0.09$  Ma (Sasso, 1997), corresponds to the early late Miocene (Lower Tortonian; Fig. 2). Regarding the fossil record from Cerro Pampa, it is represented by fresh-water bivalves and ostracodes (Moyano, 2003), a xenarthran plate (Pampatheriinae; Segovia, 2004), footprints of Charadriiformes birds (Krapovickas et al., 2009; Nasif et al., 2010), and the mesotheriine PVL 6410 herein studied.

Cerro Castillo de Las Brujas is located about 6 km from Amaicha del Valle town, Tucumán Province (Fig. 1B). In this area, the fossiliferous levels are integrated in the Saladillo Formation (= Hiladas del Saladillo in Peirano, 1946) (Fig. 2). This unit is deposited on the crystalline basement and it emerges sporadically along the Santa María Valley and through a fault in the flanks of the Aconquija range. The Saladillo Formation consists of conglomerates, sandstones and fluvial red brick siltstones (Galván and Ruíz Huidobro, 1965) with thicknesses between 100 and 350 m (Georgieff et al., 2014). The unit was locally dated on tuff level, indicating a K/Ar age of  $10 \pm 0.3$  Ma (early late Miocene, Lower Tortonian; Fig. 2) (Powell and González, 1997; González et al., 2000; Brandoni et al., 2012). The fossil record for this unit includes the megatheriine xenarthran *Anisodontherium* sp. (Brandoni et al., 2012) and the isolated small mesotheriine PVL 7569 described here.

It should be noted that, although the Santa María Group (composed by: Las Arcas, Chiquimil, Andalhuala and Corral Quemado formations, Fig. 2) was defined in the homonymous valley (Galván and Ruíz Huidobro, 1965; Bossi and Palma, 1982), its formational units were extrapolated to the Hualfín Valley based on similar lithostratigraphic features (Riggs and Patterson, 1939; Bossi et al., 1987). In turn, chronological data were used to correlate both regions (Butler et al., 1984; Marshall et al., 1979; Strecker et al., 1989). Finally, Bossi et al. (1993, 1994) proposed the Santa María-Hualfín Basin as a unified sedimentary center. In contrast, recent studies propose that several mechanisms of deformation produced different tecto-sedimentary areas in relatively close regions



**Fig. 1.** Geographical position of fossiliferous localities mentioned in the text. **A**, study area in Tucumán and Catamarca provinces, Northwestern Argentina; **B**, regional orographic features and location of fossiliferous localities. **1**, Cerro Pampa locality; **2**, Castillo de Las Brujas locality. **Abbreviations:** PCQ, Puerta de Corral Quemado [Planned for page width].



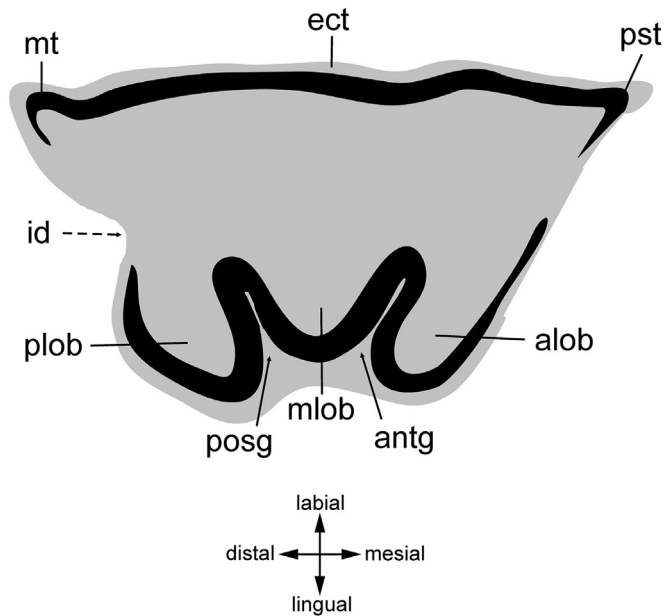
**Fig. 2.** Schematic synthesis of the lithostratigraphy and chronology of the late Miocene-Pliocene outcrops in Hualfín and Santa María valleys, Catamarca and Tucumán provinces, Northwestern Argentina. The stars indicate the stratigraphic place of the fossils herein studied and the dotted line, the undefined stratigraphic boundaries. [Planned for column width].

(Fig. 1B) and, therefore, the extrapolation of processes and the correlation of lithostratigraphic units must be performed with greater chronostratigraphic control (Georgieff et al., 2014, 2017). In this sense, the latest chronostratigraphic schemes (Georgieff et al., 2017; Herrera and Esteban, 2017), based on absolute (isotopic and paleomagnetic) data in the Hualfín Valley (Sasso, 1997; Latorre et al., 1997, in the Puerta de Corral Quemado locality; Fig. 1B) and the Santa María valley (Georgieff et al., 2014; Spagnuolo et al., 2015), show significant temporal discrepancies (Fig. 2). In this context, the validity of the Santa María-Hualfín Basin (Bossi et al., 1993, 1994) as a unified sedimentary center is under reconsideration, due to temporal differences in the evolution of sedimentary paleoenvironments and their paleoclimatic inferences (sensu Georgieff et al., 2017).

### 3. Material and methods

The studied remains are stored at the Colección Paleontología de Vertebrados Lillo of the Facultad de Ciencias Naturales e Instituto Miguel Lillo, Tucumán Province, Argentina. The anatomical study has been carried out mostly through direct comparisons, using type materials stored at the same collection and at Museo de La Plata and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires. Additionally, historical literature and papers focused on Mesotheriidae were consulted. Original photographs of *Microtypotherium choquecotense* (MNHN-Bol-V 003349) were kindly provided by G. Billet, H. Gomes Rodrigues, and B. Mamaní Quispe.

The anatomical terms (Fig. 3) follow classical papers (e.g., Francis, 1965; Villarroel, 1974a; Cerdeño and Montalvo, 2001) and more recent contributions (Billet et al., 2008; Townsend and Croft,



**Fig. 3.** Schematic upper molar morphology and terminology. **Abbreviations:** **alob**, anterior lobe; **antg**, anterior groove; **ect**, ectoloph; **id**, indentation or longitudinal posterior notch; **mlob**, median lobe; **mt**, metastyle; **plob**, posterior lobe; **posg**, posterior groove; **pst**, parastyle. [Planned for column width].

2010; Cerdeño and Schmidt, 2013). It is important to note that given the euhippodont condition of mesotheriid teeth, the occlusal relief is the product of a 'balanced wear' (Koenigswald, 2011) and the cusps are not really individually visualized even in little worn teeth; anyway, we use the terms of cusps for the areas corresponding to them (e.g., protocone, paracone) for descriptive and comparative purposes (Fig. 3).

Dental dimensions (length and width of molars) were used to evaluate size variation among mesotheriine specimens as absolute values (Table 1) and by means of bivariate plots. The index of imbrication was taken from Townsend and Croft (2010) and for *Plesiotypotherium* species was measured on digital images using the measure tool of tpsDig software (Rohlf, 2013).

**Table 1**

Upper tooth dimensions (in mm) of several mesotheriine species. ~ approximate values, \* basal portion of the crown. **A**, Chucal, Chile (Croft et al., 2004); **B**, Caragua, Chile (Flynn et al., 2005); **C**, Cerdas, Bolivia (Townsend and Croft, 2010; Croft et al., 2016); **D**, Choquecota, Bolivia (Villarroel, 1947b; Townsend and Croft, 2010); **E**, Achiri, Bolivia (Villarroel, 1974a); **F**, Casira, Bolivia (Cerdeño et al., 2012); **G**, Mendoza, Argentina (Cerdeño et al., 2006; Cerdeño, 2007); **H**, Buenos Aires, Argentina (Cabrera and Kraglievich, 1931); **I**, Catamarca, Argentina (this paper); **J**, Tucumán, Argentina (this paper); **K**, Chubut, Argentina (this paper).

Taxon	Specimen	M1		M2		M3	
		L	W	L	W	L	W
<i>Eotypotherium chico</i>	SGOPV 5157 (Holotype) <sup>A</sup>	9.5	6.4	9.6	6.5	9.8	5.8
<i>Altitypotherium chucalensis</i>	SGOPV 4100 (Holotype) <sup>A</sup>	10.4	8.6	12.9	8.5	13.1	7.6
<i>Altitypotherium paucidens</i>	SGOPV4038 (Holotype) <sup>A</sup>	12.5	8.6	12.8	8.8	14.1	~8.6
<i>Caraguatypotherium munoz</i>	SGOPV 4004 (Holotype) <sup>B</sup>	16.45	9.8	~15.67	~8.75	17.1	~9.45
' <i>Plesiotypotherium</i> ' minus	UF 133803 <sup>C</sup>	10.94	8.4	13.37	8.92	13.75	7.7
<i>Microtypotherium choquecotense</i>	GB-002 (Holotype) <sup>D</sup>	~12.1	~8.3	15.6	8.3	15.2	7.7
<i>Microtypotherium choquecotense</i>	UF 225698 <sup>C</sup>	—	—	—	—	14.8	8
<i>Plesiotypotherium achirensense</i>	MNHN-ACH 26 (Holotype) <sup>E</sup>	17	11	18.7	12.2	19.8	10.8
<i>Plesiotypotherium majus</i>	MNHN-ACH 27 (Holotype) <sup>E</sup>	20.8	12.8	21.8	12.9	24.6	12
<i>Plesiotypotherium casirensense</i>	MNHN-Bol-V 003724 (Holotype) <sup>F</sup>	18.2	11.4	18.9	12.3	21.2	12.05
cf. <i>Altitypotherium chucalensis</i>	MCNAM-PV 3648 <sup>G</sup>	—	—	>10.5	7.5	12.9	6.5
cf. <i>Altitypotherium chucalensis</i>	MLP 45-VII-10-2 <sup>G</sup>	—	—	—	—	13.3	6.5
<i>Typotheriopsis silveyrai</i>	MLP 36-XI-10-2 (Holotype) <sup>G</sup>	16	10.5	18	10.6	19	10.8
<i>Typotheriopsis chascoensis</i>	MLP 12-1666 (Holotype) <sup>H</sup>	18.3	10.4	20	10.9	21.8	11.2
<i>Plesiotypotherium aff. P. achirensense</i>	PVL 6140 <sup>I</sup>	9.9/9.2*	7.3/6.2*	11.5/9.7*	6.92/6.6*	12.8/13.03*	6.8/7.02*
Mesotheriinae indet.	PVL 7569 <sup>J</sup>	—	—	—	—	14.7	7.03
<i>Eutypotherium lehmannschei</i>	MLP 12-1701 <sup>K</sup>	—	—	17.2–16.5	10.2	17.6–17.5	9.8–9.5

### 3.1. Institutional abbreviations

GB, Servicio Geológico de Bolivia; MACN-A and PV, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional Ameghino and Colección Nacional Paleovertebrados, Ciudad Autónoma de Buenos Aires, Argentina; MCNAM, Museo de Ciencias Naturales y Antropológicas "J.C. Moyano", Mendoza, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MNHN-Bol, Museo Nacional de Historia Natural, La Paz, Bolivia; MNHN-ACH, Muséum national d'Histoire naturelle, Achiri Collection, Paris; PVL, Colección Paleontología Vertebrados Lillo, Tucumán, Argentina; SGOPV, Colección de Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; UF, Florida Museum of Natural History, Gainesville, USA.

### 3.2. Anatomical and dimensional abbreviations (text and table)

li, index of imbrication; L, length; M, upper molar; W, width.

## 4. Results

### SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903.

Suborder TYPOTHERIA Zittel, 1893.

Family MESOTHERIIDAE Alston, 1876.

Subfamily MESOTHERIINAE Simpson, 1945.

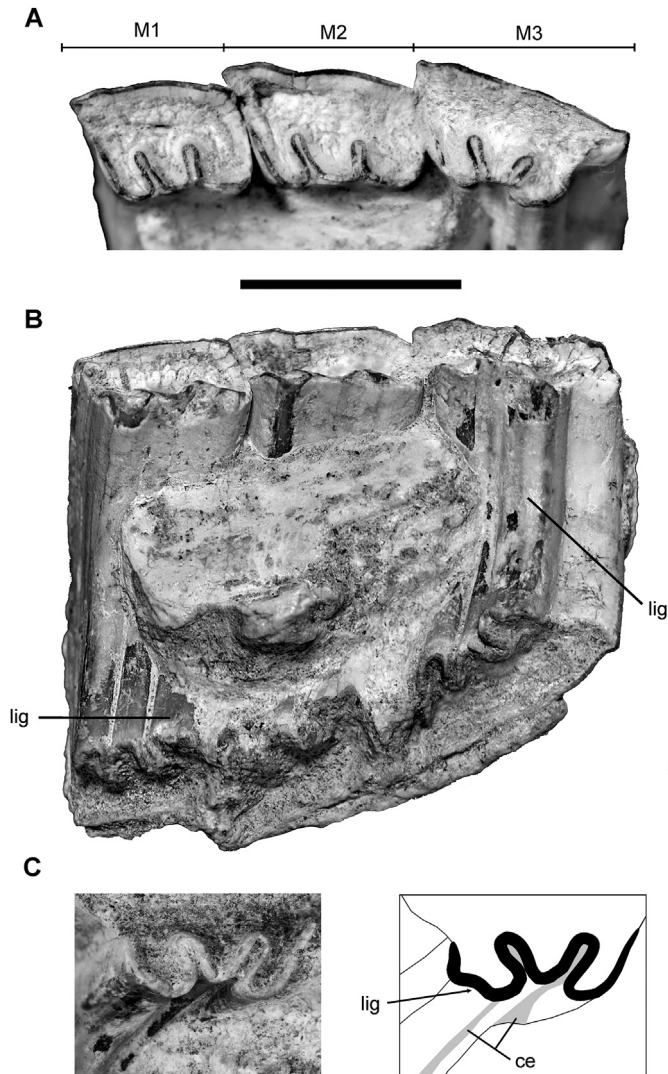
*Plesiotypotherium* aff. *P. achirensense* Villarroel, 1974a.

Fig. 4

**Referred material.** PVL 6410; left maxillary fragment with complete M1–3.

**Geographic and Stratigraphic Provenance.** Western slope of Cerro Pampa, Catamarca, Argentina (Fig. 1B). Las Arcas Formation; underlying the Chiquimil Formation dated at  $9.14 \pm 0.09$  Ma, early late Miocene (Fig. 2).

**Description.** The well-preserved trilobed molars of PVL 6410 are typical of mesotheriids (Fig. 4A). Tooth crowns are considerably high, showing no evidence of root formation (euhippodont teeth, sensu Mones, 1982) (Fig. 4B). The occlusal design of the molars is also observable at their bases (Fig. 4C), and dimensions (L and W) hardly vary throughout the crown (Table 1), which allows inferring that PVL 6410 corresponds to an adult individual. All molars lack



**Fig. 4.** *Plesiotypotherium* aff. *P. achirens*, PVL 6410, upper left series M1–3: **A**, occlusal view; **B**, detail of the lingual side; **C**, detail and scheme of the opposite end of M3, showing the smooth lingual groove on the posterior lobe. **Abbreviations:** ce, cement; lig, lingual groove. [Planned for page width].

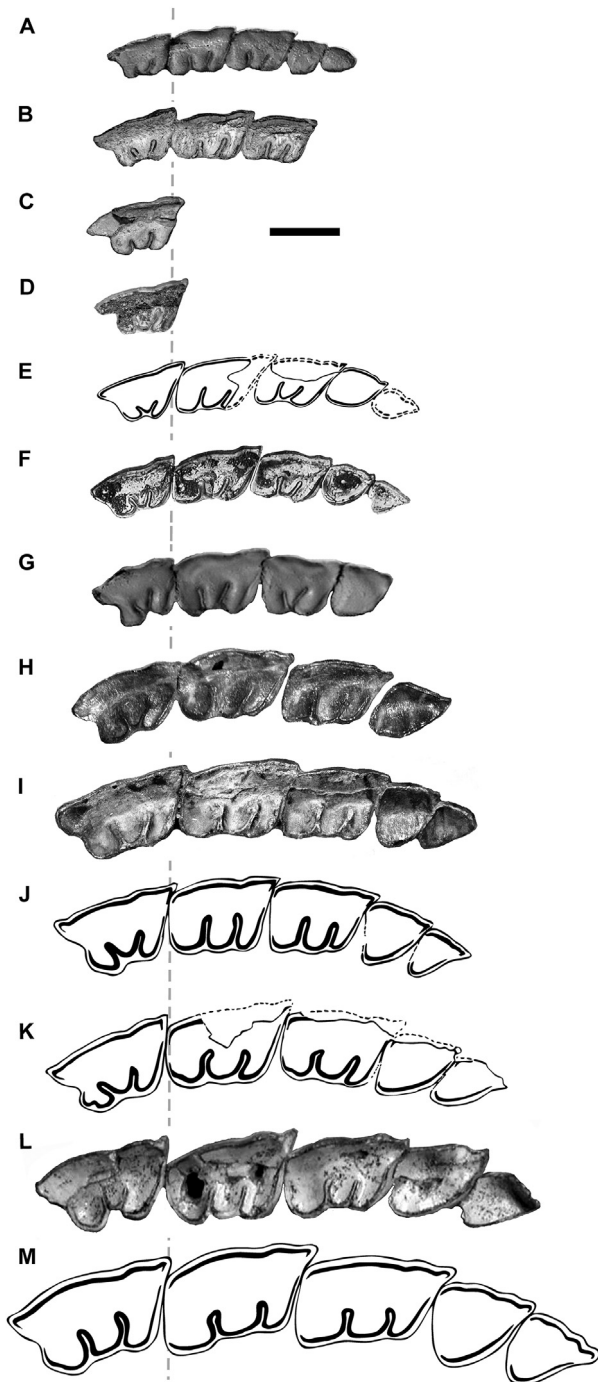
fosses, and a layer of cement covers the walls and fills the lingual grooves of each tooth. As usual for euhypsodont notoungulates, the upper molars are strongly curved medially in the coronal plane. The molar size increases from M1 to M3 (Table 1). There is a slight imbrication between M2 and M1 ( $li = 1.15$ ; following Flynn et al., 2005), similar to *Eutyptotherium lehmannitschei* Roth, 1902 (MLP 12-1701;  $li = 1.1$ ), '*Plesiotypotherium*' minus Villarroel 1978 (UF 133803;  $li = 1.12$ ), *Plesiotypotherium achirens* ( $li = 1.1–1.18$ ; measurements taken from Villarroel, 1974a: Fig. 9A–B), *Altiptotherium chucalensis* Croft et al. 2004 (SGOPV 4100;  $li = 1.12$ ) and *Eutyptotherium chico* Croft et al. 2004 (SGOPV 5157;  $li = 1.12$ ), and lesser than in *Plesiotypotherium majus* ( $li = 1.26$ ; measurements taken from Villarroel, 1974a: Fig. 9C), *Eutyptotherium superans* Ameghino 1904 (MACN 11079;  $li = 1.2$ ) and the species of *Tyotheriopsis* ( $li = 1.16–1.36$ ), *Pseudotyptotherium* ( $li = 1.46–1.8$ ), and *Mesotherium* ( $li = 1.3–1.83$ ) (see Townsend and Croft, 2010: table 4).

The M1 is not elongate ( $L/W = 1.35$ ), similar to the condition in '*Plesiotypotherium*' minus from Bolivia (Townsend and Croft, 2010) ( $L/W = 1.35$ ) and relatively longer than in *Altiptotherium chucalensis* from Chucal, Chile ( $L/W = 1.20$ ), which are the taxa with the

relatively shortest M1 among mesotheriines. In PVL 6410, M1 presents a rectangular outline (Fig. 4A), similar to the M1 of '*Plesiotypotherium*' minus from Cerdas (Townsend and Croft, 2010). The mesial face is labially inclined forward and the contact region with the last premolar can be observed (Fig. 4A and B). In the labial side, the enamel covers the whole surface including the mesial parastyle corner. Moreover, the paracone fold is weakly defined by a sulcus, which results in a hardly undulated, slightly convex ectoloph (Fig. 4A), coinciding with the outline observed in the M1 of the species of *Plesiotypotherium* (Fig. 5J–M), *Eutyptotherium chico* (Fig. 5A), and *Altiptotherium chucalensis* (Fig. 5G). The distal face of M1 is almost straight, barely convex, with a large area in contact with the M2, and without enamel. The lingual grooves of M1 are subparallel, a little convergent lingually, which render the median lobe subtriangular; this lobe has a wide, straight lingual exposure, and almost reaches the same lingual level as the other two lobes (Fig. 4A). The lingual surface of the anterior and posterior lobes is rounded. The posterior lobe is wider (anteroposteriorly) than the others and there is an incipient lingual groove, more prominent on its opposite end (Fig. 4B), similar to the holotype of *Plesiotypotherium achirens* (Fig. 5K), *Plesiotypotherium casirens* Cerdeño et al. 2012, and *Microtyptotherium choquecotense* Villarroel 1974b (Fig. 5E; see also Gomes Rodrigues et al., 2017a: Fig. 1B, MNHN-Bol-V 003349). The lingual groove pattern and the median lobe are similar to *Plesiotypotherium achirens* (Fig. 5J and K), '*P*' minus (Fig. 5F), *P. majus* Villarroel 1974a (Fig. 5M), and *Eutyptotherium chico* (Fig. 5A). In turn, it is markedly different from *Altiptotherium chucalensis* (Fig. 5G), which shows convergent lingual grooves and an enclosed median lobe.

The M2 of PVL 6410 is larger than M1 (Table 1; Fig. 4A), the median lobe is wider (anteroposteriorly), and the ectoloph is more undulated due to a marked concavity behind the paracone fold. Moreover, the posterior lobe shows an undulate lingual surface, less evident than in M1. This morphology resembles that observed in M2 of the holotype of *Plesiotypotherium achirens* (Fig. 5K) and is less developed than in the specimen MNHN-Bol-V 003349 of *Microtyptotherium choquecotense* (personal observation; Gomes Rodrigues et al., 2017a: Fig. 1B); instead, this groove is not present in other specimens of *P. achirens* (Fig. 5J) and the holotype of *M. choquecotense* (Fig. 5E).

The M3 presents a trapezoidal outline due to the posterior projection of the ectoloph and the lingual convergence of anterior and posterior lobes; 45% of M3 mesial surface contacts with M2. The ectoloph is longer and straighter, with the parastyle slightly more labially directed than in M1–2, and the metastyle strongly projected backward (Table 1; Fig. 4A), similar to *Plesiotypotherium achirens* (Fig. 5J, K), *P. majus* (Fig. 5M), '*P*' minus UF 133803 (Fig. 5F), and *Altiptotherium chucalensis* (Fig. 5G). Lingually, the grooves are convergent, similar to *P. achirens* (Fig. 5J), '*P*' minus UF 133803 (Fig. 5F), and *M. choquecotense* (Fig. 5D and E), and less than in *A. chucalensis* (Fig. 5G). In contrast, *Plesiotypotherium casirens* (Fig. 5L), *P. majus* and *Eutyptotherium chico* (Fig. 5A) present lingual grooves nearly parallel. The median lobe is triangular and a little shorter than the other two lobes, with less lingual exposure than M1–2; in turn, it is notably greater than in *Altiptotherium chucalensis* (Fig. 5G) and *M. choquecotense* (Fig. 4E; MNHN-Bol-V 003349, personal obs. and Gomes Rodrigues et al., 2017a: Fig. 1B). The posterior lobe shows a smooth lingual groove, better observed lingually than occlusally and on the opposite end (Fig. 4B–C). This groove is observed in *P. achirens*, *M. choquecotense* (MNHN-Bol-V 003349, personal obs., neither in UF 225698 nor in the holotype—Fig. 5D and E, respectively), and partially in *P. majus*, with different degree of development (*P. achirens* > MNHN-Bol-V 003349 > *P. majus* > PVL 6410). Moreover, the distal wall shows a well-marked notch or indentation (sensu Croft et al., 2004), similar



**Fig. 5.** Compared occlusal views of upper molars of mesotheriines, ordered by size. **A**, *Eotypotherium chico*, SGOPV 5157 (holotype cast; modified from Cerdeño, 2007); **B**, *Plesiotypotherium* aff. *P. achirens*, PVL 6410; **C**, Mesotheriinae indet., PVL 7569; **D**, *Microtypotherium choquecotense*, UF 225698; **E**, *Microtypotherium choquecotense*, GB 002 (holotype; from Villarroel, 1974b); **F**, '*Plesiotypotherium*' minus, UF 133803 (from Townsend and Croft, 2010); **G**, *Altitypotherium chucalensis*, SGOPV 4100 (holotype cast; modified from Cerdeño, 2007); **H**, *Eutypotherium lehmannitschei*, MLP 12-1701 (holotype); **I**, *Eutypotherium superans*, MACN-A 1079; **J**, *Plesiotypotherium achirens* (modified from Villarroel, 1974a); **K**, *Plesiotypotherium achirens*, MNHN-ACH 26 (holotype modified from Villarroel, 1974a); **L**, *Plesiotypotherium casirens*, MNHN-Bol-V 003724 (holotype; modified from Cerdeño et al., 2012); **M**, *Plesiotypotherium majus*, MNHN-ACH 27 (holotype from Villarroel, 1974a). Dotted line indicates the contact between M2–3. Scale bar equals 1 cm [Planned for column width].

to *Plesiotypotherium achirens* (Fig. 5J and K) and *Altitypotherium chucalensis* (Fig. 5G).

**Comments.** The combination of features exhibited by PVL 6410 and the fact of having only one specimen from the Las Arcas Formation prevent an accurate taxonomic assignment. However, its morphology is closer to the species of *Plesiotypotherium* in the following characters: M1 with L/W ratio = 1.35 and rectangular outline; M1–2 lingual grooves subparallel and median lobe completely exposed; M3 ectoloph slightly undulated; parastyle and metastyle pointing labially; M3 with deep posterior notch, lingual grooves convergent, but not enclosing the median lobe, and a lingual groove in the posterior lobe (Fig. 5); conversely, there are differences among them related to the tooth size (see above). In turn, it differs from *Eutypotherium*, *Typotheriopsis*, *Pseudotypotherium*, and *Mesotherium* in a smaller tooth size and lower imbrication index, and a triangular median lobe of M3, with straight lingual edge. Moreover, PVL 6410 differs from *Eotypotherium* in the slightly larger teeth and the presence of a deep posterior notch in M3, and from *Altitypotherium* and *Microtypotherium* in the greater exposure of the median lobe of M1–3. Additionally, PVL 6410 presents a smooth lingual groove on the posterior lobe of molars, which has been described in different taxa: the M3 of *Altitypotherium paucidens*, *P. achirens*, *P. majus*, *Microtypotherium* (MNHN-Bol-V 003349), and the M1 of *Plesiotypotherium casirens*, but is also present in the holotype of "*Pseudotypotherium carhuense*", as noticed by Croft et al. (2004: p. 17), which corresponds to a very young individual, but with permanent dentition (Cerdeño and Schmidt, 2013: Fig. 2A; the groove can be observed in the molars and even in P4).

Focusing in *Plesiotypotherium*, there are three recognized species, all of them from Bolivian localities: *P. achirens* and *P. majus* from Achiri, and *P. casirens* from Casira. It is important to note that the species '*Plesiotypotherium*' minus firstly assigned to this genus (i.e., Oiso, 1991; MacFadden et al., 1995) was recently recognized as a still unnamed new genus (i.e., Townsend and Croft, 2010; Croft et al., 2016).

Morphologically, the species of *Plesiotypotherium* share several features of cheek teeth, particularly the molar outline. The principal differences among them are: the length of M3 median lobe; the development of the posterior notch; the degree of development of lingual groove in the posterior lobe of molars (Fig. 5H, K, L, M); and the tooth size (Table 1). Firstly, the M3s of *P. achirens* (Fig. 5J, K) and *P. casirens* (Fig. 5L) show a triangular median lobe, different from *P. majus* (Fig. 5M), which presents a rectangular median lobe, with the lingual end straighter and slightly curved posteriorly. Moreover, despite *P. achirens* and *P. casirens* present similar median lobe, it is markedly shorter in the latter than in *P. achirens* and PVL 6410 (Fig. 5B, J, K, L). The development of the posterior notch is strong in *P. achirens*, *P. majus* and PVL 6410, in contrast with the smooth concavity of *P. casirens* (Fig. 5B, J, K, L).

Concerning the lingual groove located in the posterior lobe of molars, the holotype of *Plesiotypotherium achirens* (MNHN-ACH 26; Fig. 5K) shows a marked groove in the M3, while it is absent in other specimens of the sample referred to this species (Fig. 5J; Villarroel, 1974a: Fig. 9A). Moreover, this groove is not clearly present in the M1 and M2 of *P. achirens*, but there is an undulation in the same area (Cerdeño et al., 2012, Fig. 7C; Fig. 5K), similar to PVL 6410. *Plesiotypotherium majus* only has the lingual groove in the posterior lobe of M3, which is less developed than in *P. achirens* (Fig. 5J, K, M). In turn, *P. casirens* shows a small and marked lingual groove in the posterior lobe of M1 and none in M2–M3 (Cerdeño et al., 2012), different from *P. achirens*, *P. majus* and PVL 6410 (Fig. 5B, J, K, L, M). In PVL 6410, a smooth lingual groove is present in the 3 M, better observed in lingual than in occlusal view on the M3 (Fig. 3C). According to these data, the mentioned structure seems to be a common characteristic in *Plesiotypotherium*, with certain degree of variability related to its location in one or more molars. At

the same time, as we have noted above, this structure is also observed in the 3 M of the early and middle Miocene *Altiptotherium paucidens* (Croft et al., 2004) and *Microtyptotherium choquecotense* (MNHN-Bol-V 003349), with different development, but also in young individuals of late Miocene taxa (“*P. carhuense*”). Croft et al. (2004) indicated that this groove is a feature widespread among mesotheriids, based on its presence not only in mesotheriines but also in a juvenile specimen of *Trachytherus*, which would probably vary during ontogeny. The commented specimens showing this feature display different conditions both in development and location (one or more teeth) of the groove, which likely correspond to both ontogenetic and individual variations. At the same time, however, it could also represent an ancestral trait if considering its presence in Oligocene trachytheriines and basal mesotheriines such as *Altiptotherium* and *Microtyptotherium*. In any case, greater samples are needed to check these variations and to evaluate the phylogenetic value of this character.

**Tooth size.** One of the notable features of PVL 6410 is the small size of teeth, in contrast to the so far known mesotheriines from NWA (i.e., *Typtotheriopsis* and *Pseudotyptotherium*). In turn, it differs from the species of *Plesiotyptotherium*, with which PVL 6410 shares morphological features (Table 1; Fig. 6). Different authors give a great importance to the size as an evolutionary trait, being the small size a phylogenetically basal condition among mesotheriids (Croft et al., 2004). In this sense, the performed bivariate analysis, which includes a representative range of the size diversity among known mesotheriines, deepens the small-sized condition of PVL 6410, as it is closer to the smallest known mesotheriine, *Eotyptotherium chico*.

Regarding the M1, the bivariate analysis (Fig. 6A) shows that PVL 6410 is located between *Eotyptotherium chico* and a defined group composed of *Altiptotherium*, *Microtyptotherium* and ‘*Plesiotyptotherium*’ minus. The larger M1 belong to *Caragatyptotherium*, *Plesiotyptotherium achirensense*, *P. casirensense*, *P. majus* (the largest one) and *Typtotheriopsis* (Fig. 6A). The distribution of the species according to the L/W ratio of M2 (Fig. 6B) is similar to that obtained for M1, but in this case *Caragatyptotherium* results smaller, being closer to *Altiptotherium*, *Microtyptotherium* and ‘*Plesiotyptotherium*’ minus. Additionally, *Eutyptotherium lehmannitschei*, not included in the M1 plot, is intermediate between that group and *Typtotheriopsis*. Finally, the M3 plot (Fig. 6C) shows a more continuous distribution from small to large forms, representing the same pattern than the M1–2 plots, but without defined groups.

In summary, PVL 6410 groups with small mesotheriines, mainly *Altiptotherium* and *Microtyptotherium*, and is clearly smaller than *Plesiotyptotherium* (Table 1). This fact is discordant with the morphological study and the chronological data, which place PVL

6410 closer to *Plesiotyptotherium*.

Studies that analyzed a numerous small-sized mesotheriine sample in other localities (Cerdas, Nazareno, and Quebrada Honda from Bolivia) indicated the importance of considering each individual specimen as a member of a dynamic population (Townsend and Croft, 2010). In this context and taking into account the background around the mesotheriine taxonomy, we refer PVL 6410 to *Plesiotyptotherium* aff. *P. achirensense*, according to the morphological and chronological similarities and the scarce material still recorded in the NWA. Nevertheless, we cannot discard that PVL 6410 could represent a new small species of *Plesiotyptotherium*. In any case, it represents the first record of the genus *Plesiotyptotherium* in Argentina.

Mesotheriinae indet.

Figs. 5C and 7

**Referred material.** PVL 7569; right isolated M3.

**Geographic and Stratigraphic provenance.** Cerro Castillo de Las Brujas, Tucumán Province, Argentina (Fig. 1B). Saladillo Formation;  $10 \pm 0.3$  Ma, early late Miocene (Fig. 2).

**Description.** PVL 7569 (Fig. 7A) lacks the occlusal distolabial region. Given the degree of wear, it would correspond to an adult individual. This molar is barely larger than the M3 of PVL 6410 (Table 1). The ectoloph is convex with an undulate surface. Labially, the parastyle points mesially, not labially as PVL 6410 (Fig. 5B and C), and the metastyle curves linguallly similar to *Microtyptotherium choquecotense* GB 002 (Villarroel, 1974b) and UF 225698 (Townsend and Croft, 2010; Fig. 8B) (Fig. 5E, D). Linguallly, the grooves are less convergent (Figs. 5C and 7A) than in PVL 6410 (Fig. 4A), and similar to *M. choquecotense* UF 225698 (Fig. 5D) and *Plesiotyptotherium majus* (Fig. 5M). Moreover, the posterior lingual groove is shorter than the anterior one, it is oriented perpendicular to the major axis of the tooth series (Fig. 7A), similar to the condition in *E. chico* (Fig. 5A), *M. choquecotense* UF 225698 (Fig. 5D), *A. chucalensis* SCOPV 4100 (Fig. 5G), *Eutyptotherium lehmannitschei* MLP 12-1701 (Fig. 5H), and *E. superans* MACN-A 1079 (Fig. 5I). In contrast with the M3 of PVL 6410, the median lobe is less triangular, with more exposed surface, but seen by the opposite end it becomes clearly shorter than the other two lobes (Fig. 7A, C); the occlusal view of this lobe is similar to that in *M. choquecotense* UF 225698 (Fig. 5D), *E. chico* (Fig. 5A), and *Plesiotyptotherium majus* (Fig. 5M), but it differs from the holotype of *M. choquecotense* (GB 002, Fig. 5E). The third lobe of PVL 7569 bears a lingual groove, similar to PVL 6410, which is more evident in lingual than in occlusal view (Fig. 7B and C). Further, a cement layer is restricted to the grooves of the tooth, with no remnants on the ectoloph and lingual wall (Fig. 7B). On the

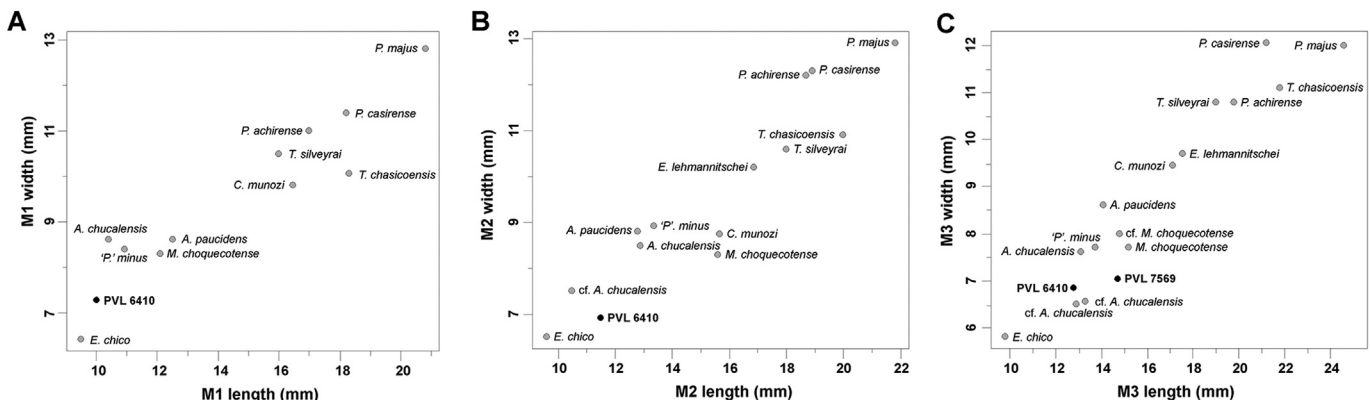
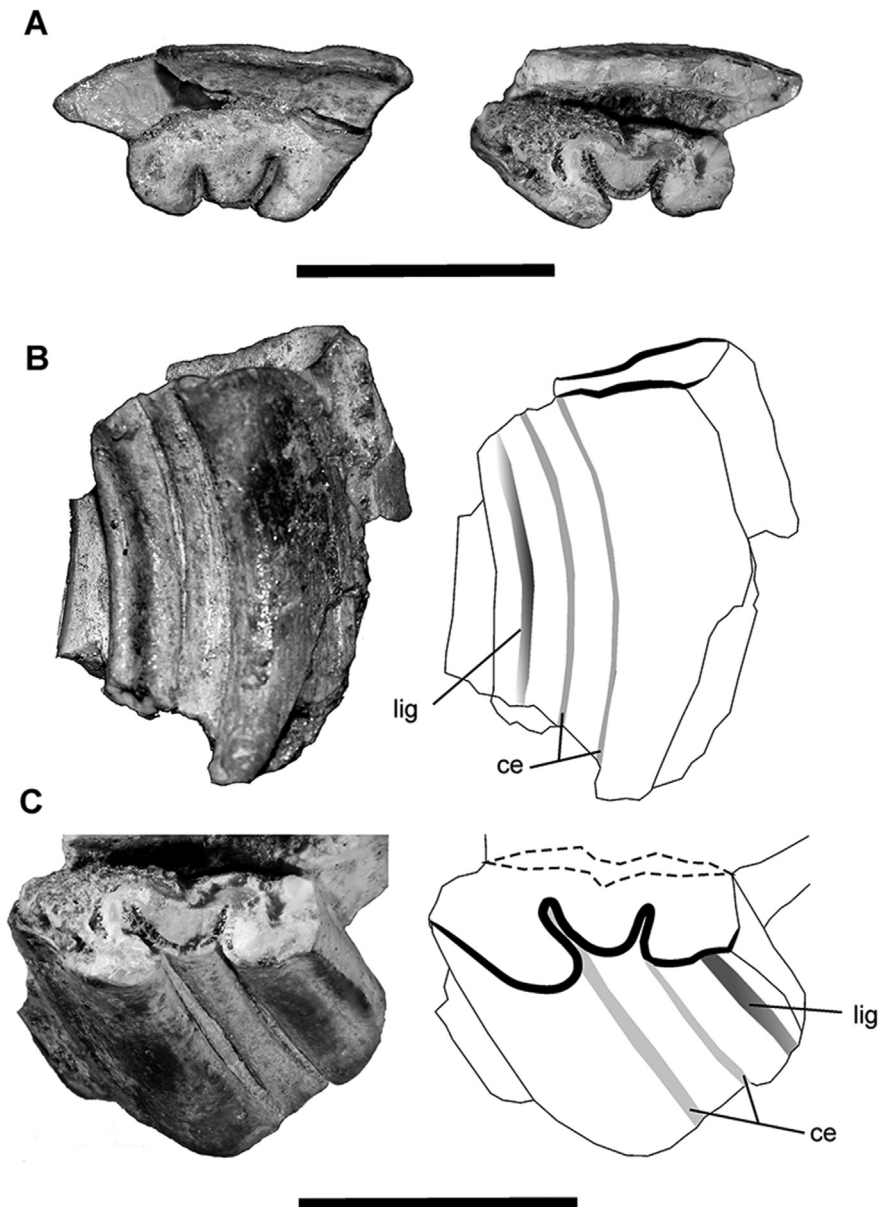


Fig. 6. Bivariate plots of upper molars of compared mesotheriines: A, M1; B, M2; C, M3. [Planned for page width].



**Fig. 7.** Mesotheriinae indet., PVL 7569: **A**, upper M3, in occlusal view (left) and opposite end of the crown (right); **B**, upper M3 in anterolingual view, and corresponding scheme; **C**, detail of the intralveolar portion of the crown of M3. **Abbreviations:** **lig**, lingual groove; **ce**, cement. Scale bar equals 1 cm [Planned for column width].

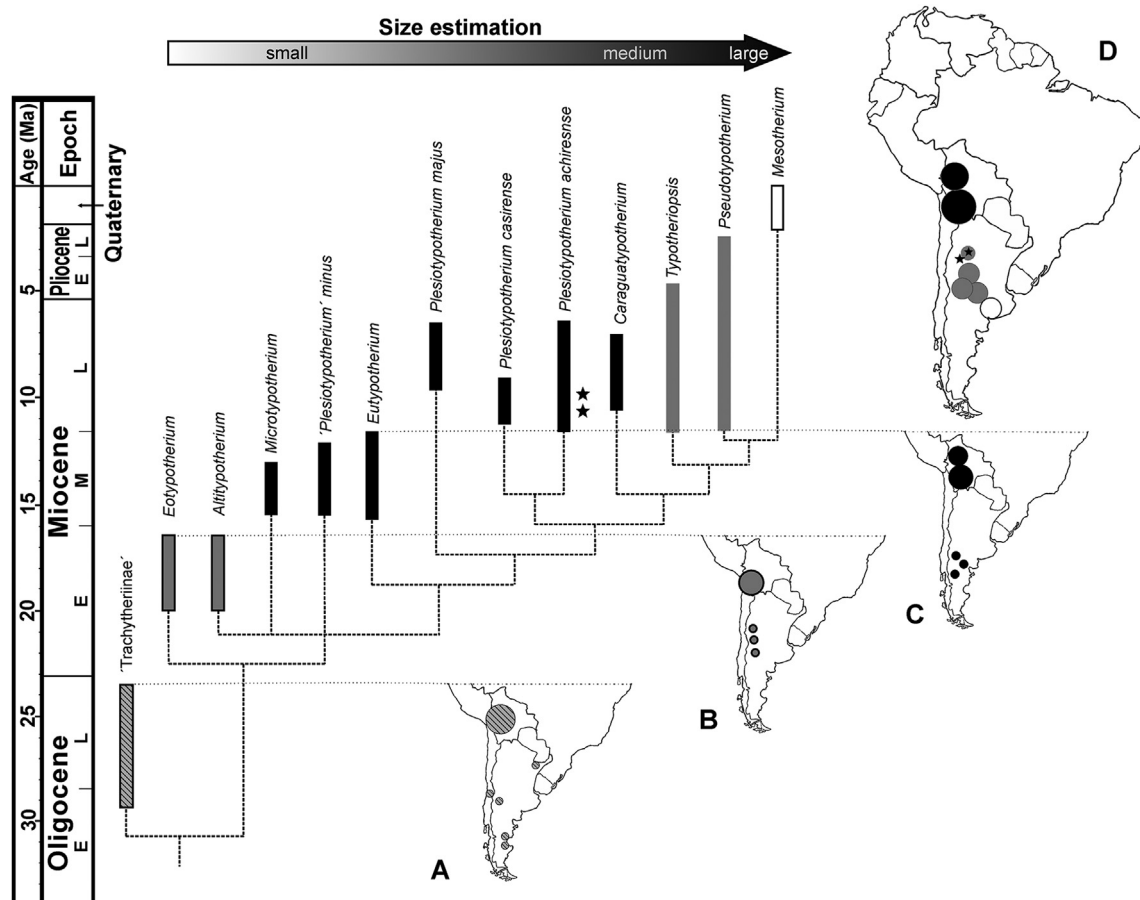
distal face, the posterior notch (Fig. 5C) is more conspicuous than in PVL 6410 (Fig. 5B), due to the more acute metastyle, and similar to *Altiypotherium chucalensis* (Fig. 5G) and *Plesiotypotherium achirense* (Fig. 5J and K).

**Comments.** The scarcity of the material recovered from the Saladillo Formation makes it difficult to assign it to a specific taxon within Mesotheriinae. Regarding PVL 6410, the main differences are related to the curvature of the parastyle and metastyle, which are pointing lingually; as a result, the M3 posterior notch is more acute in PVL 7569. Additionally, the median lobe of PVL 7569 presents its lingual surface more exposed than PVL 6410 (Fig. 5B and C). This varies in the opposite end of the tooth, where the lingual grooves are more convergent, reducing the median lobe exposure, similar to the occlusal view in PVL 6410 (Figs. 4A and 5B) and *Plesiotypotherium achirense* (Fig. 5J and K). The discrepancies among PVL 7569 and PVL 6410 could be related to different ontogenetic stages or intraspecific variability. In this sense, according to the

shared features and the chronologic similarities, the possibility that they would represent the same taxon should not be dismissed. In turn, PVL 7569 differs from the known genera of NWA (*Pseudotypotherium* and *Typotheriopsis*) and other Argentinean mesotheriines (*Eutyptotherium*) in small size, posterior lobe of M3 with a slight lingual groove, and parastyle and metastyle pointed to the lingual side.

On other hand, several of these features observed in PVL 7569 are present in Bolivian and Chilean mesotheriines (i.e., *Microtypotherium*, *Eotyptotherium*, and *Altiypotherium*), such as: ectoloph convex with undulate surface; lingual grooves convergent with the posterior fold shorter than the anterior one; median lobe well exposed; and M3 posterior lobe with a slight lingual groove. Despite that these morphological similarities are suggestive, the chronological discrepancies with these taxa hinder a direct assignment. Accordingly, we refer PVL 7569 to Mesotheriinae indet. until more materials are recovered and allow a better





**Fig. 8.** Phylogenetic relationship (modified from Cerdeño et al., 2012), size estimation, and temporal and geographical ranges of Mesotheriidae. **A**, late Oligocene 'Trachytheriinae'; **B**, early Miocene Mesotheriinae; **C**, middle Miocene Mesotheriinae; **D**, late Miocene to Pleistocene Mesotheriinae. The arrow at the top indicates the size trend (estimated from tooth size) of mesotheriids. The color of bars and circles indicates different groups of taxa. The size of the circles is related to the abundance and diversity of the taxa in their distribution areas. The stars indicate the location of the new records described in this paper. [Planned for page width].

characterization.

**Tooth size.** Undoubtedly, the small size of PVL 7569, as for PVL 6410, becomes an interesting feature (Table 1). PVL 7569 is included in the bivariate plot of M3 (Fig. 6C), being close to, but relatively longer than, PVL 6410, and forming part of the group composed of *Altiypotherium*, *Microtypotherium* and '*Plesiotypotherium*' minus. Within this group, both PVL 7569 and PVL 6410 are closer to the specimens from Mendoza referred to cf. *Altiypotherium*. However, as said above, the morphological and chronological differences with these small taxa preclude an accurate taxonomic assignment.

## 5. Chronological and paleobiogeographic implications

Most of the record of South American Native Ungulates comes from high latitudes (i.e., Patagonia, South of Argentina) (Alcalá and Morales, 1995; Bond et al., 1995; Croft et al., 2003). However, in the last decades, new findings in different localities outside Patagonia improved the knowledge of the evolution and distribution of many mammal clades, particularly Mesotheriidae (Croft et al., 2003, 2004; Flynn et al., 2005; Billet et al., 2008; Townsend and Croft, 2010; Cerdeño et al., 2012; Shockey et al., 2016; Cerdeño, 2018). Firstly, in the late Oligocene, basal mesotheriids ('Trachytheriinae') occupied a large part of the Andean region, from Bolivia (Lacayani, Río Pluma, and Salla; Billet et al., 2008; Shockey et al., 2016) to Patagonia Argentina (Cabeza Blanca and La Flecha; Reguero, 1999), including isolated specimens recorded in Mendoza Province

(Quebrada Fiera; Cerdeño, 2014) and the Argentinean 'Mesopotamia' (Curuzú-Cuatiá, Corrientes Province; Reguero and Castro, 2004; Billet et al., 2008) (Fig. 8A). This pattern bears important paleobiogeographic implications for the history of the Mesotheriidae clade, involving complex spatiotemporal events still under analysis (Shockey et al., 2016).

From early Miocene on, Mesotheriinae replace trachytheriines, and are first represented by small-sized species (see Fig. 6) with a restricted biochron. They were diverse and widely distributed from mid to high latitudes in the southern cone of South America (Bolivia, Chile, and Argentina) during the early and middle Miocene. For this lapse, three species are known in the Chucal Fauna, Chile (Fig. 8B): *Altiypotherium paucidens*, *A. chucalensis*, and *Eotyypotherium chico* from early Miocene ( $21.7 \pm 0.8$  Ma to  $17.4 \pm 0.4$  Ma, Croft et al., 2004, 2007; Riquelme, 1998; Bond and García, 2002). In Argentina, some specimens have been related to *Altiypotherium*: one from the Mariño Formation, Mendoza Province (Cerdeño et al., 2006; Cerdeño, 2007), and another from the Chinchas Formation, San Juan Province (López et al., 2011); in both cases the faunal assemblage corresponds to the Santacrucian SALMA. In addition, an older, undetermined mesotheriine comes from the Colhuehuapian Chichinales Formation, Río Negro Province (Paz et al., 2011) (Fig. 8B).

Small mesotheriines are also known in middle Miocene (Fig. 8C). The Bolivian record includes *Microtypotherium choquecotense* (16.5–15.3 Ma, Villarroel, 1974b; MacFadden et al., 1995; Townsend

and Croft, 2010) from Choquecota and *Plesiotypotherium* minus (11.96 ± 0.11 Ma to 12.83 ± 0.11 Ma, MacFadden et al., 1995; Croft et al., 2009, 2016; Townsend and Croft, 2010) from Cerdas and Quebrada Honda (Fig. 8C). Instead, in Argentina medium-sized species are recorded in middle Miocene, *Eutyptotherium lehmannnitschei* and *E. superans*, known from Friasian and Colloncuran SALMAs in Chubut, Río Negro and Neuquén provinces, with scarce but complete materials (Roth, 1899; Roth, 1902; Ameghino, 1904; Rovereto, 1914; Cabrera and Kglievich, 1931) (Fig. 8C).

According to recent phylogenetic analysis (i.e., Croft et al., 2004; Townsend and Croft, 2010; Cerdeño et al., 2012, Fig. 8) and the mesotheriid distributional patterns, the presence of the oldest and basal mesotheriid taxa, added to their great abundance in the Altiplano region (western Peru, Bolivia, and northern Chile), in contrast to the very isolated and low diversity recorded in Argentina during late early Miocene and middle Miocene, several authors (Croft et al., 2003, 2004; Shockey et al., 2016) consider that the mid-latitudes and intermediate altitudes might have been a center of diversification for mesotheriines.

By the late Miocene, all mesotheriines so far known were medium to large-sized both in Chile, Bolivia and Argentina: *Caragatypotherium munozi* from the Precordillera of northernmost Chile (Bargo and Reguero, 1989; Flynn et al., 2005; Montoya-Sanhueza et al., 2017); several species of *Plesiotypotherium* in southern Bolivia; and *Typotheriopsis* and *Pseudotypotherium* reaching a wide geographic distribution in northwest, west and Pampean region of Argentina (Catamarca, Tucumán, La Rioja, Mendoza, San Luis and La Pampa provinces), but not recorded in Patagonian areas (Fig. 8D). It is in this period when the small mesotheriines from NWA occur, which implies a break in the general trend in mesotheriid size (Fig. 8).

Finally, during the Pleistocene, the genus *Mesotherium*, which includes the largest-sized mesotheriines (Francis, 1965), is recorded in the Pampean region. It is particularly abundant in the Atlantic coast (Buenos Aires Province) where the Pleistocene outcrops are extensive (Fig. 8D).

The presence of these small mesotheriines in the NWA region, in a period of medium to large-sized mesotheriid dominance in South America, represents the persistence of a mesotheriid morphotype that was well represented in early/middle Miocene. Changes in the distribution range of mesotheriines, as well as their time of greater diversification and then their possible extinction, may be related to climatic environmental changes that occurred in their habitat. In the lapse when small-sized mesotheriines are more extended geographically (Fig. 8B), between 20 and 16 Ma, there was a climatic optimum with a period of warm and humid climate (Zachos et al., 2001; Ortiz Jaureguizar and Cladera, 2006; Goin et al., 2012; Cione et al., 2015). At this time, other groups of mammals present similar changes in their biogeographic distribution related to this climatic event and subsequent environmental changes (e.g., caviomorph rodent groups, see Pérez and Pol, 2012; Vucetich et al., 2015; hegetotheriid notoungulates, see Seoane et al., 2017). Moreover, the orogenic events, as the rising of the Andes, Aconquija, and Quilmes Ranges (Kleinert and Strecker, 2001) (Fig. 1B), shaped the landscape and modified the climate, favoring the spread of larger and phylogenetically more derived mesotheriines in lowlands at highest latitudes. The scarcity of outcrops that encompass this lapse, added to the bias of the fossil record, hinder to establish a deeper analysis about these small mesotheriines.

## 6. Conclusions

Comparison of the mesotheriid remains from Northwestern Argentina with specimens from northernmost mid-latitudes (Bolivia and Chile) has allowed the establishment of great

similarities with Bolivian species. Several features, such as the presence of a lingual groove on the posterior lobe of molars, metastyle and parastyle orientation, and the small size of the studied material, lead to determine the specimen from Las Arcas Formation, Catamarca Province, as *Plesiotypotherium* aff. *P. achirensis*, which would represent the first record of this genus in Argentina. Due to the scarcity and ambiguous features, the specimen from Saladillo Formation, Tucumán Province, is referred to a Mesotheriinae indet., until more materials could help for a better characterization.

The fossil record indicates that small-sized mesotheriines are abundant and diverse principally in the early and middle Miocene of northern Chile, Bolivia and Argentina. Instead, large-sized forms are important components of the mammal faunas in South America during the late Miocene/Pliocene and Pleistocene. In this context, the small mesotheriines herein studied represent a break in the general trend in size, as they appear during a period when medium to large-sized mesotheriines predominate in the region. The interpretation of these small late Miocene mesotheriines still remains uncertain, as they are morphologically different from the small early–middle Miocene taxa; besides, small-sized mesotheriines could be more generalized in late Neogene times than presently thought if we consider the small, still unpublished specimen from Mendoza mentioned by Cerdeño, 2018. The singularity of the landscape histories (i.e., orogenic, climatic, and environmental factors) might have favored the development of small mesotheriines in the NWA region. Thus, to understand the complex history of mammals in South America it is necessary to have well-sampled faunas with detailed chronostratigraphic provenance and an integrative analysis that involves other data sources.

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## References

- Alcalá, L., Morales, J., 1995. Ungulados sudamericanos. In: Meléndez, B. (Ed.), Paleontología, Mamíferos. Editorial Paraninfo SA, Madrid, pp. 161–197, 3(2).
- Alston, E., 1876. On the classification of the order Glires. Proc. Zool. Soc. Lond. 61–98.
- Ameghino, F., 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. Anales de la Sociedad Científica Argentina de Buenos Aires 57, 162–175.
- Ameghino, F., 1906. Les formations sédimentaires de Crétacé supérieur et du Tertiaire de Patagonie. Anales del Museo Nacional de Buenos Aires 3 (8), 1–568.
- Bargo, M.S., Reguero, M.A., 1989. El primer registro de un mamífero fósil en el extremo septentrional de Chile. Ameghiniana 26 (3–4), 239.
- Billet, G., 2011. Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters. J. Syst. Palaeontol. 9 (4), 481–497.
- Billet, G., De Muizon, C., Mamaní Quispe, B., 2008. Late Oligocene mesotheriids (Mammalia, Notoungulata) from Salla and Lacayani (Bolivia): implications for basal mesotheriid phylogeny and distribution. Zool. J. Linn. Soc. 152, 153–200.
- Bond, M., 1986. Los ungulados fósiles de Argentina: evolución y paleoambientes. In: Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, vol. 2, pp. 173–185.

- Bond, M., Cerdeño, E., López, G., 1995. Los ungulados nativos de América del Sur. Evolución biológica y climática de la región pampeana durante los últimos cinco millones de años. CSIC Monografías 12, 257–276.
- Bond, M., García, M., 2002. Nuevos restos de toxodontes (Mammalia, Notoungulata) en estratos de la Formación Chucal, Micoeno, Altiplano de Arica, norte de Chile. *Rev. Geol. Chile* 29, 81–91.
- 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 (Unpublished). Universidad Nacional de La Plata, Facultad de Ciencias Nat. y Museo de La Plata, 366 p.
- Bossi, G.E., Palma, R., 1982. Reconsideración de la estratigrafía del Valle de Santa María, provincia de Catamarca, Argentina. In: 5° Congreso Latinoamericano de Geología. Servicio Geológico Nacional, Buenos Aires, pp. 155–172.
- Bossi, G.E., Ovejero, R., Streckler, M., 1987. Correlación entre los perfiles del Terciario superior en la Puerta de Corral Quemado-Hualfín y de Entre Ríos (Chiquimil). In: Actas del X Congreso Geológico Argentino, San Miguel de Tucumán, vol. 2, pp. 117–120.
- Bossi, G.E., Muruaga, C.M., Sanagua, J.G., Hernando, A., Ahumada, A., 1993. Geología y estratigrafía de la cuenca Neógena Santa María-Hualfín (Deptos. Santa María y Belén, Prov. de Catamarca). In: Actas del XII Congreso Geológico Argentino, Mendoza, vol. 2, pp. 156–165.
- Bossi, G.E., Georgieff, S., Muruaga, C., Sanagua, J., Ahumada, A., Ibáñez, L., 1994. The Santa María-hualfín Neogene basin of northwestern Argentina. In: 14° International Sedimentological Congress, Recife, Brasil. Actas 14. G12–13.
- Bossi, G.E., Gavrilloff, I., Esteban, G., 1998. Terciario, estratigrafía, bioestratigrafía y paleogeografía. In: Gíafrancisco, M., Puchulu, M.E., Durango de Cabrera, J., Aceñolaza, G.F. (Eds.), Geología del Tucumán. Colegio de Graduados en Ciencias Geológicas de Tucumán. Publicación Especial, pp. 87–108.
- Bossi, G.E., Muruaga, C.M., Gavrilloff, I., 1999. Sierras pampeanas. Ciclo andino. Neógeno-pleistoceno. Sedimentación. In: González Bonorino, G., Omarini, R., Viramonte, J. (Eds.), Relatorio del XIV Congreso Geológico Argentino, Salta, vol. 1, pp. 329–360.
- Bossi, G.E., Georgieff, S.M., Gavrilloff, I., Ibáñez, L., Muruaga, C.M., 2001. Cenozoic evolution of the intramontane Santa María basin, pampean ranges, northwestern Argentina. *J. S. Am. Earth Sci.* 14 (7), 725–734.
- Brandoni, D., Powell, J.E., González, O.E., 2012. *Anisodontherium* from the late Miocene of North-western Argentina. *Acta Palaeontol. Pol.* 57 (2), 241–249.
- Buckley, M., 2015. Ancient collagen reveals evolutionary history of the endemic South American 'ungulates'. *Proc. R. Soc. B* 282, 20142671. <https://doi.org/10.1098/rspb.2014.2671>.
- Butler, R.F., Marshall, L.G., Drake, R.E., Curtis, G.H., 1984. Magnetic polarity stratigraphy and K-Ar dating of late Miocene and early Pliocene continental deposits, Catamarca province, NW Argentina. *J. Geol.* 92, 623–636.
- Cabrera, A., 1937. Los géneros de la familia "Thyprotheriidae". *Physis* 14, 359–372.
- Cabrera, A., Kraglievich, L., 1931. Diagnósis previas de los ungulados fósiles del Arroyo Chasicó. *Notas Preliminares del Museo de La Plata* 1, 107–113.
- Cassini, G.H., Cerdeño, E., Villafañe, A., Muñoz, N.A., 2012. Paleobiology of santacrucian native ungulates (Meridiungulata; astraprotheria, 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, UK, pp. 243–286.
- Cerdeño, E., 2007. Systematic position of the Mesotheriidae (Notoungulata) from the Mariño Formation (Miocene) in divisadero largo, Mendoza, Argentina. *Geobios* 40 (6), 767–773.
- Cerdeño, E., 2014. First record of Mesotheriidae in the late Oligocene of Mendoza province, Argentina. *Ameghiniana* 51 (4), 366–370.
- Cerdeño, E., 2018. Updated Synthesis of South American Mesotheriidae (Notoungulata) with Emphasis on West-central Argentina (In press). *Revue de Paléobiologie*, vol. Hommage à C. Guérin).
- Cerdeño, E., Bond, M., 1998. Taxonomic revision and phylogeny of *Paedotherium* and *Tremacyllus* (pachyrhinae, Hegetotheriidae, Notoungulata) from the late Miocene to the Pleistocene of Argentina. *J. Vertebr. Paleontol.* 18 (4), 799–811.
- Cerdeño, E., Montalvo, C.I., 2001. Los Mesotheriinae (Mesotheriidae, Notoungulata) del Mioceno superior de La Pampa, Argentina. *Rev. Esp. Palaontol.* 16 (1), 63–75.
- Cerdeño, E., Schmidt, G.I., 2013. Milk molars or extra premolars in Mesotheriinae (Mesotheriidae, Notoungulata): new insights into an old controversy. *Geobios* 46 (3), 195–202.
- Cerdeño, E., González Riga, B., Bordonaro, O., 2006. Primer hallazgo de mamíferos en la Formación Mariño (Mioceno) en Divisadero Largo (Mendoza, Argentina). *Ameghiniana* 43, 205–214.
- Cerdeño, E., Vera, B., Schmidt, G.I., Pujos, F., Mamaní Quispe, B., 2012. An almost complete skeleton of a new Mesotheriidae (Notoungulata) from the late Miocene of Casira, Bolivia. *J. Syst. Palaeontol.* 10 (2), 341–360.
- Cifelli, R.L., 1985. South American ungulate evolution and extinction. In: Stehli, F.G., Webb, S.D. (Eds.), *The Great American Biotic Interchange*. Plenum Press, New York, pp. 249–266.
- Cione, A., Gasparini, G., Soibelzon, E., Soibelzon, L., Tonni, E.P., 2015. The Great American Biotic Interchange: a South American Perspective. *Springer Briefs in Earth System Sciences*, 97 p.
- Croft, D.A., 1999. Placentals: endemic South American ungulates. In: R. Singer (Ed.), *The Encyclopedia of Paleontology*. Fitzroy-Dearborn, Chicago, pp. 890–906.
- Croft, D.A., 2016. Horned Armadillos and Rafting Monkeys: the Fascinating Fossil Mammals of South America. Indiana University Press, Bloomington, Indiana, 320 pp.
- Croft, D.A., Bond, M., Flynn, J.J., Reguero, M.A., Wyss, A.R., 2003. Large archaeohyracids (tyrotheria, Notoungulata) from Central Chile and Patagonia, including a revision of *archaeotytherium*. *Fieldiana Geol. (New. Ser.)* 49, 1–38.
- Croft, D.A., Flynn, J.J., Wyss, A.R., 2004. Notoungulata and litopterna of the early Miocene chucal fauna, northern Chile. *Fieldiana Geol. (New. Ser.)* 50, 1–49.
- Croft, D.A., Flynn, J.J., Wyss, A.R., 2007. A new basal glyptodontid and other Xenarthra of the early Miocene Chucal Fauna, northern Chile. *J. Vertebr. Paleontol.* 27, 781–797.
- Croft, D.A., Flynn, J.J., Wyss, A.R., 2008. In: *The Tinguiririca Fauna of Chile and the Early Stages of "modernization" of South American Mammal Faunas*, vol. 66. Arquivos do Museu Nacional, Rio de Janeiro, pp. 191–211.
- Croft, D.A., Anaya, F., Auerbach, D., Garzione, C., MacFadden, B., 2009. New data on Miocene neotropical provinciality from Cerdas, Bolivia. *J. Mamm. Evol.* 16 (3), 175–198.
- Croft, D.A., Carlini, A.A., Ciancio, M.R., Brandoni, D., Drew, N.E., Engelman, R.K., Anaya, F., 2016. New mammal faunal data from Cerdas, Bolivia, a middle-latitude neotropical site that chronicles the end of the middle Miocene climatic optimum in south America. *J. Vertebr. Paleontol.* 36 (5), e1163574 (17 pp.).
- Esteban, G., Abdala, F., 1993. Nuevos restos de *Glossotheriopsis* (Edentata-Tardigrada) de Tío Punco, Provincia de Tucumán, Análisis filogenético preliminar. *Ameghiniana* 30 (3), 328–329.
- Esteban, G., Nasif, N., 1996. Nuevos Dasypodidae (Mammalia, Xenarthra) del Mioceno tardío del valle del Cajón, Catamarca, Argentina. *Ameghiniana* 33 (3), 327–334.
- Esteban, G., Nasif, N., Georgieff, S.M., 2014. Cronobioestratigrafía del Mioceno tardío-Plioceno temprano, Puerta de Corral Quemado y Villavil, Catamarca, Argentina *Acta Geológica Lilloana* 26, 165–192.
- Flynn, J.J., Wyss, A.R., 1998. Recent advances in South American mammalian paleontology. *Trends Ecol. Evol.* 13, 449–454.
- Flynn, J.J., Novacek, M.J., Dodson, H.E., Frasinetti, D., McKenna, C., Norell, M.A., Sears, K.E., Swisher, C., Wyss, A.R., 2002. A new fossil mammal assemblage from the southern Chilean Andes: implications for geology, geochronology, and tectonics. *J. S. Am. Earth Sci.* 15, 285–302.
- Flynn, J.J., Croft, D.A., Charrier, R., Wyss, A.R., Hérail, G., García, M., 2005. New Mesotheriidae (mammalia, Notoungulata, tyrotheria), geochronology and tectonics of the Caragua area, northernmost Chile. *J. S. Am. Earth Sci.* 19, 55–74.
- Francis, J.C., 1965. Los géneros de la subfamilia Mesotheriinae (Tyrotheria, Notoungulata) de la República Argentina. *Boletín del Laboratorio de Paleontología de Vertebrados*. Montevideo 1, 7–31.
- Georgieff, S.M., Sosa Gomez, J., Schiuma, M., 2012. Análisis estratigráfico-estructural del Neógeno de Catamarca, Tucumán, Sur de Salta y Santiago del Estero. *Ameghiniana* 49 (4), 10–11.
- Georgieff, S., Ibáñez, L., Vides, M., Anis, K., Nieva, S., 2014. Paleógeno y Neógeno de Tucumán: estratigrafía y paleoambientes sedimentarios. In: Moyano, M., Puchulu, M., Fernández, D., Vides, M., Nieva, S., Aceñolaza, G. (Eds.), *Geología de Tucumán*. Colegio de Graduados en Ciencias Geológicas de Tucumán. Publicación Especial, pp. 87–108.
- Georgieff, S., Ibáñez, L., Esteban, G., Nasif, N., Bonini, R., 2016. La litoestratigrafía regional neógena y la evolución paleogeográfica de los ambientes del NOA meridional. *Ameghiniana* 53 (1), 15–16.
- Georgieff, S., Muruaga, C.M., Ibáñez, L., Spagnuolo, C., Bonini, R., Esteban, G., Nasif, N., Del Pero, M., 2017. Estilo de deformación, cronoestratigrafía y evolución paleoambiental de las unidades neógenas de las Sierras Pampeanas Noroccidentales de Catamarca y Tucumán, Argentina. In: Muruaga, C.M., Grosse, P. (Eds.), *Ciencias de la Tierra y Recursos Naturales del NOA*. Relatorio del XX Congreso Geológico Argentino, San Miguel de Tucumán, pp. 254–268.
- Galván, A.F., Ruiz Huidobro, O.J., 1965. Geología del Valle de Santa María. Estratigrafía de las formaciones mesozoico-terciarias. In: Actas Segundas Jornadas Geológicas Argentinas, San Miguel de Tucumán, vol. 3, pp. 217–230.
- Goin, F.J., Gelfo, J.N., Chornogubsky, L., Woodburne, M.O., Martin, T., 2012. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. In: Patterson, B.D., Costa, L.P. (Eds.), *Bones, Clones, and Biomes the History and Geography of Recent Neotropical Mammals*. The University of Chicago Press, Chicago, London, pp. 20–50.
- Gomes Rodrigues, H., Herrel, A., Billet, G., 2017a. Ontogenetic and life history trait changes associated with convergent ecological specializations in extinct ungulate mammals. *Proc. Natl. Acad. Sci. Unit. States Am.* 114, 1069–1074.
- Gomes Rodrigues, H., Lefebvre, R., Fernández-Monescillo, M., Mamaní Quispe, B., Billet, G., 2017b. Ontogenetic variations and structural adjustments in mammals evolving prolonged to continuous dental growth. *Roy. Soc. Open Sci.* 4, 170494.
- González, O.E., Viruel, M.E., Mon, R., Tchilinguirian, P., 2000. Hoja Geológica 2766–II San Miguel de Tucumán. Servicio Geológico Minero Argentino. Boletín 245, 1–124.
- Herbst, R., Anzótégui, L.M., Esteban, G., Mautino, L.R., Morton, S., Nasif, N., 2000. Síntesis paleontológica del Mioceno de los valles Calchaquies, noroeste argentino. *Rev. Correlación Geol.* 14, 263–288.
- Herrera, C., Esteban, G., 2017. El registro más antiguo de *Chasicotatus ameghinioi* Scillato Yané, 1977 (Xenarthra, Dasypodidae) en el Tortoniano medio de la Quebrada de Amaicha (Tucumán, Argentina): consideraciones bioestratigráficas. *Rev. Bras. Palaontol.* 20, 115–120.
- Kleinert, K., Streckler, M.R., 2001. Climate change in response to orographic barrier uplift: paleosol and stable isotope evidence from the late Neogene Santa María basin, northwestern Argentina. *Geol. Soc. Am. Bull.* 113, 728–742.
- Koenigswald, W.V., 2011. Diversity of hypsodont teeth in mammalian dentitions-construction and classification. *Palaeontographica Abt. A* 294, 63–94.
- Kraglievich, L., 1932. Diagnósis de nuevos géneros y especies de roedores cávidos y

- eumegámidos fósiles de la Argentina. An. Soc. Cient. Argent. 114, 155–181.
- Kraglievich, L., 1934. La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. El Siglo Ilustrado, Montevideo, 136 pp.
- Krapovickas, V., Ciccioli, P.L., Mángano, M.G., Marsicano, C.A., Limarino, L.O., 2009. Paleobiology and paleoecology of an arid–semiarid Miocene South American ichnofauna in anastomosed fluvial deposits. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 284, 129–152.
- Latorre, C., Quade, J., McIntosh, W.C., 1997. The expansion of the C4 gases and global changes in the late Miocene: stable isotope evidence from the Americas. *Earth Planet Sci. Lett.* 146, 83–96.
- López, G.M., 2007. Los ungulados de la Formación Divisadero Largo (Eoceno inferior?) de la provincia de Mendoza, Argentina: sistemática y consideraciones bioestratigráficas. Ph. D. Thesis (Unpublished). Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo de La Plata, 348 pp.
- López, G.M., Vucetich, M.G., Carlini, A.A., Bond, M., Pérez, M.E., Ciancio, M.R., Pérez, D.J., Arnal, M., Olivares, A.I., 2011. New Miocene mammal assemblages from Neogene manantiales basin, cordillera frontal, san Juan, Argentina. In: Salfity, J.A., Marquillas, R.A. (Eds.), *Cenozoic Geology of Central Andes of Salta*. SCS Publisher, Argentina, pp. 211–226.
- MacFadden, B.J., Anaya, F., Swisher, C.C., 1995. Neogene paleomagnetism and orocinal bending of the central Andes of Bolivia. *J. Geophys. Res.: Solid Earth* 100 (B5), 8153–8167.
- Macrini, T.E., Flynn, J.J., Ni, X., Croft, D.A., Wyss, A.R., 2013. Comparative study of notoungulate (Placentalia, Mammalia) bony labyrinths and new phylogenetically informative inner ear characters. *J. Anat.* 223, 442–461.
- Marshall, L.G., Butler, R.F., Drake, R.E., Curtis, G.H., Tedford, R.H., 1979. Calibration of the great American interchange. *Science* 204, 272–279.
- Marshall, L.G., Patterson, B., 1981. Geology and geochronology of the mammal-bearing Tertiary of the Valle de Santa María and Río Corral Quemado, Catamarca Province, Argentina. *Fieldiana Geol.* 9, 1–80.
- Marshall, L., Hoffstetter, R., Pascual, R., 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. *Paleo-vertebrata. Mémoire Extraordinaire* 1–93.
- McKenna, M., 1975. Toward a phylogenetic classification of the mammalia. In: Luckett, P., Szalay, F. (Eds.), *Phylogeny of the Primates: a Multidisciplinary Approach*. Plenum Publishing Corporation, New York, pp. 21–46.
- McKenna, M.C., Bell, S.K., 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York, 640 pp.
- Mones, A., 1982. An equivocal nomenclature: what means hypsodonty? *Paläontologische Zeitschrift* 56, 107–111.
- Montoya-Sanhueza, G., Moreno, K., Bobe, R., Carrano, M.T., García, M., Corgne, A., 2017. Peltephilidae and Mesotheriidae (mammalia) from late Miocene strata of northern Chilean Andes, Caragua. *J. S. Am. Earth Sci.* 75, 51–65.
- Moreno, F.P., Mercerat, A., 1891. Exploración arqueológica de la Provincia de Catamarca: paleontología. *Rev. Mus. La Plata* 1, 1–71.
- Moyano, M.S., 2003. Mapeo y sedimentología de los depósitos lacustres miocenos de la Formación Chiquimil en el cerro Pampa, Catamarca. Seminario (Unpublished). Universidad Nacional de Tucumán San Miguel de Tucumán, 58pp.
- Muizon, C. de, Cifelli, R.L., 2000. The “condylarths” (archaic ungulate, Mammalia) from the early Palaeocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. *Geodiversitas* 22, 47–150.
- Nasif, N., 1988. Primer registro de flamencos (Phoenicopteridae) del Terciario Superior, Valle del Cajón (Provincia de Catamarca, Argentina). *Ameghiniana* 25 (2), 169–173.
- Nasif, N., Esteban, G., Musalem, S., Herbst, R., 1997. Primer registro de Vertebrados fósiles para la Formación Las Arcas (Mioceno tardío), Valle de Santa María, Provincia de Catamarca, Argentina. *Ameghiniana* 34 (4), 538.
- Nasif, N.L., Musalem, S., Cerdeño, E., 2000. A new toxodont from the late Miocene of Catamarca, Argentina, and a phylogenetic analysis of the Toxodontidae. *J. Vertebr. Paleontol.* 20, 591–600.
- Nasif, N., Esteban, G., Cerdeño, E., Moyano, S., 2010. Un Mesotheriidae (Notoungulata) de talla pequeña del Mioceno medio alto, Formación Las Arcas, provincia de Catamarca, Argentina. In: *Actas X Congreso Argentino de Paleontología y Bioestratigrafía y VII Congreso Latinoamericano de Paleontología*, pp. 83–188.
- Oiso, Y., 1991. New land mammal locality of middle Miocene (Colloncuran) age from Nazareno, southern Bolivia. In: Suárez-Soruco, R. (Ed.), *Fósiles y Facies de Bolivia-Vol. I Vertebrados. Yacimientos Petrolíferos Fiscales Bolivianos*, Santa Cruz, pp. 653–672.
- O’leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo, Z.-X., Meng, J., et al., 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339, 662–667. <https://doi.org/10.1126/science.1229237>.
- Ortiz Jaureguizar, E., Cladera, G.A., 2006. Paleoenvironmental evolution of southern South America during the cenozoic. *J. Arid Environ.* 66, 498–532.
- Pascual, R., Ortiz Jaureguizar, E., 1990. Evolving climates and mammal faunas in Cenozoic South America. *J. Hum. Evol.* 19, 23–60.
- Patterson, B., Pascual, R., 1968. The fossil mammal fauna of South America. *Q. Rev. Biol.* 43, 409–451.
- Paz, E.R., Kramarz, A., Bond, M., 2011. Mesotheriid (mammalia, Notoungulata) remains from the colhuehuapian beds (early Miocene) of Chichinales Formation, río Negro province, Argentina. *Ameghiniana* 48 (2), 264–269.
- Peirano, A., 1943. Algunos yacimientos de fósiles de la parte central de Santa María y del Valle del Cajón (provincias de Catamarca y Tucumán). Cuadernos de Mineralogía y Geología. IV 2(14). Universidad Nacional de Tucumán, pp. 32–60.
- Peirano, A., 1946. Estudio geológico de la quebrada de Amaicha, Departamento de Tafí, provincia de Tucumán. Con referencias preliminares al valle de Santa María (parte tucumana). Cuadernos de Minería y Geología. IV (16). Universidad Nacional de Tucumán, pp. 6–37.
- Pérez, M.E., Pol, D., 2012. Major radiations in the evolution of caviid rodents: reconciling fossils, ghost lineages, and relaxed molecular clocks. *PLoS One* 7 (10), e48380.
- Powell, J.E., González, O.E., 1997. Hallazgo de mamíferos en la Formación Saladillo (Grupo Santa María), próximo al río Amaicha, provincia de Tucumán. Implicancias cronológicas. *Ameghiniana* 34 (1), 124.
- Powell, J., Mulé, P., Duarte, R., Ortíz, P., Sanagua, J., Murruaga, C., 1998. Mamíferos de la Formación Chiquimil (Mioceno superior) de la vertiente Occidental de la Sierra de Huallín, Provincia de Catamarca. *Acta Geol. Lilloana* 18 (1), 178.
- Reguero, M.A., 1999. El problema de las relaciones sistemáticas y filogenéticas de los Typotheria y Hegetotheria (Mammalia, Notoungulata): análisis de los taxones de Patagonia de la Edad-mamífero Deseadense (Oligoceno). Ph. D. Thesis (Unpublished). Universidad de Buenos Aires, Departamento de Ciencias Biológicas, 301 pp.
- Reguero, M.A., Castro, P.V., 2004. Un nuevo Trachytheriinae (Mammalia, Notoungulata) del Deseadense (Oligoceno tardío) de Patagonia, Argentina: implicancias en la filogenia, biogeografía y bioestratigrafía de los Mesotheriidae. *Revista geológica de Chile* 31 (1), 45–64.
- Reguero, M.A., Candelá, A.M., 2011. Late Cenozoic mammals from the northwest of Argentina. *Cenozoic geology of the Central Andes of Argentina* 458, 411–426.
- Reig, O., 1957. Un Mustelido del Género *Galictis* del Eocuario de la Provincia de Buenos Aires. *Ameghiniana* 1 (1–2), 33–47.
- Riggs, E.S., Patterson, B., 1939. Stratigraphy of late Miocene and Pliocene deposits of the province of Catamarca (Argentina) with notes on the faunae. *Physis* 14, 143–162.
- Riquelme, R., 1998. Evolución tectosedimentaria postoligocena del borde Occidental del Altiplano, entre Tignámar y Salar de Surire, I Región, Chile. Ph.D. Dissertation. Universidad de Chile, Santiago, 123 pp.
- Roger, C., Esteban, G., 2000. Nuevo registro de *Stromaphorus* (Xenarthra, Glyptodontidae) en el Mioceno tardío de la provincia de Catamarca. *Ameghiniana* 37, 33R.
- Rohlf, F.J., 2013. *TpsDig*. State University of New York at Stony Brook, New York. Available at: version 2.17. <http://life.bio.sunysb.edu/morph/>. (Accessed 25 January 2018).
- Roth, S., 1899. Apunte sobre la geología y la paleontología de los territorios del río Negro y Neuquén, 9, pp. 143–197. *Revista del Museo de La Plata*.
- Roth, S., 1902. Notas sobre algunos nuevos mamíferos fósiles. *Rev. Mus. La Plata* 10, 251–256.
- Roth, S., 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretáceo superior y Terciario inferior de la Patagonia. *Rev. Mus. La Plata* 11, 133–158.
- Rovereto, C., 1914. Los estratos araucanos y sus fósiles. *Anales del Museo de Historia Natural de Buenos Aires* 25, 1–247.
- Sasso, A., 1997. Geological Evolution and Hallogenic Relationships of the Farallón Negro Volcanic Complex, NW Argentina. Ph. D. Thesis (Unpublished). Queens University, Kingston, Ontario, Canadá, 268 pp.
- Scott, W.B., 1937. *A History of Land Mammals in the Western Hemisphere*, second ed. Macmillan, New York. 786 pp.
- Segovia, M.F., 2004. Icnitas fósiles de vertebrados e invertebrados del faldeo Occidental del Cerro Pampa. In: *X Reunión Argentina de Sedimentología*. Provincia de Catamarca, Argentina, pp. 161–162.
- Serres, M., 1867. De l’ostéographie du *Mesotherium* et de ses affinités zoologiques. *Comptes Rendus des Séances de l’Académie de Sciences de Paris* 65 (2), 140–148.
- Seoane, F.D., Roig Juñent, S., Cerdeño, E., 2017. Phylogeny and paleobiogeography of Hegetotheriidae (mammalia, Notoungulata). *J. Vertebr. Paleontol.* 37 (1), e1278547 (13 pp.).
- Shockey, B.J., Billet, G., Salas Gismondi, R., 2016. A new species of *Trachytherus* (Notoungulata: Mesotheriidae) from the late Oligocene (Deseadan) of Southern Peru and the middle latitude diversification of early diverging mesotheriids. *Zootaxa* 4111 (5), 565–583.
- Simpson, G.G., 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85, 1–350.
- Simpson, G.G., 1980. *Splendid Isolation: the Curious History of South American Mammals*. Yale University Press, New Haven, Connecticut, 266 pp.
- Spagnuolo, C.M., Georgieff, S.M., Rapalini, A.E., 2015. Magnetostratigraphy of the Miocene las Arcas Formation, Santa María valley, northwestern Argentina. *J. S. Am. Earth Sci.* 63, 101–113.
- Strecker, M.R., Cerveny, P., Bloom, A.L., Malizia, D., 1989. Late cenozoic tectonism and landscape development in the foreland of the Andes: northern sierras pampeanas (26°–28° S), Argentina. *Tectonics* 8 (3), 517–534.
- Tauber, A.A., 2005. Mamíferos fósiles y edad de la Formación Salicas (Mioceno tardío) de la sierra de Velasco, La Rioja, Argentina. *Ameghiniana* 42 (2), 443–460.
- Tomassini, R.L., Montalvo, C.I., 2013. Taphonomic modes on fluvial deposits of the monte hermoso formation (early Pliocene), Buenos Aires province, Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 369, 282–294.
- Tonni, E.P., 1970. *Zonotrichia robusta* n. sp. (aves, passeriformes, emberizidae) from middle Pleistocene of Buenos Aires province. *Ameghiniana* 7 (2), 161–165.
- Townsend, B., Croft, D.A., 2010. Middle Miocene mesotheriine diversity at Cerdas, Bolivia and a reconsideration of *Plesiotypotherium minus*. *Paleontol. Electron.* 13 (1), 36.

- Villarroel, C., 1974a. Les Mésothérinés (Notoungulata, Mammalia) du Pliocène de Bolivie. Leurs rapports avec ceux d'Argentine. *Ann. Paleontol.* 60, 245–281.
- Villarroel, C., 1974b. Un mésothériiné nouveau (Notoungulata, Mammalia) dans le Miocène supérieur de Bolivie. *Comptes Rendus de l'Académie des Sciences de Paris* 279, 551–554.
- Villarroel, C., 1978. Edades y correlaciones de algunas unidades litoestratigráficas del Altiplano boliviano y estudio de algunos representantes mesotheriinos. *Revista de la Academia Nacional de Ciencias de Bolivia* 1, 159–170.
- Vucetich, M.G., Arnal, M., Deschamps, C.M., Pérez, M.E., Vieytes, E.C., 2015. A brief history of caviomorph rodents as told by the fossil record. In: Vassallo, A., Antonucci, D. (Eds.), *Biology of Caviomorph Rodents, Diversity and Evolution. SAREM, Mendoza*, 11–62.
- 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.D., Rowsell, K., Porter, D.M., Kessler, B., Fischer, R., Baessmann, C., Kaspar, S., Olsen, J.V., Kiley, P., Elliott, J.A., Kelstrup, C.D., Mullin, V., Hofreiter, M., Willerslev, E., Hublain, J.-J., Orlando, L., Barnes, I., MacPhee, R.D., 2015. Ancient proteins resolve the evolutionary history of Darwin's South American ungulates. *Nature* 522, 81–84. <https://doi.org/10.1038/nature14249>.
- Westbury, M., Baleka, S., Barlow, A., Hartman, S., Pajmans, J.L.A., Kramarz, A., Forasiepi, A., Bond, M., Gelfo, J.N., Reguero, M.A., López-Mendoza, P., et al., 2017. A mitogenomic timetree for Darwin's enigmatic South American mammal *Macrauchenia patachonica*. *Nat. Commun.* 8, 1–8. <https://doi.org/10.1038/ncomms15951>.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65Ma to Present. *Science* 292, 686–693.
- Zittel, K.A., 1893. *Handbuch der Palaeontologie, IV. Vertebrata (Mammalia)*. R. Oldenbourg, Munich, 590 pp.