

Article

A Tropical Spiny Tree Rat (Rodentia, Echimyini) in the Late Quaternary of Southern South America (Argentina): Paleoenvironmental and Paleogeographic Implications

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Abstract

We report the first occurrence of an arboreal spiny rat of the tribe Echimyini in the Early Holocene of southern South America. The specimen, a lower deciduous premolar, was recovered from fluvial deposits exposed along the right bank of Doll Creek, in northeastern Argentina. Morphological comparisons indicate strong affinities with the extant Amazonian genus *Lonchothrix*, although the fossil exhibits distinct traits such as thicker enamel and a transverse, short posterior mesofossettid. The available evidence of strong climatic niche conservatism in Echimyini supports its interpretation as an indicator of the transient presence of humid, Amazonian-like forests in the region around 10,000 years ago. Sedimentological and stratigraphic evidence correlates this warming phase with an Early Holocene transgression in the Paraná Delta. The absence of aff. *Lonchothrix* in the recent fauna may be the result of a post-optimum extinction event triggered by a drier phase during the Middle Holocene. This discovery provides novel evidence for a short-lived biogeographic connection between Amazonia and the southern cone during a climatic window of expansion for tropical biotas. It also highlights the role of the fossil record of Echimyidae as a sensitive proxy for reconstructing paleoenvironmental changes in temperate South America.

Keywords: Echimyidae; Early Holocene; South America; diversity; extinctions



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1. Introduction

Echimyidae is a very diverse family of hystricognath rodents, with a variety of body plans, linked to diverse lifestyles and locomotor habits (in terms of substrate use; [1]) such as arboreal, terrestrial, fossorial, and semiaquatic [2–7]. In South America, they are currently distributed through Amazonian, coastal, and Andean forests, and, to a lesser extent, open areas such as xeric habitats in southern Brazil, and steppes and wetlands near watercourses in southern South America, i.e., Argentina and Chile [3,8]. The diversity in life modes and the types of habitats occupied are phylogenetically structured within Echimyidae [4,9],

which aligns with a certain degree of conservatism in climatic niche preferences [10]. In this context, species within the subfamily Euryzygomatomyinae have evolved terrestrial and fossorial habits, whereas, in the sister subfamily Echimyinae, the tribe Myocastorini exhibits greater adaptive diversity, including terrestrial, semiaquatic, and arboreal habits. In contrast, the tribe Echimyini demonstrates strong conservatism, with all its species developing arboreal habits in tropical forests of northern South America [3,4,11,12].

Living Echimyini, commonly known as bamboo rats, brush-tailed rats, and spiny tree rats, inhabit tropical Amazonian, Andean, and Atlantic forests in northern South America [3,12–14]. This tribe is the most taxonomically diverse among the echimyids, encompassing 14 genera and 47 living species [15]. Currently, the most southern distribution of Echimyini is represented by records of *Kannabateomys* from bamboo forests in southeastern Brazil and the northeasternmost region of Argentina [3,14,16], as well as by species of *Phyllomys* from the Paraná and Atlantic forests of southeastern Brazil [3,17], both within the Paraná Domain (sensu Morrone [18]). Molecular evidence suggests that the Echimyini clade originated in Amazonia during the Early-to-Middle Miocene [12,19,20].

Contrasting with its current diversity and distribution, there are few extinct echimyids related to the extant arboreal Echimyini, primarily distributed in southern South America. The earliest fossils clearly attributable to this tribe belong to the genus *Maruchito* (but see Verzi et al. [21] and references therein), recorded from the late Early Miocene of south-central Chile and the Middle Miocene of southern Argentina [22,23]. During the Late Miocene, Echimyini is represented by *Paralonchothrix*, known from central and north-western Argentina and western Brazil [24]. After a significant gap, Echimyini reappears in the fossil record during the Late Pleistocene–Holocene, represented by genera of the modern fauna, confined to its current distribution areas in tropical forests of northern South America ([25,26] and the literature therein). This distribution pattern of the fossil record is part of a broader trend observed throughout the overall record of Echimyidae, which exhibits temporal stages concurrent with local and global Cenozoic climatic trends. Early fossils, dating from the Early-to-Middle Miocene (or even late Oligocene, [21]), are associated with extant arboreal Echimyini, consistent with the persistence of forests containing tropical elements extending as far south as southern Argentina and Chile during this period [27]. From the late Miocene onward, southern echimyid faunas no longer include lineages related to living species from Amazonian or Atlantic forests, with the sole exception of *Paralonchothrix*. Instead, they are limited to terrestrial and fossorial lineages belonging to Euryzygomatomyinae and Myocastorini [12], which currently inhabit open, shrubby, and grassland environments, as well as dry forests of the Chacoan Domain [21,28]. In this contribution, we report the presence of an arboreal Echimyini recovered from an Early Holocene fossil deposit in southwestern Entre Ríos Province, in northeastern Argentina. We discuss the contribution of this new record to the paleogeographic pattern of Echimyidae, as well as its paleoenvironmental significance.

2. Geographical, Geological and Chronological Settings

The fossil here described was collected from a fluvial fossil-bearing level at the right bank of Doll Creek, near Molino Doll, Entre Ríos province, Argentina (32°18'19" S; 60°25'32" W; Figure 1). The fossil-bearing unit overlies in erosive unconformity on the Salto Ander Egg Formation (Late Pleistocene) (Figure 2B). The Holocene unit was recently described by Peralta et al. [29] and corresponds to a lenticular sedimentary deposit with a maximum thickness of 120 cm and a lateral extension of 300 cm (Figure 2A,B). From base to top, five levels delimited by unconformities can be identified. Level 1, a 5 cm gray clayed–silt layer with abundant fragments and complete specimens of mollusks shells, a 3 cm-thick black clayed–silt layer, and 30 cm-thick laminar light gray clay–silt layer with

mollusks shells; level 2, a layer of 10 cm-thick gray clayed-silt with abundant mollusks shells; level 3, a 30 cm-thick gray clayed-silt layer with lamination and some dispersed gastropod shells; level 4, 15 cm-thick blackish-gray clayed-silt layer with lamination and gastropod shells, lesser abundant than previous levels; level 5, 10 cm-thick blackish-gray clayed-silt layer with abundant gastropods shells and lamination, and a 10 cm-thick brownish-gray layer with some gastropod's shells, but lesser than the base. Roots are observed throughout the entire section. The specimen CICYTTP-PV-M-3-799 was found in level 2 (Figure 2B). In general, this lenticular deposit displays a fining-upward clast-bioclast (mollusk shell) pattern and demonstrates lowering water levels alternating with periods of flooding [29,30].

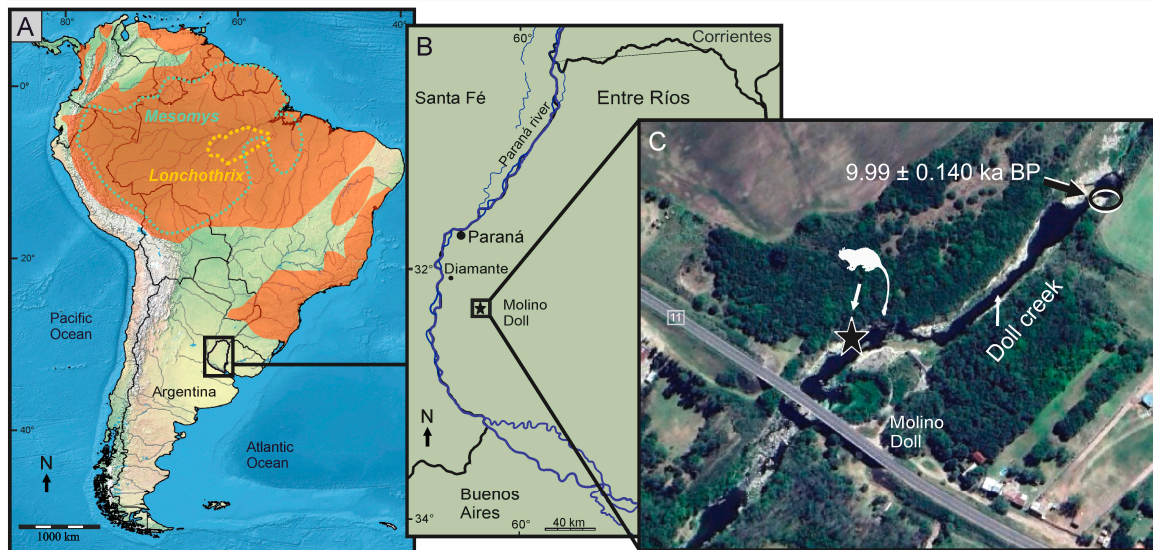


Figure 1. (A) Location map with current distribution of tribe Echimyini (orange shadow); (B,C) geographic location of Early Holocene fossil site of CICYTTP-PV-M-3-799 (black star).

Several remains of freshwater fish, anuran amphibians, squamate reptiles, birds, and mammals have also been recovered from this unit, indicating the presence of a diverse fauna [29–31].

The levels where the specimen CICYTTP-PV-M-3-799 was found lack geochronological data. However, a radiocarbon ^{14}C dating was performed in a sample of mollusk shells taken from the basal section of a lenticular deposit, also on the left bank of the Doll Creek, located 200 m east (Figure 1C). An age of 9.99 ± 0.140 ka BP (9680–9280 cal BC; 95%) was determined [32,33], corresponding to Early Holocene [34]. According to sedimentology, stratigraphy, and paleontological data, both lenticular deposits are part of the same fluvial sedimentary sequence [29,30]. The fossiliferous level where specimen CICYTTP-PV-M-3-799 was discovered is located in the lower-middle section of the lenticular deposit. Therefore, the fossil-bearing level is slightly younger than 9.99 ± 0.14 ka BP. According to Peralta [30], the eroded basal boundaries and sedimentological composition of these Holocene units provide evidence of a reactivation of the drainage system and increased water availability. These features are correlated with the last Holocene marine transgression, which occurred over 11.7–8 ka BP, as recorded in the Paraná Delta and Littoral complex [35].

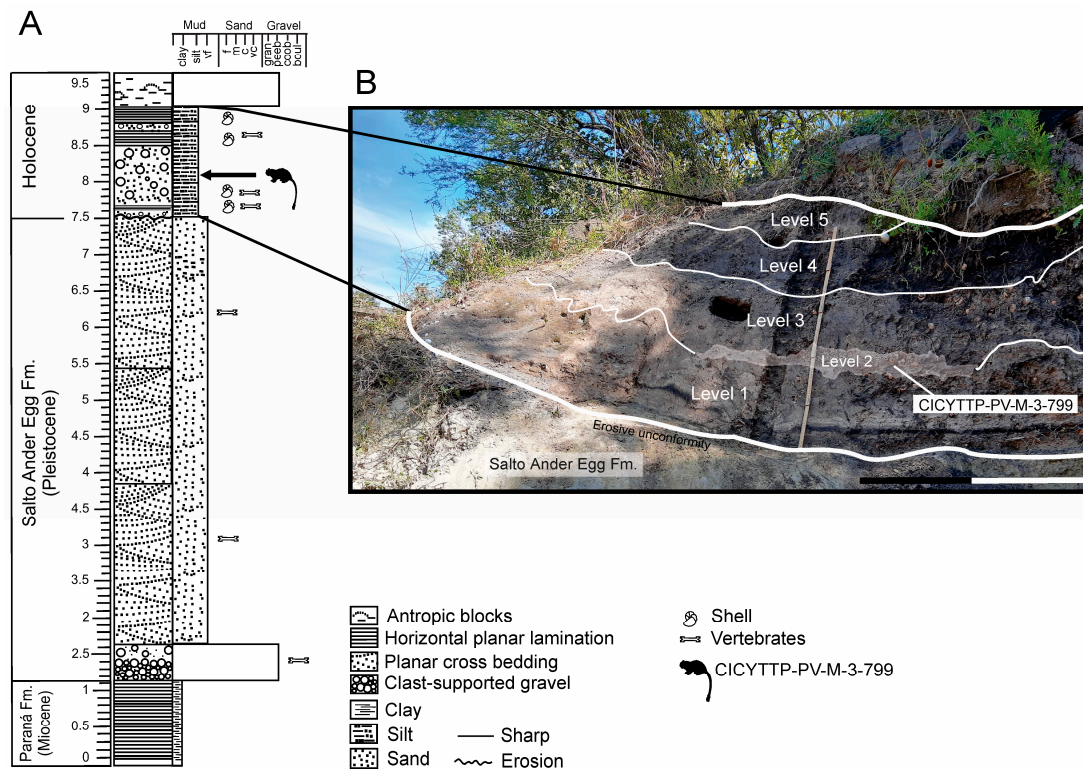


Figure 2. (A) Lithostratigraphical sequence of the right bank of Doll Creek near Molino Doll locality (Entre Ríos province), modified from Bruneto et al. [36]; (B) stratigraphic sequence of Early Holocene fossil-bearing unit (scale: 1 m).

3. Materials and Methods

The new material, CICYTTP-PV-M-3-799, corresponds to an isolated lower deciduous premolar (Dp4). The specimen examined in this study is housed in the paleontological collection (CICYTTP-PV-M) at the Centro de Investigación Científica y Transferencia Tecnológica a la Producción (CICYTTP-CONICET-Gob.E.R.-UADER), located in Diamante, Entre Ríos province, Argentina.

The material was recovered from a sediment sample collected at the site through wet screening, using two stacked sieves with mesh sizes of 4 mm and 2 mm, respectively. Subsequently, the sample was examined under magnification, and fossil remains were manually selected. Photography and measurements were taken using a LEICA DFC295 camera with LAS V3.8 software, mounted on a LEICA S8 APO stereomicroscope. CICYTTP-PV-M-3-799 was compared with pentalophodont and tetralophodont deciduous premolars from all extant and extinct genera of Echimyidae. Dental nomenclature follows Verzi et al. [37,38]; names of flexids/fossettids follow Boivin et al. [39].

Institutional Abbreviations

Paleontological collection at the Centro de Investigación Científica y de Transferencia Tecnológica a la Producción, Entre Ríos, Argentina (CICYTTP-PV-M); mammal collection and paleontological collection, Museo de La Plata, La Plata, Argentina (MLP-Mz; MLP-Pv); Museo Municipal de Ciencias Naturales ‘Carlos Darwin’, Farola Monte Hermoso collection, Buenos Aires, Argentina (MD-FM); 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); Museu de Zoologia, Universidade Federal da Paraíba, Brazil (UFPB); Universidade de Brasília, Brazil (UnB).

4. Systematic Paleontology

Order Rodentia Bowdich, 1821

Suborder Hystricomorpha Brandt, 1855

Superfamily Octodontoidea Waterhouse, 1839

Family Echimyidae Gray, 1825

Subfamily Echimyinae Gray, 1825

Tribe Echimyini Gray, 1825

Genus *Lonchothrix* Thomas, 1920

Aff. *Lonchothrix*

Figure 3A–D

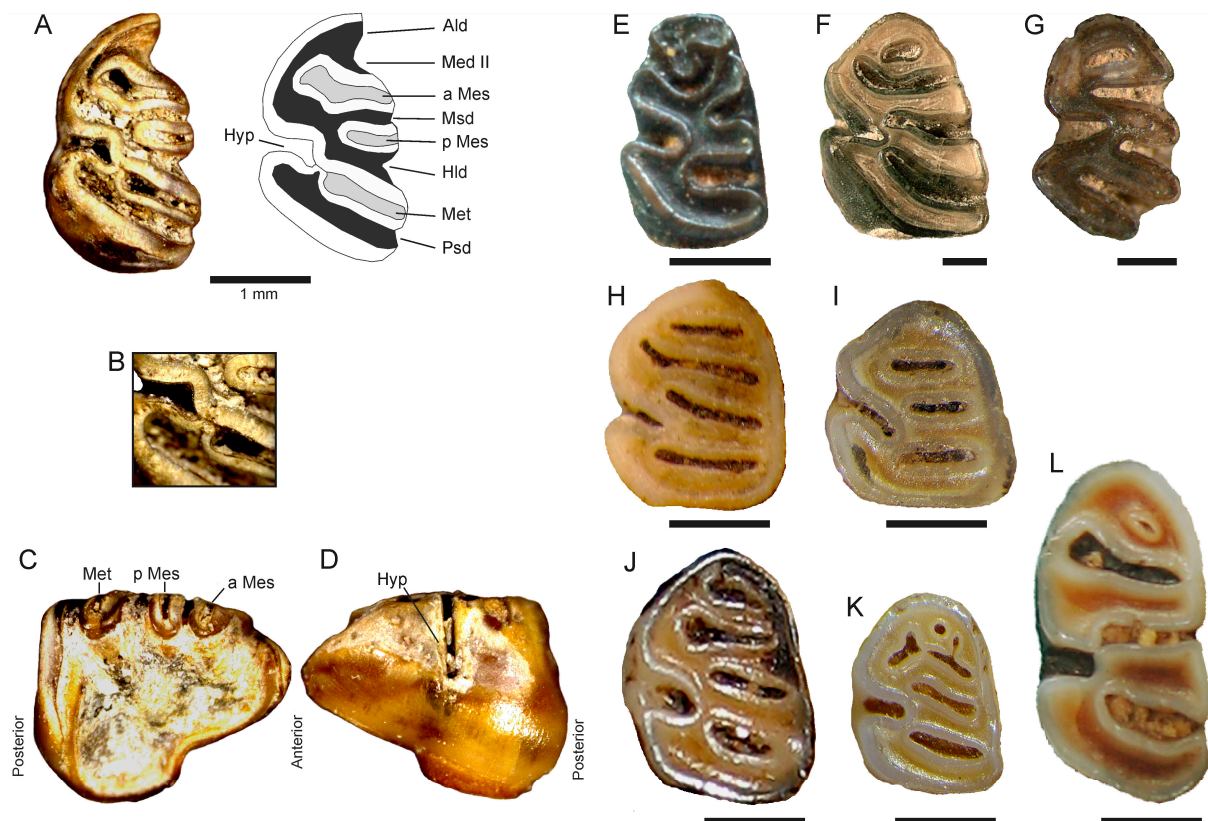


Figure 3. Left Dp4 of (A–D), aff. *Lonchothrix* CICYTTP-PV-M-3-799, (A), occlusal view; (B), detail of the posterior portion of the occlusal view; (C), lingual and (D), labial views. Occlusal views of the Dp4 of (E), *Pampamys emmonsae* GHUNLPam 2214 (holotype; inverted); (F), *Paramyocastor diligens* MD-FM 0861; (G), *Maruchito trilofodonte* MLP-Pv 90-II-20-5; (H), *Hoplomys gymnurus* MZUSP 2001; (I), *Proechimys brevicauda* MVZ 153623; (J), *Lonchothrix emiliae* MN UFRJ 4853; (K), *Mesomys hispidus* MVZ 190653; (L), *Isotrrix* sp. MN UFRJ 56811. Abbreviations: Ald, anterolophid; Hld, hypolophid; Hyp, hypoflexid; Med II, metalophulid II; a Mes, anterior mesoflexid/mesofossettid; p Mes, posterior mesoflexid/mesofossettid; Met, metaflexid/metafossettid; Msd, mesolophid; Psd, posterolophid. Scale 1 mm.

4.1. Referred Material

CICYTTP-PV-M-3-799, an isolated left Dp4.

4.2. Occurrence

Level 2 of the lenticular deposits on the right bank of Doll creek, near to Molino Doll, Entre Ríos province, Argentina (32°18'19" S; 60°25'32" W; Figures 1 and 2); Early Holocene, Greenlandian [29,30,32,33].

4.3. Description

The new material, CICYTTP-PV-M-3-799, comprises an isolated brachydont left deciduous premolar (Dp4) partially damaged on the lingual side. In the occlusal view, it is elongated and narrow. It has an anteroposterior length of 2.12 mm and an approximate transverse width of 1.25 mm. Four lophids and three lingual fossettids can be observed. However, the width of the preserved lingual portion of the first lophid indicates that this structure corresponds to the anterolophid + metalophulid II, suggesting a primarily pentalophodont pattern. This complex anterior lophid is only partially preserved, which hinders the observation of its morphology on the lingual side. However, the posterior inclination of the lingual portion of the anterior mesofossettoid suggests that an anterofossettoid must have been present in the unpreserved portion. The mesolophid is transversely oriented, while the hypolophid and posterolophid are postero-lingually oriented. The anterior arm of the hypocone and the ectolophid are slightly separated; therefore, the posterolophid is nearly isolated. The labial portion of the anterior mesofossettoid is oriented anterolabially and is wider than the lingual end, which is oriented more transversally. The posterior mesofossettoid is transverse and shorter than the other two fossettoids. The metafossettoid is long and postero-lingually oriented. The hypoflexid is wide, with the anterior margin straight and transverse. In the lateral view, the hypoflexid is markedly deeper than the lingual flexids. The outline of the protoconid area is curved and it is at the same level as the hypoconid area (Figure 3A–D).

4.4. Comparisons

Aff. *Lonchothrix* is a small-sized echimyid, smaller than the extinct *Paralonchothrix* and *Maruchito* (Echimyini), *Ullumys*, *Pampamys*, *Eumysops*, *Paramyocastor*, *Tramyocastor* (Myocastorini), *Dicolpomys*, and *Reigechimys* (Euryzygomatomyinae), and larger than *Theridomysops* (Euryzygomatomyinae). It differs from Euryzygomatomyinae and the Myocastorini *Ullumys*, *Eumysops*, and *Thrichomys* in its occlusal configuration of crests and flexids/fossettoids, which is not simplified. Euryzygomatomyinae exhibits a reduced metalophulid II and mesolophid. In contrast, *Ullumys* lacks a mesolophid, while *Eumysops* and *Thrichomys* lack a metalophulid II. *Pampamys* possesses a pentalophodont Dp4 (Figure 3E), which differs from aff. *Lonchothrix* in the morphology of the anterolophid, featuring a posterior spur (metalophulid II), and the anterolingually oriented mesolophid, as observed in *Eumysops*, *Thrichomys*, and some species of *Proechimys*. The Dp4 of the arboreal Myocastorini *Callistomys* differs markedly from that of aff. *Lonchothrix*; it is tetralophodont, with a subtriangular first lophid.

The pentalophodont Dp4 of *Myocastor* and the extinct *Paramyocastor* (Figure 3F) have an acute lingual end of the hypoflexid, with the anterior margin oriented anterolabially rather than transversely. Additionally, in these two genera, the labial portion of the anterior mesoflexid/fossettoid is oriented anterolabially and remains narrow, without the widening observed at the lingual end in aff. *Lonchothrix*.

The Dp4 of the extant Echimyini *Echimys*, *Diplomys*, *Leiuromys*, *Makalata*, *Pattonomys*, *Phyllomys*, *Toromys*, *Dactylomys*, *Kannabateomys*, and *Olallamys* differs from aff. *Lonchothrix* in that the anterior mesoflexid crosses the entire occlusal surface, opening labially. Even in the first seven genera mentioned, the posterior mesoflexid also crosses the occlusal surface and joins the hypoflexid; additionally, the posterior margin of the hypoflexid is oriented anterolingually in these genera, similar to that of extinct *Maruchito* (Figure 3G), whereas in aff. *Lonchothrix*, its orientation is posterolingual. The lower premolars of these living genera are laminar, and at least the anterolophid, metalophulid II (or anterolophid + metalophulid II), and mesolophid are subparallel. As observed in *Callistomys*, many of these genera

exhibit a pointed anterior face of the premolar. The Dp4 of the extinct *Maruchito* (Figure 3G) is laminar, with the anterior mesoflexid transverse and of uniform diameter.

Among the echimyids exhibiting a Dp4 more similar to that of aff. *Lonchothrix*, the Myocastorini *Hoplomys* (Figure 3H) and *Proechimys* (Figure 3I) differ from the new specimen in their nearly transverse metafossettid, the mesial end of the anterior mesofossettid not widened, and the transverse hypo- and posterolophid.

The new specimen shares more pronounced similarities with the *Lonchothrix*–*Mesomys*–*Isothrix* Echimyini clade (Figure 3J–L). This includes the labial end of the anterior mesofossettid being wider than the lingual end; the latter is anteriorly restricted by the arrangement of the metalophulid II and the anterior fossettid; this fossettid was very likely present but not preserved in aff. *Lonchothrix*. Additionally, it resembles *Lonchothrix* and *Mesomys* (Figure 3J,K) in having the hypo- and posterolophid oriented posterolingually, and a transverse hypoflexid. The new specimen is more similar to *Lonchothrix* than to *Mesomys* in size, with both being larger than *Mesomys*, and in the morphology of the mesolophid, which is straight rather than sigmoid, as seen in *Mesomys*. Moreover, the hypoflexid of aff. *Lonchothrix* and *Lonchothrix* is wider than that of *Mesomys* (Figure 3A,J,K). The new material differs from both *Lonchothrix* and *Mesomys* in its thicker enamel and shorter, and transverse, non-oblique posterior mesofossettid. The Dp4 of the Late Miocene *Paralonchothrix*, a sister genus to *Lonchothrix*, is unknown.

5. Discussion

The new material recovered from the Molino Doll locality is markedly similar to the living arboreal *Lonchothrix*, from which it differs by having a slightly thicker enamel and a shorter, more transverse posterior mesofossettid. The differences between the new material and the remaining Echimyini, particularly in relation to the only species of the monotypic genus *Lonchothrix*, *L. emiliae*, imply that it likely represents a new species. However, as the material consists only of a partial Dp4, we opted for the use of open nomenclature. *Lonchothrix emiliae* inhabits lowland Amazonian rainforests in central Brazil [3,14] (see Figure 1). Furthermore, the sister genus of *Lonchothrix*, *Mesomys*, also occupies upland and lowland Amazonian rainforests (Figure 1A).

The fossil record from the Early Holocene at the Molino Doll locality includes, alongside aff. *Lonchothrix*, diatoms [40], mollusks [41], and vertebrates such as freshwater fishes, anurans, squamate reptiles, aquatic and passerine birds, and small- to medium-sized mammals [29–33,42]. In particular, the avian fossil assemblage from the Molino Doll locality includes rallids (*Gallinula galeata*), tinamids (*Nothura* cf. *maculosa*), and indeterminate passerines. The mammalian fossil record includes armadillos (*Dasypus hybridus*) and rodents, such as tuco-tucos (*Ctenomys* sp.) and sigmodontines (*Calomys* sp., *Necromys* sp., and *Bibimys* sp.) [33]. This diversity is complemented by fossils of fungi, indicating the presence of wood resources [43]. All the present taxa suggest complex environments characterized by freshwater rivers and ponds with floating vegetation, as well as semi-aquatic and terrestrial habitats such as grasslands, wetlands, and gallery forests. Sedimentological and taphonomical evidence from these Early Holocene levels indicates a wet environment with water availability during deposition [29,30]. Chronologically, these units are coeval with the record of a progressively increasing sea level, which reached southwestern Entre Ríos province (Upper Paraná Delta) at the beginning of the Holocene (11.7–8 ka BP), associated with a climatic improvement [35]. There is evidence supporting that the maximum inland extension reached the Victoria area, near the study unit, ca 9.3 ka BP [44]. The complex history of the delta started at sea-level highstand before 8 ka BP and lasted to 6.5 ka BP [44]. For this time span of rising and high sea levels, the correlative fluvial sediments that were

deposited favoured a high base level [36,45,46]. During the Early Holocene, fluvial channels filled in the valleys were excavated during the preceding glacial cycle.

According to the paleoenvironmental model proposed by de Vivo and Carmignotto [47], during a warming Early Holocene phase, open forests and savannas were replaced by evergreen and semi-evergreen forests, and dense savannas, respectively (Figure 4). The evergreen and semi-evergreen forest physiognomy extended southward and eastward across South America, reaching northeastern Argentina (Figure 4). This broad-scale model provides general insights into this Holocene warming stage in South America. However, site-specific paleoclimatic evidence through diverse proxies challenges this generalized scenario by revealing a more complex and spatially heterogeneous environmental mosaic during the Early Holocene [48–52]. In this context, the occurrence of a strictly arboreal and climatically conservative *Echimyini* at the latitude of Entre Ríos in Argentina provides a valuable data point that supports the transient expansion of Amazonian-like humid forests into southern latitudes ca. 10 ka BP. Thus, this fossil not only refines the understanding of the paleogeographic dynamics of *Echimyini* but also highlights the value of local fossil evidence in uncovering fine-scale environmental complexity.

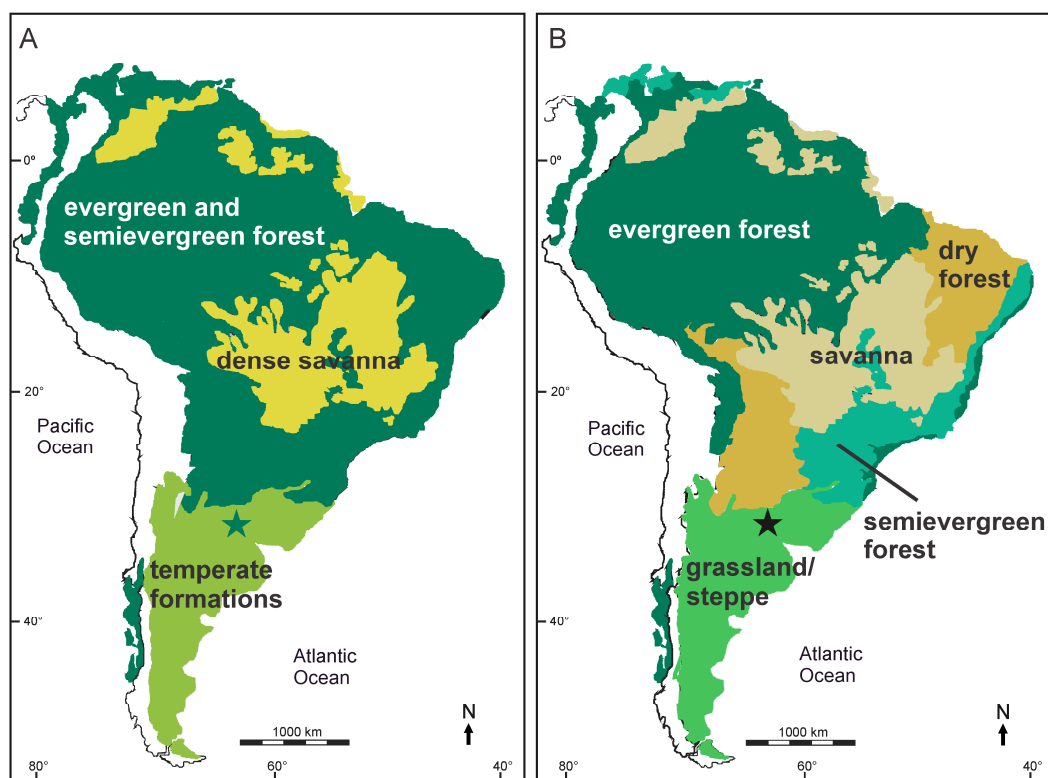


Figure 4. Major plant formations of South America during the Early Holocene warming phase (A) and Recent (B) according to the model proposed by de Vivo and Carmignotto [47]. The star indicates the geographic location of aff. *Lonchothrix* CICYTTP-PV-M-3-799.

The echimyid fossil record exhibits temporal stages that reflect faunal responses to Cenozoic climatic trends. During the late Oligocene—and with greater confidence in the Early–Middle Miocene—echimyid fossils in southern South America are exclusively represented by *Echimyini*, consistent with the expansion of forested environments with tropical elements that reached southern latitudes during that period [21,24]. This pattern shifts markedly from the Late Miocene onward, when the fossil record—perhaps with the sole exception of *Paralonchothrix* (see Piñero et al. [24])—becomes restricted to terrestrial and fossorial lineages (*Euryzygomatomyinae* and *Myocastorini*) associated with open and

arid biomes of the Chacoan Dominion [6,28,53–58]. These biogeographical and ecological shifts mirror broader environmental transformations, particularly the contraction of tropical forests and the expansion of dry ecosystems in the southern cone, driven by late Neogene cooling and Andean uplift [59–64]. The discovery of an arboreal Echimyini in the Early Holocene at the latitude of Entre Ríos Province in Argentina indicates a transient return of humid forest environments that facilitated the southward expansion of arboreal lineages. The tribe Echimyini exhibits strong climatic niche conservatism, maintaining high niche similarity and low rates of climatic niche diversification [10]. This contrasts with the more labile climatic niche of Myocastorini, which successfully colonized extratropical environments. Consistent with this conservatism, the record of aff. *Lonchothrix* supports the presence of humid, tropical, Amazonian-like forests during the Early Holocene at the latitude of Entre Ríos. The paleobiogeographic implications of this record not only reinforce the hypothesis of a transient biotic connection between Amazonia and southern South America [65] but also highlight a climatic window that temporarily enabled the expansion of Amazonian faunal elements into temperate latitudes.

The subsequent disappearance of aff. *Lonchothrix* may reflect the lineage's limited tolerance to climatic shifts, reinforcing the paleoenvironmental interpretation derived from its presence. The extinction of this arboreal Echimyini from southern South America could have been linked to subsequent climatic deterioration, such as the 8.2 ka BP cold event, a recognized period of rapid cooling and/or aridification (e.g., Alley and Ágústssdóttir [66]). Although this cold event has not been identified in South America, there is substantial evidence of drier conditions during the Middle Holocene, since approximately 8 ka (e.g., Baker et al. [67], Mayle and Power [68], and González-Pinilla et al. [69]). This event may have led to the contraction of forested habitats and the return of more open landscapes in the region, rendering it unsuitable for arboreal taxa dependent on dense canopy structures. Thus, the Early Holocene presence of aff. *Lonchothrix* may reflect a short-lived southernmost expansion, followed by local extinction driven by climatic forcing. The local extinction of the sigmodontine rodent *Bibimys*, recorded in the same levels as aff. *Lonchothrix* supports this hypothesis [32].

6. Conclusions

The Early Holocene record of an arboreal Echimyini at the latitude of Entre Ríos in northeastern Argentina provides an unexpected and informative data point for understanding the paleogeographic dynamics of the Neotropics. It reveals a transient southern incursion of a taxon strongly associated with tropical Amazonian-like forests, occurring under favorable climatic conditions during a warming Early Holocene phase. The subsequent absence of representatives of the clade to which aff. *Lonchothrix* belongs at this latitude, aligns with the regional effects of post-optimum aridification, probably occurring during the Middle Holocene, and supports a scenario of niche-driven local extinction. As such, this record adds to a growing body of evidence that links faunal composition with Quaternary climatic oscillations and emphasizes the selective filters shaping the evolutionary trajectory of South American mammalian diversity.

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