The first mammal assemblages from the Malargüe Group: Implications for the Paleogene evolution of the northern Neuquén Basin (Argentina)

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ABSTRACT

We present two new Paleogene fossiliferous sites that provide the first mammal remains for the Malargüe Group in the Neuquén basin of southeastern Mendoza Province, Argentina. Identified taxa from Agua de Flores-Agua de Isaac: *Kibenikhoria* sp., Oldfieldthomasiidae indet., ?Henricosborniidae indet., and a large Notoungulata probably related to the Isotemnidae. Taxa from Liu Malal: cf. *Kibenikhoria* and Notopithecidae gen. et sp. nov. Based on facies composition and geological distribution, we consider that the Cenozoic deposits from these fossiliferous localities correspond to the already defined Puesto Fortunata Formation. This unit is correlated to the Coihueco Formation, the top of the Malargüe Group in the northern Neuquén basin, and its mammal content supports the proposed hiatus between the ~40 Ma and 20 Ma based on chronostratigraphy. The presence of *Kibenikhoria* in the local faunas of southeastern Mendoza extends the geographic range of this genus so far known in Patagonia to central-west areas of Argentina and supports an early-middle Eocene age for the fossil-bearing levels of the Puesto Fortunata Formation.

1. Introduction

Historically, the evolution of the northern Neuquén basin located in the south of Mendoza Province (Argentina) was divided into several tecto-sedimentary cycles related to the subduction of the Pacific oceanic lithosphere beneath the western margin of South America (Ramos, 1989; Mpodozis and Ramos, 1989; Ramos and Folguera, 2005 among many others). The different scenarios of subduction produced backarc extensional, postextensional, and retroarc foreland basins along the Neuquén basin history, starting with the break-up of Pangea and ending with the Andean uplift (Vergani et al., 1995; Uliana and Biddle, 1988; Howell et al., 2005). The sedimentary infill, paleoenvironments, ages, fossil content, and duration of those cycles were intensively studied since the early 20th century and continue up with new discoveries and more precise data that complete the Neuquén basin evolution. But even with the new records, the main scheme proposed by Groeber (1946) is still useful. This author divided the sedimentary infill into three main supercycles that reflect changes in the geodynamics of the basin: 'Jurásico' (Hettangian–Kimmeridgian), 'Ándico' (Tithonian–Coniacian), and 'Riográndico' (Santonian–Danian). The latter has been divided into the 'Neuqueniano' and the 'Malalhueyano' cycles. It includes marine and marine mar-ginal sediments as product of the first Atlantic transgression into the basin during the Campanian-Danian and a dominantly continental setting at least up to the end of the Paleocene. The age studies of the sediments of the Malalhueyano cycle, currently known as Malargüe Group, are large due to their conspicuous fossil content are well known since the early years of the last century (see Rodríguez, 2011 and references therein). The next cycle starts in the early Miocene with an important orogenic event that leads to the formation of the main Andes range (Kozlowski et al., 1993; Manceda and Figueroa, 1995; Giambiagi et al., 2008 among many others). This event is registered in the northern Neuquén basin by a main disconformity below the Agua de la Piedra Formation (Criado Roque, 1950), which reflects regional shortening and crustal loading and the consequence of the foreland basin development (Combina and Nullo, 2011 and references therein). This implies that a Paleogene hiatus (~40–20 Ma) exists between the top of the Malargüe Group and the Agua de la Piedra Formation (Horton et al., 2016; Horton, 2018).

In the southernmost part of Mendoza Province (Fig. 1), Cenozoic continental deposits (e.g., Liu Malal; Groeber, 1933; González Díaz, 1979) and fossil mammals (e.g., Agua de Flores; Legarreta et al., 1985; Kozlowski et al., 1987a, b; 1989) were reported from the foothills of the Payún Matrú plateau, but these authors mislead in
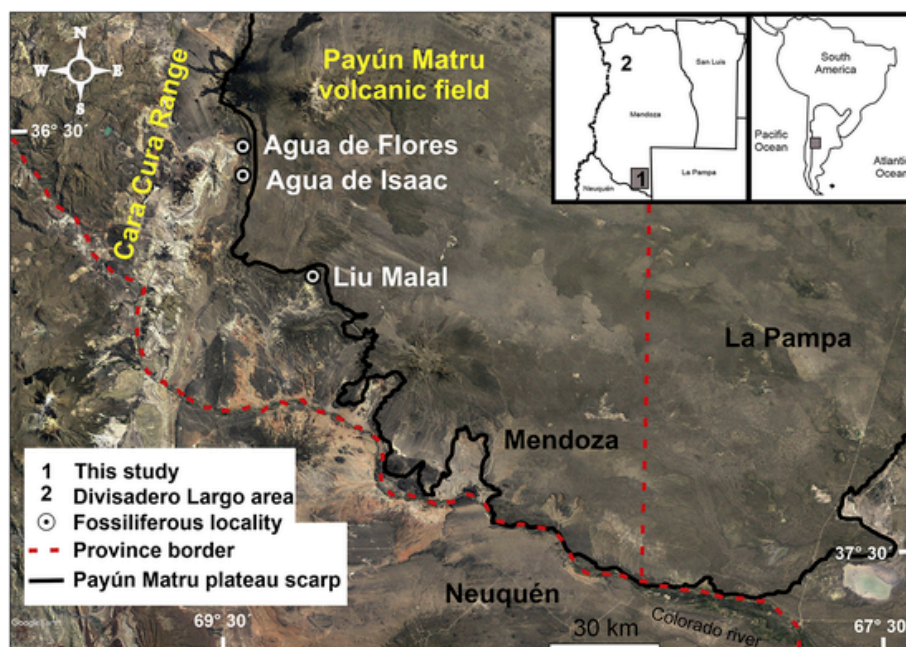
Fig. 1. Regional map showing the location of the studied area, the analyzed areas, and other localities mentioned along the text.

the age of the deposits (Miocene?) and fauna (late Oligocene), respectively, generating some confusion. Currently, these Cenozoic deposits surrounding the Payún Matrú plateau are assigned to the Malargüe Group, firstly based on litoestratigraphy, without fossil or dating data (Narciso et al., 2001) and more recently adding important data regarding the age and evolution of the northern Neuquén basin, using U–Pb age distributions (e.g., Horton et al., 2016; Gianni et al., 2018; Horton, 2018; Muñoz et al., 2018).

As a result of several fieldtrips in the area, we have located the fossil-bearing levels described in Agua de Flores (Kozlowski et al., 1987a) and those Cenozoic units in Liu Malal (Groeber, 1933; González Díaz, 1979), recovering new mammal specimens from both sites, being the first fossil record for the latter. In this paper, we provide stratigraphic information and describe the fossils from each locality, establishing bioestratigraphic correlations with other Paleogene units and faunas from Argentina (e.g., Divisadero Largo, central Patagonia, and north-western Argentina—NWA—), adding also new data on the geodynamic evolution of the Neuquén basin in southeast Mendoza.

1.1. Stratigraphy of the area

1.1.1. Liu Malal

This locality (36°50′39.04″S, 69°14′9.63″W, Fig. 1) is also known as 'Anfiteatro Liu Malal' (Liu Malal Amphitheater) by many invertebrate paleontologists due to the extensive exposition of marine fossil-bearing sequences corresponding to the Jagüel and Roca Formations (Concheyro et al., 1996; Casadío, 1998, 2008; Pires et al., 1999). However, Groeber (1933) described Tertiary conglomerates and clays and Tertiary tuffs in a schematic profile he performed northern from Liu Malal. Many years later, González Díaz (1979) analyzed the units described by Groeber (1933) and defined two continental Cenozoic formations: El Pingucho Formation (Eocene–Oligocene?) and Puesto Fortunata Formation (Miocene?), both overlying the Roca Formation and underlying the Palaoco Formation. Although neither Groeber (1933) nor González Díaz (1979) mentioned fossils from these units, both authors agreed in a pre-Miocene age for these units, based on stratigraphic relations with the upper basalt level.

Taking this background into account, we included this locality in our fieldtrip in 2016. Northern from Liu Malal (Fig. 1), in a very covered area (Fig. 2A), we recognized three sections with Cenozoic sediments exposed at the headwaters of the Liu Malal stream, near the Puesto La Fortunata. From the most complete section (36°50′8.18″S, 69°15′41.50″W) we recovered teeth and postcranial elements of mammals by means of both hand picking and dry screening of sediments (Tunik et al., 2017). The best preserved specimens are described below.

In this area, the sediments are discontinuous (Fig. 2A) and extremely covered by Quaternary debris, which prevented us to make a detailed stratigraphic section, but the presence of the conspicuous Roca and Pircala Formations allowed us to identify the onset of the Cenozoic sediments outcrop. Three divisions were distinguished in spite of been highly covered. A lower one composed of reddish and greenish shales, with an estimated thickness of 30 m located over the outcrops of the Pircala Formation after a 20 m-covered section; a 20 m-thick middle section of massive and laminated white tuffaceous sandstones, with some levels with tubular bioturbation of 0.7 cm of diameter; and a 10 m-thick top section of tuffaceous sandstones with a 2 m-thick bed of tabular massive sandstone. In the tuffaceous sandstones of the middle section, several mammal teeth and bones were found for the first time at this locality.

The remains were found in a tuffaceous wacke with quartz, feldspar, fragments of volcanic basic rocks and pumice shards immersed in an altered to clay vitreous matrix with presence of bioturbation holes filled with calcite (Fig. 2C).

Based on its stratigraphic position, lithology, sedimentary structures and thin section analyses we recognized these sediments as belonging to the Puesto Fortunata Formation defined by González Díaz (1979). At the same time, the recovered mammal remains allow us to precise the age of the unit, much older than the previously proposed Miocene (see discussion). Even though the information to assess a precise sedimentary environment is scarce, we agree with González Díaz (1979) about the proposed agradational fluvial system for these sediments.

1.1.2. Agua de Flores-Agua de Isaac

This dual name refers to a small area (36°35′30.7″S, 69°26′24.0″W) located between two very close local farms: Puesto Agua de Flores (36°31′56.66″S, 69°26′52.75″W) and Puesto Agua de Isaac (36°36′6.78″S, 69°26′52.26″W) (Fig. 1). In the surroundings of
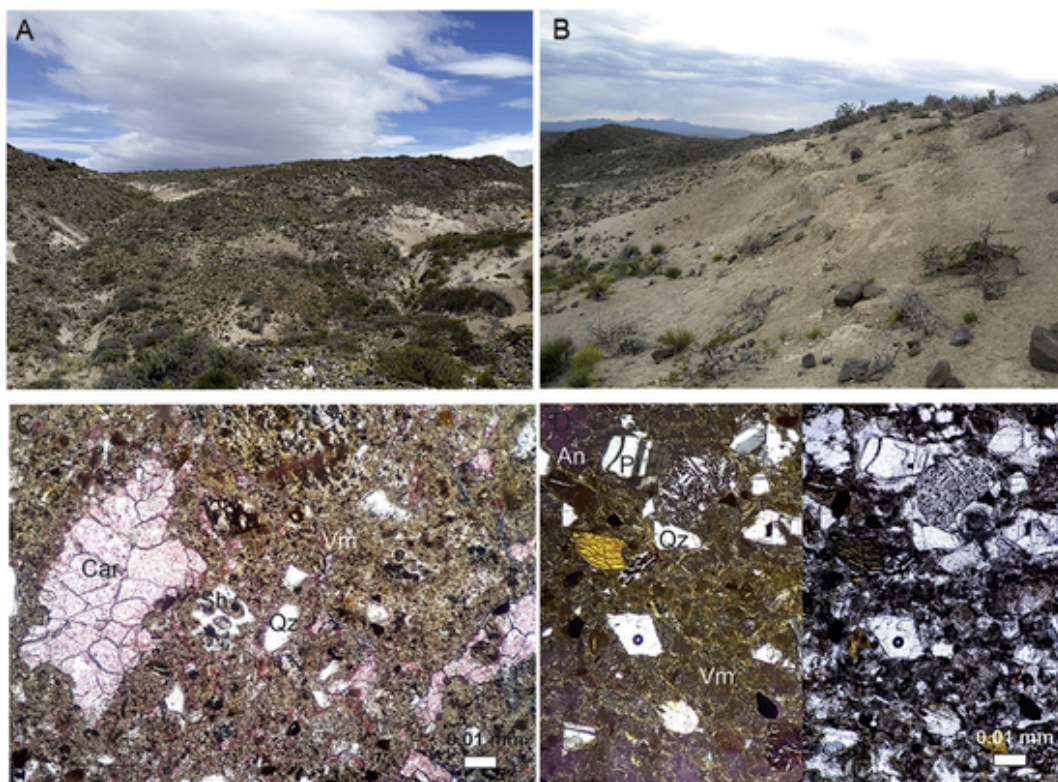
Fig. 2. A, general view of the highly covered Liu Malal section. B, general view of the Agua de Flores measured section. C, thin section of a medium wacke from Liu Malal. D, thin section of a medium wacke from Agua de Flores site. Note the presence of quartz (Qz), plagioclase (Pl), analcime replaced shards (An) and volcanic lithic fragments (Vlf) immersed in an altered volcanic matrix (Vm) with calcite cement (Car) probably filling a bioturbation hole. Left image was taken under cross-polarized light and the right one is under plane-polarized light.

Puesto Agua de Flores, Kozlowski et al. (1987a) described two integrated geologic sections, Agua de Flores I and II, where they recognized the Malargüe Group at the lower part (including, from the base to the top, the Loncoche, Roca, and Pircala Formations) and the Laguna Blanca Group (Legarreta et al., 1985) at the upper part. At the base of the Laguna Blanca Group, Kozlowski et al. (1987a) signaled that mammal bones were found in a tuffaceous wacke and emphasized that they should be stratigraphically located above the fossil-bearing levels from the Quebrada Fiera locality (Gorroño et al., 1979), which were assigned to the upper Oligocene based on the age inferred for the Laguna Blanca Group by Legarreta et al. (1985). Many years later, one of the fossils from Agua de Flores was assigned to an undetermined genus and species of 'Oldfielthomasiidae' (Notoungulata) as coming from an 'Eocene innominate lithostratigrapic unit' (Pascual and de la Fuente, 1993: 359).

After several fieldtrips prospecting the outcrops exposed in the area between the mentioned settlements, we located the Kozlowski's site in 2008 and some mammal specimens were recovered in 2014 (Vera et al., 2014; Tunik et al., 2017). It should be noted, however, that we opt to name this locality as Agua de Flores-Agua de Isaac as a substitute for Agua de Flores sensu Kozlowski et al. (1987a), because the fossiliferous bed is in fact closer to Puesto Agua de Isaac than to Puesto Agua de Flores. The fossils collected in this locality are fragmentary; some of them were found *in situ*, but others were eroded out of the outcrop.

The studied section starts with conspicuous beds with marine fossils belonging to the Roca Formation, covered by red and violet shales and sandstones assigned to the Pircala Formation (Fig. 3). Then, a clear white tuffaceous massive and laminated sandstones package (Fig. 2B) intercalated with basalts crops out below the main basaltic field

known as Payún Matru plateau. The succession in this area is characterized by fine to medium massive tuffaceous sandstones with minor interbedded fine grained massive or with cross bedded conglomerates and massive and laminated shales. Some levels with rizolite-like structures and cross-stratified sandstones were also identified. On thin section, basic to intermediate volcanic lithic fragments are the most common ones, being the quartz and feldspar subordinate components (Fig. 2D). The presence of abundant shards in the matrix indicates active volcanism. According to its stratigraphic position, lithology, and the characteristics under the polarized microscope, we correlate this outcrop with the sediments in Liu Malal (see above), which were defined as the Puesto Fortunata Formation (González Díaz, 1979). Even though these sediments were described by Kozlowski et al. (1987a) as belonging to the Laguna Blanca Group, we consider that the name Puesto Fortunata Formation should be used by priority (González Díaz, 1979) and also because the Laguna Blanca Group was defined as late Oligocene by Legarreta et al. (1985) for a volcanic unit northern from the here studied area (see Discussion).

Isolated specimens and a fragment of femur *in situ* (see below) were recovered from a tuffaceous wacke, with shards replaced by analcime with clasts of quartz, feldspar, fragments of volcanic basic rocks and shards immersed in an altered to clay vitreous matrix (Fig. 2D). This level is located approximately 95 m above the top of Pircala Formation and even though the Puesto Fortunata Formation sediments continue few meters above this level, as it is highly covered, it could not be measured.

The association of shales and fine sandstones with bioturbation, together with the presence of fine conglomerate in wide channels, suggests a distal fluvial setting with active volcanism influence.
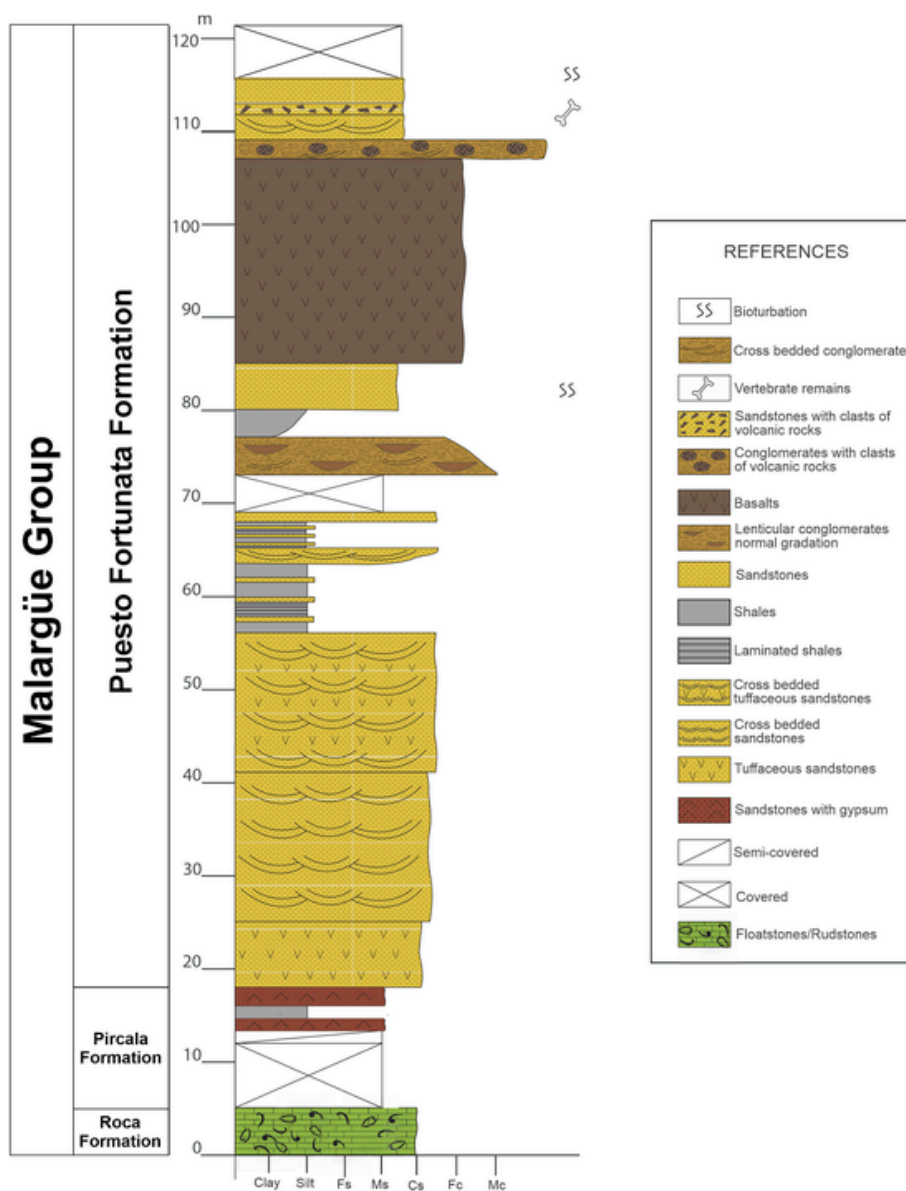
Fig. 3. Measured stratigraphic section of the sediments assigned to the Puesto Fortunata Formation with the position of the fossil-bearing level at the Agua de Flores-Agua de Isaac locality.

2. Materials and methods

All new fossils from Agua de Flores-Agua de Isaac and Liu Malal were collected during austral spring and autumn field seasons from 2009 to 2016 and recorded with Global Positioning System (GPS).

The fossils studied in this paper are curated at the MLP and IANIGLA (see acronyms below). In the MLP, we identified two lots of fossils containing the specimens collected by Dr. Kozlowski in the Agua de Flores area (MLP 96-VIII-15-1 and MLP 96-VIII-15-2).

All material has been compared with native ungulates (mainly attributed to Henricosborniidae and Oldfieldthomasiidae) described in other better known Eocene faunas from Mendoza (Divisadero Largo Formation), Patagonia (Sarmiento and Las Flores Formations), and NWA (Geste and Lumbrera Formations) in Argentina, and the Itaboraian fauna (Itaboraí Formation) in Brazil. The comparisons are based on literature and direct observation of specimens housed at several institutions: *Henricosbornia lophodonta* Ameghino (1901) (holotype MACN-A10808; AMNH FM 28968; Simpson, 1948); *Peripantostylops minutus* (Ameghino, 1901) (holotype MACN-A 10711; AMNH FM 28494;

Simpson, 1948); ?*Peripantostylops orehor* Simpson (1935a) (paratype AMNH FM 28555); *Selenoconus agilis* Ameghino (1901) (holotype MACN-A 10796); *Kibenikhoria get* Simpson (1935a) (holotype AMNH FM 28542; AMNH FM 28544; AMNH FM 28563; *Colbertia magellanica* (Price and Paula Couto, 1950) (DGM 357-M, DGM 2450-M, DGM 2585-M, MN, 1871-V; Paula Couto, 1952; Bergqvist and Bastos, 2009); *Othnielmarshia lacunifera* Ameghino (1901) (holotype MACN-A 10807); *O. pristina* (Paula Couto, 1978; DGM 400-M); *Xenostephanus chiotti* Simpson et al. (1962) (MCNAM 3008; AMNH FM 45947; AMNH FM 45948); *Brachystephanus postremus* Simpson et al. (1962) (AMNH FM 45945); *Allalmeia atalaensis* Rusconi (1946) (MCNAM-PV 507; Lorente et al., 2014); *Notopithecus adapinus* Ameghino (1897) (holotype MACN-A 10822, MACN-A 10786, MPEF-PV 1113; Vera, 2012, 2013, 2016); *Antepithecus brachystephanus* Ameghino (1901) (MACN-A 10842, MACN-A 10859a, MACN-A 10861, MLP 74-IV-27-15/16; Vera, 2013, 2016; Vera and Cerdeño, 2014); *Punapithecus minor* López and Bond (1995) (MLP 88-V-10-1); *Pleurostylodon modicus* Ameghino (1897) (AMNH FM 29878, Shockey and

Flynn, 2007); *Archaeopithecus rogeri* Ameghino (1897) (MMdP-M 727, Vera, 2017); *Homalostylops atavus* Paula Couto, 1954 (MN, 1992-V).

Specifically, specimens IANIGLA-PV 518 and IANIGLA-PV 519 were photographed using a Scanning Electron Microscope at the Laboratorio de Microscopía Electrónica de Barrido y Microanálisis (MEByM), IANIGLA-CONICET, Mendoza, Argentina. Postcranial terminology follows Cifelli (1983) and the International Committee on Veterinary Gross Anatomical Nomenclature (2005).

2.1. Institutional abbreviations

AMNH FM, American Museum of Natural History, Fossil Mammals, New York, USA; **DGM**, ex-Direção de Geologia y Mineralogia, Rio de Janeiro, Brasil; **IANIGLA-PV**, Paleovertebrate collection of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; **MACN-A**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Ameghino collection, Buenos Aires, Argentina; **MGP-PD-PD**, Museo de Geologia e Paleontologia, Università degli Studi di Padova , Padova , Italia; **MLP**, Museo de La Plata, La Plata, Argentina; **MCNAM**, Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano', Mendoza, Argentina; **MCT**, Museu de Ciências da Terra, Rio de Janeiro, Brasil; **MMdP**, Museo de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia', Mar del Plata, Argentina.

2.2. Other abbreviations in text and tables

APD, anteroposterior diameter; **cfc**, cuboid facet; **ffc**, fibular facet; **H**, height; **L**, length; **M/m**, upper/lower molar; **md**, mandible; **max**, maximum; **min**, minimum; **P/p**, upper/lower premolar; **PDD**, proximodistal diameter; **Px-dis**, proximo-distal; **SALMA**, South American Land Mammal Age; **sust**, sutentaculum; **TD**, transverse diameter; **TL**, total length; **tr**, trochlea; **W**, width.

3. Results

3.1. Systematic paleontology

PANPERISSODACTYLA Welker et al. (2015).
Notoungulata Roth, 1903.
Oldfieldthomasiidae Simpson, 1945.
Kibenikhoria Simpson, 1935a.

3.1.1. Type species
Kibenikhoria get Simpson (1935a).

3.1.2. Holotype
AMNH FM 28542, maxillary fragment with left P2–M1.

3.1.3. Diagnosis
Note: Simpson (1935a) provided the diagnosis of *Kibenikhoria* based only on upper teeth (P1 two-rooted and longer than wide, P2 simpler than P3–4 and not developing a closed fossette, P1–3 less transverse, slightly less prominent metacone than paracone on molars, and hypocone equal to or smaller than protocone and not projecting so far internally). However, one of us (BV) has recently revised the genus and a more complete diagnosis is provided in a manuscript already evaluated and presently under revision (Vera and Krause, J. of Vert. Paleontology). This new diagnosis include several features of lower dentition that allow the following interpretations (some specimens included in the mentioned revision are referred to in the comparisons below).

3.1.4. Referred material
MLP 96-VIII-15-1, a lot including two mandible fragments of different individuals, here named MLP 96-VIII-15-1a and MLP 96-VIII-15-

1b for descriptive purposes: MLP 96-VIII-15-1a, right m1–2; MLP 96-VIII-15-1b, right m2–3.

3.1.5. Geographic and stratigraphic origin
Agua de Flores-Agua de Isaac (Agua de Flores sensu Kozlowski et al., 1987a), Mendoza, Argentina. Puesto Fortunata Formation. Early–middle Eocene, Riochican–lower Casamayoran? SALMAs.

3.1.6. Description and comparisons
MLP 96-VIII-15-1a (Fig. 4A–B) preserves a very low (Table 1) and thin horizontal ramus with short-crowned and rooted m1–2. Both molars are characterized by having labially convex trigonid and talonid, very short protolophid, and lacking paralophid (Fig. 4A–B). They have a low and short mesial cingulid that descends labiolingually. The hypolophid is well developed but short, and a high distal cingulid closes a fossettid between hypolophid and entolophid (Fig. 4A). This fossettid is shallower and more reduced in m1 than in m2 because of the greater wear of the former tooth. The trigonid is a bit higher than the talonid, and the cristid obliqua is not fused yet to the metalophid, even in the more worn m1. The entolophid is comma-shaped in occlusal view, widening to the entoconid. The metalophid of m2 extends mesially in its middle part, forming a marked angle that is not observed in m1; distally, the metalophid widens downward filling the basin of talonid. The m1 is much smaller than m2 (Fig. 4A–B; Table 1), with the talonid nearly as short as the trigonid, while the talonid is longer than the trigonid in m2.

The specimen MLP 96-VIII-15-1b bears right m2–3 too badly preserved to be illustrated. However, the general aspect is very similar to the molars of MLP 96-VIII-15-1b, sharing a very low and thin horizontal ramus and short-crowned, although more worn, teeth. The m3 is similar to the m2 of MLP 96-VIII-15-1a in having a short and distinct hypolophid, but differs from it in the distolabially-mesiolingually oriented entolophid.

3.1.7. Taxonomic assessment
MLP 96-VIII-15-1a (Fig. 4A–B) was previously considered as cf. *Peripantostylops* by López (2008). This genus was included by Simpson (1948) in the Family Henricosborniidae, together with *Henricosbornia* and *Othnielmarshia*. Within *Peripantostylops*, Simpson (1948) differentiated the two species of the genus based only on size and wear, *P. minutus* (holotype MACN-A 10711, upper molar) from the 'Casamayoran' levels of 'Oeste de Río Chico' (Chubut Province) and ?*Peripantostylops orehor* (holotype AMNH FM 28526, left M1; paratype AMNH FM 28555, lower jaw) from the upper levels of Las Flores Formation of Cañadón Hondo (Chubut Province). Based on the differences between the mandible AMNH FM 28555 of ?*P. orehor* and the mandible MACN-A 10796 (holotype of *Selenoconus agilis* Ameghino, 1901), Simpson (1948) inferred that the latter represented the lower jaw of *P. minutus*, and therefore he proposed *S. agilis* as a synonymous name of *P. minutus*. Thus, probably MACN-A 10796 is the specimen on which López (2008) based his comparison of MLP 96-VIII-15-1a to consider the latter as cf. *Peripantostylops*. In turn, Simpson (1948) considered *Selenoconus centralis* Ameghino (1901) (holotype MACN-A 10797), *S. senex* Ameghino (1901) (holotype MACN-A 10792), and *S. spiculatus* Ameghino (1902) (holotype MACN-A 10795) synonymous names of *Henricosbornia lophodonta*. At present, Vera and Krause (MS under revision) have also proposed ?*P. orehor* as a synonymous of *H. lophodonta*. Other henricosborniid taxa are still pending a deep revision.

Comparatively, MLP 96-VIII-15-1a is similar in size to MACN-A 10796 ('*Selenoconus agilis*'; Table 1), sharing several features: m1 smaller than m2, trigonid with a low mesial cingulid, short protolophid, lack of paralophid, and high distal cingulid. However, MLP 96-VIII-15-1a differs from MACN-A 10796 in having the m2 with a more rounded talonid (versus triangular and labially pointed), a
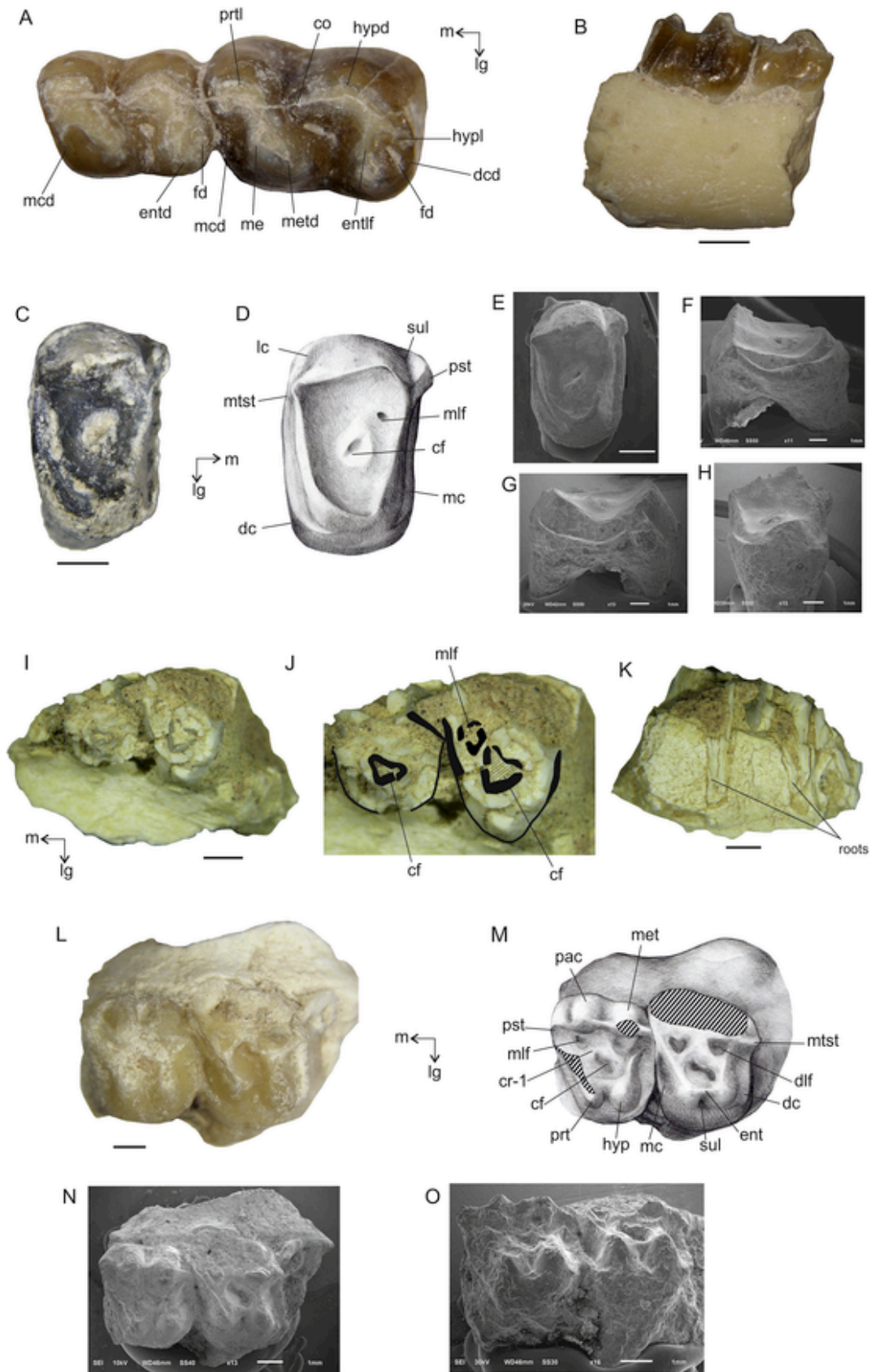
Fig. 4. A–J, Oldfieldthomasiidae. A–D, *Kibenikhoria* sp. A–B, MLP 96-VIII-15-1a, lower jaw with right m1–2, in occlusal (A) and labial (B) views. C–H, cf. *Kibenikhoria*, IANIGLA-PV 519, right P4, in occlusal (C–E), lateral (F–G), and lingual (H) views. I–L, Oldfieldthomasiidae indet., IANIGLA-PV 85, maxillary fragment with left P3–4, in occlusal (I–J) and labial (K) views. L–O, Notopithecidae Gen. et sp. nov., IANIGLA-PV 518, fragment of maxilla with little worn left M1–2, in occlusal (L–N) and lingual (O) views. D and M, artistic illustrations; E–H

and N–O, scanning electron microscope images. Scale bars equal 2 mm, except in F–H and N–O that equal 1 mm. Arrows indicate mesial (m) and lingual (lg) sides. Abbreviations: **cf**, central fossette; **co**, cristid oblique; **dc/dcd**, distal cingulum/distal cingulid; **dlf**, distolabial fossette; **ent**, entoloph; **entd**, entoconid; **entlf**, entolophid; **fd**, fossettid; **hyp/hypd**, hypocone/hypoconid; **hypl**, hypolophid; **lc**, labial cingulum; **mc/mcd**, mesial cingulum/mesial cingulid; **me**, mesial expansion; **met/metd**, metacone/metaconid; **mlf**, mesiolabial fossette; **mtst**, metastyle; **pac**, paracone; **prt**, protocone; **prtl**, protolophid; **pst**, parastyle; **sul**, sulcus.

Table 1
Measurements of lower molars (in mm) compared in the text. Acronyms for each specimen are detailed in text.

	m1 L W	m2 L W	m3 L W	H md at m1
Kibenikhoria sp. MLP 96-VIII-15-1a	3.1 2.5	4.5 3.0		5.7
'*Seleneoconus agilis*' MACN-A 10796	>2.7 2.6	4.0 3.3	5.3 3.0	6.3
Peripantostylops minutus AMNH FM 28494	3.7 2.6	3.9 2.9	5.3 2.9	
?*Peripantostylops orehor* AMNH 28555	3.7 3.15	4.4 3.7	5.5 3.5	7.2
Kibenikhoria get AMNH FM 28544	5.3 4.3	6.6 4.8		
Colbertia magellanica MN 1871-V	5.5 3.8	6.1 4.6	8.5 4.9	11.7
Homalostylops atavus MN 1992-V	4.4 3.0	5.0 3.0	6.3 3.1	
Xenostephanus chiotti AMNH 45948	5.4 4.8	6.3 4.6		
Brachystephanus postremus AMNH 45945	4.1 3.1	4.7 3.2		
Allalmeia atalaensis MCNAM-PV 507	4.5 3.8	5.0 4.0	5.0 4.2	
Notopithecus adapinus MACN-A 10786	5.1 3.6	5.4 3.8		13.7

mesial expansion in the middle of the metalophid (absent in MACN-A 10796), and the posterior border of the latter straight at the contact point with the cristid obliqua (concave in MACN-A 10796). Conversely, the mesial extension of the metalophid and the convex labial and lingual faces resemble the morphology observed in some specimens (e.g., AMNH FM 28544, MGP-PD-PD 31561, MGP-PD-PD31720, MGP-PD-PD 32034) attributed to *Kibenikhoria get*, an oldfieldthomasiid identified in the upper levels of Las Flores Formation in Cañadón Hondo and Bajo Palangana, Chubut Province (Simpson, 1935a; Vera and Krause, MS under revision).

Therefore, in our opinion, MLP 96-VIII-15-1a is morphologically closer to *Kibenikhoria* than to *Peripantostylops*, although it is smaller than *K. get* (Table 1). As noted above, *K. get* was originally based on upper teeth, and lower dentition was indirectly associated (Simpson, 1935a, 1967). However, new remains (MGP-PD-PD 31561, MGP-PD-PD 31720, MGP-PD-PD 32034) have been recently ascribed to this species, leading to a deep revision and a more complete diagnosis of the species (Vera and Krause, MS under revision), which allows us (based on BV's personal data) to propose MLP 96-VIII-15-1a,b belong to *Kibenikhoria*. Due to the scarce material, we cannot be sure whether or not it could be a new species of the genus and so we identify these specimens as *Kibenikhoria* sp.

3.1.8. Referred material
IANIGLA-PV 518, fragment of maxilla with left M1–2

3.1.9. Geographic and stratigraphic origin
Liu Malal, Mendoza, Argentina. Puesto Fortunata Formation. Early–middle Eocene, Riochican–lower Casamayoran? SALMAs.

3.1.10. Description and comparisons
IANIGLA-PV 519 was recovered by hand picking of sediments from Liu Malal (Fig. 1). It is a brachydont tooth, much wider than long (L = 5.6 mm; W = 8.4 mm), with three roots, and a rectangular general outline, which allows us to identify this premolar as a P4. It is a moderately worn tooth, showing a deep, mesiolabially-distolingually oriented central fossette , and a tiny and circular mesiolabial fossette (Fig. 4C–D). The enamel forms a triangular occlusal outline, softly undulated on the mesial and distal edges that converge in a rounded lingual apex. No sulcus is observed on the lingual face. There is a mesiolabially folded parastyle and a deep sulcus behind it. The ectoloph is barely convex and backwardly inclined, with an insinuated metastyle. The mesial and distal cingula are low, concave in the middle, and well-extended from the labial to the lingual border (Fig. 4F–G). The mesial cingulum is lower and shorter than the distal one; the latter is a bit more extended lingually (Fig. 4H). There is also a labial cingulum, very low and narrow at the base and more developed on the distal half of the crown (Fig. 4C–E).

3.1.11. Taxonomic assessment
The presence of low and long cingula in upper premolars is characteristic of early Eocene small brachydont notoungulates, such as *Henricosbornia* and *Kibenikhoria*, whereas in late-diverging forms, such as *Notopithecus* and *Archaeopithecus*, the cingula are higher and relatively much reduced, mainly the mesial cingulum. Regarding the P4 of *Henricosbornia lophodonta* (MACN-A 10808; Table 2), IANIGLA-PV 519 has a larger W/L ratio (1.5 versus 1.3) and a wider protocone, while the P4 in MACN-A 10808 is more triangular, the protocone is narrower and sharper, the central fossette is larger, and the paracone and metacone folds are pronounced. On the contrary, IANIGLA-PV 519 (Fig. 4C–H) shares with *Kibenikhoria get* (e.g., AMNH FM 28542; Simpson, 1935a; Vera and Krause, under revision) a comparable size (Table 2), a similar W/L ratio, a small metastyle, a nearly flat ectoloph, and similarly-shaped mesiolabial and central fossettes. However, *K. get* has a more undulated occlusal contour, more folded parastyle and metastyle, and a larger mesiolabial fossette. These differences and the scarce material lead us to identify IANIGLA-PV 519 as cf. *Kibenikhoria*. Contrary to the previous case, the identification of IANIGLA-PV 519 is not so confident, but it clearly closes *Kibenikhoria*. On the other hand, IANIGLA-PV 519 could represent a different taxon from MLP 96-VIII-15-1a, which is supported by the large general dimensions of IANIGLA-PV 519 (Tables 1–2), even though both specimens are not homologous elements.

3.1.12. Referred material
IANIGLA-PV 85, maxillary fragment with left P3–4.

3.1.13. Geographic and stratigraphic origin
Agua de Flores-Agua de Isaac, Mendoza, Argentina. Puesto Fortunata Formation. Early–middle Eocene, Riochican–lower Casamayoran? SALMAs.

3.1.14. Description and comparisons
The fragment of maxilla IANIGLA-PV 85 has two rooted and low-crowned teeth, here interpreted as the left P3–4 (Fig. 4I–K). The premolars are badly preserved and show an advanced wear. They are characterized by having a large, heart-shaped and long-lived central fossette, and a conspicuous mesiolabial fossette, which is more evident in the P4. The enamel is thick around the crown and in the central fossette (Fig. 4I). The P4 has a sub-squared outline, with the proto-

Table 2

Measurements of upper teeth (in mm) compared in the text. Acronyms for each specimen and abbreviations are detailed in text. Approximate values in parentheses; –, missing data.

	P3		P4		M1		M2	
	L	W	L	W	L	W	L	W
Oldfieldthomasiidae indet. IANIGLA-PV 85			>5.0	(5.9)				
Notopithecidae IANIGLA-PV 518					4.0	4.1	3.8	4.8
cf. *Kibenikhoria* IANIGLA-PV 519			5.6	8.4				
Peripantostylops minutus MACN-A 10711							4.3	4.9
Xenostephanus chiotti AMNH FM 45947	5.6	7.4	5.5	(8.0)	6.8	8.3	(6.5)	–
Brachystephanus postremus AMNH FM 45945	2.9	4.3	3.4	5.2	4.4	6.1	(5.0)	(6.0)
Allalmeia atalaensis MCNAM-PV 507	3.7	6.2	4.1	7.0	5.0	7.9	5.5	9.7
Kibenikhoria get AMNH FM 28542	(5.1)	6.6	5.4	7.9	6.0	8.4		
Henricosbornia lophodonta MACN-A 10808	4.8	(5.0)	4.5	5.8	4.9	6.1	5.5	6.2
Colbertia magellanica DGM 357-M	4.3	6.3	4.9	7.5	6.2	8.2	7.1	9.2
Othnielmarshia pristina DGM 400-M	3.9	5.8	4.4	6.9	4.7	7.2	5.7	7.8
Notopithecus adapinus MACN-A 10822	3.6	4.2	4.3	4.6	–	–	4.7	4.8
Antepithecus brachystephanus MACN-A 10859a	–	(4.4)	4.2	5.1	4.9	5.4	5.1	>3.9
Punapithecus minor MLP 88-V-10-1					3.2	2.8	3.4	2.9
Archaeopithecus rogeri MMdP-M 727	4.1	6.4	4.5	(6.8)	4.2	6.6	(4.9)	(7.6)

cone centrally placed on the lingual face that is shorter than the labial face; the distal face is convex (Fig. 4J). The P3 is smaller than P4, but it is too incomplete to be measured (Table 2). It does not seem mesial and distal cingula are present, but unfortunately it cannot be assured due to the bad preservation.

3.1.15. Taxonomic assessment

IANIGLA-PV 85 is comparable in size to *Henricosbornia lophodonta*, *Peripantostylops minutus*, and the notopithecids (*sensu* Vera, 2016) *Notopithecus adapinus* and *Antepithecus brachystephanus* (Table 2). However, it differs from *H. lophodonta* because its P4 is squarer (versus nearly triangular), with a convex mesial face and long-lived central and labial fossettes (versus undulated mesial face and short-lived central and labial fossettes). The large central fossette present in both teeth of IANIGLA-PV 85 (Fig. 4I–J) also distinguishes this specimen from *P. minutus*. Among other comparable small and brachydont Eocene notoungulates, teeth of IANIGLA-PV 85 are larger than those of the oldfieldthomasiid *Brachystephanus postremus* and differ from it in having a larger and long-lived central fossette; in turn, the archaeopithecid *Archaeopithecus rogeri* differs from IANIGLA-PV 85 in having a higher W/L ratio (1.5), a larger mesiolabial fossette, and a smaller and more complex central fossette.

The characteristics described for IANIGLA-PV 85, including the premolar W/L ratio, the occlusal contour, the long-lived central fossette, and the thick enamel, resemble the general aspect of the notopithecids (e.g., *N. adapinus* and *A. brachystephanus*) and the oldfieldthomasiid *Kibenikhoria get*. Premolars of both groups differ from each other mainly in their proportions and development of cingula. In this aspect, however, the poor preservation of IANIGLA-PV 85 does not allow a confident evaluation on the presence of cingula, while its proportions are closer to *Kibenikhoria* (with a low mesial cingulum and a very well-developed distal cingulum). With respect to the other remains here described from southeast Mendoza, upper premolars IANIGLA-PV 85 are much larger than the lower molars of MLP 96-VIII-15-1a (*Kibenikhoria* sp.) and differ from IANIGLA-PV 519 (cf. *Kibenikhoria*; Fig. 4C–H) in having a lower W/L ratio on P4 (1.2 versus 1.5) and larger central and labial fossettes. Therefore, we consider that IANIGLA-PV 85 represents an oldfieldthomasiid (discarding notopithecids after the premolar proportions), but a more accurate determination cannot be achieved.

3.1.16. Referred material

IANIGLA-PV 518, fragment of maxilla with left M1–2.

3.1.17. Geographic and stratigraphic origin

Liu Malal, Mendoza. Argentina. Puesto Fortunata Formation. Early–middle Eocene, Riochican–lower Casamayoran? SALMAs.

3.1.18. Description and comparisons

The specimen IANIGLA-PV 518 shows little worn M1–2, the M2 with broken ectoloph (Fig. 4L–M). They are brachydont teeth and very similar in morphology to each other. It is interesting to note that the M1 is a nearly square tooth, while the M2 is longer than wide and larger (Table 2). The smaller size of M1 with respect to M2 is a common condition in Eocene notoungulates (e.g., *Kibenikhoria*, *Notopithecus*, *Colbertia*), whereas in post-Eocene taxa the M1 acquires larger size than M2 (e.g., *Protypotherium*). The M1 has an undulate ectoloph, with well-developed parastyle, paracone, metacone, and metastyle (Fig. 4M–N). The metacone is wider than the paracone and the sulcus between them is deeper than the parastyle sulcus. The metastyle forms a sharp corner and is distally extended (Fig. 4M, O). There are two nearly equally-sized and heart-shaped labial fossettes. The central fossette is larger than the labial ones, with a sigmoid contour more clearly visible in M2 (Fig. 4M). Protoloph and metaloph are well-separated by the central fossette, but there is a short and wide crest (entoloph) between them, which isolates the central fossette from the lingual sulcus. The protoloph is distolingually inclined, whereas the metaloph is transverse to the ectoloph. Both mesial and distal cingula are low and long, although the distal cingulum is wider than the mesial one (Fig. 4O). In both molars, protocone and hypocone are practically at the same lingual level, but the protocone is a bit internally placed with respect to the hypocone in M1.

3.1.19. Taxonomic assessment

IANIGLA-PV 518 is characterized by its very small size with respect to other known Eocene notoungulates, such as *H. lophodonta*, *K. get,* the notopithecids, and the taxa from the Divisadero Largo (Argentina) or Itaboraí (Brazil) Formations (Table 2). Although IANIGLA-PV 518 cannot be directly compared with IANIGLA-PV 85 (Oldfieldthomasiidae indet.; Fig. 4L–O), its molars are much smaller than the premolars of the latter (Table 2). Squarer molars with well-defined crista 1 and crochet, larger labial fossettes, and a lower and wider distal cingulum differentiate IANIGLA-PV 518 from *Henricosbornia*. In turn, *Kibenikhoria* has the protoloph shorter than metaloph, which implies that the hypocone is lingually extended with respect to the protocone, the protocone

and hypocone are lingually joined, and the ectoloph is less folded. IAN-IGLA-PV 518 differs from *Brachystephanus postremus* and *Xenostephanus chiotti* from Divisadero Largo Formation in having labial fossettes, which are absent in both species; in addition, *B. postremus* has a shorter and more inclined protoloph. IANIGLA-PV 518 is larger than *Punapithecus minor*, a basal interatheriid from the Geste Formation, NWA (Table 2), and differs from it in having squarer molars, lingual crest between the metaloph and protoloph, and a wider central fossette. In relation to the Itaboraian fauna from the Itaboraí Formation, IANIGLA-PV 518 shares with *Colbertia magellanica* the low and well-developed mesial and distal cingula and a folded ectoloph, but *C. magellanica* lacks the lingual crest and has ephemeral labial fossettes. On the other hand, *Othnielmarshia pristina* presents very short-lived labial fossettes, a wider lingual crest, and a thin mesial cingulum.

General morphology of IANIGLA-PV 518 (square molars, long and wide cingula, labial fossettes, lingual crest uniting metaloph with protoloph, lingual sulcus, and a large and isolated central fossette) closes this specimen to the Notopithecidae morphotype (e.g., *Notopithecus* and *Antepithecus*). However, it differs from *N. adapinus* and *A. brachys-tephanus* in having more convex labial folds and deeper sulci on the ectoloph, simpler central fossette, hypocone more lingually placed than protocone, and a narrower crest uniting the protocone with hypocone. Therefore, we consider that IANIGLA-PV 518 could represent a new taxon of the Family Notopithecidae.

3.1.20. Referred material

MLP 96-VIII-15-2, associated right astragalus and calcaneum.

3.1.21. Geographic and stratigraphic origin

Agua de Flores-Agua de Isaac, Mendoza, Argentina. Puesto Fortunata Formation. Early–middle Eocene, Riochican–lower Casamayoran? SALMAs.

3.1.22. Description and comparisons

The astragalus MLP 96-VIII-15-2 (Fig. 5A−E) is characterized by having almost parallel trochlear crests and the medial crest higher (PDD) than the lateral one, although this asymmetry is not as evident as in *Notopithecus adapinus* (Vera, 2012). The lateral crest is
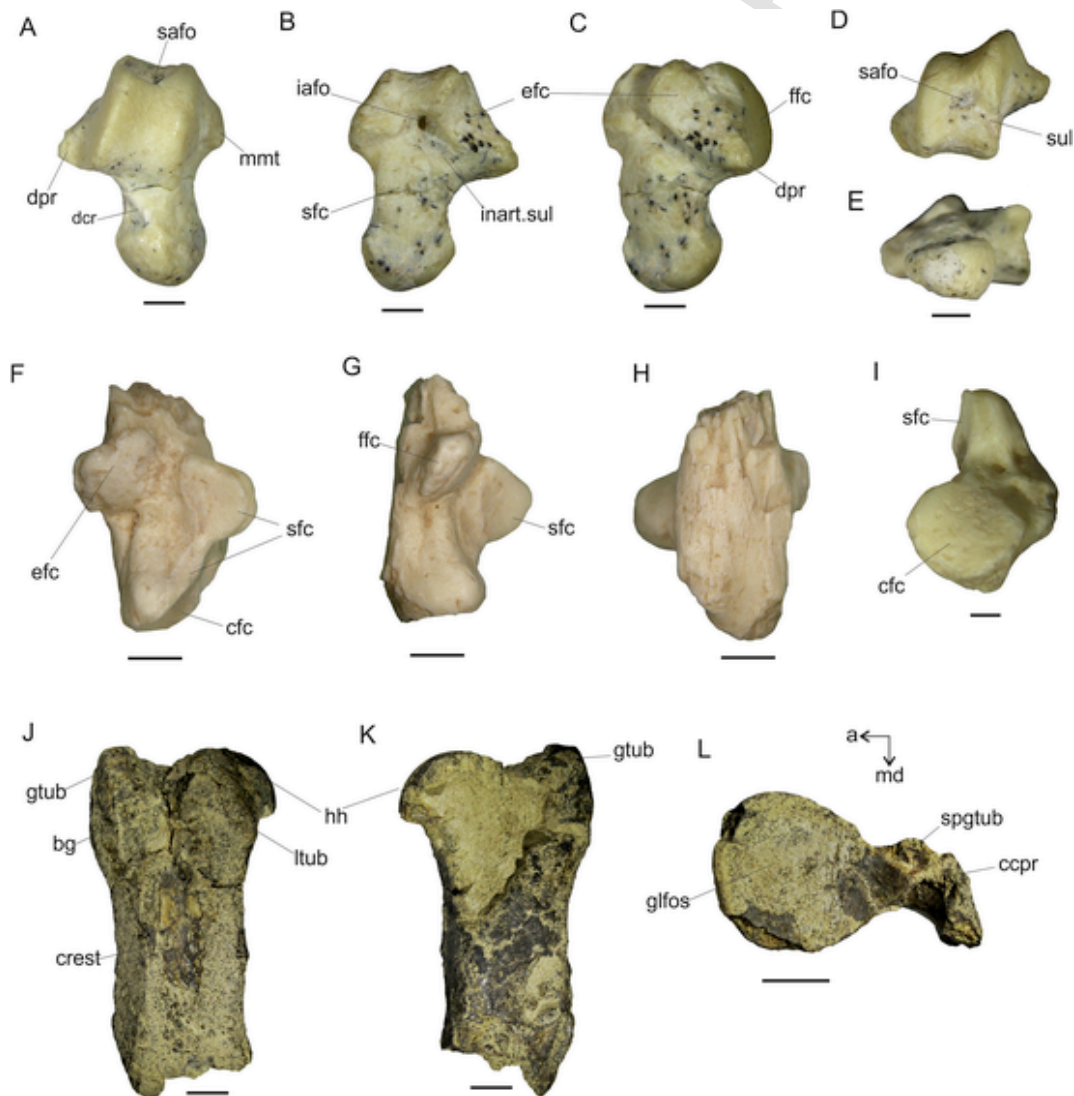

Fig. 5. A−I, ?Henricosborniidae indet., MLP 96-VIII-15-2, right astragalus (A−E) and calcaneum (F−I), in anterior (A and F), posterior (B and H), medial (C and G), proximal (D), and distal (E and I) views. J−L, Notoungulata indet., IANIGLA-PV 542, proximal right humerus (J−K) and fragment of scapula (L), in anterior (J), posterior (K), and ventral (L) views. Scale bars equal 2 mm in A−I, and 10 mm in J−L. Arrows indicate anterior (a) and medial (md) sides. Abbreviations: **bg**, bicipital groove; **ccpr**, coracoid process; **cfc**, cuboid facet; **dcr**, dorsal crest; **dpr**, distal process; **efc**, ectal facet; **ffc**, fibular facet; **glfos**, glenoid fossa; **gtub**, greater tubercle; **hh**, humeral head; **iafo**, inferior astragalar foramen; **inart. sul**, inarticular sulcus; **ltub**, lesser tubercle; **mmt**, medial malleolus of tibia; **safo**, superior astragalar foramen; **sfc**, sustentacular facet; **spgtub**, supraglenoid tubercle; **sul**, sulcus; **tr**, trochlea.

deeper (APD) than the medial crest, and surpasses the latter anteriorly. In anterior view, the trochlea is oblique in relation to the vertical neck, and its articular surface is mildly concave (Fig. 5A). The TD/APD ratio of the trochlea is greater than in *Notopithecus*, but lower than in *Colbertia* (Table 3). The dorsal crest is long and obliquely oriented on the anterior face (Fig. 5A). In posterior view, the ectal facet is concave, obliquely oriented, and widens proximally (Fig. 5B). Proximally, the ectal facet forms a crest with the trochlea and distally extends in a prominent process (Fig. 5C), which is not as laterally extended as in *Colbertia*. Comparatively, the proximal crest is much more developed and posteriorly projected in *Notopithecus* (Vera, 2012: Fig. 5B), whereas in *Colbertia* it is similarly developed, as in MLP 96-VIII-15-2. The sustentacular facet has an ellipsoidal contour with the major axis proximomedially-distolaterally oriented; its convex surface is wide and long, covering almost all the posterior face of the body of the astragalus (Fig. 5B). The fibular facet is almost flat and widens distally, and covers the entire anterolateral side (Fig. 5C). A large superior astragalar foramen is anterolaterally placed on proximal view (Fig. 5A, D). A wide and deep sulcus runs posterolaterally from the foramen, reaching the lateral border of the trochlea (Fig. 5D), like in *C. magellanica* (Cifelli, 1983: Fig. 11G) but different from *Notopithecus*, in which the foramen is more posteriorly placed and a sulcus is not discernible (Vera, 2012: Fig. 5). The superior astragalar foramen is connected to the inferior astragalar foramen that opens in a deep and wide interarticular sulcus (Fig. 5B). The superior foramen was described as typical for Eocene notoungulates (e.g., *Colbertia magellanica*, *Thomashuxleya*, and *Anisotemnus*), while it is less common in post-Eocene forms (e.g., interatheriines) (Shockey and Flynn, 2007). The medial malleolus for the tibia is as developed as in *Notopithecus*, but more vertically oriented (Fig. 5A). The articular head is anteroposteriorly narrow (Fig. 5E); its facet is well expanded on both lateral and medial faces and widens medially, while in *Notopithecus* the head is spherical and its facet is less expanded laterally, being much better developed medially to the navicular facet (Vera, 2012: Fig. 5B). In general terms, MLP 96-VIII-15-2 is more similar to *C. magellanica* (Cifelli, 1983: Fig. 11) than to other compared Eocene astragali, sharing with this species the presence of a large superior astragalar foramen, a prominent medial malleolus for the tibia, and a prolonged fibular facet, but differing from it by its smaller size (Table 3), a longer and stylized neck, a laterally shorter and anteroposteriorly deeper trochlea, and a narrower cuboid facet. In the ?oldfieldthomasiid *Allalmeia* (Lorente et al., 2014), the lateral crest is evidently higher than the medial, as in *Notopithecus* (Vera, 2012), and both crests diverge proximodistally.

The calcaneum MLP 96-VIII-15-2 (Fig. 5F–I; Table 4) lacks the tuber, but its body is rather well-preserved. The ectal facet is crescent-shaped, medially oriented, narrow, and very convex anteriorly (

Table 3

Measurements (in mm) of astragali compared in the text. Acronyms for each specimen are detailed in text.

	TL	Px-dis. max. tr.	TD tr.	TD max.	APD tr.	TD head	APD head
?Henricosborniidae indet. MLP 96-VIII-15-2	11.6	8.4	5.3	8.5	4.9	4.8	3.3
Colbertia magellanica DGM 2450-M	15.2	8.5	9.7	12.7	6.7	7.3	5.3
Allalmeia atalaensis MCNAM-PV 507		8.8	6.4				
Notopithecus adapinus MPEF-PV 1113	8.9	5.2	4.1	5.0	4.4	2.7	2.9

Table 4

Measurements (in mm) of calcanei compared in the text. Acronyms for each specimen and abbreviations are detailed in text. –, missing data.

	TL	D max. cfc	D min. cfc	H sust.	APD max. sust.	TD max. ffc
?Henricosborniidae indet. MLP 96-VIII-15-2	–	4.3	3.4	3.6	2.4	2.1
Colbertia magellanica DGM 2585-M	26.3	7.6	6.1	5.2	3.2	3.3
Notopithecus adapinus MPEF-PV 1113	13.0	4.4	3.1	3.1	6.6	5.9

Fig. 5G). The fibular facet is wedge-shaped, obliquely oriented on the lateral face and narrows distally (Fig. 5F). The presence of a fibular tubercle cannot be determined because the bone is broken in this part (Fig. 5H). The facet for cuboid is nearly circular, barely concave anteroposteriorly, and medially inclined (Fig. 5I). The sustentacular facet has two sections (Fig. 5F): the proximal one is wide, fan-shaped, and slightly concave; it continues distally in a thin slice-shaped subfacet that contacts medially the cuboid facet. This configuration is also present in *C. magellanica*, but in this species the distal part is triangular, clearly larger and better developed, forming a larger articular surface with the proximal part. In addition, *C. magellanica* has a reduced fibular facet in relation to the ectal facet, whereas in MLP 96-VIII-15-2 such a difference is not so obvious. The calcaneum of *Allalmeia*, in turn, has a large sustentaculum, as wide as the calcaneal tuber, and a well-developed plantar tubercle (Lorente et al., 2014). This tubercle is equally developed in *Notopithecus*, which also has a broader protuberance (coracoid process) housing the ectal and fibular facets (Table 4), but this taxon differs from MLP 96-VIII-15-2 in having a circular and moderately concave sustentacular facet without the distal subfacet.

3.1.23. Taxonomic assessment

The astragalus and calcaneum MLP 96-VIII-15-2 (Fig. 5A–I) have several tarsal traits that occur in pre-Oligocene notoungulates, whereas they are rare in Oligocene or younger taxa (see Shockey and Flynn, 2007). In this sense, the presence of an astragalar foramen, a well-developed tibial protuberance in the astragalus, and a sustentacular distal subfacet in the calcaneum are shared with Eocene taxa such as *Colbertia* (Cifelli, 1983), *Notostylops* (Lorente et al., 2019), *Thomashuxleya* (Simpson, 1936; Shockey and Flynn, 2007), *Anisotemnus* (Shockey and Flynn, 2007), *Notopithecus* (Vera, 2012), and *Allalmeia* (Lorente et al., 2014). Among these taxa, the generalized morphology of MLP 96-VIII-15-2 is closer to *Colbertia* than to the others. However, the differences observed in both tarsal bones do not allow a confident taxonomic determination, but it is reasonable to consider these bones could belong to the Family Henricosborniidae, supporting Vera (2012), who previously identified the astragalus MLP 96-VIII-15-2 as ?Henricosborniidae. Nevertheless, associated dentition and postcranium are not know for this particular group of notoungulates, which prevents more precise comparisons.

3.1.24. Referred material

IANIGLA-PV 542, associated fragments of right humerus and scapula.

3.1.25. Geographic and stratigraphic origin

Agua de Flores-Agua de Isaac, Mendoza, Argentina. Puesto Fortunata Formation. Early–middle Eocene, Riochican–lower Casamayoran? SALMAs.

3.1.26. Description and comparisons

IANIGLA-PV 542 includes a proximal fragment of right humerus (Fig. 5J–K) and a fragment of scapula (Fig. 5L) of the same individual. These bones were found *in situ* in tuffaceous sandstones above the Pircala Formation, in the Agua de Flores-Agua de Isaac profile (Fig. 3 and see above). According to the dimensions of the humerus (proximal epiphysis: APD = 29.4 mm; TD = 46.4 mm), this specimen belongs to a large-sized animal, too large to correspond to any of the much smaller specimens described above (e.g., teeth and tarsal bones). The proximal epiphysis of the humerus is anteroposteriorly flattened with a rectangular cross-section and straight lateral borders. The greater tubercle is a broad crest running parallel to the anteroposterior axis and widens in the same direction, although it is practically at the same level than the head (Fig. 5J). The crest of the greater tubercle runs distally on the anterior face, forming a slightly marked lateral border. The epiphysis is deeply excavated between the high lateral border and the medial side of the humerus. The bulbous lesser tubercle is barely insinuated on the anterior face, at a lower level than the head (Fig. 5K). The humeral head is moderately convex and posteromedially directed; it is slightly lower than the greater tubercle. The posterior face of the epiphysis is broken, thus it is not possible to observe the complete extension of the greater tubercle and humeral head (Fig. 5K). The bicipital groove is wide and moderately deep (Fig. 5J).

The associated scapula IANIGLA-PV 542 (Fig. 5L) preserves the glenoid fossa, supraglenoid tubercle, and coracoid process. The glenoid fossa is smoothly concave and has a teardrop contour (APD = 22.0 mm; TD = 26.2 mm). The coracoid process is a well-developed, strong, and curved projection medially extended. This projection connects to the glenoid fossa by a wide and short neck with strongly concave lateral and medial borders. Posterior to the lateral concavity, a broken but moderately expanded supraglenoid tubercle is insinuated.

Few large-sized humeri and scapulae are known among Eocene notoungulates. This is the case for the isotemnids *Thomashuxleya externa* and *Anisotemnus distentus* from Cañadón Vaca (Chubut Province) in Patagonia (Carrillo and Asher, 2017; Shockey and Flynn, 2007). Humeri MPEF-PV 8166 (*T. externa*; Carrillo and Asher, 2017: Fig. 4) and AMNH FM 28906 (*A. distentus*; Shockey and Flynn, 2007: Figs. 1 and 2) mainly differ from IANIGLA-PV 542 in having a high greater tubercle, a sharply defined lesser tubercle, a well-developed deltopectoral crest, and a well-defined bicipital groove, as well as an anteroposteriorly elongated glenoid fossa. Another significant difference is that the proximal epiphysis and the diaphysis of the humerus IANIGLA-PV 542 are aligned in the proximo-distal axis; that is, the greater tubercle runs in the same axis than the lateral face of the diaphysis. On the contrary, in the isotemnid humeri the crest of the greater tubercle curves medially, giving a twisted aspect to the proximal epiphysis, as it is observed as well in toxodontids (Scott, 1912). The humerus IANIGLA-PV 542 is comparable in size to the isotemniid *Pleurostylodon similis* (e.g., AMNH FM 28904; Shockey and Flynn, 2007, Table 1), but the humeral proximal epiphysis in the latter is restored, impeding full comparisons.

Concerning the scapula, the described features of IANIGLA-PV 542 are rather similar to those of *Anisotemnus* (AMNH 28906; Shockey and Flynn, 2007).

We cannot accurately discard the correspondence of IANIGLA-PV 542 to other native ungulates (e.g., Litopterna), but humeri and scapula associated with taxonomically identified dentition are unknown for Eocene representatives. In the case of Litopterna, the Eocene taxa show a small tooth size that is not compatible with IANIGLA-PV 542. In sum, we consider that IANIGLA-PV 542 could belong to an indeterminate large-sized notoungulate.

4. Discussion

4.1. The Malargüe Group in the studied area: age and geodynamic scenario

The Malargüe Group (Uliana and Dellapé, 1981) is integrated in the northern part of the Neuquén Basin by marginal marine and marine deposits at the base, known as Loncoche, Jagüel and Roca Formations, and continental sediments of the Pircala and Coihueco Formations at the top (Fig. 6). These continental formations were sometimes combined into the same unit, named as the Pircala-Coihueco Formation (Yrigoyen, 1993) because of its difficulty for differentiation. The age of the Malargüe Group was established as late Campanian–Paleocene (?) based on fauna from the marine deposits (Rodríguez, 2011; Parras and Griffin, 2013 and references therein) and K/Ar data (Parras et al., 1998) that allowed locating the K/Pg boundary within the sediments of Pircala Formation in the Arroyo Loncoche area, situated 180 km approximately to northwest from the studied area.

A few years ago, Horton et al. (2016) considered the Coihueco Formation as an independent unit and provided an absolute age for the top of it, using detrital zircons, with a weighted mean U–Pb age of 41.4 ± 1.1 Ma (Eocene, Lutetian–Bartonian). However, no fossils were recorded that provide biostratigraphic correlations. The facies analyses and the zircon U–Pb age signatures indicated that the Coihueco Formation represents slow accumulation rates that are compatible with an insignificant topographic loading and the absence of a well-developed zone of upper crustal shortening between the arc and retroarc basin (Horton, 2018: Fig. 9A2 and 9A3).

In the studied area, the lower part of the Malargüe Group is identified by the presence of the conspicuous outcrops of the Roca and Pircala Formations in both localities (Fig. 1). Now, the lithology, stratigraphic position, sedimentary structures, facies analysis, thin section studies, and fossil content of the studied sediments allow us to recognize them as belonging to the Puesto Fortunata Formation defined in Liu Malal area (González Díaz, 1979) and propose this unit can be laterally correlated to the Coihueco Formation known in other outcrops of the northern Neuquén basin (Fig. 6). This is relevant as the deposition of Coihueco sediments marks the end of the pre-orogenic Paleogene sedimentary sequences of the Neuquén basin, so the absolute age of the Coihueco Formation (Horton et al., 2016) allows constraining the duration of the gap between the Riográndico cycle and the following one, the onset of the Miocene orogenic phase (Silvestro and Atencio, 2009; Horton, 2018). This is reinforced as well by the relative early–middle Eocene age inferred from the mammal content for the Fortunata Formation sediments.

4.2. Mammal composition

According to their general morphology and sizes, the mammal fossils recovered from Agua de Flores-Agua de Isaac and Liu Malal can be gathered in four different groups. On the one hand, MLP 96-VIII-15-1a,b and probably IANIGLA-PV 519 represent the oldfieldthomasiid *Kibenikhoria*, although they are different from the only known species, *K. get*, which implies the first mention of *Kibenikhoria* out of Patagonia.

IANIGLA-PV 85 shows characters that close it to both *Kibenikhoria* and notopitheciids. However, the tooth W/L ratio allows discarding these premolars from notopithecids whereas the large and long-lived central fossette differs from *Kibenikhoria*. The latter feature, which is regarded as primitive, constitutes a peculiarity for this specimen and this is why we identify IANIGLA-PV 85 as Oldfieldthomasiidae indet.

IANIGLA-PV 518 displays the typical characteristics (e.g., square molars, long and wide cingula, presence of labial fossettes, lingual crest uniting metaloph with protoloph, lingual sulcus, and large isolated central fossette) of the Notopithecidae *Notopithecus* and *Antepithecus*, although some peculiarities (e.g., smaller size, a more folded ectoloph,
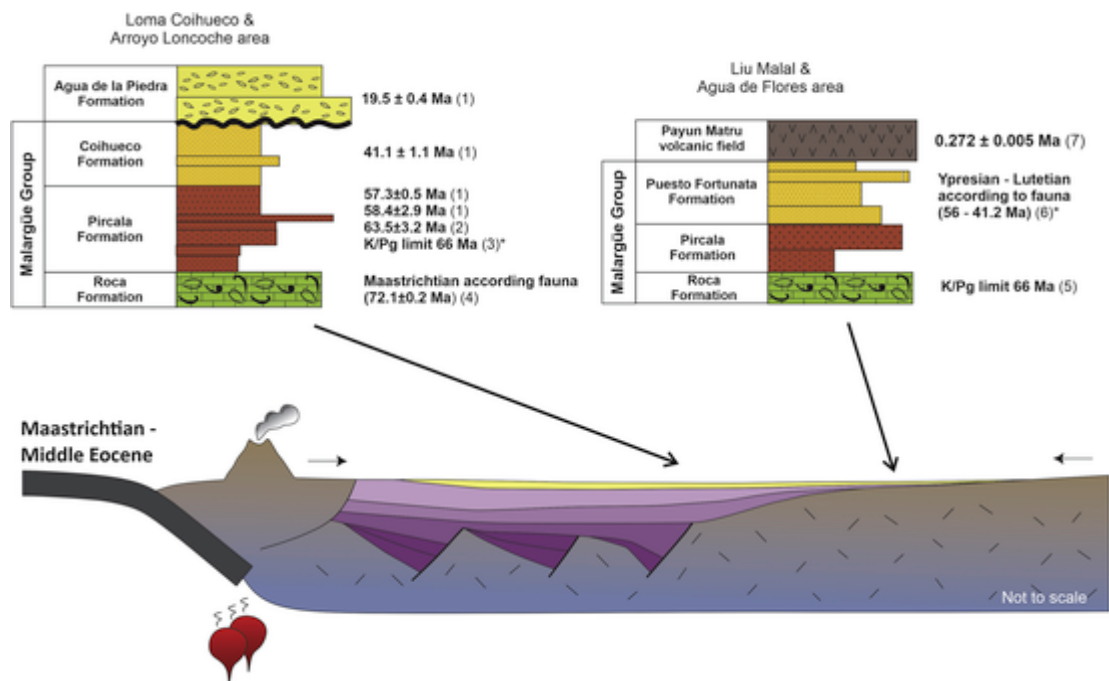
Fig. 6. Simplified stratigraphic columns (not to scale) of the Liu Malal and Agua de Flores-Agua de Isaac areas and Arroyo Loncoche and Loma Coihueco areas located in the schematic cross section reconstructions at the latitude of the studied area. The sketches are based on Horton et al. (2016; Fig. 11d) and redrew according to our stratigraphic data for the Maastrichtian-middle Eocene setting. The ages were taken from: 1, Horton et al. (2016); 2, Parras et al. (1998); 3, Parras and Casadío (1999); 4, Parras and Griffin (2013); 5, Pires et al. (1999); 6, this work; 7, Ramos and Folguera (2010). *The duration of the stages and the K/Pg limit are according to the International Commission on Stratigraphy.

a narrower occlusal crest) separate it from these genera and could represent a new genus and species of this group.

The size and morphology of the astragalus and calcaneum MLP 96-VIII-15-2 differ from well-known Eocene notoungulates, such as old-fieldthomasiids (e.g., *Colbertia*), notopithecids (e.g., *Notopithecus*) and notostylopids (e.g., *Notostylops*), which leads to consider them as possibly belonging to Henricosborniidae, whose tarsus has not been described before.

Finally, the humerus and scapula IANIGLA-PV 542 are recognized as Notoungulata indet., close in size to the Isotemniidae *Pleurostylodon*. This specimen implies the presence of a large taxon, expanding the range of body sizes represented within the notoungulate assemblage from southeast Mendoza.

4.3. Faunal relationships

Both the teeth and postcranium from southeast Mendoza are recognized into the henricosborniid, notopithecid, oldfieldthomasiid, and possibly isotemniid (*Pleurostylodon*) morphotypes. These groups constitute the typical Riochican and Casamayoran mammal communities from Patagonia, which implies a faunal relationship between both areas. Moreover, the recognition of *Kibenikhoria* in Mendoza links this fauna more closely to the Riochican associations from Cañadón Hondo and Bajo Palangana (Chubut Province), where this genus was identified (Simpson, 1935a, b; Vera and Krause, MS under revision).

Noteworthy, there are not common taxa between southern (e.g., Agua de Flores-Agua de Isaac, Liu Malal) and northern Mendoza (Divisadero Largo Formation), which reinforces the idea that some kind of ecologic isolation favored the particular endemism of the 'Divisaderan' fauna (Simpson et al., 1962; Cerdeño et al., 2008). A biogeographic isolation was also hypothesized between the most austral region of South America (Patagonia) and the NWA (Lumbrera and Geste Formations, Salta and Catamarca provinces) during Eocene times, given the absence of common elements in the notoungulate record (Scarano, 2009; Powell et al., 2011).

4.4. Age inferences

Regarding the fossil-bearing levels from Liu Malal and Agua de Flores-Agua de Isaac, no absolute ages are available yet, although the data published by Horton et al. (2016) from Loma Coihueco, located 150 km to the NW, indicate that the top of the Malargüe Group has a Lutetian–Bartonian age (middle Eocene). On the other hand, the recognition of *Kibenikhoria* in southeast Mendoza relates the studied assemblages to the *Kibenikhoria* local fauna (Simpson, 1935b), defined from the upper levels of Las Flores Formation at Cañadón Hondo (Chubut), which is discussed and considered as mid–late Ypresian, early Eocene, in the recent revision by Vera and Krause (MS under revision). Therefore, the fauna from the Fortunata Formation at Agua de Flores-Agua de Isaac and Liu Malal could be as old as the Riochican SALMA or represent a lapse between the latter and the lower Casamayoran SALMA (Vacan subage, ca. ~45–42 Ma, Lutetian; Krause et al., 2017).

In sum, this fauna evolved in a low rate accumulation environment just before the end of deposition of the Malargüe Group and its presence add new data to constrain the Paleogene hiatus (~40–20 Ma) existing between the top of the Malargüe Group and the Agua de la Piedra Formation (Horton et al., 2016; Horton, 2018). The recognition of these Eocene notoungulates adds precise data in the span of the pre-orogenic stage of the basin in the Malargüe fold and trust belt (Fig. 6).

5. Conclusions

Two new sites, Agua de Flores-Agua de Isaac and Liu Malal, with early Paleogene sediments bearing Eocene mammal fossils are identified in southeast Mendoza Province, which constitute the first paleontological mammal record for the Malargüe Group.

Based on facies composition and geological distribution, we consider that the Cenozoic deposits from these fossiliferous localities correspond indeed to the already defined Puesto Fortunata Forma-

tion, which is equivalent to the Coihueco Formation, the top of the Malargüe Group.

Among the studied mammals, at least four groups of notoungulates are represented in the localities Agua de Flores-Agua de Isaac and Liu Malal: (1) the Oldfieldthomasiidae are represented by MLP 96-VIII-15-1a, b, IANIGLA-PV 85, and IANIGLA-PV 519; in particular, MLP 96-VIII-15-1 and IANIGLA-PV 519 are interpreted as *Kibenikhoria* sp. and cf. *Kibenikhoria*, respectively, but different from *K. get* from Patagonia; (2) the tarsal bones MLP 96-VIII-15-2 resemble the Oldfieldthomasiidae *Colbertia*, but present some differences that lead to tentatively propose they belong to Henricosborniidae, a group whose tarsals have not been described before; (3) IANIGLA-PV 518 is recognized as a probable new genus of Notopithecidae; and (4) IANIGLA-PV 542 represents a large taxon probably related to the Isotemnidae.

The presence of *Kibenikhoria* in southeast Mendoza implies the first record of the genus out of Patagonia, extending its geographic distribution.

On the basis of the paleontological content, we suggest these Eocene mammals from Mendoza may fill the current early to middle Eocene gap in the South American fossil record. This means they are not younger than the Vacan fauna and not older than the Riochican fauna (upper Las Flores Formation; mid-late Ypresian).

Our paleontological results for this unit reinforce recent studies regarding the duration of the preorogenic stage of the Malargüe fold and trust belt and constitute the first mammal remains of the Paleogene (Eocene), a period of low accommodation in the retroarc region.

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