Eocene mammals from volcaniclastic deposits of the Somun Cura Plateau: biostratigraphic implications for north Patagonia Paleogene

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ABSTRACT. The Paleogene terrestrial faunal succession and its associated bearing volcaniclastic deposits has been exhaustively studied in central Patagonia, but there is still no acceptable litho-bio-chronostratigraphic ordering for the extra-Andean North Patagonia. The only references on Paleogene mammals bearing deposits north to Chubut River are imprecise and contradictory. West to Ingeniero Jacobacci (Río Negro Province, Argentina), the paleontologist and archaeologist Rodolfo Casamiquela reported a fossiliferous succession with Casamayoran or Mustersan (Eocene) and Deseadan (Oligocene) mammals from rocks currently mapped as the Las Chacras Formation. This unit includes acid to intermediate tuffs, ignimbrites, paleosols, conglomerates, and basalts originated in a perivolcanic fluvial system, under a seasonal subhumid-humid climate according to predominant pedogenic features. As a result of our fieldworks and fossil collection in the area of Ingeniero Jacobacci, and the revision of the materials collected by Casamiquela in the forties and fifties (with well-known stratigraphic origin), we identified a single mammal association from the lower section of the Las Chacras Formation (here named the Lower Las Chacras fauna) composed by: Plesiofelis schlosseri Roth, 1903 (Sparassodonta), Trigonostylops Ameghino, 1897, Astraponotus Ameghino, 1901 (Astrapotheria), Propyrotherium Ameghino, 1901 (Pyrotheria), Pseudhyrax eutrachytheroides Ameghino, 1901, Eohetoetherium priscum Ameghino, 1901, Puelia sigma (Ameghino, 1901), Periphragnis Roth, 1899 (Notoungulata), Isutaetus depictus Ameghino, 1902 (Cingulata), and a new member of Adianthidae (Litopterna) and probably of Pichipilidae (Paucituberculata). This assemblage is closer to that derived from the Rosado Member of the Sarmiento Formation at Gran Barranca, central Patagonia (type locality of the Mustersan Land Mammal Age) dated in ca. 38 Ma (late middle Eocene). A pyroclastic flow
associated to the bearing deposits of Ingeniero Jacobacci was dated (K-Ar) in 39.2±2 Ma, value compatible with the Mustersan age here inferred for the Lower Las Chacras fauna. The alleged occurrence of Deseadan mammals in these levels was based on remains of an isotemnid notoungulate incorrectly identified as a leontinid. The presence of the Tinguirirican (early Oligocene) notoungulate *Eohegetotherium priscum*, with more apomorphic dental traits than in its Eocene allies, and of an astrapotheriid more derived than *Astraponotus* suggests that some advanced faunal elements would have been established in North Patagonia earlier than in central Patagonia.

**Keywords:** Paleogene, Mustersan, Ingeniero Jacobacci, Las Chacras Formation, Fossil mammals, Biostratigraphy

**RESUMEN.** Mamíferos eocenos en depósitos volcániclásticos de la meseta de Somun Cura: implicaciones bioestratigráficas para el Paleógeno del norte de la Patagonia. La sucesión faunística terrestre del Paleógeno y sus depósitos volcániclásticos portadores asociados han sido exhaustivamente estudiados en Patagonia central, pero aún no hay un ordenamiento lito-bio-chronoestratigráfico aceptable para la región Norpatagónica extraandina. Las únicas referencias sobre depósitos portadores de mamíferos Paleógenos al norte del río Chubut son imprecisas y contradictorias. Al oeste de Ingeniero Jacobacci (Provincia de Río Negro, Argentina), el paleontólogo y arqueólogo Rodolfo Casamiquela reportó una sucesión fosilífera con mamíferos casamayorenses o mustersenses (Eoceno) y deseadenses (Oligoceno) de rocas actualmente mapeadas como Formación Las Chacras. Esta unidad incluye tobas ácidas a intermedias, ignimbritas, paleosuelos, conglomerados y basaltos originados en un sistema fluvial perivolcánico, bajo un clima estacional subhúmedo de acuerdo a los caracteres pedogénicos predominantes. Como resultado de nuestros trabajos de campo y recolección de fósiles en el área de Ingeniero Jacobacci y la revisión de los materiales colectados por Casamiquela en los años cuarenta y cincuenta (con procedencia estratigráfica bien conocida), identificamos una única asociación de mamíferos proveniente de la sección inferior de la Formación Las Chacras (aquí denominada “Lower Las Chacras fauna”) compuesta por: *Plesiofelis schlosseri* Roth, 1903 (Sparassodonta), *Trigonostylops* Ameghino, 1897, *Astraponotus* Ameghino, 1901 (Astrapotheria), *Propyrotherium* Ameghino, 1901 (Pyrotheria), *Pseudhyrax eutrachytheroides* Ameghino, 1901, *Eohegetotherium priscum* Ameghino, 1901, *Puelia sigma* (Ameghino, 1901), *Periphragnis* Roth, 1899 (Notoungulata), *Isutaetus depictus* Ameghino, 1902 (Cingulata), y un nuevo miembro de Adianthidae (Litopterna) y probablemente de Pichipilidae (Paucituberculata). Esta asociación es más parecida a la proveniente del Miembro Rosado de la Formación Sarmiento en Gran Barranca, Patagonia central (localidad tipo de la Edad Mamífero Mustersense) datada en ca. 38 Ma (Eoceno...
medio tardío). Un flujo piroclástico asociado a los depósitos portadores de Ingeniero Jacobacci fue datado (K-Ar) en 39.2±2 Ma, valor compatible con la edad Mustersense inferida aquí para la “Lower Las Chacras fauna”. La supuesta presencia de mamíferos deseadenses en estos niveles estaba basada sobre restos de un notoungulado isoténmido incorrectamente identificado como un leontínido. La presencia del notoungulado tinguiririquense (Oligoceno temprano) *Eohegetotherium priscum*, con caracteres dentarios más apomórficos que sus aliados eocénicos, y de un astrapotérido más derivado que *Astraponotus*, sugiere que algunos elementos faunísticos más avanzados se habrían establecido en Norpatagonia más temprano que en Patagonia central.

**Palabras clave:** Paleógeno, Edad Mustersense, Ingeniero Jacobacci, Formación Las Chacras, Mamíferos fósiles, Bioestratigrafía.

1. **Introduction**

   The Andean foreland of central Patagonia was draped by a huge volume of volcanic ashes and coarser volcaniclastic sediments during much (30 Ma) of the middle Cenozoic (Feruglio, 1949; Mazzoni, 1985; Bellosi, 2010a). This process involved both large depocenters (*e.g.*, San Jorge, Cañadón Asfalto, Valdés basins) and smaller, low-subsiding areas related to valleys infills. These volcaniclastic deposits preserved a vast number of fossil remains that document the Paleogene—early Neogene evolution of mammals and other vertebrates in continental landscapes of southern South America. Age and divisions of the volcaniclastic successions were defined according to fossil mammals grouped into several assemblages (Ameghino, 1900-1902, 1906), that later became the standards for the South America land mammal ages (SALMAs) (*e.g.* Simpson, 1940; Pascual *et al.*, 1965).

   The stratigraphic framework, chronology, and allocation of SALMAs for this Paleogene—early Neogene succession (mostly the Sarmiento Formation and equivalents) was outlined in central Patagonia, particularly at the Gran Barranca South of Colhué-Huapi Lake (Bellosi, 2010b; Ré *et al.*, 2010; Dunn *et al.*, 2013; Bellosi and Krause, 2014) (Fig. 1).

   However, stratigraphy, chronology, and fossil mammal content of coeval deposits in North Patagonia are not well delineated yet (Franchi *et al.*, 1984; Ardolino *et al.*, 1999). There are very few documented occurrences of Paleogene mammals in rocks exposed north of the Chubut River. They include the still little known early Oligocene association from the Bajada de los Ingleles Formation at Río Negro Province (Bond *et al.*, 1997), and undetermined deposits in Neuquén Province presumably bearing Eocene and Oligocene mammals (Ameghino, 1889, 1906; Kraglievich, 1957; Kramarz *et al.*, 2011). Somewhat better documented are the Paleogene volcaniclastic deposits interbedded with lava flows at the west slope of the Somun Cura Plateau in Río Negro Province, near Ingeniero Jacobacci (Ardolino *et al.*, 1999) (Fig. 1).
Figure 1. A. Map of Southern South America showing the main localities discussed in the text. B. location of the studied area (red star) in the west margin of the Somun Cura Plateau and adjacent Paleogene volcanic belts in North Patagonia. 1, Gran Barranca South of Colhué Huapi Lake. 2, Cerro del Humo. 3, Gran Hondonada. 4, Tinguiririca. 5, Antofagasta de la Sierra.

During the late forties and early fifties, the Argentine archaeologist and paleontologist Rodolfo Casamiquela collected several fossil remains in the vicinities of Ingeniero Jacobacci, at the area of Puesto Marileo, a site also known locally as Cerro Yeso (Fig. 2). Casamiquela (1963) first reported the occurrence of Paleogene mammals in Cerro Yeso but did not supply precise locality information. Some years later, Casamiquela (1969: 291) indicated that these remains were collected from whitish tuffs of Mustersan or Casamayoran age, bearing “Astraponotus sp. o Albertogaudrya sp., Palaeothentes sp., etcetera”, overlaid by pumiceous tuffs of Deseadan or Colhuehuapian age, bearing remains of a leontinid notoungulate. Thus, Casamiquela interpreted that at least two distinct faunal associations occur at Cerro Yeso, based on the taxonomic identifications by R. Pascual and L. Parodi (MLP). The same interpretation was followed by Pascual et al. (1984), who listed Eocene and Oligocene mammals from the Puesto Marileo locality. More recently, González...
Figure 3. Studied fossiliferous outcrops of the Las Chacras Formation, west of Ingeniero Jacobacci (Río Negro province). **A.** Cerro Yeso section showing position of the mammal bearing beds CY 1 and CY 2 (a person at CY 1 for scale). **B.** Lower basalt with columnar jointing near Puesto Marileo. **C.** Measured section at Chucair farm showing location of the mammal bearing bed CH 1 and stacked pyroclastic beds (PF). **D.** Detail of the lower pyroclastic flow with non-erosive, flat basal contact overlying a thin paleosol (hammer 30 cm). **E.** The fossiliferous conglomerate CH 1 showing low angle cross-bedding and erosive lower contact (scale 1 m). **F.** Weakly-developed paleosol exhibiting A horizon with Fe-Mn nodules, Bw or Bg horizon with mottles and drab-haloed rhizoliths, and BC / C horizons (scale 1 m).

The taxonomic identifications supporting this age was never re-examined.

In October 2017 and April 2018, our team prospected the Cerro Yeso locality, as well as other correlated beds exposed at Chucair farm, 2 km west of Cerro Yeso (Fig. 2).
As a result of these fieldworks, we collected dozens of additional vertebrate remains (mostly mammals). In this contribution, we present an integrative study of the Paleogene volcaniclastic deposits exposed in the area of Ingeniero Jacobacci, in SW Río Negro Province (Argentina), and of the mammals and other vertebrates exhumed from these rocks. We discuss the presumed occurrence of at least two distinct Paleogene faunal associations and its stratigraphic implications with other faunal units in central Patagonia and elsewhere in South America.

Figure 2. Distribution of lava flows and volcaniclastic deposits of the Las Chacras Formation at south of Huahuel Niyeo valley (Río Negro, Argentina). See location in Fig. 1. Modified from Coira (1979) and González et al. (2000).
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Figure 4. A. Simplified stratigraphic profile of the Las Chacras Formation at the south margin of the Huahuel Niyeo river, Ingeniero Jacobacci (modified from González et al., 2000). Stars correspond to K/Ar ages. Blue stars after Coira et al. (1985); red star after Mazzoni and Benvenuto (1990). B. Stratigraphic and sedimentologic profiles of the lower section of the Las Chacras Formation bearing Paleogene mammals, at Chucair farm and Cerro Yeso, west of Ingeniero Jacobacci (Río Negro Province).

2. Materials and methods

Twelve of the fossil specimens collected by R. Casamiquela studied here are stored in the Museo Jorge H. Gerhold (Ingeniero Jacobacci); they were included in the original Casamiquela’s collection and catalogued under the acronym MJHG Pa. Other seven specimens are stored in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” at Buenos Aires (MACN). Fossils collected by our team (58 specimens) are
also stored in the Museo Jorge H. Gerhold, but are part of a separate collection and
catalogued under the acronym MJHG-NCP (New Paleontological Collection). Systematic
descriptions, inventory numbers, provenance of the studied fossil specimens,
nomenclatorial discussions, and additional figures are provided in Supplementary
Information S1. Dental measurements are included in Supplementary Information S2. Taxa
between quotation marks indicate the lack of consensus concerning its monophyly.

2.1. Institutional abbreviations
MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires,
Argentina); MJHG, Museo de Ciencias Naturales, Antropológico e Histórico “Jorge H.
Gerhold” (Ingeniero Jacobacci, Río Negro, Argentina); MLP, Museo de La Plata
(Argentina).

2.2. Anatomical abbreviations
C/c, upper/lower canine; P/p, upper/lower premolar; M/m, upper/lower molar.

3. Geological and stratigraphic setting
The Las Chacras Formation is a ~80 m thick succession of volcaniclastic deposits
interbedded with lava flows accumulated in the Jacobacci basin (Dalla Salda and Franzese,
1987), at the northwest margin of the Somun Cura Plateau, and adjacent to the North
Patagonia volcanic arcs (Fig. 1). This unit is preserved south of the Huahuel Niyeo River,
with the best expositions in the area of Ingeniero Jacobacci (Fig. 2), where it lies over the
Cretaceous Coli Toro and the Paleogene Huitrera formations (Casamiquela, 1969;
González et al., 2000).

The Las Chacras Formation includes two volcaniclastic sections, 34 and 7 m thick,
intercalated with three intervals of basalt flows (Figs. 3, 4A). The volcaniclastic rocks are
formed by glass shards and fragments acid to intermediate in composition (Coira, 1979;
Coira et al., 1985). They comprise primary and reworked massive tuffs, graded pyroclastic
flow deposits composed of poorly-sorted and angular pumice clasts, fine tuff breccias,
clast-supported conglomerates, fine to medium sandstones, and intercalated paleosols.
Lower basalts (4 m thick) present columnar jointing, while middle (15-20 m thick) and
upper basalts (~ 7 m thick) are massive.

The measured profile at Cerro Yeso (77 m thick) corresponds to the lower section
(Figs. 3A, 4B) and is bounded by basalt flows at the base and top (Figs. 3B). Few hundred
meters NW, this section shows a faulted contact with marine sandstones and claystones of
the Upper Cretaceous Coli Toro Formation. The lower part of the profile includes light
greenish to yellowish gray, laminated or massive volcaniclastic mudstones, intercalated
with fine tuffs. Rhizoliths and fragmentary leaves and stems were also recognized. The
middle and upper parts of the profile are composed of fine tuffaceous sandstones showing
trough cross-bedding and erosive lower contact, and thinner conglomeratic lenses with
pumice fragments and intraformational tuff clasts. These beds intercalate with pinkish gray,
very fine, laminated tuffs, and volcaniclastic mudstones. The fossiliferous site CY1 (41°
21’ 51.0” S 69° 37’ 27.3” W) occurs 22 m from the base in a massive volcaniclastic
mudstone showing pedogenic features (Fig. 3A). This is the site where Casamiquela
collected all his fossils (according to Mr. Marileo, a local farmer who accompanied
Casamiquela in his prospections). CY1 also provided the bulk of the mammal remains
unearthed by us at Cerro Yeso associated with few anuran remains. The site CY2 occurs in
laminated tuffs, 55 m above the base of the unit in the same profile than CY1 (Fig. 3A), but
only produced very few fossil remains. A third site, CY3 (41° 21’ 42.46” S  69° 37’ 38.1”
W) preserved several micromammal and scarce anuran remains; it occurs nearly 300 m
west of the measure profile, 11 m meters above the contact with the Coli Toro Formation,
and its stratigraphic position might be slightly lower than CY1 (Fig. 4B).

The profile from Chucair farm presents a similar thickness (67 m), but shows
coarser deposits and more frequent and developed paleosols (Figs. 3C, 4B). The lower
contact is on the Coli Toro Formation, and a basalt flow occurs at the top. The lower half
consists of yellowish gray to very pale orange, fine-grained tuffs displaying horizontal
lamination, small-scale cross-bedding or are massive; fine and massive, thin matrix-
supported pyroclastic flow deposits and subordinated volcaniclastic mudstones showing
horizontal lamination. The upper half comprises fine, clast-supported conglomerates (Fig.
3E), showing erosive base, through cross-bedding, finning-upward sets and rounded clasts
of volcanic rocks. Stacked, whitish pyroclastic flow deposits, up to 13 m thick are also
present (Fig. 3D). They are non-erosive and graded, show cross-bedding or parallel
stratification, cut and fill structure, brecciated or deformed zones, and include 0.5-15 cm,
angular pumice clasts along with common wood fragments. Paleosols exhibit weak
horzonation, fine clayey rhizoliths and rhizohaloes, Fe-Mn nodules, mottles, blocky and
granular peds, and solitary bee cells (*Celliforma* isp.) (Fig. 3F). The fossiliferous sites CH1
(41° 21’ 55.3” S  69° 38’ 48.9” W) (Fig. 3C, 4B) and CH2 (41° 22’ 12.2” S 69° 39’ 01.3”
W) occur in the same clast-supported conglomerate, 45 m above the base and 3 m below
the major pyroclastic flow of the upper half of the measured section (Fig. 3C, 4B). Both
sites are located ~ 300 m apart and produced abundant macro and micromammals including
the best preserved materials (partial skulls and mandibles) collected by our team.

The continuity of the upper basalt at Cerro Yeso and Chucair farm allows
correlating both profiles (fig. 4B). Differences between them are due to lateral facies
changes and bed morphology resulting from differences between fallout, flow (ignimbrite),
and subordinated reworked deposits. Volcaniclastic sediments of the Las Chacras
Formation were sourced from the Pilcaniyeu-El Maiten volcanic belt system (Fig. 1), and
accumulated in a fluvial system next to volcanic edifices. At Cerro Yeso, pyroclastic flow deposits are represented by thin, lenticular and non-erosive bodies. Prevailing well-sorted massive tuffs formed as ash falls, suggest sustained eruptions probably as co-ignimbrite deposits (Lajoie and Stix, 1992). Massive mudstones and tuffs were deposited in vegetated floodplains; which also supported shallow ponds where fine laminated pyroclastic muds accumulated. Paleosols formed in tuffaceous material and showing a very weakly development degree are comparable to vitric Entisols (Soil Survey Staff, 2014). The Chucair section presents coarser deposits, recording gravelly braided channels that reworked tuffaceous floodplains and volcanic clasts. Pyroclastic flow deposits are more frequent and thicker. They show non-erosive, flat and horizontal lower contact (Fig. 3D). Soil forming processes in this area were more intense and modified both fluvial channel and floodplain deposits, but did not affected pyroclastic flows. Pedogenesis produced weakly developed paleosols with typical A - Bg/Bw - BC/C profiles, showing numerous gleying features such as rhizohaloes, low-chroma irregular zones (drab mottles) and iron-manganese nodules (Fig. 3F) in surface and subsurface horizons. Volcaniclastic material and dominant redoximorphic attributes of paleosols correspond to aquic Andisols, mostly formed under alternated lapses of reduction (prevailing) and oxidation, associated with water saturation and drying respectively (Soil Survey Staff, 2014). Aquic soil moisture regime is more frequent in areas where ground-water level is shallow. These characteristics are compatible with seasonal subhumid-humid conditions (Retallack, 2001).

4. Correlations and age

Volcaniclastic beds from Cerro Yeso and Chucair were previously assigned to the Marileo Member of the Miocene Collon Cura Formation by Coira (1979). This author placed the Eocene mammals reported by Casamiquela (1969) into the Huitrera Formation that is not exposed from this area. Later, Coira et al. (1985) reassigned these deposits to two Paleogene volcanic-sedimentary phases based on new K-Ar dates. The older one (Eocene) comprises thylotic dacitic tuffs bearing the Casamayoran or Mustersan mammals reported by Casamiquela (1969) (see also Pascual et al., 1984), covered by alkaline basalts dated between 44 and 39 Ma. The second phase (Oligocene) shows a similar composition with silicic tuffs, presumably preserving the Deseadan mammals reported by Casamiquela (1969), and basalt flows dated at 34 – 28 Ma (Coira et al., 1985).

Direct and reliable correlation between basalts observed in our profiles and those dated by Coira et al. (1985) in the same area (south margin of Huahuel Niyeo valley) is possible (Fig. 4B). Relative stratigraphic position suggests that the older lava flows (44 – 39 Ma) recognized by Coira et al. (1985) would correspond to the lower basalts at the base of the Las Chacras Formation, that show similar columnar jointing; while younger lavas (34 – 28 Ma) would correspond to the uppermost basalts described by González et al.
(2000), which are not included in our measured sections (Fig. 4B). Such stratigraphic inferences are also supported by the K-Ar date (39.2 ± 2 Ma) of a whitish and vitric ignimbrite at Corte Blanco locality, near Ojos de Agua (Mazzoni and Benvenuto, 1990) (Figs. 2 and 4A). This ignimbrite was originally attributed to the Ojos de Agua Member of the Pliocene La Cabaña Formation (Nullo, 1978; Coira, 1979), but the absolute age and stratigraphic position discard such assignation (González et al., 2000). Similarity between this ignimbrite and the pyroclastic flow recognized in the Chucair profile (Fig. 4B), particularly the abundance and size of pumice fragments, allow assigning both beds to the Las Chacras Formation.

5. Fossil mammals of the lower Las Chacras Formation

5.1. Notoungulata

As in most Paleogene South American vertebrate associations, fossils of notoungulate mammals are abundant and diverse. The most abundant remains belong to maxillary and mandibular fragments with partial dentition and isolated teeth of the small typotherian *Pseudhyrax eutrachytheroides* (Fig. 5A, B), with protohypsodont cheek teeth, interpreted as the sister taxon of the archaehyracids, hegetotheriids, and mesotheriids (Billet, 2011). A single specimen (an isolated upper molar) differs from all the *Pseudhyrax* specimens in being smaller (see Supplementary Information S2) and having comparatively higher crown, more ephemeral enamel lakes and larger mesial and distal bands of exposed dentine (Fig. 5C and Supplementary Information S1, Fig. S1.). This specimen is assigned to *Eohegetotherium priscum* Ameghino, 1901 (=*Protarchaeohyrax gracilis*, Reguero et al., 2003; see Supplementary Information S1), a more advanced and undisputable archaehyracid typothere (Billet, 2011). Interatheres are represented by few and fragmentary remains with low crowned teeth (Fig. 5D), likely corresponding to the subfamily Notopithecinae, interpreted by Vera (2016) as a small, middle to late Eocene monophyletic group of early diverging typotherians.

Toxodontian notoungulates are represented by abundant remains of the basal “notohippid” *Puelia sigma* (Fig. 5E, F) and at least two species of the isotemnid genus *Periphragnis*: *P. circumflexus* (Fig. 5G) and *P. palmeri* (Fig. 5H), the former being larger sized (see Supplementary Information S2) and without basal cingulids. A specimen with much worn cheek teeth in Casamiquelas’s collection (MJHG 148Pa) is catalogued as Leontiniidae. Nevertheless, the lower premolars differ from those of leontiniids in having shorter and simpler talonid, and the lower molars lack the deep lingual flexid between the trigonid and talonid (Fig. 5I) characteristic of the leontiniids (even in worn teeth). Size and morphology of the preserved premolars indicate that MJHG 148Pa belongs unquestionably to an Isotemnidae, and could belong to a third, still undetermined species of *Periphragnis*. 
5.2. Astrapotheria

Astrapotheres are the most conspicuous components of the mammal association derived from the Las Chacras Formation. Although less abundant than notoungulates, they are represented by many cranial, mandibular, and dental remains of very large specimens and they are clearly identifiable as belonging to the astrapotheriid genus *Astraponotus* (Fig. 6 A, B, C). The most complete specimen consists of associated right and left mandibular fragments and a maxillary fragment with partial dentition of a juvenile specimen (Fig. 6A) collected by R. Casamiquela in 1953. This specimen is catalogued in the MJHG collection with the number 146Pa as belonging to *Astraponotus* sp. or *Albertogaudrya* sp., according to identification by R. Pascual (MLP) (*in schedula*), and almost surely Casamiquela (1969) reported the occurrence of one of these taxa in Cerro Yeso based upon this specimen (see above). In addition, we unearthed a partial skull with complete right upper dental series (Fig 6 B, C) and additional fragmentary dental remains. Three isolated and incomplete vertebrae of a large mammal could also pertain to *Astraponotus* (whose postcranial skeleton is almost entirely unknown). However, some few isolated dental remains might not belong to *Astraponotus*, but to a somewhat smaller sized (see Supplementary Information S2) and more advanced taxon (Fig. 6 D, E), although they definitively do not match with any known Oligocene astrapothere. A third astrapothere taxon is represented by an isolated upper molar referable to *Trigonostylops*, much smaller than the formers (see Supplementary Information S2) and with a typical trigonodont pattern (see Simpson, 1967a; MacPhee *et al.*, 2021). The specimen could not be found in MJHG collection, but a drawing was provided by Carbajal *et al.* (1977: fig. 1d).
Fig. 5. Notoungulata from Las Chacras Formation. A. MJHG-NCP 255, probably associated left p3 or p4, and m1-m3 of *Pseudhyrax eutrachytheroides*. B. MJHG-NCP 8, left maxillary fragment with P4-M1 of *Pseudhyrax eutrachytheroides*. C. MJHG-NCP 264, isolated right M1 or M2 of *Eohegetotherium priscum*. D. MJHG-NCP 28, right maxillary fragment with C1-P1 and roots for P2 of Interatheriidae indet. E. MJHG-NCP 2, left maxillary fragment with roots of P4, complete P3, M1-M3 of *Puelia sigma*. F. MJHG-NCP 5, right mandibular fragment with m2-m3 of *Puelia sigma*. G. MJHG-NCP 252, associated p3, p4, m1 and partial m2 or m3 of *?Periphragnis circunflexus*. H. MJHG-NCP 11, partial left mandibular ramus with p2-m2 of *Periphragnis palmeri*. I. MJHG 148Pa, associated left p3-m1 of *Periphragnis sp.*
Fig. 6. Astrapotheria and Pyrotheria from Las Chacras Formation. A. MJHG 146Pa, left mandibular fragment with erupting p3 - p4, erupted m1 - m2 and encrypted m3 of *Astraponotus* sp. B-C. MJHG-NCP 251, partial skull of *Astraponotus* sp. B. right palate with in complete right C1-M3 series. C. skull in right lateral. D. MJHG-NCP 269a, right upper premolar (P3?) of cf. *Astraponotus*. E. MJHG-NCP 269b right lower premolar in occlusal and lingual views cf. *Astraponotus*. F. MJHG 254Pa, isolated tusk of *Propyrotherium saxeum*. G. MJHG-NCP 3, isolated right lower molar (m2?) of *Propyrotherium saxeum*. H. MJHG-NCP 268, isolated right lower molar (m1?) of *Propyrotherium saxeum*. 
5.3. Pyrotheria

Pyrotheres are infrequent in most Paleogene mammal associations. Among large mammals of the Las Chacras Formation, pyrotheres are represented by an isolated tusk (probably lower) (Fig. 6F) and two isolated lower molars with the typical bilophodont pattern of *Propyrotherium* (Fig. 6 G, H), and much more bunodont than in the Oligocene *Pyrotherium*. We also recovered a lower cheek tooth, doubtfully associated with a tusk fragment. The cheek tooth is not bilophodont, but it has a single, massive, conical cuspid, with a minute distal heel and a crenulated labial? cingulid (see Supplementary Information S1). The latter feature resembles the basal crenulations observed in some cheek teeth of *Propyrotherium* and *Pyrotherium* (see Kramarz and Bond, 2014). This tooth might belong to an anterior lower premolar (p2?) of a pyrothere, although its attribution to an astrapothere cannot be discarded.

5.4. Litopterna

Among all mammals collected in Cerro Yeso, both by Casamiquela and by us, litopterns are represented by an isolated, very low crowned, and bunolophodont upper cheek tooth (Fig. 7A). Although it displays some “condylarth” appearance, it is more likely a deciduous tooth of an undetermined litoptern (Proterotheriidae?). We also recovered a small mandibular fragment with p3-m1 (Fig. 7B), very likely representing a new member of Adianthidae. Although the dentition of this still little known family shows superficial resemblances with some member of Notopterna (Soria, 1989), adianthids are traditionally referred to Litopterna (Cifelli and Soria, 1983 and references therein), probably allied to the Macraucheniidae (Cifelli, 1993), a position accepted herein.

5.5. Cingulata

Cingulates are frequent and diverse in Eocene mammalian assemblages. However, all cingulates in our sample are referable to a single species, *Isutaetus depictus* Ameghino, 1902, represented by more than a dozen osteoderms, some probably associated. This is a medium-size armadillo with very numerous piliferous foramina on the caudal and lateral margins of the osteoderms (Fig. 7C), evidencing a well-developed piliferous system.

5.6. Marsupialia

Sparassodont metatherians are represented by a large mandible with partial dentition (Fig. 7D, E). It is referable to the borhyaenid *Plesiofelis schlosseri* by having premolars with reduced distal cingulid, molars with lingual border of the talonid reaching the lingual
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base of the protoconid, cheek teeth with the bulbous roots, among other features (see Supplementary Information S1). This is the only predator recovered to date from the Las Chacras Formation. The body mass has been estimated in ~40 kg (Prevosti and Forasiepi, 2018), which is on the range of the living jaguar (*Panthera onca*).

Paucituberculatans are only represented by two, very fragmentary specimens referable to a pichipilid palaeothentoid (Fig. 7F, G), an extinct allied of the living shrew possums *Caenolestes*, and might belong to a new taxon (see Supplementary Information S1).

Fig. 7. Litopterna, Cingulata, and Metatheria from Las Chacras Formation. **A.** MJHG-NCP 256, isolated upper tooth (deciduous?) of Litopterna indet. **B.** MJHG-NCP 257, left mandibular fragment with p3-m1 of Adianthidae sp. nov. **C.** MJHG-NCP 26, fixed osteoderm of *Isutaetus depictus* in external (left), lateral (center), and caudal (right) views. **D.** MJHG-NCP 58, almost complete left jaw in lateral view of *Plesiofelis schlosseri*. **E.** MJHG-NCP 58, left p1-p3, m3-m4 m1, roots of m2, and alveolus for c1 in occlusal view of *Plesiofelis schlosseri*. **F.** MJHG-NCP 277, left lower molar (m2?) of Pichipilidae sp. nov? **G.** MJHG-NCP 278, left mandibular fragment with a premolar (p3?) in lateral view of Pichipilidae sp. nov?
6. Faunal comparisons

The comparisons among the fossil mammals of the five sites of the Las Chacras Formation prospected herein reveal that the notoungulates *Pseudhyrax eutrachytheroides* and *Puelia sigma*, the cingulate *Isuetaetus depictus*, the astrapothere *Astraponotus*, and the pyrothere *Propyrotherium* occur both in the lower part of the lower section exposed in CH1 and CH3 and in the upper part of the same section in CY1 and CY2 (Figs. 3, 4). The notoungulate *Periphragnis* is also represented in the lower and upper levels of the studied section, although likely represented by different species. The sparassodont *Plesiofelis schlosseri*, the Adianthidae gen. et sp. nov., the astrapothere *Trigonostylops*, and the notoungulate *Eohegetotherium priscum* are respectively represented by a single specimen and do not allow direct comparisons, as well as those taxa for which we were not able to supply at least a generic identification. Consequently, we find no significant differences in taxonomic composition through the studied interval in the lower section of Las Chacras Formation, and we consider all these mammals to represent a single faunal association, herein named the Lower Las Chacras fauna.

Comparing with other Paleogene assemblages (see Table 1), the Lower Las Chacras fauna shares only one genus, *Trigonostylops*, with the Casamayoran (Vacan and Barrancan) assemblages from central Patagonia. *Trigonostylops* has a long biochron, spanning throughout almost the entire Eocene (Simpson, 1967a; Kramarz et al., 2019). No specimen collected by Casamiquela or by us is referable to the Casamayoran genus *Albertogaudrya*, and its possible occurrence alleged by Casamiquela (1969) and Pascual et al. (1984) is almost surely based on specimens unambiguously belonging to *Astraponotus*.

Table 1. Comparison among the Lower Las Chacras fauna and other middle Eocene – early Oligocene associations. Only taxa identified at generic level are included. Bibliographic sources: Roth (1899, 1901, 1903), Ameghino (1901), Simpson (1936, 1967a, b), Flynn et al. (2003), Reguero et al. (2003), Croft et al. (2003), Cladera et al. (2004), Bond and Deschamps (2010), López et al. (2010), Bradham et al. (2015), Babot et al. (2017).

| Taxon\locality | Lower Las Chacras | Casamayoran | Mustersan | Tinguirirican |
|---------------|-------------------|-------------|-----------|--------------|
|               | Lower Las Chacras | Cerro del Humo (Colhue Huapi Norte) | Rosado (Gran Barranca) 38.16-37.4 Ma. | Gran Hondonada | Antofagasta de la Sierra 37- 35 Ma | La Cancha 33.5 Ma | Tinguiririca 31.6 Ma |
| *Plesiofelis* | x                  | x           |           | x            |
| *Isuetaetus*  | x                  | x           |           | x            |
| *Propyrotherium* | x                  | x           |           | x            |
Most taxa of the Lower Las Chacras fauna are shared with the comparatively more diverse mammal assemblage from the Rosado Member of the Sarmiento Formation at Gran Barranca South of Colhué-Huapi Lake, proposed as the type locality of the Mustarian SALMA (Bond and Deschamps, 2010): Astraponotus, Trigonostylops, Periphragnis, Pseudhyrax eutrachytheroides, and Puelia sigma (Table 1). The same taxa plus Plesiofelis schlosseri are shared with the assemblage from the lower section of the Sarmiento Formation exposed at Gran Hondonada in central Patagonia (Fig. 1A), assigned to the Mustarian SALMA (Odreman Rivas, 1978; Cladera et al., 2004) (Table 1). Propyrotherium saxenum, Pseudhyrax eutrachytheroides, Astraponotus, and Periphragnis are also shared with the taxonomic grouping derived from the Ameghino’s locality Colhué Huapi Norte (Simpson, 1967b) (Table 1). Similarly, the Lower Las Chacras fauna shares with the faunal assemblage described by Roth (1899, 1901, 1903) for his “Cretáceo Superior Lago Musters” Plesiofelis schlosseri, Isutaetus depictus, Pseudhyrax eutrachytheroides, Puelia sigma, and Periphragnis palmeri, in addition to the genera Astraponotus, and Trigonostylops (Table 1). Ameghino’s Colhué Huapi Norte and Roth’s “Cretáceo Superior Lago Musters” are presumably equivalent to the Mustarian Simpson’s (1936) Cerro del Humo Locality (Fig. 1A), although precise stratigraphic origin of these ensembles is still uncertain (see Bond and Deschamps, 2010 and references therein).

The Lower Las Chacras fauna shares only a single taxon (Pseudhyrax) with the still little known, presumable Mustarian fauna of Los Helados derived from the Abanico Formation in central Chile (Engelman et al., 2018). Pseudhyrax, along with Propyrotherium, are also shared with the Mustarian fauna of the middle member of the Geste Formation at Antofagasta de la Sierra, in northwestern Argentina (Fig. 1A) (Babot et al., 2017 and references therein) (Table 1).

Compared with the early Oligocene Tinguiririca fauna of central Chile (type of the Tinguirirican SALMA) (Fig. 1A), the Lower Las Chacras fauna shares only two species, Pseudhyrax eutrachytheroides and Eohegetotherium prisum (Flynn et al., 2003; Reguero
et al., 2003), and one genus (*Periphragnis*) although represented by different species (Bradham et al., 2015). *Eohegetotherium priscum* and *Puelia sigma* are the only taxa shared with the early Oligocene La Cancha mammal assemblage at Gran Barranca South of Colhué Huapi lake in central Patagonia (the Vera Member of the Sarmiento Formation) (Table 1), which is slightly older than the Chilean Tinguirirican fauna (Dunn et al., 2013). These taxa were treated as *Protarchaeohyrax gracilis* and *Puelia plicata* respectively (see López et al., 2010; Reguero and Prevosti, 2010).

In sum, the taxonomic composition of the Lower Las Chacras fauna is much closer to the Mustersan assemblages of the Rosado Member and Gran Hondonada than to any known Casamayoran and Tinguirirican assemblages. It should be noted the Lower Las Chacras fauna does not share any species or genera with late Oligocene and younger faunas elsewhere in South America. The alleged occurrence of Leontiniidae (a typical but not exclusive late Oligocene – early Miocene notoungulate clade), as stated by Casamiquela (1969) and Pascual et al. (1984), is almost surely based on the specimen MJHG 148Pa (Fig. 51) labeled as Leontiniidae in the MJHG catalogue, after identification of R. Pascual (MLP). As discussed above, this specimen belongs to an undetermined species of the isotemnid *Periphragnis*, a genus unknown in faunas younger than early Oligocene. Similarly, the alleged presence of the paucituberculate marsupial *Palaeothentes* in this fauna (Casamiquela, 1969; Pascual et al., 1984) might be based on the specimen MJHG 150Pa, which is the only specimen derived from Cerro Yeso catalogued as belonging to this genus in Casamiquela’s collection. The specimen could not be found by us in the MJHG collection, and thus we are unable to confirm the taxonomic identification. Nevertheless, *Palaeothentes* is only known for Miocene beds (Abello, 2013). Its alleged occurrence in the Lower Las Chacras fauna is clearly incongruent with the geochronologic and faunistic context and might be consequence of an erroneous identification (probably influenced by the fact that *Palaeothentes* was interpreted in the 60’s as oldest known paucituberculate marsupial, when R. Pascual made the identification). Therefore, we prefer provisionally to omit this taxon from the faunistic list of Table 1 until further evidences confirm or reject its record in the Lower Las Chacras fauna.

7. **The age of the Lower Las Chacras fauna**

The proposed stratigraphic correlations and geochronological dates of the Las Chacras Formation indicate that the stratigraphic interval bearing the Lower Las Chacras fauna is younger than the maximum age estimated for the lower basalt flow exposed at Cerro Yeso (44 Ma.) (Fig. 4A). This interval is necessarily older than the minimum age obtained for the pyroclastic flow 3 m above the fossil bearing conglomerate at Chucair farm (37.2 Ma.) (Fig. 4A). This interval would span at most 6.9 Ma, from the Lutetian to the earliest Priabonian, which overlaps the Vacan and Barrancan subages of the
Casamayoran SALMA and the Mustersan SALMA (Rê et al., 2010; Dunn et al., 2013). The strong similarity with the Mustersan assemblage from the Rosado Member at Gran Barranca South of Colhué Huapi Lake, with a well constrained age of 38.16 – 37.4 Ma. (Dunn et al., 2013), suggests that the Lower Las Chacras Formation and its fauna is more likely of late Bartonian or early Priabonian age.

*Eohegetotherium* is the only element not shared with other Mustersan associations. It exhibits more advanced dental features than *Pseudhyrax* and was previously considered as an exclusive Oligocene taxon (Reguero et al., 2003). This brings the possibility that the Lower Las Chacras fauna is somewhat younger than the Mustersan Rosado assemblage. However, several Eocene typotheres had a moderately long biochron and coexisted with their morphologically more advanced relatives. For example, *Pseudhyrax*, traditionally assumed to be typically Mustersan (e.g., Simpson, 1967a; Marshall et al., 1983), also co-occurs with *Eohegetotherium* in the Tinguiuririca fauna (Flynn et al., 2003). García-López et al. (2020) also reported several archaeohyracids with different degrees of hypsodonty coexisting in Eocene units of NW Argentina. Similarly, the interatheriid typothere *Eopachyrucos* (previously considered as limited to the Oligocene) co-occurs with its less hypsodont relative *Guilielmoscottia* in the Rosado fauna (Reguero and Prevosti, 2010). These evidences suggest the coexistence of short and long lasting lineages of typotheres instead of successive replacements of short lasting lineages, and thus their biochronological value is inconclusive. Since the middle Eocene, the Somun Cura Massif became a high plateau in the retroarc area dividing the extra-Andean Patagonia and would have acted as a permanent topographic, climatic, and selective migration filter for some mammals (Aragón et al., 2011). In this context, the absence of *Eohegetotherium* in Mustersan assemblages of central Patagonia might be explained by paleobiogeographic rather than chronological differences.

The cingulate *Isutaetus depictus*, were previously known only from specimens described by Ameghino (1902) as derived from his “couches à *Astraponotus*” at an unknown locality and a specimen from Roth’s (1903) “Cretáceo Superior Lago Musters” locality (Simpson, 1967a; Ciancio and Carlini, 2008). Similarly, the isotemnid *Periphragnis palmeri* was only known from “Cretáceo Superior Lago Musters” (Roth, 1903), whereas *Periphragnis circunflexus* only from the “couches à *Astraponotus*” at an imprecise Colhué Huapi locality (Ameghino, 1901). These taxa have been traditionally accepted as part of the Mustersan fauna (Simpson, 1948, 1967a), although their stratigraphic origins are dubious and their association with other localities bearing Mustersan mammals (e.g., the Rosado) are still unclear. The Lower Las Chacras fauna documents for the first time the occurrence of these three taxa within a defined faunistic and stratigraphic context and confirms their occurrence in sediments of Mustersan age.
8. Conclusions

Las Chacras Formation is a succession of volcaniclastic deposits interbedded with basalt flows accumulated in the Jacobacci basin, at the northwest margin of the Somun Cura Plateau. This succession includes two sedimentary sections: the lower (34 m thick) was deposited during the middle – late Eocene, the upper (7 m thick) during the early Oligocene. Acid to intermediate tuffs, tuffites (ash fallout deposits), and pumiceous pyroclastic flow deposits accumulated in a fluvial system during an eruptive lapse. Short lapses of ambient stability are recorded in intercalated weakly-developed paleosols, testifying a seasonal subhumid climate.

The analysis presented here of the fossil mammals collected by our team from exposures of the Las Chacras Formation and the re-examination of the specimens unearthed by Casamiquela (1969) revealed that this unit bears a single mammal association (Lower Las Chacras fauna), which is restricted to the lower section of the unit. The occurrence of fossil vertebrates in the upper section is still unknown.

The Lower Las Chacras fauna is composed by at least 16 mammal species corresponding to almost all typical Eocene South American orders (Sparassodonta, Paucituberculata, Cingulata, Astrapotheria, Pyrotheria, Litopterna, and Notoungulata). The notoungulates are the most abundant and diverse, represented by basal members of Toxodontia (i.e., Isotemnidae and Notohippidae) and Typotheria (Archaeohyracidae and Interatheriidae). Other mammal groups, which are diverse in other Eocene associations (e.g. cingulates, litopterns, etc.) seem to be underrepresented in our sample.

The composition of the Lower Las Chacras fauna is much closer to the type Mustersan fauna from the Rosado Member of Gran Barranca South of Colhué Huapi Lake and to the Mustersan fauna of Gran Hondonada than to any other Paleogene faunal association in Patagonia or elsewhere in South America. It is also similar to the faunal ensemble from Cerro del Humo locality (equivalent to Ameghino’s Colhué Huapi Norte and Roth’s Cretácio Superior del Lago Musters), but exact stratigraphic origin of the later is not well determined.

According to isotopic dates of intercalated basalt flows, the stratigraphic interval of the Las Chacras Formation bearing the Lower Las Chacras fauna is geochronologically constrained between 44 and 37.2 Ma. However, the age of the fossiliferous beds would be closer to the younger limit of this interval (i.e., 37.2 Ma) based on biochronological correlation with the Rosado Member (with a constrained age of 38.16 – 37.4 Ma). Consequently, that lower section of Las Chacras Formation and its fauna is more likely of late Bartonian or early Priabonian age.

Casamiquela (1969) and Pascual et al. (1984) stated that the Paleogene deposits near to Ingeniero Jacobacci also bear Deseadan mammals represented by a leontinid notoungulate. Re-examination of the only specimen in Casamiquela’s collection labelled as
Leontiniidae revealed that it belongs to an isotemnid (likely *Periphragnis*), and consequently the Lower Las Chacras fauna bears no known element shared with the Deseadan associations. The presence of the Miocene marsupial *Palaeothentes* in this fauna alleged by Casamiquela (1969) and Pascual *et al.* (1984) is unproven.

The typothere *Eohegetotherium priscum* is clearly more advanced than its Eocene counterparts and is the only element of the Lower Las Chacras fauna shared with early Oligocene Tinguirirican associations of central Patagonia and Chile but not with Mustersan ones. Likewise, the Lower Las Chacras fauna documents the occurrence of an astrapotheriid (described above as cf. *Astraponotus*) with more derived dental features than *Astraponotus* or any other Eocene astrapothere, although in this case there are no undisputable Tinguirirican known astrapothere to compare with. These records suggest that some advanced faunal elements settled in North Patagonia earlier than in central Patagonia. The Somun Cura Massif could have acted as a biogeographic barrier for the southern dispersion of these mammals.

The Lower Las Chacras fauna is the only known Mustersan and the better known Paleogene association for North Patagonia. The Mustersan age is unknown in low latitudes of South America. In middle latitudes, this age is represented only by the roughly coeval fauna of the Geste formation in NW Argentina, which bears a moderately diverse mammalian assemblage. Consequently, the Lower las Chacras Fauna represents a substantial increasing of our knowledge of the Paleogene faunal succession and mammal diversity, not only in Patagonia but also in entire South America.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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