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Late Miocene mammals from the Calchaquí Valley (Palo Pintado Formation, northwestern Argentina): Biogeographic and paleoenvironmental implications for the southern central Andes

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ABSTRACT

With noteworthy outcrops in the Angastaco Basin (Salta Province), the Palo Pintado Formation is perhaps one of the most intensely studied late Miocene stratigraphical unit of northwestern Argentina from geological, paleoecological, and paleobotanical approaches. In contrast, the mammals from this unit are scarcely known, most of them lacking a precise stratigraphical and geochronological adjustment. In this contribution, we report new caviomorph rodents from the Palo Pintado Fm, exposed at Calchaquí Valley (Eastern Cordillera, Angastaco Basin). The stratigraphical and geochronological control of the new specimens indicate a time window ranging from ~9.3 Ma to ~6.1 Ma. The first records of brachydont mammals of the Palo Pintado Fm, represented by the caviomorph Erethizontidae (Erethizontidae sp. nov. cf. *Microsteiromys* sp.) and Echimyidae (cf. "*Eumysops" parodii*, and cf. *Thrichomys* sp.), are described. Dinomyidae (cf. *Ferigolomys* sp.), small Caviidae (gen. and sp. indet. A and B), and the abrocomid *Protabrocoma paranensis* are also identified. Caviomorphs from the Palo Pintado Fm (containing the oldest and more recent taxa of different Neotropical linages) allow us to suggest Angastaco Basin as "museum" and "cradle" of biodiversity during the Tortonian and Messinian ages. Our analysis indicates that the late Miocene mammals of the Palo Pintado Fm are compatible with the occurrence of forested environments developed under humid and warm conditions, in agreement with independent paleoenvironmental and paleoclimatic proxies. A close biogeographic relationship between the area of the Calchaquí Valley, the Brazilian Acre, and the Argentinian Mesopotamia during the late Miocene is also suggested.

1. Introduction

The late Miocene is recognized as a period of important climatic, environmental, and geological changes, which greatly altered the diversity of the continental ecosystems (Cerling et al., 1993, 1997; Zachos, 2001; Rohrmann et al., 2016; Herbert et al., 2016; Amidon et al., 2017; Carrapa et al., 2019). During the Tortonian age (11.6–7.25 Ma), with a global warming characterized by a mean annual temperature higher than present time, a warmer and wetter world is expected (Pound et al., 2011). Instead, during the Messinian age (7.25–5.33 Ma), a global late Miocene cooling was coeval with the "Messinian Salinity Crisis", the spread of C4 photosynthesis pathway plants, and a remodeling of the terrestrial faunas (e.g. Cerling et al., 1993, 1997; Zachos, 2001; Edwards et al., 2010; Dupont et al., 2013; Herbert et al., 2016; Amidon et al., 2017; Carrapa et al., 2019; Domingo et al., 2020). In the southern central Andes at northwestern Argentina (NWA), active tectonic–orographic processes were synchronous with regional and global late Miocene climatic changes (e.g. Kleinert and Strecker, 2001; Garzione

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et al., 2008; Hain et al., 2011; Hynek et al., 2012; Galli et al., 2014; Pingel et al., 2016; Amidon et al., 2017; Carrapa et al., 2019). However, the eco-evolutionary history of the late Miocene vertebrates of NWA and their potential relationships with the Andean uplift and climate changes has so far remained unclear. For example, it has not yet been assessed whether the Tortonian warming has impacted the taxonomic and ecological diversity of vertebrates in NWA, or whether the climatic changes close to the Tortonian–Messinian boundary can be perceived as variations of the faunal composition.

At the Calchaquí Valley (Salta Province, NWA), situated in the southern part of the Eastern Cordillera (between 25°41′34″S–66°03′31″W and 25°37′17″S–66°03′26″W), the late Miocene age corresponding to Tortonian and Messinian is represented by the Palo Pintado Fm (Grupo Payogastilla; Díaz and Malizzia, 1983), which was deposited in the Angastaco Basin (AB), from 10.29 ± 0.11 Ma (K/Ar) to 5.27 ± 0.28 Ma (206 P b/238U; Coutand et al., 2006; Carrapa et al., 2006; Galli et al., 2008, 2014). The Palo Pintado Fm (PPF) is perhaps one of the most intensely studied late Miocene units of NWA, with sedimentological, geochronological, isotopic, paleoecological, faunistic, and paleobotanical studies (e.g. Anzótegui and Cuadrado, 1996; Morton, 1992; Anzótegui, 1998; Stark and Anzótegui, 2001; Hain et al., 2011; Bywater-Reyes et al., 2010; Galli et al., 2011, 2014, 2019; Carrapa et al., 2012, 2014; Reguero et al., 2015; Pingel et al., 2016; Rohrmann et al., 2016; Garralla et al., 2016; Zimicz et al., 2018; Robledo et al., 2020, in press). In contrast to the above mentioned evidence, and compared with that of other late Miocene areas of Argentina (e.g. Entre Ríos, Catamarca, Buenos Aires, and La Pampa provinces; e.g. Esteban et al., 2014; Montalvo et al., 2019; Prevosti et al., 2021; Schmidt et al.,

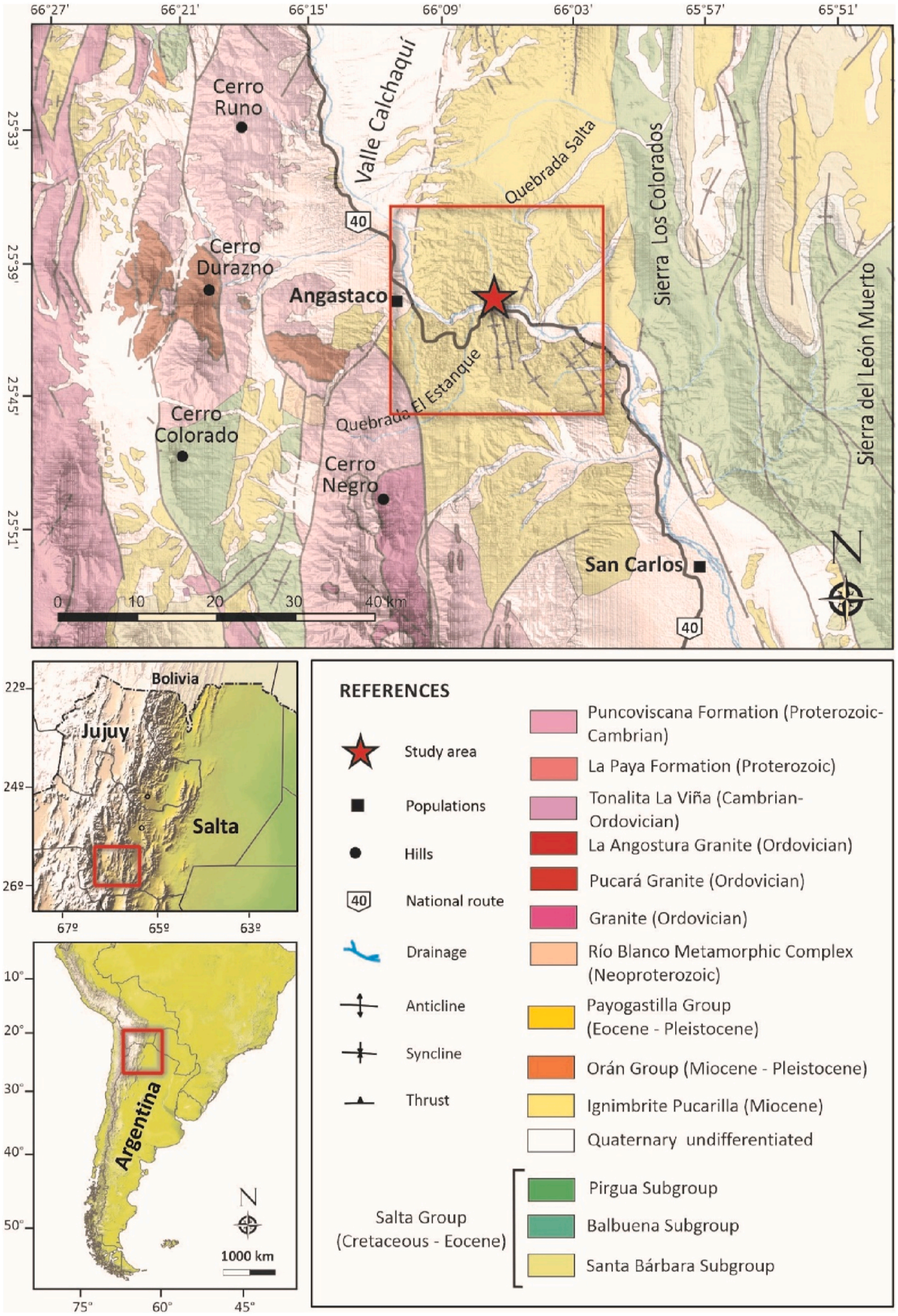

Fig. 1. Geological map of the southern Calchaquí Valley, Salta Province, northwestern Argentina, showing the Angastaco Basin area and the fossil-bearing sites (red star) of Palo Pintado Formation (modified from Galli et al., 2014).

2020), the mammals from the PPF at the Calchaquí Valley are still poorly known, most of them lacking a precise stratigraphic and geochronological adjustment (Díaz et al., 1989; Starck and Anzótegui, 2001; Reguero et al., 2015).

Herein, we describe new caviomorph specimens recovered from the PPF at the Calchaquí Valley. Based on recent geochronological analyses and the knowledge of their stratigraphic provenance, the age of each new specimen is provided. We studied their systematics and, combining previously published mammal records from this unit, we scrutinized the diversity and the evolutionary and biogeographic significance of the mammals of the PPF, as well as their value as paleoenvironmental proxies.

2. Geochronology and stratigraphical setting

The study area is located in the AB, in the southern part of the Eastern Cordillera (NWA, Salta Province), at the Calchaquí Valley, from 25°42′55″ S to 66°10′44″ W and 25°40′42″ S to 66°05′30″ W (Fig. 1). The narrow, NS trending AB is located in the distal part of a formerly contiguous Paleogene Retroarc Foreland basin (Jordan and Alonso, 1987). The AB includes >6 km of Eocene–Pliocene continental deposits of the Payogastilla Group (Díaz and Malizzia, 1983; Starck and Vergani, 1996), comprising (from base to top) Los Colorados, Angastaco, Palo Pintado and San Felipe formations. The AB is bounded to the west by the Precambrian–early Cambrian metasedimentary Puncoviscana Formation over the Cenozoic basin strata, and to the east by the Cretaceous rocks of the Sierra de Los Colorados and Sierra León Muerto (Galli et al., 2014).

The new fossils were found at the PPF, in outcrops exposed along the Calchaquí River (Galli et al., 2014), from Quebrada Los Colorados to Quebrada Piedras Blancas, close to a left tributary of the Calchaquí River (Fig. 1). Both at the top and base, the contacts of the PPF are transitional and concordant with the San Felipe and Angastaco formations, respectively. The PPF ranges from 10.29 ± 0.11 Ma at the base (Galli et al. 2008, 2011) to 5.27 ± 0.28 Ma (Coutand et al., 2006) - 5.98 ± 0.32 Ma (Bywater-Reyes et al., 2010) at the top of the unit. Recently, two tuff levels were dated in 6.3 ± 0.08 Ma and 6.8 ± 0.05 Ma in the PPF at Quebrada El Estanque (Galli et al., 2014; Pingel et al., 2016). The PPF is 800 m thick at the Calchaquí River section and encompasses thickening and coarsening-upward cycles, including matrix supported conglomerates, fine to medium sandstone, and fine grained sublithic sandstones that end in levels of green, brown, and gray siltstones beds. The PPF lithofacies are characteristic of an intermediate stage between low-sinuosity, multiple channel rivers (classic braided rivers) and high-sinuosity, single channel rivers (classic meandering rivers; Galli et al., 2011, 2014, 2019). In some sections, these rivers can develop a simple channel, whereas in others, they develop multiple channels. This fluvial system would have developed wide floodplains, which would have been drained in the dry season, as it is evidenced by desiccation cracks and gypsum levels pedogenetic features. The general characteristics of the fluvial architecture indicates that the PPF was developed as a sinuous sandy-gravel fluvial system with swamps and lagoons, under a warm, humid, tropical to subtropical climate with a slight seasonality (Starck and Anzótegui, 2001; Galli et al., 2011, 2014). This interpretation is supported by X-ray diffraction data from floodplain clay minerals that revealed the presence of illite, smectite and kaolinite generated by hydrolysis produced under a temperate and humid climate (Galli et al. 2011, 2014).

The lithofacies boundaries as well as the characteristics and geometries of the architectural elements of the profile in the Calchaquí River Section were analyzed in detail by Galli et al. (2011, 2014). A magnetostratigraphic study of the PPF was recently performed at this section (Galli et al., 2014), notably around the site where the new fossils were found, thereby allowing us to bracket the age of the mammal-bearing sediments between ~9.3 Ma and ~6.1 Ma. In Fig. 2 the stratigraphic provenance and the estimated age of the new specimens are indicated in the PPF stratigraphic column, showing the local magnetostratigraphic column vs. the stratigraphic level (Calchaquí River), and the Global Magnetic Polarity Time Scale (following Galli et al., 2014).

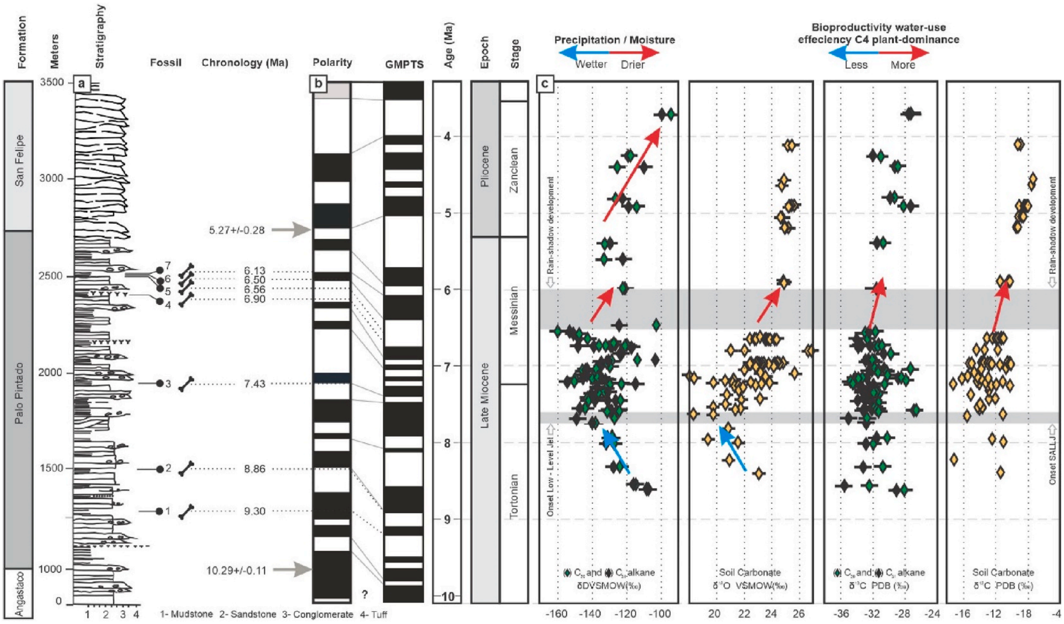

Fig. 2. (a) Stratigraphic column of Palo Pintado Formation at the Calchaquí River section, including provenance of caviomorph fossils (1, cf. *Ferigolomys* sp., S. Sal. Scar.Paleo. 2012–055; 2, Erethizontidae sp. nov. cf. *Microsteiromys* sp., S. Sal.Scar.Paleo. 2012-044a-c; 3, cf. *"Eumysops" parodii*, S. Sal.Scar.Paleo. 2012–036; 4, Caviidae Gen. et. sp. indet. A, S. Sal.Scar.Paleo. 2012–058; 5, *Protabrocoma paranensis*, S. Sal.Scar.Paleo. 2012–023; 6, cf. *Thrichomys* sp., S. Sal.Scar.Paleo. 2012–033; 7, Caviidae Gen. et. sp. indet. B, S. Sal.Scar.Paleo. 2012–034), and dated tuff beds (taken from a: Carrapa et al., 2006, and b: Galli et al., 2011); (b) correlation of local magnetostratigraphy (taken from Galli et al., 2014) to the Global Magnetic Polarity Time Scale (GMPTS, Cande and Kent, 1995); (c) stable isotope compilation (modified from Rohrmann et al., 2016) of leaf wax δDwax (a function of plant transpiration), soil carbonate δ^{18}Osc (a function of soil evaporation), stable isotopes of leaf wax δ^{13}Cwax, and soil carbonate $\delta\ ^{13}$Csc (as proxies of C4/C3 vegetation type). Vienna Standard Mean Ocean Water (VSMOW). Pee Dee Belemnite (PDB).

3. Materials and methods

The new specimens described below are housed in the vertebrate paleontology collections of the Museum of San Carlos (S.Sal.Scar.Paleo), Salta Province, Argentina. The whole new specimens were found *in situ* in the sandy facies of the bearing horizon. The fossils were recovered by direct collection from the sedimentary exposures. Each material, previously photographed, geo-referenced and recorded, was extracted with part of the bearing sediment by using chisels. In the laboratory, each sample was partially immersed in water for several hours to facilitate the detachment of the hardened sandstone. Finally, the remaining sediment adhered to the fossils was removed under a stereomicroscope. The adhering matrix is a fine sandstone which was deposited by large subaqueous dunes in fast-flowing confined channels. Further, the preservation of all specimens indicates that they were no transported far, and that there were no other potential source horizons in the immediate vicinity.

Measurements were made to the nearest 0.1 mm using digital calipers. Comparative data were obtained from research collections at the Museo de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Buenos Aires, and Museo de La Plata (MLP), La Plata, Argentina. Specimens were compared with materials of reference, mainly type specimens; additional data used in comparative studies were gathered from published sources. Information on the new specimens that justify their proposed taxonomic assignments was provided. Only in those cases, when a new species is proposed, detailed descriptions were given. The use of open nomenclature follows the recommendations given by Matthews (1973) and Bengtson (1988). Teeth growing terminology follows Mones (1982). Hypsodont teeth are high-crowned, in contrast to low-crowned brachydont teeth. Protohypsodonty refers to high-crowned and limited growing teeth, and euhypsodonty, to high-crowned and ever growing teeth.

3.1. *Age of the fossil record*

The record of the fossils has been located in the stratigraphic column of the Calchaquí River (Galli et al., 2014) and then the stratigraphic location of each one (GPS) was interpolated, with the local and international paleomagnetic column of Cande and Kent (1992) to obtain the age of each of the records (Fig. 2). The age of the fossils was estimated from magnetostratigraphical data reported by Galli et al. (2014) at PPF, where a local paleomagnetical section and two absolute dates, one at the base (10.29 ± 0.11 Ma, Galli et al. 2011) and the other at the top (5.27 ± 0.28 Ma, Carrapa et al. 2006) were obtained. The samples were collected in siltstones or mudstones to increase the probability that the magnetic minerals be sufficiently fine-grained to deliver a reliable magnetic signal. A total of 97 sites were collected in a stratigraphical section 1730 mts thickness at PPF. Ninety three out of 97 sample sites studied by Galli et al. (2014) were Class I sites, in which the mean orientation of the samples produced statistically significant results using Watson's criteria (see Galli et al., 2014). Class II sites were only used to support adjacent Class I sites of the same polarity; therefore, polarity zones were never defined only by Class II sites. Galli et al. (2014) obtained a total of 22 reversals, which define 23 polarity zones. The fossils were found in siltstones or claystones beds that correspond to the paleomagnetical stations sampled; it is for this reason that we have a high degree of confidence about the age of the deposits and therefore about the age of the fossils.

3.2. *Anatomical terminology and abbreviations*

The terminology of cheek teeth structures of Chinchilloidea, Erethizontidae, and Octodontoidea follows that proposed by Candela (1999), and Rasia and Candela (2019) for the upper cheek teeth, and Candela (2000, 2002), Candela and Rasia (2012), and Rasia et al. (2021) for the lower ones (see also Boivin and Marivaux, 2020). The dental and mandibular terminology for Cavioidea follows Pérez (2010). M/m: upper/lower molar; DP/dp: upper/lower deciduous premolar.

4. Results

4.1. *Systematic paleontology*

Class Mammalia Linnaeus, 1758.
Order Rodentia Bowdich, 1821.
Suborder Hystricognathi Tullberg, 1899.
Infraorder Caviomorpha Wood and Patterson in Wood (1955).
Superfamily Erethizontoidea Bonaparte, 1845.
Family Erethizontidae Bonaparte, 1845.
Erethizontidae sp. nov. cf. *Microsteiromys* sp.
Fig. 3a–c.

Referred material. S. Sal.Scar.Paleo. 2012-044a, left M1 or M2, S. Sal. Scar.Paleo. 2012-044b, left M3 (a young individual), and S. Sal.Scar. Paleo. 2012-044c, left dp4.

Description and comments. The new specimens were found together, and, because of their compatible size and similar general molar morphology, they are considered a single species. S. Sal.Scar.Paleo. 2012-044a is an upper molar (M1 or M2) with a longer than wide occlusal outline and tetralophodont pattern. It has distinct labial (para- and mesostyle) cusps, even with a moderate stage of wear, as observed in several Paleogene caviomorphs (Arnal et al., 2020; Boivin et al., 2017a,b, 2018), and the paraflexus, mesoflexus and posteroflexus still open labially at this stage of wear. The posterior arm of the protoloph (lingual protoloph) is represented by a short and low projection. The protocone is relatively short mesiodistally. The protoloph is transverse and connects to the paracone labially. The mure is short and slightly oblique with respect to the mesiodistal axis of the molar. The mesoflexus is slightly divergent labially in occlusal view (open labially). The mesolophule is transversely oriented, slightly sinuous (probably as a consequence of the union of lingual and labial portions of this loph), and connected with the mesostyle labially. The hypoflexus is narrow and poorly penetrating in the occlusal outline. There is a constriction immediately located posterodistally to the hypocone. The posteroloph is convex distally and extends to the labial side of the molar without connecting to the mesostyle.

The M3 (S.Sal.Scar.Paleo. 2012-044b), which is preserved at a very early stage of wear (just erupted), also has a longer than wide occlusal outline and is smaller than the M1 or M2 (Sal.Scar.Paleo. 2012-044a). As in the M3s of erethizontids and other caviomorphs, the posterior portion is narrower than the anterior one, and the hypocone is labially displaced with respect to the protocone. Lophs show slight constrictions and crenulations and a very low obliquity. The paracone is bulky and distinct from the anteroloph and mesoflexus, and the mesostyle is well differentiated but smaller than the paracone. The protoloph is transversely oriented and connects to the paracone labially. The posterior arm of the protoloph (lingual protoloph) is represented by a short and low projection, so that a connection, even though superficial, exists between the paraflexus and hypoflexus. This trait expresses a pseudo-taeniodont pattern.

As in S. Sal.Scar.Paleo. 2012-044a, the mure is short and slightly oblique, the mesolophule is transversely oriented and connected with the mesostyle, and the metaflexus is labially open. There is a constriction posterodistally located to the hypocone that is deeper than in S. Sal.Scar. Paleo. 2012-044a. The posteroloph extends mesiolabially until the distolabial wall of the tooth. As in others caviomorphs, it is possible that in the M1 or M2 and M3, the metacone and the metaloph are subsumed with the posteroloph in a posteroloph-metaloph-metacone complex.

The Sal. Scar.Paleo. 2012-044c is assigned to a dp4 because it has similar proportions and general morphology to the deciduous teeth of both extant and extinct porcupines, i.e., relatively longer than wide with respect to the definitive premolars (Candela, 2000). The dp4 (Sal.Scar. Paleo. 2012-044c) is longer than wide and tetralophodont, similar to

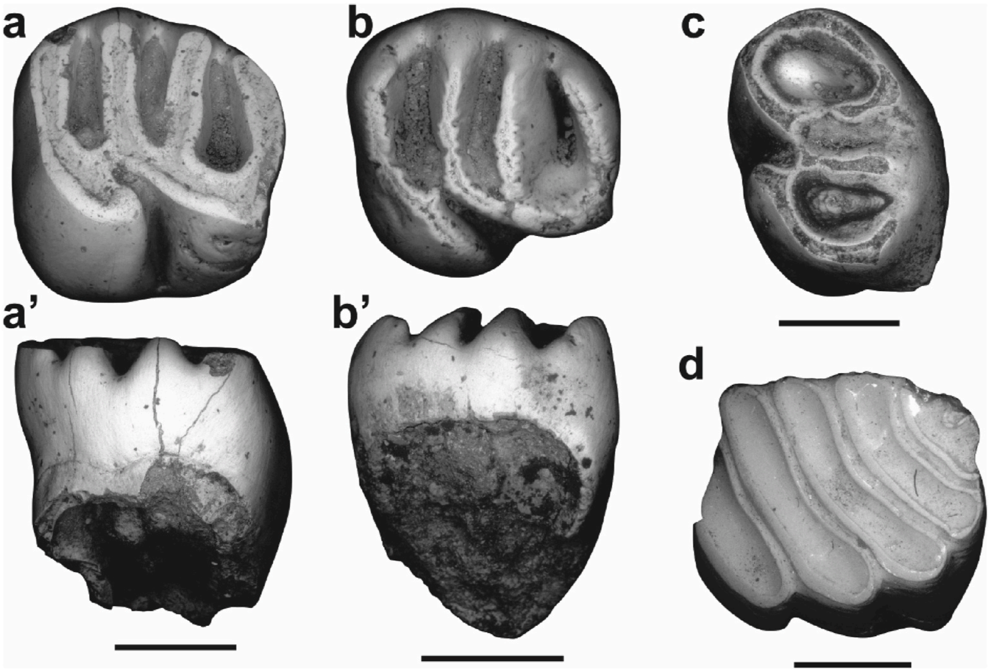

Fig. 3. (a–c) Erethizontidae sp. nov. cf. *Microsteiromys* sp., S. Sal.Scar.Paleo. 2012-044a, left M1 or M2 in occlusal (a) and labial (a') views; S. Sal.Scar.Paleo. 2012-044b, left M3 in occlusal (b) and labial (b') views; (c) S. Sal.Scar.Paleo. 2012-044c, left dp4 in occlusal view. (d) cf. *Ferigolomys* sp., S. Sal.Scar.Paleo. 2012–055, left upper molariform in occlusal view. Scale bar 1 mm in a-c, 3 mm in d.

that of some extinct and extant porcupines, such as *Hypsosteiromys* (Candela, 2002). Unlike the pentalophodont dp4s of erethizontids, as in those of the extinct *Branisamyopsis*, *Steiromys* and *Eosteiromys* (Candela, 2000, 2002, 2003), there is no evidence of mesolophid and mesostylid. As in other erehtizontids, the dp4 has a shallow, wide, and closed (with scarcely wear) anterofossettid, and a wide and nearly closed posterofossettid. The entoconid is the only well-distinctive lingual cusp.

The size of the new dental specimens is compatible with that of the teeth of the erethizontid *Microsteiromys jacobsi* Walton (1997) (from the late middle Miocene of La Venta, Colombia; Walton, 1997), the smallest known representative of New World porcupines, and to cf. *Microsteiromys* sp., recovered from the middle Miocene locality MD-67 (Madre de Dios, Peruvian Amazonia; Antoine et al., 2013). *Microsteiromys jacobsi* is known only by lower cheek teeth (Walton, 1997), while the specimens form locality MD-67 are represented by two upper teeth, which are comparable in size to those of *M. jacobsi* (Antoine et al., 2013). The small size, the longer than wide occlusal outline of upper molars, the persistence of the labial flexi, the low loph obliquity, the short lingual protoloph, the narrow hypoflexus, the presence of the posterodistal constriction posteriorly to the hypocone, and the low crowns suggest that the new material is closely related to specimens from MD-67 assigned to cf. *Microsteiromys* sp. However, the S. Sal.Scar.Paleo. 2012-044ba-b differ from cf. *Miocrosteiromys* sp. (MD-67) in having upper molars with a tetralophodont and pseudo-taeniodont outline. Several features of the upper molars (the small size, brachydonty, longer than wide upper molars, the presence of distinctive cusps, the poorly penetrant and narrow hypoflexus) are shared with small stem Cavioidea *Palaeosteiromys amazonensis* (from the late Oligocene of Peru; Boivin et al., 2017b; Marivaux et al., 2020a). However, *P. amazonensis* mainly differs from the S. Sal.Scar.Paleo. 2012-044ba-b in having pentalophodont and non-taeniodont upper molars. S. Sal.Scar.Paleo. 2012-044a-b are similar in size and in the presence of a tetralophodont pattern to the erethizontid *Plesiosteiromys newelli* (from the late Oligocene of Peru; Boivin et al., 2017b), known by just one upper molar. On the other hand, this Peruvian species differs from S. Sal.Scar.Paleo. 2012-044a-b in having a more transverse occlusal outline (displaying a longer and curved anteroloph and posteroloph, respectively), a marked labiolingual expansion of the hypoflexus, non-taeniodont occlusal pattern, and close labial flexi. The S. Sal.Scar.Paleo. 2012-044a-b are similar to the erethizontid *Kichkasteiromys raimondii* (based on a single tooth from the early Oligocene of the Peruvian Amazonia; Boivin et al., 2018) in its small size, brachydont molars, and the presence of a weak and short lingual protoloph. However, the S. Sal.Scar.Paleo. 2012-044a-b differ from *Kichkasteiromys raimondii* in having tetralophodont upper molars longer than wide (less transverse).

Concerning to dp4, tetralophodont dp4s are also present in other extinct caviomorphs (e.g. Candela, 2002), but the suite of characters of the dp4 (S.Sal.Scar.Paleo. 2012-044c) indicates erethizontoid affinities. The dp4 differs from *M. jacobsi* in having a simpler (tetralophodont) pattern (Walton, 1997). Among Paleogene caviomorphs, the dp4 of *Mayomys confluens* (from the early Oligocene of Peruvian Amazonia; Boivin et al., 2018) is also tetralophodont with a wide and closed anterofossetid, similar to that of S. Sal.Scar.Paleo. 2012-044c. However, *M. confluens* mainly differs from the new materials in having a smaller size, and closed labial flexi on the upper molars.

In sum, the new material is recognized as a small erethizontid, with a particular character combination, which indicates that it represents a new species, probably more closely related to cf. *Microsteiromys* sp. from the middle Miocene of Peru. The new erethizontid is characterized by the following combination of features: brachydont cheek teeth, upper molars longer than wide, with moderate unilateral hypsodonty, tetralophodont occlusal pattern, pseudo-taeniodonty, labial cusps (paracone and mesostyle) well-distinct (mainly on M3), persistent paraflexus and metaflexus, even with moderate wear (M1 or M2), narrow and scarcely penetrant hypoflexus, and constriction posterodistally located with respect to the hypoflexus; lower deciduous tooth (dp4) mesiodistally elongated, with a tetralophodont pattern, having the anterofossetid wide mediodistally, the mesoflexid narrow, and the posteroflexid wide and shallow. Given the current uncertainty with respect to the generic assignment, we prefer to leave the unnominated new species (in open nomenclature) as Erethizontidae sp. nov. cf. *Microsteiromys* sp. Further phylogenetic analyses of caviomorphs should help to resolve its closer affinities and generic assignment.

Superfamily Chinchilloidea Kraglievich, 1940.

Family Dinomyidae Alston, 1876.

cf. *Ferigolomys* sp.

Fig. 3d.

Referred material. S. Sal.Scar.Paleo. 2012–055, an isolated left upper cheek tooth.

Description and comments. The tooth is pentalophodont, with all lophs slightly curved, large, forming laminae, isolated from each other, and with interlaminar cement. The enamel band of each laminar loph is slightly wider in the leading edge than in the trailing edge. With more wear, the last three laminar lophs will join lingually, as is observed in the root apex of the tooth. The S. Sal.Scar.Paleo. 2012–055 is similar to *Ferigolomys pacarana* from the late Miocene (Solimões Formation) of Brazil (Kerber et al., 2018), the only species of the genus, known only through the holotype, because it has pentalophodont occlusal pattern, with the last three lophs attached lingually (a feature seen towards the base of the tooth). In upper teeth of *Ferigolomys pacarana*, the leading and trailing edges of each lamina have similar thickness (Kerber et al., 2018). In contrast on the upper teeth of other late Miocene dinomyids, such as *Arazamys*, *Tetrastylus*, and *Eumegamys* (e.g. Rinderknecht et al., 2011; Candela et al., 2013), the leading edge is wider and higher than the trailing edge. In S. Sal.Scar.Paleo. 2012–055, the differences in thickness and height between the leading and trailing edges are less marked than in these genera, being more similar to the condition of *F. pacarana*. As in the latter species, a small fossette on the last loph indicates an additional distal loph, such as was inferred for an earlier ontogenetic stage of this species. S. Sal.Scar.Paleo. 2012–055 is less worn than the M1 of the holotype of *F. pacarana*, having the lingual and labial flexi still open, as the M2 of this species. As in *F. pacarana*, the laminar lophs have no crenulation and are less compressed than in *Potamarchus* (Kerber et al., 2016a). S. Sal.Scar.Paleo. 2012–055 is similar in size to the M1 of *F. pacarana*, but we were unable to attest its degree of hypsodonty (protohypsodonty, like the holotype of *F. pacarana*, or euhypsodonty, like the giant Eumegamyinae). In relation to the systematics of Chinchilloidea, it was widely recognized that the dinomyids change their molar morphology during the ontogenetic development (e.g. Nasif and Abdala, 2016; Rinderknecht et al., 2018; Rasia and Candela, 2019; Rasia et al., 2021), which, in principle, would difficult the taxonomic assignment of an isolated molar. However, it is also proved that extinct dinomyids acquire the final occlusal pattern of the cheek teeth very early in their ontogenetic development (Rinderknecht et al., 2018). The traits of S. Sal.Scar.Paleo. 2012–055, evaluated against the traits of juvenile and adult specimens of other dinomyids, suggest its assignment as cf. *Ferigolomys* sp. This combination of features and the scarcity of the material do not allow to reach a confident determination of the new specimen at the generic and species level. Consequently, we maintain the taxonomic assignment of S. Sal.Scar. Paleo. 2012–055 as cf. *Ferigolomys* sp. Further findings of more complete specimens should help resolve its specific status and confirm the suggested generic assignment.

Superfamily Octodontoidea Waterhouse, 1839.

cf. "*Eumysops*" *parodii* Kraglievich (1945).

Fig. 4b.

Referred material. S. Sal.Scar.Paleo. 2012–036, fragmentary right maxilla with DP4–M3.

Description and comments. According to Olivares et al. (2012), the generic designation of the species "*Eumysops*" *parodii*, known only through the holotype (Kraglievich, 1945; Nasif et al., 2013, Fig. 4a), reported in the "Mesopotamiense" (Ituzaingó Formation, late Miocene; Schmidt et al., 2020), remains to be formalized, because this species does not belong to *Eumysops*. Thus, an open nomenclature for the generic determination of this species is maintained in the present study until transferred to another genus (Olivares et al., 2012). S. Sal.Scar. Paleo. 2012-036 shares with the holotype of "*E*". *parodii* the general size of DP4–M3 (length P4–M3: 12.9 mm), an equivalent degree of hypsodonty (having lower crowns than *Eumysops* species), a conspicuous unilateral hypsodonty, a subquadrangular outline of the cheek teeth, a tetralophodont occlusal pattern with a slight thickening in the last loph, and a similar degree of persistence of the flexi (more persistent than any species of *Eumysops*; Olivares et al., 2012). Thus, S. Sal.Scar.Paleo. 2012-036 has a combination of characters that indicates its greater affinity with "*E*". *parodii* than with any other species of Octodontoidea, sharing most of these features with this species. S. Sal.Scar.Paleo. 2012-036 differs from the type of "*E*". *parodii* in having a more robust ventral zygomatic root and a greater degree of divergence of the mesoflexid (with the mesolophule more posterolabially oriented). These features suggest that the new specimen could represent a new species, closely related to "*E*". *parodii*. However, intraspecific and ontogenetic variation within this species cannot be ruled out, considering that the new specimen is more worn than the type of "*E*". *parodii* (displaying the hypoflexus still connected to the paraflexus in M3, and the paraflexus open in all cheek teeth). Given the current uncertainty, we opt to refer S. Sal.Scar.Paleo. 2012–036 (in open nomenclature) as cf. "*E*". *parodii.*

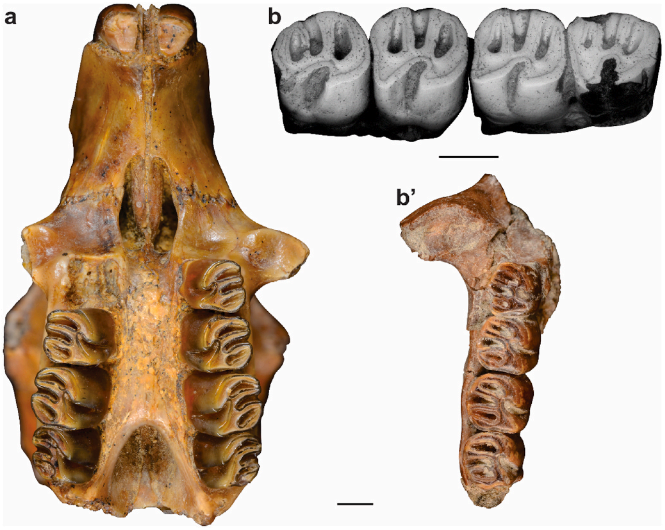

Fig. 4. (a)"*Eumysops*" *parodii*, MLP 41-XII-13-272 (holotype), anterior portion of the skull with left DP4–M3 and right M1–M3 in ventral view; (b-b') cf. "*Eumysops*" *parodii*, S. Sal.Scar.Paleo. 2012–036, DP4–M3 in occlusal view (b) right maxilla with DP4–M3 in ventral view (b'). Scale bar 2 mm.

Family Echimyidae Gray, 1825.

Subfamily Eumysopinae Rusconi, 1935.

cf. *Thrichomys* sp.

Fig. 5a–a′.

Referred material. S. Sal.Scar.Paleo. 2012–033, left mandibular fragment with a portion of the incisor and dp4–m2.

Description and comments. S. Sal.Scar.Paleo. 2012-033 shares most of its characters with the genus *Thrichomys*, known since the Pleistocene of Brazil (Kerber et al., 2016b), and represented today by at least four valid species: *T. apereoides*, *T. inermis*, *T. laurentius*, and *T. pachyurus* (Pessôa et al., 2015). Some characters (see below) of S. Sal.Scar.Paleo. 2012–033 are shared with *Ullumys* Olivares et al. (2017), known by the species *U. intermedius* (=*Eumysops intermedius* Rovereto, 1914, =*Thrichomys intermedius* Bond, 1977) and *U. pattoni* Olivares et al. (2017), both from the late Miocene of northwestern Argentina (Olivares et al., 2017). The mandible of S. Sal.Scar.Paleo. 2012–033 is similar in size and morphology to that of *Thrichomys* (the mandibular corpus is strong, the notch for the tendon of the medial masseter muscle is located at the level of dp4–m1 and continuous with the masseteric crest, the lateral crest is oblique and starts at the level of m1, and the masseteric crest is markedly projected from a deep masseteric fossa). The location of the lateral crest and the depth of the masseteric fossa are traits also present in *U. intermedius* (Olivares et al., 2017). With respect to the cheek teeth, S. Sal.Scar.Paleo. 2012–033 has a combination of characters shared with *Thrichomys*: the dp4 is tetralophodont with a well-developed

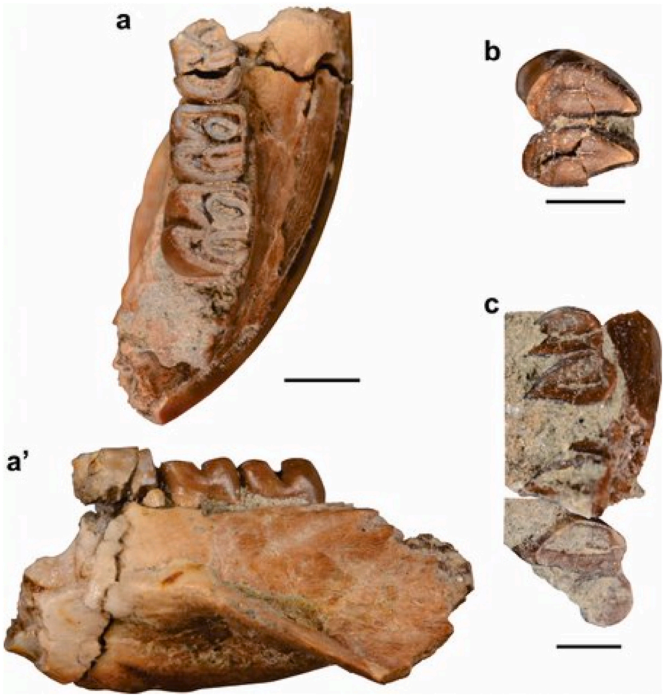

Fig. 5. (a-a') cf. *Thrichomys* sp., S. Sal.Scar.Paleo. 2012–033, left mandible with dp4–m2 in occlusal (a) and lateral (a') views; (b–c) Caviidae; (b) Gen. et. sp. indet. A, S. Sal.Scar.Paleo. 2012–058, right upper molar in occlusal view; (c) Gen. et. sp. indet. B, S. Sal.Scar.Paleo. 2012–034, left maxilla with M1-M3 in occlusal view. Scale bar 2 mm.

metalophulid II and a persistent metaflexid, the lower molars are trilophodont, having the metaflexid clearly more persistent than the mesoflexid in m1–m2 (Pessôa et al., 2015; Kerber et al., 2016b; Olivares et al., 2017). The latter character allows us to distinguish S. Sal.Scar.Paleo. 2012–033 from *Ullumys*, in which the closure of the metaflexid and the mesoflexid in the m1 is almost synchronous, a feature that was recognized as diagnostic of this genus (Olivares et al., 2017). According to the wear stage of the cheek teeth, S. Sal.Scar.Paleo. 2012–033 is an adult (Neves and Pessôa, 2011), having lower crowns than those of adult specimens of *T. apereoides* with a similar degree of wear. However, more specimens at different ontogenetic stages are necessary to assess the degree of crown height of the new specimen in the context of the extant species of *Thrichomys*. Concerning the variability of the occlusal morphology of *Thrichomys*, an exhaustive analysis throughout the ontogeny of the extant *T. laurentius*, *T. inermis* and *T. pachyurus* indicated that each species has a distinct ontogeny, showing different patterns of wear of the cheek teeth, so that the occlusal wear occurred in different ways among the three taxa (Neves and Pessôa, 2011). Significant variation was also found in the skull shape of species of *Thrichomys* (Carvalhaes et al., 2019). In view of the observed variability in extant species of *Thrichomys*, the occlusal pattern and crown height of S. Sal.Scar.Paleo. 2012–033 may fall within the variability limits of this genus. In S. Sal.Scar.Paleo. 2012–033, the mesofossettid is broader in relation to the thickness of the lophids than what occurs in *Thrichomys*, thereby resembling *Ullumys* in this feature. Both species of *Ullumys* differ between them, among other features, in their degree of hypsodonty (Olivares et al., 2017). So, the degree of hypsodonty coupled to the pattern of tooth wear are variable traits in both *Thrichomys* and *Ullumys*. Accordingly, a wider sample is necessary to evaluate crown high and relative width of the fossettids in the new specimen.

In sum, this comparative study indicates that most of the characters of S. Sal.Scar.Paleo. 2012–033 correspond to *Thrichomys*, but these are not sufficiently informative to assign it to a specific level. On this basis, we maintain the taxonomic identity of the S. Sal.Scar.Paleo. 2012–033 as cf. *Thrichomys* sp. Further findings of more complete specimens should help resolve its specific status and confirm the suggested generic assignment. Nevertheless, this comparative study supports the inclusion of S. Sal.Scar.Paleo. 2012–033 in the *Ullumys*-*Thrichomys* clade (Olivares et al., 2017).

Family Abrocomidae Miller and Gidley, 1918.
Genus *Protabrocoma* Kraglievich, 1927.
Type species *Protabrocoma paranensis* Kraglievich (1927).
Protabrocoma paranensis Kraglievich (1927).
Fig. 6a–d.

Referred material. S. Sal.Scar.Paleo. 2012–023, right mandibular fragment bearing dp4–m2.

Description and comments: Kraglievich (1927) erected the extinct genus *Protabrocoma*, based on the species *P. paranensis* Kraglievich 1927 known only through the holotype (MACN 9024, a left mandibular fragment with dp4–m2), from the late Miocene ("Mesopotamiense"; Ituzaingó Formation) of Entre Ríos Province (Kraglievich, 1927, 1940). According to Kraglievich (1927, 1940), *Protabrocoma* differs from the extant *Abrocoma* in having the anterior portion of dp4 narrower and more rounded than that of *Abrocoma*, and less sharp edges of the lower molars. S. Sal.Scar.Paleo. 2012–023 is very similar in size and general morphology to the holotype of *Protabrocoma paranensis* (Kraglievich, 1940: fig. a); the notch for the tendon of the masseter muscle is rounded, well distinctive, and located below half the height of the mandible. As in the holotype of *P. paranensis*, S. Sal.Scar.Paleo. 2012–023 presents the anterior portion of dp4 with its anterior margin rounded and the m1–2 with the lateral edges of the lophids less angular than in the extant *Abrocoma*. In all teeth, the bottom of the hypoflexid is distally located

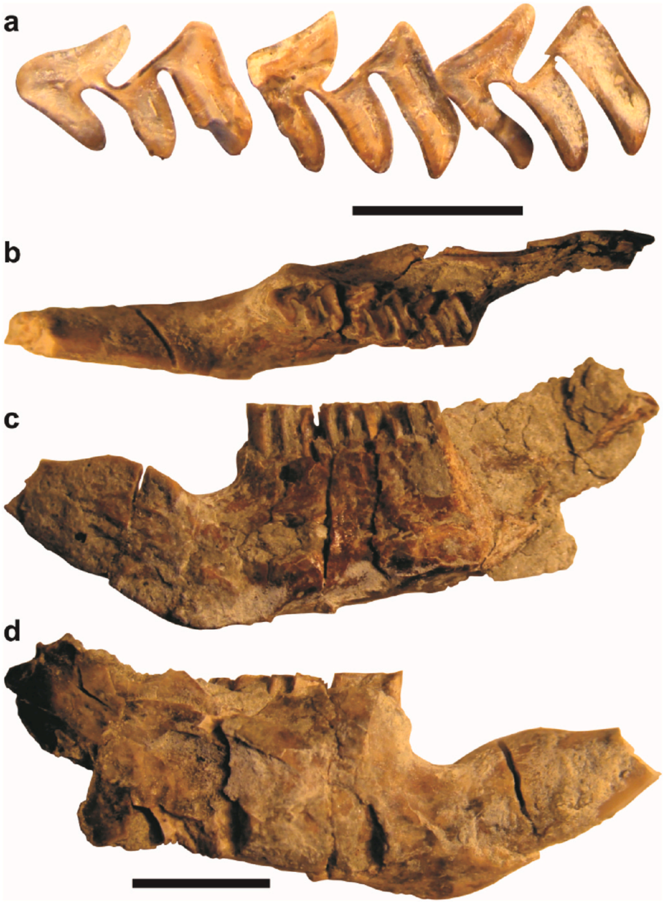

Fig. 6. (a–d) *Protabrocoma paranensis*, S. Sal.Scar.Paleo. 2012–023, right mandibular fragment with dp4–m2; (a) dp4–m2 in occlusal view; (b–d) mandible in occlusal (b), medial (c), and lateral (d) views. Scale bar 2 mm in a, 5 mm in b-d.

with respect to the bottom of the anterior lingual flexi; consequently, the bottom of the hypoflexid is located between the two lingual flexids, as in the holotype of *P. paranensis*. This feature may change with wear, so, we were unable to confirm its diagnostic value here. As the holotype of *P. paranensis*, the lophids are wider mesiodistally with respect to the flexid than those of *Abrocoma* (Verzi and Quintana, 2005). In sum, shared characters of S. Sal.Scar.Paleo. 2012–023 and the holotype of *P. paranensis* justify the specific determination of this new specimen.

Another abrocomid from the late Miocene of Argentina, *Abrocoma antiqua* Rovereto (1914), was identified for the "Araucanense" of Catamarca Province. After its original description, *Abrocoma antiqua* was included in the genus *Protabrocoma* (Marshall and Patterson, 1981; Verzi and Quintana, 2005; Kihn, 2009). *Protabrocoma* is widely recorded in the late Miocene. It was reported for the late Miocene of Catamarca (Chiquimil and Andalhualá formations; Marshall and Patterson, 1981; Esteban et al., 2014), La Rioja (Toro Negro Formation; Rodríguez-Brizuela and Tauber, 2006), La Pampa and Buenos Aires (Cerro Azul Formation; Pascual, 1966; Kihn, 2009), Mendoza ("Guayquerías de San Carlos"; Rovereto, 1914; Prevosti et al., 2021), and San Juan (Lomas de las Tapias; Contreras et al., 2019) provinces. *Protabrocoma* was also reported from the late Miocene of Muyu Huasi Bolivia (Villarroel and Marshall, 1989). A study on abrocomids from the late Miocene of Cerro Azul Formation proposed *P. antiqua* and *P. paranensis* as synonymous, and considered that the variability identified in the late Miocene *Protabrocoma* specimens corresponds to ontogenetic and/or intraspecific variation (Kihn, 2009). Pending future taxonomic analyses of extant and living abrocomid, we retain here the validity of the extinct species *P. paranensis* and *P. antiqua*. *Abrocoma* cf. *A. boliviensis* was recently reported for the El Jarilla Member (Chiquimil Formation; Esteban et al., 2014), being until now the oldest record of *Abrocoma*. Concerning the extant *Abrocoma boliviensis* (Glanz and Anderson, 1990), Verzi and Quintana (2005) assigned this species to the extant arboreal abrocomid *Cuscomys* (Emmons, 1999), on the basis of similar features of cheek teeth (broad anteroposterior lophs, as opposed to narrow anteroposterior lophs of *Abrocoma*) and the relative size of the coronoid process (moderate in *Abrocoma*, reduced in *Cuscomys*). Later, Patton and Emmons (2015), retained *boliviensis* in *Abrocoma*, pending a phylogenetic analysis. *Abrocoma boliviensis* along with *Cuscomys* would be the morphologically least specialized extant Abrocomidae (Emmons, 1999). As mentioned above, S. Sal.Scar.Paleo. 2012–023 and the holotype of *Protobrocoma paranensis* have lophids mesiodistally wider with respect to the flexids than in most of the species of *Abrocoma* (Kraglievich, 1940: fig. b; Pascual et al., 1966: lam 52F, 59B; Verzi and Quintana, 2005: Fig. 6E). This occlusal pattern is more similar to those of *Cuscomys* (Emmons, 1999: Fig. 7C and D) and *A. boliviensis* (Glanz and Anderson, 1990: Fig. 9; Verzi and Quintana, 2005).

Superfamily Cavioidea Fischer, 1817.

Family Caviidae Fischer, 1817.

Gen. et sp. indet. A.

Fig. 5b.

Referred material. S. Sal.Scar.Paleo. 2012–058, rigth isolated upper molariform.

Description and comments. The upper tooth is euhypsodont and bilobed, with a constriction in the apex of each lobe, being the posterior one more pronounced. Both lobules are similar in size and have a crest in the middle of each one. The fundamental internal flexus (= hypoflexus) contains cement on its lingual portion and is funnel-shaped, with its anterior border (= posterior border of the anterior lobule) slightly sinuous and less divergent to the posterior one. The labial border of the tooth is not enameled except in the labial flexus, which has a moderate depth and is opposed to the bottom of the hypoflexus. There is no evidence of the accesory labial primary and secundary fissures. The size and general occlusal morphology of S. Sal.Scar.Paleo. 2012–058 are similar to that of *Microcavia*, *Orthomyctera*, and *Prodolichotis prisca* (Quintana, 1996; Madozzo-Jaén, 2019), but smaller than the latter. The only tooth known here described does not allow us to reach a determination at the generic and species levels.

Gen. and sp. indet. B.

Fig. 5c.

Referred material. S S. Sal.Scar.Paleo. 2012–034, left maxilar with M1–M3 with the M2 partially complete.

Description and comments. As in other caviids, the molars are euhypsodont and bilobed, with-heart-shaped lobes. As in S. Sal.Scar. Paleo. 2012–058, the lobules are subequal in size, with a transverse dentine crest in the middle of the occlusal surface of each lobe. There is no accesory primary or secondary fissures on the labial border of the lobule. The enamel is interrupted along the labial sides of the molars, except in the labial flexus. The hypoflexus is funnel shaped, with cement in the lingual portion.

Molars of S. Sal.Scar.Paleo. 2012-034 differ from S. Sal.Scar.Paleo. 2012–058 in having a larger size and shallower labial flexi, which is somewhat more displaced towards the posterior lobe (not directly opossed to the hypoflexus), although certain variability is observed in this trait.

Since the alpha taxonomy of extinct caviids is currently under intensive study, and revised diagnoses for most of the extinct genera and species are still neccesary (Madozzo-Jaén et al., 2018; Madozzo-Jaén, 2019), we assigned S. Sal.Scar.Paleo. 2012–034 as gen. and sp. indet. On the basis of the aforementioned differences, S. Sal.Scar.Paleo. 2012–034 and S. Sal.Scar.Paleo. 2012–058 are provisionally considered different taxa, pending taxonomic studies of extinct caviids, including analyses of intraspecific and ontogenetic variability.

4.2. Diversity and age

A recent paleomagnetic study at the Río Calchaquí section on the PPF (Galli et al., 2014), together with the stratigraphic provenance of each studied specimen, allow us to date the fossil bearing sediments (Fig. 2). On this basis, the age of the bearing sediments of the Dinomyid cf. *Ferigolomys* sp. (S.Sal.Scar.Paleo. 2012–055) is estimated at 9.3 Ma, and that of the Erethizontidae sp. nov. cf. *Microsteiromys* sp. (S.Sal.Scar. Paleo. 2012-044a-c) at 8.86 Ma. The age of the echimyid cf. "*Eumysops" parodii* (S.Sal.Scar.Paleo. 2012–036) is estimated at 7.43 Ma, and that of the echimyid cf. *Thrichomys* sp. (S.Sal.Scar.Paleo. 2012–033) is estimated at 6.5 Ma. The age of the abrocomid *Protabrocoma paranensis* (S. Sal.Scar.Paleo. 2012–023) is estimated at 6.56 Ma, and those of the caviids gen. et sp. indet. A (S.Sal.Scar.Paleo. 2012–058) at 6.9 Ma, and gen. et sp. ifndet. B (S.Sal.Scar.Paleo. 2012–034) at 6.13 Ma. In addition, the paleomagnetic data allow us to precise the age of *Paedotherium kakai* -but see Seoane and Cerdeño (2019) with respect to the assignment of this species to *Pachyrukhos*-reported at Quebrada Piedras Blancas at 8.8 Ma, coincidently with the previous estimated age for this species (Reguero et al., 2015).

5. Discussion

5.1. Diversity and age of the vertebrates of the Palo Pintado Formation

The rodents cf. *Thrichomys* sp. and cf. "*Eumysops" parodii* are the first echimyids described from the PPF. Late Miocene echimyids of NWA are represented by the Eumysopinae *Theridomysops parvulus* Rovereto (1914), *Paralonchothrix ponderosus* Piñero et al. (2021) (= *Eumysops ponderosus* Rovereto, 1914; = *Proechimys ponderosus* Bond, 1977), and the genus *Ullumys* Olivares et al. (2017), represented by *U. intermedius*, from the Valle de Santa María (Catamarca Province; Rovereto, 1914), and *U. pattoni*, from Lomas de las Tapias locality (San Juan Province; Olivares et al. (2017). With the exception of *U. pattoni*, whose holotype (the only known specimen) comes from a level below a tuff dated at 7.0 Ma, and *P. ponderosus*, recently recorded in this same locality, the remaining late Miocene echimyids of NWA lack stratigraphic provenance. Consequently, the new specimen identified as cf. *Thrichomys* sp., with an estimated age at 6.5 Ma, increases the late Miocene diversity of extinct echimyids of Argentina in a temporally controlled setting. In addition, the echimyid cf. *Thrichomys* sp. reported in the PPF provides the minimum age of divergence for the clade containing *Ullumys* and *Thrichomys*. The late Miocene echimyid *"Eumysops" parodii* (Kraglievich, 1945) is known only by the holotype, which comes from the "conglomerado osífero" (= "Mesopotamiense", Ituzaingó Formation, Entre Ríos Province). In the absence of geochronological dating, the age of the Mesopotamian fauna was estimated evaluating the faunal relationship between the "Mesopotamiense" and other Neogene units. On this basis, it was proposed that the Mesopotamian fauna would have been deposited during the end of the Tortonian or early Messinian (Schmidt et al., 2020). cf. "*Eumysops" parodii* from the PPF, with an estimated age at 7.43 Ma, provides the first geochronological dating of this species, indicating a late Tortonian age. So, the record of this echimyid in PPF is biochronologically significant for the correlation with the bearing level of the holotype of cf. "*Eumysops" parodii* reinforcing a late Tortonian age for the Mesopotamian fauna.

The abrocomid *Protobrocoma paranensis* Kraglievich, 1927 is the first record of this species described from the PPF. Until now, *P. paranensis* was known only for the "Mesopotamiense" (Nasif et al., 2013); therefore, the record of this species in the PPF extends its geographic distribution. The new specimen of *P. paranensis* (dated at 6.56 Ma) also represents the first record of this species associated to geochronological data.

The dinomyid cf. *Ferigolomys* sp. from the PPF constitutes the first record of this family in the unit. The late Miocene dinomyids of Argentina were widely distributed, with numerous genera and species from La Pampa, Entre Ríos, Catamarca, and Buenos Aires provinces (Candela and Nasif, 2006; Nasif et al., 2013, 2019; Esteban et al., 2014; Montalvo et al., 2019). In spite of their taxonomic diversity and wide geographic distribution, many of the late Miocene dinomyids of Argentina lack stratigraphical and geochronological data. The dinomyids recovered from the Solimões Formation (Brazilian Amazonia) also show a high taxonomic diversity (Kerber et al., 2016a, 2018). The species *Ferigolomys pacarana* was recorded in the upper levels (horizont B) of the Solimões Formation, at Niterói locality (Kerber et al., 2018). These levels were dated by U–Pb methods that revelead an age of 8.5 ± 0.5 Ma (Bissaro-Júnior et al., 2019).

Therefore, cf. *Ferigolomys* sp. from the PPF, with an absolute age at 9.3 Ma, is one of the few late Miocene dinomyids of Argentina associated to geochronological data and, if its generic assignment was confirmed, it would indicate that the temporal range of this dinomyid is restricted to the Tortonian age.

The Erethizontidae sp. nov. cf. *Microsteiromys* sp. is the first porcupine recovered from the PPF. Late Miocene erethizontids of Argentina are represented by *Neosteiromys bombifrons* Rovereto, 1914, and *N. pattoni* Candela, 2004, both species known only by their holotypes, lacking stratigraphic information. *Paradoxomys cancrivorus*, another erethizontid, was reported at the "Mesopotamiense" (Vucetich and Candela, 2001). Consequently, the new erethizontid specimens here reported, with an estimated age at 8.86 Ma, represent the only late Miocene erethizontid with known stratigraphic provenance and geochronological data associated with its bearing unit. The new Erethizontidae sp. nov. cf. *Miocrosteiromys* sp. would represent the earliest and southernmost distributed record of this small Miocene erethizontid, if its generic assignment is confirmed, hitherto known from the late middle Miocene of Colombia (Walton, 1997) and Peru (Antoine et al., 2013; Marivaux et al., 2020b).

Small caviids are well represented in the late Miocene of Argentina (Madozzo-Jaén and Pérez, 2017; Madozzo-Jaén, 2019) but, unlike those here reported, most of them have scarce stratigraphic and geochronological associated information.

Among ungulates, *Paedotherium kakai*, reported in the PPF, with an estimated age of 8.8 Ma, constitutes one of the few late Miocene representatives of *Paedotherium* (Reguero et al., 2015) with precise stratigraphic provenance and geochronological data.

Recently, among vertebrates with known stratigraphic provenance, a specimen of *Caiman* cf. *latirostris* (Alligatoridae, Caimaninae) was recovered from upper levels of the PPF, situated above a tuff dated at 5.98 ± 0.32 Ma, so that the specimen should be slightly younger than 6 Ma (Bona et al., 2014).

Diverse vertebrate taxa from the PPF were reported in previous studies. Russo (1948, in Stark and Anzótegui, 2001) cited the xenarthran *Pleurolestodon avitus*, Herbst et al. (1987) the presence of fish scales, and Anzótegui and Stark (2001), the Toxodontidae cf. *Xotodon* sp., Glyptodontidae, and turtle plates assigned to the family Chelidae. More recently, Armella and Bonini (2020) identified the cingulates *Macroeuphractus morenoi*, *Chorobates villosissimus*, *Chasicotatus* sp. and cf. *Paraeuphractus* (Dasypodidae), and the notoungulate cf. *Andinotoxodon bolivarensis* (Toxodontidae).

These records indicate a high vertebrate diversity for PPF. However, neither of these taxa have been yet the subject of descriptions that support their taxonomic determinations, nor have been reported their precise stratigraphic provenances at PPF.

In this context, rodents from the PPF at Calchaquí Valley increase the knowledge of the late Miocene mammal diversity from NWA in a temporally controlled setting, and provide valuable data to correlate their bearing sediments with other fossiliferous late Miocene sites of South America. At Tonco Valley, from the lower levels of the PPF, the Dasypodidae (Cingulata) *Macrochorobates*, *Vetelia gandhi*, Euphractini gen et sp. indet. a and b, the ungulates *Protypotherium minutum*, *Typotheriopsis*, and the caviomorphs *Procardiomys*, Caviidae gen. et sp. indet. *Protabrocoma* sp. and *Lagostomus* (Zimicz et al., 2018) were reported. With respect to the chinchillids, Rasia et al. (2020) considered the record of *Prolagostomus* from Tonco Valley (Zimicz et al., 2018) as *Lagostomus* sp., because of the lacking of diagnostic features of *Prolagostomus*.

5.2. Mammals from Palo Pintado formation as paleoenvironmental proxies

5.2.1. Brachydont mammals

The new specimens of Echimyidae and Erethizontidae represent the first brachydont mammals of the PPF. Erethizontidae (porcupines or coendús), are currently represented by numerous highly arboreal species distributed from Mexico to northern Argentina and Uruguay. They inhabit Amazonian rain-forests, the mountain forests and the Atlantic Forest, but also the Bolivian and Paraguayan Chaco and the Brazilian Cerrado and Caatinga (Voss, 2015). Echimyids (spiny rats, bamboo rats, tree rats, coypus) include small to medium size taxa, currently represented by more than 20 genera and about 99 extant species, distributed throughout all Neotropical forests (Amazonian, Andean, and Atlantic forests; Emmons et al., 2015). Some echimyid species also occur in the Paraguayan and Bolivian Chaco and the Brazilian Cerrado, and Caatinga. Particularly, the echimyid *Thrichomys* includes five terrestrial species that inhabit the Chaco, Pantanal, Cerrado and Caatinga ecoregions, ranging from northeastern, central, and southeastern Brazil to Paraguay and Bolivia (Emmons et al., 2015). So, species of *Thrichomys* occur in heterogenous habitats with different degree of development of trees, shrubs, and grasses, where exist zones of transition between arboreal and open areas.

Based on their mainly tropical distribution, the brachydont dental morphology, and the arboreal habits (in the case of the neotropical porcupines), the presence of erethizontids and echimyids in PPF is compatible with forested environments under warm and mainly humid climatic conditions. This inference is in line with the occurrence of *Caiman* cf. *latirostris* recovered at Quebrada El Estanque (Bona et al., 2014), which indicates that the climatic conditions during the late Miocene at Calchaquí Valley were comparatively more warmer and humid than today. The paleoenvironmental inference based on vertebrates of the PPF is in turn strengthened with the sum of independent data provided by the sedimentological and floristic studies. Paleoflora from the PPF indicated the following paleo-communities: aquatic (e.g.

floating aquatic *Salvinia*, and the submerged and rooted wetland plants such as *Mayaca aff. M. fluviatilis* and *Cabomba aff. C. caroliniana*); marsh (e.g. *Equisetum* sp., *Acrostichum paleoaureum, Blechnum serrulatiformis*); riparian forests (e. g., *Lycopodiella* sp., and *Reboulisporites* sp. in the cespitose strata; *Nectandra saltensis*, *Ficus tressensii*, *Cedrella fissiliformis*, *Sapium haematospermoides*, the climbing lieane *Ranunculodendron anzoteguiae,* in the arboreal stratum, and *Schinus herbstii* in the shrub stratum); montane forests with arboreal species (e.g. *Podocarpidites marwickii*); and xeric communities (e.g. *Caesalpinia stuckerti*, an endemic shrub species constituting xerophytic forests in the Western Chaco; Anzótegui and Horn, 2011; Anzótegui et al., 2017). The paleoflora as a whole has been developed under a humid subtropical climate, with a relatively brief period of seasonality and scarce xeric representation (Anzótegui and Cuadrado, 1996; Anzótegui, 1998; Starck and Anzótegui, 2001; Anzótegui and Horn, 2011; Galli et al., 2011; Garralla et al., 2016). As noted above, sedimentological and mineralogical analyses indicated a river system with low and high sinuosity, and the development of wide floodplains with lagoons and marshes developed under a hot and humid climate (Stark and Anzótegui, 2001; Galli et al., 2011, 2014). During a relatively short dry season, savannas and grasslands would have also developed. In the coasts of the lakes and marshes, which intermingled with fluvial riverbeds, the gallery forests would have been stable. Environments and climatic condition without significant changes were inferred during the deposition period of the PPF (Robledo et al., in press). Recently, isotopic data performed in the AB indicated humid conditions and the predominance of C3 plants (Bywater Reyes et al., 2010; Rohrmann et al., 2016; see below).

Therefore, the occurrence of echimyids, erethizontids, and *Caiman* cf. *latirostris* during the late Miocene at Calchaquí Valley supports the paleoenvironmental and climatic inferences provided by independent and multidisciplinary approaches. The record of the echimyid cf. *Thrichomys* sp. suggests that the PPF could have been deposited in an overall setting similar to the present-day Chaco.

5.2.2. Hypsodont mammals

Euhypsodonty indicates high rates of tooth wear and is one of the most intensively studied dental traits of mammals from a paleoecological point of view (e.g. Janis, 1988; Damuth and Janis, 2011; Madden, 2015). The increasing number of hypsodont mammalian species registered during the late Miocene and Pliocene of Argentina was traditionally related to the development of widespread plains and to the expansion of grasslands in arid and open areas; a period commonly known as *Edad de las Planicies Australes"* ("Age of the Austral Plains"; Pascual and Bondesio, 1982; Ortiz Jaureguizar and Cladera, 2006). However, it is now widely recognized that hypsodonty is not mainly or exclusively related with the ingestion of grasses but also with the consumption of grit or abrasive components in the diet (Janis, 1988; Williams and Kay, 2001; Mendoza and Palmqvist, 2008; Damuth and Janis, 2011; Domingo et al., 2020). Currently, the close relationship between the advent and expansion of grasslands and the rise and evolution of grazers continues under debate (e.g. Strömberg et al., 2013; Bellosi et al., 2021).

Despite the relatively important diversity of the late Miocene hypsodont mammals of Argentina (except for some recent contributions), they remain poorly understood from a paleobiological point of view (Candela et al., 2013; Reguero et al., 2015; Ercoli et al., 2021; Scarano et al., 2021; Solórzano and Núñez-Flores, 2021), and its paleoenvironmental significance was not analyzed by contrasting it with independent (geochemical, paleofloristic, sedimentological) data in a stratigraphically controlled context. Following, we assess the paleoenvironmental significance of each of the hypsodont mammalian taxa from the PPF (both those described here and those previously reported).

Abrocomids (chinchilla rats), known since the late Miocene, are euhypsodont caviomorphs, today represented by the genera *Abrocoma* and *Cuscomys*. *Abrocoma* includes eight living species: *Abrocoma bennettii,* which is restricted to the Andean slopes of north-central Chile, *Abrocoma boliviensis*, from the east-central Andes of Bolivia, and six species of the *cinerea* complex, which are distributed along the Andes from southern Peru to central Argentina (Patton and Emmons, 2015). The species of the *cinerea* complex are specialized for life in rocky cliffs (Patton and Emmons, 2015). *Cuscomys*, the largest living abrocomid, is instead the only adapted taxon for an arboreal lifestyle (Emmons, 1999). *Cuscomys ashaninka* Emmons, 1999 was reported in the montane, wet, mossy cloud forest of the Cordillera de Vilcabamba (Peru), whereas *C. oblativus* occurs in the mountain forests of Machu Picchu (Peru; Ochoa et al., 2020). Because living abrocomids inhabit at different habitats and have dissimilar substrate preferences, the presence of abrocomids in the fossil record cannot be directly associated with a particular type of environment. As noted above, the molar morphology of *Protabrocoma paranensis* shares an occlusal pattern more similar to that of *Cuscomys* (both taxa having mesiodistally wide lophids with rounded border) than that of *Abrocoma* species (Emmons, 1999; Verzi and Quintana, 2005). These traits suggest that *P. paranensis* had a dietary habit more similar to that of *Cuscomys*, which includes fruit as part of the diet (Emmons, 1999), than that of *Abrocoma*. It is also expected that *P. paranensis* would have occupied mountain forests (perhaps like those conformed by *Podocarpidites marwickii*), more similar to the high-altitude forests inhabited by *Cuscomys* than to the arid and desert environments inhabited by *Abrocoma*. Lower molars with narrower lophids and sharp angulous borders of *Abrocoma* species can be related to the higher efficiency of the enamel ridges to cut fibrous foods, such as leaves, stems, twigs, roots or grasses (Schmidt-Kittler, 2002). This morphology could be a specialization to a type of food associated to arid and desertic conditions, like those detected with the global cooling and drying event near the Plio-Pleistocene boundary (Verzi and Quintana, 2005; Prevosti et al., 2021). Therefore, abrocomids from the late Miocene of the PPF do not necessarily indicate arid or desert environments, suggesting instead the presence of a similar habitat to that of the arboreal *Cuscomys*. The adaptation to typical arid conditions would have arisen later during the evolutionary history of abrocomids.

The lagostomine *Lagostomus* (vizcacha) was recorded at lower levels of the PPF (Zimicz et al., 2018). The extant *L. maximus* inhabits lowland areas from subtropical grasslands to dry scrublands in Argentina, Bolivia and Paraguay. *Lagostomus* had a wider past distribution than at present time, extending it to western Bolivia, Patagonia, and southern Brazil (Rasia and Candela, 2019; Rasia et al., 2021), which suggests that this chinchillid inhabited more heterogeneous environments. A previous evolutionary analysis of Chinchillidae showed that the origin of euhypsodonty was before the late Miocene, at least early Miocene (Rasia et al., 2021). So, the presence of euhypsodont chinchillids in PPF cannot be undoubtedly related to arid conditions or grassland-dominated environments.

At present, the small caviids (cuises or cavies) inhabit a wide variety of habitats, including open (mesic and xeric) grasslands, dry steppes, forest edges, marsh and rocky mountainous areas (from see level to 5000 masl) (Dunnum, 2015). On this basis, small caviids of PPF suggest the presence of heterogenous habitats, probably similar to present day xerophytic forests.

Within Caviidae, the extinct Hydrochoerinae known as 'cardiomyines' were medium-sized caviomorph rodents characterized by ever-growing teeth. They were first known from the middle Miocene of Patagonia, reaching their greatest taxonomic diversity during the late Miocene–late Pliocene of Argentina (Pérez et al., 2017). "Cardiomyines" are represented in the PPF by cf. *Procardiomys* sp. (Zimicz et al., 2018). Considering that the paleoenvironments in which occurred "cardiomyines" were probably semiaquatic (Vucetich et al., 2015), the presence of these caviids in PPF could be interpreted as compatible to humid rather than to arid climatic conditions. It has been documented that the origin of euhypsodonty in the Caviidae, including the "cardiomyines", occurred earlier than the late Miocene.

The Dinomyidae (pacaranas) are medium-sized to gigantic caviomorphs, including the single living species, *Dinomys branickii*. This species inhabits forested areas of the eastern Andes of Brazil, Peru, Ecuador, Bolivia, Venezuela and Colombia, spanning the western margins of lowland Amazonian rainforest to upper montane tropical forest on the Andean slopes (Patton, 2015). The pacarana eats palm and other fruits, tender stems, and leaves (Patton, 2015). Extinct dinomyids had a rich record during the middle/late Miocene of the tropical latitudes of South America (e.g. Nasif et al., 2013; Rinderknecht et al., 2011; Kerber et al., 2016a; Kerber et al., 2018). As noted above, dinomyids from the Solimões Formation are particularly diverse. A massive wetland, similar to the current environment of the modern ecosystem of Pantanal, with rivers associated with megafan systems and lakes and marshes, the presence of open environments, and gallery forests were inferred for the uppermost levels of the Solimões Formation with wet and humid conditions (Kerber et al., 2016a). A paleobiological study of the late Miocene *Eumegamys paranensis*, a dinomyid from the "Mesopotamiense" (Entre Ríos Province), suggested that soil consumption could explain the high degree of hypsodonty in this species (Candela et al., 2013). The crown complexity of *E. paranensis* indicated that this species would have been a mixed feeder, consuming a variable diet obtained close to the ground. This feeding behaviour is compatible with the heterogeneous and forested environments inferred for the Mesopotamic area during the late Miocene (Candela et al., 2013). The dinomyid cf. *Ferigolomys* sp. has a complex molar morphology similar to that of *Ferigolomys pacarana*, *Dinomys* or *Eumegamys*, and may have had similar habits to those of these dinomyids. Therefore, the record of the dinomyid in the PPF is compatible with forested and humid environments.

The ungulates reported in the PPF are exclusively represented by euhypsodont species. They include the Hegetotheriidae *Paedotherium kakai*, and *P. minor*, the Interatheriidae *Protypotherium* sp., and the Mesotheriidae cf. *Typotheriopsis* (Reguero et al., 2015; Zimicz et al., 2018). *Paedotherium kakai* would have been a mixed feeder, consuming a variable diet obtained close to the ground (Reguero et al., 2015). A recent paleobiological analysis indicated that the configuration of the masticatory apparatus of pachyrukhines (*Paedotherium* and *Tremacyllus*) is more compatible with hard and brittle or turgid fruit food consumption than to specialized folivorous, and particularly grazing habits (Ercoli et al., 2020). *Protypotherium* was likely a generalized terrestrial ungulate, with a tendency toward cursoriality (Croft and Anderson, 2007). According to Muñoz (2017), *Protypotherium* would have been ambulatory with the ability to run but would also have had climbing ability. *Protypotherium* cf. *antiqus* was reported in the Chiquimil Formation (ca. 9 Ma, Tortonian), at Cerro Pampa (Catamarca Province), in sediments for which values of the isotope data (δ1 ^{13}C) indicate that C3 plants were the dominant (or exclusive) vegetation (Armella and Bonini, 2020). A decreasing tendency in the number of species of *Protypotherium* throughout the Miocene to the beginning of the Pliocene was recognized, probably correlated with a climatic deterioration (Scarano and Vera, 2021), and the C3/C4 biomass change at the Tortonian–Messinian boundary (Armella and Bonini, 2020).

Recently, Solórzano and Núñez-Flores (2021) revealed that in the evolution of Typotheria and Toxodontia there was an active trend of increased hypsodonty through time, suggesting that these ungulates reflect adaptive responses to the increased availability of volcanic or other terrigenous particles, at the south of South America (south of 15°S). Andean growth was regarded as a more likely driver for the long-term hypsodonty evolution in notoungulates than the development of grasses, the increased availability of open environments, or the global temperature change (Solórzano and Núñez-Flores, 2021). In this line, it is possible to hypothesize that the building of the Central Andes and its associated generation of volcaniclastic particles by the Tortonian and Messinian ages, have influenced the evolution of the hypsodonty during the late Miocene in the AB.

Studies on evolutionary trends of hypsodonty in the late Miocene caviomorphs and ungulates of subtropical latitudes at the NWA, and their probable drivers, as the Central Andes growth or the global climatic deterioration throughout the late Miocene-Pliocene, are still needed.

In summary, the hypsodont ungulates and rodents from the PPF do not indicate predominant arid and open grassland-dominated environments. Their records are compatible with forested habitats or heterogeneous environments, like today Western Chaco, developed under mainly warm and humid climatic conditions, in agreement with independent evidence.

5.3. The Angastaco Basin as "museum" and "cradle" of biodiversity during the late Miocene

Several hypotheses to explain the global increase of species richness toward the equator have been proposed (e.g. Mittelbach et al., 2007; Wiens and Donoghue, 2004; Rolland et al., 2014). Some of them highlight the higher net diversification rates as the main cause underlying the tropical species richness: the "tropics as cradle" hypothesis emphasizes the role of high speciation rates, whereas the "tropics as museum" hypothesis emphasizes the role of low tropical extinction rates (e.g. Arita and Vázquez-Domínguez, 2008; Mittelbach et al., 2007). The "tropical-niche conservatism" hypothesis proposes that current tropical richness species can be explained by the evolutionarily conserved ancestral tolerances of species to the warm environments in which most clades originated (Wiens and Donoghue, 2004). In the latter hypothesis, lineages originate in the tropics and have difficulties to disperse and adapt into temperate regions, so they were accumulating in tropical regions. According to the "out-of-the-tropics hypothesis", most species originated in the tropics then migrated to higher latitudes (Jablonski et al., 2006; Jansson et al., 2013). Under both hypotheses, the origin of diversity is tropical. The proposal of Neotropics as a "sink" of diversity, conversely, suggests high dispersal rates from other regions into the Neotropics, thus acting as a "species attractor" (Meseguer et al., 2020). The effect of these factors affecting the high tropical mammalian species richness remains debated (Mittelbach et al., 2007; Wiens and Donoghue, 2004; Rolland et al., 2014; Boucher-Lalonde et al., 2015). Here, we use the terms "cradles" (areas that present a particular set of characteristics that maximize potential for the origination of new species) and "museums" (areas of environmental stability for a higher number of surviving species from early radiations that persisted or dispersed there), following the original concepts of Stebbins, 1974 (see Vasconcelos et al., in press for a discussion of these terms).

On this basis, we propose that during the Tortonian and at least the onset of the Messinian, the AB was both a "cradle" and a "museum" of mammalian diversity. The presence in the PPF of the erethizontid Erethizontidae sp. nov. cf. *Microsteiromys* sp., with close affinities with the late middle Miocene erethizontids of Colombia and Peru (Walton, 1997; Antoine et al., 2013; Marivaux et al., 2020b), suggests that by the late Miocene the AB can be recognized as a reservoir of the oldest tropical lineages that were probably extinct in lower latitudes during the Neogene of South America. Similarly, it was proposed that the Pliocene San Gregorio assemblage (Venezuela) served as a reservoir for rodent taxa that had already became extinct in southern South America (Vucetich et al., 2010). These authors identified in the San Gregorio fauna old lineages restricted to Intertropical South America.

Sedimentological studies indicate the presence of arid conditions within the AB prior to the deposition of the PPF (Starck and Anzótegui, 2001). With the onset of the deposition of the PPF, ca. 10-9 Ma and up to 7.6 Ma, multi-proxy isotope data (δDwax, δ ^{18}Osc; Fig. 2) indicated a trend towards wetter conditions and an enhanced orographic rainfall, possibly as a result of topographic growth along the Eastern Cordillera (Rohrmann et al., 2016). The presence of a C3 forest ecosystem in the AB during this time is suggested by the δ ^{13}Cwax and ^{13}Csc values (Bywater Reyes et al., 2010; Rohrmann et al., 2016, Fig. 2), and the paleoflora (Starck and Anzótegui, 2001; Garralla et al., 2016).

Between 7.6 and 6.5 Ma a large variability in isotope values of Dwax and δ ^{18}Osc records, reflecting changes in rainfall variability, indicates the existence of a paleo South American Low-Level Jet, which would have facilitated Amazonian moisture transport into the AB (Rohrmann et al., 2016, Fig. 2). The carbon isotope records of δ ^{13}Cwax and δ ^{13}Csc of the PPF also reflect a C3 forest ecosystem (Bywater Reyes et al., 2010), coincidently with the evidence provided by the pollen and paleoflora (Starck and Anzótegui, 2001; Garralla et al., 2016; Robledo et al., in press). Consequently, until ca 6.5 Ma, the eco-hydrological conditions and landscape inferred for the PPF were suitable for the diversification of erethizontids, echimyids, and dinomyids. The habitats associated with the increased humidity, in a contiguous low-elevation open foreland (<500 m) (Starck and Anzótegui, 2001), would have allowed the faunal dispersal from lower tropical latitudes. Dispersal events, or a southern extension of Brazilian radiations, were suggested to explain the presence of the late Miocene echimyids of Argentina (Olivares et al., 2017). A forested corridor may have favored the dispersal from tropical latitudes of adapted forest-dwelling species, to subtropical latitudes, even as far as the Mesopotamian, after the withdrawal of the middle–late Miocene Paranense Sea (Candela et al., 2013).

On the other hand, the record of the extant echimyid cf. *Thrichomys* sp. in PPF allows us to propose the AB at ~7 Ma as a “cradle” of tropical biodiversity. This is in line with the Neogene origin postulated for the modern Amazon rainforests, which is supported by palynological and paleobotanical data (Jaramillo et al., 2010). Molecular data suggested that mammalian taxa that live today in the forest of Amazonia were already present by the middle Miocene (or even earlier; Galewski et al., 2005). Upham and Patterson (2015) dates the stem divergence leading to *Thrichomys* at 15.5 Ma, and Nascimento et al. (2013) dated the *Thrichomys* crown group to the late Miocene (~8.5 Ma). The phylogenetic analyses also suggest that the lineage of *Thrichomys* would have differentiated at least during the late Miocene (Candela and Rasia, 2012; Olivares et al., 2017). The new record of cf. *Thrichomys* sp. is in agreement with these proposals.

The δ^{13}C and δ^{18}O values of the upper part of the PPF suggest a shift from C3 photosynthetic pathway at the base to a greater proportion of C4 plants at the top of this formation, supporting a progressive aridification starting ca. 6 Ma, with sustained aridity by ca. 5 Ma (Bywater Reyes et al., 2010), and the onset of coarse-grained fluvial-alluvial deposition of the suprajacent San Felipe Formation. Coincidently, isotope values (δDwax, δ 18Osc, glass shards) of the AB revealed that the humid conditions ended after 6.5 Ma, as a local orographic barrier uplift farther east forcing cooler and drier conditions in the AB (Rohrmann et al., 2016, Fig. 2). A sedimentation rate increased to 0.66 mm/year in the upper third of the deposits to 4.9 Ma, close to the timing of the transition from the PPF to the San Felipe Formation (*ca*. 5.2 Ma; Galli et al., 2014).

The record of cf. *Thrichomys* sp., caviids, and abrocomids at 6.9–6.1 Ma in the AB (Fig. 2) could be linked with the starting of some degree of aridification in the AB, and the global late Miocene cooling (Bywater Reyes et al., 2010; Rohrmann et al., 2016; Herbert et al., 2016; Carrapa et al., 2019). However, more information based on a wider mammalian sample reported near of the Tortonian and Messinian boundary is needed to support this hypothesis.

Concerning biogeographic relationships, the record of cf. “*Eumysops” parodii*, cf. *Ferigolomys* sp. and *Protabrocoma paranensis* advocates close biogeographic relationships between AB and the Mesopotamian area during the late Miocene (Cozzuol, 2006; Kerber et al., 2016a). This is in agreement with what was proposed by palynologic and paleofloristic data of the PPF (Garralla et al., 2016). Relationships between PPF flora and the phytogeographic Paranaense Province were detected, as well as similarities with the current Paranaense flora of southwest Brazil (Starck and Anzótegui, 2001; Garralla et al., 2016; Anzótegui et al., 2017).

A debate exists on whether the topographically induced changes in atmospheric circulation patterns or global climatic changes (e.g. Bywater Reyes et al., 2010; Rohrmann et al., 2016) should be identified as the controlling factors for environmental changes during the late Miocene and Pliocene in the AB. In any case, global and/or local climatic and topographical changes affecting the AB must have had an important impact on the evolution of the mammals in the AB. As other mountain ranges, it is possible that the Andes in the NWA played a key role as both “cradles” and “museums” of biodiversity due to the habitat complexity created by the orogenic uplift (Hain et al., 2011; Garzione et al., 2008; Galli et al., 2014).

6. Conclusions

The first record of brachydont mammals is reported for the PPF, represented by the Echimyidae cf. “*Eumysops*” *parodii* and cf. *Thrichomys* sp., and the Erethizontidae sp. nov. cf. *Microsteiromys* sp. The first record of the dinomyid (cf. *Ferigolomys* sp.) and the abrocomid *Protabrocoma paranensis* are also reported for this unit. Dinomyids, echimyids (cf. *“E”. parodii*), and erethizontids of the PPF inhabited forested areas, developed under humid and warm climate, in agreement with the global warning inferred for the Tortonian age. Near the Tortonian–Messinian boundary, coincident with the onset of climatic changes in the AB, echimyid cf. *Thrichomys*, abrocomids and small caviids are recorded.

The Angastaco Basin is suggested as a “museum” and “cradle” of biodiversity during the late Miocene. A close biogeographic relationship among the fauna of the PPF and those of the Amazonian (Acre) and the Mesopotamian areas during the late Miocene is proposed.

Late Miocene mammals of the AB recorded over the last ~10 Ma, represented by the oldest and more recent taxa of different linages, are key to the understanding of the origin and the evolution of the modern latitudinal diversity gradient in mammals. The faunas of the partially correlated temporally Guanaco Formation (late Miocene-Pliocene; Hain et al., 2011), as well as those of the more recent San Felipe and El Piquete formations (Lerma Basin), should be scrutinized in an integrated manner in futures works in order to understand the role of the Central Andes in the evolution of the subtropical biodiversity during the Neogene.

In summary, this contribution sheds light on the temporally calibrated mammalian diversity during the late Miocene in NWA, which is intended to provide valuable evidence for future studies exploring how the vertebrates of the AB respond to climatic, topographic, and floristic changes in the southern-central Andes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Alston, E.R., 1876. On the classification of the order Glires. Proc. Zool. Soc. Lond. 67–98.
Amidon, W.H., Fisher, G.B., Burbank, D.W., Ciccioli, P.L., Alonso, R.N., Gorin, A.L., Silverhart, P.H., Kylander-Clark, A.R.C., Christoffersen, M., 2017. Mio-Pliocene aridity in the south-central Andes associated with Southern Hemisphere cold periods. Proc. Natl. Acad. Sci. Unit. States Am. 114, 6474–6479.
Antoine, P.-O., Roddaz, M., Brichaeu, S., Tejada-Lara, J., Salas-Gismondi, R., Altamirano, A.J., Louterbach, M., Lambs, L., Otto, T., Brusset, S., 2013. Middle Miocene vertebrates from the amazonian madre de Dios subandean zone, perú. J. S. Am. Earth Sci. 42, 91–102.

Anzótegui, L., 1998. Hojas de angiospermas de la Formación Palo Pintado, Mioceno Superior, Salta, Argentina. Parte I: anacardiaceae, Lauraceae y Moraceae. Ameghiniana 35, 25–32.

Anzótegui, L.M., Cuadrado, G., 1996. Palinología de la Formación Palo Pintado, mioceno superior, provincia de Salta, república Argentina. Parte I: taxones nuevos. Rev. Espanola Micropaleontol. 28, 77–92.

Anzótegui, L.M., Horn, M.Y., 2011. Megaflora de la Formación Palo Pintado (mioceno superior) Salta, Argentina. Parte II. Rev. Bras. Palaontol. 14, 239–254.

Anzótegui, L.M., Mautino, L.R., Garralla, S.S., Herbst, R., Robledo, J.M., Horn, M.Y., 2017. Paleovegetación cenozoica del Noroeste Argentino. In: Muruaga, C., Grosse, P. (Eds.), Ciencias de la Tierra y Recursos Naturales del NOA, Relatorio del Congreso Geológico Argentino, No. 20, 767–781. Asociación Geológica Argentina, Tucumán.

Arita, H.T., Vázquez-Domínguez, E., 2008. The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. Ecol. Lett. 11, 653–663. https://doi.org/10.1111/j.1461-0248.2008.01197.

Armella, M.A., Bonini, R., 2020. Biostratigraphic significance of the presence of *Protypotherium* cf. *P. antiquum* ameghino 1885 (Interatheriidae, notoungulata) in the late Miocene of northwestern Argentina. J. S. Am. Earth Sci. 102 https://doi.org/10.1016/j.jsames.2020.102676.

Arnal, M., Kramarz, A.G., Vucetich, M.G., Frailey, C., Campbell Jr., K.E., 2020. New palaeogene caviomorphs (Rodentia, Hystricognathi) from Santa rosa, Peru: Systematics, biochronology, biogeography and early evolutionary trends. Papers in Palaeontology 6, 193–216.

Bellosi, E., Genise, J.F., Zucol, A., Bond, M., Kramarz, A., Sánchez, M.V., Krause, J.M., 2021. Diverse evidence for grasslands since the Eocene in Patagonia. J. S. Am. Earth Sci. 108, 103357.

Bengtson, P., 1988. Open nomenclature. Palaeontology 31, 223–227.

Bissaro-Júnior, M.C., Kerber, L., Crowley, J., Ribeiro, A.M., Ghilardi, R.P., Guilherme, E., Negri, F.R., Hsiou, A.S., 2019. Detrital zircon U-Pb geochronology constrains the age of Brazilian Neogene deposits from Western Amazonia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 516, 64–70. https://doi.org/10.1016/j.palaeo.2018.11.032.

Boivin, M., Marivaux, L., 2020. Dental homologies and evolutionary transformations in Caviomorpha (Hystricognathi, Rodentia): new data from the Paleogene of Peruvian Amazonia. Hist. Biol. 32, 528–554.

Boivin, M., Marivaux, L., Orliac, M.J., Pujos, F., Salas-Gismondi, R., Tejada-Lara, J.V., Antoine, P.O., 2017a. Late middle Eocene caviomorph rodents from contamana, Peruvian Amazonia. Palaeontol. Electron. 20, 19A.

Boivin, M., Marivaux, L., Candela, A.M., Orliac, M.J., Pujos, F., Salas-Gismondi, R., Tejada-Lara, J.V., Antoine, P.-O., 2017b. Late Oligocene caviomorph rodents from contamana, Peruvian Amazonia. Papers in Palaeontology 3, 69–109.

Boivin, M., Marivaux, L., Pujos, F., Salas-Gismondi, R., Tejada-Lara, J.V., Varas-Malca, R. M., Antoine, P.-O., 2018. Early Oligocene caviomorph rodents from shapaja, Peruvian Amazonia. Palaeontograph. Abteilung 311, 87–156.

Bona, P., Starck, D., Galli, C., Gasparini, Z., Reguero, M., 2014. *Caiman* cf. *latirostris* (Alligatoridae, Caimaninae) in the late Miocene Palo Pintado Formation, Salta province, Argentina: paleogeographic and paleonvironmental considerations. Ameghiniana 51, 26–36.

Bonaparte, C.L.J.L., 1845. Catalogo methodico dei mammiferi Europei. Luigi di Giacomo Pirola, Milano, p. 36.

Bond, M., 1977. Revisión de los Echimyidae (Rodentia, Caviomorpha) de la Edad Huayqueriense (Plioceno medio) de las Provincias de Catamarca y Mendoza. Ameghiniana 14, 312.

Boucher-Lalonde, V., De Camargo, R.X., Fortin, J.-M., Khair, S., So, R.I., Vázquez Rivera, H., Watson, D., Zuloaga, J., Currie, D.J., 2015. The weakness of evidence supporting tropical niche conservatism as a main driver of current richness–temperature Gradients. Global Ecol. Biogeogr. 22, 344–350.

Bowdich, T.E., 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers. Smith, Paris, p. 115.

Bywater-Reyes, S., Carrapa, B., Clementz, M., Schoenbohm, L., 2010. Effect of late Cenozoic aridification on sedimentation in the Eastern Cordillera of northwest Argentina (Angastaco basin). Geology 38, 235–238.

Candela, A.M., 1999. The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity of *parasteiromys* ameghino, 1904. Palaeovertebrata 28, 53–73.

Candela, A.M., 2000. Los Erethizontidae (Rodentia, Hystricognathi) fósiles de Argentina. Sistemática e historia evolutiva y biogeográfica. Ph.D. thesis, Universidad Nacional de La Plata.

Candela, A.M., 2002. Lower deciduous tooth homologies in Erethizontidae (Rodentia, Hystricognathi): evolutionary significance. Acta Palaeontol. Pol. 47, 717–723.

Candela, A.M., 2003. A new porcupine (Rodentia, Hystricognathi, Erethizontidae) from the early and middle Miocene of Patagonia. Ameghiniana 40, 483–494.

Candela, A.M., 2004. A new giant porcupine (Rodentia, Erethizontidae) from the late Miocene of northwestern Argentina. J. Vertebr. Paleontol. 24, 732–741.

Candela, A.M., Rasia, L.L., 2012. Tooth morphology of Echimyidae (Rodentia, Caviomorpha): homology assessments, fossils, and evolution. Zool. J. Linn. Soc. 164, 451–480.

Candela, A.M., Cassini, G.H., Nasif, N.L., 2013. Fractal dimension and cheek teeth crown complexity in the giant rodent *Eumegamys paranensis*. Lethaia 46, 369–377.

Carrapa, B., Strecker, M.R., Sobel, E.R., 2006. Cenozoic orogenic growth in the Central Andes: evidence from sedimentary rock provenance and apatite fission track thermochronology in the Fiambalá Basin, southernmost Puna Plateau margin (NW Argentina). Earth Planet Sci. Lett. 247, 82–100.

Carrapa, B., Bywater-Reyes, S., DeCelles, P., Mortimer, M., Gehrels, G.E., 2012. Late Eocene-Pliocene basin evolution in the Eastern Cordillera of northwestern Argentina (25°e26°S): regional implications for Andean orogenic wedge development. Basin Res. 24, 249–268.

Carrapa, B., Huntington, K.W., Clementz, M., Quade, J., Bywater-Reyes, S., Schoenbohm, L.M., Canavan, R.R., 2014. Uplift of the Central Andes of NW Argentina associated with upper crustal shortening, revealed by multiproxy isotopic analyses. Tectonics 33, 1039–1054.

Carrapa, B., Clementz, M., Feng, R., 2019. Ecological and hydroclimate responses to strengthening of the Hadley circulation in South America during the Late Miocene cooling. Proc. Natl. Acad. Sci. Unit. States Am. 116, 9747–9752.

Carvalhaes, J.G., Cordeiro-Estrela, P., Hohl, L.S.L., Vilela, R.V., D'Andrea, P.S., Rocha-Barbosa, O., 2019. Variation in the skull morphometry of four taxonomic units of *Thrichomys* (Rodentia: Echimyidae), from different Neotropical biomes. J. Morphol. 280, 436–445.

Cerling, T.E., Wang, Y., Quade, J., 1993. Expansion of C4 Ecosystems as anIndicator of global ecological change in the late Miocene. Nature 361, 344–345.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153–158.

Contreras, V.H., Bracco, A.I., Baraldo, J.A., 2019. Estratigrafía, bioestratigrafía y cronología del Mioceno superior de la provincia de San Juan (Argentina). In: Nasif, N., Esteban, G.I., Chiesa, J., Zurita, A., Georgieff, S. (Eds.), Mioceno al Pleistoceno del Centro y Norte de Argentina, vol. 52. Opera Lilloana, pp. 177–206.

Coutand, I., Carrapa, B., Deeken, A., Schmitt, A.K., Sobel, E.R., Strecker, M.R., 2006. Propagation of orographic barriers along an active range front: insights from sandstone petrography and detrital apatite fission-track thermochronology in the intramontane Angastaco basin, NW Argentina. Basin Res. 18, 1–26.

Cozzuol, M., 2006. The Acre vertebrate fauna: diversity, geography and time. J. S. Am. Earth Sci. 21, 185–203.

Croft, D.A., Anderson, L.C., 2007. Locomotion in the extinct notoungulate *Protypotherium*. Paleontologia Electronica 11, 1A.

Damuth, J., Janis, C.M., 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. Biol. Rev. 86, 733–758.

Díaz, J.I., Malizzia, D.C., 1983. Estudio geológico y sedimentológico del Terciario Superior del valle Calchaquí (departamento de San Carlos, provincia de Salta). Boletín Sedimentológico 2, 8–28.

Domingo, L., Tomassini, R.L., Montalvo, C.I., Sanz-Pérez, D., Alberdi, M.T., 2020. The Great American Biotic Interchange revisited: a new perspective from the stable isotope record of Argentine Pampas fossil mammals. Sci. Rep. 10, 1608.

Dunnum, J.L., 2015. Family Caviidae. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America, Rodents, vol. 2. The University of Chicago Press, Chicago, pp. 690–726.

Dupont, L.M., Rommerskirchen, F., Mollenhauer, G., Schefuß, E., 2013. Miocene to Pliocene changes in South African hydrology and vegetation in relation to the expansion of C4 plants. Earth Planet Sci. Lett. 375, 408–417.

Edwards, E.J., Osborne, C.P., Strömberg, C.A., Smith, S.A., 2010. C4 Grasses Consortium. The origins of C4 grasslands: integrating evolutionary and ecosystem science. Science 328, 587–591.

Emmons, L.H., 1999. A new genus and species of abrocomid rodent from Peru (Rodentia: Abrocomidae). Am. Mus. Novit. 3259, 1–14.

Emmons, L.H., Leite, Y.L.R., Patton, J.L., 2015. Family Echimyidae. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America, Rodents, vol. 2. The University of Chicago Press, Chicago, pp. 877–1022.

Ercoli, M.D., Álvarez, A., Moyano, S.R., Youlatos, D., Candela, A.M., 2020. Tracing the paleobiology of Paedotherium and Tremacyllus (pachyrukhinae, notoungulata), the latest sciuromorph south American native ungulates – Part I: snout and masticatory apparatus. J. Mamm. Evol. https://doi.org/10.1007/s10914-020-09516-7.

Esteban, G., Nasif, N., Georgieff, S.M., 2014. Cronobioestratigrafía del Mioceno tardío-Plioceno temprano, Puerta de Corral Quemado y Villavil, provincia de Catamarca, Argentina. Acta Geol. Lilloana 26, 165–192.

Fischer de Waldheim, G., 1817. Adversaria zoologica. Mémoires de la Société Impériale des Naturalistes de Moscou 5, 357–428.

Galewski, T., Mauffrey, J.F., Leite, Y.L.R., Patton, J.L., Douzery, E.J., 2005. Ecomorphological diversification among South American spiny rats (Rodentia: Echimyidae): a phylogenetic and chronological approach. Mol. Phylogenet. Evol. 34, 601–661.

Galli, C.I., Ramirez, A., Barrientos, C., Reynolds, J., Viramonte, J.G., Idleman, B., 2008. Estudio de proveniencia de los depósitos del Grupo Payogastilla (Mioceno Medio-Superior) aflorantes en el río Calchaquí, provincia de Salta, Argentina. In: Actas 17° Congreso Geológico Argentino. Jujuy, Argentina, pp. 353–354.

Galli, C.I., Anzoátegui, L.M., Horn, M.Y., Morton, L.S., 2011. Paleoambiente y paleocomunidades de la Formación Palo Pintado (Mioceno-Plioceno), provincia de Salta, Argentina. Rev. Mex. Ciencias Geol. 28, 161–174.

Galli, C.I., Coira, B., Alonso, R., Reynolds, J., Matteini, M., Hauser, N., 2014. Evolución de la cuenca de antepaís Cenozoica del Grupo Payogastilla, en los valles Calchaquí, Tonco y Amblayo, noroeste Argentina. In: XIX Congreso Geológico Argentino. Córdoba, Argentina, pp. 22–23.

Galli, C.I., Alonso, R.N., Coira, B.L., Herrera Oviedo, P., Constantini, O.E., Barrientos Ginés, A., Villalba Ulberich, J.P., 2019. Estratigrafía y paleoambientes de los depósitos del Plioceno de la Cordillera Oriental Argentina. Opera Lilloana 52, 367–388.

Garralla, S.S., Anzótegui, L.M., Mautino, L.R., 2016. Relaciones paleoflorísticas del Mioceno-Plioceno del norte argentino. Publicación Electrónica de la Asociación Paleontológica Argentina 16.

Garzione, C.N., Hoke, G.D., Libarkin, J.C., Withers, S., MacFadden, B., Eiler, J., Ghosh, P., Mulch, A., 2008. Rise of the Andes. Science 320, 1304–1307.

Glanz, W.E., Anderson, S., 1990. Notes on Bolivian mammals. 7. A new species of Abrocoma (Rodentia) and relationships of the Abrocomidae. Am. Mus. Novit. 2991, 1–32.

Gray, J.E., 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera appertaining to each tribe. Ann. Philos. 10, 337–344.

Hain, M.P., Strecker, M.R., Bookhagen, B., Alonso, R.N., Pingel, H., Schmitt, A.K., 2011. Neogene to Quaternary broken foreland formation and sedimentation dynamics in the Andes of NW Argentina (25° S). Tectonics 30, 1–27. https://doi.org/10.1029/2010TC002703.

Herbert, T.D., Lawrence, K.T., Tzanova, A., Peterson, L.C., Caballero-Gill, R., Kelly, C.S., 2016. Late Miocene global cooling and the rise of modern ecosystems. Nat. Geosci. 9, 843–847.

Herbst, R., Anzótegui, L.M., Jalfin, L.G., 1987. Estratigrafía, paleoambiente y dos especies de Salvinia Adanson (Filicopsida), del Mioceno superior de Salta, Argentina. Facena 7, 15–42.

Hynek, S.A., Passeya, B.H., Prado, J.L., Brown, F.H., Cerling, T.E., Quadec, J., 2012. Small mammal carbon isotope ecology across the Miocene- Pliocene boundary, northwestern Argentina. Earth Planet Sci. Lett. 321–322, 177–188.

Jablonski, D., Roy, K., Valentine, J.W., 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science 314, 102–106. https://doi.org/10.1126/science.1130880.

Janis, C.M., 1988. Estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. Muséum national d'Histoire naturelle Memoir série C 53, 367–387.

Jansson, R., Rodriguez-Castaneda, G., Harding, L.E., 2013. What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. Evolution 67, 1741–1755.

Jaramillo, C., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M.J., de la Parra, F., Morón, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, F., Alvarán, M., Osorno, J., Crowley, J.L., Valencia, V., Vervoort, J., 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. Science 330, 957–961.

Jordan, T., Alonso, R., 1987. Cenozoic stratigraphy and basin tectonics of the Andes Mountains, 20°-28° south latitude. American Association of Petroleoum Geologists Bulletin 71, 49–64.

Kerber, L., Negri, F.R., Ribeiro, A.M., Vucetich, M.G., Souza-Filho, J.P., 2016a. Late Miocene potamarchine rodents from southwestern Amazonia, Brazil: with description of new taxa. Acta Palaeontol. Pol. 61, 191–203. https://doi.org/10.4202/app.00091.2014.

Kerber, L., Mayer, E.L., Ribeiro, A.M., Vucetich, M.G., 2016b. Late Quaternary caviomorph rodents (Rodentia: Hystricognathi) from the Serra da Capivara, northeastern Brazil, with description of a new taxon. Hist. Biol. 28, 439–458.

Kerber, L., Bissaro Júnior, M.C., Negri, F.R., de Souza-Filho, J.P., Guilherme, E., Hsiou, A. S., 2018. A new rodent (Caviomorpha: Dinomyidae) from the upper Miocene of southwestern Brazilian Amazonia. Hist. Biol. 30, 985–993.

Kihn, R.G., 2009. Análisis de la variabilidad de los representantes de la familia Abrocomidae (Rodentia) en la Formación Cerro Azul (Mioceno tardío, La Pampa). Ph.D. Thesis. Universidad Nacional de La Pampa.

Kleinert, K., Strecker, M.R., 2001. Climate change in response to orographic barrier uplift: paleosol and stable isotope evidence from the late Neogene Santa Maria basin, northwestern Argentina. Geol. Soc. Am. Bull. 113, 728–742.

Kraglievich, L., 1927. Nota preliminar sobre nuevos géneros y especies de roedores de la fauna Argentina. Physis 8, 591–598.

Kraglievich, L., 1940. Los roedores de la familia extinguida Neoepiblemidae. In: Torcelli, A.J., Marelli, C.A. (Eds.), Obras en Geología y Paleontología. La Plata: Talleres de Impresiones Oficiales, pp. 741–764.

Kraglievich, J.L., 1945. Un nuevo roedor del Entrerriano: *Eumysops parodii* n. sp. An. Soc. Cient. Argent. 140, 16–21.

Linnaeus, C., 1758. Systema Naturae Per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio decima, reformata. Holmiae [Stockholm]. L. Salvii.

Madozzo-Jaén, M.C., 2019. Systematic and phylogeny of *Prodolichotis prisca* (Caviidae, Dolichotinae) from the Northwest of Argentina (late Miocene–early Pliocene): advances in the knowledge of the evolutionary history of maras. Comptes Rendus Palevol 18, 33–50.

Madozzo-Jaén, M.C., Pérez, M.E., 2017. The most ancient caviine rodent (Hystricognathi, Cavioidea) comes from the late Miocene of Northwest Argentina (South America). Hist. Biol. 29, 376–383.

Madozzo-Jaén, M.C., Pérez, M.E., Montalvo, C.I., Tomassini, R.L., 2018. Systematic review of *neocavia* from the Neogene of Argentina: phylogenetic and evolutionary implications. Acta Palaeontol. Pol. 63, 241–260.

Marivaux, L., Vélez-Juarbe, J., Merzeraud, G., Pujos, F., Viñola Lopez, L.W., Boivin, M., Santos-Mercado, H., Cruz, E.J., Grajales, A., Padilla, J., Vélez-Rosado, K.I., Philippon, M., Léticée, J.-L., Münch, P., Antoine, P.O., 2020a. Early Oligocene chinchilloid caviomorphs from Puerto Rico and the initial rodent colonization of the West Indies. Proceedings of the Royal Society B 287, 20192806.

Marivaux, L., Aguirre-Díaz, W., Benites-Palomino, A., Billet, G., Boivin, M., Pujos, F., Salas-Gismondi, R., Tejada-Lara, J.V., Varas-Malca, R., Antoine, P.-O., 2020b. New record of *neosaimiri* (cebidae, platyrrhini) from the late middle Miocene of Peruvian Amazonia. J. Hum. Evol. 146, 102835.

Marshall, L.G., Patterson, B., 1981. Geology and geochronology of the mammal-bearing tertiary of the valle de Santa María and río corral quemado, Catamarca province, Argentina. Fieldiana Geol. 9, 1–80.

Matthews, S.C., 1973. Notes on open nomenclature and on synonymy lists. Palaeontology 16, 713–719.

Mendoza, M., Palmqvist, P., 2008. Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? J. Zool. 274, 134–142.

Meseguer, A., Antoine, P.-O., Fouquet, A., Delsuc, F., Condamine, F., 2020. The role of the Neotropics as a source of world tetrapod biodiversity. Global Ecol. Biogeogr. 29, 1565–1578 ff10.1111/geb.13141ff. ffhal-03006032f.

Miller Jr., G.S., Gidley, J.W., 1918. Synopsis of the supergeneric groups of rodents. J. Wash. Acad. Sci. 8, 431–448.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A. R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M., Turelli, M., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10, 315–331.

Montalvo, C.I., Tomassini, R.L., Sostillo, R., Cerdeño, E., Verzi, D.H., Visconti, G., Folguera, A., Schmidt, G.I., 2019. A Chasicoan (late Miocene) vertebrate assemblage from Cerro Azul Formation, central Argentina. Geomorphological and biochronological considerations. J. S. Am. Earth Sci. 95, 102218. https://doi.org/10.1016/j.jsames.2019.102218.

Morton, L.S., 1992. Bivalvos de agua dulce de la Formación Palo Pintado (Mioceno Tardío) del Valle Calchaquí, provincia de Salta, Argentina. Revista de la Facultad de Ciencias Exactas y Naturales y Agrimensura 9, 77–91.

Muñoz, N.A., 2017. Esqueleto apendicular de tipoterios (Notoungulata) y caviomorfos (Rodentia) de la Formación Santa Cruz (Mioceno Inferior alto). Ph.D. Thesis. Facultad de Ciencias Naturales y Museo. Universidad Nacional de La Plata.

Nasif, N.L., Abdala, F., 2016. Craniodental ontogeny of the pacarana *Dinomys branickii* peters 1873 (Rodentia, Hystricognathi, Caviomorpha, Dinomyidae). J. Mammal. 96, 1224–1244.

Nasif, N.L., Candela, A.M., Rasia, L., Madozzo-Jaen, M.C., Bonini, R., 2013. Actualizacion del conocimiento de los roedores de la Mesopotamia Argentina: aspectos sistematicos, evolutivos y paleobiogeograficos [Updating the knowledge on rodents of Mesopotamia Argentina: systematic, evolutionary and paleobiogeographic aspects]. Asociacion Paleontologica Argentina - Publicacion Especial 14, 153–169.

Nasif, N.L., Esteban, G., Georgieff, S.M., Ibañez, L., Spagnuolo, C.M., 2019. Biocronoestratigrafía y paleoambientes del Mioceno tardío de Catamarca, Tucumán y Santiago del Estero, Argentina. Opera Lilloana 52, 229–250.

Neves, A.C.A., Pessôa, L.M., 2011. Morphological distinction of species of *Thrichomys* (Rodentia: Echimyidae) through ontogeny of cranial and dental characters. Zootaxa 2804, 15–24.

Ochoa, J.A., Quispe, R., Moscoso, N.J., Cossios, D., 2020. Confirmación de la presencia de la enigmática "rata chinchilla arborícola de Machupicchu" *Cuscomys oblativus* (Abrocomidae) Confirmation on the presence of the enigmatic "Machupicchu Arboreal Chinchilla Rat" *Cuscomys oblativus* (Abrocomidae). Rev. Peru. Biol. 27, 251–254. https://doi.org/10.15381/rpb.v27i2.17882.

Olivares, A.I., Verzi, D.H., Vucetich, M.G., 2012. Definición del género *Eumysops* Ameghino, 1888 (Rodentia, Echimyidae) y revisión de las especies del Plioceno temprano de Argentina central. Ameghiniana 49, 198–216.

Olivares, A.I., Verzi, D.H., Contreras, V.H., Pessôa, L., 2017. A new Echimyidae (Rodentia, hystricomorpha) from the late Miocene of southern South America. J. Vertebr. Paleontol. 37, 1. https://doi.org/10.1080/02724634.2017.1239204.

Ortiz Jaureguizar, E., Cladera, G.A., 2006. Paleoenvironmental evolution of southern South America during the cenozoic. J. Arid Environ. 66, 498–532.

Pascual, R., Bondesio, P., 1982. Un roedor Cardiatheriinae (Hydrochoeridae) de la Edad Huayqueriense (Mioceno tardı'o) de La Pampa. Sumario de los ambientes terrestres en la Argentina durante el Mioceno. Ameghiniana 19, 19–36.

Pascual, R., Cattoi, N., Francis, J.C., Gondar, D., Ortega Hinojosa, E., Tonni, E., Pisano, J. A., Ringuelet, A.B., Zetti, J., 1966. Vertebrata, fascículo IV. In: Borrello, A.V. (Ed.), Paleontografía Bonaerense. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, La Plata, pp. 1–202.

Patton, J.L., 2015. Family Dinomyidae. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America, Rodents, vol. 2. The University of Chicago Press, Chicago, pp. 783–786.

Patton, J.L., Emmons, L.H., 2015. Family Abrocomidae. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America, vol. 2. The University of Chicago Press, Chicago, pp. 805–818. Rodents.

Pérez, M.E., 2010. A new rodent (Cavioidea, Hystricognathi) from theMiddle Miocene of Patagonia, mandibular homologies, and the origin of the crown group Cavioidea sensu stricto. J. Vertebr. Paleontol. 30, 1848–1859.

Pérez, M.E., Deschamps, C.M., Vucetich, M.G., 2017. Diversity, phylogeny and biogeography of the South American 'cardiomyine' rodents (Hystricognathi, Cavioidea) with a description of two new species. Papers in Palaeontology. https://doi.org/10.1002/spp2.1095.

Pessôa, L.M., Tavares, W.C., Neves, A.C.A., da Silva, A.L.G., 2015. Genus *Thrichomys* E.-L. Trouessart, 1880. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America, ume 2. Rodents. University of Chicago Press, Chicago, Illinois, pp. 989–999.

Piñero, P., Olivares, A., Verzu, D., Contreras, V., 2021. Paralonchothrix gen. Nov., the first record of echimyini (Rodentia, Octodontoidea) in the late Miocene of southern South America. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 112, 147–158. https://doi.org/10.1017/S175569102100027X.

Pingel, H., Mulch, A., Alonso, R.N., Cottlee, J., Hynek, S.A., Poletti, J., Rohrmann, A., Schmitt, A.K., Stockli, D.F., Strecker, M.R., 2016. Surface uplift and convective rainfall along the southern central Andes (Angastaco Basin, NW Argentina). Earth Planet Sci. Lett. 440, 33–42.

Pound, M.J., Haywood, A.M., Salzmann, U., Riding, J.B., Lunt, D.J., Hunter, S.J., 2011. A Tortonian (late Miocene, 11.61–7.25 Ma) global vegetation reconstruction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 300, 29–45.

Prevosti, F.J., Romano, C.O., Forasiepi, A.M., Hemming, S., Bonini, R., Candela, A.M., Cerdeño, E., Madozzo Jaén, M.C., Ortiz, P., Pujos, F., Rasia, L., Schmidt, G.I., Taglioretti, M., MacPhee, R.D.E., Pardiñas, U.F.J., 2021. New radiometric ^{40}Ar–^{39}Ar dates and faunistic analyses refine evolutionary dynamics of Neogene vertebrate assemblages in southern South America. Sci. Rep. 11, 9830. https://doi.org/10.1038/s41598-021-89135-1.

Quintana, C., 1996. Diversidad del roedor *Microcavia* (Caviomorpha, Caviidae) de América del Sur. Mastozool. Neotrop. 3, 63–86.

Rasia, L.L., Candela, A.M., 2019. Upper molar morphology, homologies and evolutionary patterns of chinchilloid rodents (Mammalia, Caviomorpha). J. Anat. 234, 50–65.

Rasia, L.L., Bonini, R.A., Candela, A.M., 2020. Nuevos registros de *Lagostomus* Brookes (Rodentia, Chinchillidae) en el Mioceno tardío de Argentina y su importancia bioestratigráfica. Andean Geol. 47, 430–445.

Rasia, L.L., Candela, A.M., Cañón, C., 2021. Comprehensive total evidence phylogeny of chinchillids (Rodentia, Caviomorpha): cheek teeth anatomy and evolution. J. Anat. 239, 405–423. https://doi.org/10.1111/joa.13430.

Reguero, M.A., Candela, A.M., Galli, C.I., Bonini, R., Voglino, D., 2015. A new hypsodont notoungulate (Hegetotheriidae, Pachyrukhinae) from the late Miocene of the eastern Cordillera, Salta province, northwest of Argentina. Andean Geol. 42, 56–70.

Rinderknecht, A., Bostelmann, E., Ubilla, M., 2011. New genus of giant Dinomyidae (Rodentia: Hystricognathi: Caviomorpha) from the late Miocene of Uruguay. J. Mammal. 92, 169–178.

Rinderknecht, A., Bostelmann, E., Ubilla, M., 2018. Making a giant rodent: cranial anatomy and ontogenetic development in the genus *Isostylomys* (Mammalia: Hystricognathi: Dinmyidae). J. Syst. Palaeontol. 16, 245–261. https://doi.org/10.1080/14772019.2017.1285360.

Robledo, J.M., Contreras, A.C, Baez J., Galli, C.I. In press. First Miocene megafossil of arrowhead, alismataceous plant *Sagittaria*, from South America. Acta Paleontologica Polonica.

Robledo, J.M., Horn, M.Y., Galli, C.I., Anzótegui, L.M., 2020. InferenciasPaleoclimáticas para el Mioceno tardío en la cuenca de Angastaco basadas en el análisis fisionómico foliar: formación Palo Pintado, Salta, Argentina. Andean Geol. 47, 418–429.

Rodríguez-Brizuela, R., Tauber, A., 2006. Estratigrafía y mamíferos fósiles de la Formación Toro Negro (Neógeno), Departamento Vinchina, noroeste de la provincia de La Rioja, Argentina. Ameghiniana 43, 257–272.

Rohrmann, A., Sachse, D., Mulch, A., Pingel, H., Tofelde, S., Alonso, R.N., Strecker, M.R., 2016. Miocene orographic uplift forces rapid hydrological change in the southern central Andes. Sci. Rep. 6, 35678. https://doi.org/10.1038/srep35678.

Rolland, J., Condamine, F.L., Jiguet, F., Morlon, H., 2014. Faster speciation and reduced extinction 590 in the tropics contribute to the mammalian latitudinal diversity gradient. PLoS Biol. 12, 591 e1001775.

Rovereto, C., 1914. Los Estratos Araucanos Y sus Fósiles, vol. 25. Anales del Museo Nacional de Historia Natural de Buenos Aires, pp. 1–247.

Rusconi, C., 1935. Tres nuevas especies de mamíferos del Puelchense de Villa Ballester. Bol. Paleontol. B. Aires 5, 1–4.

Scarano, A.C., Vera, B., Reguero, M., 2021. Evolutionary trends of Protypotherium (Interatheriidae, notoungulata) lineage throughout the Miocene of south America. J. Mamm. Evol. https://doi.org/10.1007/s10914-020-09534-5.

Schmidt, G.I., Diederle, J.M., Góis, F., Vallone, E.R., Tarquini, J., Fernández Osuna, M.A., Gottardi, M.G., Brandoni, D., 2020. New vertebrates from the late Miocene of Entre Ríos province, Argentina: diversity, age, and paleoenvironment. J. S. Am. Earth Sci. 101, 102618.

Schmidt-Kittler, N., 2002. Feeding specializations in rodents. Senckenberg. Lethaea 82, 141–152.

Seoane, F.D., Cerdeño, E., 2019. Systematic revision of *hegetotherium* and *Pachyrukhos* (Hegetotheriidae, notoungulata) and a new phylogenetic analysis of Hegetotheriidae. J. Syst. Palaeontol. https://doi.org/10.1080/14772019.2018.1545146.

Solórzano, A., Núñez-Flores, M., 2021. Evolutionary trends of body size and hypsodonty in notoungulates and their probable drivers. Palaeogeogr. Palaeoclimatol. Palaeoecol. 568 https://doi.org/10.1016/j.palaeo.2021.110306.

Starck, D., Anzótegui, L., 2001. The late Miocene climatic change-persistence of a climatic signal through the orogenic stratigraphic record in northwestern of Argentina. J. S. Am. Earth Sci. 14, 763–774.

Starck, D., Vergani, G., 1996. Desarrollo tecto-sedimentario del Cenozoico en el sur de la Provincia de Salta-Argentina. In: Actas XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos, pp. 433–452. Buenos Aires, Argentina.

Stebbins, G.L., 1974. Flowering Plants. Evolution above the Species Level. The Belknap Press of Harvard University Press, Cambridge, MA, USA, p. 633.

Strömberg, C.A., Dunn, R.E., Madden, R.H., Kohn, M.J., Carlini, A.A., 2013. Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. Nat. Commun. 4, 1–8.

Tullberg, T., 1899. Ueber das System der Nagethiere: eine phylogenetische Studie. Nova Acta Regiae Societatis Scientiarium Upsaliensis 3, 1–514.

Vasconcelos, T., O'Meara, B. C., Beaulieu, J. M. In press). Retiring "cradles" and "museums" of biodiversity. Am. Nat.

Verzi, D.H., Quintana, C.A., 2005. The caviomorph rodents from the San Andrés Formation, east-central Argentina, and global Late Pliocene climatic change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 219, 303–320.

Villarroel, A.C., Marshall, L.G., 1989. A new fossil land mammal locality of Late Miocene (Huayquerian) Age from Muyu Huasi, southcentral Bolivia. Bol. Serv. Geol. Boliv. 4, 27–40 (ser. A).

Voss, R., 2015. Family Erethizontidae. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America, vol. 2. Rodents. The University of Chicago Press, Chicago, pp. 786–805.

Vucetich, M.G., Candela, A.M., 2001. *Paradoxomys cancrivorus* ameghino, 1885 (Rodentia, Hystricognathi, Erethizontidae): the first porcupine from the "mesopotamiense" (late Miocene). Ameghiniana 38, 147–150.

Vucetich, M.G., Carlini, A.A., Aguilera, O., Sánchez-Villagra, M.R., 2010. The tropics as reservoir of otherwise extinct mammals: the case of rodents from a new Pliocene faunal assemblage from northern Venezuela. J. Mamm. Evol. 17, 265–273.

Vucetich, M.G., Deschamps, C.M., Pérez, M.E., 2015. The First Capybaras (Rodentia, Caviidae, Hydrochoerinae) Involved in the Great American Biotic Interchange. Ameghiniana 52, 324–333.

Walton, A.H., 1997. Rodents. In: Kay, R.F., Madden, R.H., Cifelli, R.L., Flynn, J.J. (Eds.), Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, pp. 392–409.

Waterhouse, G.R., 1839. Mammalia; pp. vii–ix, 49–97. In: Darwin, C. (Ed.), The Zoology of the Voyage of the H.M.S. Beagle under the Command of Captain Fitz Roy, R. N., during the Years 1832–1836, Fascicle 10. Smith, Elder and Co., London.

Wiens, J.J., Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19, 639–644.

Williams, H.S.H., Kay, R., 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. J. Mamm. Evol. 8, 207–229.

Wood, A.E., 1955. A revised classification of the rodents. J. Mammal. 36, 165–187.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.

Zimicz, N., Payrola, P., del Papa, C., 2018. New, late Miocene mammalian assemblage from the Palo Pintado Formation (northwestern Argentina). J. S. Am. Earth Sci. 81, 31–44.