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# Recognition of a new nothrotheriid genus (Mammalia, Folivora) from the early late Miocene of Achiri (Bolivia) and the taxonomic status of the genus *Xyophorus*

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**Running Head –** NEW NOTHROTHERIID SLOTH GENUS FROM BOLIVIA

## Abstract

New remains of a relatively plesiomorphic nothrotheriid sloth have been recovered from upper Miocene-aged deposits near the village of Achiri in the Altiplano of Bolivia. The new specimens appear allied to other middle and late Miocene remains from Argentina and Bolivia that have been assigned to the pseudo-genus "*Xyophorus*." "*Xyophorus*" has not previously been recognized as a distinct genus because of the paucity of material it encompasses. The new specimens, however, include a well-preserved squamosal with attached auditory region, and an isolated astragalus. These elements, which are described in detail, provide a sufficient number of distinctive characters to place the previous fossils assigned to "*Xyophorus*" into a new monotypic genus. Beyond exhibiting a suite of distinctive autapomorphies which justify its formal taxonomic designation, the new taxon shares several synapomorphies with more derived members of Nothrotheriidae, but also retains a number of plesiomorphies characteristic of basal megatherioid taxa, and shows a number of intermediate features. Although the new taxon is too incomplete to justify a full phylogenetic analysis, it appears to represent a basal member of Nothrotheriidae. Resolution of the taxonomic status of the genus *Xyophorus* awaits a better understanding of the taxonomy of early Miocene-aged basal megatherioids.

**Keywords**: Xenarthra, Pilosa, sloth, auditory region, astragalus, skull, skeleton, late Miocene

## Introduction

Intensive, ongoing fieldwork in Neogene deposits from the Altiplano of Bolivia over the past two decades have yielded numerous remains of extinct sloths, including the large megatheriine *Megatherium altiplanicum* (St-André and De Iuliis 2001), both scelidotheriine (cf. *Proscelidodon*; Pujos et al. 2012) and mylodontine sloths (*Simomylodon uccasamamensis*; St-André et al. 2010; Boscaini et al. 2019, 2021) representing the Mylodontidae, with the latter the most abundant taxon, the nothrotheriid sloths *Lakukullus anatisrostratus* (Pujos et al. 2014) and *Aymaratherium jeani* (Pujos et al. 2016), and the peculiar megatherioid sloth *Hiskatherium saintandrei* (Pujos et al. 2011). Included among these remains are specimens reputedly pertaining to the enigmatic genus *Xyophorus.* The taxonomic status and phylogenetic relationships of this genus are controversial and have been widely discussed (e.g., De Iuliis et al. 2011; Pujos et al. 2011; Brandoni 2014; Bargo et al. 2019; Brandoni et al. 2019), in part because the fossil remains assigned to it are broadly distributed in time and space, spanning a geographic range from the Bolivian Altiplano in the north to the southern tip of Argentine Patagonia in the south, and a temporal range of nearly 12 Ma from the late early Miocene Santacrucian SALMA of Santa Cruz Province to the early Pliocene Montehermosan SALMA of La Rioja Province (Rodríguez Brizuela and Tauber 2006; Brandoni 2014; Brandoni et al. 2019). The taxon is also controversial because the remains assigned to it are so fragmentary and poorly preserved. Ameghino (1887) erected the genus based on partially preserved maxillary and mandibular specimens from the Santa Cruz Formation (Santacrucian SALMA, late early Miocene), which he placed in two species, *Xyophorus rostratus* (Ameghino, 1887) and *X. simus* (Ameghino, 1887), solely because of size differences. The type specimens of both species have subsequently been lost (Bargo et al. 2019). Another four fragmentary specimens from Santa Cruz were assigned to four new species by Ameghino (1891, 1894; the former is a paper in which he also synonymizes *Xyophorus* with Mercerat's [1891] genus *Eurysodon*) based on size and minor morphological differences in the size and outline of the teeth: *X. sulcatus* (Ameghino, 1891), *X. atlanticus* (Ameghino, 1891), *X. andinus* (Ameghino, 1891) and *X. crassissimus* (Ameghino 1894). Bargo et al. (2019) recently assigned new mandibular and postcranial specimens to *X. atlanticus*, including a complete femur and astragalus. partial ulnae, and a partial radius and tibia. New species of *Xyophorus* from later in the late Miocene (Chasicoan–Huayquerian SALMAs) were erected by Scillato-Yané (1979; *X. bondesioi*) and St-André (1996; *X. villarroeli*), the former based on a partial mandible and the latter based on a partial right mandible (Figure 1) and an isolated astragalus. Frailey (1988) described a partial anterior skull and mandible from slightly younger Laventan (Laventan SALMA) aged deposits at Quebrada Honda, in southern

Bolivia, which he assigned to *Hapalops angustipalatus*, but these were subsequently placed in *Xyophorus* (*X.* cf. *bondesioi*) by Scillato-Yané and Carlini (1999). Additional partial mandibles were allocated to *Xyophorus* by Rodríguez Brizuela and Tauber (2006; *X.* cf. *bondesioi*) from the early Pliocene (Montehermosan–Chapadmalalan SALMAs) of La Rioja Province (Argentina), and Croft et al. (2009; *X.* cf. *bondesioi*) from the late early–middle Miocene (Friasian–Colloncuran SALMAs) of Cerdas (Bolivia), the latter study also allocating a manual and pedal ungual to the genus.

Given the paucity of remains, it is perhaps not surprising that the diagnoses provided for the genus itself, and for its constituent species, have been less than compelling. St-André (1996, p. 96) offered the following diagnosis for the genus *Xyophorus*: "[cf1] *déplacée vers la symphyse mandibulaire et séparée des autres dents par un diastème de longueur inférieure au diamètre antéropostérieur de [mf1]. Dents postérieures prismatiques*." (our translation: cf1 displaced in front of the posterior edge of the mandibular symphysis [in dorsal view] and separated from the molariforms by a diastema of length less than the anteroposterior diameter of mf1. Posterior molariforms prismatic). The last of these features is characteristic of all megatherioid sloths (Gaudin 2004) in all but the very earliest stages of life, and is therefore not diagnostic. Pujos et al. (2011) also noted the strong resemblance between the astragali of *Hapalops* and *Xyophorus*. It is perhaps not surprising, then, that Scott (1904; followed by Lydekker 1894; Perea 1999), based on Ameghino's (1887, 1891, 1894) Santacrucian-aged specimens, considered *Xyophorus* a junior synonym of the much better known and highly variable genus *Hapalops*. Brandoni (2014) and Brandoni et al. (2019) suggested that the post-Santacrucian SALMA material placed in *Xyophorus* (in the species *X. bondesioi* and *X. villarroeli*) belongs in a separate genus from the Santacrucian species, but, given the sparse record of the group, they did not feel a genus could be adequately diagnosed, and hence they referred to this younger material as "*Xyophorus*" (following the "Open nomenclature" style of Bengston 1988).

Although the published diagnoses do not establish this unambiguously, we agree with Brandoni (2014) and Brandoni et al. (2019) that the post-Santacrucian aged material assigned to *X. bondesioi* and *X. villarroeli* is marked by distinctive features that might be useful in distinguishing these species from other nothrotheriids. These include traits highlighted by St-André (1996), De Iuliis et al. (2011), and Brandoni (2014), i.e., cf1 displaced in front of the posterior edge of the mandibular symphysis [in dorsal view] and separated from the molariforms by a short diastema of length less than the anteroposterior diameter of mf1, postero-external opening of mandibular canal on lateral surface of the coronoid process, mf1 not mesiodistally compressed, and deep apicobasal grooves on the lingual and labial surfaces of mf1 and mf2. That said, the case for recognizing a distinct genus for this material would be bolstered greatly by the addition of new traits from new areas of the skeleton and not just the isolated and fragmentary material currently available.

The goal of the present report is to provide such characters and to reconsider the validity of post-Santacrucian SALMA *Xyophorus* species. We report here on an isolated squamosal and intact attached ear region, along with an isolated complete astragalus, recovered from deposits dating to the late Mayoan–early Chasicoan SALMAs (late Miocene, Fernández-Monescillo et al. 2019) near Achiri village, in the Bolivian Altiplano. This material clearly pertains to a nothrotheriid, and we reasonably consider it to be allied with the post-Santacrucian material assigned to "*Xyophorus*" by Brandoni (2014) and Brandoni et al. (2019). These specimens display a distinctive array of traits that include plesiomorphic features shared with basal megatherioids, derived features shared with undoubted members of Nothrotheriidae (i.e., taxa included in Varela et al. 2019, excluding *Thalassocnus* [following Amson et al. 2017], and any Santacrucian megatherioids), some transitional features, and a number of autapomorphies. These characteristics allow us to recognize the new specimens, and related material, as pertaining to a new extinct sloth genus. Moreover, they will allow us to better understand the phylogenetic affinities of this new taxon.

## Materials & Methods

The basis of this report are two new specimens. The first, MNHN-Bol-V 012690, is a right squamosal and attached auditory region, including a complete auditory bulla and petrosal. The second specimen, MNHN-Bol-V 011887, is an isolated right astragalus. Both specimens were recovered from the Cerros Pisakeri and Virgen Pata, Mauri 6 Formation, Unit IV (Mayoan–early Chasicoan SALMAs; Evernden et al. 1977; Fernández-Monescillo et al. 2019) 3-4 km southeast the village of Achiri (Pacajes Province, La Paz Department, Bolivia) roughly 50 km southwest of the capital city, La Paz (Figure 2).

The two new specimens are compared to other late Miocene and Pliocene nothrotheriids, in particular *Pronothrotherium typicum,* a species from the late Miocene–early Pliocene of southern South America (Huayquerian–Chapadmalalan SALMAs), represented by several nearly complete skulls, one with a well-preserved auditory region (Patterson et al. 1992; Gaudin et al. 2020), as well as a published description of an isolated astragalus (Kraglievich 1928). We will also compare the skull material to *Mionothropus cartellei*, a species from the late Miocene (Huayquerian SALMA) of Peruvian Amazonia, represented by a single complete skull with a well-preserved auditory region (De Iuliis et al. 2011). In addition, we will use the basal megatherioid sloth *Hapalops,* best known from the Patagonian Santa Cruz Formation (Santacrucian SALMA, late early Miocene; Scott 1904), as a reference taxon, in order to provide information on the plesiomorphic condition of megatherioid sloths.

The anatomical terminology utilized in the present study follows that of Wible and Gaudin (2004), Wible (2010), De Iuliis et al. (2011), and Gaudin (2011). Measurements for all specimens were taken with a digital caliper to the nearest 0.1 mm.

**Museum Acronyms:** CRILAR-PZ, Colección de Paleozoología, Departamento de Geociencias, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Anillaco, Argentina; FMNH, The Field Museum, Chicago, IL, USA; LIEB PV, Laboratorio de Investigaciones en Evolución y Biodiversidad (-PV, Paleovertebrados), Esquel, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MNHN-Bol, Museo Nacional de Historia Natural, La Paz, Estado Plurinacional de Bolivia; MNHN.F, Muséum national d'Histoire naturelle, Paris, France (ACH indicating Achiri); MPEF-PV, Colección de Paleontología de Vertebrados del Museo Paleontológico Egidio Feruglio, Trelew, Argentina; UATF, Universidad Autónoma Tomás Frías, Potosí, Estado Plurinacional de Bolivia; UF, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA; YPM-PU, Princeton Collection, Peabody Museum, Yale University, New Haven, CT, USA.

**Other Abbreviations: aptt,** anteroventral process of the tegmen typmani; **Cf1/cf1,** caniniform tooth; **CN,** cranial nerve; **gtvp,** groove for the muscle *tensor veli palatini*; **iam,** internal acoustic meatus; ICZN, International Code of Zoological Nomenclature**; Mf1-4/mf1-3,** molariform teeth; **SALMA,** South American Land Mammal Age.

## Systematic Paleontology

XENARTHRA Cope, 1889

PILOSA Flower, 1883

FOLIVORA Delsuc et al., 2001

NOTHROTHERIIDAE Gaudin, 1994

*Mcdonaldocnus* new genus

Type species: *Xyophorus bondesioi* Scillato-Yané 1979

Figures 1, 3–5

***Diagnosis*—** Small bodied member of Nothrotheriidae, similar to or smaller in size than *Pronothrotherium.* It lacks derived features of more derived nothrotheriids (i.e., *Pronothrotherium*, *Aymaratherium*, *Mionothropus*, *Nothrotherium*, and *Nothrotheriops*) or retains megatherioid symplesiomorphies, including: lack of a canal from occipital artery system perforating the paroccipital process; anterolaterally directed root of zygoma; lack of an odontoid process on astragalus; lack of broad dorsal exposure of fibular facet; broad astragalar neck; ectal facet not transversely oriented; small sustentacular facet; cuboid facet on plantar surface of astragalus; presence of a ridge connecting the head to the distal lateral trochlea in distal view; presence of a non-articular area on the plantar edge of the lateral trochlea, lateral to the head in distal view; distal contact between the fibular and ectal facets in lateral view; and, minimal lateral exposure of ectal facet in lateral view.

Can be distinguished from both basal megatherioids and other nothrotheriids by the following autapomorphies: elongated mandibular symphysis, with cf1 anterior to posterior edge of symphysis; short diastema, less than the maximum mesiodistal length of mf1; deep longitudinal grooves on the labial and lingual surfaces of mf1 and mf2; very rugose external surface of ectotympanic; contact between styliform process of ectotympanic and pterygoid; very high stapedial ratio; very small anteroventral process of tegmen tympani; subarcuate fossa strongly reduced; presence of medial prominence of petrosal; wide sulcus tali on ventral surface of astragalus; shallowly concave ectal facet.

***Etymology***—'McDonald' is in honor of Dr. H. Greg McDonald, recently retired from the U.S. Bureau of Land Management, and the unquestioned dean of fossil sloth experts. He has been a tremendously important role model, mentor and friend to T.J.G, F.P., and A.B., and we are pleased to name this taxon in his honor, and to thank him for his unflagging enthusiasm for sloths and for his years of encouragement and collaboration with all who work on these fascinating animals. 'Ocnus' comes from the Greek 'ocno,' meaning 'hesitating or inactive,' and is an ending frequently used in sloth genus names.

***Referred material***—Largely following Brandoni et al. (2019), we recognize material assigned to "*Xyophorus*" *bondesioi*, "*Xyophorus*" *villarroeli*, and "*Xyophorus*" sp. as pertaining to a new nothrotheriid genus, *Mcdonaldocnus,* including: "*Xyophorus*" *bondesioi* MLP 32-V-20-1, partial left mandible (Scillato-Yané 1979); "*Xyophorus*" cf. *bondesioi* CRILAR-PZ 262, partial left mandible (Rodríguez Brizuela and Tauber 2006); "*Xyophorus*" cf. *bondesioi* UATF-V-000871, partial right mandible, UATF-V-0008850, manual ungual phalanx, UATF-V-0008825, pedal ungual phalanx (Croft et al. 2009); "*Xyophorus" villarroeli* MNHN.F. ACH 15, right astragalus, MNHN.F ACH 43, partial right mandible (St-André 1996); "*Xyophorus"* sp. MPEF-PV 3264, partial left mandible (Brandoni 2014); "*Xyophorus"* sp. LIEB PV 5129, right mandibular fragment (Brandoni et al. 2019); as well as the material from the present study - MNHN-Bol-V 012690 right squamosal with auditory region, MNHN-Bol-V 011887, right astragalus.

***Questionably Referred material***—"*Xyophorus"* cf. *bondesioi* UF 26668, palatal portion of skull and partial mandible with complete dentition, UF 24200, partial left mandible with symphysis, which possesses some but not all of the diagnostic characters of the genus, though it falls within the appropriate age range (Laventan SALMA, middle Miocene; Frailey 1988; Brandoni et al. 2019).

***Distribution***—late early–early middle Miocene Friasian SALMA to early Pliocene Montehermosan SALMA, roughly 16/15-6/5 Ma; known from multiple localities in Argentina and Bolivia (see map in Brandoni 2014, Figure 3).

†***Mcdonaldocnus bondesioi*** (Scillato-Yané 1979), new combination

***Holotype***—MLP 32-V-20-1, partial left dentary (Scillato-Yané 1979)

***Referred material***— As for genus listed above.

***Distribution***—As for genus listed above.

***Diagnosis***—Because the newly constituted genus is monotypic, the diagnosis for this species, the type and only species, is the same as for the genus as a whole.

***Remarks***—In prior works, "*Xyophorus*" *bondesioi* and "*Xyophorus*" *villarroeli* were distinguished on the basis of size and the cross-sectional shape of the lower caniniform (St-André, 1996; Croft et al. 2009; Brandoni 2014; Brandoni et al. 2019), but we do not believe that either is sufficiently reliable as a basis for species definition (see, e.g., discussion in De Iuliis 2018 on use of size for diagnosing sloth taxa), so we choose instead to place all the material in the same species. "*Xyophorus*" *bondesioi* has priority (see Article 23 of the ICZN 1999), and so all the material of the new genus is assigned to this species for the time being, recognizing that this makes for a very long-lived species that may require subdivision pending discoveries of new, more anatomically extensive materials.

## Description

Specimen MNHN-Bol-V 012690 is an isolated right squamosal, preserving much of the ear region, but missing the zygomatic process (Figure 3).

*Ectotympanic*- The ectotympanic is complete and apparently tightly sutured to the skull. This bone is horseshoe-shaped, surrounding a dorsoventrally elongated porus acousticus. In both respects, *Mcdonaldocnus* resembles nothrotheriid sloths and differs from more basal megatherioids like *Hapalops* in which the ectotympanic is more circular and more loosely attached to the skull (Patterson et al. 1992; Gaudin 1995, 2004). As in most sloths the anterior crus is larger than the posterior crus (Figures 3A, C, 4). The posterior crus is attached dorsally to the post-tympanic region of the squamosal laterally; posteromedially, it is connected to a bridge of bone linking the mastoid petrosal and the squamosal, as in other sloths (Figure 3A, C-D; Gaudin 1995). The inner surface of the ectotympanic is visible at the tip of the posterior crus, so that the sulcus tympanicus and crista tympanica for the attachment of the tympanum are evident (Figure 3A, C-D). Immediately behind the posterior crus and the bridge of bone to which it attaches is the opening of the stylomastoid foramen (Figures 3C, 4). The ventral portion of the ectotympanic is somewhat expanded transversely in ventral view, more so than in *Hapalops* but less than in early nothrotheriids such as *Mionothropus* and *Pronothrotherium* (Patterson et al. 1992; De Iuliis et al. 2011). The surface of this portion of the ectotympanic is highly rugose (Figures 3A, C, 4). Although this may be exaggerated by post-mortem erosion, we note that a rugose ectotympanic surface is characteristic of nothrotheriids and their relatives, including *Pronothrotherium*, *Hapalops*, and *Analcimorphus* (Gaudin 1995, 2004). The ventral portion of the ectotympanic is deep in lateral view, especially anteriorly, i.e., it is much broader than either the anterior or posterior crura. In this respect it resembles *Pronothrotherium* (Patterson et al. 1992; Gaudin et al. 2020) and differs from *Mionothropus*, *Hapalops*, and *Analcimorphus* (Scott 1904; Patterson et al. 1992; De Iuliis 2011), where the ectotympanic ring has more uniform proportions. This ventral segment of the ectotympanic appears to be attached medially to the tympanohyal and the entotympanic, with the opening for the Eustachian tube situated between the ectotympanic and the latter element (Figure 3C-D). An elongated styliform process of the ectotympanic forms the anterior margin of this opening, and forms a small distal contact with the pterygoid (Figure 3A). Although a sizable styliform process is present in *Hapalops*, *Pronothrotherium*, and *Mionothropus* (Patterson et al. 1992; De Iuliis et al. 2011), the process does not contact the pterygoid in any of these taxa. The anterior crus is more massive and rugose than the posterior crus, and is exclusively attached to the squamosal (Figures 3A, 4). The Glaserian fissure passes between the anterior crus of the ectotympanic and the squamosal (Figure 3A, C).

*Entotympanic*- As in most sloths, the entotympanic in *Mcdonaldocnus* is composed of two vertical plates separated by an anteroposteriorly elongated sulcus for the internal carotid artery (Figure 3C). The lateral plate appears to be damaged posteriorly in the vicinity of the stylohyal fossa but the bone is otherwise nearly complete. In front of the stylohyal fossa, the ventral margin of the entotympanic lateral plate is thickened and rugose, and extends clearly ventral to the ectotympanic along its entire length (Figure 3C-D). The anteroventral process of the entotympanic appears to be missing but this is likely due to taphonomic damage. The medial portion of the entotympanic is deeper than that of *Hapalops*, similar in proportions to the basal nothrotheriids *Pronothrotherium* and *Mionothropus* (Patterson et al. 1992; De Iuliis et al. 2011). The carotid sulcus is quite broad posteriorly but narrows dramatically roughly at the midpoint of the entotympanic, becoming a transversely narrow trough that curves medially and dorsally into the carotid foramen (Figure 3D). The entotympanic contacts the petrosal dorsally, the ectotympanic, mastoid, and tympanohyal laterally, and has a small anterior contact with the pterygoid (Figure 3C-D).

*Stylohyal fossa*- The stylohyal fossa is likely comprised of the same four elements that are typical for sloths: tympanohyal, mastoid portion of petrosal, entotympanic, and the paracondylar process of the exoccipital, although the latter is missing and the posterior portion of the entotympanic is damaged (Figure 3C-D). As preserved, the outline of the depression is oval as is in nothrotheriids, in contrast to the circular outline of *Hapalops* and other basal megatherioids (Gaudin 1995: char. 54, 2004). The bulk of the fossa is comprised by the circular head of the ventralmost portion of the tympanohyal.

*Petrosal*- The lateral surface of the petrosal is visible through the porus acusticus (Figure 4). As is typical for sloths, the promontorium of the petrosal is rounded posteriorly but carries an anterodorsal extension with a flat lateral surface. The fenestra vestibuli is the largest aperture observable on the promontorium (stapedial ratio = 1.93). It is an anteroposteriorly elongated, oval, perhaps more elongated than in any other known sloth (Gaudin 2011: stapedial ratios for *Neocnus*, *Choloepus*, and *Bradypus* 1.5–1.6; Boscaini et al. 2018: stapedial ratio for *Glossotherium* 1.35). There is a broad, triangular crista interfenestralis separating the fenestra vestibuli from the aperture for the cochlear fossula (Figure 4; note the latter opening leads to the fenestra cochleae, and the latter term has been used for this opening; Wible 2010). Immediately lateral to the fenestra vestibuli is a deep and very narrow facial sulcus flanked laterally by a strong crista parotica. At its posterior end, the crista gives rise to the base of the tympanohyal. At its anterior end is a small expansion that represents the anteroventral process of the tegmen tympani (aptt). The small size of the aptt stands in stark contrast to the condition in basal megatherioids like *Hapalops* where the aptt forms a large concave plate that contacts the anterior crus of the entotympanic; in nothrotheriids, the aptt is even further enlarged (Gaudin 1995, 2004). Lateral to the crista parotica, there appears to be a deep epitympanic sinus as in typical for megatheroid sloths.

*Medial surface*- The medial surface of the petrosal in MNHN-Bol-V 012690 is well preserved (Figure 3B). Its most prominent feature is the large deep posteromedially directed internal acoustic meatus (iam) characteristic of sloths (Gaudin 1995). Recessed at the bottom of the canal, the openings of CN VII and VIII are visible. The cluster of dorsal openings (including the facial foramen and the superior vestibular area of the vestibulocochlear nerve; Wible 2010) is larger than the ventral cluster (including the remaining openings for branches of CN VIII, the inferior vestibular area, the spiral cribriform tract and the foramen singular; Wible 2010), the two clusters separated by a sharp-edged crest. The area posterodorsal to the iam shows only the barest impressions of a very shallow subarcuate fossa, an unusual condition for a xenarthran. Most sloths have a broad, fairly shallow but distinct subarcuate fossa (e.g., Stock 1925; Patterson et al. 1992; Gaudin et al. 2015; Boscaini et al. 2018; Gaudin and Broome 2021). The fossa is also well developed in cingulates (e.g., Wible 2010; Gaudin and Lyon 2017). The fossa is very deep in some anteaters, but is reduced in *Myrmecophaga* (Guth 1961; Patterson et al. 1992; Gaudin and Branham 1998). The latter taxon most closely approximates the condition in *Mcdonaldocnus* among xenarthrans, but the fossa is less well developed in *Mcdonaldocnus*. Above the iam, there is a strong crista petrosa that marks the boundary of the cerebellar surface of the petrosal. Anterior to the iam is a broad anteroposteriorly directed groove that may accommodate a portion of the inferior petrosal sinus (following Gaudin and Lyon 2017). Below this groove is an extremely large medially directed prominence of the petrosal. To our knowledge, this prominence has neither been described or identified previously in sloths.

*Posterior surface of the petrosal*- The lateral most feature of the petrosal is a prominent paraoccipital process (Figure 3C-D). This forms the lateral boundary to the ventral opening for the occipital artery. The artery travels within a partially closed canal inside the mastoid portion of the petrosal as in some megatheriids (i.e., *Megatherium* and *Eremotherium*), as opposed to the primitive condition observed in basal megatherioids where the artery is in an open groove (e.g., *Hapalops*, *Analcimorphus*, and *Schismotherium*), or the more derived condition in *Nothrotherium* and *Planops* where the artery is completely enclosed in a bony canal (Gaudin 1995, 2004). *Mcdonaldocnus* also lacks the canals which perforate the paroccipital process in Nothrotheriidae (Gaudin 1995; De Iuliis et al. 2011; Gaudin et al. 2020), marked by openings on the lateral surface of the skull posterodorsal to the process.

*Lateral surface of the squamosal*- As noted previously, the lateral surface of the squamosal serves as the point of attachment for the ectotympanic. Just anterior to the attachment point between the anterior crus and squamosal is a well-developed postglenoid foramen (Fig. 3A). The postglenoid foramen is generally reduced or absent in pilosans (Gaudin 1995). It has been observed in other fossil sloths, mostly in taxa that are not one anothers' close relatives, e.g., *Mionothropus* (De Iuliis et al. 2011), *Neocnus* (Gaudin 2011), *Parocnus* (Fischer 1971: fig. 9) and in a few other sloth taxa identified by Gaudin (2004 - *Megatherium*, *Nematherium*, and *Analcimorphus*), but it is rarely this prominent. Ventral to the postglenoid foramen and anterior to the opening for the Eustachian tube is another large opening between the squamosal and ectotympanic. This opening emerges into a deep anteroventrally directed groove that has been identified as accommodating the tensor veli palatini muscle (gtvp; Figure 3A, C; Gaudin 1995). This groove is present in *Hapalops* and in Megatheriidae and Nothrotheriidae (Gaudin 2004). The foramen ovale opens medial to the end of the gtvp. It would appear that the foramen ovale is almost entirely surrounded by the squamosal bone with a small ventral contribution to its rim from the pterygoid (Figure 3C). This is typical for most megatherioid sloths (Gaudin 2004), with the exception of *Pronothrotherium*, where the aperture lies entirely within the alisphenoid (Gaudin et al. 2020).

*Zygomatic process*- The zygomatic process of the squamosal is mostly preserved (Figure 3A, C-D). It is anterolaterally directed in ventral view with a flat lateral face and a sharp dorsal margin (Figure 3C). On its ventral surface, it carries a glenoid fossa with a well-demarcated medial edge. The fossa appears to be wider transversely than it is elongated anteroposteriorly, and its medial limit is marked by a low, anteroposteriorly elongated entoglenoid process (Figure 3C). The fossa is deeply concave transversely and nearly flat anteroposteriorly. The post glenoid region is marked by numerous longitudinal ridges. This differs from the condition in basal megatherioids, *Pronothrotherium*, and megatheriids, where the post-glenoid region is characterized by rugose bone, but is similar to the condition in *Mionothropus* and *Nothrotheriops* (Gaudin 1995, 2004; De Iuliis et al. 2011; Gaudin et al. 2020).

*Astragalus*- Two astragali of *Mcdonaldocnus* are available (Figure 5A-F). The astragalus was originally described by St-André (1996), as part of the type specimen of "*Xyophorus*" *villarroeli* (MNHN.F.ACH 15, Figure 5A-C; St-André 1996). This specimen is well preserved, missing only a chunk of bone along its proximal edge, affecting the tibial trochlea and ectal facet (Figure 5B-C). The new isolated right astragalus we recovered from Achiri (MNHN-Bol-V 011887; Figure 5D-F) is almost perfectly preserved, with the exception of a small amount of surface erosion around the margins of the sustentacular facet on the ventrolateral side of the bone, and a small break at the distal end of the lateral trochlea.

The dorsal surface of the bone in MNHN-Bol-V 011887 is dominated by the medial and lateral trochleae of the tibial facet (Figure 5E). The latter is relatively narrow transversely and elongated proximodistally, of uniform width, with a straight lateral edge. It is convex transversely, and strongly convex proximodistally, and its surface faces medially. The medial trochlea is confluent with the lateral trochlea at its medial end, but diverges distally at roughly a 70º angle. The medial trochlea is convex both transversely and proximodistally, and is also fairly uniform in width. The medial and lateral trochleae are similar in MNHN.F.ACH 15 (Figure 5B; St-André 1996), in *X. atlanticus* (Bargo et al. 2019), and in the basal megatherioid genus *Hapalops* (Figure 5H)*,* except that in the latter three taxa the medial trochlea is less divergent from the lateral trochlea. The distal angle between the medial and lateral trochleae is roughly 40º in MNHN.F.ACH 15*,* 25º in *X. atlanticus* (Bargo et al. 2019, fig. 6)*,* and it varies between 35º - 57º in *Hapalops* (35º in *H. elongatus* FMNH P13123; 57º in *Hapalops* sp. MLP 88-X-2-1.4 [Figure 5H]; 45º in *H. longiceps* YPM-PU 15523), whereas in the nothrotheriid *Pronothrotherium typicum* (FMNH P15223; Kraglievich 1928), the medial trochlea is a fully developed odontoid process typical of many derived sloths (McDonald 2012), oriented at a 90º angle to the lateral trochlea. *Pronothrotherium* also differs from the other taxa in that the fibular facet is broadly exposed dorsally, and extends far laterally, making the astragalus much broader transversely in dorsal view.

Immediately distal to the junction of the medial and lateral trochleae in MNHN-Bol-V 011887 is a deep pit. A similar pit is described on the dorsal astragalar surface in *Hapalops longiceps* – Scott (1904) suggested its function is to accommodate the elongate anterior distal tibial process at the end of the tibia, serving as a stop to avoid hyper-dorsiflexion. The pit is also present in *Pronothrotherium* (FMNH P15523)*,* albeit a bit more distally located along the medial edge of the lateral trochlea than in MNHN-Bol-V 011887, whereas it is more centrally located in *X. atlanticus* (Bargo et al. 2019), in *Hapalops longiceps* (YPM-PU 15523; Scott 1904, plate 33, fig. 4) and *H. elongatus* (FMNH P13123), and is situated along the lateral edge of the medial trochlea in *Hapalops* sp. (MLP 88-X-2-1.4; Figure 5H). The depression is poorly developed in MNHN.F.ACH 15 (Figure 5B; St-André 1996). The astragalar neck, which connects the tibial facets to the distal articulation for the navicular on the head, is relatively broad in all of the taxa described here (Figure A, D, E), nearly as wide as the tibial facets themselves in *Mcdonaldocnus, X. atlanticus* and *Hapalops.* The neck is more constricted medially and laterally in *Pronothrotherium* (FMNH P15223; Kraglievich 1928).

The plantar astragalar surface is largely occupied by two facets for the calcaneus, the lateral ectal facet and the medial sustentacular facet (Figure 5C, F). In *Hapalops*, the ectal facet is boomerang-shaped, i.e., it has a strong lateral indentation and a medial edge that is either medially convex (Figure 5I) or straight, with the distal and proximal ends extended laterally above and below the lateral indentation (Figure 5I). The facet is oriented mostly proximodistally, but tilted slightly laterally at its distal end. In MNHN-Bol-V 011887, the ectal facet has a similar orientation, but the lateral indentation is weaker than in *Hapalops,* and the facet only extends laterally at its proximal end, the distal end being rectangular in shape (Figure 5F). The preserved portion of the ectal facet in MNHN.F.ACH 15 (Figure 5C) is identical to that of MNHN-Bol-V 011887 (Figure 5F). Nearly the opposite condition prevails in *X. atlanticus* (Bargo et al. 2019), with the distal end extended laterally but the proximal end only weakly so. In *Pronothrotherium* (FMNH P15223)*,* the ectal facet differs in both shape and orientation. In shape it is nearly rectangular, with slight indentations along its long edges, and it is oriented almost transversely, with only a slight distolateral tilt.

The sustentacular facet is roughly quadrangular in all the taxa examined here, and is much smaller than the ectal facet (though less so in *Pronothrotherium*), separated from that facet by a deep groove, the sulcus tali. The sulcus is fairly wide in *Mcdonaldocnus* (Figure 5C, F) and in *X. atlanticus* (Bargo et al. 2019). It is somewhat narrower in *Hapalops* sp. (MLP 88-X-2-1.4), and is quite narrow in the other *Hapalops* specimens (FMNH P13123 and YPM-PU 15523) and in *Pronothrotherium* (FMNH P15223). The orientation of the sustentaculum varies among these taxa. In *Hapalops,* it faces not only in the plantar direction, but also somewhat medially and proximally (Figure 5I). It has a similar orientation in *X. atlanticus* (Bargo et al. 2019) and in MNHN.F.ACH 15 (Figure 5C). It is tilted proximally to a much lesser degree in MNHN-Bol-V 011887, and in *Pronothrotherium* it faces directly proximally.

The distal navicular facet is extended proximally onto the ventromedial surface of the astragalus (Figure 5D-F). In MNHN.F.ACH 15 (Figure 5A, C) and *Hapalops* sp. (MLP 88-X-2-1.4, Figure 5G, I), this extension is broadly confluent with the cuboid facet, separated by only a broad, shallow proximal indentation. The indentation between proximal navicular facet extension and cuboid facet is deeper in MNHN- Bol-V 011887, in *X. atlanticus* (Bargo et al. 2019), and in the other two *Hapalops* specimens (FMNH P13123 and YPM-PU 15523). The cuboid facet itself lies on the plantar surface of the astragalus in *Mcdonaldocnus* (Figure 5C, F), *X. atlanticus* (Bargo et al. 2019) and *Hapalops* (Figure 5I), as noted by Scott (1904) in the case of the latter. The facet is pointed proximally in MNHN.F.ACH 15, whereas it has a broad rounded proximal margin in MNHN-Bol-V 011887, *X. atlanticus* (Bargo et al. 2019), and *Hapalops*. In *Pronothrotherium* (FMNH P15223), the cuboid facet lies on the lateral side of the head, widely separated from the proximal extension of the navicular facet. *Pronothrotherium* also differs from the other taxa due to the presence of a large non-articular area occupying the proximomedial astragalar surface in ventral view, an area largely absent in the other forms.

The head of the astragalus is covered by a concave navicular facet in all the taxa examined for the present study (Figure 5D). A concave navicular facet is a synapomorphy of Pilosa (Hoffstetter 1958; Gaudin and McDonald 2008). In MNHN.F.ACH 15 (Figure 5A), the facet is nearly circular (ratio of maximum dorsoplantar depth to maximum transverse width = 0.98), whereas in the others (Figure 5D, G) the facet is somewhat elongated transversely (ratio of depth/width: MNHN-Bol-V 011887 = 0.71; *Hapalops* sp. MLP 88-X-2-1.4 = 0.77; *Hapalops longiceps* YPM-PU 15523 = 0.72; *X. atlanticus* = 0.77 [based on Bargo et al. 2019, fig. 6]; *Pronothrotherium typicum* FMNH P15223 = 0.82). The head is connected by a strong, rounded ridge to the ventral edge of the lateral trochlea in MNHN-Bol-V 011887, as well as in *X. atlanticus* (Bargo et al. 2019) and in *Hapalops.* The ridge is sharper but weaker in MNHN.F.ACH 15, and is absent entirely in *Pronothrotherium.* There is a sizable, non-articular area visible in distal view, lateral to the head abutting the distal edge of the lateral trochlea, in *Mcdonaldocnus* (Figure 5D), *Hapalops* (Figure 5G), and *X. atlanticus* (Bargo et al. 2019). This is also missing in *Pronothrotherium.* The latter also differs from the others in that the lateral trochlea is much taller in distal view, and the odontoid process has a large distal exposure that the medial trochlea lacks in the other taxa.

The fibular facet has a similar shape in lateral view among all the taxa observed in the present study. It contacts the ectal facet in *Mcdonaldocnus* (Figure 5F), *Hapalops* (Figure 5I), and *X. atlanticus* (Bargo et al. 2019), whereas this contact is missing in *Pronothrotherium.* The latter taxon also has a broad exposure of the ectal facet and a globose cuboid facet in lateral view. These are missing in *Mcdonaldocnus* and *Hapalops.*

In medial view, MNHN-Bol-V 011887 strongly resembles *Pronothrotherium* (FMNH P15223) in that the lateral trochlea is much taller than the medial trochlea, and has a semicircular dorsal edge, whereas in *Hapalops* the lateral trochlea is lower and less strongly curved. In addition, the medial trochlea is proximodistally narrower, as in *Pronothrotherium,* and is bordered distally by a strong indentation. This indentation is missing in *Hapalops,* and the medial trochlea is more elongated proximodistally in medial view. The medial view shows that MNHN-Bol-V 011887 differs from both *Pronothrotherium* and *Hapalops* in the curvature of the ectal facet, with the concavity of the facet much less in the first taxon.

## Discussion

Brandoni (2014) and Brandoni et al. (2019) both suggested that post-Santacrucian sloths assigned to the nothrothere genus *Xyophorus* (i.e., *X. bondesioi* and *X. villarroeli*) likely comprised a distinct lineage from the material originally placed in this clade by Ameghino (1887, 1891, 1894).

Ameghino's specimens were older, all deriving from the Santa Cruz Formation of Patagonia, which is late early Miocene in age (Santacrucian SALMA). However, Brandoni (2014) and Brandoni et al. (2019) hesitated to erect a new taxon for this material, because of the paucity of material available at the time and the consequent lack of a sufficient number of diagnostic features for such a clade, choosing instead to refer to these specimens with the generic epithet "*Xyophorus*," following the open nomenclature convention of Bengston (1988), but rendering the understanding of this genus very difficult. Moreover, the majority of specimens assigned to "*Xyophorus*" were partial mandibles which, though distinct in several respects from the older *Xyophorus* material, indeed provide a very limited basis for erecting a new taxon (De Iuliis 2018).

The new specimens from Achiri described in the present report, and especially the skull fragment with ear region, significantly increase the information available for basal nothrotheriids. The astragalus we recovered is similar to another astragalus from Achiri reported by St André (1996, part of the type of "*Xyophorus*" *villarroeli*), although it is better preserved. It bears a more medially divergent medial trochlea, more closely approaching the odontoid facet of derived nothrotheriids (Stock 1925; Kraglievich 1928; Cartelle and Fonseca 1982); it possesses a dorsal pit alongside the lateral trochlea that receives the anterior distal tibial process, and a less proximally tilted sustentacular facet. However, the strong similarities between these two astragali (Figure 5A-F), confirm for the moment the presence of a single small-sized megatherioid species in the Bolivian locality of Achiri. However, the squamosal with its attached auditory region is even more indicative of the anatomy of *Mcdonaldocnus*, as it bears a significant number of diagnostic features of this genus. The ear region of mammals has long been recognized as one of the most complex regions of the skull (Novacek 1993), and one that is evolutionarily labile, such that it has proved particularly useful and sometimes fundamental as a source of taxonomically and phylogenetically informative characters for mammals in general (Rougier and Wible 2006; O'Leary et al. 2013) and xenarthrans in particular (e.g., Patterson et al. 1989, 1992; Gaudin 1995), as in the present case. The new ear region clearly shows that this new taxon *Mcdonaldocnus*, incorporating the remains of relatively primitive, small bodied nothrotheres from the late early–early middle Miocene (Friasian–Colloncuran SALMAs) and early Pliocene (Montehermosan–Chapadmalalan SALMAs) of Argentina and Bolivia, is a basal member of the clade Nothrotheriidae, but one lacking some of the traits of more derived members of the group. Nothrotheriid characters it shares from the auditory region include a dorsoventrally elongated ectotympanic with an elongated styliform process that is tightly sutured to skull, an ovate stylohyal fossa, and the presence of longitudinal ridges in postglenoid region (Figure 3). Additional nothrotheriid characters from the astragalus include a lateral trochlea of the astragalar tibial facet with a semicircular dorsal edge in medial view; a proximodistally narrow medial trochlea bordered distally by strong indentation in medial view; and a pit on the dorsal surface of the astragalus, medial to lateral trochlea, for the anterior distal tibial process (present only in the new specimen).

However, *Mcdonaldocnus* lacks features of more derived nothrotheriids (*Pronothrotherium*, *Aymaratherium*, *Mionothropus*, *Nothrotherium*, and *Nothrotheriops*) as noted in the diagnosis above. These include a canal from the occipital artery system perforating the paroccipital process, an odontoid process on the astragalus, a broad dorsal exposure of the fibular facet on the astragalus, and a transverse orientation of the ectal facet of the astragalus. In addition, it retains numerous megatherioid symplesiomorphies, among them: an anterolaterally directed root of the zygoma; a broad astragalar neck; a small sustentacular facet; a cuboid facet on the plantar surface of astragalus; a ridge connecting the head to the distal lateral trochlea in distal view; a non-articular area on the plantar edge of the lateral trochlea, lateral to the head in distal view; a distal contact between the fibular and ectal facets in lateral view; and minimal lateral exposure of the ectal facet in lateral view.

Moreover, *Mcdonaldocnus* expresses some features that are transitional between basal megatherioids like *Hapalops* from the Santacrucian SALMA and more derived nothrotheriids like *Pronothrotherium* and *Mionothropus,* both from the Huayquerian SALMA*,* including: ectotympanic expanded transversely in ventral view (more than *Hapalops*, less than derived Nothrotheriidae); medial portion of the entotympanic is deeper than that of *Hapalops*, similar in proportions to the more derived nothrotheriids *Pronothrotherium* and *Mionothropus*; medial astragalar trochlea medially divergent (variable, more than *Hapalops* and *Xyophorus atlanticus*, less than derived Nothrotheriidae); ectal facet expands laterally at distal end only (extends laterally at both ends in *Hapalops,* not expanded at either end in *Pronothrotherium*); sustentacular facet less proximally oriented than in *Hapalops* and *X. atlanticus,* more so than in *Pronothrotherium* (variable); lateral trochlea elevated in medial view relative to medial trochlea (more than *Hapalops* and *X. atlanticus*, less than *Pronothrotherium*).

Although we have assigned all specimens included in "*Xyophorus*" by Brandoni (2014) and Brandoni et al. (2019) to our new genus, we have singled out one assignment as questionable. A partial skull and mandible reported by Frailey (1988) from sediments in Quebrada Honda, Bolivia, assigned to the Laventan SALMA (middle Miocene, 13.1–12.4 Ma [see Gibert et al., 2020]), were originally placed in the species *Hapalops angustipalatus,* but were subsequently moved to "*Xyophorus*" cf. '*X' bondesioi* by Scillato-Yané and Carlini (1999). There is a second mandible from the same locality (UF 242000) that we also questionably refer to the new genus. Although these specimens are of the right age to be included in *Mcdonaldocnus* – indeed, there is older material from Cerdas (Friasian – Colloncuran SALMAs; Croft et al. 2009) that we subsume in the new taxon – and the two mandibles do have a short diastema and elongated mandibular symphysis, as in other *Mcdonaldocnus* specimens, we note that these mandibles lack the most distinctive dental feature of *Mcdonaldocnus,* the deeply grooved first and second molariforms. The grooves are not entirely absent, they are just weakly developed, and hence more similar to the condition in basal megatherioids like *Hapalops* (Scott 1904). And though De Iuliis et al. (2011) caution against the use of apicobasal grooves on the lingual and labial surfaces of the molariforms as phylogenetic characters in nothrotheriids, given their variable expression in well-sampled taxa like the stem megatherioid *Hapalops* and the highly-derived nothrothere *Nothrotheriops,* we note that the grooves are particularly deep in the lower molariforms of other *X. bondesioi* and *X. villarroeli* (Figure 1), and so their poor development in the Quebrada Honda specimens merits some caution when assessing their taxonomic affinities. The partial skull recovered by Frailey (1988) may eventually be helpful in more clearly determining the taxonomic provenance of the Quebrada Honda specimens, but only the palate is illustrated and described. Frailey (1988, p. 7) states that "a portion of the basicranium [is] preserved," but he provides no further information, and of course, the only other partial skull of *Mcdonaldocnus,* the one from Achiri, preserves neither the basicranium itself, nor any portion of the palate. Although on balance, given its age and geographic provenance, we feel there is reason enough to hypothesize a connection between the Quebrada Honda material and other specimens more confidently assigned to *Mcdonalocnus,* we also recognize that the morphological evidence for its inclusion is less compelling, and perhaps warrants some question pending the availability of more material.

It is important at the end to emphasize that the present study does not resolve the taxonomic status of the original material assigned to *Xyophorus* by Ameghino (1887, 1891, 1894). As noted in the Introduction to the present study, other authors (e.g., Lydekker 1894; Scott 1904; Perea 1999) have considered *Xyophorus* to be a junior synonym of *Hapalops,* based solely on Ameghino's specimens. Bargo et al. (2019) provide an extensive discussion of the confusing taxonomy of this material. Although they suggest some of the original *Xyophorus* species (*X. andinus, X. atlanticus*, and *X. crassissimus*) might represent a distinct clade from other Santacrucian basal megatherioids based on dental features; and, moreover, that some of the new skeletal remains they assign to *X. atlanticus* exhibit autapomorphic traits, yet they do not attempt to formally designate any new genera or formally emend the diagnosis of any existing *Xyophorus* species. We consider that the ultimate fate of *Xyophorus* cannot be determined without an extensive revision of *Hapalops* and "allied genera" (e.g., *Pseudohapalops*, *Amphihapalops*, etc), like that recently completed for its fellow Santacrucian-aged megalonychid taxon *Eucholoeops* (Santacrucian SALMA; De Iuliis et al. 2014). Such an analysis could provide a clearer understanding of what should and should not be included in *Hapalops.* Until such systematic revision is completed, however, only those species erected by Ameghino and with a provenance from Santacrucian levels of Santa Cruz Province, must be included in the genus *Xyophorus.* In the absence of a comprehensive revision of *Hapalops* and its allies*,* which is well beyond the scope of the present study, we will refrain from making any definitive statement regarding the legitimacy of *Xyophorus* itself as a separate genus. That said, it is noteworthy that several of Ameghino's specimens do not satisfy the definition of *Xyophorus* as regards diastema length, possessing a diastema longer than the mesiodistal length of mf1 (Brandoni 2014, Table 1). Some also lack apicobasal grooves on the lower molariforms (Bargo et al. 2019). Clearly, the taxonomy of *Xyophorus* requires further study before it can be resolved, though we are comfortable excluding this material from *Mcdonaldocnus,* following Brandoni (2014) and Brandoni et al. (2019).

Finally, beyond an assignment to Nothrotheriidae, with the implication that it represents a fairly basal member of that clade, we have not yet attempted to better resolve the phylogenetic position of *Mcdonaldocnus*. At this point, there remains very little information on the skeletal anatomy of this taxon. The sum total of all the specimens assigned to date provide us with information on most of the mandible, but only the squamosal, auditory region and possibly the palatal portion of the skull, along with the astragalus and a few ungual phalanges. This ultimately represents a fairly small portion of its overall skeletal anatomy, and therefore we are not convinced that a formal phylogenetic analysis of *Mcdonaldocnus* is warranted as of yet. We are conscious that the specimens included in *Mcdonaldocnus* represent a lineage of 10 Ma and it is possible that new discoveries may justify the recognition of other species within this new genus, or even its division into multiple genera. We think that a greater diversity of skeletal material needs to be recovered and described in detail before a more definitive resolution of its affinities can realistically be achieved. It is our hope that ongoing field work in Bolivia and Argentina by our group, and others, will ultimately provide such a resolution.

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**Data Availability Statement**

The fossils described in the present study are housed in the Museo Nacional de Historia Natural, La Paz, Estado Plurinacional de Bolivia. Any requests for further information about the data presented in this study should be directed to the corresponding author.

**Declaration of Interests Statement**

The authors report there are no competing interests to declare.

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## Figure Captions

Figure 1 Caption:. Right dentary of the nothrotheriid sloth *Mcdonaldocnus bondesioi* (MNHN.F.ACH 43) from the late Miocene Bolivian locality of Achiri in lateral (A), medial (B), and occlusal (C) views. Abbreviations: cf1, lower caniniform; mf1-3, lower molariforms 1-3. Scale bar = 50mm.

Figure 1 Alt text: Fragmentary right dentary, including caniniforms and molariforms, of the nothrotheriid sloth *Mcdonaldocnus bondesioi* (MNHN.F.ACH 43) shown in lateral, medial, and occlusal views with teeth labeled and a scale bar provided.

Figure 2 Caption: Location map of the late Miocene fossil-bearing locality of Achiri (La Paz Department) and Cerros Pisakeri and Virgen Pata where the new remains of *Mcdonaldocnus bondesioi* were discovered; (B), general map of Bolivia.

Figure 2 Alt Text: Location map of the late Miocene fossil-bearing locality of the village of Achiri (La Paz Department) and fossil localities of Cerros Pisakeri and Virgen Pata, where the new remains of *Mcdonaldocnus bondesioi* were discovered, shown next to a general map of Bolivia indicating the location of Achiri relative to the major cities in the country.

Figure 3 Caption: Right posterolateral portion of the skull attributed to the nothrotheriid sloth *Mcdonaldocnus bondesioi* (MNHN-Bol-V 012690) from the Bolivian locality of Achiri in lateral (A), internal (B), lateroventral (C), and ventral (D) views. Abbreviations: bo, basioccipital; cf, carotid foramen; crp, crista petrosa; cs, cerebral surface; eam, external auditory meatus; ec, ectotympanic; egp, entoglenoid process; ent(lp), entotympanic (lateral plate); eps, epitympanic sinuses; fG, fissura Glaseri; fo, foramen ovale; gEt, groove for the Eustachian tube; gf, glenoid fossa; gvn, groove for the vidian nerve; gtvp , groove for m. tensor veli palatini; iam, internal acoustic meatus; jf, jugular foramen; mpp, medial prominence of petrosal; oaf, occipital artery foramen; p, parietal; pcp, paracondylar process of exoccipital; pgf, postglenoid foramen; pop, paroccipital process of the petrosal (= mastoid process of squamosal of Patterson *et al.* 1992); prp, promontorium of the petrosal; pt(lp), pterygoid (lateral plate); saf, subarcuate fossa; sips, sulcus for inferior petrosal sinus; sq/f(?)s, suture between the squamosal and the frontal(?); shf, stylohyal fossa; stmf, stylomastoid foramen; zpsq, zygomatic process of the squamosal. Scale bar = 50mm.

Figure 3 Alt Text: Right posterolateral portion of the skull attributed to the nothrotheriid sloth *Mcdonaldocnus bondesioi* (MNHN-Bol-V 012690) shown in lateral, internal, lateroventral, and ventral views, with structural details labeled, and a scale bar provided.

Figure 4 Caption: Ear region in lateral view from the skull attributed to the nothrotheriid sloth *Mcdonaldocnus bondesioi* (MNHN-Bol-V 012690) from Bolivian locality of Achiri. Abbreviations: cp, crista parotica; ec, ectotympanic; ent(lp), entotympanic (lateral plate); fv, fenestra vestibuli (= fenestra ovalis); gEt, groove for the Eustachian tube; gtvp , groove for tensor veli palatini muscle; oaf, occipital artery foramen; pcp, paracondylar process of exoccipital (= paraoccipital process of Patterson *et al.* 1992); pgf, postglenoid foramen; pop, paroccipital process of the petrosal (= mastoid process of squamosal of Patterson *et al.* 1992); prp, promontorium of the petrosal; shf, stylohyal fossa; sq, squamosal; stmf, stylomastoid foramen. Scale bar = 10mm.

Figure 4 Alt Text: Ear region in close-up lateral view from the skull attributed to the nothrotheriid sloth *Mcdonaldocnus bondesioi* (MNHN-Bol-V 012690), with structural details labeled, and a scale bar provided.

Figure 5 Caption: Photographs of two astragali of the nothrotheriid sloths *Mcdonaldocnus bondesioi* MNHN.F.ACH 15 (A-C) and MNHN-Bol-V 011887 (D-F) and the basal megathrioid sloth *Hapalops* sp. MLP 88-X-2-1.4 (G-I) in anterior (A, D, G), dorsal (B, E, H), and plantar (C, F, I) views. Abbreviations: ah, astragalar head; an, astragalar neck; cuf, cuboid facet; ef, ectal facet; ff, fibular facet; lt, lateral trochlea; mt, medial trochlea; nf, navicular facet; st, sulcus tali; suf, sustentacular facet. Scale bar = 50mm.

Figure 5 Alt Text: Photographs of two astragali of the nothrotheriid sloth *Mcdonaldocnus bondesioi* (MNHN.F.ACH 15 and MNHN-Bol-V 011887) and the basal megathrioid sloth *Hapalops* sp. (MLP 88-X-2-1.4), each shown in anterior, dorsal, and plantar views, with structural details labeled, and a scale bar provided.

**Fig. 1**

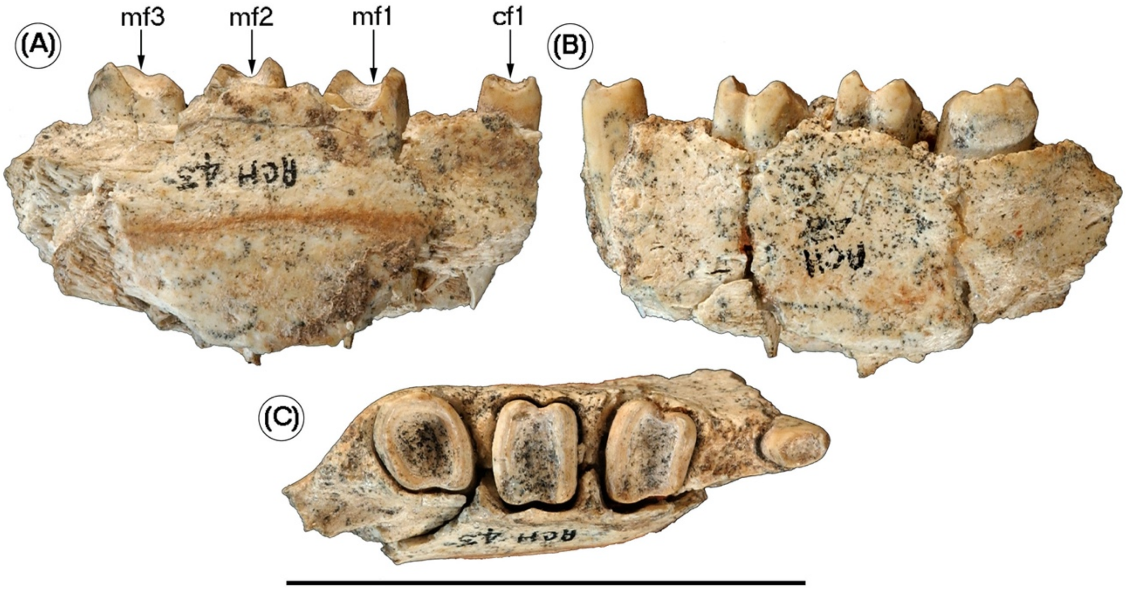
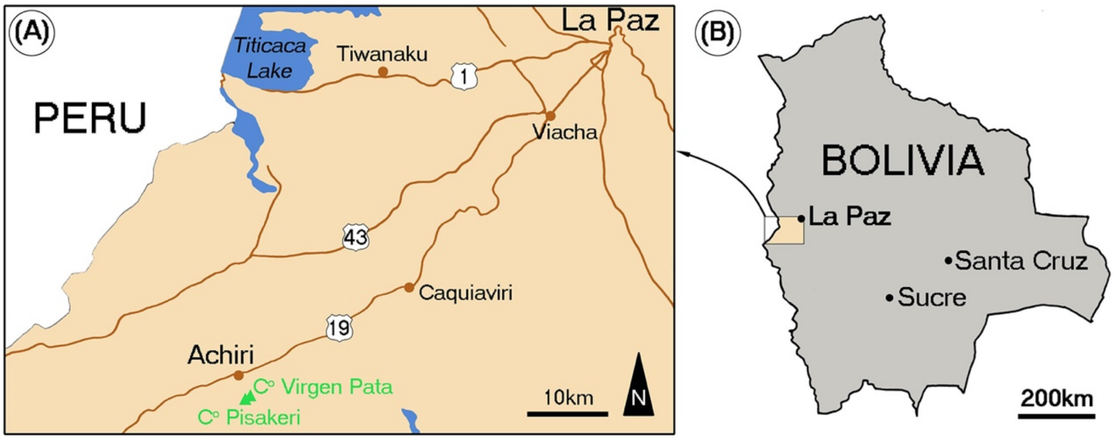


**Fig. 2**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Santa Cruz
Sucre
200km

**Fig. 3**

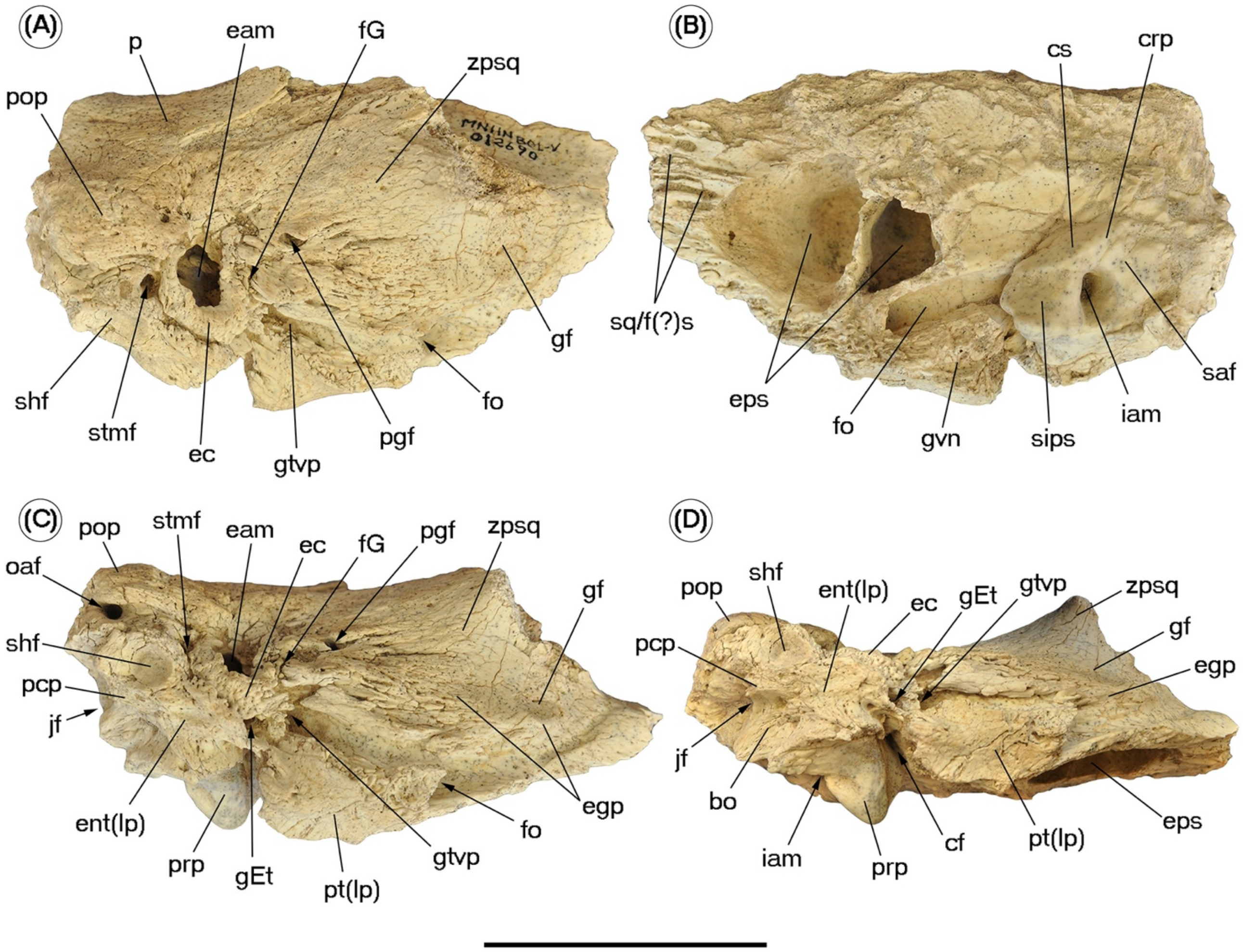
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**Fig. 4**

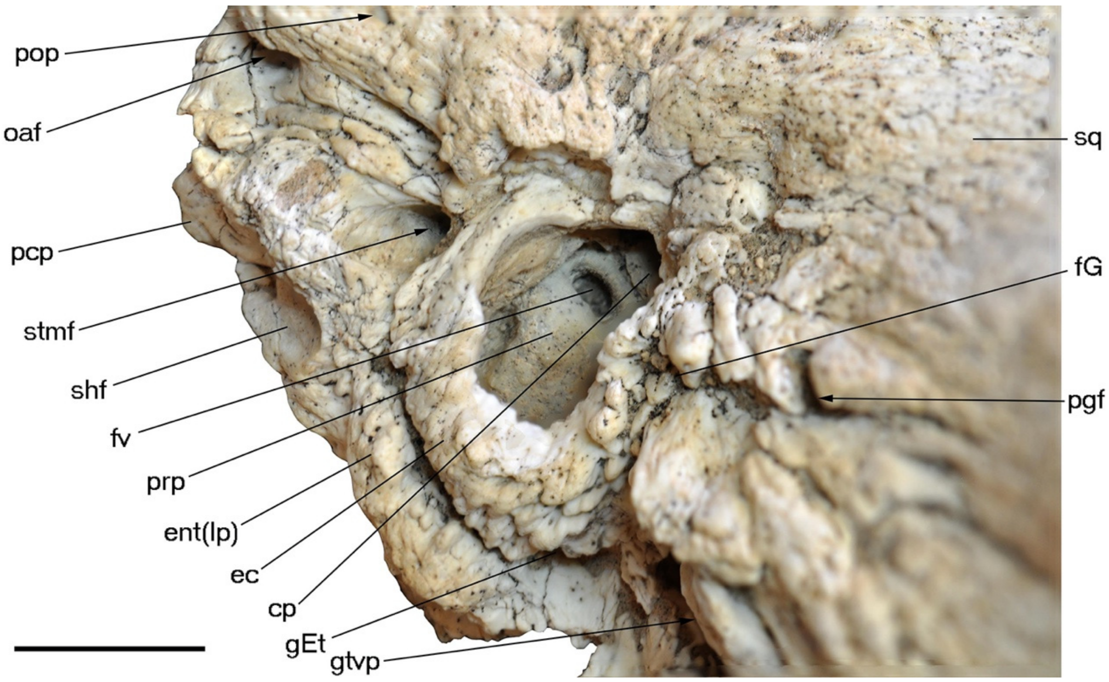

**Fig. 5**