

Article

Paralonchothrix gen. nov., the first record of Echimyini (Rodentia, Octodontoidea) in the late Miocene of Southern South AmericaPedro PIÑERO^{1*} , A. Itatí OLIVARES¹ , Diego H. VERZI¹  and Victor H. CONTRERAS²¹ CONICET, Sección Mastozoología, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 1900 La Plata, Argentina.² Gabinete de Estratigrafía, Instituto de Geología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Ignacio de la Roza y Meglioli S/N°, 5400 Rivadavia, San Juan, Argentina.*Corresponding author. Email: ppinero@fcnym.unlp.edu.ar

ABSTRACT: Echimyidae is the most widely diversified family among hystricognath rodents, both in the number of species and variety of lifestyles. In the Patagonian Subregion of southern South America, extinct echimyids related to living arboreal species (Echimyini) are recorded up to the middle Miocene, whereas all the known southern fossils since the late Miocene are linked to terrestrial and fossorial lineages currently inhabiting the Chacoan open biome in eastern South America. In this work, we describe a new genus of echimyid rodent, *Paralonchothrix* gen. nov., from the late Miocene of northwestern Argentina and western Brazil. Its single recognised species, *Paralonchothrix ponderosus* comb. nov., is represented by two hemimandibles. One of them comes from a level of Loma de Las Tapias Formation, underlying a tuff dated at 7.0 ± 0.9 Ma (Huayquerian age, late Miocene); the other specimen comes from the ‘Araucanense’ of Valle de Santa María (type locality, Huayquerian age, late Miocene). A phylogenetic analysis linked *Paralonchothrix* to *Lonchothrix*, both being the sister group to *Mesomys*. Thereby, for the first time, an echimyid linked to living Amazonian arboreal clades is recognised for the late Miocene of southern South America. *Paralonchothrix* gen. nov. thus represents an exceptional record that raises the need to review the postulated evolutionary pattern for echimyids recorded at high latitudes since the late Miocene. The new genus provides a minimum age (*ca.* 7 Ma) in the fossil record for the divergence between *Mesomys* and *Lonchothrix*. The palaeoenvironmental conditions inferred for the late Miocene in western and northwestern Argentina suggest savanna-type environments, with areas with more closed woodlands in peri-Andean valleys. The record of *Paralonchothrix* gen. nov. supports the hypothesis that this area would have maintained connections with tropical biomes of northern South America during the late Miocene.



KEY WORDS: Argentina, Echimyidae, late Neogene, *Paralonchothrix ponderosus* comb. nov., phylogeny, systematics.

Echimyidae is the most widely diversified family among hystricognath rodents, both regarding number of living taxa and variety of lifestyles (arboreal, terrestrial to fossorial, and semiaquatic; Eisenberg & Redford 1999; Galewski *et al.* 2005; Emmons *et al.* 2015; Fabre *et al.* 2016). Extant species are distributed mainly in northern South America, inhabiting Atlantic, Amazonian, and Andean forests, and occasionally the Cerrado and Caatinga (Eisenberg & Redford 1999; Emmons & Feer 1999; Patton *et al.* 2015; Fabre *et al.* 2016). The only living echimyid distributed up to high latitudes of South America is *Myocastor* (Woods *et al.* 1992; Patton 2015a). According with timetrees and fossils, the family is at least as old as the late Oligocene or even late Eocene (Wood & Patterson 1959; Patterson & Pascual 1968; Frailey & Campbell 2004; Upham & Patterson 2015; Verzi *et al.* 2016; Álvarez *et al.* 2017; Courcelle *et al.* 2019). Late Oligocene to Pliocene echimyids are known essentially from southern South America. Late Oligocene to middle Miocene representatives are related to living arboreal Echimyini

(*sensu* Fabre *et al.* 2017) from Amazonian and Atlantic forests, which agrees with the persistence of forests with tropical elements as far as southern Argentina in this period (Palazzesi & Barreda 2007). From the late Miocene on, southern fossil echimyids belong to lineages of terrestrial and fossorial Euryzygomatomyinae and Myocastorini (*sensu* Fabre *et al.* 2017) that currently inhabit open, shrubby to grassland environments, and dry forests (Reig 1986; Verzi *et al.* 1994, 1995, 2014, 2016, 2019; Vucetich 1995; Vucetich *et al.* 1997; Cartelle 1999; Hadler *et al.* 2008; Olivares *et al.* 2012b, 2017, 2020; Sostillo *et al.* 2015; Candela *et al.* 2020). This taxonomic composition of the fossil record of echimyids is concurrent with Cenozoic palaeoclimatic changes (Pascual & Ortiz Jaureguizar 1990; Janis 1993; Denton 1999; Zachos *et al.* 2001, 2008; Tripathi *et al.* 2009; Arakaki *et al.* 2011; Le Roux 2012; Palazzesi & Barreda 2012; Dunn *et al.* 2015). The expansion of open environments in southern South America since the late Miocene progressively restricted the distribution of echimyids to northern tropical habitats, starting with

the forest-adapted lineages and following with the open-adapted ones except for *Myocastor* (Pascual 1967; Verzi *et al.* 2018).

In this context, one of the fossils that remains controversial is *Eumysops ponderosus* Rovereto, 1914 from the late Miocene of northwestern Argentina. This extinct species has lower molars with occlusal morphology somewhat more complex than that of species from open environments, which is why it was more recently linked to the Amazonian genus *Proechimys* (Bond 1977; but see Reig 1989). Besides the holotype, no other material of this species had been found so far. In this work, we describe a new mandibular remain from an additional locality of the late Miocene of western Argentina and revise the taxonomic status and phylogenetic affinities of this peculiar echimyid. We erect a new genus for this species and discuss its evolutionary meaning relative to the modern radiation of the family.

1. Material and methods

The specimens studied are housed in the following institutions: Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, Argentina (MACN-Pv); Museo de La Plata, Mastozoología, La Plata, Argentina; Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil (MN UFRJ); Museum of Vertebrate Zoology, University of California, USA (MVZ); Museu de Zoologia, Universidade de São Paulo, Brazil (MZUSP); Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, Argentina (PVSJ); Museu de Zoologia, Universidade Federal da Bahia, Brazil; Universidade Federal da Paraíba, Brazil; Universidade de Brasília, Brazil. Nomenclature of craniomandibular traits follows Woods & Howland (1979) and Verzi *et al.* (2016). Dental nomenclature follows Verzi *et al.* (2016) and modifications by Verzi *et al.* (2019) (Fig. 1). The third lower molar (m3) of PVSJ 319 was damaged anterolingually when obtaining its cast (Victor H. Contreras, pers. obs. 2020), but the missing portion was preserved in the latter. Both the original specimen and the cast are stored together.

A parsimony analysis was performed based on a combined matrix of morphological characters and nine genes (supplementary material available at [https://doi.org/10.1017/](https://doi.org/10.1017/S175569102100027X)

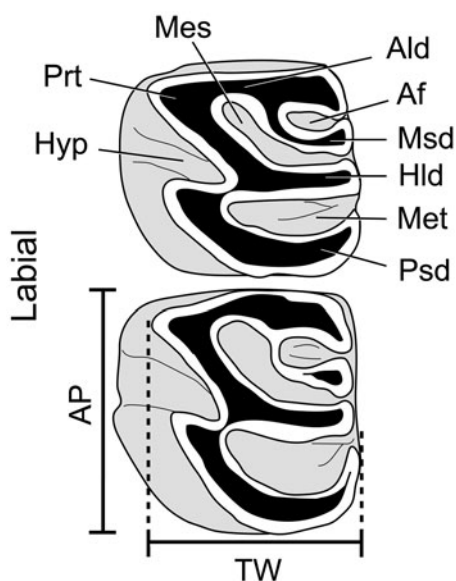


Figure 1 Nomenclature and measurements of lower molars (right m1–2, inverted, MACN-Pv 8377). Abbreviations: Af = antero-flexid/fossettoid; Ald = anterolophid; AP = antero-posterior length; TW = transverse width; Hld = hypolophid; Hyp = hypoflexid; Mes = mesoflexid/fossettoid; Met = metaflexid/fossettoid; Msd = mesolophid; Prt = protoconid area; Psd = posterolophid.

[S175569102100027X](https://doi.org/10.1017/S175569102100027X)). The morphological matrix is based on Verzi *et al.* (2016) and Olivares *et al.* (2017). The nine gene fragments were obtained from GenBank: five mitochondrial genes, ribosomal subunits 12S (975 bp), and 16S (819 bp); cytochrome *c* oxidase subunit I (COI, 1545 bp), and II (COII, 684 bp); cytochrome *b* (cytb, 1118 bp), and four nuclear genes, growth hormone receptor (GHR, 850 bp); interphotoreceptor retinoid binding protein (irbp, 1183 bp); transthyretin gene (TTH, 932 bp), and the von Willebrand factor (vWF, 1140 bp). Gene selection followed Upham & Patterson (2012) and Álvarez *et al.* (2017). Gene sequences were aligned using BioEdit 7.2.0 (Hall 1999) with the default values of gap opening and gap extension. This matrix contained a total of 9311 characters (64 morphological) and 64 taxa, including *Dasyprocta*, *Cavia*, *Dolichotis* (Caviioidea), and *Chinchilla*, *Lagidium*, and *Lagostomus* (Chinchilloidea) as outgroups. The parsimony analysis of the combined morphological and DNA matrix was carried out treating gaps as missing data in TNT 1.5 (Goloboff *et al.* 2008a, b). The analysis was based on 1000 random stepwise-addition replicates and tree bisection reconnection (TBR) branch swapping, saving 100 trees per replicate. In addition, we performed an extra round of TBR on the optimal trees to increase the possibility of finding all minimum-length topologies (Bertelli & Giannini 2005). Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (Coddington & Scharff 1994). Branch support was calculated using bootstrap absolute and bootstrap GC (for ‘Group present/Contradicted’), and with absolute and relative Bremer support indices (Bremer 1994). All characters were considered equally weighted, and multistate characters were coded as non-additive.

2. Systematic palaeontology

Order Rodentia Bowdich, 1821

Suborder Hystricomorpha Brandt, 1855

Superfamily Octodontoidea Waterhouse, 1839

Family Echimyidae Gray, 1825

Subfamily Echimyinae Gray, 1825

Tribe Echimyini Gray, 1825

Paralonchothrix gen. nov.

(Figs 2A–C, 3)

1914 *Eumysops* Rovereto: 67, fig. 32 (*partim*).

1977 *Proechimys* Bond: 312.

LSID. urn:lsid:zoobank.org:act:DE1B0202-A174-40E8-BC7D-3AA0BC80916D.

Etymology. Greek, *para*, alongside, and *Lonchothrix*, referring to it being closely related to this genus.

Type and only species. *Paralonchothrix ponderosus* comb. nov.

Distribution. Late Miocene of western and northwestern Argentina and western Brazil (Fig. 4).

Diagnosis. Medium-sized echimyid diagnosed by the following unique combination of characters: tetralophodont and subquadrangular m1–3; protoconid area acuminate, extended labially; mesolophid short, curved, and joined to the middle part of the anterolophid; antero-flexid/fossettoid transverse; metaflexid and mesoflexid quite similar in length; metaflexid more persistent than mesoflexid; hypoflexid not very penetrating, extended through less than half of the occlusal surface of the molar; mesial portion of the hypoflexid facing the mesial portion of the metaflexid (Fig. 2A, B); lower incisor thick; bottom of lower incisor posterior to m3; mandibular symphysis scarcely

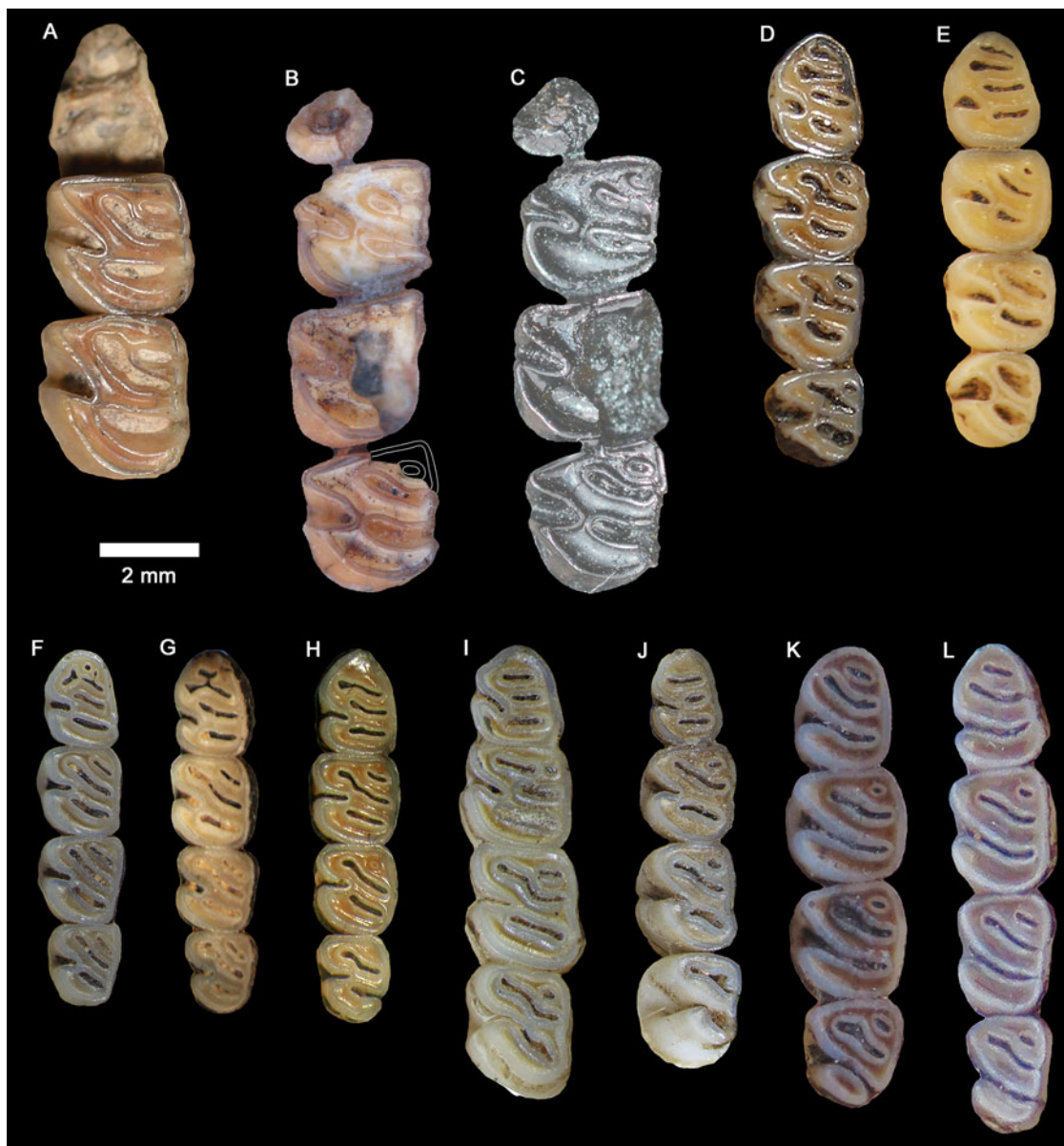


Figure 2 Occlusal morphology of left lower molars. (A) m1–2 and roots of dp4 of *Paralonchothrix ponderosus* comb. nov. MACN-Pv 8377 (holotype); (B) m1–3 and root of dp4 of *P. ponderosus* comb. nov. PVSJ 319; (C) cast of PVSJ 319; (D) dp4–m3 of *Lonchothrix emiliae* MN UFRJ 4853; (E) dp4–m3 of *L. emiliae* MZUSP 3939; (F) dp4–m3 of *Mesomys hispidus* MVZ 190653; (G) dp4–m3 of *Mesomys* sp. MZUSP S/N; (H) dp4–m3 of *M. hispidus* MN UFRJ 27956; (I) dp4–m3 of *Proechimys brevicauda* MVZ 153623; (J) dp4–m3 of *Proechimys roberti* MVZ 197578; (K) dp4–m3 of *Trinomys paratus* MZUSP 29419; (L) dp4–m3 of *T. paratus* MZUSP 20420 (inverted right molars in A, I, L).

protruding, with the chin process slightly anterior to the fourth lower deciduous premolar (dp4); notch for the tendon of the infraorbital part of the medial masseter muscle elongated and located at the level of m1; anterior border of the masseteric fossa, delimited by the lateral crest and the origin of the masseteric crest, curved; base of coronoid process at level of the m3 (Fig. 3).

2.1. Remarks

The upper teeth and maxillae of *Paralonchothrix* gen. nov. are unknown. Sant'Anna-Filho (1994) reported an isolated lower molar (AMNH 55836; plate VIII, fig. 5) of 'Eumysopinae' indet. from the late Miocene deposits of the upper Juruá River (Acre region, southwestern Amazonia) (see Cozzuol 2006; Kerber *et al.* 2017). This m1 or m2 (antero-posterior length: 2.37 mm; transverse width: 2.15 mm) is somewhat smaller than the molars studied here, but it shares the following characteristics with the latter: short and curved mesolophid joined to the middle part

of the anterolophid, elongated metaflexid with a similar length to that of the mesoflexid, and hypoflexid extended through less than half of the occlusal surface. In addition, the hypolophid is straight and transverse, and the mesoflexid is notably curved anterolabially as in MACN-Pv 8377. These morphological similarities allow us to refer this specimen to *Paralonchothrix* gen. nov.

Paralonchothrix ponderosus comb. nov. (Rovereto, 1914)

(Figs 2A–C, 3)

1914 *Eumysops ponderosus* Rovereto: 67, fig. 32.

1977 *Proechimys ponderosus* Bond: 312.

2012 '*Eumysops*' *ponderosus* Olivares *et al.*, 2012a.

Holotype. MACN-Pv 8377, right mandibular fragment with intra-alveolar portion of incisor, m1–2, and roots of the dp4 (Figs 2A, 3A–C).

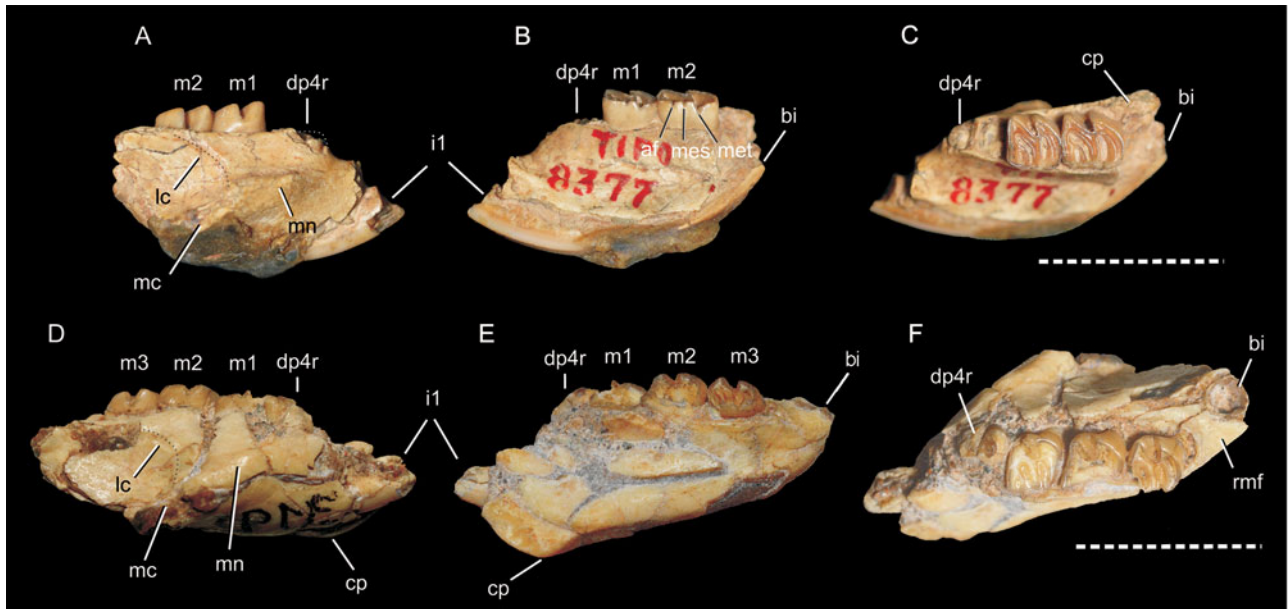


Figure 3 *Paralonchothrix ponderosus* comb. nov. (A–C) Right hemimandible of MACN-Pv 8377; (D–F) left hemimandible inverted of PVSJ 319. (A, D) lateral; (B, E) medial; (C, F) occlusal views. Abbreviations: af = anteroflexid; bi = base of the lower incisor; cp = chin process; dp4r = deciduous premolar roots; i1 = lower incisors; lc = lateral crest; mc = masseteric crest; mes = mesoflexid; met = metaflexid; mn = mandibular notch for the tendon of medial masseter muscle; rmf = retromolar fossa. Scale bar = 10 mm.

Referred material. PVSJ 319, left mandibular fragment with intra-alveolar portion of incisor, broken m1–3, and roots of the dp4 (Figs 2B, C, 3D–F).

Geographical and stratigraphical provenance. The holotype comes from Valle de Santa María, Catamarca Province, north-western Argentina; ‘Araucanense’ (*sensu* Rovereto 1914), late

Miocene. PVSJ 319 was found in Loma de Las Tapias, Ullum, San Juan Province, western Argentina; Loma de las Tapias Formation, Albardón Member, late Miocene (Serafini *et al.* 1986; Rodríguez 2004; Contreras & Baraldo 2011); the specimen of this locality comes from a level below a tuff dated at 7.0 ± 0.9 Ma (Bercowski *et al.* 1986; Fig. 4).

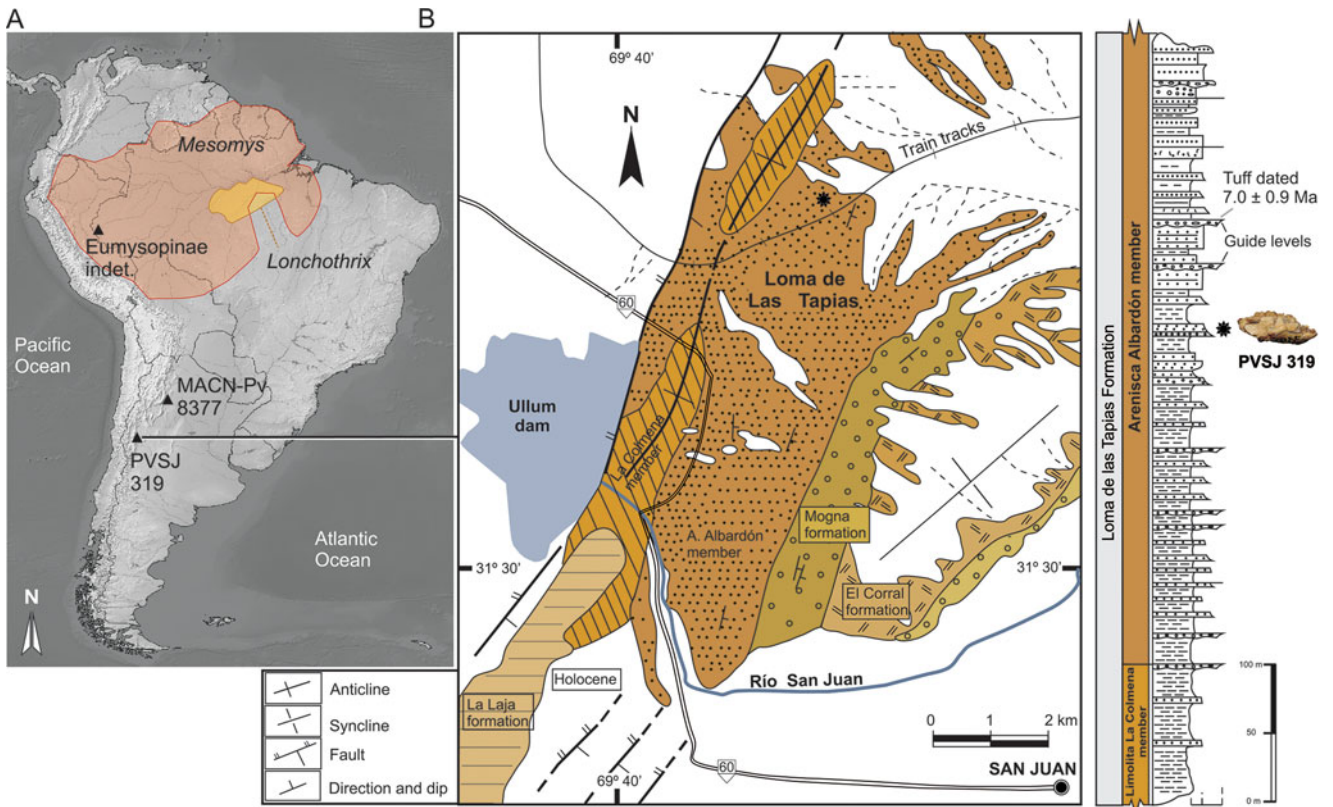


Figure 4 (A) Location map showing localities bearing specimens studied, PVSJ 319 from Loma de Las Tapias Formation, Ullum, San Juan Province; MACN-PV 8377 from ‘Araucanense’, Valle de Santa María, Catamarca Province (both in Argentina), and *Eumysopinae* indet. from upper Juruá River, Acre region, southwestern Amazonia, Brazil (Sant’Anna-Filho 1994); (B) geologic map of Loma de Las Tapias Formation and stratigraphic section located in the N area of rail tracks of this formation. Black star indicates the location of PVSJ 319. Modified from Olivares *et al.* (2017).

Emended diagnosis. Same as for the genus.

Measurements. See Table 1.

2.2. Description

Medium-sized echimyid, larger than the extinct *Ullumys*, *Pam-pamys*, *Dicolpomys*, *Theridomysops*, and *Reigechimys*, and smaller than *Paramyocastor*; it is larger than the living *Thrichomys*, *Proechimys*, *Mesomys*, *Lonchothrix*, and euryzygomatomyines, and smaller than *Isothrix*, *Kannabateomys*, *Dactylomys*, *Makalata*, and *Myocastor*. The holotype, MACN-Pv 8377, corresponds to a juvenile individual, whereas the specimen PVSJ 319 corresponds to an adult, non-senile individual.

Only the roots of the dp4 are preserved in both specimens. The lower molars are subquadrangular and tetralophodont, different from those in the most of extinct southern Echimyidae that are trilophodont (see Verzi *et al.* 1994, 1995, 2015, 2018; Vucetich 1995; Olivares *et al.* 2012a, b, 2017; Olivares & Verzi 2015; Candela *et al.* 2020). The extinct *Paramyocastor* (see Verzi *et al.* 2002) and *Tramyocastor* (see Rusconi 1936), and the extant *Myocastor coypus* also have tetralophodont molars, with the mesolophid as a complete crest. In contrast, the m1–3 of *Paralonchothrix* gen. nov. have a short mesolophid connected to the middle part of the anterolophid, being curved in shape. This latter pattern is represented in the living *Lonchothrix*, *Proechimys*, *Mesomys*, and most of the *Trinomys* species (see Fig. 2). The anteroflexid/fossettid is transverse in the new taxon, whereas it is more obliquely oriented in *Mesomys*, *Lonchothrix*, *Proechimys*, and *Trinomys*. Unlike these latter genera, the metaflexid/fossettid and mesoflexid/fossettid of *Paralonchothrix* gen. nov. are similar in length. The mesoflexid is anterolabially oriented in *Paralonchothrix* and *Lonchothrix*, and oriented towards the protoconid area in *Mesomys*. The hypoflexid extends through less than half of the occlusal surface, as in *Mesomys*, *Lonchothrix*, and the m1–2 of *Proechimys*. The mesial portion of the hypoflexid is facing the mesial portion of the metaflexid; only in the m1 of the holotype of *Paralonchothrix ponderosus*, the hypoflexid is somewhat displaced anteriorly with respect to the mesial portion of the metaflexid, as in *Mesomys*. In *Mesomys* and *Proechimys*, the hypoflexid is anterior to the mesial portion of the metaflexid. In the holotype MACN-Pv 8377, the lingual portion of the hypolophid is markedly straight and transverse to the sagittal axis of the molar. In PVSJ 319, this lingual portion is slightly oriented posteriorly and aligned with the protoconid area. The described m1–3 have the posterolophid connected labially to the hypolophid via the anterior arm of the hypoconid. This configuration is like that of *Lonchothrix*, *Mesomys*, and *Proechimys* (except for the juvenile m3), and different to that of *Trinomys* in which the metaflexid is connected to the hypoflexid. In *P. ponderosus*, the labial end of the protoconid area of m1–3 is more extended than in *Mesomys*, *Trinomys*, and *Proechimys*, similar to that in *Lonchothrix*.

Unlike octodontids, the mesoflexid closes earlier than the metaflexid. In the juvenile m1–2 of the holotype MACN-Pv 8377, the metaflexid is open when the anteroflexid and mesoflexid are almost closed (Fig. 2A). In lingual view (Fig. 3B, E),

Table 1 Dental measurements (in mm) of *Paralonchothrix ponderosus* comb. nov. Abbreviations: AP = antero-posterior length; TW = transverse width; IW = incisive width; IT = incisive thickness; Dm = depth of mandible below m1.

Specimen	AP m1	AP m2	AP m3	TW m1	TW m2	TW m3	IW	IT	DM
MACN-Pv 8377	2.74	3.47	–	2.96	2.61	–	2.00	2.35	~6.67
PVSJ 319	2.72	3.08	2.72	2.55	~2.58	2.81	2.18	2.50	6.85

the depth of the anteroflexid is only slightly lesser than that of the mesoflexid in m1–2, evidencing an almost synchronic closure. In the adult PVSJ 319, the m1 shows a little anterofossettid, a long mesofossettid, and the metaflexid nearly closed (Fig. 2B, C). The m3 shows an anterofossettid long, the mesoflexid almost closed, and the metaflexid open. The m2 of this specimen is slightly larger than the subequal m1 and m3. The posterior margin of the teeth is curved.

In labial view, the difference in height of the hypoflexid between the m1 and m2 is greater in MACN-Pv 8377 than in PVSJ 319 (Fig. 3A, D). Moreover, the anterior and posterior walls of the molars are more vertically straight in the former. These differences denote variation in hypsodonty – that is, MACN-PV 8377 has higher crowned molars than PVSJ 319, even taking into account that the former is ontogenetically younger. The same pattern is present between *Ullumys intermedius* from the ‘Araucanense’ of Catamarca Province and *Ullumys pattoni* from Loma de Las Tapias in San Juan Province (Olivares *et al.* 2017). It is possible that the two specimens assigned to *Paralonchothrix* gen. nov. also represent two morphologies resulting from a temporal pattern of change.

The mandible is represented by partially preserved hemimandibles lacking the anterior part of the diastema, coronoid process, and angular process. The posterior portion of the diastema is excavated, with a moderate ledge in the anterior alveolar border of the dp4. The symphysis is scarcely protruding, and the chin process is slightly anterior to the dp4; the ventral margin, posterior to the symphysis, is gradually ascending backwards. In *Lonchothrix* and *Mesomys*, the chin process is located at the level of dp4, and the ventral margin of the mandible is more markedly ascending; as a result, the symphysis appears more prominent in these genera. The mandibular notch (for the tendon of the infraorbital part of the medial masseter muscle) reaches the level of dp4 in the juvenile MACN-Pv 8377 and the m1 in the adult PVSJ 319. This change in the position of the masseteric notch is observed in the ontogeny of other echimyids (see Gaudioso *et al.* 2021). The anterior border of the masseteric fossa is at the level of the posterior portion of m1 or m2. It is curved as in *Lonchothrix* and different to *Mesomys* and the rest of Echimyini, Myocastorini, and Euryzygomatomyinae, in which it is more acute. The lateral crest is shorter than that of *Eumysops* and *Ullumys*, extending between the posterior portion of m1 and the middle portion of m2 in the juvenile MACN-Pv 8377, and between the middle portions of m2 and m3 in the adult PVSJ 319. The base of the coronoid process is located at the level of the m3. In PVSJ 319, the posterior portion of the lower incisor, near to the bottom of its alveolar sheath, is located posterolaterally to the m3 (Fig. 3). The base of the incisor is damaged in the holotype MACN-Pv 8377.

2.3. Remarks

Eumysops ponderosus was originally described by Rovereto (1914), who provided a plate illustrating the occlusal view of the specimen MACN-Pv 8377. This species was named *ponderosus* because of its large size, representing the largest among the new species described by this author as members of the extinct *Eumysops*. Later, Kraglievich (1965) considered this species as not belonging to *Eumysops* and transferred it to the genus *Cercomys* (= *Thrichomys*) but without any justification. Bond (1977) assigned *E. ponderosus* to the extant *Proechimys*; however, Reig (1989) regarded this assignment as not convincing. Similarly, Olivares (2009) agreed in transferring it to a different genus other than *Eumysops* and *Thrichomys*, but considered that its attribution to *Proechimys* is contingent on a revision. In this regard, Olivares (2009) was cautious and favoured the use of open nomenclature for this species, suggesting the assignment to *Proechimys? ponderosus*. Indeed, although this taxon

Table 2 Characters of extinct *Paralonchothrix*, and the extant *Lonchothrix* and *Mesomys*.

	<i>Paralonchothrix ponderosus</i> comb. nov.	<i>Lonchothrix emiliae</i>	<i>Mesomys hispidus</i>
Size	Medium	Small	Small
Relative size of m1 vs m3	Similar in size	Larger	Larger
Anteroflexid/fossetid	Transverse	Oblique	Oblique
Mesoflexid	Anterolabially oriented	Anterolabially oriented	Oriented towards the protoconid
Mesoflexid vs metaflexid	Similar in length	Longer	Longer
Mesial hypoflexid vs mesial metaflexid	Faced	Faced	Anteriorly displaced
Hypoflexid	Broad	Broad	Narrow
Metalophulid II of dp4	–	Complete	Reduced
Protoconid area	Labially extended, acuminate	Labially extended, acuminate	Shorter, more curved
Anterior border of the masseteric fossa	Curved	Curved	Acute
Symphysis	Scarcely protruding	Protruding	Protruding

presents some similarities with the living *Proechimys*, especially in the morphology of the anterolophid–mesolophid, there are some characteristics that preclude the attribution to that genus, such as the morphology of the protoconid area and configuration of the masseteric fossa. In addition, Olivares *et al.* (2017) discarded including *E. ponderosus* within the variation of the extinct *Ullumys*.

Besides *E. ponderosus*, Rovereto (1914) recognised four other new species within the variation of *Eumysops*, two for the Valle de Santa María, Catamarca Province, and two for the Huayquerías de San Carlos, Mendoza Province, all from the late Miocene of western Argentina. These species are currently not considered as belonging to *Eumysops* (Bond 1977; Vucetich 1995; Verzi *et al.* 1999; Olivares *et al.* 2012a, 2017), except for *Eumysops seridensis*, assigned to *Thrichomys* by Bond (1977; although see Reig 1989), and which is pending a formal revision.

Despite its significantly larger size, the new taxon shows morphological similarities with the living *Mesomys*, *Lonchothrix*, and some species of *Proechimys*. These taxa share the presence of mesolophid connected to the middle part of the anterolophid, hypoflexid not very penetrating, and the posterolophid labially connected to the hypolophid through the anterior arm of the hypoconid. The morphology of the protoconid is similar to that of *Lonchothrix*. However, when compared in detail, some morphological differences such as less obliquely oriented anterofossetid, presence of more transversally oriented lingual portion of the hypolophid, metaflexid and mesoflexid with similar length, m1 similar in size to the m3, and lesser protruding mandibular symphysis, justify the erection of a new genus (Table 2).

2.4. Phylogeny

The parsimony analysis of the echimyids based on morphological and molecular characters resulted in eight most parsimonious trees, 14,081 steps long (consistency index, CI = 0.382; retention index, RI = 0.442; Fig. 5). *Paralonchothrix ponderosus* comb. nov. was recovered as the sister species of *Lonchothrix emiliae*, with which it shares the anterior margin of masseteric fossa curved (character 63.1), and the protoconid area of m1–2 labially extended, acuminate, and posterolabially oriented (character 64.1). This clade had moderate support but no character conflict (i.e., high relative Bremer support values; Fig. 5). *Paralonchothrix* and *Lonchothrix* formed a clade with *Mesomys*, supported by one morphological character-state – that is, supraorbital ridges conspicuous, extending in parallel along frontals and squamosal–parietal suture (character 20.1; absent in *Paralonchothrix*). These three genera clustered with the brush-tailed rat *Isothrix*, in a clade that also had moderate support but no character conflict. This clade, together with the Miocene *Maruchito trilofodonte* and other arboreal echimyids ((*Santamartamys* + *Diplomys*) (*Olallamys* (*Kannabateomys* + *Dactylomys*))) (*Pattonomys* (*Leiuromys* + *Toromys*)) (*Makalata* (*Echimyis* +

Phyllomys))) form the Echimyini tribe in recent phylogenetic analyses (Álvarez *et al.* 2017; Fabre *et al.* 2017; Emmons & Fabre 2018; Courcelle *et al.* 2019). The monophyly of the Myocastorini was recovered in four out of the eight most parsimonious trees.

3. Discussion and conclusions

The new genus *Paralonchothrix* increases the diversity of both the extinct echimyids in southern South America (Olivares *et al.* 2017; Candela *et al.* 2020) and the clade that includes the living *Mesomys* and *Lonchothrix* (Lara *et al.* 1996; Leite & Patton 2002; Galewski *et al.* 2005; Upham & Patterson 2012, 2015; Emmons & Fabre 2018). Our systematic and phylogenetic analyses show that the closest relative of *Paralonchothrix* is the monotypic *Lonchothrix*, and both are sister to *Mesomys*. Hence, *Paralonchothrix* becomes the first extinct genus known among the spiny tree-rats (Echimyini *sensu* Fabre *et al.* 2017) recorded in the late Miocene of southern South America.

The precise stratigraphic provenance of the holotype of *Paralonchothrix ponderosus* is unknown (Rovereto 1914). The ‘Araucanense’ of Valle de Santa María represents the late Miocene–Pliocene interval (Marshall & Patterson 1981; Bossi & Muruaga 2009; Reguero & Candela 2011; Esteban *et al.* 2014). However, the specimen recovered from Loma de las Tapias, assigned to this species, comes from a deposit below a tuff dated at 7.0 ± 0.9 Ma (Bercowski *et al.* 1986; Fig. 4). The Loma de las Tapias Formation includes two successive late Miocene faunal associations assigned to the Chasicuan Stage/Age (assemblage A) and the Huayquerian Stage/Age (assemblage B). The specimen PVSJ 319 was collected from the middle levels of the Arenisca Albardón Member (Fig. 4), and it is included in the younger faunal assemblage B (Contreras & Baraldo 2011; Contreras *et al.* 2019).

Therefore, the late Miocene *Paralonchothrix* provides a minimum age for the divergence between the living *Mesomys* and *Lonchothrix*. Molecular dating indicated that the split between these last two genera took place during the Pliocene (Leite & Patton 2002) or previously, from 7.6 Ma (Upham & Patterson 2012; 2015; Upham *et al.* 2013; Fabre *et al.* 2014) to 14.05 Ma (Álvarez *et al.* 2017). Using the minimum date provided by *Paralonchothrix* (ca. 7.0 Ma), the divergence time among spiny tree-rats could be more accurately constrained.

The evolutionary history of echimyids is linked to forested areas of Central America and especially northern South America. Living representatives primarily occupy Amazonian and Atlantic forests, with only a few lineages having colonised open areas (Patton *et al.* 2015; Wilson *et al.* 2016). Echimyids recorded in the late Oligocene–middle Miocene of the current Patagonian Subregion (*sensu* Hershkovitz 1958) are related to living arboreal clades currently inhabiting Amazonian or Atlantic forests

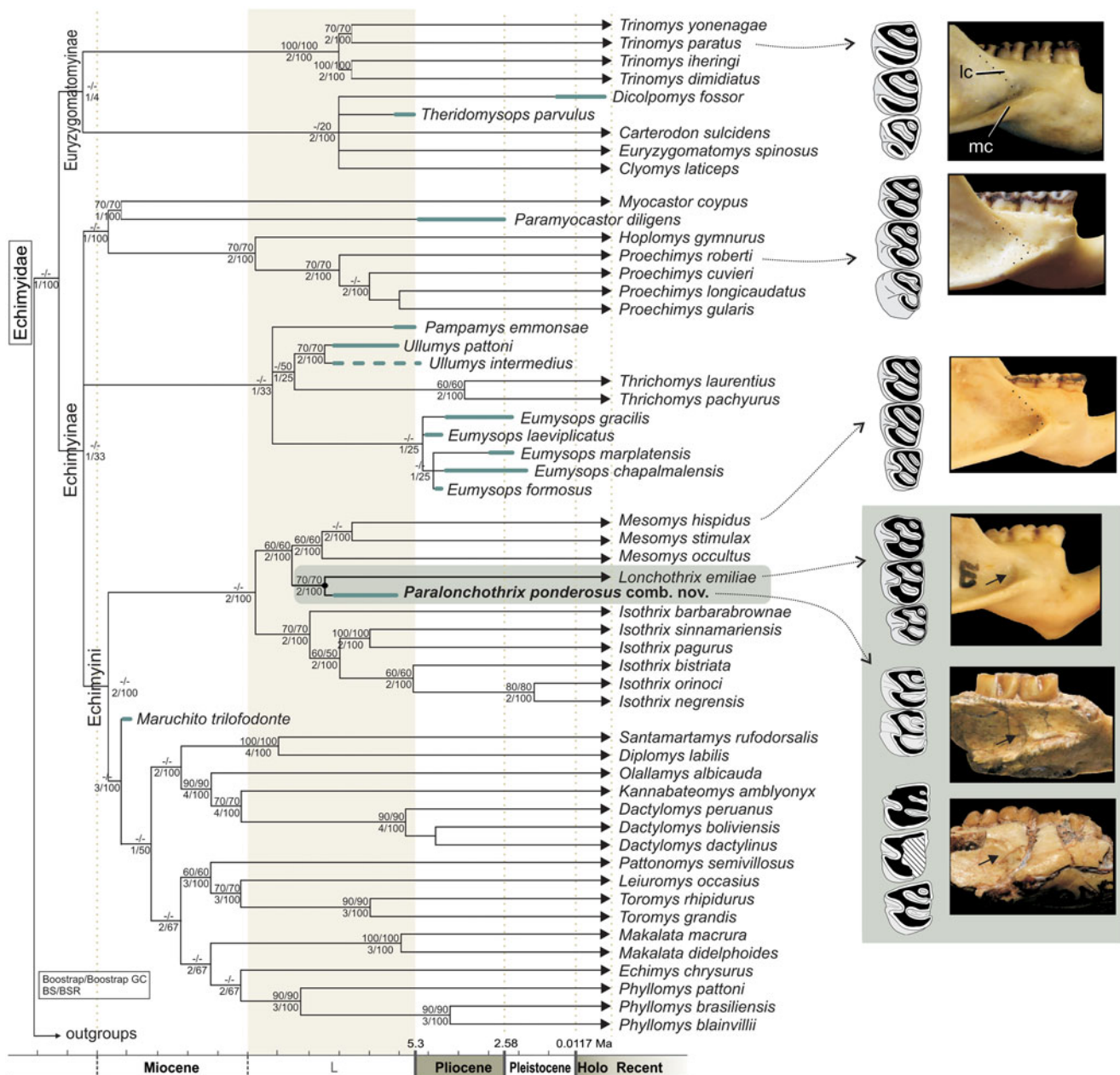


Figure 5 Strict consensus of eight most parsimonious trees of 14,080 steps resulting from parsimony analysis of morphological and molecular data. Nodal support is indicated with bootstrap absolute frequency/absolute frequency (above), and Bremer support/relative Bremer support values (below), next to each node. Biochrons of extinct Echimyidae are shown. On the right, occlusal view of molars of tetralophodont echimyids (except *Myocastor*, which has four complete lophids), and lateral view of mandibles showing the morphology of anterior portion of the masseteric fossa (black arrow). Abbreviations: Holo = Holocene; lc = lateral crest; mc = masseteric crest.

(Emmons & Vucetich 1998; Carvalho & Salles 2004; Verzi *et al.* 2014, 2015, 2016; Olivares & Verzi 2015; Olivares *et al.* 2017). From these echimyids, the genus *Maruchito* from the middle Miocene of central–southern Argentina and Chile (Vucetich *et al.* 1993; Solórzano *et al.* 2020) was so far the last record of an Echimyini in southern South America.

Global Cenozoic drying and cooling trends following the middle Miocene Climatic Optimum (Denton 1999; Zachos *et al.* 2001, 2008; Tripathi *et al.* 2009), along with Andean orogeny promoting a rain shadow in most of southern South America (see Le Roux 2012), favoured aridification spread in tandem with expansion of open habitats (Pascual & Ortiz Jaureguizar 1990; Janis 1993; Arakaki *et al.* 2011; Hynek *et al.* 2012; Palazzesi & Barrada 2012; Dunn *et al.* 2015; Amidon *et al.* 2017; Carrapa *et al.* 2019). These ecological transitions promoted changes in the taxonomic composition of the fossil echimyid fauna from the Patagonia Subregion. Thereby, southern echimyids recorded

since the late Miocene are restricted to lineages of Euryzygomatomyinae (*sensu* Emmons 2005) and Myocastorini (*sensu* Fabre *et al.* 2017) that currently occupy open, shrubby to grassland environments and dry forests in the Chacoan Dominion (*sensu* Morrone 2014) (e.g., Reig 1986; Verzi *et al.* 1994, 1995, 2004, 2015, 2016, 2018; Vucetich 1995; Cartelle 1999; Hadler *et al.* 2008; Olivares *et al.* 2012a, b, 2017; Olivares & Verzi 2015; Sostillo *et al.* 2015; Candela *et al.* 2020). That is the case of some material assigned to Eumysopinae indet. from the Andahuala Formation (Catamarca province; Nasif 1998), *Theridomysops* from the ‘Araucanense’ of Catamarca (Rovereto 1914), *Ullumys* from the ‘Araucanense’ of Catamarca and the Loma de Las Tapias Formation (San Juan Province; Olivares *et al.* 2017), and ‘*Eumysops*’ *serridens* from the Mendoza province (see Rovereto 1914), all from southern peri-Andean areas. Therefore, the Echimyini *Paralonchothrix* is an exceptional record that raises the need to review the postulated evolutionary pattern for

echimyids recorded at high latitudes since the late Miocene (Vucetich *et al.* 1997; Olivares *et al.* 2012a, b; Verzi *et al.* 2015, 2016, 2018).

The living *Lonchothrix* and *Mesomys* have arboreal modes of life. *Lonchothrix emiliae* lives in lowland mature and secondary (capoeira) rainforests in a limited area of eastern Brazilian Amazonia (Patton 2015b; Fabre *et al.* 2016). *Mesomys* has a wider geographic range, occupying lowland rainforest throughout the Amazon Basin and the Guianan region, and even extending up to an elevation of 2000 m in the upper montane forests along the eastern slope of the Andes (Patton *et al.* 2000; Voss *et al.* 2001; Orlando *et al.* 2003; Upham *et al.* 2013; Patton & Emmons 2015; Dias de Oliveira *et al.* 2019). Preserved morphology in *Paralonchothrix* does not allow reliable inference on its habits. Nevertheless, some indicative features may be mentioned. *Paralonchothrix* differs from all arboreal echimyids in its less protruding mandibular symphysis (see Olivares *et al.* 2020). In addition, the PVSJ 319 specimen preserves the posterior portion of the incisor, which is long, thick, and with its base located posterolateral to the m3. This position of the base of the incisor of *P. ponderosus* is slightly more posterior than that observed in *Mesomys* and *Lonchothrix*, and markedly more posterior than that in the rest of arboreal echimyids and the semiaquatic *Myocastor*, which have shorter incisors; it is similar to that of the terrestrial *Thrichomys* and *Proechimys*, and more anterior than that observed in fossorial echimyids (supplementary Fig. S1). A deeper insertion of the lower incisors is linked to the frequency of use of them and the development of forces at their tips (Verzi & Olivares 2006). This condition implies relatively longer incisors, with the basal generative zone far from the point in which the pressure is exerted (Landry 1957; Lessa 1990; Stein 2000; Zuri & Terkel 2001). Furthermore, *P. ponderosus* has a retromolar fossa located posterior to the dental series (Fig. 3), as in the terrestrial *Thrichomys* and fossorial genera. This fossa is lateral and shallower in arboreal echimyids and the semiaquatic *Myocastor*. The retromolar fossa is the insertion area of the orbital portion of the temporal muscle, whose function is mainly the elevation of the mandible (Woods 1972; Woods & Howland 1979).

Palaeoecological data discernible from the faunal association B at the Loma de las Tapias site, where *P. ponderosus* is recorded, suggest the dominance of open environments. *Paralonchothrix* is associated to the xenarthrans *Vasallia* sp., *Chorobates villosissimus*, Euphractinae indet., the notoungulates *Hoplophractus* sp., *Tyotheriopsis ?silveyrai* and *Paedotherium* sp. cf. *P. borrelloii*, and with the rodents *Protastrocoma* sp., *Ullumys pattoni*, *Lagostomopsis* sp. (= *Lagostomus*; see Rasia 2016; Rasia & Candela 2017), dolichotines, and caviines (Contreras & Baraldo 2011; Contreras *et al.* 2019; pers. obs. 2019). The pampatheriid *Vasallia*, registered too in the 'Araucanense' of Catamarca province (Esteban *et al.* 2014), has been interpreted as feeding on grasses (grazer), consuming mainly coarse vegetation (Vizcaíno *et al.* 1998). The dasyproctid *Chorobates* has been inferred as a dweller of temperate to warm, open environments (Carlini & Scillato-Yané 1996; Contreras *et al.* 2013), similar to those currently occupied by the euphractines *Zaedyus* and *Euphractus* (Wetzel *et al.* 2007). *Chorobates* has also been recorded in the 'Araucanense' of Catamarca province (Esteban *et al.* 2014). The glyptodontid *Hoplophractus* has been described as a bulk-feeding inhabitant of moderately open habitats (Vizcaíno *et al.* 2011). *Tyotheriopsis* (Notoungulata) is considered as an inhabitant of open, dry areas, with fossorial abilities and masticatory specialisations for the consumption of hard food items (Fernández-Monescillo *et al.* 2018; Ercoli & Armella 2021). *Paedotherium* was a small terrestrial herbivorous that resembles extant leporids, probably adapted to open and semi-arid habitats (Cerdeño & Bond 1998; Reguero *et al.* 2007; Tomassini *et al.*

2017 and references therein). The living abrocomid rodents related to *Protastrocoma* are specialised for life in rocky cliff faces in Andean regions (Patton *et al.* 2015). The chinchillid rodent *Lagostomus* currently occupies grasslands and lowland deserts (Patton *et al.* 2015). The other echimyid rodent recorded in the Loma de Las Tapias Formation, *Ullumys*, has a peculiar craniomandibular morphology, with wide and posterior orbits, reflecting specialisations to open environments (Olivares *et al.* 2017, 2020).

Sedimentological analyses of deposits from the El Jarillal Member (Chiquimil Formation) and the base of the Andalhuala Formation, dated to between 9.14 ± 0.09 Ma and 6.70 ± 0.05 Ma, at the Catamarca province, Araucanense, suggested the presence of a savanna-type environment with areas with closed tree vegetation and an annual wet season (see Pascual & Odreman Rivas 1971; Esteban *et al.* 2014).

On the other hand, the evidence of stable carbon isotope data from tooth enamel of extinct mammals in Argentina, including the Valle de Santa María, suggested an increase in C4 plant contribution to herbivore diets after ~ 8 Ma (MacFadden *et al.* 1996), as expected for temperate and tropical savanna-type environments. Expansion of C4 plants at about 8 Ma in the southern central Andes has been linked to an increase in seasonality (Latorre *et al.* 1997). Recently, other evidence from stable isotopes record from paedogenic carbonates preserved in southern central Andes suggested subtropical aridification and a shift toward expansion of C4 grasses during the late Miocene cooling (Carrapa *et al.* 2019; see also Domingo *et al.* 2020).

These available data are consistent with palaeoenvironmental inference proposed by Pascual & Odreman Rivas (1971) favouring the predominance of open environments. Nevertheless, based on the record of fossil trees and climate-sensitive mammals, these authors suggested the presence of forested environments in peri-Andean valleys of western and northwestern Argentina during the late Miocene (see also Vucetich 1986; Esteban *et al.* 2014). More recent palaeobotanical (Anzótegui *et al.* 2019), palaeozoological (Ercoli *et al.* 2021), and geological evidence (Strecker *et al.* 2007) supports this interpretation. This area, already biogeographically differentiated from the Pampean plains of central Argentina by that time, would have maintained connections with tropical biomes of northern South America (Pascual & Odreman Rivas 1971; Ercoli *et al.* 2021). Such a scenario could explain the presence of *Paralonchothrix* in western and northwestern Argentina and western Brazil, and its absence in contemporary deposits from the Pampean region where large samples of small mammals were collected; nevertheless, biases in the fossil record explaining this pattern should not be discarded.

The current outstanding diversity of Echimyidae contrasts with the paucity of its southern fossil record, which does not match geographically with the main area where this clade radiated (Reig 1986; Verzi *et al.* 2018). The Amazonian region exhibits low diversity of fossil echimyids, with scarce remains reported from the late Miocene of Acre River and Upper Juruá River in Brazil (including *Paralonchothrix*) and the Upper Purus River in Peru (Frailey 1986; Sant'Anna-Filho 1994; Campbell *et al.* 2006; Kerber *et al.* 2017). Fossil echimyids are mainly known from Patagonia Subregion (Flynn *et al.* 2008; Vucetich *et al.* 2015; Verzi *et al.* 2016; Olivares *et al.* 2017), probably as a consequence of the biased distribution of fossil deposits or bias in the fossil collecting methodology (Marshall *et al.* 1983; Hoffstetter 1986; MacFadden 2006; Kerber *et al.* 2017). The late Miocene–Holocene echimyids from southern South America have been interpreted as being part of episodes of southward drift extension of their distributions from the Brazilian Subregion (*sensu* Hershkovitz 1958), the southern record representing an impoverished sample of the extraordinary diversity reached by this family in the northern tropical and subtropical

areas (Vucetich *et al.* 1997; Verzi 2002; Verzi *et al.* 2014, 2016, 2018; Olivares *et al.* 2017). Following this interpretation, the ancestor to all tree spiny tree-rats (*Paralonchothrix*, *Lonchothrix*, and *Mesomys*) is most likely to have occupied an Amazonian range. Consequently, *Paralonchothrix* would have adapted to more open habitats after its dispersal from the Amazonian basin to the Patagonian Subregion during the late Miocene. The occurrence of *Paralonchothrix* in the late Miocene of the Amazonian Acre region supports this idea. There are indeed studies showing that lineages tend to originate in the tropics and then expand out of the tropics to encompass also temperate zones (e.g., Jablonski *et al.* 2013; Jansson *et al.* 2013). Although a S–N transition cannot be excluded, this is a most unlikely scenario. Upham *et al.* (2013) identified at least four transitions between the Andes and Amazonia within arboreal echimyids. According to these authors, reciprocal exchange between Andean and Amazonian lineages has been a continual process since the late Miocene (ca. 12 Ma). However, this biogeographical pattern does not involve latitudinal changes.

The record of *Paralonchothrix* in western and northwestern Argentina supports the hypothesis of faunistic exchanges between the tropical biomes of northern South America and the Patagonian Subregion. New studies are necessary to test whether the corridor represented by peri-Andean valleys (Pascual & Odreman Rivas 1971) and that from plains of central Argentina (Verzi *et al.* 2018) could have functioned selectively according to the ecological requirements of echimyids and other small mammals.

4. Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

5. Supplementary material

Supplementary material is available online at <https://doi.org/10.1017/S175569102100027X>

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