



# AMEGHINIANA

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# AN ENIGMATIC NOTHROTHERIINAE (XENARTHRA, TARDIGRADA) FROM THE PLEISTOCENE OF ARGENTINA

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**Key words.** Ground Sloths. Notrotheriidae. South America. North America. Femur. Dentary.

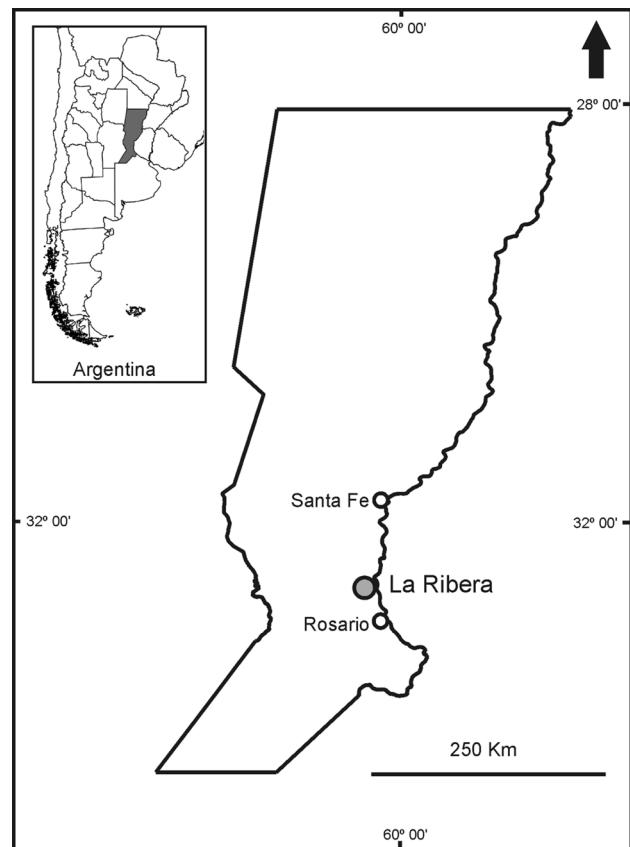
Most of the genera and species that were traditionally considered as nothrotheres (*sensu lato*) currently are considered as restricted to the Notrotheriinae clade (e.g., *Nothropus* Burmeister, 1882, *Nothrotherium* Lydekker, 1889, *Pronothrotherium* Ameghino, 1907, *Nothrotheriops* Hoffstetter, 1954, *Mionothropus* De Iuliis, Gaudin and Vicars, 2011) or as basal megatherioids (e.g., *Hapalops* Ameghino, 1887, *Schismotherium* Ameghino, 1887, *Pelecyodon* Ameghino, 1891) (see Burmeister, 1882; Ameghino, 1887, 1891, 1907; Lydekker, 1889; Hoffstetter, 1954; Gaudin, 2004; De Iuliis *et al.*, 2011; Pujos *et al.*, 2011). Members of the Notrotheriinae are known from middle Miocene (Langhian–Serravallian Stage/Age) rocks in Bolivia and Argentina, represented by the genus "*Xyophorus*" (see Brandoni, 2014 for a discussion of these records). They are also known from Quaternary deposits of South America (Lujanian South America Land Mammal Age) and North America (Irvingtonian and Rancholabrean North America Land Mammal Ages). Quaternary taxa of this group are mainly included in two genera, *i.e.*, *Nothrotherium*, mainly recorded from the Pleistocene of Brazil (Hoffstetter, 1954; Paula Couto, 1971; Cartelle and Fonseca, 1983) –but also reported from the Pleistocene of Argentina and Uruguay (Kraglievich, 1926; Perea, 2007)– and *Nothrotheriops*, recorded in the Quaternary of the United States, Mexico and Belize (McDonald, 1985, 1995; McDonald and Jefferson, 2008; Akersten and McDonald, 1991; Bell *et al.*, 2004; De Iuliis *et al.*, 2015; among others). Hofreiter *et al.* (2003) reported sloth dung from Cuchillo

Curá, Neuquén Province (southwestern Argentina). This dung sample yielded DNA belonging to a nothrothere. As no body-fossil of a nothrothere is known from that region, assignment to a lower taxonomic level is not possible at this time. Remains of both the South and North American genera are relatively common and many of their species (e.g., *Nothrotherium maquinense* [Lund, 1839], *Nothrotheriops texanus* [Hay, 1916], *Nothrotheriops shastensis* [Sinclair, 1905]) are represented by large samples and in some cases by nearly complete specimens, along with mummified remains and dung.

The nothrotheriine sloth, *Nothropus priscus* Burmeister, 1882, was erected on the basis of an isolated mandible with teeth from the Pleistocene of Argentina. An additional specimen was identified by Ameghino (1907) as *Nothropus taricensis* (Burmeister, 1887) from the Pleistocene of Bolivia, also based on a partial dentary. *Nothropus carcaranensis* Bordas, 1942, was based on a partial dentary from the Pleistocene of Santa Fe Province, Argentina (see below). Species of *Nothropus* are characterized by their bilophodont and rectangular molariforms with a shape and occlusal surface very similar to the morphology present in *Nothrotherium* and *Nothrotheriops*. However *Nothropus priscus* and *Nothropus taricensis* retain an alveolus for a small anterior caniniform tooth, separated by a diastema from the three posterior molariforms, whereas in the genera *Nothrotherium* and *Nothrotheriops* and in *Nothropus carcaranensis* the caniniform is absent.

The type specimen of *Nothropus carcaranensis* was collected by Osvaldo Coronel from the cliffs along the Carcarañá River, near the village of La Ribera, Santa Fe Province. Coronel donated many fossil remains collected at Carcarañá River –including the type of *Nothropus carcaranensis*– to the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN). Bordas (1942) studied the dentary collected by Coronel and assigned it to the genus *Nothropus* as *N. carcaranensis* despite the absence of the caniniform, the primary defining feature of the genus distinguishing it from *Nothrotherium*.

Among the fossil remains collected by Coronel at Carcarañá River and donated to the MACN, there are also two undescribed ground sloth femora showing several features in common with the femora of the Quaternary nothrotheriines. The aim of this contribution is to describe the femora, provide a taxonomic assignment for them, and to discuss some of the taxonomic and biogeographical aspects of these records.



**Figure 1.** Location map. Grey circle indicates the location of village of La Ribera, Santa Fe Province, Argentina.

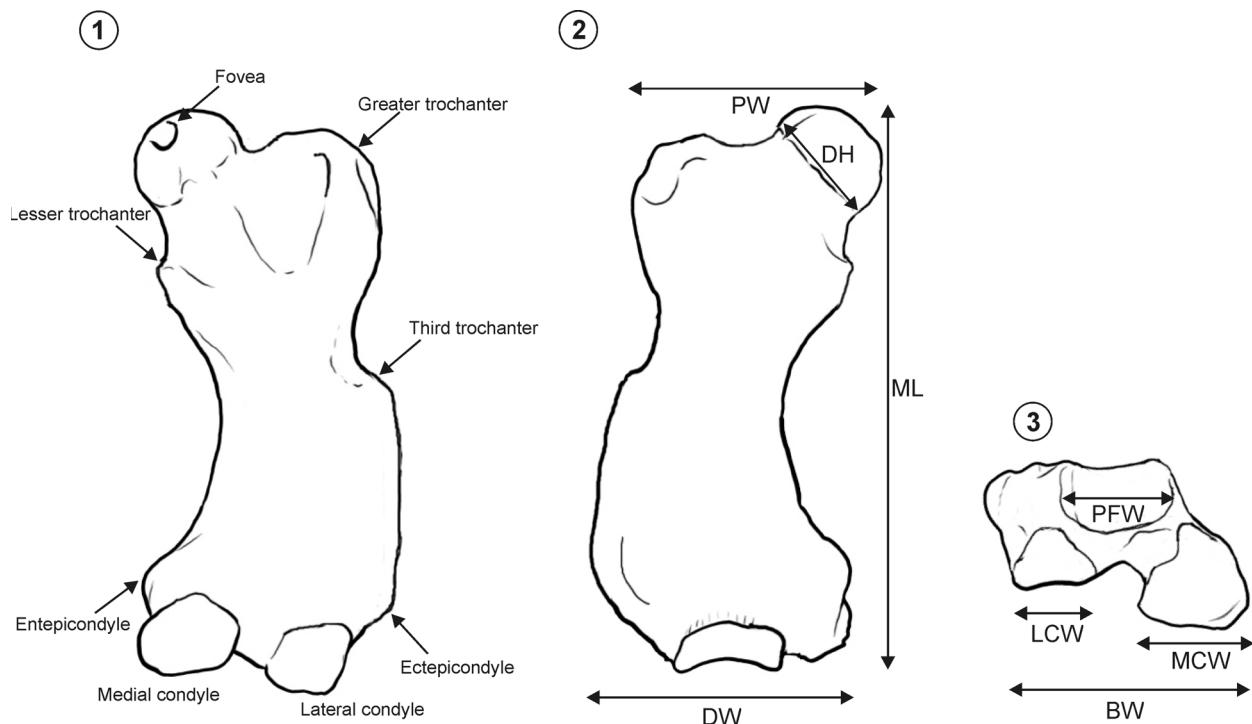
**Institutional abbreviations.** FMNH, Field Museum of Natural History, Chicago, USA; GRCA, Grand Canyon National Park, USA; LACM-HC, Hancock Collection, Natural History Museum of Los Angeles County, Los Angeles, USA; MACN A, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Ameghino de Paleovertebrados, CABA, Argentina; MACN Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional de Paleovertebrados, CABA, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; NSMLV-BLM, Nevada State Museum, Las Vegas-Bureau of Land Management, Las Vegas, USA; UA, University of Arizona, Tucson, USA; 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; ZMUC, Zoological Museum University of Copenhagen, Copenhagen, Denmark.

**Anatomical abbreviations.** AL, alveolar length; BW, bicondylar width; DH, diameter of the head; DW, distal width; LCW, lateral condyle width; MCW, medial condyle width; MD, mandible depth; ML, medial length; PW, proximal width; PFW, patellar facet width.

## GEOLOGICAL SETTING

Most of the fossils remains collected by Osvaldo Coronel and his son (see Bordas, 1942) were found near the railway bridge over the Carcarañá River, at the village of La Ribera, Santa Fe Province, Argentina ( $32^{\circ} 38' 20''$  S,  $60^{\circ} 48' 52''$  W), at 25 meters above the sea level. However, their exact stratigraphic provenance is unknown. Two late Pleistocene units are present at this site (Fig. 1), i.e., the Timbúes and the Puerto San Martín (overlying the former) formations.

The Puerto San Martín Formation derives from the discontinuous accumulation of fine aeolian sediments. The accumulation environment was semi-permanent swamps, with intercalated periods of subaerial conditions (loess) (Iriondo and Kröhling, 2009). In several places in Santa Fe Province the Puerto San Martín Formation overlies the Ituzaingó Formation (late Miocene–Pliocene), but at some sites (e.g., the Carcarañá River at the village of La Ribera), between the two mentioned formations there are several intercalated paleochannels in-filled with alluvial and palu-



**Figure 2.** Morphology of the femur of Nothrotheriinae and measurements used; 1, posterior view; 2, frontal view; 3, distal view.

dal deposits (*i.e.*, the Timbúes Formation) (see Iriondo and Kröhling, 2009).

## MATERIALS AND METHODS

For the femora, eight measurements were taken on 21 specimens (Fig. 2; Tab. 1); for the dentaries, two measurements were taken on 25 specimens (Tab. 2). All measurements are in millimeters.

## SYSTEMATIC PALEONTOLOGY

TARDIGRADA Latham and Davies in Forster, 1795

NOTHROTHERIIDAE Ameghino, 1920

NOTHROTHERIINAE Ameghino, 1920

**Nothrotheriinae indet.**

Figure 3

**Referred material.** MACN Pv 14148, complete right femur (Fig. 3.1–4); MACN Pv 14149 almost complete left femur (Fig. 3.5–8).

**Geographic provenance.** Railway bridge over the Carcarañá

River, village of La Ribera, Santa Fe Province, Argentina ( $32^{\circ} 38' 20''$  S;  $60^{\circ} 48' 52''$  W) (Fig. 1).

**Stratigraphic provenance.** Cliffs along the Carcarañá River; either the Timbúes or Puerto San Martín Formation (late Pleistocene).

## Description and Comparisons

MACN Pv 14148 is a complete femur (Fig. 3.1–4) and MACN Pv 14149 is almost complete, but lacking the ectepicondyle (Fig. 3.5–8).

As is characteristic in most femora of late Pleistocene sloths, the shaft of MACN Pv 14148 and MACN Pv 14149 is wide and antero-posteriorly flattened. Both femora are similar to that of *Nothrotheriops shastensis* in size (Tab. 1), and resemble it also in being medio-laterally broader distally than proximally, and because the third trochanter distally forms a continuous surface with the lateral epicondyle (ectepicondyle). In other Nothrotheriinae such as *Nothrotherium*, *Pronothrotherium*, and *Mionothropus* the femur is more elongated and gracile and the third trochanter is distinct from the ectepicondyle as also occurs in the basal megatheriid *Hapalops*.

TABLE 1. Femur measurements (in mm).

Taxon	Catalog Number	MD	DH	PW	DW	LCW	MCW	BW	PFW
<i>Nothrotheriops shastensis</i>	LACM 21620	379.7	77.9	162.9	184.1	—	71.5	—	—
<i>Nothrotheriops shastensis</i>	LACM 21614	368.2	80.4	168.3	183.2	60.2	76.6	158.4	72.1
<i>Nothrotheriops shastensis</i>	LACM 18919	—	77.5	145.6	170.5	49.1	69.6	142.2	62.8
<i>Nothrotheriops shastensis</i>	LACM HC 428	398.1	86.2	182.1	193.6	59.9	74.6	167.6	71.1
<i>Nothrotheriops shastensis</i>	LACM 21744	347.6	79.3	155.4	171.4	—	—	—	59.8
<i>Nothrotheriops shastensis</i>	NSMLV-BLM-P149	359.2	81.9	163.5	187.2	60.5	66.1	157.2	64.9
<i>Nothrotheriops texanus</i>	UF 81500	341	78.1	168.3	172.3	50.4	66.5	149.9	62.1
<i>Nothrotheriops texanus</i>	UF 86733	362.2	82.9	175.2	171.8	52.3	67*	158.2	—
<i>Nothrotheriops texanus</i>	UF 80038	367.7	86	160.9	195.5	59.1	74.1	163.8	67.3
<i>Nothrotheriops texanus</i>	UF 64350	—	73.3	156.8	—	—	—	—	—
<i>Nothrotheriops texanus</i>	UF 84931	347	82	—	185.8	—	66.9	153.9	69.7
<i>Nothrotheriops texanus</i>	UF 86355	361.2	81.2	172.8	181.7	—	—	—	58.7
<i>Nothrotheriops texanus</i>	UF 80211	362.7	80	167.2	—	62	68.5	161.4	—
<i>Nothrotheriops texanus</i>	UF 81362	347.3	76.8	160	—	54.4	—	—	—
<i>Nothrotheriops texanus</i>	UF 87012	374	81.5	171.7	186.7	—	70.3	163.4	63.8
<i>Nothrotheriops texanus</i>	UF 86734	359.5	82.2	174.1	178.5	44.2	68.6	160	—
<i>Pronothrotherium typicum</i>	FMNH P14515	297	67	146.7	148.2	45.4	57.6	123.2	45.7
<i>Nothrotherium maquinense</i>	ZMUC 5711	243.5	50	94.7	93.5	28.7	35.8	85.7	37.3
<i>Nothrotherium torresi</i>	MLP 4-50	410	88	194	205	50*	55	146.1*	55*
<i>Nothrotheriinae indet.</i>	MACN Pv 14148	394	98	190	218	77.8	94.5	207.6	74.1
<i>Nothrotheriinae indet.</i>	MACN Pv 14149	365	85	180	—	63.7	77.5	183.3	72.3

\*, approximate measurement.

The head is spherical and prominent (Fig. 3.1, 5), especially in MACN Pv 14149, whereas in *Mionothropus* and *Hapalops* it is relatively smaller. In MACN Pv 14148 the fovea ligamentum teres is a shallow and semi-oval depression on the posteromedial part of the articular surface of the head, with its long diameter of 25 mm and the lesser diameter 17 mm; the fovea is connected to the periphery of the head by a shallow sulcus of 17 mm in width. In MACN Pv 14149, the fovea is also semi-oval in outline, its long diameter is 31 mm and its lesser diameter is 14 mm, and it presents a little scar that closes the canal connecting the fovea with the periphery. In *Nothrotheriops shastensis* and *Nothrotheriops*

*texanus* the fovea is small and entirely enclosed by the articular surface of the head. In *Mionothropus* and *Nothrotherium torresi* Kraglievich, 1926 (MLP 4-50) the fovea is relatively deep and also enclosed by the articular surface of the head.

The greater trochanter is prominent (86 mm for the antero-posterior diameter in MACN Pv 14148 and 70 mm in MACN Pv 14149, Fig. 3.1, 5) and placed distally with respect to the distal margin of the head (Fig. 3.2, 6). In *Nothrotheriops* and *Mionothropus* the position of the greater trochanter is also similar to that of MACN Pv 14148 and MACN Pv 14149; whereas in *Hapalops* the proximal margin of the

TABLE 2. Dentary measurements (in mm).

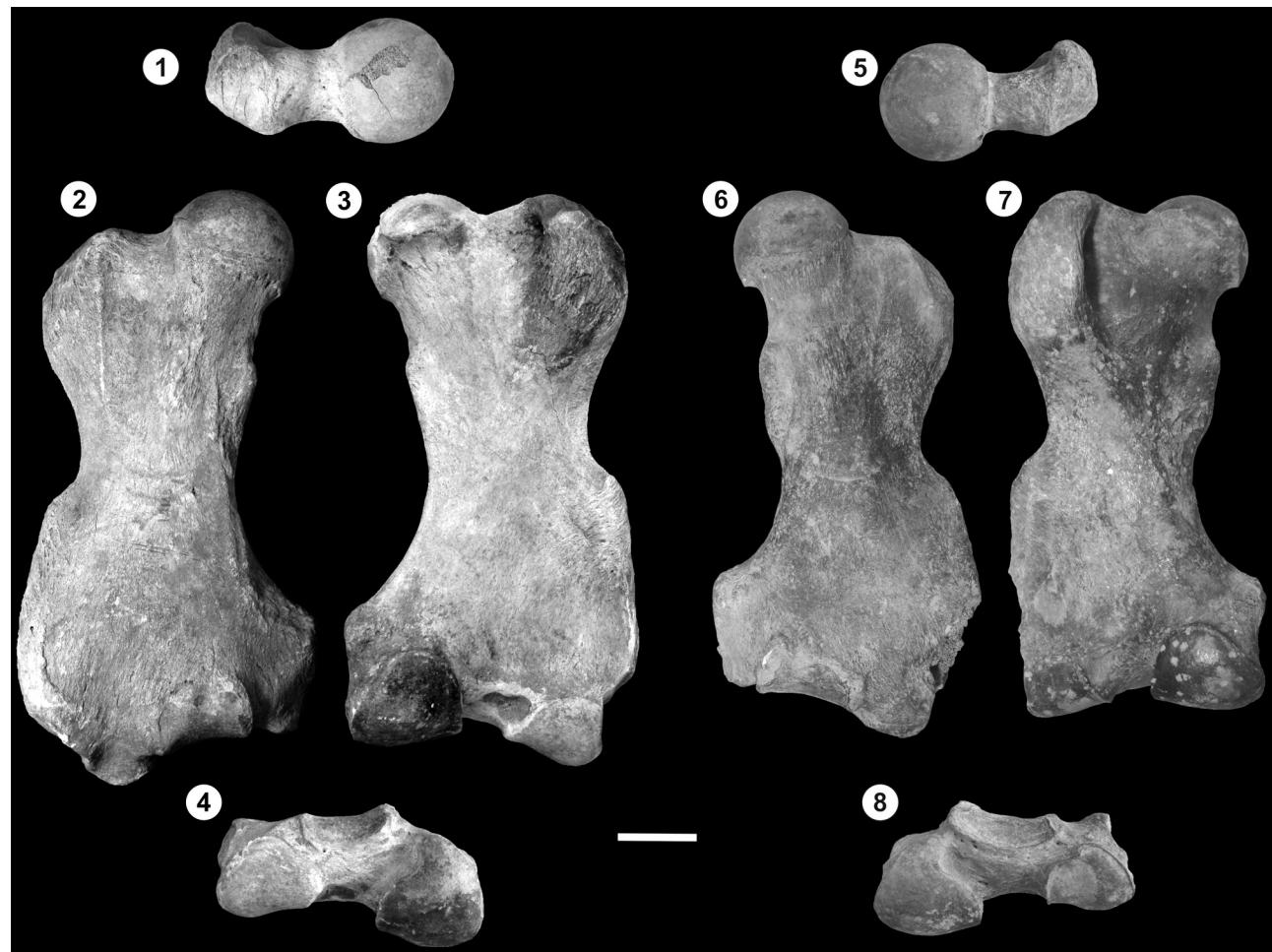
Taxon	Catalog Number	AL	MD
<i>Nothropus priscus</i>	MACN Pv 975	33.5	36.1
<i>Nothropus taricensis</i>	MACN A 1112	53.9	54.2
<i>Nothropus carcaranensis</i>	MACN Pv 11555	44.1	47.7
<i>Nothrotheriops texanus</i>	UF 64348	44.2	42.5
<i>Nothrotheriops texanus</i>	UF 64349	31.9	28.5
<i>Nothrotheriops texanus</i>	UF 86899	45.4	46.2
<i>Nothrotheriops texanus</i>	UF 86121	45.7	44.3
<i>Nothrotheriops texanus</i>	UF 84626	45.6	46.8
<i>Nothrotheriops texanus</i>	UF 83100	47.5	43.9
<i>Nothrotheriops texanus</i>	UF 83594	44.5	46.4
<i>Nothrotheriops texanus</i>	UF 86984	43.1	41.8
<i>Nothrotheriops texanus</i>	USNM 11665	47.7	51
<i>Nothrotheriops texanus</i>	UMMP V3352	45	50.3
<i>Nothrotheriops shastensis</i>	LACM 3029	54.6	56.9
<i>Nothrotheriops shastensis</i>	LACM 3031	53.5	51.5
<i>Nothrotheriops shastensis</i>	LACM 15125	53.5	51
<i>Nothrotheriops shastensis</i>	LACM HC 636	53.7	53.5
<i>Nothrotheriops shastensis</i>	LACM HC 637	50	60.3
<i>Nothrotheriops shastensis</i>	LACM HC 418	52.3	52.7
<i>Nothrotheriops shastensis</i>	LACM HC 166	57.3	54.3
<i>Nothrotheriops shastensis</i>	LACM HC 203	57.3	57.7
<i>Nothrotheriops shastensis</i>	LACM 5-5-9	42.9	38.7
<i>Nothrotheriops shastensis</i>	LACM 21749	42.3	40.8
<i>Nothrotheriops shastensis</i>	GRCA 21959	50.1	48.6
<i>Nothrotheriops shastensis</i>	UA no Numb.	53	52.4

greater trochanter nearly reaches the level of the head. In *Nothrotherium* the position is intermediate between that described for *Hapalops* and that for *Nothrotheriops* and *Mionothropus*.

In MACN Pv 14148 the crest between the head and the greater trochanter is slightly concave (Fig. 3.2); whereas in MACN Pv 14149 it is straight (Fig. 3.6). In *Mionothropus* the crest resembles that of MACN Pv 14149. In *Nothrotherium*

*maquinense* (ZMUC 5711) and *Nothrotherium torresi* the crest is more similar to that of MACN Pv 14149, whereas in *Hapalops* the crest is very concave. In *Nothrotheriops texanus* this crest is straight.

As in some specimens of *Nothrotheriops*, the lesser trochanter is not prominent as in other nothrotheriines (*i.e.*, *Nothrotherium*, *Mionothropus*, *Pronothrotherium*) and *Hapalops*. In MACN Pv 14149 the lesser trochanter is more



**Figure 3.** Femora of *Nothrotheriinae* indet. 1–4, MACN Pv 14148, right femur; 5–8, MACN Pv 14149, left femur. 1, 5, proximal view; 2, 6, frontal view; 3, 7, posterior view; 4, 8, distal view. Scale bar= 50 mm.

prominent than in MACN Pv 14148, forming a rugose protuberance projecting from the medial surface of the femur.

Distal to the greater trochanter and to the lesser trochanter, the shaft of the femur decreases in width. This is the result of the very concave lateral margin at mid-shaft (Fig. 3.2–3, 6–7).

As in *Nothrotheriops*, the third trochanter is prominent, and forms a rugose surface that is connected with the ectepicondyle (Fig. 3.2–3, 6–7). Thus, the distal half of the femur is wider than the proximal. In *Hapalops*, *Pronothrotherium*, and *Nothrotherium maquinense* the third trochanter is well developed and projects laterally, while in *Nothrotherium torresi* the projection of the third trochanter is less pronounced than in *Nothrotherium maquinense*.

As in *Nothrotherium*, *Nothrotheriops*, and *Pronothrotherium*, the patellar trochlea is separated from the medial and

lateral condyles (Fig. 3.4, 8); whereas in *Mionothropus* the medial condyle is almost in contact with the patellar facet. The prominent medial margin of the patellar trochlea results from the medio-laterally concave surface of the patellar trochlea; the dorsal margin is not straight (it is sigmoid).

The medial condyle is pyriform in outline (Fig. 3.4, 8); in MACN Pv 14148, its apex is separated from the medio-distal margin of the patellar trochlea by a surface of 20 mm of non-articular bone, and in MACN Pv 14149 the separation is 11 mm. In *Nothrotheriops* and *Nothrotherium* the separation between the medial condyle and the patellar trochlea resembles that of MACN Pv 14148 and MACN Pv 14149.

As in *Nothrotheriops*, the lateral condyle is pentagonal in outline (Fig. 3.4, 8); in MACN Pv 14148 it is separated from the patellar trochlea by a 13 mm wide sulcus, whereas in MACN Pv 14149 the width of the sulcus is 11 mm.

## DISCUSSION

The general morphology of MACN Pv 14148 and MACN Pv 14149 more closely resembles the femur of *Nothrotheriops* than any of the other known South American late Pleistocene nothrotheriines. Although a bit larger, both specimens are also more similar in size to those of *Nothrotheriops shastensis* and share several features with this species, *i.e.*, shape and position of the greater trochanter, development of the lesser trochanter, presence of connection between the third trochanter and the ectepicondyle, distal half of the femur wider, locations and relationships of the distal condyles. However, MACN Pv 14148 and MACN Pv 14149 differ from the femur of *Nothrotheriops shastensis* by the shape of the fovea ligamentum teres. Based on their morphology, MACN Pv 14148 and MACN Pv 14149 could be referred to *Nothrotheriops*, a genus exclusively recorded from the Pleistocene of North America and Belize, making this the first record of the genus outside its known geographical distribution. An alternative hypothesis is also plausible: MACN Pv 14148 and MACN Pv 14149 were recovered from the same locality where the type specimen

of *Nothropus carcaranensis* (MACN Pv 11555) was collected; however, the femur of *Nothropus carcaranensis* is unknown, the species is based only on a partial mandible (Fig. 4) and there are no known associations of cranial and post-craniol remains of this taxon.

The dentary of *Nothropus carcaranensis* (Fig. 4) is similar in size to those of *Nothrotheriops texanus*, and is slightly smaller than most of the specimens assigned to *Nothrotheriops shastensis* (Fig. 5, Tab. 2). Additionally, *Nothropus carcaranensis*, *Nothrotheriops texanus*, and *Nothrotheriops shastensis* share several features: the caniniform is absent, and the molariforms are nearly rectangular in outline, with the mesial and distal lophids separated by a labially open transverse valley, and with vertical grooves on the labial and lingual faces (Fig. 4); in contrast, the caniniform is present in *Nothropus priscus* and *Nothropus taricensis*.

Given the close similarity in size of the dentaries of *Nothrotheriops* and *Nothropus*, it is not unreasonable to expect that they may also have femora similar in size. Specimens MACN Pv 14148 and MACN Pv 14149 have a *Nothrotheriops*-type morphology and are similar in size to those of *Nothrotheriops shastensis*, so the assignment of

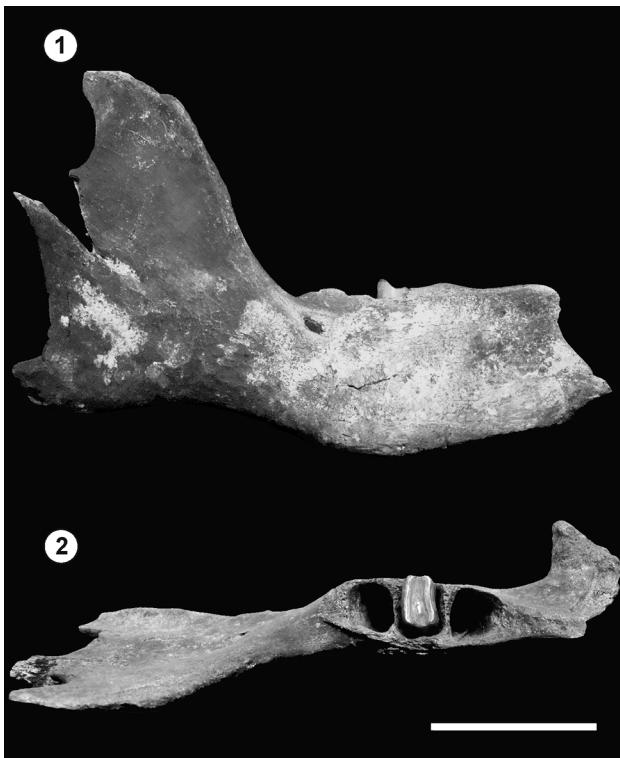


Figure 4. *Nothropus carcaranensis*; MACN Pv 11555, right dentary in 1, lateral view; 2, occlusal view. Scale bar= 50 mm.

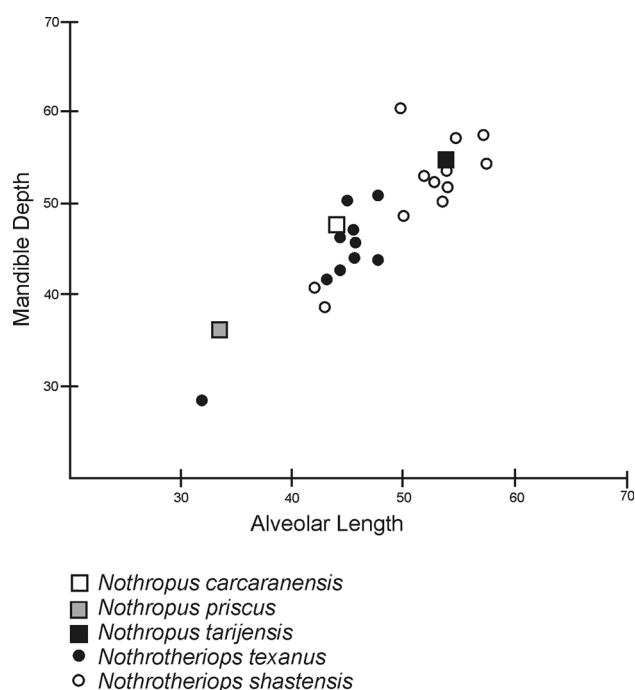


Figure 5. Comparison of mandible depth and alveolar length. Measurements in mm.

MACN Pv 14148 and MACN Pv 14149 to *Nothropus* could be appropriate. However, the fact that the type mandible of *Nothropus carcaranensis* lacks the caniniform raises the possibility that it should not be placed in *Nothropus* and this option should be considered. If it can eventually be demonstrated that the femora described here belong to specimens of *Nothropus carcaranensis*, then a taxonomic option to be considered would be to transfer *Nothropus carcaranensis* to *Nothrotheriops*. Unfortunately *Nothropus carcaranensis*—like *Nothropus priscus*—is based on the type mandible only. The current lack of associated skeletons including both the mandible and femur for both taxa precludes assignment to either a genus or species. It is possible that these femora could be assigned to either species if both were actually species of *Nothropus*, which would indicate that the morphology of the femur of *Nothropus* is more similar to that of *Nothrotheriops* than to the other South American nothrotheriine genus. Pending the discovery of associated skeletal material we are left with three possible options, which cannot be resolved at this moment: 1) the femora may belong to species of *Nothropus*, as the femur of that genus is unknown; 2) they may go with *N. carcaranensis* which is not *Nothropus* but we are not sure to what genus the type mandible should be assigned; or 3) they may in fact belong in *Nothrotheriops* and thus are the first evidence for the genus in South America.

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