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A new early Miocene Mesotheriidae (Notoungulata) from the Mariño Formation (Argentina): Taxonomic and biostratigraphic implications

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ABSTRACT

Old and new specimens from the early Miocene middle member of the Mariño Formation (Mendoza, Argentina) allow for a reinterpretation of a controversial Mesotheriidae taxon. Earlier known remains come from the Divisadero Largo locality and were, depending on the specimen, either previously described as *Trachytherus? mendocensis* or referred to a coeval taxon from Chile, *Altitypotherium chucalensis*. Based on new specimens, here described in detail for the first time, we propose that all mesotheriid material from Divisadero Largo, as well as new material from the Potrerillos locality belong to a new mesotheriid taxon. Recognition of the same taxon from these two localities establishes a sound biostratigraphic correlation. The combination of morphological characters leads to the proposal of a new generic name, *Rusconitherium*, for *Trachytherus? mendocensis*, establishing *Rusconitherium mendocense* New genus and New Combination. This nomenclatural act is due to the fact that *T.? mendocensis*, formerly thought as a Trachytheriinae from the Paleogene Divisadero Largo Formation, actually comes from the Mariño Formation and belongs to the same taxon as the new material. The missing holotype of *T.? mendocensis* prompts us to propose a neotype and a new diagnosis for this species, which better characterize the Santacrucian mesotheriids from Mendoza. A phylogenetic analysis does not support a close relationship between this species and *Altitypotherium* (or any other mesotheriine genus) counter to a previous hypothesis. An unnamed new taxon from the Chinches Formation (San Juan Province) could belong to *Rusconitherium*, but its full description is pending, as well as a thorough revision of most Mesotheriinae members. Sediments at Potrerillos reveal two paleoenvironmental scenarios: dune fields, influenced by volcanic events, and capillary water that provided humid conditions encouraging vegetation and fauna.

1. Introduction

The Mariño Formation (Biondi, 1936, nom. subst. Rolleri and Criado Roque, 1970) is a continental clastic sequence comprised of Cenozoic fill in the Cuyo Basin (Ramos, 1999). It reaches up to 1900 m of thickness, and is classically subdivided in three members: Conglomerados Violáceos at the base, Areniscas Entrecruzadas or Areniscas Inestratificadas in the middle section, and Estratos de Mariño or Serie del Higueral at the top (Chiotti, 1946). These three members present inter-discordant or pseudo-concordant relationships (Sepúlveda, 2001), depending on the observed outcrops. Lower and upper members correspond to fluvial and alluvial environments, respectively, deposited under arid and semi-arid conditions, whereas the medium member is interpreted as eolian deposits (Irigoyen, 1997). This formation has been recognized in two main areas near Mendoza city, Divisadero Largo and Cacheuta-Potrerillos (Mendoza Province, central-west Argentina; Fig. 1).

Divisadero Largo, 8 km to the west from the city, is a well-known fossiliferous area, where a mammal assemblage is known since the beginning of the 20th century (Simpson et al., 1962 and references therein), coming from the Divisadero Largo Formation, which underlies the Mariño Formation. This fauna has been recently re-studied, which led to the reinterpretation of some taxa and the revision of the Divisaderan South American Land Mammal Age (SALMA) and its biostratigraphic position, currently considered as middle Eocene (López, 2008, 2010; Cerdeño et al., 2008; and references therein).

The Mariño Formation at Divisadero Largo has recently yielded fossil remains. Although very scarce, the remains from the middle

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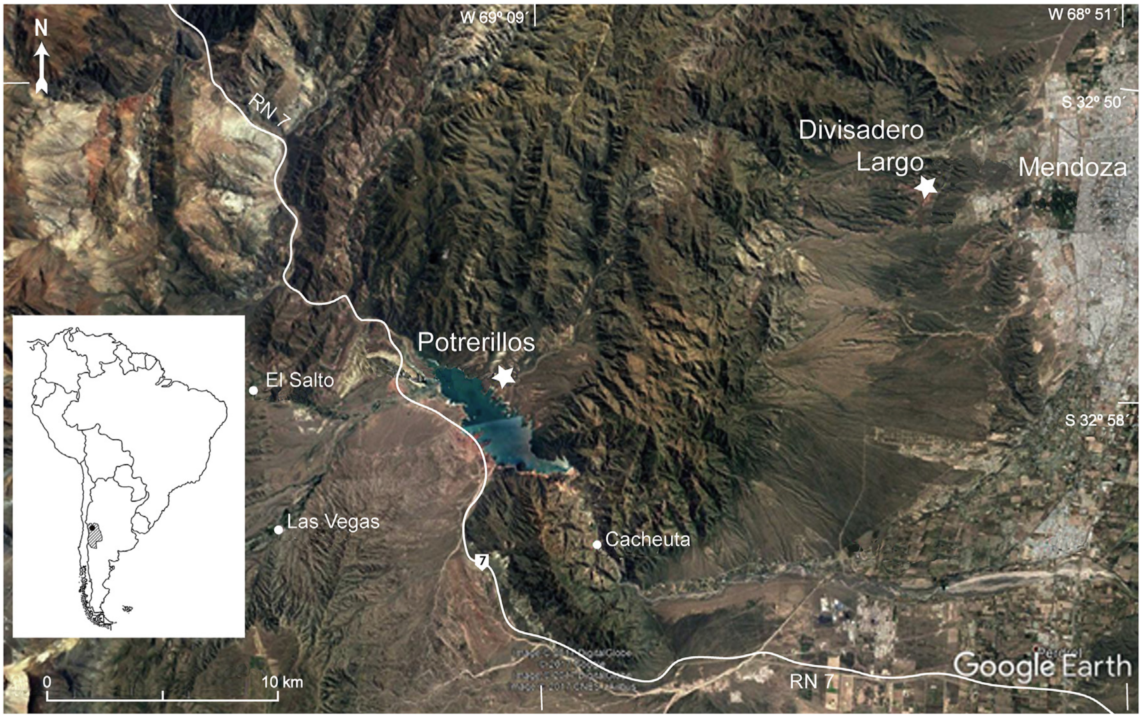

Fig. 1. Geographical location of the fossiliferous localities (stars) of the Mariño Formation at Divisadero Largo and Potrerillos, Mendoza Province, Argentina.

member of the Mariño Formation allow the recognition of two taxa (a mesotheriid and a rodent) indicating an early Miocene age (Santacrucian SALMA) for this unit (Cerdeño et al., 2006; Cerdeño, 2007; Cerdeño and Vucetich, 2007; see below).

The area of Cacheuta and Potrerillos villages, about 45–70 km southwest of Mendoza city, also presents thick sections of Cenozoic sediments, including levels of both Divisadero Largo and Mariño formations (Yrigoyen, 1993; Irigoyen et al., 2000, 2002). Thick exposures of the latter are at both the northern and southern margins of the Potrerillos dam (Irigoyen et al., 2000, 2002). The first fossils known from the exposures in Cacheuta area correspond to continental bivalves, described by Rusconi (1949) as *Corbicula elchaensis*. The presence of mammals in the area is known only from a maxillary fragment referred to the Proterotheriidae *Thoatheriopsis mendocensis* Soria, 2001, afterward revised and discussed by Villafañe et al. (2012; see references therein).

Irigoyen et al. (2000, 2002) dated the Mariño Formation after paleomagnetic and isotopic dating (^{40}Ar-^{39}Ar) at the Arroyo del Agua Blanca section in the Cacheuta area, providing an age of 12.03 ± 0.45 Ma for the upper levels and between ~15.4 and 14.7 Ma for the middle member. These data led the authors to establish a temporal range of deposition for the Mariño Formation between ~15.7 and ~12.0 Ma, which corresponds to the middle Miocene (Langhian–Serravalian Stages; Cohen et al., 2013-updated). Nevertheless, the mammals from the middle member of the Mariño Formation at Divisadero Largo (Cerdeño et al., 2006; Cerdeño, 2007; Cerdeño and Vucetich, 2007) indicate an older age for this fauna, as they are comparable to Santacrucian taxa, late early Miocene. In fact, both the rodent (Cerdeño and Vucetich, 2007) and the mesotheriine (Cerdeño, 2007) resemble taxa from Patagonia, Argentina (*Scleromys* Ameghino, 1887, from the Pinturas Formation) and Chile (*Altitypotherium chucalensis* Croft et al., 2004, from the Chucal Formation), respectively, which correspond to the Santacrucian SALMA (see also Fleagle et al., 2010, for absolute dating of the Pinturas and Santa Cruz formations). Considering that the rodent was not identified at specific level and the mesotheriine is now recognized as an endemic species, a possible middle Miocene age for them could be argued according with the absolute ages. However, morphological similarities with Santacrucian taxa are evident, *Scleromys* is confidently recognized only during early Miocene (see discussion in Cerdeño and Vucetich, 2007), and the absolute ages for the Mariño Formation were obtained from the top of the sequence; therefore, with the present data, an early Miocene age for the middle Member of the formation seems still more plausible.

1.1. Taxonomic background on the mesothere from Divisadero Largo

The mesotheriid species *Trachytherus mendocensis* Simpson and Minoprio, 1949 from the Divisadero Largo area was first assigned to this Paleogene genus in part because of the authors assumed it came from the Paleogene (pre-Deseadan SALMA) Divisadero Largo Formation, despite of the fact that its stratigraphic origin was not established with precision: "… near its type locality [Divisadero Largo Formation] around and south of the eastern end of the Cerro Divisadero Largo" (Simpson and Minoprio, 1949: 2). However, Simpson et al. (1962: 272–273) harbored some doubts about this determination, reflected by later adding a question mark to the name. The recovery in recent years of remains of a mesotheriid (maxillary fragment MCNAM-PV 3648) and a rodent from the overlying Mariño Formation at the Divisadero Largo locality allowed for a reinterpretation of both the stratigraphic origin and the taxonomic identification of *T.? mendocensis* (Cerdeño et al., 2006, 2008; Cerdeño, 2007; Cerdeño and Vucetich, 2007; López and Manassero, 2008). Further, the study of the first mesotheriine remains from the Mariño Formation (Cerdeño, 2007) led to the discovery that the holotype for *T.? mendocensis* (MCNAM 2494) is missing. The only specimen of this taxon that provides any comparative value is the isolated M3 of MLP 45-VII-10-2 (Simpson et al., 1962).

Concerning the loss of the holotype MCNAM 2494, it is worth mentioning that one of us (EC) was in charge of ordering and cataloguing the entire paleontological collection of the MCNAM (see Cerdeño, 2005), and there is no doubt that the holotype is missing. The history of this museum includes several location changes, many years of decay, and even a fire, all of which contributed to the loss of many fossils (Cerdeño, 2005). Fortunately, some vertebrate specimens have been recovered through happenstance, including the holotypes of *Adiantoides* *leali* Simpson and Minoprio, 1949 and '*Cunampaia simplex*' Rusconi, 1946 (Agnolín and Pais, 2006) from the Divisadero Largo Formation. The former was located in the AMNH (New York), where Dr. G. G. Simpson could likely have taken it in the 1950s as part of his study of this fossil assemblage (Simpson et al., 1962). As the South American ungulates in the AMNH collections have been thoroughly revised by different Argentinean and other researchers without citing the presence of MCNAM 2494, we can infer, rather confidently, that the holotype of *T.? mendocensis* is actually not there either.

While Cerdeño (2007) recognized similarities between MCNAM-PV 3648 from the Mariño Formation and the Chilean species *Altitypotherium chucalensis*, she also stated the probable correspondence of MCNAM-PV 3648 with *T.? mendocensis* (or to be more specific, the M3 MLP 45-VII-10-2). The lack of published photographs of the lost holotype (MCNAM 2494) somewhat complicated an accurate assessment. Concerning the schematic drawing of P2–3 (Simpson and Minoprio, 1949: Fig. 6), it was reinterpreted as P3–4 by Cerdeño et al. (2008), a fact that indirectly implied the lack of P2 as in most mesotheriines (see Cerdeño and Schmidt, 2013, about this character) and contrary to trachytheriines; in addition, the recognition of MCNAM 2494 as a mesotheriine agreed with the proposed origin of that material from the Mariño Formation, that is from the early Miocene, when trachytheriines were already extinct.

Now the new findings of mesotheriines from both Divisadero Largo and Potrerillos allow a more complete characterization of the taxon, which leads to the recognition of a new early Miocene mesotheriid as exposed below.

2. Material and methods

The newly recovered remains from Divisadero Largo area are two fragments of the mandible of the same mesothere individual described some years ago from a maxillary fragment (MCNAM-PV 3648; Cerdeño, 2007). At the time of recovery of MCNAM.PV 3648, it seemed that the hard sediment did not contain more material, but time and erosion have provided new remains at exactly the same point; first, most part of the left horizontal ramus of the mandible was found, and years later the symphysis together with part of the right ramus completed the specimen (MCNAM-PV 4005). Although there is no doubt about its belonging to the same animal as the maxilla, two different collection numbers were provided for both anatomical elements due to the time span separating the findings and the management of the collection. Both the maxillary and mandibular fragments are deposited in the Vertebrate Paleontology Collection of the Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano', Mendoza. The material from Potrerillos area (IANIGLA-PV 151), found at the northern margin of the Potrerillos dam, belongs to the Vertebrate Paleontology collection of the IANIGLA, CCT-CONICET-Mendoza.

The comparative work here has focused on other early Miocene, Santacrucian mesotheriines. Santacrucian mesotheres are best represented in the Chucal Formation (Chile), with three recognized species: *Altitypotherium chucalensis*, *A. paucidens* Croft et al., 2004, and *Eotypotherium chico* Croft et al., 2004. Other Santacrucian records are those from the Aisol Formation (Mendoza Province), provisionally referred to *Eutrachytherus modestus* Roth, 1903, but also comparing favorably to *Altitypotherium* (Garrido et al., 2014: 149–151, tab. 3, Fig. 6), and from the Chinches Formation (San Juan Province), where two taxa were recognized: one of them related to *Altitypotherium* from Chile and the second one considered as an unnamed new taxon (López et al., 2011: Fig. 4h–j).

Comparative data were observed from mesotheriid material stored in different institutions (MACN, MLP; specimens are detailed in the text when appropriate), as well as bibliographic sources (e.g., Croft et al., 2004; Flynn et al., 2005; Croft, 2007; Townsend and Croft, 2010; Montoya-Sanhueza et al., 2017). Some casts of the species from Chile are stored in MCNAM and we had access to some original photographs of *A. chucalensis* and the maxilla from the Aisol Formation.

A phylogenetic analysis has been performed through the computer program TNT 1.1 (Goloboff et al., 2008a; b), as detailed in the corresponding section.

2.1. *Institutional abbreviations*

AMNH, American Museum of Natural History, New York; IANIGLA-PV, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Vertebrate Paleontology, Mendoza; MACN, Museo Argentino de Ciencias Naturales 'B. Rivadavia', Buenos Aires; MCNAM-PV, Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano', Vertebrate Paleontology, Mendoza; MHNM, Museo de Historia Natural de Mendoza (presently MCNAM); MHNSR-PV, Museo de Historia Natural de San Rafael, Vertebrate Paleontology, San Rafael; MLP, Museo de La Plata, La Plata; SGOPV, Vertebrate Paleontology collections, Museo Nacional de Historia Natural, Santiago de Chile.

2.2. *Anatomical abbreviations*

C/c, upper/lower canine; H, height; I/i, upper/lower incisor; L, length; M/m, upper/lower molar; P/p, upper/lower premolar; W, width.

3. Geological data

The studied fossils come from the Areniscas Entrecruzadas, the middle Member of the Mariño Formation, in both Divisadero Largo and Potrerillos outcrops (Fig. 1). The stratigraphic section at Divisadero Largo was detailed by Cerdeño et al. (2006). Concerning Potrerillos, approximately 250 m of continuous and homoclinal sedimentation can be observed (Rb N355°, Bz 34°W) (Fig. 2). The sedimentary layers were analyzed through the identification and description of lithofacies and facies associations, detailed in Table 1. The eolian facies associations were analyzed according to the architectural elements, the limiting surfaces, and their spatial distribution (Tripaldi, 2012; Armas and Sánchez, 2013; Jones et al., 2016). For the fluvial facies associations, we used the Miall's (1984, 1985) classical methodology; for pyroclastic deposits, we follow Branney and Kokelaar (2002).

Irigoyen (1997) considered that the deposit environment of the Areniscas Entrecruzadas Member of the Mariño Formation is eolian, although Cerdeño et al. (2006) also pointed out fluvial and lacustrine environments developed during the sedimentation of this member. The present study at Potrerillos reveals that two different paleoenvironments evolved. One is represented by dune fields with straight ridge dunes (MF element), which interdigitate with sand fields (MA element). Among the straight-crested dunes, the IDh element developed. This sea of sand was influenced by a volcanic event, associated with the Miocene volcanic arc, which deposited a thin stratum of very fine ash, enriched in amphibole crystals, typical of ash fall, inside of the interdune (lithofacies mT). Simultaneously, the tephra that fell on the dunes generated the Shmp lithofacies, where the sediments were enriched in amphibole crystals (providing the characteristic greenish color). Due to the dynamics of the eolian sedimentation, the finest and lightest pyroclastic material was transported out of the study area.

The other recognizable paleoenvironment is represented by the IDh elements, characterized by conspicuous desiccation cracks, water droplet marks, bioturbations, ripples, and adhesion warts, indicating the presence of water at the capillary level that avoided the continuous deflation of the sediment. The level of humidity of the IDh would allow the presence of vegetation and fauna adapted to this environment. At times, the phreatic level would rise above the surface (Mountney and Thompson, 2002) and generate small, very shallow water bodies, where sedimentation prevailed by decantation. Subsequent evaporation then generated desiccation cracks. The presence of concretions (Cc) in the Sme layers could be associated with early cementing processes, due to

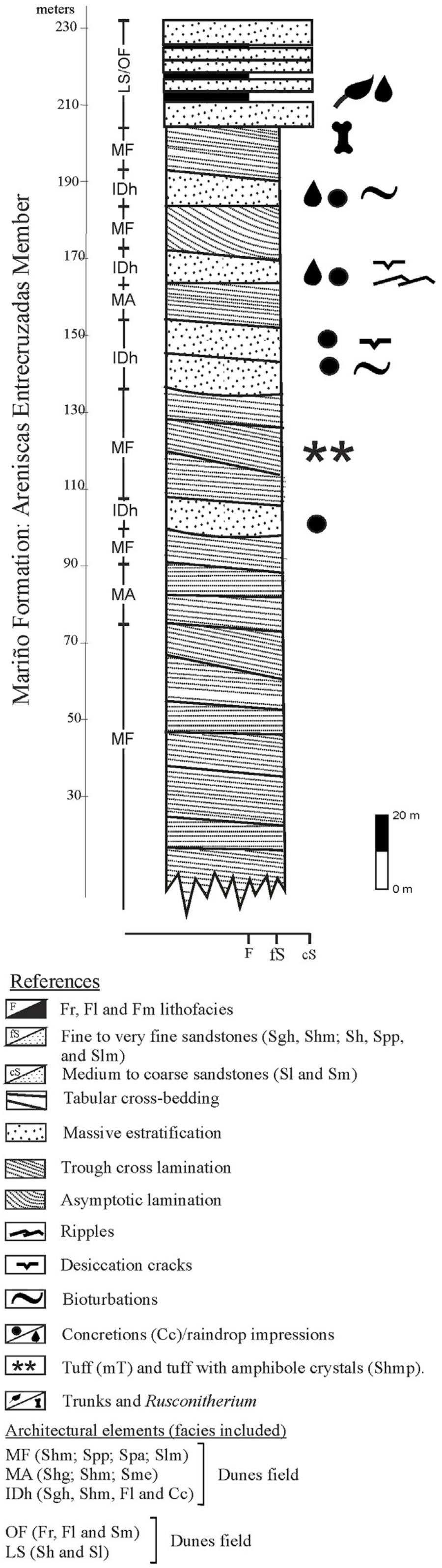

Fig. 2. Stratigraphic profile of the middle Member of the Mariño Formation at Potrerillos locality.

the moisture in the sediment.

These conditions of eolian sedimentation were interrupted locally by the development of an ephemeral fluvial system interlaced with the sandy system, with very diffuse channels, wide and very shallow, without net edges, which generated tabular to slightly wedged bodies (SL element). In these channels, when there was no aqueous flow, the finest facies belonging to the OF element were deposited, mainly by decanting. This more humid environment generated suitable conditions for the development of paleoflora (fossil wood remains; Franco et al., 2014 and collaboration in progress). Subsequently, these conditions disappeared and the eolian system was reinstalled, with the development of MA and MF elements.

Probably, the water-table level fluctuation, strongly influenced by the rainfall regime, controlled the development of the ephemeral systems within the interdunes.

The facies architecture, characterized by successive sets of eolian dunes of straight ridges, wet interdunes, and the ephemeral fluvial system, generated a humid eolic system, where the water table or its capillary fringe intercepts the interdune surface, controlling the eolian accumulation and the evolution of interdunes (Mountney and Thompson, 2002), while the presence of ephemeral fluvial systems could be indicating an interconnection between the interdunes (Jones et al., 2016). These humid eolic systems are characterized by small-sized dunes and sand sheets, because it is the humidity of the water table or its capillary fringe that controls the angle of growth of the dune and the availability of loose sediment to be transported.

The sandstones at Potrerillos are equivalent to those at Divisadero Largo (Cerdeño et al., 2006), reflecting the same sedimentary environment. The described pyroclastic lithofacies could probably be correlated with the levels dated by Irigoyen et al. (2002) at the top of the Mariño Formation in Cacheuta-Potrerillos area.

4. Systematic paleontology

Order NOTOUNGULATA Roth, 1903
Suborder TYPOTHERIA Zittel, 1893
Family MESOTHERIIDAE Alston, 1876
Subfamily MESOTHERIINAE Simpson, 1945
Rusconitherium NEW GENUS

Type species. *Trachytherus mendocensis* Simpson and Minoprio, 1949

Diagnosis. As for the type and only species.

Etymology. Dedicated to Carlos Rusconi (1898–1969), a prestigious Argentinean naturalist who devoted more than 30 years to advancing the knowledge of paleontology and archaeology of Mendoza; and therium (from Greek, beast), usual ending of mesotheriid generic names.

Rusconitherium mendocense (Simpson and Minoprio, 1949) New combination Figs. 4 and 5

Trachytherus mendocensis Simpson and Minoprio, 1949: 18, Fig. 6 (original description); Simpson and Minoprio, 1950: 249, Fig. 2.

Trachytherus? mendocensis Simpson and Minoprio, 1949: Simpson et al., 1962: 272, Figs. 16–17.

Mesotheriinae indet.: Cerdeño et al., 2006: 211, Fig. 5.

cf. *Altitypotherium chucalensis* Croft et al., 2004: Cerdeño, 2007: Figs. 2 and 3.

Note. The specific epithet changes the ending to be concordant with the generic name in this new combination, according to the ICZN (2000:art. 31).

Holotype. MCNAM (ex-MHNM) 2494: right P3–4 (according to Cerdeño et al., 2008), M1, and parts of right M2, and left P3?–M1. Presently lost.

The holotype was originally described as “four associated upper cheek teeth and fragments of at least three others …,” (Simpson and Minoprio, 1949: 18), without catalogue number, and it was later indicated as belonging to Minoprio's collection by Simpson and Minoprio (1950: 249). Simpson et al. (1962: 272) provided the inventory number corresponding to the MHNM (presently MCNAM). The three mentioned papers illustrated the same schematic drawing of four upper teeth of the holotype, then recognized as P2–3 and M1–2, but the premolars later interpreted as P3–4 by Cerdeño et al. (2008; see below).

Neotype (here designated). MCNAM-PV 3648, right maxilla with

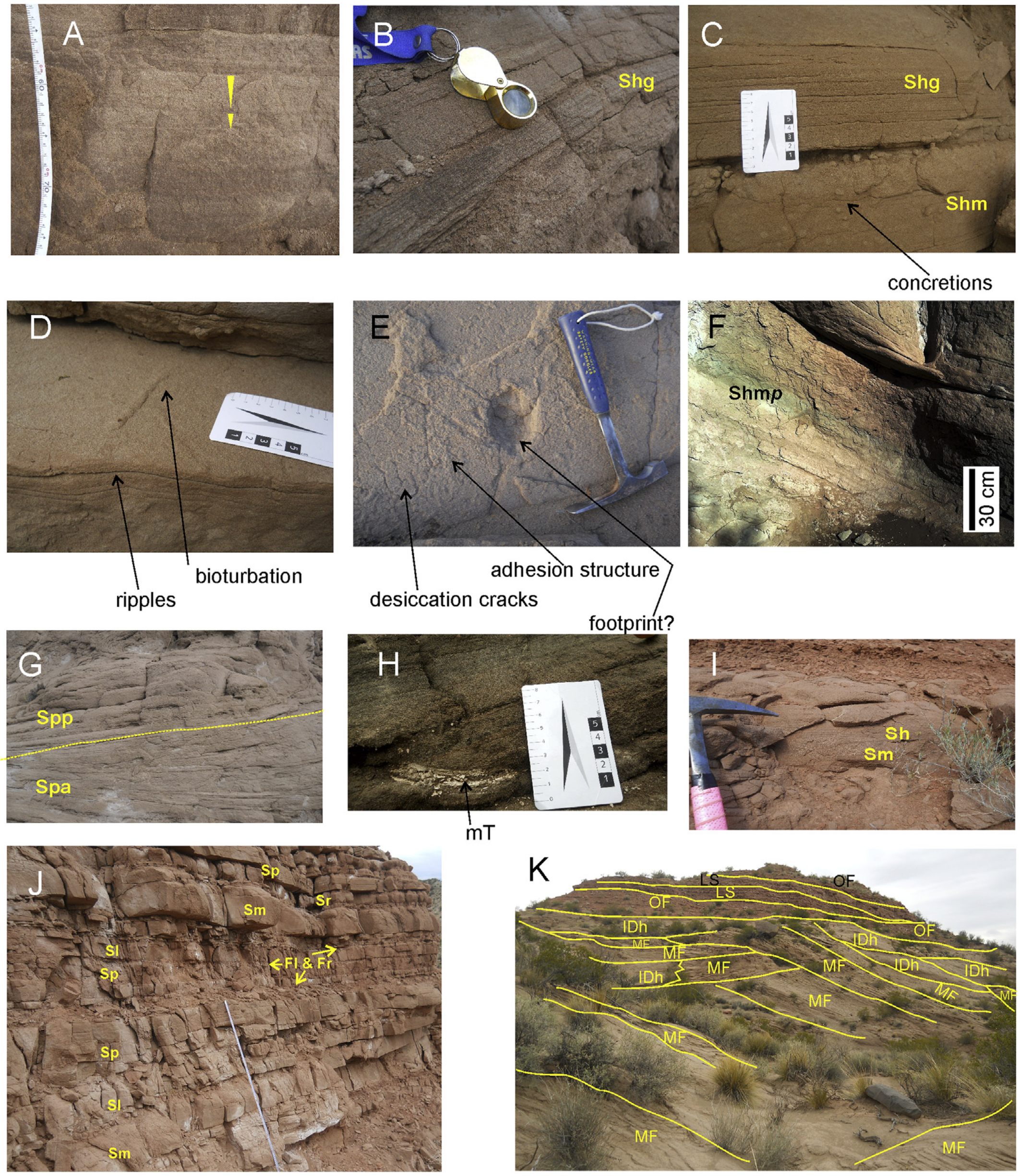

Fig. 3. **A–I**, details of lithofacies of the Mariño Formation at Potrerillos locality: **A–G**, eolian lithofacies; **H**, pyroclastic lithofacies; **I**, fluvial lithofacies. **J**, general view of stratification; **K**, architectural elements recognized in the outcrops of the Mariño Formation. **LS** and **OF**, fluvial elements; **MA** and **MF**, dune fields; **IDh**, interdunes. See Table 1 for explanation of different facies and elements.

P3–M3, and MCNAM-PV 4005, incomplete mandible preserving right i1–2, p3–m1 and left m1–3, corresponding to the same individual (see Material and methods for explanation of the different collection numbers).

Referred material. Holotype, neotype, and MLP 45-VII-10-2, right M3, from Divisadero Largo locality; and IANIGLA-PV 151, maxillary fragment with incomplete left P3–M3 and associated mandibular fragment with left m3, from Potrerillos locality. The specimen MLP 45-VII-10-2 was described by Simpson et al. (1962).

Neodiagnosis. *Rusconitherium mendocense* is characterized by an i1/i2 ratio between 1.5 and 1.99, subcylindrical and reduced p3, very procumbent symphysis, and short posterolingual interruption of enamel along the crown height of m3. Differs from *Altitypotherium chucalensis* and *A. paucidens* in: relatively smaller i2, more triangular P4, with straighter mesial wall, lower length/width ratio in m2, and m3 with deeper lingual groove on the talonid and short posterolingual interruption of enamel. *R. mendocense* shares with *A. chucalensis* the proportion of M1: length/width ≤1.30 in contrast to other mesotheriines. With respect to *A. paucidens*, the mandible of *R. mendocense* has a more procumbent symphysis and lower, slenderer, and less divergent horizontal ramus, with more convex ventral border.

Geographic and stratigraphic origin. Divisadero Largo and Potrerillos (northern margin of the Potrerillos dam) localities, Mendoza Province, Argentina. Middle Member of the Mariño Formation, Santacrucian SALMA, early Miocene.

4.1. Comparative description

Upper dentition. MCNAM-PV 3648 (Fig. 4A) was previously described by Cerdeño (2007), who also considered that the material identified as *Trachytherus? mendocensis*, especially the isolated M3 MLP 45-VII-10-2 (Simpson et al., 1962), corresponds to the same taxon (Fig. 4B). Although material for this taxon has been described before, the description here includes the heretofore undescribed IANIGLA-PV

Table 1
Lithofacies and architectural elements in the Mariño Formation section at Potrerillos locality.

Eolian lithofacies	Description	Interpretation	
Shg	Very fine, well-selected, brown sandstones, with fine to very fine planar lamination. Internally, the sheets have an inverse gradation and concentration of felsic minerals (Fig. 3A–C).	Migration of eolian waves on small-sized mesoforms or flattening of pre-existing wavelets due to strong winds (Hunter, 1977) on eolian beds or interdunes.	
Shm	Fine sandstones to very fine brown with thick to very thick, massive planar lamination. They present spherical to massive ellipsoidal concretions of fine to very fine sandstone, massive, with an average diameter of 0.8 to 1.5 cm. Internally, they do not have a growth nucleus or concentric lamination (Cc), they generate tabular bodies with slightly wedge-shaped bodies, which form sets (40 cm to 60 cm) with flat net contacts. Small desiccation cracks in some of the planes can be observed (Fig. 3C).	Fall of grains in mesoforms of small size or migration of eolian waves in interdunes and eolian beds.	
Sme	Fine brown, massive sandstones with bioturbation, desiccation cracks, and ripples (Fig. 3D–E).	Deflation levels within the interdunes.	
Shmp	Very fine, greenish brown sandstones, very well selected, with planar crisscross lamination from low fine to very fine angle. They form a tabular body. The characteristic greenish color is given by the presence of amphibole crystals, mixed in the sediment (Fig. 3F).	Fall of grains in mesoforms of small size or migration of wind waves in interdunes and eolian beds, with pyroclastic rework.	
Spa	Well-selected, very fine brown sandstones, with asymptotic planar intertwined stratification. They form sets with crossed stratification of high angle (NE 20°) that generate cuneiform or tabular bodies with flat non-erosive contacts (Fig. 3G).	Generated by migrant straight crested dunes (2D), with fall processes and grain flows to leeward.	
Spp	Well-selected, very fine, brown sandstones, with crisscross planar stratification (Fig. 3G).	Generated by migrant straight crested dunes (2D), dominated by fall processes and grain flows.	
Pyroclastic lithofacies	**Description**	**Interpretation**	
mT	Small, white, massive lapillite with amphibole crystals visible in magnifying glass. The body is slightly lenticular, with net contacts (Fig. 3H).	Fall tuff, related to the presence of distant pyroclastic clouds. Associated with Shmp.	
Fluvial lithofacies	**Description**	**Interpretation**	
Sm	Medium to fine, reddish brown, massive sandstones that generate 30 cm-thick tabular bodies, with net contacts (Fig. 3I).	Decantation or flat layer deposits of low flow rate.	
Sp	Medium to fine, reddish brown sandstones, in 5 to 10 cm-thick layers, with scalloped net contacts (Fig. 3J).	Megaondules with straight ridges (2D).	
Sl	Medium to thick reddish brown sandstones, with planar lamination of very low angle (Fig. 3J). The sheets are interspersed with sheets of larger and smaller granulometry. They generate tabular bodies of irregular (concave) bases and plane roof.	Deposit generated by mantiform currents of high flow regime.	
Fr	Reddish brown, laminated, very bioturbated pelites and current marks (Fig. 3J).	Deposits associated with floodplains, interchannel areas or ephemeral bodies of water.	
Fl	Reddish brown, laminated pelites, interspersed with very thin sheets of fine sand (Fig. 3J).	Deposits associated with floodplains or ephemeral bodies of water.	
Fm	Reddish brown, massive pelites.	Decanting deposits in interchannel areas, interdunes or ephemeral water bodies.	
Eolian Architectural Elements[a]	**Description**	**Interpretation**	
MF	Generated by tabular and cuneiform bodies, with an average thickness of 0.80 to 1.20 m. Present lithofacies are Shm, Spp, Spa, and Slm. The bodies are limited by overimposed flat to slightly curved surfaces, or very little inclined.	Formed by migration of straight-crested eolian dunes.	Dune field
MA	Formed by tabular bodies, 1 m thick. Present lithofacies are Shg, Shm, and Sme (with and without bioturbations). This element is associated with FM.	Vertical accretion of the sandy sheet by migration of eolian waves. Bioturbations can be associated with a vegetal cover and to organic activity.	
IDh	Tabular bodies, 0.3 to 0.5 m thick, formed by Sgh, Shm, and Fl. Very thin plates of pelites are observed, with bioturbations, desiccation cracks, ripples and adhesion warts, and concretions (Cc). Associated with MF.	Wet interdunes. Bioturbations and desiccation cracks indicate the presence of sporadic water.	Interdune
Fluvial Architectural Elements[b]	**Description**	**Interpretation**	
LS	Formed by tabular to slightly wedged bodies, generated by lithofacies Sp, Sh, and Sl.	Recognized as the product of sudden and episodic floods that deposit sand in high flow regime conditions.	Ephemeral system
OF	Formed by tabular bodies at the base and flat roofs, where lithofacies Fr, Fl, Fs, and subordinate Sm predominate.	Deposits of floodplain or ephemeral bodies of water, where decantation and evaporation prevail.	

[a] Tripaldi (2012).
[b] Miall (1984).

151 specimen, which allows for a more complete anatomical assessment of the taxon concerning upper dentition.

IANIGLA-PV 151 belongs to an adult individual, and the teeth (P3–M3) are badly preserved (Fig. 4C–F). Only the M2–3 (Fig. 4E and F) display most of the occlusal surface, as both teeth are separated from the rest of the series (lower part of ectoloph of M2 together with the series); the remaining teeth (P3–4 and M1; Fig. 4C and D) are broken at mid height of the crown and the cross section is altered due to the lack or displacement of some fragments. There are remains of a thin cement layer on every tooth. Despite the bad preservation, the general subtriangular outline of premolars is observable, especially P4 that is relatively shorter and wider than P3 (Table 2; Fig. 4C). In addition, the ectoloph of P4 presents a narrow anterolabial groove that limits a short parastyle, more forwardly directed than in the P4 of MCNAM-PV 3648. The middle lobe in M1 (breakage level) and M2 is wider than in M3; in the latter, the middle lobe is more triangular and shorter, being more enclosed by the other two lobes which, in turn, are convergent; the posterior face of M3 makes a marked notch. The morphology in IANIGLA-PV 151 is broadly coincident with that of MCNAM-PV 3648 (Fig. 4A), although some minor differences can be noted: in the M1 of IANIGLA-PV 151 the median lobe is well developed in comparison with the shorter and triangular lobe in MCNAM-PV 3648; in addition, the anterior border of the protoloph in M2–3 of IANIGLA-PV 151 shows a smooth inflexion that is not present in the M2 (that area is lacking in M3) of MCNAM-PV 3648.

Based on the short premolars, the short median lobe of M1 and M3, and the general tooth size, Cerdeño (2007) stated that MCNAM-PV 3648 was very close to *Altitypotherium chucalensis*. Therefore, the greater development of median lobe of M1 in IANIGLA-PV 151 not only differs from MCNAM-PV 3648 but also from *A. chucalensis*; instead, IANIGLA-PV 151 shares with the latter the smooth inflexion of the anterior border of the protoloph in M2–3. One attribute stated by Croft et al. (2004) for this species is the proportion of M1, $L/W \leq 1.30$, which is also true for MCNAM-PV 3648 (1.09) and IANIGLA-PV 151 (~ 1.26).

In turn, compared with the maxillary fragment MHNSR-PV 1152 (Fig. 4G) from the early Miocene Aisol Formation (Garrido et al., 2014), the series MCNAM-PV 3648 and the M1 and M2 individually are shorter (Table 2); in the case of MHNSR-PV 1152, the proportion L/W of M1 (after the photograph) is ~ 1.4, barely greater than in the studied specimens, but this value would correspond to a different state of character according to Croft et al. (2004) and Cerdeño et al. (2012) (see Phylogenetic Analysis, character 26). Concerning morphology, the P4 in MHNSR-PV 1152 is also triangular, without lingual sulcus, and with a more conspicuous paracone fold; the median lobe of M1 is subtriangular but reaches the same lingual level as the posterior lobe, being closer to the condition in IANIGLA-PV 151 than in MCNAM-PV 3648; and the median lobe of M2 has more parallel sides in MHNSR-PV 1152. Even though MHNSR-PV 1152 presents these differences, it is rather close to the specimens from the Mariño Formation and could belong to the same taxon. In addition, the tentative assignment of MHNSR-PV 1152 to the Colloncuran *Eutrachytherus modestus* by Garrido et al. (2014) is not justified. The teeth recognized by Roth (1899) as canine and premolars are small and simple, with labial enamel surrounding the mesial and distal corners, nothing of which resembles the studied teeth from the Mariño Formation; and the described M3 differs by its straight ectoloph and the enamel with the same distribution as the anterior teeth.

Regarding the mesotheriid taxa from the Chinches Formation, San Juan Province (López et al., 2011), the maxilla LH-08-38 determined as cf. *Altitypotherium* (López et al., 2011: Fig. 4h) compares well with the specimens from Mendoza in having triangular outlined premolars (P3–4) with a narrow anterolabial groove and short parastyle, and without lingual sulcus; subtriangular (slightly wider) median lobe in M1 and M3, not reaching the lingual level of the other two lobes (closer to the condition in IANIGLA-PV 151 and MHNSR-PV 1152 than to MCNAM-PV 3648). The authors did not provide upper dental characters for the second taxon from the Chinches Formation.

An early Miocene Argentinean mesotheriid was recovered within the faunal assemblage from Chichinales Formation, Paso Córdova locality, Río Negro Province, assigned to the Colhuehuapian SALMA (Paz et al., 2011). These authors compared the teeth from Paso Córdova with specimens from both Chucal and Mariño formations, but did not reach a taxonomic determination under subfamily level. They described two incomplete M1 (and a third fragment with doubts), which share a short middle lobe with MCNAM-PV 3648 and *A. chucalensis*.

The small size of the studied material precludes its assignment to other mesotheriids of younger age (e.g., *Pseudotypotherium* or *Typotheriopsis* among others; MLP, MACN, and GHUNLPam materials; Cerdeño and Montalvo, 2001), with the exception of two small, middle Miocene Bolivian taxa: *Microtypotherium choquecotense* Villarroel, 1974a, from Choquecota, and '*Plesiotypotherium*' *minus* Villarroel, 1978, from Cerdas (Townsend and Croft, 2010; Croft et al., 2016), both attributed to the Colloncuran SALMA. *'P.' minus* is also recorded at Quebrada Honda, corresponding to the Laventan SALMA (Croft, 2007), but note that *'P.' minus* is considered to represent a still unnamed genus, different from *Plesiotypotherium* (Townsend and Croft, 2010). In both species, the P4 is less triangular, more rounded than in MCNAM 3648 and IANIGLA-PV 151, and the M1 has the middle lobe longer and wider than in MCNAM 3648, but still a little shorter than the other lobes. The size is slightly greater (e.g., *M. choquecotense*: P3, 6.5 mm × 5.3 mm; P4, 8.3 mm × 6.5 mm, after Villarroel, 1974a; *'P.' minus*: P3, 5.6 mm × 6.9 mm; P4, 6.8 mm × 7.3 mm, after Townsend and Croft, 2010).

Late middle Miocene (Mayoan SALMA) mesotheriids from Laguna Blanca (Chubut Province) assigned to *Eutypotherium* Roth, 1901 (see Kraglievich, 1930) also present differences. The holotype of *E. lehmannitschei* Roth, 1901, MLP 12–1701, differs from the studied material by its more quadrangular P4, with a short but marked lingual groove, and more developed median lobe in M1, with subparallel sides (also in M2). In turn, *E. superans* (Ameghino, 1903) has more triangular premolars, without lingual sulcus, but the median lobe of M1–2 is also more developed (MLP 26-VI-15-1, cast of the holotype). Both species of *Eutypotherium* have larger size than the specimens from Mendoza (e.g., M1 of *E. lehmannitschei* = 15.4 mm × 9.9 mm; *E. superans* = 15.3 mm × 10.0 mm; EC's personal data).

Mandible and lower dentition. The specimen MCNAM-PV 4005 (Fig. 5A–C) has a wide and low horizontal ramus ($W = 12.5$ mm, $H = 20.7$ mm at m2 level). Its ventral border is convex and the vertical ramus forms a nearly acute angle with the occlusal plane, a similar condition to that in *Altitypotherium chucalensis* (SGOPV 4100; Croft et al., 2004: Fig. 10A). The symphysis is particularly procumbent and very narrow and long, reaching posteriorly the level of the talonid of p4 (Fig. 5B and C); this area is lacking in SGOPV 4100. The other Chilean species of the genus, *A. paucidens* (Croft et al., 2004: Fig. 8), shows the mandible with more upraised symphysis, reaching also the p4 level, and higher, more robust, and more divergent horizontal ramus, with less convex ventral border. In *'Plesiotypotherium' minus*, the mandibular symphysis also reaches the posterior end of p4, but its angle cannot be evaluated as this specimen was not figured in lateral view. In turn, the mandible MLP 12–1701 of *Eutypotherium lehmannitschei* has a longer symphysis, reaching the level of m1, and it is not as procumbent as in MCNAM-PV 4005.

MCNAM-PV 4005 bears i1 and i2, showing a large difference in size between them (Fig. 5D–E), i2 being clearly shorter than i1 (Table 2). Both teeth are very procumbent; the angle between the horizontal ventral border of the ramus and the line on the external face of i1 does not reach 30°. The occlusal face of i1 is trapezoidal, with the labial wall convex and longer than the nearly straight lingual wall; the enamel is discontinuous at the anterolingual and posterolingual areas. The i2 has a triangular outline and a distribution of enamel similar to i1. The incisors length ratio ($Li1/Li2 = 1.72$) is greater than in the species of *Altitypotherium*, which have an index of 1.3 for *A. chucalensis* and 1.2

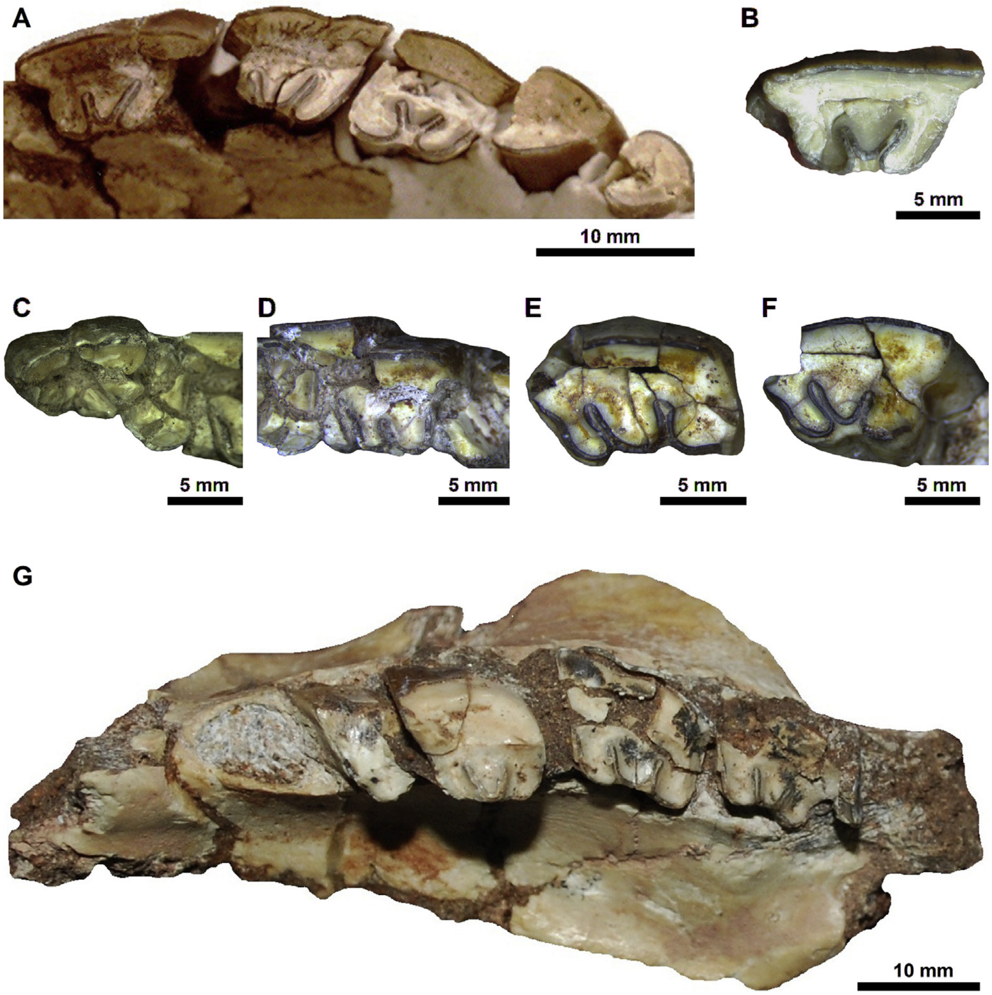

Fig. 4. A–F, *Rusconitherium mendocense* from the Mariño Formation (**A–B** from Divisadero Largo; **C–F** from Potrerillos): **A**, MCNAM-PV 3648 (neotype), right upper series P3–M3, occlusal view; **B**, MLP 45-VII-10-2, right M3, occlusal view; **C–F**, details of the left upper series IANIGLA-PV 151, occlusal view: **C**, P3–4; **D**, M1; **E**, M2; **F**, M3. **G**, Mesotheriinae indet., MHNSR-PV 1152, from the Aisol Formation.

Table 2
Measurements (mm) of the upper and lower dentition of *Rusconitherium mendocense* from the Mariño Formation. l., left; r., right.

	P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W
MCNAM-PV 3648	5.2	5.8	5.9	6.9	9.1	8.3	> 10.5	7.5	12.8	6.9
MLP 45-VII-10-2									13.3	6.6
IANIGLA-PV 151	(4.6)	(4.7)	(5.8)	(7.4)	(10)	(7.9)	> 11.0	7.6	> 12.0	7.5
	p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W
MCNAM-PV 4005 l.	—	—	—	—	8.9	5.3	9.5	6.1	11.7	4.8
MCNAM-PV 4005 r.	2.0	2.7	6.3	4.3	9.0	5.5	—	—	—	—
IANIGLA-PV 151									11.2	4.4
	i1		i2							
	L	W	L	W						
MCNAM-PV 4005 l	6.2	3.9	—	—						
MCNAM-PV 4005 r	6.2	3.8	3.6	2.7						

and 1.4 for *A. paucidens*, after dimensions provided by Croft et al. (2004: Tables 2 and 4). Similarly, *'P.' minus* has an index of 1.4 (Townsend and Croft, 2010: tab. 6) and *E. lehmannitschei* (MLP 12–1701) of 1.5 (EC's personal data).

The right cheek tooth series of MCNAM-PV 4005 preserves a reduced p3 (Fig. 5B–C, F–G), a premolar that is not usually present in mesotheriines, but when present it is well developed (see Cerdeño and Schmidt, 2013, about this character). The p3 in MCNAM-PV 4005 is a subcylindrical, simple, and small tooth, which is separated from the incisor by a short diastema. This reduced p3 constitutes, therefore, a singular feature (character 35[1], see below) of MCNAM-PV 4005; the area corresponding to the left p3 is broken (Fig. 5C). The p4 is long and subtriangular, with the trigonid shorter and narrower than the talonid; the lingual and labial grooves are rather shallow (Fig. 5F).

Molars of MCNAM-PV 4005 (Fig. 5H–J, Table 2) present a relatively shorter trigonid than premolars and a deep labial groove that crosses most of the occlusal surface, slightly inclined backward; its end faces the shallow lingual groove. The talonid has convex labial and lingual walls in m1–2. The L/W ratio in m2 is less than 1.60 (character 37[2], see below), a feature shared only with *Microtypotherium choquecotense*. In m3, the talonid is longer, with a shallow, but marked lingual groove in the middle; the labial face is smoothly convex, pointing posterolingually (Fig. 5I). A layer of cement covers the teeth; where it is lacking, the vertically striated enamel is observed. The m3 of IANIGLA-PV 151 (Fig. 5 K–L, Table 2) is very similar to the homologous molar in MCNAM-PV 4005 (Fig. 5I and J), but the lingual groove is smoother, just as a soft, regular concavity. In both m3, there is a posterolingual interruption of the enamel (character 38[1], see below); in occlusal view, this is better observed on IANIGLA-PV 151 (Fig. 5K) due to its occlusal border is complete whereas it is slightly eroded in MCNAM-PV 4005; in both cases, the enamel interruption is well observed along the lingual wall at sight (Fig. 5J, L). Differences in tooth size are not significant (Table 2).

Compared with *Altitypotherium chucalensis*, the p4 of MCNAM-PV 4005 has a less marked labial groove and is not pointing anteriorly, but this feature could be due to the fact of having another premolar ahead of it and/or to a different degree of wear; in this sense, the mandible SGOPV 4100 of *A. chucalensis* (Croft et al., 2004: Fig. 10) would be of a younger individual than MCNAM-PV 4005, as it shows remnants of a posterior fossettid in molars. The p4 of *A. paucidens* (Croft et al., 2004: Fig. 8) has a smoother labial groove than that of *A. chucalensis*, but still more marked than in MCNAM-PV 4005.

Concerning molars, the m3 of the specimens from Mendoza seems to have a relatively shorter talonid than the species of *Altitypotherium*, and displays a more acute lingual groove, even considering the differences between MCNAM-PV 4005 and IANIGLA-PV 151. Instead, ‘*Plesiotypotherium*' *minus* also has an acute lingual groove on the talonid of m3 (Townsend and Croft, 2010: Fig. 10). On the other hand, *A. chucalensis* and *A. paucidens* do not present the posterolingual interruption of the enamel in m3 that is observed in the two studied specimens. In contrast, this interruption has been described for the new taxon from the Chinches Formation (López et al., 2011: 219). With respect to this character, Villarroel (1974a, b, 1978) published schematic drawings of lower teeth of *Microtypotherium choquecotense*, *Plesiotypotherium achirense*, *‘P’. minus*, and *Eutypotherium lehmannitschei*, in which the occlusal enamel line of m3 is posterolingually interrupted; however, the author did not mention this feature in the descriptions; after our data, neither in *E. lehmannitschei* (MLP 12–1701) nor in *P. achirense* (M. Fernández Monescillo, pers. comm.) this interruption exists, which renders dubious the Villarroel's published schemes; in the case of *‘Plesiotypotherium’ minus*, there are specimens that present continuous enamel (Townsend and Croft, 2010: Figs. 10 and 11.1), but others seems to have some interruptions although more posteriorly placed (Townsend and Croft, 2010: Fig. 11.2).

Concerning the lingual convexity of the talonid of m1 and m2 in MCNAM-PV 4005, it is observed that some compared species present this convexity in m1, but not in m2 in which a more or less shallow groove appears (e.g., *Altitypotherium chucalensis*—SGOPV 4100—; *‘Plesiotypotherium’ minus*; barely evident in *Eutypotherium lehmannitschei*—MLP 12-1701—; *Typotheriopsis chasicoensis*—MLP 60-VI-18-116 and MLP 67-XII-27-1—); nevertheless, the development of this groove is probably related to the ontogeny, which would explain its more frequent presence in m2 than in m1. The development of grooves in mesotheriid teeth can be subject to great changes with wear, as shown by Cerdeño and Schmidt (2013). Considering the euhypsodont condition of these teeth, changes probably occurred even within the full adult period of individuals, and in consequence, variation of some characters should be taken into account when comparing taxa.

4.2. Phylogenetic analysis

In order to evaluate the position of the taxon from Mendoza, *Rusconitherium mendocense*, among mesotheriids, a cladistic analysis was performed with the computer program TNT 1.1 (Goloboff et al., 2008a; b), applying heuristic searches with the Tree Bisection Reconnection swapping algorithm (TBR), and using 1000 random addition sequences and saving 10 trees. Subsequent searches were repeated from previously obtained trees. Support values were calculated using Bremer and Jackknife indices (the latter is a resampling technique that is summarized using absolute frequencies and GC frequencies; see Goloboff et al., 2003).

The data matrix is composed of 25 taxa and 39 morphologic and meristic characters (Appendices 1–2); it was slightly modified from the matrix in Cerdeño et al. (2012). These modifications are: former character 20 (P2) is here considered two separated characters (no. 21 and 22: presence/absence and developed/reduced condition, respectively); former character 22 (premolar ectoloph with two or one sulcus) has been eliminated from the present analysis, as it is not obvious how it was evaluated and we do not see two clear sulci in the taxa that are supposed to have them (Cerdeño et al., 2012, reproduced this character from Croft et al., 2004: character 27); character 23 (P3) adds a third state referring to the absence of P3 in *Altitypotherium paucidens*; character 35 includes one more character state that refers to reduced condition of p3 in the studied material; and former character 38 has been replaced. The former character 38 considered the presence of two lingual sulci on m3 talonid in the species *Caraguatypotherium munozi* (Cerdeño et al., 2012: App. 1), but this condition was recently rejected for this species by Montoya-Sanhueza et al. (2017) and, therefore, the character does not provide any information within mesotheriids; instead, a new character 38 is now included, which refers to the presence of a posterolingual discontinuity of the enamel in m3. With respect to the terminal taxa, the present analysis adds the material recognized as *Rusconitherium mendocense* New Combination, the specimen MHNSR-PV 1152 from the Aisol Formation, and the two mesotheriids from San Juan after the data provided by López et al. (2011). Mesotheriinae indet. material from the oldest Chichinales Formation, Colhuehuapian SALMA (Paz et al., 2011), was not included in the analysis due to its fragmentary condition.

Some characters were scored as polymorphic, when more than a character state is present in a taxon (e.g., 1&2), and as non-applicable (NA) when a character is not present. All characters are treated as unordered, a method that minimizes the number of postulated evolutionary transformations. They are referred to in brackets with the character state in superscript. The data matrix was assembled with Mesquite (Maddison and Maddison, 2009). Maximum parsimony under equal weights was assumed.

The analysis yielded ten most parsimonious trees (108 steps length) with a CI = 0.69 and RI = 0.75, whose common synapomorphies are shown in the strict consensus (Fig. 6). This topology displays very poorly resolved relationships, especially for the taxa under study. However, when we analyze each tree separately (e.g., tree 0/10; Fig. 7A), we observe that *Rusconitherium mendocense* and the new taxon from San Juan forms a monophyletic group in all of the trees (Figs. 6, 7A–B), sharing a synapomorphy, the posterolingual short interruption in the enamel of m3 [38[1]]; in turn, MHNSR-PV 1152 from the Aisol Formation is nested with the other taxon from San Juan (cf. *Altitypotherium*), but no synapomorphy was recovered in the node. Observing the position of both clades among the trees, the first one represents an early diverging group from the rest of mesotheriines in most of the topologies (Fig. 7A and B), whereas the second clade displays a more changing position, from basally placed, close to the first clade (Fig. 7A), to being nested in the *Eutypotherium* clade in five of the ten topologies (Fig. 7B).

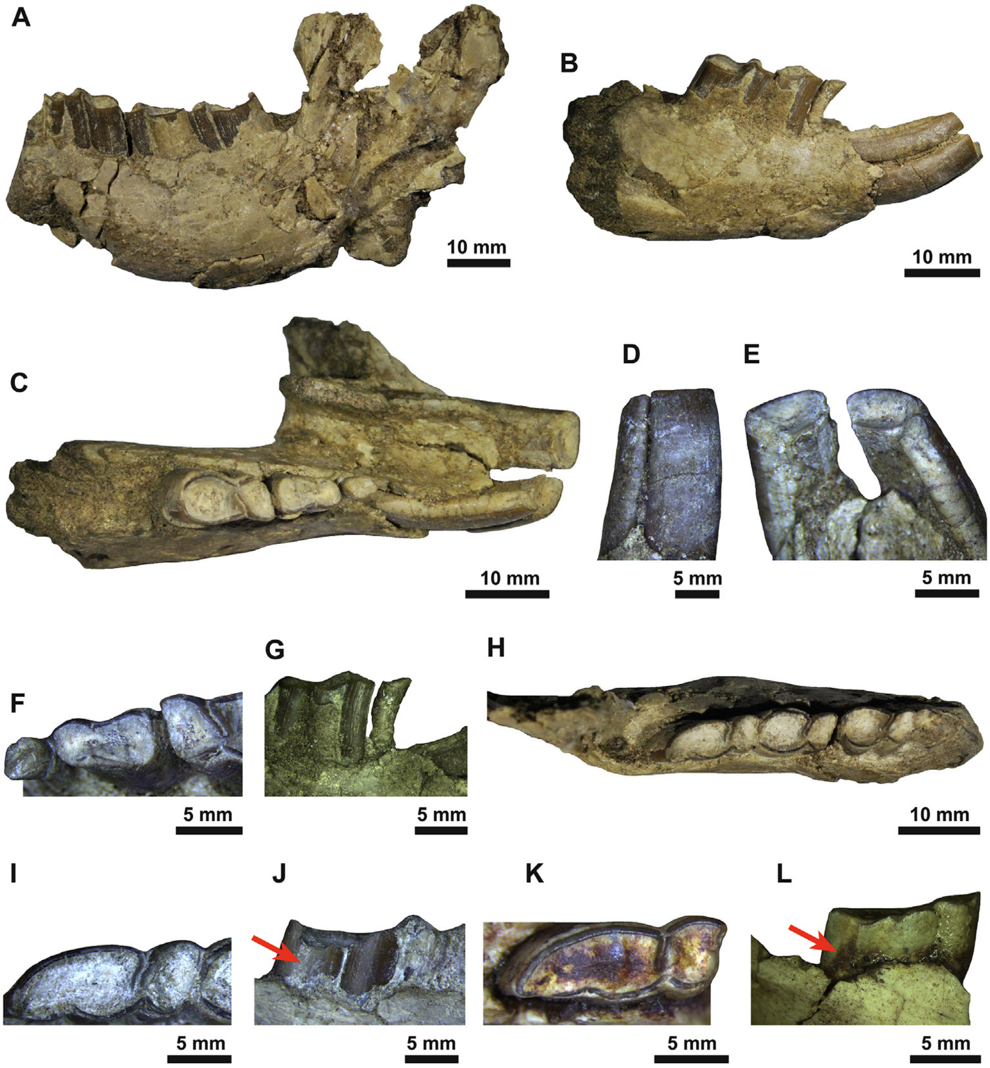

Fig. 5. *Rusconitherium mendocense* from the Mariño Formation. **A–J**, mandible MCNAM-PV 4005 (neotype) from Divisadero Largo: **A**, left horizontal ramus, labial view; **B–C**, right horizontal ramus and symphysis: **B**, labial view; **C**, occlusal view; **D**, detail of right i1–2, labial view; **E**, detail of left and right i1 and right i2, lingual view; **F–G**, detail of p3–4, occlusal and labial views; **H**, left molar series m1–3, occlusal view; **I–J**, detail of m3, occlusal and lingual views; **K–L**, IANIGLA-PV 151, mandibular fragment with left m3, occlusal and lingual views. Arrows indicate the enamel interruption on m3.

Based on the present results, the only unquestionable monophyletic group is the genus *Mesotherium*, supported by a single synapomorphy (I1 with more transverse implantation and procumbent [18^{2}]; Fig. 6). *Pseudotypotherium* and *Plesiotypotherium* are recovered as monophyletic groups in eight of 10 trees (80%), with *Ps. hystatum* and *Pl. casirense* being the itinerant species of the respective genera. In the case of *Typotheriopsis*, it appears monophyletic in all of the trees (e.g., Fig. 7A and B), but it is not recovered as a clade in the strict consensus (Fig. 6), reflecting the lack of synapomorphies supporting this group, as also happens with *Pseudotypotherium* and *Plesiotypotherium*. Interestingly, two clades in the strict consensus deserve special considerations. The group including *Plesiotypotherium majus* and *Pl. achirense* (Figs. 6, 7A–B) is supported by one synapomorphy (third lobe of M3 with lingual sulcus [32^{1}]); however, this character should be viewed with caution as the presence of the lingual sulcus in the third lobe could depend on the ontogenetic state. Secondly, the clade including the species of *Pseudotypotherium* and *Mesotherium* (Fig. 6) is strongly supported by four unambiguous synapomorphies: P4 bilobed, with short and poorly defined or well developed lingual plication groove [24^{2,3}]; P4 length/width ratio ≥ 1.50 [25^{1}]; M1 length/width ratio > 1.75 [26^{2}], and m2 length/width ratio > 2.30 [37^{1}], and high Bremer and GC support values. In addition, another well-supported clade contains the middle/late Miocene–Pleistocene representatives of Mesotheriinae, including *Caraguatypotherium munozi* and its descendants (Fig. 6), sharing three synapomorphies: parallel or gently convex upper and lower diastemata [3^{2}], subparallel or lingually divergent anterior and posterior sides of M1 middle lobe [27^{1,2}], and length ratio i1/i2 > 1.5 [33^{1,2,3}]. In contrast, the relationships between the early–middle Miocene representatives (e.g., *Altytipotherium*, *Microtypotherium*, *Eutypotherium*) are poorly defined in our analysis (Fig. 6), which could be due to the still poor knowledge of some taxa such as *Eutypotherium* from the middle Miocene of Patagonia.

Concerning *Altitypotherium*, it is not recovered as a clade in any of the trees, a result that contrasts with that obtained by Croft et al. (2004). These authors diagnosed the genus based on two synapomorphies, presence of a single labial sulcus on the premolar ectoloph and the presence of upper first incisors that are subtriangular, pointed distally, with two lingual sulci. As explained above, the presence of one or two labial sulci in premolars is not clear enough to us, and we did not want to use it as long as we cannot check the character adequately in all taxa. The upper incisor morphology (character 19) is not available in the taxa from Mendoza or San Juan, and the character state 19^{4}, although is present in both species of *Altitypotherium*, does not appear as a synapomorphy for this genus.

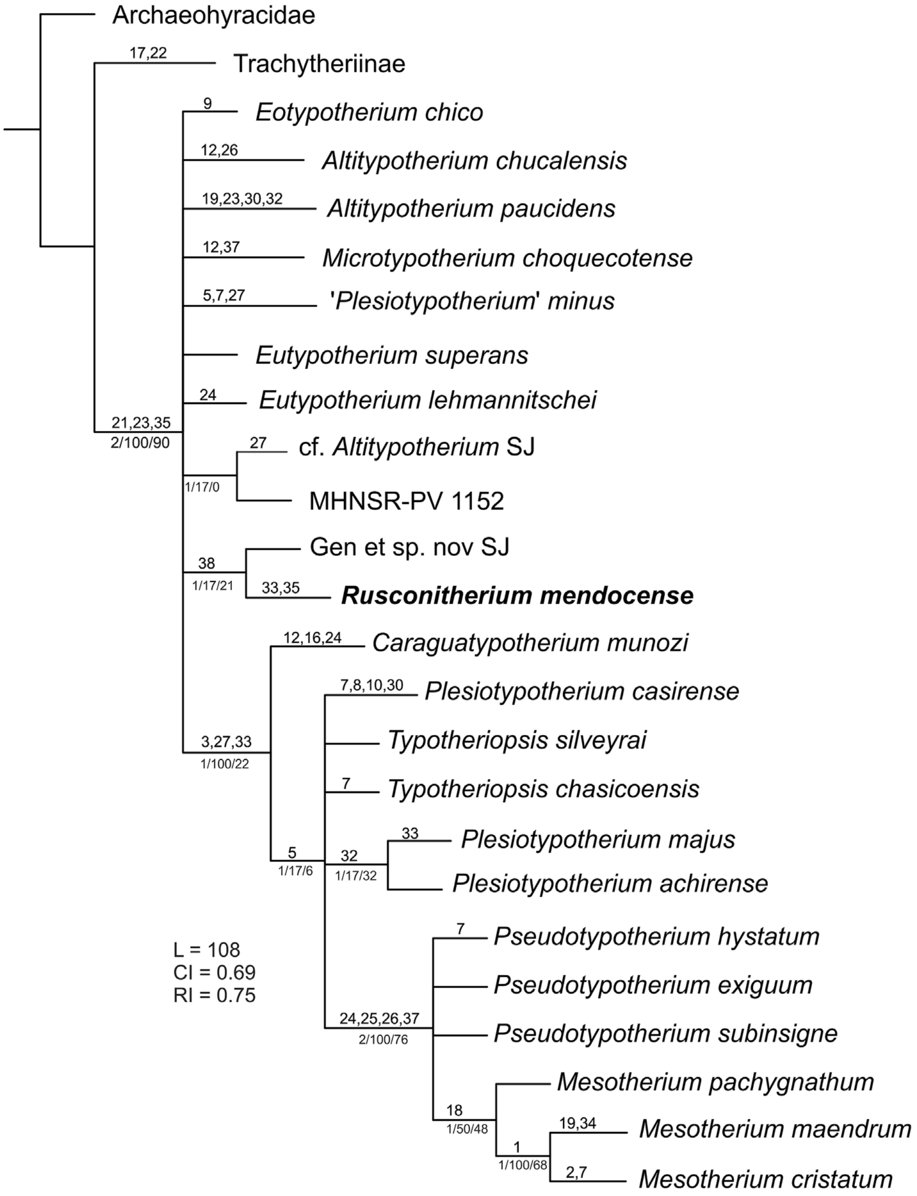

Fig. 6. Strict consensus of ten most parsimonious trees obtained in the cladistic analysis (L = 108; CI = 0.69; RI = 0.75). Numbers above and below branches are synapomorphies and Bremer and Jackknife indices, respectively.

5. Discussion and conclusions

The initial description of a mesotheriid from the Mariño Formation at Divisadero Largo (MCNAM-PV 3648) (Cerdeño et al., 2006; Cerdeño, 2007) indicated a close relationship of this upper dentition with the species *Altitypotherium chucalensis* from Chucal Formation (Santacrucian SALMA; Croft et al., 2004). The new material herein described adds new morphological data on the mandible and lower teeth (MCNAM-PV 4005) of the same individual described by Cerdeño (2007), as well as it provides the first record of mesotheriids (IANIGLA-PV 151) from the Mariño Formation at the Potrerillos locality. Based on the comparisons presented above, we determine that these specimens belong to the same species and the few differences observed between them are due to intraspecific variation.

In this context, the new material allows for establishing some differences with respect to other Santacrucian mesotheriines. The most remarkable feature of MCNAM-PV 4005 is the presence of a reduced p3 (character 35), a condition that differentiates this taxon not only from *A. chucalensis* (Croft et al., 2004: 20–21) but from all other mesotheriines. The presence of p3 (and P2) in mesotheriines is an old controversy that has been recently restudied (Cerdeño and Schmidt, 2013). These authors concluded that these teeth can be present, not being deciduous dental elements. Though mostly discussed for upper dentition with P2, Cerdeño and Schmidt (2013: Table 1) also described some mandibular specimens bearing the p3. This tooth is well developed in these cases, very different from the p3 described here. As far as we know, there is no previous mention of a mesotheriine with a reduced p3, which becomes then a particular feature for the species from the Mariño Formation. Other differences observed in the studied material with respect to the species of *Altitypotherium* concern the relatively smaller i2 (see proportional values above and character 33) and the enamel interrupted at the posterolingual end of m3 (character 38). All these features and likely the very procumbent symphysis (not comparable in *A. chucalensis* but greater than in *A. paucidens*) support that the taxon from Mendoza is different from *Altitypotherium* from Chile.

Concerning the mesotheriid from the Aisol Formation, general similarities with *Rusconitherium mendocense* are evident and it could belong to the same taxon, but mandibular material from Aisol would be

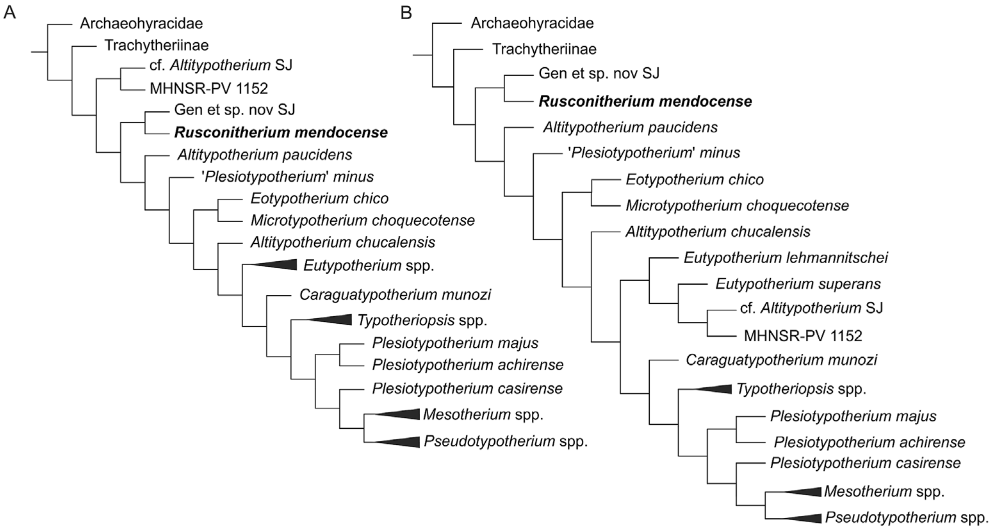

Fig. 7. **A**, one of the alternative topologies (4/10) showing a particular resolution of the polytomies of the strict consensus in Fig. 6; **B**, another alternative topology (0/10).

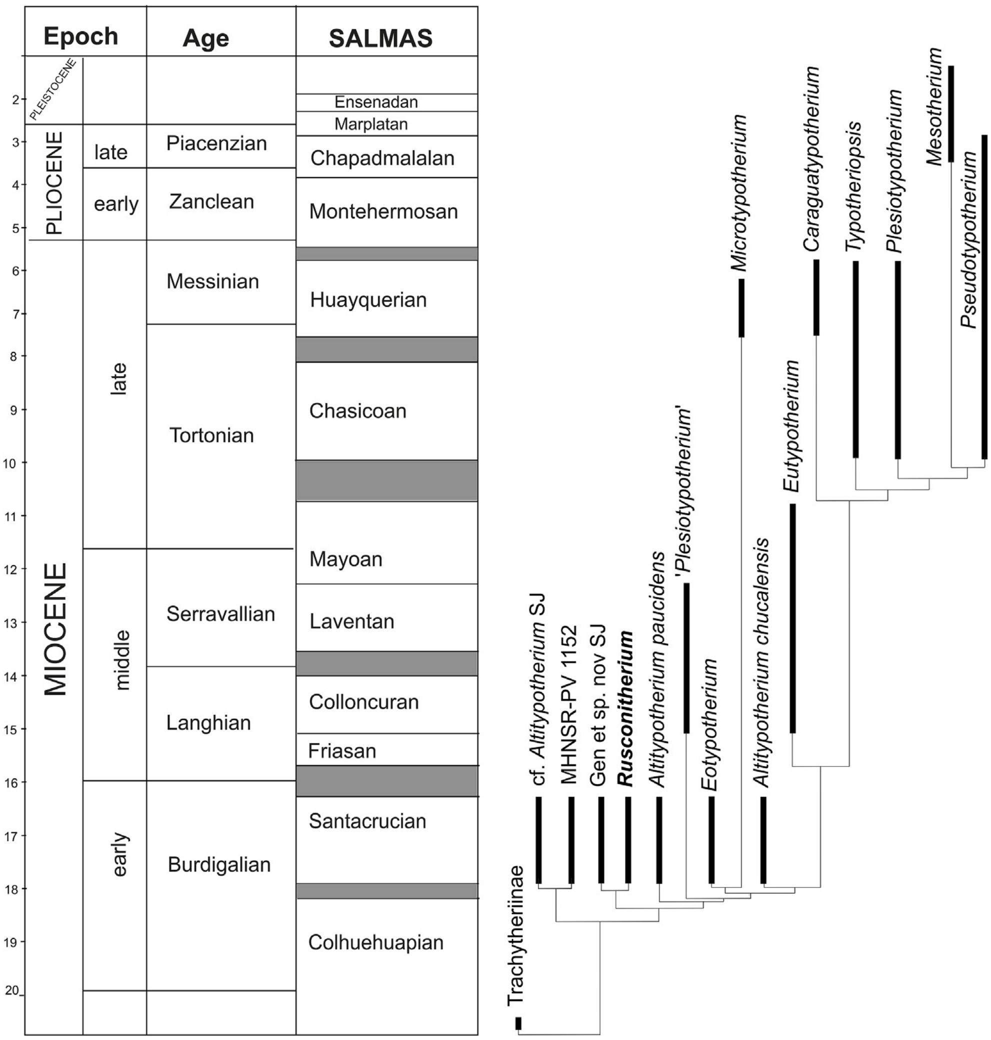

Fig. 8. Biostratigraphic distribution of mesotheriid genera relative to the topology of the strict consensus in Fig. 6. South American Land Mammal Ages after Croft et al. (2016), Cohen et al. (2013-updated), and Cerdeño (in press).

necessary to check this hypothesis. With respect to the Santacrucian faunal assemblage from the Chinches Formation (López et al., 2011), despite the lack of a detailed study, we can also establish some similarities. On the one hand, the maxilla determined as cf. *Altitypotherium* (López et al., 2011: Fig. 4h) shares with the new taxon from the Mariño Formation the triangular premolars, without lingual sulcus, narrow anterolabial groove and short parastyle; median lobe in M1 and M3 subtriangular (although a little wider) and not reaching the lingual level of the other two lobes. On the other hand, the mandible assigned to a new taxon (López et al., 2011: 219) shares a narrow and long symphysis, and a posterolingual band without enamel in the m3; in contrast, however, this mandible lacks p3 and has subequal lower incisors. Considering the coincident age of the fossiliferous levels and the geographic proximity of the areas (central and northern Mendoza and southern San Juan), it would be expected that there were common taxa, but more material in the case of Aisol Formation and a deeper comparison with the remains from the Chinches Formation are needed before reaching a confident conclusion about this hypothesis.

In summary, the morphometric comparisons allow us to consider the mesothere from the Mariño Formation as a new genus, *Rusconitherium*. We also include in this new taxon the mesotheriid first known from the Divisadero Largo area, originally assigned to the older Divisadero Largo Formation and described as the Trachytheriinae ***Trachytherus? mendocensis*** (Simpson and Minoprio, 1949; Simpson et al., 1962; Cerdeño, 2007; Cerdeño et al., 2008). This fact implies the priority of this specific epithet and, consequently, the establishment of the name *Rusconitherium mendocense* New combination. At the same time, the lost condition of the holotype, the lack of confident illustrations of it, the absence in the holotype of the diagnostic features herein established, and the lack of precision of its stratigraphic origin (but within the Mariño Formation) lead us to formally propose a neotype for *Rusconitherium mendocense* New genus and New Combination, according to the ICZN (2000: art. 75.3), and a neodiagnosis.

The phylogenetic analysis does not support a close relationship of the material from the Mariño Formation with the genus *Altitypotherium* as firstly proposed (Cerdeño, 2007), but neither with any other genus in a confident way, excepting the new Mesotheriinae from the Chinches Formation (San Juan Province; López et al., 2011). This fact would indicate a probable taxonomic identity between them, as well as the biostratigraphic correlation between the respective faunal assemblages and formations. Therefore, these results, together with the exclusive morphological characters described above, support the proposal of a new generic name for the taxon from the Mariño Formation.

At the same time, the genus *Altitypotherium* appears as a paraphyletic assemblage, with *A. paucidens* at a basal position with respect to *A. chucalensis*, which suggests the need of a taxonomic revision of these taxa from the Chucal Formation.

Taking into account the stratigraphic position of the mesotheriids relative to their phylogeny (Fig. 8), two groups may be clearly distinguished: the well-supported clade including the late Miocene–Pleistocene members, such as *Caraguatypotherium munozi* and its descendants, which share unquestionable synapomorphies (see Fig. 6), and all early-middle Miocene members, whose relationships are poorly resolved. Just the late Miocene *Microtypotherium* appears at a more basal position than the coeval taxa. In any case, we must keep in mind that mesotheres lack a contemporary, thorough revision that addresses the great variability observed across some dental features. Important also is the fact that significant material found in recent years is still pending detailed study (e.g., from Mendoza—see Cerdeño, in press, for preliminary data— or Bolivia—Fernández Monescillo's Doctoral dissertation in progress).

From a biostratigraphic point of view, the establishment of shared taxa between the fossil material from Divisadero Largo and Potrerillos areas provides a confident basis for the correlation between both outcrops of the Mariño Formation. The mesotheriid remains in both cases were found at the top of a level of sandstones corresponding to the middle Member of the formation, the Areniscas Entrecruzadas. The sedimentary characteristics observed at the Potrerillos section reveal two paleoenvironmental scenarios: 1) dune fields with development of straight ridge dunes, which interdigitate with sand fields, which was influenced by volcanic events associated with the Miocene volcanic arc; 2) the presence of water at the capillary level which prevented the continuous deflation of the sediment, and allowed for the presence of vegetation and fauna adapted to this environment.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jsames.2018.06.016

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