

Beyond the desert: new paleoenvironmental evidence for Nothrotheriops (Xenarthra, Folivora) from the Late Pleistocene of Argentina

Diego Brandoni

dbrandoni@cicyttp.org.ar

CICYTTP

Raúl I. Vezzosi

CICYTTP

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Abstract

Nothrotheriops is mainly recorded during the Pleistocene of the United States, but it is also present in South America. Among the species of *Nothrotheriops*, *N. texanus* differs from *N. shastensis* in size (*N. shastensis* being larger) and in cranial and dental proportions (regarding the mandible, the relationship of the predental length and the length of the molariform toothrow). A dentary fragment (MRP-G-Pv 041) from the Puerto San Martín Formation (Late Pleistocene, Santa Fe Province, Argentina) is herein described. The size and general morphology of MRP-G-Pv 041 allow to locate the specimen in *Nothrotheriops*. Given it is not possible to calculate the relative length of the molariform toothrow of MRP-G-PV 041, the assignment to *N. shastensis* or *N. texanus* is not possible. In addition, the fact that the type mandible of *Nothropus carcaranensis* lacks the caniniform suggests that *Nothropus* could represent a junior synonym of *Nothrotheriops*. Taking into account 1) differences between *N. shastensis* and *N. texanus*, and 2) the assignment of *Nothropus carcaranensis* to *Nothrotheriops*; referring MRP-G-PV 041 to any of the known species of *Nothrotheriops* is not sustained, justifying its assignment to *Nothrotheriops* sp. Sedimentological, stratigraphic, and paleontological evidence from the Puerto San Martín Formation suggest a heterogeneous and complex paleoenvironment, contrasting with the mostly dry/desert ones in which *Nothrotheriops* is typically recorded in North America.

Introduction

Folivora (Xenarthra, Pilosa), commonly known as sloths, represents one of the most characteristic groups of Cenozoic mammals from South America, later expanding into Central and North America. The earliest record of the clade is tentatively referred to *Pseudoglyptodon*, whereas extant diversity is restricted to the arboreal genera *Bradypus* and *Choloepus*. The fossil record reveals a wide ecological diversity, including arboreal, semiarboreal, and terrestrial forms.

Traditionally four main clades are recognized within Folivora: Megatheriidae, Megalonychidae, Nothrotheriidae, and Mylodontidae (Gaudin 2004; Brandoni et al. 2016). However, molecular analyses support a more subdivided arrangement, recognizing families such as Acratocnidae, Parocnidae, Choloepodidae, Megalonychidae, Mylodontidae, Megatheriidae, Nothrotheriidae, and Bradypodidae (Delsuc et al. 2019). Within Nothrotheriidae, Nothrotheriinae represents the most diverse and widely distributed subclade during the Neogene and Quaternary. Members of this group—including *Nothropus*, *Nothrotherium*, *Pronothrotherium*, *Nothrotheriops*, *Mionothropus*, *Lakukullus*, *Aymaratherium*, and *McDonaldocnus*— are known from the Middle Miocene of Bolivia and Argentina to the Late Pleistocene of South America, Central America, and North America (see Brandoni 2014; Pujos et al. 2014; De Iuliis et al. 2015; Brandoni and McDonald 2015; Brandoni and Vezzosi 2019). During the Pleistocene, the group is mainly represented by *Nothrotherium*, recorded from Brazil, Argentina, and Uruguay (Kraglievich 1926; Hoffstetter 1954; Paula Couto 1971; Cartelle and Fonseca 1983; Perea 2007; Costa da Silva et al. 2019; Vezzosi et al. 2019a); *Nothrotheriops*, recorded from the United States, Mexico, Belize, Argentina, and Uruguay (McDonald 1995; McDonald and Jefferson 2008; De Iuliis et al. 2015; Brandoni and Vezzosi

2019; Varela et al. 2023; Vazquez et al. 2025; McDonald et al. 2026); and *Nothropus*, recorded from Argentina and Bolivia (Brandoni and McDonald 2015; Quiñones et al. 2017).

In Argentina, species of Quaternary Nothrotheriinae were reported from several Pleistocene localities in Buenos Aires (e.g., *Nothrotherium torresi*) and Santa Fe [e.g., *Nothropus carcaranensis*, *Nothrotherium escrivanense*, *Nothrotherium roverei*, *Nothrotherium* cf. *torresi*, *Nothrotheriops* sp.] provinces (Brandoni and McDonald 2015; Vezzosi et al. 2019a; Brandoni and Vezzosi 2019; Brambilla et al. 2019). Additionally, molecular evidence from dung recovered at Cuchillo Curá (Neuquén Province) indicates the presence of a nothrotheriine, although the absence of associated skeletal remains prevents a more precise taxonomic assignment (Hofreiter et al. 2003).

Pleistocene deposits of Santa Fe Province are dominated by lithologically homogeneous sequences of sandy silts and silty sand of aeolian (loess) and/or fluvial origin, with intercalated paleosols and calcretes (Iriondo and Kröhling 2009; Iriondo 2010). These deposits have historically been locally known as the 'Pampas Formation' (Roth 1888) or 'Belgranense' deposits (sensu Castellanos 1943), both included within the traditional concept of the Pampean Formation sensu lato (see Toledo 2011; Tonni 2011; Prado et al. 2021; Voglino et al. 2023; among others). Under the current lithostratigraphic framework, they are subdivided into several Middle–Late Pleistocene units, including the Puerto San Martín, Palo Negro, Timbúes, Fortín Tres Pozos, Carcarañá, and Tezanos Pinto formations (Iriondo and Kröhling 2009; Brunetto et al. 2010; Iriondo 2010; Kröhling and Brunetto 2013; Brunetto et al. 2017). These units are highly fossiliferous and have yielded abundant remains of continental vertebrates (Frenguelli 1928; Castellanos 1945; Vezzosi 2016; Vezzosi and Kerber 2018; Vezzosi et al. 2019a, 2019b; Carrillo-Briceño et al. 2023; Le Verger 2023). Particularly, the most abundant records include large Xenarthra, with fragments of dorsal carapace and/or isolated osteoderms of various cingulate armored species, as well as isolated cranial and postcranial remains of giant sloths, including members of Megatheriidae, Mylodontidae, and Nothrotheriinae (Brandoni and McDonald 2015; Brandoni and Vezzosi 2019; Vezzosi et al. 2019b, Zamorano et al. 2026).

Along the right margin of the Paraná River (Santa Fe Province), the Late Pleistocene Puerto San Martín, Timbúes, and Carcarañá formations crop out extensively (Iriondo and Kröhling 2009; Vezzosi 2015). Particularly, the Puerto San Martín Formation crops out discontinuously in the cliffs between Coronda and San Lorenzo localities (Iriondo and Kröhling 2009) and has yielded a relatively scarce terrestrial mammalian record (see Vezzosi 2015). However, fossil mammals reported from this sector were originally assigned to the Pampean Formation sensu lato (Roth 1888; Frenguelli 1926; Rusconi 1931; Castellanos 1945, 1973, 1980; Carrillo-Briceño et al. 2023; Le Verger 2023), prior to the establishment of the current lithostratigraphic framework.

Here, we report and describe a mandibular fragment referred to *Nothrotheriops* sp. from the Late Pleistocene of Santa Fe Province, Argentina, providing morphological insights and ecological flexibility in a heterogeneous paleoenvironment.

Material and methods

In order to identify and characterize the specimen described herein, comparative analyses were conducted using mandibular material referred to several species of Nothrotheriinae. The sample includes Miocene to Pleistocene taxa: *Nothrotheriops shastensis*, *Nothrotheriops texanus*, *Nothrotherium maquinense*, *Nothropus carcaranensis*, *Nothropus tarijensis*, *Nothropus priscus*, *Pronothrotherium typicum*, *Pronothrotherium mirabilis* (including *Pronothrotherium figueirasi*, see Gaudin et al. 2020) and *Mionothropus cartellei* (Table 1). For chronological purposes, we follow the International Chronostratigraphic Chart (Cohen et al. 2013; ICS 2026). Measurements were taken using a digital caliper (accuracy: 0.01 mm) and are reported in millimeters; additional measurements were obtained using the open-source software ImageJ.

Linear regression analysis was performed using mandibular depth vs molariform tooththrow length (see Supplementary Electronic Data). The hypsodonty index ($HI = \text{mandibular depth} / \text{molariform tooththrow length}$) was calculated for each complete specimen and used to compare Neogene and Quaternary Nothrotheriinae (Table 1).

Institutional abbreviations. **CMGS**, Ghizzoni Personal Collection, Salto, Uruguay; **FC-DPV**, Facultad de Ciencias - Colección de Vertebrados Fósiles, Montevideo, Uruguay. **GRCA**, Grand Canyon National Park, (US National Park Service), Arizona, USA; **INAH**, Instituto Nacional de Antropología e Historia, México; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, USA; **LACM HC**, Natural History Museum of Los Angeles County, Hancock collection at the Rancho La Brea Tar Pits and Museum, Los Angeles, USA; **MACN A**, Colección Ameghino, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, CABA, Argentina; **MACN Pv**, Colección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, CABA, Argentina; **MNRJ**, Museu Nacional, Rio de Janeiro, Brazil; **MRP-G-Pv**, Museo del Río Paraná, Puerto San Martín, Santa Fe, Argentina; **UA**, University of Arizona, Tucson, USA; **UCMG**, Universidade Catolica de Minas Gerais, Minas Gerais, Brazil; **UF**, Florida Museum of Natural History, University of Florida, Gainesville, USA; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, USA; **USNM**, United States National Museum of Natural History, Washington D.C., USA.

Anatomical abbreviations. **mf**, molariform; **po**, posterolateral opening of the mandibular canal.

Geological setting

Three major geomorphological regions are recognized in Santa Fe Province: the Austral Chaco, Northern Pampa, and Southern Pampa plains (Iriondo 2010). The specimen MRP-G-Pv 041 (herein described) was recovered near the historical site known as Bajada Quebracho (32° 40' 41.69640" S, 60° 43' 35.84280" W), between the industrial area and the vicinity of Puerto San Martín city, Santa Fe Province, Argentina (Fig. 1A). The study area is located within to the Northern Pampa plain (NPP), as defined in regional geological maps, and is characterized by the Unequal Blocks Area (Iriondo 2010; Brunetto et al. 2025). The lithostratigraphic and chronological framework of the NPP comprises Middle Pleistocene–Holocene

fluvial, lacustrine, and eolian sedimentary sequences (Kröhling and Iriondo 1999, 2003; Iriondo 2010; Kröhling and Brunetto 2013; Kröhling and Carignano 2014; Brunetto et al. 2017).

Based on field observations, MRP-G-Pv 041 comes from deposits of the Puerto San Martín Formation (Iriondo and Kröhling 2009; Brunetto et al. 2025). This unit is exposed at the base of the cliff from the mouth of the Coronda River to the locality of Puerto San Martín (Iriondo 1987, 2010; Iriondo and Kröhling 2009), and it is overlain by younger Late Pleistocene deposits (Fig. 1B). Depending on the exposure, the overlying units correspond to the Palo Negro, Ituzaingó, Carcarañá, or Tezanos Pinto formations (Iriondo and Kröhling 2009). The Puerto San Martín Formation consists mainly of yellowish-brown to olive silty deposits with pedogenic structure, locally including ferruginous mottles, carbonate rhizoconcretions, and calcretized horizons (Iriondo and Kröhling 2009; Franco et al. 2019). These deposits record the alternation of low-energy fluvial–palustrine environments with intervals of eolian sedimentation, reflecting phases of increased accommodation and aggradation. The fossil-bearing levels analyzed here occur below the calcretized upper sector of the succession.

Recent Optically Stimulated Luminescence (OSL) dating and sequence stratigraphic analyses from the Frías Stream, south of the study area, provide novel chronological constraints (see Vezzosi 2015; Vezzosi et al. 2019a; Brunetto et al. 2023). At this stream, exposed basal deposits that underlie deposits correlated with the Puerto San Martín Formation are interpreted as being at least Middle Pleistocene in age (Chibanian; Cohen et al. 2013; Brunetto et al. 2023; ICS 2026). Thus, the fossil-bearing levels of the Puerto San Martín Formation from which MRP-G-PV 041 derives are interpreted as belonging to the early part of the Late Pleistocene, an interpretation consistent with their subsequent correlation to the Last Interglacial (MIS 5).

At a broader regional scale, the Northern Pampa and Southern Mesopotamia preserve sedimentary successions that record the interglacial–glacial cyclicity characteristic of the Quaternary (Brunetto et al. 2010, 2015; Ferrero et al. 2017; Thalmeier et al. 2021). At these latitudes, high sea-level stands are associated with humid periods typical of interglacial stages (Vezzosi et al. 2019a; Brunetto et al. 2010, 2025), exerting a strong control on fluvial dynamics through variations in the regional base level. In this context, the Puerto San Martín Formation records humid intervals associated with high sea-level conditions and enhanced fluvial aggradation during the Last Interglacial MIS 5 (Iriondo, 2010, 2012; Brunetto et al., 2015, 2017, 2025). Comparisons with nearby fluvial successions, including those of the Carcarañá River, further support this interpretation (Vezzosi et al. 2019b).

Systematic paleontology

Superorder XENARTHRA Cope, 1889

Order FOLIVORA Delsuc, Catzefflis, Stanhope, and Douzery, 2001

Family NOTHROTHERIIDAE Ameghino, 1920

Subfamily NOTHROTHERIINAE Ameghino, 1920

Type species. *Nothrotheriops shastensis*.

Nothrotheriops sp.

Figure 2, Table 1

Referred material. MRP-G-Pv 041 fragment of the right dentary.

Geographic and Stratigraphic provenance. Bajada Quebracho (32° 40' 41.69640" S, 60° 43' 35.84280" W), vicinity of Puerto San Martín locality, Santa Fe Province (Fig. 1A), NPP, Unequal Blocks Area (Iriondo 2010; Brunetto et al. 2025), central Argentina; Puerto San Martín Formation, Late Pleistocene (Fig. 1B).

Description and comparison

MRP-G-Pv 041 is similar in size to most of the specimens of *N. texanus* and *Nothropus carcaranensis*; whereas *Mionothropus cartellei*, *Pronothrotherium typicum*, *P. mirabilis*, and *Nothrotherium maquinense* are smaller, and most of the specimens of *N. shastensis* and *Nothropus tarijensis* are larger (Fig. 3, Table 1).

As in *M. cartellei*, *P. typicum*, *P. mirabilis*, *N. texanus*, *N. shastensis*, *Nothropus priscus*, *N. tarijensis*, and *N. carcaranensis*, in MRP-G-Pv 041 the ventral margin of the dentary (i.e., ventral margin of the bulge) is convex (Fig. 2A, B, D), with its maximum depth at the plane of the mf2; whereas in *N. maquinense* it is nearly horizontal with the ventral bulge less pronounced. The hypsodonty index (HI=mandibular depth/molariform toothrow length) is 1.01 in MRP-G-Pv 041; whereas in *N. shastensis* ranges from 0.9 to 1.20, in *N. texanus* ranges from 0.89 to 1.1, and in *Nothropus* spp. ranges from 1.005 to 1.08 (see Table 1).

As in *M. cartellei*, *P. typicum*, *P. mirabilis*, *N. texanus*, *N. shastensis*, *N. priscus*, *N. tarijensis*, and *N. carcaranensis*, in MRP-G-Pv 041 the anterior margin of the coronoid process is posterior to the posterior plane of mf3, making this tooth visible in lateral view (Fig. 2A). The posterolateral opening of the mandibular canal is closer to the anterior margin of the coronoid process, entirely posterior to the plane of the mf3, and below to the occlusal plane (Fig. 2A). The described position of posterolateral opening of the mandibular canal is similar in most other Nothrotheriinae, but in *P. typicum* the posterolateral opening of the mandibular canal is slightly anterior, close to the plane of the posterior margin of the mf3.

As in *Nothrotherium* and *Nothrotheriops*, in MRP-G-Pv 041 the toothrow is composed by three molariforms (Fig. 2C), and the caniniform is considered to be absent (see Casali et al. 2026); whereas in *Mionothropus cartellei* and the species of *Pronothrotherium* the caniniform is present and separated from the mf1 by a short diastema. In *N. carcaranensis* a very small foramen appears in front of the anterior margin of m1, which was considered by Quiñones et al. (2017) to be the alveoli of the caniniform. In

MRP-G-Pv 041 a small foramen is located near the anterior wall of the m1 (Fig. 4A), but as occur in *N. carcaranensis* (Fig. 4B) and *Nothrotheriops* (Figure 4C) it seems like it is a vascular foramen and not de alveoli of a caniniform.

The occlusal surface of the molariforms has mesial and distal lophids separated by an open transverse 'V' valley, and as in other Nothrotheriinae the molariforms (mf1 and mf2) have lingual and labial vertical grooves (Fig. 2C). The mf1 is subtrapezoidal in outline (length: 11.02 mm; width: 14.53 mm), has its anterior face slightly concave and the posterior one convex; the mf2 is subrectangular in outline (length: 11.72 mm; width: 14.00 mm) has its anterior face slightly convex and the posterior one convex, and as was mentioned above, has lingual and labial vertical grooves; the mf3 is quadrangular in outline (length: 13.00 mm; width: 13.33 mm) having its anterior face slightly convex and the posterior one flat.

Linear regression analysis of mandibular depth against molariform toothrow length ($N = 36$, $r = 0.9221$, $p < 0.0001$; see Supporting Electronic Data) places MRP-G-Pv 041 (within the 95% bootstrapped confidence interval) closest to *Nothrotheriops texanus* and slightly distant to *N. shastensis* and *Nothropus carcaranensis* (Fig. 3). This quantitative result is consistent with the qualitative morphological comparisons presented above, in which MRP-G-Pv 041 is similar to specimens referred to *Nothrotheriops*.

Discussion

In the Pleistocene of America, Nothrotheriinae is represented by *Nothrotherium*, *Nothrotheriops*, and *Nothropus*. Among these, *Nothrotherium* and *Nothrotheriops* (clade Nothrotheriini; De Iuliis et al. 2011) are relatively well-studied, based on multiple specimens, whereas *Nothropus* is mainly represented by isolated dentaries (see Burmeister 1882; Bordas 1942; Quiñones et al. 2017). Morphological differences between *Nothrotheriops* and *Nothrotherium* were discussed by Paula Couto (1971) and De Iuliis et al. (2011), among others. In the dentary, the main differences are related to size, with *Nothrotherium* being smaller than *Nothrotheriops*, and the shape of the ventral bulge, which is convex in *Nothrotheriops* and horizontal in *Nothrotherium*.

The dentary of *Nothropus carcaranensis* is similar in size to those of *Nothrotheriops texanus*, and slightly smaller than most of the specimens assigned to *Nothrotheriops shastensis* (Table 1, Fig. 3). Additionally, in both *Nothrotheriops texanus* and *Nothrotheriops shastensis* the caniniform is absent; whereas in *Nothropus carcaranensis* it is likewise absent or at least not observable (but see Quiñones et al. 2017). However, this tooth is present in *Nothropus priscus* and *Nothropus tarijensis*.

The general morphology of MRP-G-Pv 041, including the presence of three molariforms and absent caniniform, the shape of the ventral bulge, and overall size, supports its assignment to *Nothrotheriops*. Among the species of this genus, *N. texanus* differs from *N. shastensis* in size (*N. shastensis* being larger than *N. texanus*) and in cranial and dental proportions, particularly in the relationship between predental length and molariform toothrow length (McDonald 1995; McDonald and Jefferson 2008). In this sense, the molariform toothrow of *N. shastensis* is relatively larger than that in *N. texanus*. Given the predental

region is not preserved in MRP-G-PV 041, this ratio cannot be assessed, precluding assignment to either species. In addition, as noted by Brandoni and McDonald (2015), the absence of a caniniform in the type mandible of *Nothropus carcaranensis* and the convexity of the ventral margin of the bulge raises the possibility that this taxon may not belong to *Nothropus*, and could instead be assigned to *Nothrotheriops*. Taken together, these considerations support the assignment of MRP-G-Pv 041 to the genus *Nothrotheriops*. However, taking into account the abovementioned considerations regarding the 1) the diagnostic differences between *N. shastensis* and *N. texanus*, and 2) the taxonomic uncertainty surrounding *N. carcaranensis*, the assignment of MRP-G-PV 041 to a particular species is not sustained, then its assignment to *Nothrotheriops* sp. results appropriate.

For the Late Pleistocene of Santa Fe Province, Nothrotheriinae comprises *Nothropus carcaranensis*, *Nothropus priscus*, *Nothrotherium escrivanense*, *Nothrotherium roverei*, *Nothrotherium* cf. *torresi*, and *Nothrotheriops* sp. (see Quiñones et al. 2017; Vezzosi et al. 2019b; Brandoni and Vezzosi 2019; Brambilla et al. 2019; Le Verger 2023). Although this taxonomic diversity seems to be high for a relatively small geographical area, most taxa are represented by isolated, non-overlapping elements from different parts of the skeleton (e.g., dentaries for *Nothropus* spp., a humerus for *Nothrotherium roverei*, a partial femur for *N.* cf. *torresi*), precluding direct comparisons among them. This issue and its systematic implications have been discussed by Brandoni and McDonald (2015) for several femora referred as Nothrotheriinae indet., which show similarities to a femur assigned to *Nothrotheriops* sp. by Brandoni and Vezzosi (2019). Besides, Quiñones et al. (2017) considered *N. priscus* as a species inquirenda (“a species of doubtful identity needing further investigation.” ICZN, 1999: 116), suggesting that the diversity of Nothrotheriinae in the Late Pleistocene of Santa Fe Province may be overestimated.

In the case of *N. escrivanense*, the specimen PIMUZ A/V 477 (Roth collection at PIMUZ) was collected from the cliffs of the Carcarañá River. Although Le Verger (2023) suggested a possible Plio–Middle Pleistocene age for this fossil and other xenarthran remains recovered from the area, the exposed cliffs are predominantly composed of deposits of Late Pleistocene age sensu stricto (Kröhling 1999; Iriondo and Kröhling 2009; Brunetto et al. 2017, 2023, 2025; Vezzosi et al. 2019b), suggesting a younger age for *N. escrivanense*. Thus, although the available geological evidence favors a Late Pleistocene age, a Middle Pleistocene age for this taxon cannot be completely ruled out. A comprehensive systematic revision of Pleistocene Nothrotheriinae, incorporating precise stratigraphic and geographic data, is needed to better resolve the taxonomic diversity of the group.

The exact age of the sediments where the specimen MRP-G-Pv 041 was recovered (i.e. Puerto San Martín Formation) is unknown; however, taking into consideration the evidence from chronological dates from deposits correlated with the Puerto San Martín Formation (see Vezzosi 2015; Brunetto et al 2017), the available chronology indicates that this stratigraphic sequence in the area was deposited during the last Pleistocene interglacial interval (MIS 5), approximately 90 to 118 kyr ago. The MIS 5 interval has been interpreted as a relatively warm and humid climatic phase in northeastern Argentina, characterized by the expansion of fluvial systems and wetlands (Brunetto et al. 2017), environmental conditions that may have favored the southward expansion of warm-adapted mammals. The record of *Nothrotheriops*

sp. from Santa Fe Province (herein reported) chronologically coincides with the earliest records of *Nothrotheriops shastensis*, suggesting a broad geographic distribution of *Nothrotheriops* during the Late Pleistocene, ranging from 33°–36°N (e.g., states of California and Arizona, USA) to 32°S (Bajada Quebracho, Santa Fe Province, Argentina). Thus, *Nothrotheriops* would have dispersed from North America (where *Nothrotheriops* has early records, Calabrian–Middle Pleistocene) to South America where localities bearing *Nothrotheriops* or its allies are Late Pleistocene in age (Brandoni and Vezzosi 2019), a dispersal that may have been facilitated by the favorable paleoenvironmental conditions prevailing during the MIS 5 interglacial.

In general, species of Nothrotheriinae have been interpreted as inhabitants of predominantly open environments, browsing on a variety of xerophytic vegetation (Thompson et al. 1980; Ghilardi et al. 2011). In North America, *Nothrotheriops* has likewise been considered well adapted to arid and semi-arid environments, although it was also associated with a greater variety of habitats, including mesic and riparian environments (see McDonald and Jefferson 2008; Green 2009; McDonald 2023; Kurre and DeSantis 2025; McDonald and Ruddell 2025). Additional lines of evidence, including paleobotanical and molecular data, have also supported a more opportunistic browsing or mixed-feeding strategy for *Nothrotheriops shastensis* (see Poinar et al. 1998; Hofreiter et al. 2000). In sum, compared with other sloths recorded during the Pleistocene of North America, *Nothrotheriops* is the most adapted genera to xeric environments (McDonald 2023); however, the occupation of heterogeneous environments was also considered.

In South America, *Nothrotheriops* has been recorded from Pleistocene deposits of Argentina, Brazil, and Uruguay (Oliveira et al. 2017; Brandoni and Vezzosi 2019; Varela et al. 2023). Stable isotope data from the Arroyo del Vizcaíno site, Uruguay (ca. 30 ka, Late Pleistocene; Fariña et al. 2014) indicate $\delta^{13}\text{C}$ values consistent with C_3 plant-dominated diets, and $\delta^{18}\text{O}$ values suggesting relatively dry and/or warm climatic conditions (Varela et al. 2023). Records from central Brazil likewise suggest drier conditions with expanded open vegetation during the Pleistocene–Holocene transition (Oliveira et al. 2017). However, studies in America have emphasized that *Nothrotheriops* was capable of inhabiting a wide range of environmental conditions, from cold and arid to warm and humid (De Iuliis et al. 2015; Brandoni and Vezzosi 2019; Vezzosi et al. 2019a). In this context, Brandoni and Vezzosi (2019) proposed relatively more humid conditions for the lowlands of southern South America (including Santa Fe Province) during interglacial phases of the Late Pleistocene.

As was mentioned, the sedimentological and stratigraphic evidence from the Puerto San Martín Formation indicates deposition in low-energy fluvial–palustrine systems developed under conditions of increased accommodation and aggradation, consistent with extensive wetlands and relatively humid climatic conditions. Paleobotanical data, including the occurrence of Proteaceae fossil wood (*Scalarixylon* sp.), further support the presence of heterogeneous vegetation cover and environmentally dynamic conditions, reflecting alternating humid and relatively drier phases during deposition, as well as the development of forested or densely vegetated sectors under warmer and humid conditions (Franco et al. 2019). The mammalian assemblage, including both mega- and micromammals (Equidae, Cervidae,

Chinchillidae, Chlamyphoridae, Gomphotheriidae, and Protheriidae; Vezzosi et al. 2019), supports the interpretation of environmentally heterogeneous landscapes composed of open woodland. Furthermore, chronological constraints indicate that these deposits were formed during the Last Interglacial (MIS 5), a period characterized in this region by increased humidity and higher base levels.

The presence of *Nothrotheriops* in Puerto San Martín Formation suggests that *Nothrotheriops* was capable of exploiting heterogeneous and environmentally complex landscapes during the Late Pleistocene. Together, the sedimentology, stratigraphy, and paleontological evidence further supports the interpretation of dynamic environmental mosaics in the NPP during MIS 5, within which *Nothrotheriops* likely occupied a broad range of available habitats. Such ecological flexibility, together with the expansion of suitable habitats during the Last Interglacial, may also have facilitated the southward dispersal of the genus into southern South America.

Conclusion

The record of *Nothrotheriops* sp. from the Late Pleistocene of Santa Fe Province expands the known distribution of the genus in southern South America and provides new insights into its paleoecology. The geo-paleontological evidence indicates that the specimen likely derives from fluvial–palustrine deposits of the Puerto San Martín Formation, formed under low-energy floodplain conditions during MIS 5. Paleoenvironmental data suggest the development of heterogeneous landscapes, including wetlands, open areas, and vegetated patches associated with Proteaceae, under relatively humid climatic conditions. The contrasting paleoenvironmental conditions documented across the Pleistocene record of *Nothrotheriops*, together with the paleoenvironmental framework reconstructed here for Puerto San Martín Formation, are consistent with the occurrence of the genus across a broad range of paleoenvironmental conditions. These conditions may have provided suitable environments and plant resources during interglacial phases, potentially facilitated the dispersion of the genus into southern South America during the Late Pleistocene, as proposed for other taxa under interglacial regimes.

Declarations

Author Contribution

D.B. and R.I.V conceptualized the research and wrote the manuscript. R.I.V. prepared the figures.

References

1. Ameghino F (1920) Sur les édentés fossiles de l'Argentine. Examen critique, révision et correction de l'ouvrage de M. R. Lydekker. Obras Completas y Correspondencias Científicas 11:447–909.
2. Bordas AF (1942) Observaciones sobre algunos Nothrotheriinae (Gravirada). Physis 19:173–179.
3. Brambilla L, Haro JA, Ibarra DA (2019) New remains and considerations on Nothrotheriidae from the late Pleistocene of La Ribera, Santa Fe, Argentina. Boletín del Instituto de Fisiografía y Geología

89:1–8.

4. Brandoni D (2014) “*Xyophorus*” sp. en el Mioceno Medio de Chubut: implicancias sistemáticas, biogeográficas y biocronológicas del registro de un Nothrotheriinae en el Neógeno de la Argentina. *Ameghiniana* 51:94–105.
5. Brandoni D, McDonald HG (2015) An enigmatic Nothrotheriinae (Xenarthra, Tardigrada) from the Pleistocene of Argentina. *Ameghiniana* 52:294–302.
6. Brandoni D, Scillato-Yané GJ, Miño-Boilini AR, Favotti E (2016) Los Tardigrada (Mammalia, Xenarthra) de Argentina: diversidad, evolución y biogeografía. In: Agnolin FL, Lio GL, Brissón Egli F, Chimento NR, Novas FE (eds.) *Historia evolutiva y paleobiogeográfica de los vertebrados de América del Sur*, Buenos Aires, 6:263–274.
7. Brandoni D, Vezzosi RI (2019) *Nothrotheriops* sp. (Mammalia, Xenarthra) from the Late Pleistocene of Argentina: implications for the dispersion of ground sloths during the Great American Biotic Interchange. *Boreas* 48(4):879–890.
8. Brunetto E, Iriando M, Zamboni L, Gottardi G (2010) Quaternary deformation around the Palo Negro area, Pampa Norte, Argentina. *J South Am Earth Sci* 29:627–641.
9. Brunetto E, Ferrero B, Noriega JI (2015) Late Pleistocene lithostratigraphy and sequences in the south-western Mesopotamia (Argentina): evidences of the last interglacial stage. *J South Am Earth Sci* 58:111–128. <https://doi.org/10.1016/j.jsames.2014.12.003>.
10. Brunetto E, Krohling DM, Zalazar MC, Francisconi C (2017) Analysis of the interaction between neotectonic and surface processes in a low-land intracratonic setting of South America. *Quat Int* 438:141–159.
11. Brunetto E, Vezzosi RI, Kröhling DM, Thalmeier MB, Zalazar MC (2023) Estratigrafía secuencial en la región distal de la cuenca pericratónica del Río Paraná, durante el Cuaternario Tardío. XVIII Reunión Argentina de Sedimentología y IX Congreso Latinoamericano de Sedimentología, Actas XVIII RAS y IX CLS. La Plata, Buenos Aires, p 39.
12. Brunetto E, Kröhling DM, Cello PA, Thalmeier MB, Zalazar C (2025) Tectonic Shallow Lakes of the Northern Pampa Plain. In: Piovano EL, Stutz S, Morales JA, Ariztegu D (eds): *Pampean lakes*, Chap. 7:151–181 pp. Springer Cham. Springer Nature Switzerland AG. <https://doi.org/10.1007/978-3-031-86028-7>.
13. Burmeister H (1882) *Nothropus priscus*, ein bisher unbekanntes fossiles Faulthier. *Sitzungsberichte der königlich preussischen Akademie der Wissenschaften*, Berlin, 613–620.
14. Carrillo-Briceño JD, Vezzosi RI, Ming KM, Christen, ZM, Mothé D, Ruiz-Ramoni D, Sánchez-Villagra MR (2023) Nearctic Pleistocene ungulates from the Pampean region (Argentina) in the historical collections of Santiago Roth in Switzerland: an overview. *Swiss J Palaeontol* 142:12. <https://doi.org/10.1186/s13358-023-00273-7>
15. Cartelle C, Fonseca JS (1983) Contribuição ao melhor conhecimento da pequena preguiça terrícola *Nothrotherium maquinense* (Lund) Lydekker, 1889. *Revista Lundiana* 2:127–181.

16. Casali DM, Costa CG, Barbosa FHS, Muniz FP, Mestriner G, Parisi Dutra R, Narducci RE, McDonald HG, Fonseca Tostes C, de Abreu Lima IL, Manzi FR, Vilaboim Santos L (2026) The presence of an atavistic caniniform alveolus in *Nothrotherium maquinense* (Xenarthra, Folivora, Nothrotheriidae). *Journal of Mammalian Evolution* 33:25. <https://doi.org/10.1007/s10914-026-09823-5>
17. Castellanos A (1943) El Preenssenadense ¿es un horizonte geológico o una facies? *Publicaciones del Instituto de Fisiografía y Geología* 18:1–83.
18. Castellanos A (1945) Nota sobre algunas cornamentas de ciervos de los géneros *Epieuryceros*, *Antifer* y *Paraceros* y descripción de la de *Epieuryceros proximus* n. sp. *Publicaciones del Instituto de Fisiografía y Geología de la facultad de Ciencias Físico–Químicas y Naturales aplicadas a la Industria de la Universidad Nacional del Litoral* 24:5–23.
19. Castellanos A (1973) Estratigrafía y génesis de los valles fluviales en los bloques tectónicos pampeanos. La vida orgánica a través de los últimos tiempos geológicos en cada uno de los bloques. *Instituto de Fisiografía y Geología* 4:1–14.
20. Castellanos A (1980) Estratigrafía geológica de un sector del área de influencia del gran Rosario. *Instituto de Fisiografía y Geología*, 64:1–28.
21. Cohen KM, Finney SC, Gibbard PL, Fan J-X (2013 updated) The ICS International Chronostratigraphic Chart. *Episodes* 36:199–204.
22. Cope ED (1889) The Edentata of North America. *American Naturalist* 23:657–664.
23. Costa da Silva R, Berbert-Born M, Ferreira Bustamante DE, Novaes Santoro T, Sedor F, Avilla LS (2019) Diversity and preservation of Pleistocene tetrapods from caves of southwestern Bahia, Brazil. *Journal of South American Earth Sciences* 90:233–254.
24. Darwin C (1846) Geological observations on South America. Being the third part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, R.N. during the years 1832 to 1836. Smith Elder and Co. 280 pp., London.
25. De Iuliis G, Gaudin TJ, Vicars M (2011) A new genus and species of nothrotheriid sloth (Xenarthra, Tardigrada, Nothrotheriidae) from the late Miocene (Huayquerian) of Peru. *Palaeontology* 54(1):171–205.
26. De Iuliis G, McDonald HG, Stanchly N, Spenard J, Powis TG (2015) *Nothrotheriops shastensis* (Sinclair) from Actun Lak: First record of Nothrotheriidae (Mammalia, Xenarthra, Pilosa) from Belize. *Ameghiniana* 52:153–171.
27. Delsuc F, Catzeflis FM, Stanhope MJ, Douzery EJP (2001) The evolution of armadillos, anteaters and sloths depicted by nuclear and mitochondrial phylogenies: implications for the status of the enigmatic fossil *Eurotamandua*. *Proceedings of the Royal Society B* 268:1605–1615.
28. Delsuc F, Kuch M, Gibb GC, Karpinski E, Hackenberger D, Szpak P, Martínez JG, Mead JI, McDonald HG, MacPhee RDE, Billet G, Hautier L, Poinar HN (2019) Ancient mitogenomes reveal the evolutionary history and biogeography of sloths. *Current Biology*, 29(12):2031–2042.e6. [doi.org](https://doi.org/10.1016/j.cub.2019.09.025).
29. Fariña RA, Tambusso PS, Varela L, Czerwonogora A, Di Giacomo M, Musso M, Bracco R, Gascue A (2014) Arroyo del Vizcaíno, Uruguay: a fossil-rich 30-ka-old megafaunal locality with cut-marked

- bones. *Proceedings of the Royal Society B* 281(1774):20132211.
30. Ferrero BS, Noriega JI, Brunetto E, Nuñez Otaño N (2017) Vertebrate continental assemblage from the last interglacial in southern South America (Entre Ríos, Argentina). *Biostratigraphy and paleoenvironment. Palaeogeography, Palaeoclimatology, Palaeoecology* 466:89–99.
 31. Franco MJ, Vezzosi RI, Brunetto E (2019) First fossil wood from the Northern Pampa (Upper Pleistocene), Santa Fe province, Argentina. *Ameghiniana* 56:493–500.
<https://10.5710/AMGH.13.08.2019.3267>
 32. Frenguelli J (1926) Las barrancas del puerto de Rosario: apuntes sobre su estructura geológica y las causas que determinan su derrumbe. *Publicación del Ministerio de Obras Públicas de la Nación* 1:3–34.
 33. Frenguelli J (1928a) Sobre un perfil geológico del río Carcarañá. *Anales Facultad de Ciencias de la Educación de Paraná* 3:101–130.
 34. Frenguelli J (1928b) Observaciones geológicas en la región costanera sur de la Provincia de Buenos Aires. *Anales de la Facultad de Ciencias Educativas de Paraná* 2:1–145.
 35. Gaudin TJ (2004) Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society* 140:255–305.
 36. Ghilardi AM, Fernandes MA, Bichuette ME (2011) Megafauna from the Late Pleistocene-Holocene deposits of the Upper Ribeira karst area, southeast Brazil. *Quaternary International* 245:369–378.
 37. Green JL (2009) Dental microwear in the orthodontine of the Xenarthra (Mammalia) and its use in reconstructing the palaeodiet of extinct taxa: the case study of *Nothrotheriops shastensis* (Xenarthra, Tardigrada, Nothrotheriidae). *Zoological Journal of the Linnean Society* 156:201–222.
 38. Hoffstetter R (1954) Les Gravigrades (Édentés Xénarthres) des cavernes de Lagoa Santa (Minas Gerais, Brésil). *Annales de Sciences Naturelles, Zoologie* 16:741–764.
 39. Hofreiter M, Poinar HN, Spaulding WG, Bauer K, Martin PS, Possnert G, Pääbo S (2000) A molecular analysis of ground sloth diet through the last glaciation. *Molecular Ecology* 9:1975–1984.
 40. Hofreiter M, Betancourt JL, Pelliza de Sbriller A, Markgraf V, McDonald HG (2003) Phylogeny, diet and habitat of an extinct ground sloth from Cuchillo Curá, Neuquén Province, southwest Argentina. *Quaternary Research* 59:364–378.
 41. ICS (2026) International Commission on Stratigraphy (ICS). International Chronostratigraphic Chart. Last version available in. <http://www.stratigraphy.org/index.php/ics-chart-timescale> (v2026/06).
 42. Iriondo MH (1987) Geomorfología y Cuaternario de la Provincia de Santa Fe (Argentina). *D'Orbignyana* 4:1–54.
 43. Iriondo MH (2010) Geología del Cuaternario de Argentina. Museo Provincial De Ciencias Naturales “Florentino Ameghino”, Santa Fe, Argentina. *Moglia Ediciones* 437 pp.
 44. Iriondo MH, Kröhling DM (2009) From Buenos Aires to Santa Fe: Darwin's observations and modern knowledge. *Rev Asoc Geol Arg* 64:109–123.

45. Iriondo MH (2012) Paleoclimas del Hemisferio Sur. Primeros resultados. Cuaternario y Geomorfología 12:95–104.
46. Kraglievich L (1926) Presencia del género "*Nothrotherium*" Lydek. (= "*Coelodon*" Lund) en la fauna pampeana *Nothrotherium torresi*, n. sp. Revista del Museo de La Plata 29:169–186.
47. Kurre A, DeSantis LRG (2025) Lost giants, lost functions: palaeodietary insights into the ecological niches of Pleistocene ground sloths. Biol. Lett. 21: 20250158.
<https://doi.org/10.1098/rsbl.2025.0158>
48. Kröhling DM (1999) Upper Quaternary geology of the lower Carcarañá Basin, North Pampa, Argentina. Quat In 57/58:135–148.
49. Kröhling DM, Brunetto E (2013) Marco geológico y geomorfología de la cuenca del Arroyo Cululú, provincia de Santa Fe. Bases Conceptuales y Metodológicas para el Ordenamiento Territorial en el Medio Rural – Región Centro, Argentina. In: Giayetto O, Plevich J, Lallana V, Pilatti M (eds) Parte 3: Territorio Santafesino, 1ra Ed. Río Cuarto, pp. 483–512. Libroclíc Ediciones.
50. Kröhling DM, Carignano C (2014) La estratigrafía de los depósitos cuaternarios, en Geología y recursos naturales de la provincia de Córdoba: Córdoba, Argentina. Asoc Geol Arg. Relatorio del XIX Congreso Geológico Argentino, pp 673–724.
51. Kröhling DM, Iriondo M (1999) Upper Quaternary Paleoclimates of the Mar Chiquita Area (North Pampa, Argentina). In: Partridge T, Kershaw P, Iriondo M (eds.) "Paleoclimates of the Southern Hemisphere". Quat In 57/58:149–164.
52. Kröhling DM, Iriondo M (2003) El loess de la Pampa Norte en el bloque de San Guillermo. Rev Asoc Arg Sed 10:137–150.
53. Le Verger K (2023) Xenarthrans of the collection of Santiago Roth from the Pampean Region of Argentina (Pleistocene), in Zurich, Switzerland. Swiss J Palaeontol 142:3.
<https://doi.org/10.1186/s13358-023-00265-7>
54. McDonald HG (1995) Gravigrade Xenarthrans from the early Pleistocene Leisey Shell Pit 1A, Hillsborough County, Florida. Bulletin off Florida Museum of Natural History 37:345–373.
55. McDonald HG (2023) A Tale of Two Continents (and a Few Islands): Ecology and Distribution of Late Pleistocene Sloths. Land 12:1192. <https://doi.org/10.3390/land12061192>.
56. McDonald HG, Jefferson GT (2008) Distribution and habitat of *Nothrotheriops* (Xenarthra, Nothrotheridae) in the Pleistocene of North America. In: Wang X, Barnes LG (eds.) Geology and Vertebrate Paleontology of Western and Southern North America, Contributions in Honor of David P. Whistler. Natural History Museum of Los Angeles County Science Series 41:313–331.
57. McDonald HG, Ruddell MW (2025) First record of the ground sloth *Nothrotheriops* (Xenarthra: Nothrotheriidae) from the central Mississippi River drainage in Arkansas. In: Lucas SG, Morgan GS, Hunt AP, Lichtig AJ (eds.) Fossil Record 10. New Mexico Museum of Natural History and Science Bulletin, 100:145–151 pp.
58. McDonald HG, Dantas MAT, Espinasa-Pereña R, Espinasa L (2026) Xenarthrans from Sistema Calera Cave, Mexico, and radiocarbon and stable isotope analyses of the cave fauna. Revista Mexicana de

59. Oliveira A M, Becker-Kerber B, Cordeiro LM, Borghezán R, Avilla LS, Forancelli Pacheco MLA, Santos CMD (2017) Quaternary mammals from central Brazil (Serra da Bodoquena, Mato Grosso do Sul) and comments on paleobiogeography and paleoenvironments. *Revista Brasileira de Paleontologia* 20:31–44.
60. Paula Couto C de (1971) On two small Pleistocene ground sloths. *Anales de la Academia Brasileira de Ciências (Suplemento)* 43:499–513.
61. Perea D (2007) *Nothrotherium* cf. *N. maquinense* (Xenarthra, Tardigrada) en la Formación Sopas (Pleistoceno tardío de Uruguay). *Revista de la Sociedad Uruguaya de Geología* 14:5–9.
62. Prado JL, Alberdi MT, Bellinzoni J (2021) Pleistocene mammals from Pampean region (Argentina). Biostratigraphic, biogeographic, and environmental implications. *Quaternary* 4(2):1–15.
63. Pujos F, De Iuliis G, Mamani Quispe B, Andrade Flores R (2014) *Lakukullus anatisrostratus*, gen. et sp. nov, a new massive nothrotheriid sloth (Xenarthra, Pilosa) from the middle Miocene of Bolivia. *Journal of Vertebrate Paleontology* 34(5):1243–1248.
64. Quiñones SF, Miño-Boilini AR, Zurita AE (2017) Revisión del perezoso terrestre *Nothropus* (Mammalia, Xenarthra, Tardigrada) del Pleistoceno de Argentina y Bolivia. *Revista Brasileira de Paleontologia* 20(1):121–132.
65. Roth S (1888) Beobachtungen über Entstehung und Alter der Pampas formation in Argentinien. *Zeitschrift Der Deutschen Geologischen Gesellschaft* 40(3):375–464.
66. Rusconi C (1931) La presencia del género *Paleolama* en los yacimientos pleistocénicos de la provincia de Santa Fe. *Publicaciones del Museo "Florentino Ameghino"* pp1–16.
67. Scillato-Yané GJ, Carlini AA, Tonni EP, Noriega JI (2005) Paleobiogeography of the late Pleistocene pampatheres of South America. *Journal of South American Earth Sciences* 20: 131–138.
68. Thalmeier MB, Kröhling DM, Brunetto E (2021) The geomorphology and Late Quaternary sediment record of the Salado/Juramento fluvial megafan, Central Andes foreland basin (Chaco plain, Argentina). *Geomorphology* 373:107495. <https://doi.org/10.1016/j.geomorph.2020.107495>.
69. Thompson RS, Van Devender TR, Martin PS, Foppe T, Long A (1980) Shasta ground sloth (*Nothrotheriops shastense* Hoffstetter) at Shelter Cave, New Mexico: environment, diet and extinction. *Quaternary Research* 14:360–376.
70. Toledo M (2011) El legado Lujanense de Ameghino: revisión estratigráfica de los depósitos Pleistocenos-Holocenos del valle del río Luján en su sección tipo. Registro paleoclimático en la pampa de los estadios OIS 4 al OIS 1. *Revista de la Asociación Geológica Argentina* 68(1):121–167.
71. Tonni EP (2011) Ameghino y la estratigrafía pampeana un siglo después. *Asociación Paleontológica Argentina: Publicación Especial* 12:69–79.
72. Varela L, Tambusso PS, McDonald HG, Vezzosi RI, Fariña RA (2023) Occurrence of the ground sloth *Nothrotheriops* (Xenarthra, Folivora) in the Late Pleistocene of Uruguay: new information on its dietary and habitat preferences based on stable isotope analysis. *Journal of Mammalian Evolution* 30:561–576. <https://doi.org/10.1007/s10914-023-09660-w>.

73. Vázquez M, Montellano Ballesteros M, Barrón Ortiz CI, Ramos Heredia JE, Escoto Moreno JA (2025) Nuevo material de *Nothrotheriops* sp. (Mammalia: Xenarthra) de la fauna El Cedazo, Aguas calientes, México. Boletín de la Sociedad Geológica Mexicana 77(1)A021024:1–13. <http://dx.doi.org/10.18268/BSGM2025v77n1a021024>.
74. Vezzosi RI (2015). Diversidad de los mamíferos del Pleistoceno de la Provincia de Santa Fe, Argentina: aspectos taxonómicos, bioestratigráficos y paleobiogeográficos relacionados. PhD thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Plata, La Plata, Buenos Aires. <http://naturalis.fcnym.unlp.edu.ar/id/20151130001422>.
75. Vezzosi RI, Kerber L (2018). The southernmost record of a large erethizontid rodent (Hystricomorpha: Erethizontoidea) in the Pleistocene of South America: biogeographic and paleoenvironmental implications. J. South Am Earth Sci 82:76–90. <https://doi.org/10.1016/j.jsames.2017.12.015>.
76. Vezzosi RI, Brunetto E, Zalazar MC (2019a) El registro fósil de vertebrados del Cuaternario de Santa Fe (Argentina): primera Actualización. In: Nasif N, Esteban G, Chiesa J, Zurita A, Georgieff S (eds) Mioceno al Pleistoceno del Centro y Norte de Argentina. Opera Lilloana, Tucumán, Argentina, pp. 52:638–670.
77. Vezzosi RI, Brandoni D, Brunetto E, Zalazar MC (2019b.) New remains of Nothrotheriinae (Mammalia, Xenarthra) from late Pleistocene fluvial deposits of Northern Pampa (Santa Fe Province, Argentina). J. South Am Earth Sci 89:47–54.
78. Weinstock J, Shapiro B, Prieto A, Marín JC, González BA, Gilbert MTP, Willerslev E (2009) The Late Pleistocene distribution of vicuñas (*Vicugna vicugna*) and the “extinction” of the gracile llama (*Lama gracilis*): New molecular data. Quaternary Science Reviews 28:1369–1373.
79. Voglino D, Carrillo-Briceño JD, Furrer H, Balcarcel A, Rangel-de Lazaro G, Fernández GA, Forasiepi AM (2023) Pampean megamammals in Europe: the fossil collections from Santiago Roth. Swiss J Palaeontol 142:25. <https://doi.org/10.1186/s13358-023-00283-5>.
80. Zamorano M, Vezzosi RI, Mones A (2026) Anatomy of the most reinforced caudal tube in an enigmatic specimen of *Panochthus* (Xenarthra, Glyptodontidae): chronology and paleoenvironmental implications, and taxonomic revision of *Panochthus florensis*. Quat In 769:110288. <https://doi.org/10.1016/j.quaint.2026.110288>.
81. Zurita AE, Miño-Boilini AR, Francia A, Arenas-Mosquera (JE 2012) The Pleistocene Glyptodontidae Gray, 1869 (Xenarthra: Cingulata) of Colombia and some considerations about the South American Glyptodontinae. Revista Brasileira de Paleontologia 15(3):273–280.

Table

TABLE 1. Measurements (in mm) of molariform toothrow length and mandibular depth of Nothrotheriinae hemimandibles compared with MRP-G-Pv 041. The hypsodonty index (HI) was calculated for each complete specimen and is provided in the table.

Taxon / Specimen	Length	Depth	HI
<i>Mionothropus cartellei</i> / LACM ⁴⁶⁰⁹ / ₁₁₇₅₃₃	36.8	45	1.223
<i>Nothropus carcaranensis</i> / MACN Pv 11555	44.1	47.7	1.081
<i>Nothropus priscus</i> / MACN Pv 975	33.5	36.1	1.077
<i>Nothropus tarijensis</i> / MACN A 1112	53.9	54.2	1.005
<i>Nothrotherium maquinense</i> / CMGS-c10-1.	40.5	36.5	0.901
<i>Nothrotherium maquinense</i> / MNRJ 2115	33	30	0.909
<i>Nothrotherium maquinense</i> / UCMG 1020	37	31.4	0.849
<i>Nothrotheriops</i> sp. / INAH PF 2050-428	46.7	43.2	0.925
<i>Nothrotheriops</i> sp. / MRP-G-PV 041	43.3	44	1.016
<i>Nothrotheriops shastensis</i> / GRCA 21959	50.1	48.6	0.970
<i>Nothrotheriops shastensis</i> / LACM 1840	45.5	48.3	1.062
<i>Nothrotheriops shastensis</i> / LACM 5-5-9	42.9	38.7	0.902
<i>Nothrotheriops shastensis</i> / LACM 3029	54.6	56.9	1.042
<i>Nothrotheriops shastensis</i> / LACM 3031	53.5	51.5	0.963
<i>Nothrotheriops shastensis</i> / LACM 15125	53.5	51	0.953
<i>Nothrotheriops shastensis</i> / LACM 21749	42.3	40.8	0.965
<i>Nothrotheriops shastensis</i> / LACM HC 166	57.3	54.3	0.948
<i>Nothrotheriops shastensis</i> / LACM HC 203	57.3	57.7	1.007
<i>Nothrotheriops shastensis</i> / LACM HC 418	52.3	52.7	1.008
<i>Nothrotheriops shastensis</i> / LACM HC 636	53.7	53.5	0.995
<i>Nothrotheriops shastensis</i> / LACM HC 637	50	60.3	1.206
<i>Nothrotheriops shastensis</i> / UA no #	53	52.4	0.989
<i>Nothrotheriops texanus</i> / UF 64348	44.2	42.5	0.962
<i>Nothrotheriops texanus</i> / UF 64349	31.9	28.5	0.893
<i>Nothrotheriops texanus</i> / UF 83100	47.5	43.9	0.924
<i>Nothrotheriops texanus</i> / UF 83594	44.5	46.4	1.043
<i>Nothrotheriops texanus</i> / UF 83900	43.1	41.8	0.970
<i>Nothrotheriops texanus</i> / UF 84626	45.6	46.8	1.026

<i>Nothrotheriops texanus</i> / UF 86121	45.7	44.3	0.969
<i>Nothrotheriops texanus</i> / UF 86899	45.4	46.2	1.018
<i>Nothrotheriops texanus</i> / UMMP V3352	45	50.3	1.118
<i>Nothrotheriops texanus</i> / USNM 11665	47.7	51	1.069
<i>Pronothrotherium mirabilis</i> / FC DPV 271	25.7	29.2	1.136
<i>Pronothrotherium mirabilis</i> (= <i>P. figueirasi</i>) / FC DPV 270	30.3	26.5	0.875
<i>Pronothrotherium typicum</i> / MACN Pv 8140	37	34.5	0.932

Figures

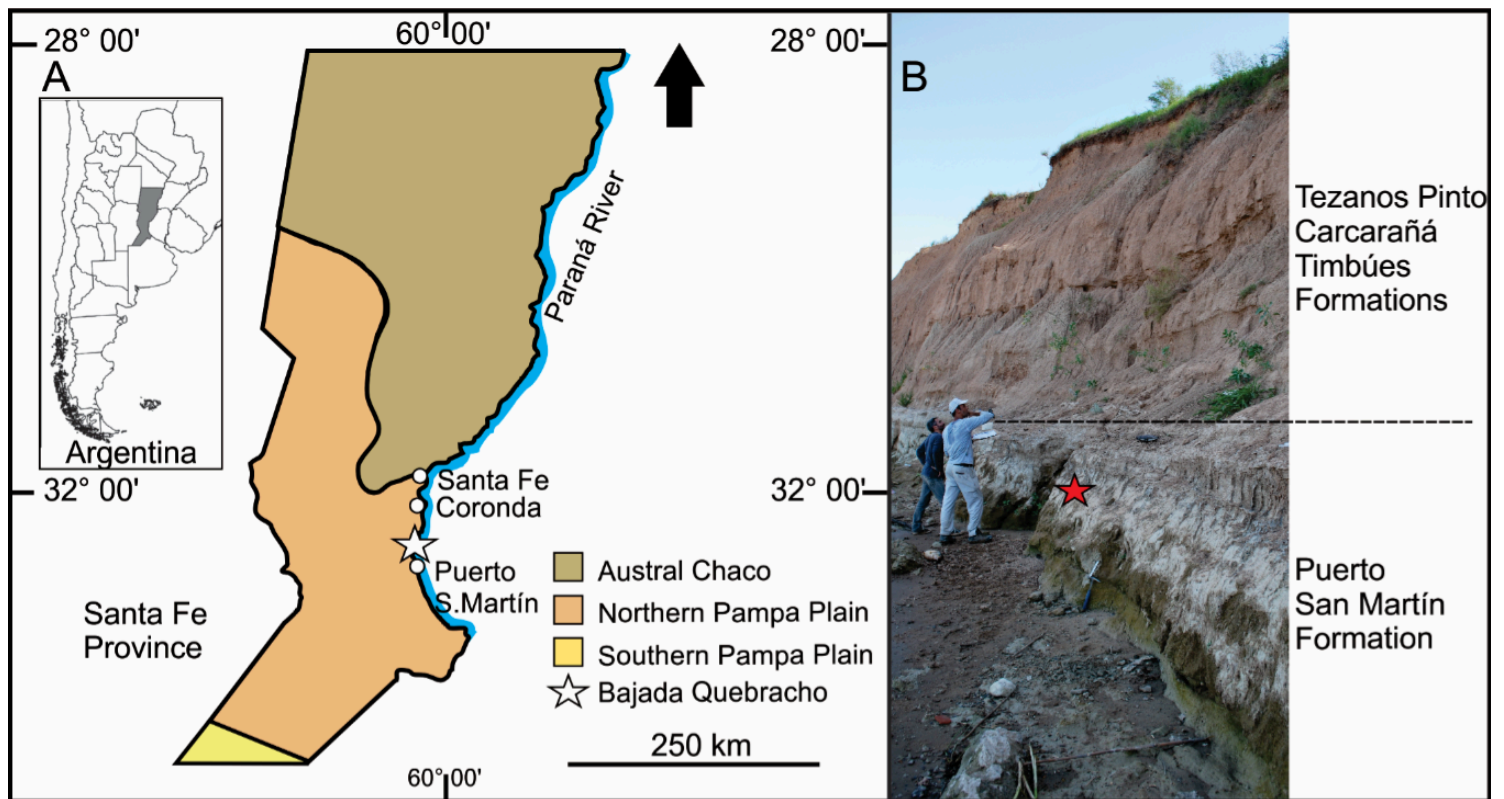


Figure 1

A) Sketch map showing the *Nothrotheriops* sp. (MRP-G-Pv 041) record from Northern Pampa plain, Santa Fe Province, Argentina. B) deposits of the Puerto San Martín Formation at Bajada Quebracho from which *Nothrotheriops* sp. (MRP-G-Pv 041, red star) was recovered.

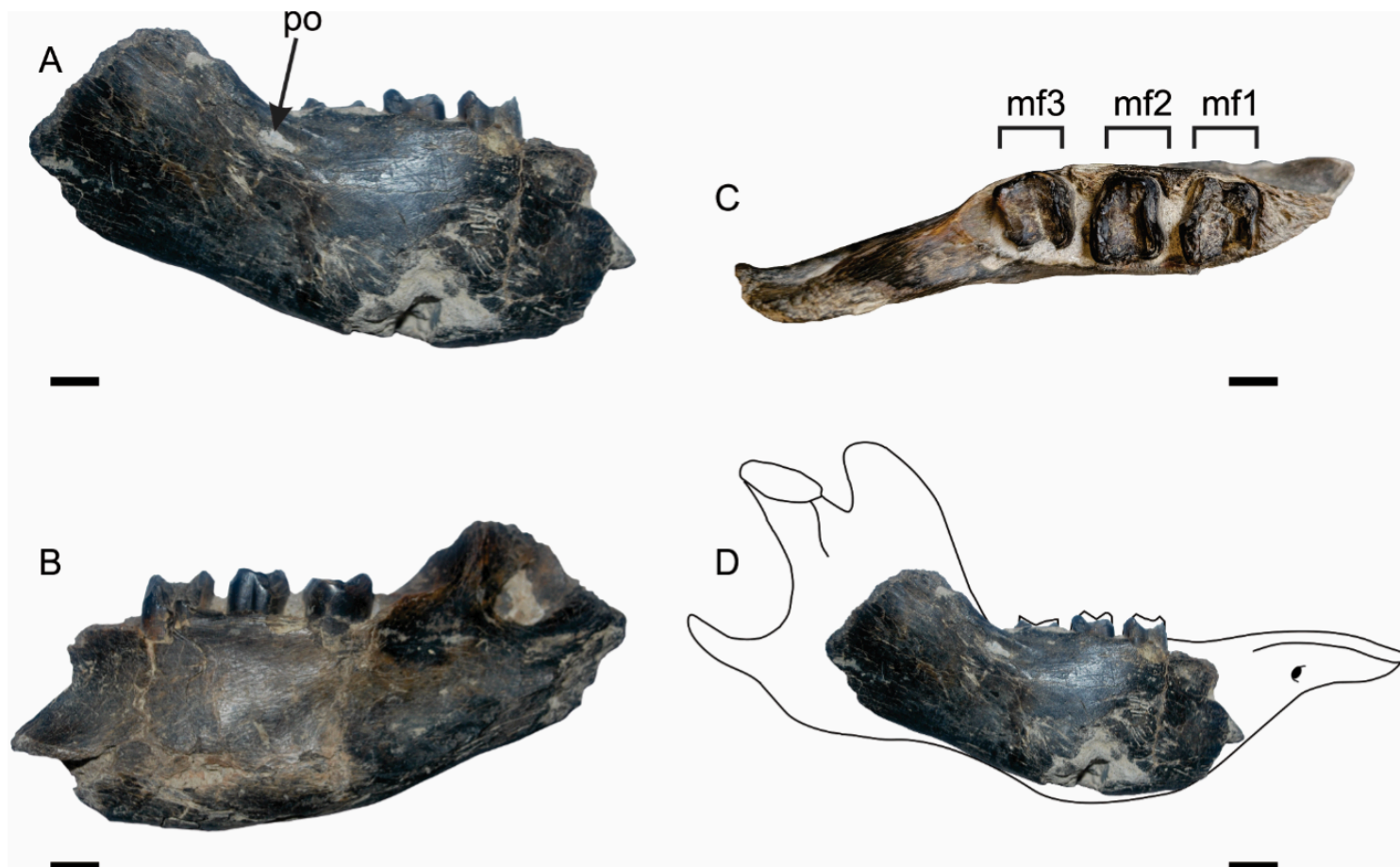


Figure 2

Fragment of the right dentary of MRP-G-Pv 041 in A) labial, B) lingual, C) occlusal views, and D) schematic reconstruction of the right dentary in labial view. Abbreviations: mf, molariform tooth; po, posterolateral opening of the mandibular canal. Scale bars equal 1 cm.

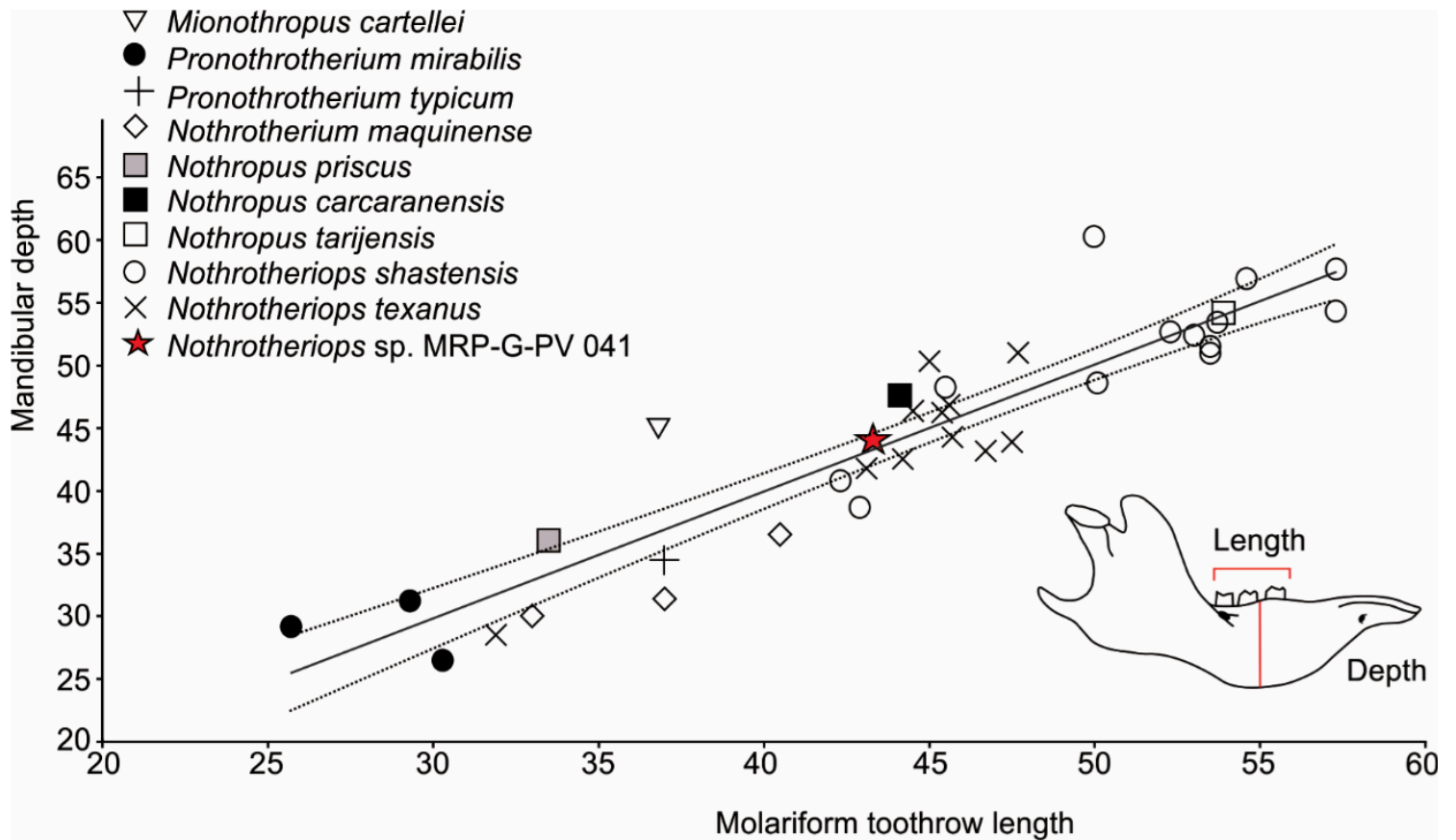


Figure 3

Linear regression of mandibular depth against molariform toothrow length for fossil Neogene and Quaternary American Nothrotheriinae. The position of MRP-G-Pv 041 (red star) is indicated for comparison. Dotted lines represent the 95% bootstrapped confidence interval.



Figure 4

Comparison in occlusal view of A) MRP-G-Pv 041, B) *Nothropus carcaranensis* from South America (MACN 11555, Santa Fe, Argentina), and C) *Nothrotheriops* sp. from North America (INAH PF 2050-428, Aguas Calientes, México). Abbreviation: mf, molariform tooth Scale bars equal 1 cm.

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