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Updated synthesis of South American Mesotheriidae (Notoungulata) with emphasis on west-central Argentina

Esperanza CERDEÑO

Paleontología, IANIGLA, Centro Científico Tecnológico-CONICET-Mendoza. Avda. Ruiz Leal s/n. 5500 Mendoza, Argentina. E-mail: espe@mendoza-conicet.gob.ar

Abstract
Doctor Claude Guérin dedicated many years of his research to fossil rhinoceroses, but also to some of the interesting mammals that evolved in South America. This is why I contribute to this volume in his memory with a synthesis on one of the families that are known as South American Native Ungulates. The order Notoungulata was the most diverse and abundant of these native ungulates throughout the Cenozoic, and is mainly gathered in two suborders, Toxodontia and Typotheria, which in turn include up to 11-12 families, not all presently considered as monophyletic groups. The family Mesotheriidae includes the largest-sized typotheres and is recorded from Early Oligocene to Early Pleistocene. Mesotheriids are mainly known from Argentina, but are also present in Chile, Bolivia, and Peru. The record of Argentinean mesotheriids has increased in recent years, both from Paleogene and Neogene levels, and some emphasis is made in the new records from west-central areas such as Mendoza Province. The systematics of mesotheriids is far from being well resolved. Recent studies have evidenced a marked change in tooth morphology, size, and proportions along the ontogeny within mesotheriines, which have led to questioning some assumed diagnostic features. Research in progress on new findings from several localities in Mendoza could help elucidate some taxonomic issues, especially among Miocene taxa.

Keywords
Mesotheriids, Typotheria, Paleogene, Neogene, Mendoza, Argentina.

1. INTRODUCTION

South America was isolated during most of the Cenozoic and different biotas developed independently of northern faunas and floras (e.g., Seoane *et al.,* 2017 and references therein). Dr Claude Guérin dedicated some years of his broad research to the so-called South American Native Ungulates (SANU), especially to the last representatives found in faunal assemblages from Brazil. For this reason, I chose to contribute to his memory with this synthesis on Mesotheriidae, one of the families of this large group of mammals, emphasizing the current research and findings in west-central Argentina.

Among the SANU, the order Notoungulata is the most diverse and widespread. Notoungulates are recorded throughout the Cenozoic, from Paleocene to early Holocene. They are mainly grouped in two suborders: Toxodontia and Typotheria, composed of up to 11-12 families, not all presently considered as monophyletic groups (Billet, 2011; Vera, 2016). Among Typotheria, the family Mesotheriidae gathers small to medium-sized notoungulates, the largest representatives reaching the size of a sheep (Shockey *et al*., 2007, 2016). They are characterized by ever-growing (= euhypsodont or hypselodont; e.g., Mones, 1982; Ungar, 2010; Koenigswald, 2011) incisors with enamel restricted to the labial wall; cheek teeth hypsodont (trachytheriines) or euhypsodont (mesotheriines); and postcranial skeleton (forelimb, hind limb and sacro-pelvic complex) presenting some features associated with a digging behavior and, at least, semi-fossorial habits (Shockey *et al*., 2007, 2016). The biochron of mesotheriids ranges from Early Oligocene to Early Pleistocene. They are mainly known from Argentina, but also from Chile, Bolivia, and Peru (see references in following sections). Two subfamilies, Trachytheriinae and Mesotheriinae, are classically accepted within Mesotheriidae. However, despite the relatively abundant remains, the systematics of this family is far from being well established. In this context, different localities in Mendoza Province, west-central Argentina, have recently provided new mesotheriid remains that contribute to the knowledge of the family. Herein, an updated summary on Mesotheriidae, including preliminary data on new findings from Mendoza (still under study), is presented.

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Abbreviations (text and figure captions): CRILAR, Centro Regional de Investigaciones de La Rioja, La Rioja, Argentina; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCNAM-PV, Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano' – Vertebrate Paleontology, Mendoza, Argentina; MHNSR, Museo de Historia Natural de San Rafael, San Rafael, Argentina; MNHN-Bol-V, Museo Nacional de Historia Natural de Bolivia – Vertebrate Paleontology, La Paz, Bolivia; SALMA, South American Land Mammal Age.

2. PALEOGENE RECORD

The Paleogene mesotheriids correspond to the subfamily Trachytheriinae and only one genus is presently recognized, *Trachytherus* Ameghino, 1889 (Reguero, 1999; Billet *et al*., 2008). The first record of trachytheriines seems to correspond to the Tinguirirican SALMA (Early Oligocene) from Río Negro Province, Argentina (Fig. 1) (Reguero & Castro, 2004), and the locality of Cachapoal, Chile (Croft *et al*., 2008; Shockey *et al*., 2016), but remains are too incomplete to be accurately determined at generic level. It is during the Late Oligocene (Deseadan SALMA; Fig. 1) that the record increases and is referred to the genus *Trachytherus*, which includes four species. *Trachytherus spegazzinianus* Ameghino, 1889 (= *Anatrachytherus soriai* Reguero & Castro, 2004; Billet *et al*., 2008) is mainly known from different Patagonian localities in Neuquén, Chubut and Santa Cruz provinces (Ameghino, 1889; Reguero, 1999; Reguero & Prevosti, 2010), but also from the Fray Bentos Formation ('*T. curuzucuatiense*' Podestá, 1899) in Corrientes Province, northeast Argentina (Reguero & Castro, 2004; Billet *et al*., 2008). Recently, a specimen from the Quebrada Fiera locality (Agua de la Piedra Formation) in Mendoza Province was determined as *Trachytherus* cf. *T. spegazzinianus* (Cerdeño, 2014). The presence of *Trachytherus* in the Divisadero Largo Formation, also in Mendoza Province (Reguero, 1999; Reguero & Castro, 2004), was rejected after taxonomic and stratigraphic reinterpretations (Cerdeño, 2007 and see below).

Out of Argentina, *T. spegazzinianus* has been recognized at Lacayani, Bolivia (Marshall & Sempere, 1991; Billet *et al*., 2008). In this country, two other species were defined: *T. subandinus* Villarroel, Sempere & Marshall, 1994 from Río Pluma, Cochabamba Department, and *T. alloxus* Billet, De Muizon & Mamaní Quispe, 2008 from the well-known locality of Salla (Fig. 1).

Very recently, another species, *Trachytherus ramirezi* Shockey, Billet & Salas-Gismondi, 2016, has been described for the Moquegua Formation, Moquegua, southern Peru (Fig. 1).

As a whole, the Paleogene record of mesotheriines is little diversified. The only recognized genus *Trachytherus* is present in Argentina with one species whereas three are present in a relatively small geographic area in western Bolivia and southern Peru (Fig. 1), which led Shockey *et al*. (2016) to propose a Bolivian Orocline Region as an ancestral area for diversification of mesotheriids.

3. NEOGENE RECORD

Mesotheriids from Neogene levels are more abundant (Fig. 2) and at least nine genera have been recognized (Fig. 3), all taxa grouped in the subfamily Mesotheriinae. The first mesotheriine remains are known from the Colhuehuapian SALMA (Early Miocene) in Río Negro Province (Chichinales Formation), Argentina (Paz *et al*., 2011), just determined at the subfamily level.

In the following age, Santacrucian SALMA (late Early Miocene), two genera are recorded in northern Chile (Figs 2-3): *Altitypotherium* Croft, Flynn & Wyss, 2004 with two species, and *Eotypotherium chico* Croft, Flynn & Wyss, 2004; they belong to the Chucal faunal assemblage, whose age is constrained between ~17 and ~22.5 Ma (Croft *et al*., 2004, 2016).

Some west-central Argentinean findings from Mendoza and San Juan provinces have been related to the Chilean genus *Altitypotherium*. On the one hand, one specimen from the Mariño Formation, in the Divisadero Largo area, Mendoza Province, was determined as cf. *Altitypotherium chucalensis* Croft, Flynn & Wyss, 2004 (Cerdeño, 2007); in addition, the material from Divisadero Largo, previously considered as *Trachytherus mendocensis* (Simpson & Minoprio, 1949) (Simpson *et al*., 1962), was reinterpreted as coming from the Mariño Formation and related to the other mesotheriine material from this formation (Cerdeño, 2007; Cerdeño *et al*., 2008). Besides, new remains recently recovered from the Mariño Formation in two areas of Mendoza (Divisadero Largo and Potrerillos; Combina *et al*., 2016) enlarge the knowledge of the taxon from this formation, as they are mandibular fragments that add to the published maxilla (Cerdeño, 2007); the presence of a small p3 and the interrupted enamel in m3 are distinctive features of this new material that has been very recently recognized as a new taxon (Cerdeño *et al.*, 2018). On the other hand, one of the two mesotheriines from the Chinches Formation, San Juan Province, was also related to *Altitypotherium* whereas the second one was proposed as a new taxon (López *et al*., 2011). Both taxa from San Juan are still lacking a detailed description, and a full comparison with the remains from Mendoza is pending. The mentioned localities in both provinces are geographically very close (Fig. 2: points 3-4) and taxonomic similarities between them would be expected for coeval faunas.

Another Early Miocene mesotheriine in Mendoza Province comes from the Aisol Formation, San Rafael area. It was considered as an undetermined mesotheriid (Garrido *et al*., 2014: tab. 3), maybe related to *Eutrachytherus modestus* Roth, 1899, a species poorly defined in the Colloncuran SALMA (Middle Miocene)

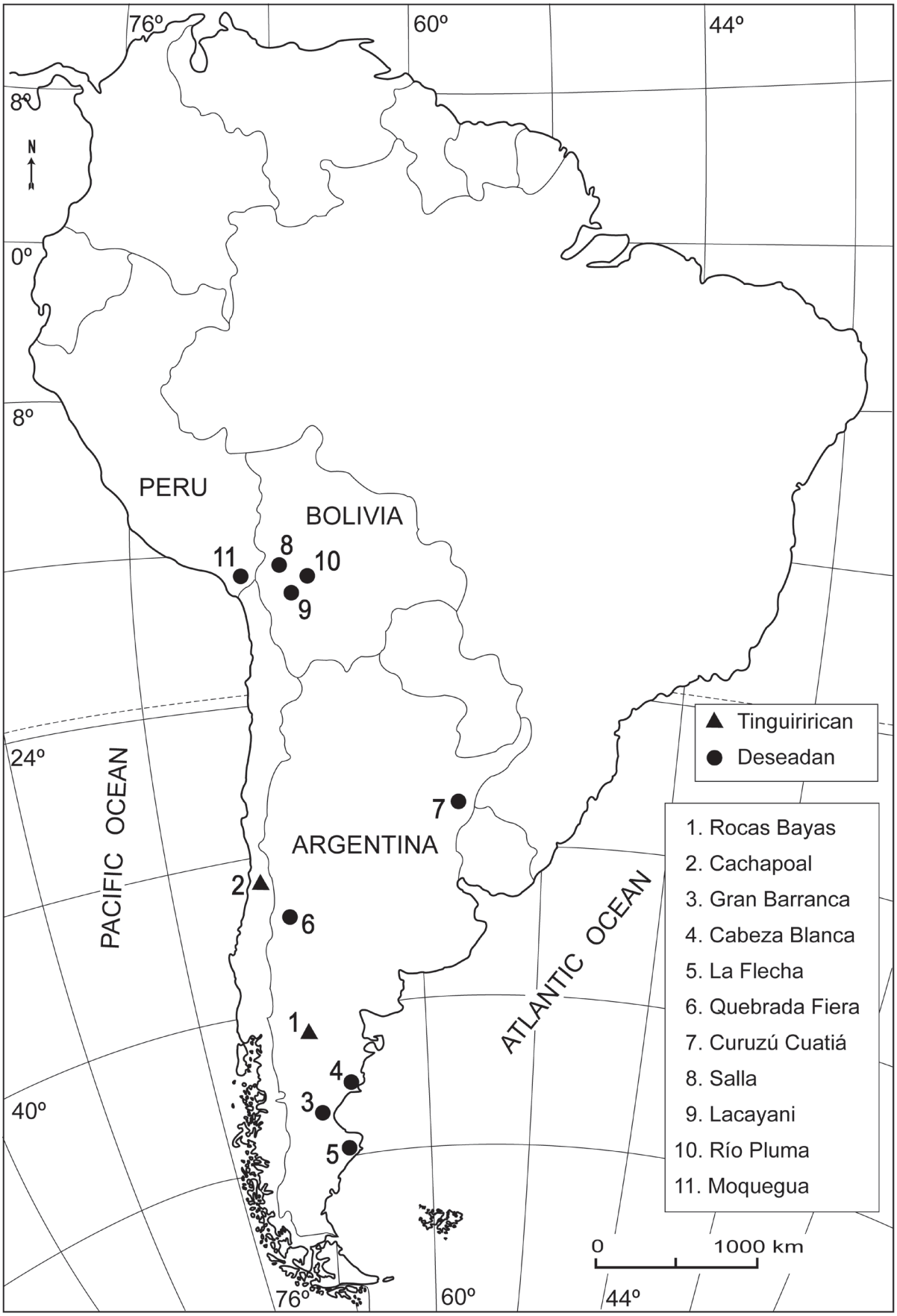

Fig. 1: Geographical distribution of Paleogene localities with Mesotheriidae.

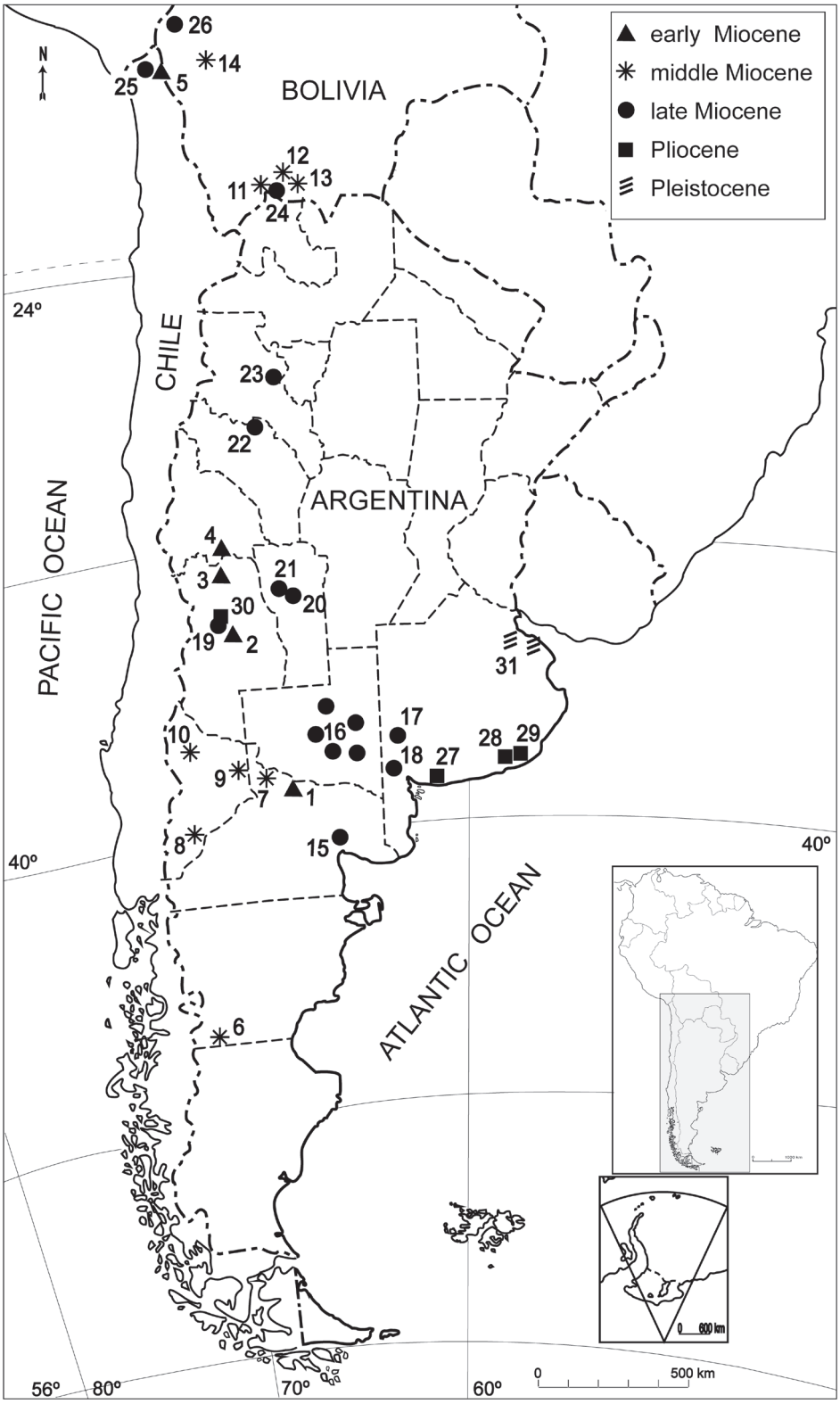

Fig. 2: Geographical distribution of Neogene-Quaternary localities with Mesotheriidae. 1-5, Early Miocene: 1, Chichinales Fm.; 2, Aisol Fm.; 3, Mariño Fm.; 4, Chinches Fm.; 5, Chucal. 6-13, Middle Miocene: 6, Laguna Blanca; 7, Vaca mahuida; 8, Río Collón Curá, 9, Bajada del Palo; 10, Chos Malal; 11, Cerdas; 12, Nazareno; 13, Quebrada Honda; 14, Choquecota. 15-22, Late Miocene: 15, Salinas del Gualicho; 16, Cerro Azul Fm. (up to 15 localities throughout the province); 17, Adolfo Alsina ('Fm. Epecuén'); 18, Arroyo Chasicó; 19, Huayquerías Fm.; 20, Río Quinto Fm.; 21, Los Llanos; 22, Salicas Fm.; 23, Andalhuala Fm.; 24, Casira; 25, Caragua; 26, Achiri. 27-29, Pliocene: 27, Monte Hermoso; 28, Miramar; 29, Chapadmalal; 30, San Carlos and San Rafael areas. 31, Pleistocene, La Plata River coastal area.

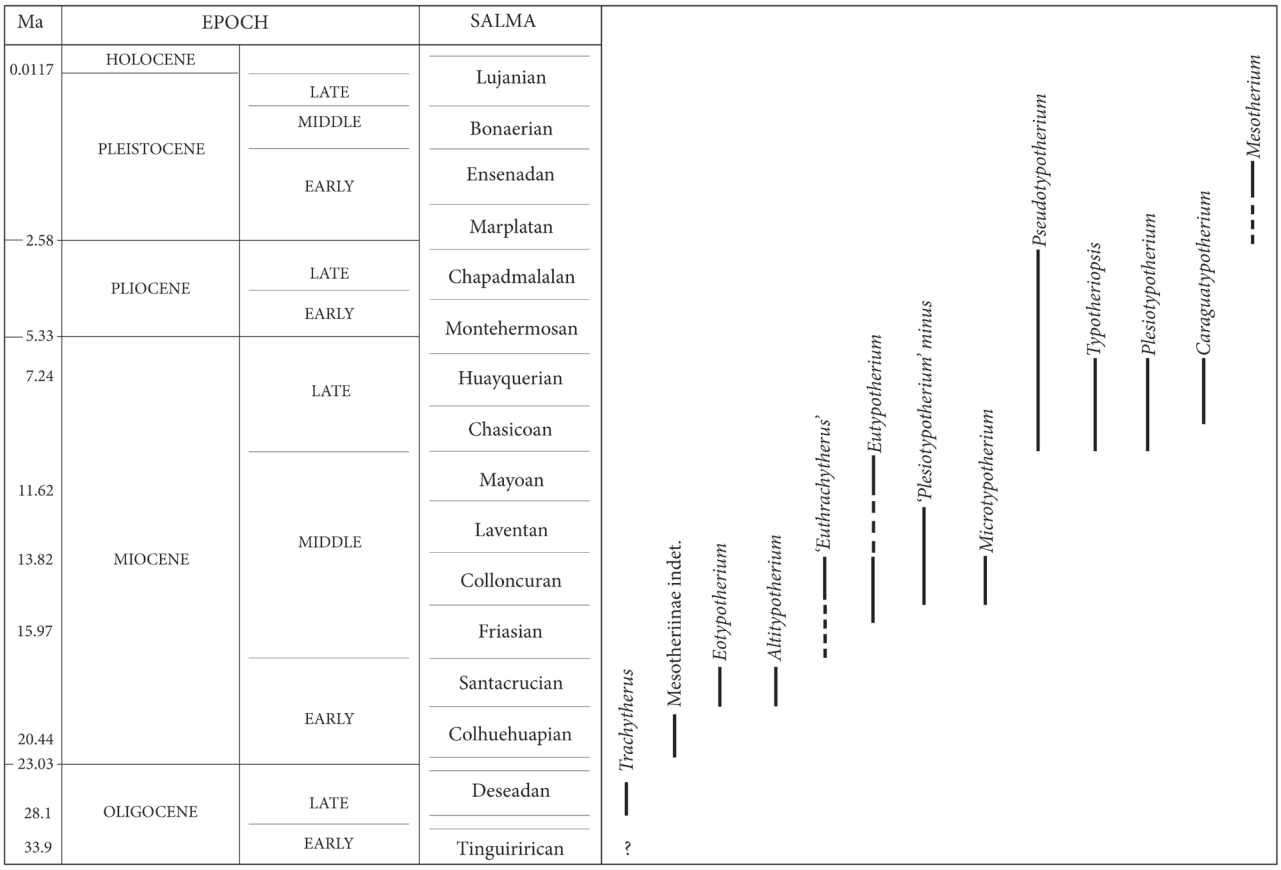

Fig. 3: Biostratigraphic distribution of mesotheriid taxa mentioned in the text. Ma, megaannum.

of the Collon Curá Formation, Neuquén Province (Roth, 1899; see Kramarz *et al*., 2011 for more data on Neuquén fossil faunas). Preliminarily, the preserved cheek teeth (P4-M3) of this maxilla from Aisol are similar in size and morphology to those from the Mariño Formation, although the M1 does not show the middle lobe as short as in the latter specimen (Cerdeño, 2007; Cerdeño *et al.,* 2018).

In contrast to these mentioned Argentinean records, no Early Miocene mesotheriine is known from higher latitudes in Patagonia, being absent from Chubut (Reguero & Prevosti, 2010) and the typical Santacrucian localities of Santa Cruz Province (Santa Cruz Formation; Cassini *et al*., 2012) (Fig. 2).

During the Friasian and Colloncuran SALMAs (Middle Miocene), the mesotheriid diversity increases (Fig. 3). Taxa from Argentina are referred to the genus *Eutypotherium* Roth, 1901, with the species *E. lehmannitschei* Roth, 1901 and *E. superans* Ameghino, 1904 (Rovereto, 1914; Kraglievich, 1930; Francis, 1965; Pascual & Bondesio, 1985; Cerdeño & Montalvo, 2001; Townsend & Croft, 2010; Cerdeño *et al*., 2012), and are present in Chubut, Río Negro and Neuquén provinces (Roth, 1899; Pascual & Bondesio, 1985; Kramarz *et al*., 2011) (Fig. 2). Nevertheless, there is no detailed taxonomic revision of this genus as neither is on the abovementioned *Eutrachytherus* from Neuquén Province.

Middle Miocene mesotheriines show a wider geographic distribution than the Early Miocene ones, as they are also known in Bolivia (Figs 2-3). The locality of Cerdas is assigned to the Colloncuran SALMA (Townsend & Croft, 2010; Croft *et al*., 2016) and has provided good remains of a mesothere preliminarily identified as '*Plesiotypotherium' minus* Villarroel, 1978; this species is also present in the fauna from Quebrada Honda, corresponding to the Laventan SALMA (Croft, 2007). Its assignation to the genus *Plesiotypotherium* is questioned due to the differences of '*Pl.' minus* with the Late Miocene species of *Plesiotypotherium* Villarroel, 1974a (see below), and likely represents a different genus (Townsend & Croft, 2010). Another Bolivian taxon of probably Colloncuran age is the small *Microtypotherium choquecotense* Villarroel, 1974b, from Choquecota.

Late Miocene mesotheriines (Figs 2-3) are present in Argentina, Bolivia, and Chile. In Argentina, they are absent from Patagonian areas, with the exception of Salinas del Gualicho locality (Pascual & Bondesio, 1985) in Neuquén Province (Fig. 2). The Argentinean record is grouped in two genera: *Typotheriopsis* Cabrera & Kraglievich, 1931 and *Pseudotypotherium* Ameghino, 1904 (Francis, 1960, 1965) (Fig. 4.1-2).

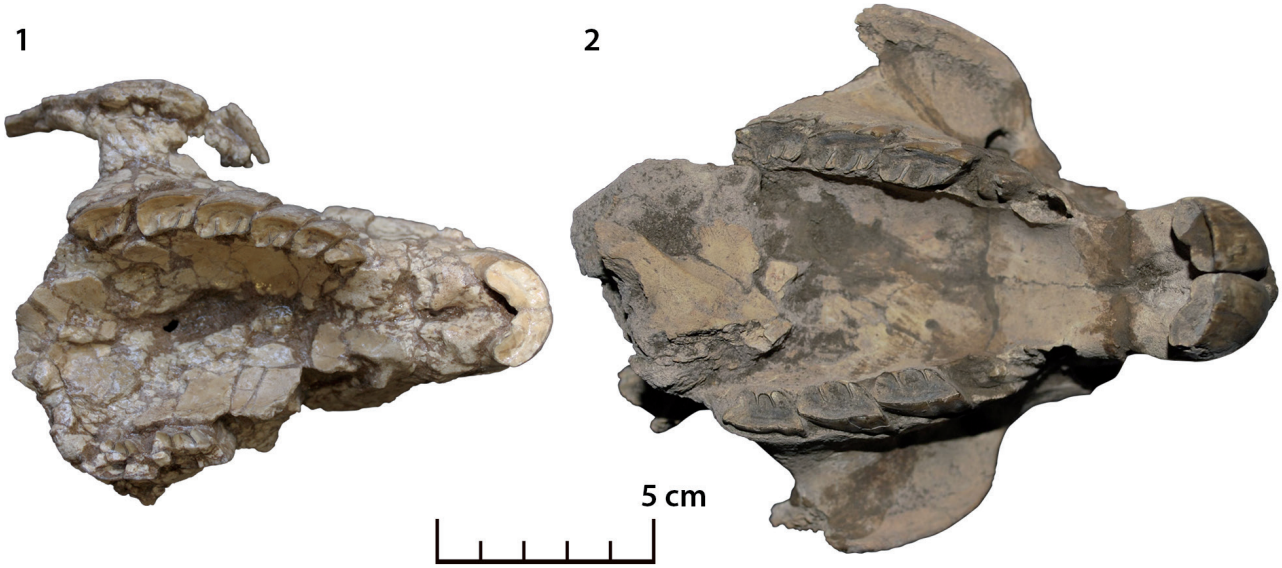

Fig. 4: Cranial fragments of *Pseudotypotherium*. 1, CRILAR Pv 433 from the Salicas Fm., La Rioja, Huayquerian SALMA; 2, MACN 7846 from Monte Hermoso, Buenos Aires, Montehermosan SALMA. Occlusal views.

Typotheriopsis is represented by *T. chasicoensis* Cabrera & Kraglievich, 1931 in the Chasicoan SALMA, whose type locality is Arroyo Chasicó, Buenos Aires Province. A second species, *T. silveyrai* Cabrera, 1937, is known in the Huayquerian SALMA (Late Miocene, but extending to Early Pliocene, e.g., Tomassini *et al.,* 2013), coexisting in some localities with the genus *Pseudotypotherium* (e.g., Cerdeño & Montalvo, 2001).

The Huayquerian SALMA is represented in different areas of Argentina: 1) the Pampean-central region ('Epecuen Fm.', Buenos Aires; Cerro Azul Fm., La Pampa, and Río Quinto Fm., San Luis; Cerdeño & Montalvo, 2001; Chiesa *et al*., 2011, and references therein); 2) west-central region (Mendoza and San Juan provinces; Rovereto, 1914; Cabrera, 1937; Rusconi, 1947; and see below); and 3) north-west region (Andalhuala Fm., Catamarca, and Salicas Fm., La Rioja – Fig. 4.1; i.e., Ameghino, 1891; Moreno & Mercerat, 1891; Marshall & Patterson, 1981; Cerdeño & Schmidt, 2013). The revision achieved by Cerdeño & Montalvo (2001) on Huayquerian mesotheriids led to consider only two species for this age in Argentina: *Typotheriopsis silveyrai* and *Pseudotypotherium subinsigne* (Rovereto, 1914), but see also Armella *et al.* (2018).

Both species have been recorded in Mendoza Province. In fact, *Typotheriopsis silveyrai* was defined based on a skull found in the area of Tupungato (Cabrera, 1937), in sediments that seem to correspond to the Río de los Pozos Formation (Irigoyen *et al*., 2000), correlated with the Huayquerías Formation (Yrigoyen, 1993, 1994) in the Huayquerías de San Carlos area. Concerning *Ps. subinsigne*, the type material described by Rovereto (1914) comes from the Huayquerías de San Carlos, but from the transitional levels between the 'Araucanense' and the 'Hermosense', later recognized as Tunuyán Formation, Pliocene in age (Yrigoyen, 1994). Recent investigations have provided mesotheriine remains from the Huayquerías Formation (Late Miocene) for the first time; among them, a partial skull and a maxillary fragment show the P4 with marked lingual groove, which would indicate its correspondence to *Pseudotypotherium* (but see Cerdeño & Schmidt, 2013, about the variation of this character), discarding *Typotheriopsis*. The full study of these new remains from Mendoza is still in progress.

As said above, Late Miocene mesotheriids are also known from Bolivia and Chile (Fig. 2). The Bolivian taxa are included in the genus *Plesiotypotherium* with the species *Pl. achirense* Villarroel, 1974a and *Pl. majus* Villarroel, 1974a from different levels in the locality of Achiri, and *Pl. casirense* Cerdeño, Vera, Schmidt, Pujos & Mamaní Quispe, 2012 from Casira (Fig. 5). In northern Chile, a different genus and species was described from the Caragua area, *Caraguatypotherium munozi* Flynn, Croft, Charrier, Wyss, Hérail & García, 2005. Very recently, new remains of this species were recovered; Montoya-Sanhueza *et al*. (2017) revised the whole sample and rejected one of the diagnostic characters of *Caraguatypotherium* established in the original description (Flynn *et al*., 2005).

The Pliocene (Montehermosan and Chapadmalalan SALMAs) record of mesotheriines is limited to Argentina, so far restricted to Buenos Aires and Mendoza provinces, and reflects a low diversity with respect to previous periods, with only one genus, *Pseudotypotherium* (Fig. 4.2).

Different Montehermosan species of *Pseudotypotherium* were defined from the type locality Monte Hermoso, Buenos Aires Province (Rovereto, 1914) (Fig. 2), but

Fig. 5: Skull and mandible of the skeleton MNHN-Bol-V-3724, holotype of *Plesiotypotherium casirense*, Casira, Bolivia (also published in Cerdeño *et al.,* 2012). Lateral view.

Fig. 6: Posterior portion of the skeleton in anatomical connection (MHNSR still unnumbered) from the Tunuyán Fm., Mendoza.

Cerdeño & Montalvo (2001) considered only one, *Ps. exiguum* (Ameghino, 1887). However, a detailed taxonomic revision of material from this age is pending (partially included in Fernández-Monescillo, 2018. The Pliocene levels of Tunuyán Formation in Mendoza Province have provided new remains that confirm the presence of *Pseudotypotherium subinsigne* (Rovereto, 1914) in this formation as originally stated. Therefore, new findings allow establishing that this species ranges from Huayquerian to Montehermosan SALMAs at least in west-central Argentina.

On the other hand, a new locality of Mendoza, near San Rafael city, has yielded an almost complete skeleton of mesotheriid in anatomical connection (Fig. 6), though the skull and mandible are almost destroyed except two teeth that allow some description. The fossil-bearing level is preliminarily correlated with the Tunuyán Formation. The particularity of this individual is its small size, with relatively long metapodials, being clearly smaller than the species of *Pseudotypotherium*, *Typotheriopsis* or *Plesiotypotherium*. A hypothetical relationship with the older small-sized mesotheriines from Middle Miocene (e.g., *Altitypotherium*, *Eotypotherium*, *Microtypotherium*, "*Pl.*" *minus*, or the small form from Catamarca – Nasif *et al.,* 2010; Armella *et al.*, 2018) needs to be checked.

In the Chapadmalalan SALMA (Fig. 3), *Pseudotypotherium* is represented by *Ps. hystatum* Cabrera, 1937 (see comments on this species in Cerdeño *et al*., 2012: 359) in Buenos Aires Province. In Mendoza, La Huertita Formation (San Rafael area) has yielded some remains of Montehermosan–Chapadmalalan age (Garrido *et al*., 2014), including a skull that presents some features similar to both *Ps. subinsigne* and *Ps. hystatum*.

The low diversity of mesotheriines is maintained in the Early Pleistocene, with the species *Mesotherium cristatum* Serres, 1867 (Cabrera, 1937; Francis, 1960, 1965) (Fig. 7), which in fact is the type genus of the family Mesotheriidae. The species is mainly known from levels of the Ensenadan SALMA (Early Pleistocene) in the coastal areas of La Plata River, Buenos Aires Province. Until now, mesotheres have not been recorded in the Pleistocene of west-central Argentina (Forasiepi *et al*., 2010).

4. FINAL REMARKS

Many taxa of Mesotheriidae were described since the second half of the XIX century, but not always well defined, which eventually led to a confusing systematics of the group. To a great degree, it was clarified by Francis (1960, 1965), who summarized the systematic background and established the valid taxa at generic level within the subfamily Mesotheriinae. One of the aspects that he tried to elucidate was the controversy on taxa based on supposedly juvenile specimens of other species known from adult individuals, a matter previously discussed by different authors. Francis' papers concluded that the specimens with three upper or two lower premolars were actually individuals with deciduous dentition, referable to known species whose adults only bear two upper and one lower permanent premolars. However, this controversy has recently been discussed again (Cerdeño & Schmidt, 2013), reaching a different interpretation: specimens previously considered to bear milk dentition are recognized as young adults with permanent cheek teeth, including well-developed P2/p3 (Fig. 4.1); at the same time, these authors evidenced a great change along the tooth crown that is reflected in morphological and proportional changes in the occlusal surface according to the ontogenetic stage. As stated by Cerdeño & Schmidt (2013), a deep revision of all mesotheriines is needed in order to establish inter- or intraspecific variations and the systematic value of this character, and to obtain a confident taxonomic classification of the group. At the same time, the ontogenetic changes have to be

Fig. 7: Life reconstruction of *Mesotherium* (created by Jorge Blanco).

taken into account when comparing samples, mainly when they are isolated teeth or incomplete tooth series, because dental morphology is rather homogeneous and even the number and shape of grooves can change with wear (Cerdeño & Schmidt, 2013). This is particularly important with respect to the lingual groove in P3–4, whose presence differentiates *Pseudotypotherium* from *Typotheriopsis*, but some variation in the morphology of the groove has been observed within the studied sample of *Pseudotypotherium* (Cerdeño & Montalvo, 2001; Cerdeño & Schmidt, 2013). Increasing number of mesotheriine samples from localities different in time and space require a revision of this group to supplement our knowledge about this important group of SANU.

From a paleobiogeographic point of view, Shockey *et al*. (2016) proposed a relatively small geographic area in Bolivia (the Bolivian Orocline Region) as an ancestral area for diversification of mesotheriids, both the earlier forms (Trachytheriinae) and the post-Deseadan taxa, based on the high diversity of mesotheriids in that region. In the context of Paleogene faunas, the oldest records of Trachytheriinae would be the Tinguirirican remains from northern Patagonia and central Chile (Fig. 1). In turn, within the Deseadan faunas, the assemblage from Quebrada Fiera, Mendoza, provides interesting paleobiogeographic data due to its latitudinal position, intermediate between Patagonia and lower latitudes (e.g., Bolivia, Peru) (see Cerdeño & Reguero, 2015 and references therein). In this sense, the mesotheriid from Quebrada Fiera fills a geographical gap for this group of notoungulates between Patagonian localities and Lacayani, Bolivia. Nevertheless, an outstanding fact is the scarcity of mesotheriid remains at that site, contrasting with the representation of other notoungulates and with the abundance of the family in other Deseadan localities, differences that are presently difficult to explain (Cerdeño, 2014).

The geographical range of mesotheriines suffered expansions and retractions throughout the Neogene-Quaternary. The Early Miocene record (Figs 2-3) concentrates in a latitudinal range between 38ºS (Chichinales Fm., Río Negro) and 32ºS (Chinches Fm., San Juan Province) around the Andes range, with a northern record at 18ºS (Chucal Fm., Chile). In Middle Miocene, two main distribution areas are detected, mid-northern Patagonia (~45º-37ºS) and Bolivia (~21º-17ºS),

the latter showing higher taxonomic diversity of mesotheriids. Late Miocene record shows a continuous distribution from ~38ºS (west of Buenos Aires Province) to ~16º (Achiri, west-central Bolivia), with localities along central, central-west and north-west Argentina and southern Bolivia. At this time, mesotheres are absent from Patagonia (except the record from Neuquén, see above). Pliocene and Pleistocene records show a low taxonomic diversity of mesotheriids, with only one genus each, becoming extinct in Middle Pleistocene. These records are mainly concentrated in Buenos Aires Province, except for the Pliocene taxa in Mendoza Province.

A paleobiogeographical pattern of mesotheriids cannot be precisely established from the observed diversity and geographical distribution, which are likely biased from two different aspects. On the one hand, the taxonomy of the group still needs a deep revision, including the search of unpublished material in old collections; on the other hand, the geographical findings depends on the extension of sediments of each age, and likely also on the existence of working teams close to the potentially fossiliferous outcrops. However, comparing with the paleobiogeographical study recently presented for the family Hegetotheriidae (Seoane *et al*., 2017), the retraction from Patagonia from Middle Miocene on is common to both families of notoungulates: the mesotheriids have a very scarce record in northern Patagonia and hegetotheriids are totally absent (Seoane *et al*., 2017: fig. 5).

Further analyses, including a more detailed phylogeny of mesotheriids and biogeographic methodologies (as used with hegetotheriids), would allow a more precise estimation of the ancestral areas of diversification, along with vicariance, dispersal, and extinction events within the family Mesotheriidae, and relate them to major climatic changes occurred throughout the Cenozoic.

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