



## NEW POSTCRANIAL REMAINS OF GROUND SLOTHS (XENARTHRA, FOLIVORA, MYLODONTIDAE) FROM SOUTHERN BRAZIL

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**ABSTRACT** – Diagnoses of Mylodontidae species are generally based on skull, mandibular, and tooth characteristics, and rarely on postcranial morphology, due to the lack of postcranial material associated with the cranial material. The studies of postcranial anatomy have generally a biomechanical focus and reflect a set of functions of skeletal structures, but their interpretation in phylogenetic analysis is still limited. In Pleistocene deposits of Rio Grande do Sul State, Brazil, an important set of postcranial specimens was collected, belonging to Mylodontidae. They were morphologically and morphometrically analyzed, allowing us to observe some diagnostic characters such as the humeral entepicondylar foramen and crests, shape of the radial shaft, angle of distal articulation of the tibia, as well as the angle of proximal articulation of the astragalus. The material was also compared with specimens from other South American localities. Most of the remains were assigned to *Glossotherium robustum* and *Lestodon armatus*. In addition, a new Scelidotheriinae was recorded for Rio Grande do Sul State. The study indicated significant differences in the postcranial morphology, which allowed the recognition of some specific diagnostic characters.

**Keywords:** Mylodontinae, Scelidotheriinae, hindlimb, forelimb, Pleistocene, Rio Grande do Sul.

**RESUMO** – As diagnoses de espécies de Mylodontidae são baseadas principalmente em características cranianas, mandibulares e dentárias e, raramente, em morfologia pós-craniana, devido à falta de esqueletos completos associados a material craniano. Os estudos de anatomia pós-craniana têm se limitado, em geral, a biomecânica, com foco nas funções das estruturas esqueléticas, mas suas interpretações filogenéticas ainda são poucas. Nos depósitos pleistocênicos do Estado do Rio Grande do Sul, Brasil, um importante conjunto de espécimes pós-cranianos pertencentes a Mylodontidae foi morfológica e morfometricamente analisado, o que nos permitiu observar algumas características diagnósticas como o forame entepicondilar e as cristas do úmero, formato da diáfise do rádio, ângulo da articulação distal da tibia, bem como o ângulo da articulação proximal do astrágalo. Os materiais também foram comparados com espécimes de outras localidades da América do Sul. A maioria do material foi atribuída a *Glossotherium robustum* e *Lestodon armatus*. Ademais, um novo Scelidotheriinae é registrado para o Rio Grande do Sul. O estudo indicou diferenças significativas na morfologia pós-craniana, que permitiram o reconhecimento de caracteres diagnósticos específicos.

**Palavras-chave:** Mylodontinae, Scelidotheriinae, membro anterior, membro posterior, Pleistoceno, Rio Grande do Sul.

## INTRODUCTION

Xenarthra is a clade that is divided into two main groups: Cingulata and Pilosa. The former is composed of extant armadillos and the extinct lineages popularly known as giant armadillos, while Pilosa contains two main groups: Vermilingua (anteaters) and Folivora (sloths). Currently, there are six species of sloths distributed into two genera, *Bradypus* Linnaeus, 1758 and *Choloepus* Linnaeus, 1758, which mainly inhabit the Atlantic and Amazon forests regions (Pujos *et al.*, 2017).

According to the phylogenetic analysis based on craniodental characters made by Gaudin (2004), the extinct families that compose Folivora are Megalonychidae, Nothrotheriidae, Megatheriidae, and Mylodontidae, but recent studies using molecular data revealed new relationships within the group, where Scelidotheriidae and Mylodontidae + Choloepodidae form Mylodontoidea (Delsuc *et al.*, 2019; Presslee *et al.*, 2019).

The fossil record of Folivora indicates that the group had a great geographic distribution, ranging from southern South America to northern North America, reflecting a significant morphological diversity that allowed a wide occupation of niche types (Delsuc *et al.*, 2004). During the South American Cenozoic there was an increase in Folivora diversity, which can be observed from the Miocene onwards because of the better preservation and abundance of the fossil record (Varela *et al.*, 2019).

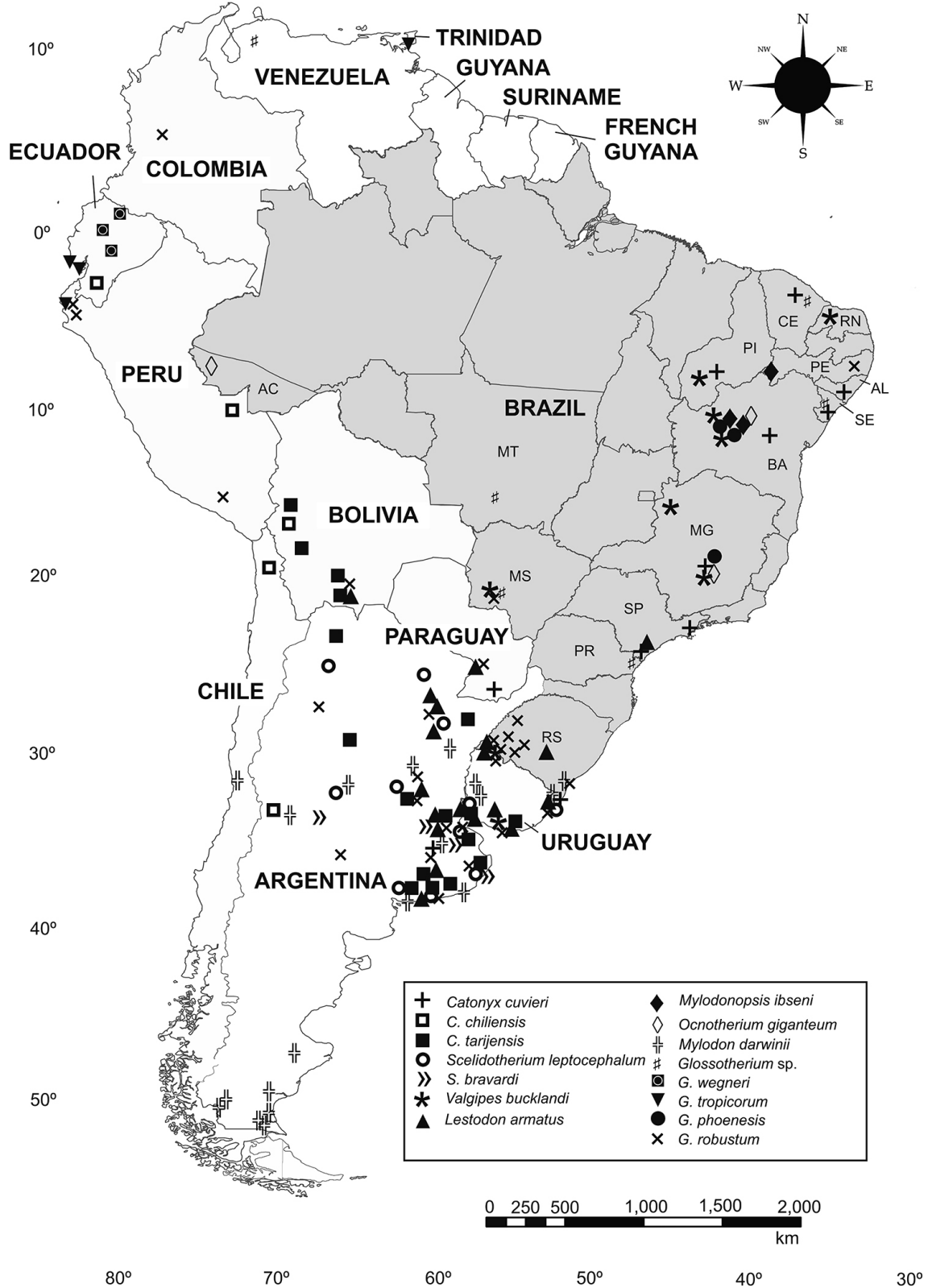
Mylodontidae have been reported from the late Oligocene to the Holocene in South America and from the early–middle Miocene to late Pleistocene in North America (Carlini *et al.*, 1990, 2006a; McDonald & De Iuliis, 2008; Saint-André *et al.*, 2010; Shockey & Anaya, 2011; Boscaini *et al.*, 2019a; Cartelle *et al.*, 2019). This group comprises two monophyletic taxa currently considered valid: Scelidotheriinae and Mylodontinae (Mylodontini + Lestodontini) (Boscaini *et al.*, 2019a). Urumacotheriinae, Octomyodontinae and Nematheriinae are also considered subfamilies by some authors (see Engelmann, 1985; McKenna *et al.*, 1997; Gaudin, 2004; Negri & Ferigolo, 2004; McDonald & De Iuliis, 2008; Rinderknecht *et al.*, 2010; Miño-Boilini, 2012; Casali *et al.*, 2022).

Mylodontinae Lestodontini has been reported from the late Miocene to late Pleistocene in several countries with five genera recognized: *Thinobadistes* Hay, 1919, *Bolivartherium* Carlini, Scillato-Yané & Sánchez, 2006, *Lestobradys* Rinderknecht Bostelmann, Perea & Lecuona, 2010, *Sphenotherus* Ameghino, 1891 and *Lestodon* Gervais, 1855 (Boscaini *et al.* 2019a). The latter has a wide distribution over the Pleistocene of South America (Figure 1) (Czerwonogora & Fariña, 2013) and one record for the late Pliocene in Argentina (Deschamps *et al.*, 2001), while the other genera are from the Cenozoic of South America and *Thinobadistes* from North America (Boscaini *et al.*, 2019a). This group is characterized by Cfl/cfl (caniniforms) with oblique/nearly vertical wear facet, intermediate development of coronoid and angular processes, moderate length of the mandibular condyloid

process, mandibular condyle extending both medially and laterally in dorsal view, mandible with weakly developed fossa posterior to cfl, orthogonal or acute odontoid process–discoid angle of the astragalus and fusion of the mesocuneiform and second metatarsal (Boscaini *et al.*, 2019a, characters 20, 47, 48, 51, 57, 76, 368, and 377, respectively).

Mylodontinae Mylodontini was richer in number of species than Lestodontini, with taxa reported from the middle Miocene to the Holocene (see Kraglievich, 1925; Scillato-Yané, 1978, 1981; Hirschfeld, 1985; McDonald, 1997; Esteban, 1999; Villarroel, 2000; Rinderknecht *et al.*, 2007, 2010; Saint-André *et al.*, 2010; Boscaini *et al.*, 2019a, 2021), and widely distributed during the Quaternary. This group was recorded in Argentina, Bolivia, Brazil, Chile, Ecuador, Colombia, Peru, Paraguay, Uruguay, Venezuela, and the United States of America. The known taxa are: *Mylodon* Owen, 1839, *Glossotherium* Owen, 1839, *Oreomyodon* Hoffstetter, 1949, *Paramylodon* Brown, 1903, *Mylodonopsis* Cartelle, 1991, *Ocnotherium* Lund, 1842, *Glossotheridium* Kraglievich, 1934, *Pleurolestodon* Rovereto, 1914, *Simomyodon* Saint-André, Pujos, Cartelle, De Iuliis, Gaudin, McDonald & Quispe, 2010, *Kiyumylodon* Rinderknecht, Perea & McDonald, 2007 and *Archaeomyodon* Brambilla & Ibarra, 2019 (Boscaini *et al.*, 2019a). It is characterized by the cfl being the smallest tooth of the upper tooth row, Mf2 and Mf3 (upper molariforms) with a square outline in cross section, irregularly lobate cross section of mf2 (lower molariforms), presence of an oblique medial ridge on the ascending ramus of the mandible, medial and lateral palatal processes of maxilla of equivalent anterior extent, flat surface contour of the astragalus discoid process in lateral view and the presence of osteoderms (Boscaini *et al.*, 2019a, characters 13, 32, 34, 44, 111, 369, and 383, respectively).

Scelidotheriinae were endemic to South America throughout all their existence. The first records are from the middle Miocene, and they were extinct in the Pleistocene–Holocene transition (Corona *et al.*, 2013; Lobato *et al.*, 2021). The group has a wide geographic distribution in South America, with fossils found in several countries such as Colombia, Uruguay, Ecuador, Bolivia, Argentina, Chile, Paraguay, Peru, and Brazil (Corona *et al.*, 2013). Since its first descriptions, the group had several phylogenetic issues (Lobato *et al.*, 2021) with some taxa considered a “nomenclature nightmare” by some authors (*e.g.*, Paula-Couto, 1973). Cartelle *et al.* (2009) elucidated some nomenclature issues about Brazilian taxa. Currently, there are three genera recognized for the Quaternary: *Catonyx*, *Scelidotherium* and *Valgipes* (Miño-Boilini & Quiñones, 2020). In Brazil, only remains of *Catonyx* and *Valgipes* have been described so far and were mainly recovered at intertropical latitudes (Miño-Boilini & Quiñones, 2020). Scelidotheriinae had typical morphological features, such as a tubular and elongated skull, parallel dental series, laterally compressed molariforms, quadrangular and anteroposteriorly compressed femur, and astragalus with a concave cuboidal facet (Miño-Boilini *et al.*, 2019).



**Figure 1.** Geographic distribution of Mylodontidae during the Quaternary in South America according to Cartelle (1991), Esteban (1993), Cartelle *et al.* (2009), Brandoni *et al.* (2010), Silva *et al.* (2010), Corona *et al.* (2013), Miño-Boilini *et al.* (2014), Favotti *et al.* (2015), Varela & Fariña (2015), De Iuliis *et al.* (2017, 2020), Varela *et al.* (2018), Cartelle *et al.* (2019), Boscaini *et al.* (2020), Gaudin & Broome (2021) and Lobato *et al.* (2021).

### Rio Grande do Sul mylodontids

The fossils of Mylodontinae are known from several Pleistocene localities in Rio Grande do Sul State, Brazil. *Lestodon armatus* has been reported from Sanga dos Borba (Rio Pardo Municipality), Arroio do *Lestodon* (Caçapava do Sul Municipality), Hermenegildo Beach, Chui Creek (Santa Vitória do Palmar Municipality) and Osório Municipality (Paula-Couto, 1953; Oliveira *et al.*, 2005; Ribeiro & Scherer, 2009; Vargas-Peixoto *et al.*, 2021). Remains assigned to *Glossotherium robustum* were reported from Barranca Grande, Cerro da Tapera, Sanga da Cruz, Rincão dos Fialho, Banhado do Inhatium (Uruguaiana, Quaraí, Alegrete, Rosário do Sul and São Gabriel municipalities, respectively) and Hermenegildo Beach (Oliveira, 1992, 1996; Pitana *et al.*, 2013).

The records of Scelidotheriinae considered valid so far are few and limited to some remains attributed to *Catonyx* cf. *C. cuvieri* collected in Chui Creek and in the Coastal Plain, in the Santa Vitória do Palmar Municipality (Lopes & Pereira, 2010).

The diagnoses of the two groups of Mylodontidae (Mylodontinae and Scelidotheriinae) are mainly based on cranial and mandibular features (Gaudin, 2004; Boscaini *et al.*, 2019a). This can be attributed to the lack of postcranial material associated with cranial remains, and because postcranial morphology is considered to have fewer variables compared to the skull and mandible, which has restricted its importance in morphological comparative studies and phylogenetic analyses. Thus, this paper aims to identify and to describe new postcranial remains belonging to Mylodontidae from the Pleistocene of Rio Grande do Sul (Brazil) and to improve morphological data to better understand the isolated remains of this group.

### MATERIAL AND METHODS

The postcranial materials corresponds to two humeri, two radii, one femur, 29 tibiae and 25 astragali from various Pleistocene localities of Rio Grande do Sul State (Figure 2) and they are deposited in the Paleovertebrate Scientific Collection of the Museu de Ciências Naturais, Secretaria Estadual do Meio Ambiente e Infraestrutura (MCN/SEMA-RS), Porto Alegre, and Universidade Federal do Rio Grande (FURG), both in Rio Grande do Sul State, Brazil, under the acronyms MCN-PV and LGP-Q, respectively.

The identification of the material was carried out on the basis of comparisons with Quaternary mylodontids from Argentina (*Lestodon armatus*, *Glossotherium robustum*, *Scelidotherium leptcephalum*), Uruguay (*L. armatus*, *G. robustum*), Bolivia (*G. robustum*) and northeastern Brazil (*Ocnotherium giganteum*, *Glossotherium phoenesis*, *Valgipes bucklandi* and *Catonyx cuvieri*), megatheriids (*Eremotherium laurillardii* and *Megatherium americanum*), and megalonychids (*Ahytherium aureum* and *Australonyx aquae*). A comparison with the specialized literature (Cartelle *et al.*, 2009; Miño-Boilini, 2012; Amson *et al.*, 2014; Cartelle *et al.*, 2019; Boscaini *et al.*, 2021) was made.

Principal Component Analyses (PCA) were performed using the software PAST (Hammer *et al.*, 2001) for the tibiae and astragali, as they were the elements with a considerable number of specimens (Supplementary material). All measurements were made with a calliper, ruler, and protactor.

**Institutional abbreviations.** FMNH, Field Museum of Natural History, Chicago, United States; LGP-Q, Laboratório de Geologia e Paleontologia da Fundação Universidade de Rio Grande, Rio Grande, Brazil; MCL, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MCN-PV, MCN-D, Museu de Ciências Naturais, Secretaria do Meio Ambiente e Infraestrutura, Porto Alegre, Brazil, Paleovertebrados and Mastozoologia collections, respectively; MCP-PV, Museu de Ciências e Tecnologia of Pontifícia Universidade Católica of Rio Grande do Sul, Porto Alegre, Brazil; MHD-P, Museo Histórico Departamental de Artigas, Uruguay; MLP, Museo de La Plata, La Plata, Argentina; MNPA-V, Museo Nacional Paleontológico Arqueológico, Tarija, Bolivia. **Other abbreviations:** Cf, upper caniniforms; cf, lower caniniforms; Mf, upper molariforms; mf, lower molariforms; RSCP, Rio Grande do Sul Coastal Plain.

### SYSTEMATIC PALEONTOLOGY

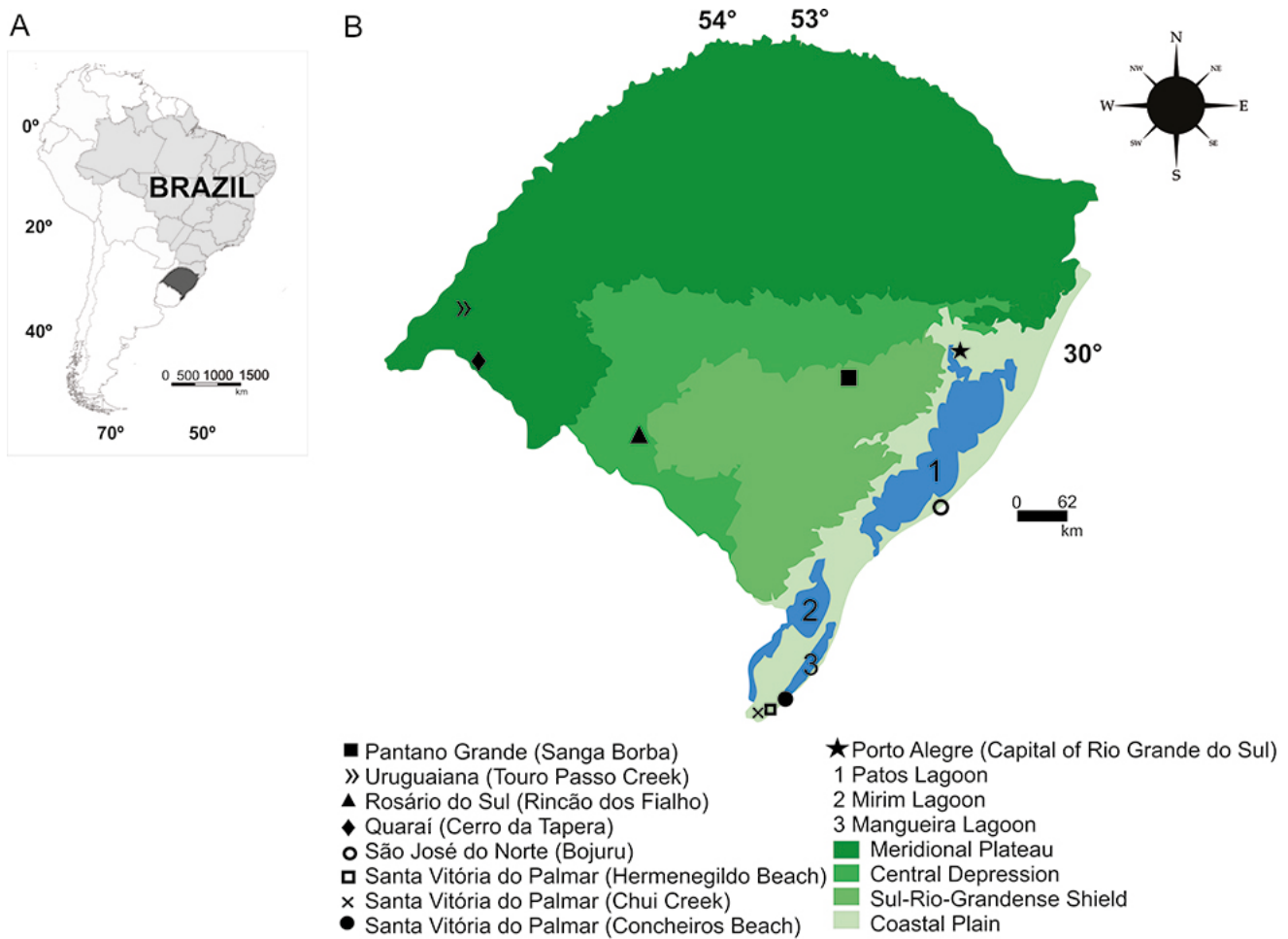
FOLIVORA Delsuc, Catzeflis, Stanhope & Douzery, 2001  
MYLODONTIDAE Gill, 1872  
MYLODONTINAE Gill, 1872  
LESTODONTINI Ameghino, 1889 *sensu* Gaudin (2004)

*Lestodon* Gervais, 1855

**Type species.** *Lestodon armatus* Gervais, 1855.

*Lestodon armatus* Gervais, 1855  
(Figure 3)

**Material and geographic provenance.** Pantano Grande, Sanga Borba: MCP-674-PV (right tibia); São José do Norte, Bojuru: MCN-PV 1809 (left astragalus); Quaraí, Cerro da Tapera: MCN-PV 2090 (left tibia); Santa Vitoria do Palmar, Coastal Plain: MCN-PV 438, 447 (left tibiae); MCN-PV 838, 1112 (right tibiae); MCN-PV 338, 31808 (distal portions of left tibiae); MCN-PV 36991 (proximal portion of left tibia); MCN-PV 93, 31821 (proximal portions of right tibiae); MCN-PV 287, 32113, 36992 (distal portions of right tibiae); MCN-PV 31734 (left astragalus); Hermenegildo Beach: MCN-PV 340 (proximal portion of left radius); MCN-PV 1927 (incomplete left radius); MCN-PV 5708 (right tibia); MCN-PV 5705, 5707, 5709 (distal portions of right tibiae); MCN-PV 5711, 9685 (distal portions of left tibiae); MCN-PV 5719, 5720, 5721, 5722, 5723, 6065, 6201, 7928, 8653, 9652, 9655, 9656, 9657 (left astragali); MCN-PV 5715, 5717, 6899, 9654 (right astragali); Concheiros Beach: MCN-PV 1591 (distal portion of right radius); MCN-PV 2543 (left radius); MCN-PV 2555, 2561 (distal portions of right tibiae); MCN-PV 2385, 3616 (left astragali); MCN-PV 2514 (right



**Figure 2.** A, South America map showing the State of Rio Grande do Sul in dark gray; B, localities where the specimens of this study were collected.

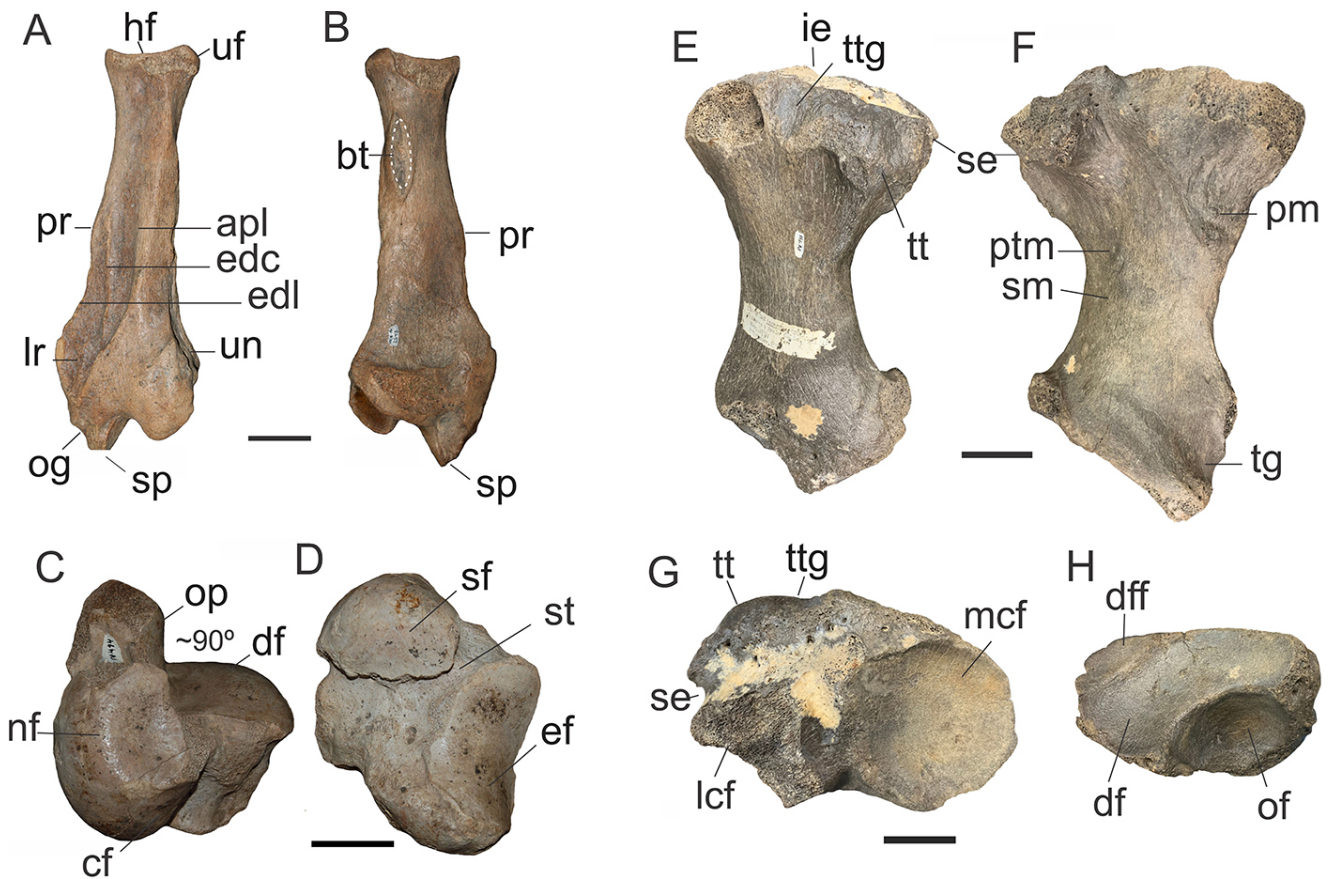
astragalus); Duna Tadeu: MCN-PV 3224 (right astragalus); Chui Creek: MCN-PV 414 (left astragalus) (Figure 2).

**Age.** Late Pleistocene.

**Description.** *Radius* (Figures 3A, B): the proximal end has an ovoid shape, with two articular surfaces, one for the ulna and one for the humerus. The humeral facet is concave, proximally oriented and larger than the ulnar facet. The ulnar facet is formed by two contiguous portions; the larger one is slightly convex and proximoposteriorly oriented, whereas the smaller one is flat and distoposteriorly oriented. The shaft of the radius is proximodistally elongated and lateromedially compressed; its anterior border in lateral view is formed by a convex pronator ridge. In lateral view, there are two descendent crests for attachment of the muscular tendons of the antebrachium: *m. abductor pollicis longus* (posterior), *m. extensor digitorum communis* (central), and *m. extensor digitorum lateralis* (anterior margin). The posterior and central crests are confluent and reach the anterior portion of the shaft. Distoanterior to the anteriormost crest there is a short longitudinal ridge. The bicipital tuberosity is medially oriented, near the anterior margin, proximodistally elongated, and has a rugose surface. The anterior surface of the shaft has a styloid process (suprastyloid tuberosity) distally, just

proximal to the styloid process there is an oblique groove for a *digitorum* musculature. The posterior border is straight, with a rugose surface corresponding to the interosseous ligament scar near the middle axis of the shaft; distal of this scar there is the ulnar notch. The distal end bears two articular facets, which are subtly separated by a ridge. The lunar facet is the anterior one, while the posterior one corresponds to the scaphoid facet.

*Tibia* (Figures E–H): the tibiae are flattened and narrow in the shaft, both anteroposterior and lateromedially, reaching their minimum thickness in the middle portion. This narrowing results in lateral, medial, and posterior concave margins. The shaft is short with its medial surface rugose, which extends to the medial portion of the shaft for attachment of the *m. popliteus*. The proximal end is larger lateromedially than the distal one and has two condyles, the medial and the lateral, both articulating with the femur and separated by a nonarticular area: the intercondylar eminence. The intercondylar eminence is the most projected structure in the proximal portion, resulting in a convex appearance in anterior and posterior views. The medial condyle facet is concave and oval, and is considerably larger than the lateral facet, which has a circular shape and a more flattened surface. In anterior view, the tibial tuberosity is wider in the proximal



**Figure 3.** *Lestodon armatus*. **A, B**, Left radius (MCN-PV 2543), lateral and medial views, respectively. **C, D**, left astragalus (MCN-PV 414), anterior and distal views, respectively. **E—H**, left tibia (MCN-PV 447) anterior, posterior, proximal and distal views, respectively. **Abbreviations:** **apl**, *m. abductor pollicis longus* crest; **bt**, bicipital tuberosity; **cf**, cuboid facet; **df**, discoid facet; **dff**, distal fibular facet; **edc**, *m. extensor digitorum communis* crest; **edl**, *m. extensor digitorum lateralis* crest; **ef**, ectal facet; **hf**, humeral facet; **ie**, intercondylar eminence; **lcf**, lateral condylar facet; **lr**, longitudinal ridge; **mcf**, medial condylar facet; **nf**, navicular facet; **of**, odontoid facet; **og**, oblique groove; **op**, odontoid process; **pm**, *m. popliteus* crest; **pr**, pronator ridge; **ptm**, *m. posterior tibialis* crest; **se**, *sulcus extensorius*; **sf**, sustentacular facet; **sm**, *m. soleus* crest; **sp**, styloid process; **st**, *sulcus tali*; **tg**, tendinal groove; **tt**, tibial tuberosity; **ttg**, tibial tuberosity groove; **uf**, ulnar facet; **un**, ulnar notch. Scale bars = 50 mm.

portion tapering distally, giving it a triangular appearance. The most proximal portion is medially limited by the tibial tuberosity groove. The *sulcus extensorius* is proximolaterally oriented to the tibial tuberosity. The lateral condyle projects posterolaterally and has an articulating facet for the proximal portion of the fibula, which occupies a more proximal position. The distal fibular facet has a semilunar outline; the joint surface is slightly concave and slants proximally, forming an obtuse angle with the discoid facet. The discoid facet has a semilunar outline, is slightly concave medially, and is thick laterally. The facet for the odontoid process of the astragalus is deep, with a rounded outline, forming a right angle ( $\pm 90^\circ$ ) with the entire margin of the discoid facet, which is separated by a prominent articular ridge. The malleolus appears to have a single wide and shallow tendinal groove in some specimens and two in other specimens. This groove is directed obliquely proximolaterally and distomedially.

*Astragalus* (Figures 3C, D): the proximal portions of the astragali bear two facets, the discoid and the odontoid. The discoid facet is horizontally oriented; its joint surface is

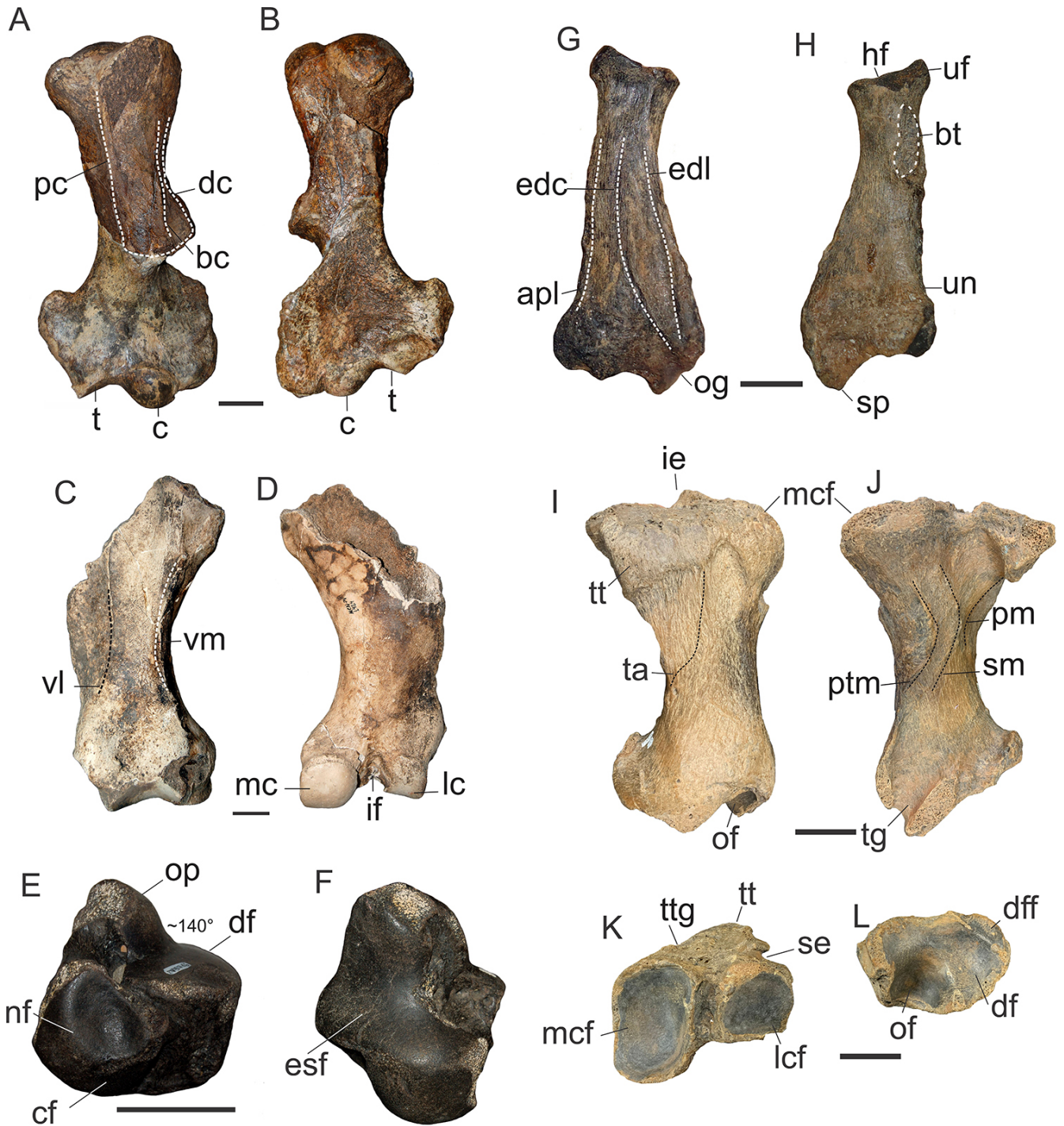
flat, with the lateral margin convex. The odontoid process is elliptical, robust and elongated, forming a right angle ( $\pm 90^\circ$ ) with the discoid facet on its lateral side. The lateral facet of the astragalus, which articulates with the fibula, is slightly convex anteroposteriorly and proximodistally, forming an acute angle ( $\pm 45^\circ$ ) with the discoid facet. The navicular facet is slightly concave in its anteriormost portion and convex dorsally. The cuboid facet is convex and has a triangular surface. On the distal portion, the two facets of the calcaneus, ectal and sustentacular, are separated by the *sulcus tali*.

MYLODONTINI Saint-André, 1994

*Glossotherium* Owen, 1839

**Type species.** *Myloodon robustus* Owen, 1842.

*Glossotherium robustum* (Owen, 1842)  
(Figure 4)



**Figure 4.** *Glossotherium robustum*. A–B, left humerus (LGP-Q0004), anterior and posterior views, respectively. C–D, right femur (MCN-PV 1424), anterior and posterior views, respectively. E–F, left astragalus (MCN-PV 5716), anterior and distal views, respectively. G–H, right radius (MCN-PV 9718), lateral and medial views, respectively. I–L, right tibia (MCN-PV 8247), anterior, posterior, proximal, and distal views, respectively. **Abbreviations:** **apl**, *m. abductor pollicis longus* crest; **bc**, brachiocephalic crest; **bt**, bicipital tuberosity; **c**, capitulum; **cf**, cuboid facet; **dc**, deltoid crest; **df**, discoid facet; **dff**, distal fibular facet; **edc**, *m. extensor digitorum communis* crest; **edl**, *m. extensor digitorum lateralis* crest; **esf**, ectal + sustentacular facet; **hf**, humeral facet; **ie**, intercondylar eminence; **if**, intercondylar fossa; **lc**, lateral condyle; **lcf**, lateral condylar facet; **mc**, medial condyle; **mcf**, medial condylar facet; **nf**, navicular facet; **of**, odontoid facet; **og**, oblique groove; **op**, odontoid process; **pm**, *m. popliteus* crest; **ptm**, *m. posterior tibialis* crest; **pc**, pectoral crest; **se**, *sulcus extensorius*; **sm**, *m. soleus* crest; **sp**, styloid process; **t**, trochlea; **ta**, *m. tibialis anterior* crest; **tg**, tendinal groove; **tt**, tibial tuberosity; **ttg**, tibial tuberosity groove; **uf**, ulnar facet; **un**, ulnar notch; **vl**, *m. vastus lateralis* crest; **vm**, *m. vastus medialis* crest. Scale bars = 50 mm.

**Material and geographic provenance.** Santa Vitória do Palmar, Chui Creek: LGP-Q0004 (left humerus); Hermenegildo Beach: MCN-PV 8247 (right tibia); MCN-PV 59, 36611 (left tibia); MCN-PV 325 (distal portion of left tibia); MCN-PV 7929 (distal portion of right tibia); MCN-PV 5716 (left astragalus); MCN-PV 6603 (right astragalus); MCN-PV 9718 (right radius); Concheiros: MCN-PV 2388 (right tibia); Rosário do Sul, Rincão dos Fialho: MCN-PV 1424 (incomplete right femur); Uruguaiana, Touro Passo: MCN-PV 1482 (right tibia).

**Age.** Late Pleistocene.

**Description.** *Humerus* (Figures 4A, B): the shaft is straight, anteroposteriorly flat with three well-developed crests on its deltopectoral plate. The pectoral crest (medial) begins below the anterior portion of the greater tuberosity and extends to the medial portion of the shaft; the deltoid crest (lateral one) partially covers the musculospiral groove. The central brachiocephalic crest is shorter than the other two. The brachiocephalic and deltoid crests are distally coalescent. The greater tuberosity is elongated and anteroposteriorly oriented; the lesser one is anteromedially oriented. The two tuberosities are separated by a wide and shallow groove, which corresponds to the tendon of the *m. pectoralis*. The distal end of the humerus is mediolaterally expanded; the medial epicondyle is well developed and has a rugose surface. The lateral epicondyle is elongated and is part of the supinatory crest. The olecranon fossa is slightly concave.

*Radius* (Figures 4G, H): the head is ovoid with a convex medioproximal surface that is smaller than the lateral one. The latter is markedly concave. The shaft is mediolaterally compressed; its lateral surface is slightly flat with two oblique descendent crests, oriented proximoanteriorly, for the muscular tendons of the antebrachium. This condition is similar to that observed in *Lestodon armatus*, although in *Glossotherium robustum* the crests occupy only the anterior half of the shaft, while in *L. armatus* the posteriormost crest almost reaches the posterior border of the bone. In lateral view, the anterior margin is straight. The distal end is triangular and formed by two concave joint facets: the scaphoid facet (posterior) and lunar facet (anterior). The first facet is wide, quite concave and is quadrangular-shaped; the anterior one is narrow and elongated, flat laterally and slightly concave medially. Like in *L. armatus*, just proximal to the styloid process there is an oblique groove for a digitorum musculature.

*Femur* (Figures 4C, D): the bone has a rectangular outline, with a slight medial arch along its axis. The shaft is narrow; its anterior view is flat with a well-developed longitudinal crest for the attachment of the *m. vastus medialis*. The posterior surface of the shaft is flat, with a rugose region for the *facies poplitea*. The lesser trochanter is vertically rounded, forming a distally oriented “depressed tuberosity”, limited by a short crest, which is distally continuous with a rough surface for attachment of the *m. vastus lateralis*. There is no third trochanter. The femoral condyles are asymmetrical; the intercondylar fossa is small and continuous with the popliteal plane, without an osseous bridge.

*Tibia* (Figures 4I–L): the tibia of *G. robustum* is smaller than that of *L. armatus* (Figure 5). As in *L. armatus*, the tibia is flattened and narrow in the shaft resulting in lateral, medial and posterior concave margins. The proximal surface bears the two femoral facets, where the medial one is almost twice as large as the lateral one. The intercondylar eminence is the most proximally projected structure. The lateral surface of the tibia has a slightly rugose surface for the attachment of the *anterior tibialis muscle*. The tibial tuberosity is wide, with the lateral surface slightly flat, that is medially limited by the *sulcus tuberositatis tibiae*. Proximolaterally to the tibial tuberosity there is the *sulcus extensorius*, which extends posteriorly, limiting the proximal fibular facet. The posterior surface of the shaft has rugose surfaces for the attachment of the *m. popliteus*, *m. soleus* and *m. tibialis posterior*. In the distal portion, the discoid facet has a flat, small middle portion, slightly concave and thick laterally. The odontoid facet for the astragalus is rounded and slightly concave and forms a right angle with the anterior edge of the discoid facet and an obtuse angle with the lateral portion of the discoid facet. The malleolus has a single wide and deep tendinal groove.

*Astragalus* (Figures 4E, F): the astragalus of *Glossotherium robustum* is smaller than its homologues of *Lestodon armatus* (Figure 6); the discoid facet is horizontally oriented, flat and wide posteriorly, and narrow anteriorly. The lateral facet is convex with a rugose surface and forms an almost right angle with the discoid facet. The odontoid process is semicylindrical in shape and forms an obtuse angle with the discoid facet. The navicular facet is slightly concave anteriorly and convex dorsally, continuous with the cuboid facet. The cuboid facet is convex and triangular. In distal view, the sustentacular and ectal facets are contiguous, forming a wide calcaneal facet, which means that there is no *sulcus tali*. The cuboid facet is continuous to the calcaneal facet.

#### SCOLIDOTHERIINAE Ameghino, 1904

##### Scelidotheriinae indet.

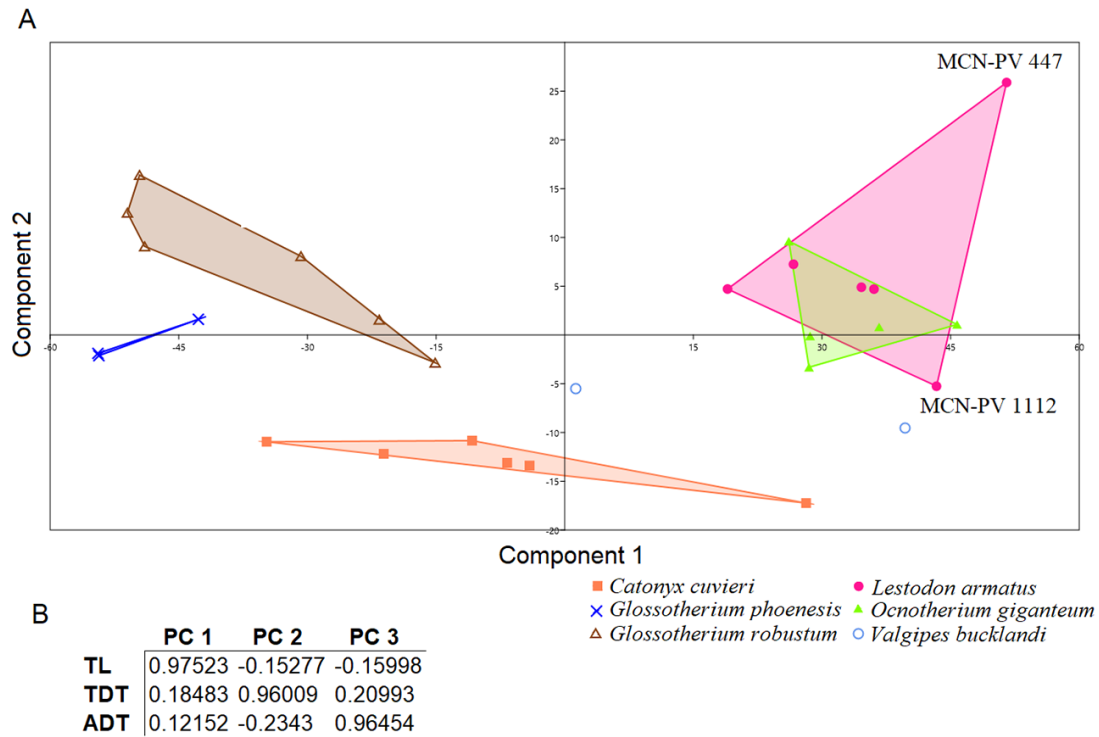
(Figure 7A)

**Material and geographic provenance.** Hermenegildo Beach, Santa Vitória do Palmar: MCN-PV 038 (fragment of distal portion of the left humerus).

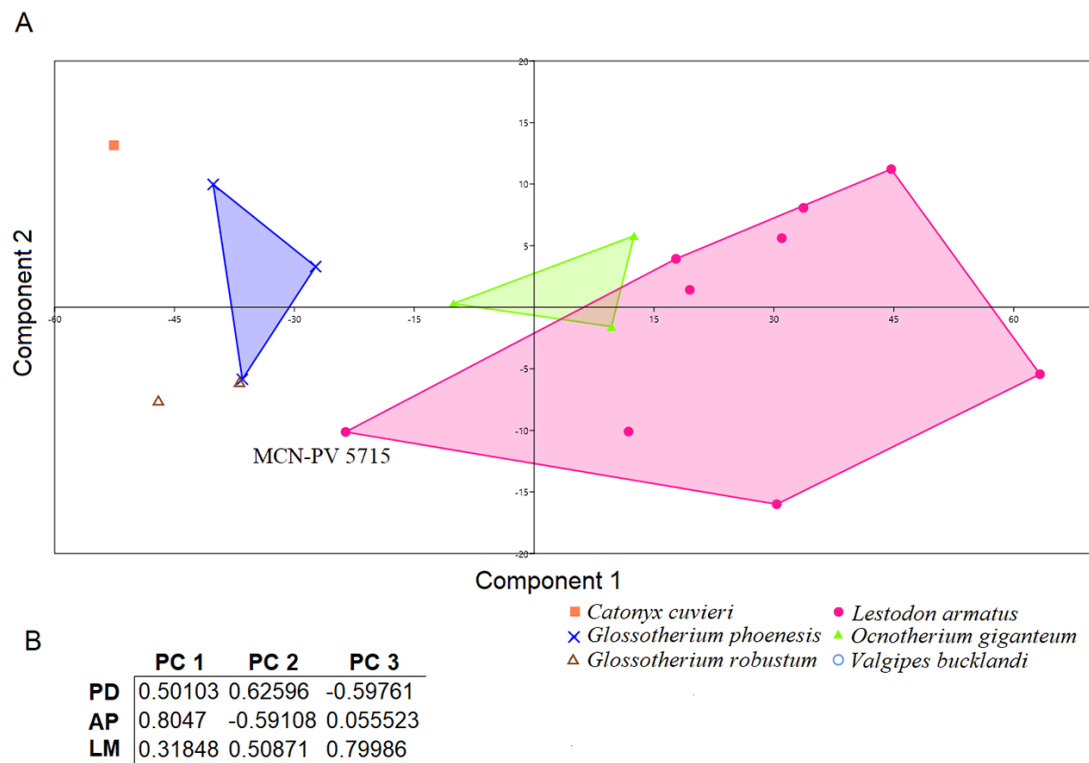
**Age.** Late Pleistocene.

**Description.** *Humerus* (Figure 7A): the specimen has an elliptical entepicondylar foramen (37.4 mm x 18.3 mm) with a single aperture; the bone bar that covers the foramen anteriorly is horizontally oriented. Laterally to the foramen, the distal area of the deltopectoral plate is anteriorly positioned with a portion that projects laterally. The entepicondylar ridge is aligned with the bone bar and the distalmost portion of the deltopectoral plate; the medial epicondyle is strongly projected medially. Posteriorly, the fragment is flattened.

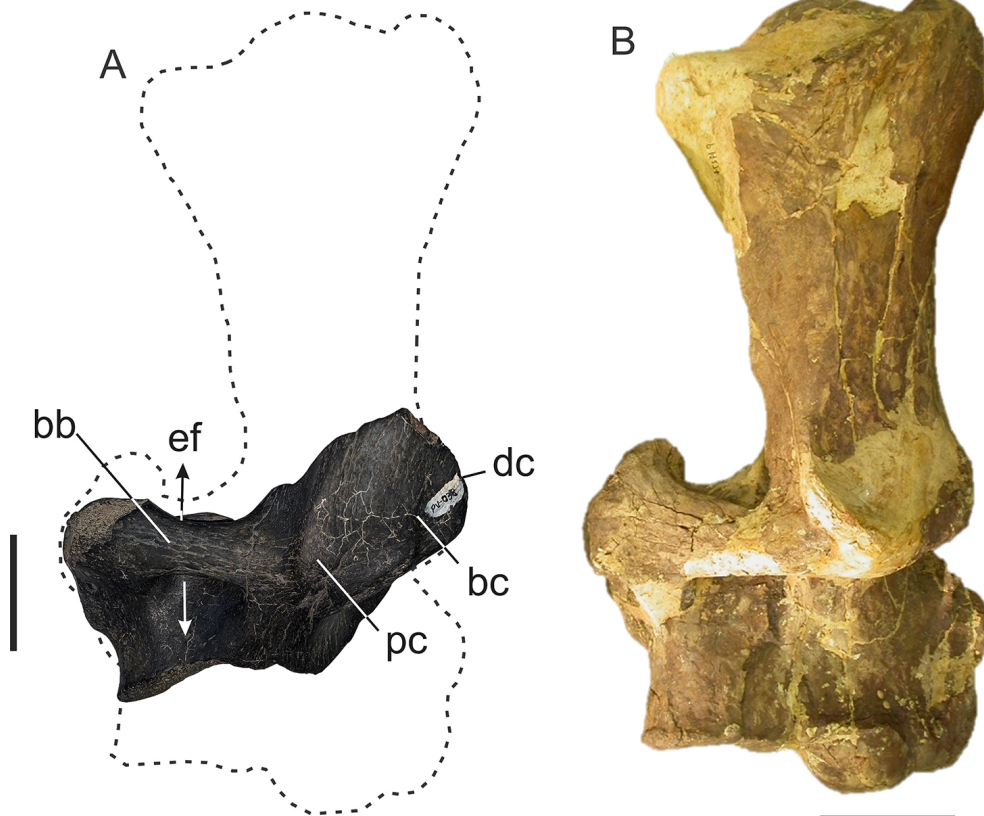




**Figure 5.** A, tibial morphospace based on Principal Component 1 (PC 1, variance of 91,532%) and Principal Component 2 (PC 2, variance of 6,4158%). B, contribution of each measure to the PCA. **Abbreviations:** TL, total length; TDT, transverse diameter of tibia at midshaft; ADT, anteroposterior diameter of tibia at midshaft.



**Figure 6.** A, astragalar morphospace based on Principal Component 1 (PC 1, variance of 93,217%) and Principal Component 2 (PC 2, variance of 5,2812%). B, contribution of each measure to the PCA. **Abbreviations:** PD, proximodistal length; AP, anteroposterior length; LM, lateromedial length.



**Figure 7.** A, *Scelidotheriinae* indet., fragment of the distal portion of the left humerus (MCN-PV 038), in anterior view; B, *Scelidotherium leptocephalum*, right humerus (FMNH P 14274), in anterior view. Image of FMNH P 14274 given by Ángel Miño-Boilini. **Abbreviations:** bb, bone bar; bc, brachiocephalic crest; dc, deltoid crest; ef, entepicondylar foramen; pc, pectoral crest. Scale bars = 50mm.

## DISCUSSION

As previously discussed in other studies (*e.g.*, Lopes, 2013; Cruz *et al.*, 2016), the fossils collected from the Rio Grande do Sul Coastal Plain (**RSCP**) (Santa Vitória do Palmar and São José do Norte municipalities) are mostly disarticulated, with signs of postmortem fractures, abrasion due to reworking caused by waves; and associated actual marine and terrestrial fauna. This implies a lack of articulated individuals, and there are few specimens that have structures clearly preserved. Differently, the material from Chui Creek (Santa Vitória do Palmar Municipality) are better preserved, since they did not suffer the same actions caused by the waves as in the RSCP case (see Pereira *et al.*, 2012; Lopes & Simone, 2012; Lopes, 2013; Lopes & Ferigolo, 2015). Similar conditions were observed for specimens collected in the Uruguaiana Municipality (Touro Passo Formation), which are mostly isolated with incrustations that result in fossil deformation (Kerber *et al.*, 2014). Those from Pantano

Grande Municipality (Sanga Borba) are also isolated and very fragmentary, while those from Rosário do Sul Municipality (Rincão dos Fialho) are sometimes recovered articulated, but unfortunately, this locality still has scarce associated information.

The postcranial morphology of fossil sloths has been considered conservative, because their corporal design is apparently less complex than that of other mammal groups; some sloth postcranial bones (*e.g.*, humerus, tibia) are considered classic examples of the conservative nature of the appendicular skeleton (De Iuliis, 2003). Recently, works described postcranial remains of extinct Folivora (Toledo *et al.*, 2013, 2014, 2015; Amson *et al.*, 2015a, b; Haro *et al.*, 2016; Vargas-Peixoto *et al.*, 2021; Boscaini *et al.*, 2021; Casali *et al.*, 2022), focusing mainly on morphological information and, sometimes, on phylogenetic affinities. Regarding the primitive or derived condition of the characters, little attention was given.

Despite the fragmentary nature of the studied material, some relatively complete humeri, radii, femora, tibiae, and astragali of Mylodontidae from the Quaternary localities of the Rio Grande do Sul could be analyzed and compared with material of this group from other South American regions.

### Humerus

Both described humeri were collected in the Santa Vitória do Palmar Municipality, one relatively complete from Chui Creek (LGP-Q0004, Figures 4A–B) and one fragment of distal portion from Hermenegildo Beach (MCN-PV 038, Figure 7A). The first was attributed to *Glossotherium robustum* due to its size and some morphological characteristics, such as a wide and shallow groove separating the two proximal tuberosities, and the lesser tuberosity significantly less protruded than the greater tuberosity (characteristic of Mylodontidae; Boscaini *et al.*, 2019a; Boscaini *et al.*, 2021); deltopectoral plate oriented anterolaterally, trochlea, and capitulum with similar mediolateral width and posteriorly directed medial epicondyle in distal view (characteristic of Mylodontini; Boscaini *et al.*, 2019a).

Specimen MCN-PV 038, although very incomplete, was assigned to Scelidotheriinae mainly because it has a distinct entepicondylar foramen, which is a typical feature of some species of Scelidotheriinae. Currently, there are three genera of Scelidotheriinae recognized for the Quaternary, with only two species recorded in Brazil so far (*Valgipes bucklandi* and *Catonyx cuvieri*). The specimen MCN-PV 038 differs from *V. bucklandi* humerus because the bone bar is markedly obliquely oriented (see Figure 8B). *Catonyx* has three species: *C. cuvieri*, *C. chiliensis* and *C. tarijensis*. MCN-PV 038 differs from *C. cuvieri* because the humerus of this one does not bear an entepicondylar foramen; on the other hand, *C. chiliensis* and *C. tarijensis* bear an entepicondylar foramen with the bone bar transversally oriented (Miño-Boilini, 2012, characters 17 and 18, respectively). *Scelidotherium* is a genus with three valid species, *S. parodii* (Pliocene), *S. bravardii* (early–middle Pleistocene), and *S. leptocephalum* (late Pleistocene, Figure 7B) (Miño-Boilini *et al.*, 2014, Nieto *et al.*, 2020; Haro *et al.*, 2023), all of them showing an entepicondylar foramen and a transversal bone bar, as *C. chiliensis* and *C. tarijensis* (see Miño-Boilini, 2015, fig. 2A). The available characters in the specimen MCN-PV 038 are not enough for some specific or even generic attribution once the material is isolated and very fragmentary. Nevertheless, the specimen MCN-PV 038 indicates the presence of another species of Scelidotheriinae different from *Valgipes bucklandi* and *Catonyx cuvieri*, the two species of Scelidotheriinae with Brazilian records so far.

*Remarks on the entepicondylar foramen.* The entepicondylar foramen is a canal in the medial epicondyle at the distal end of the humerus (Figure 8), usually pierced by the median nerve and brachial artery. It is a primitive structure in the humerus of mammals, and it is also considered a primitive amniote feature (Romer, 1945; Landry Jr., 1958). Some groups never developed an entepicondylar foramen (*e.g.*, lagomorphs, cetaceans, chiropterans, humans), but in other groups, this characteristic is variable (Landry Jr., 1958), as in living and

fossil xenarthrans, although it has received little attention, in particular in what concerns ground sloths.

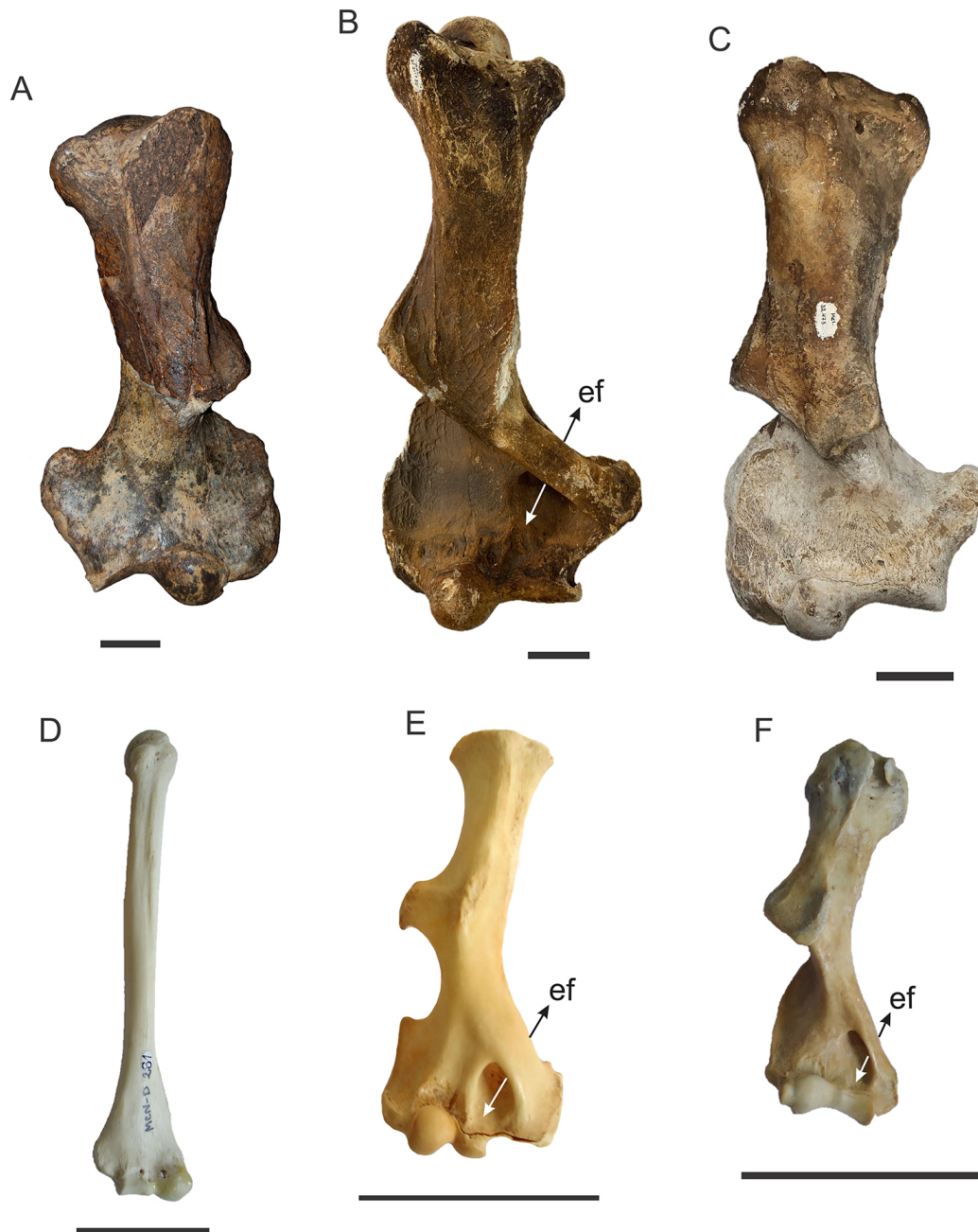
Early mylodontids, *Pseudopreotherium venezuelanum* (Collins, 1934) and *Bolivartherium urumaquensis* do not bear an entepicondylar foramen, while *Pseudopreotherium confusum* Hirschfeld, 1985 and *Urumacotherium garciai* Bocquentin-Villanueva, 1984 have such a structure. The Pleistocene Mylodontini *Glossotherium robustum* (LGP-Q 0004; Figures 4A, 8A), *Myloodon darwini* Owen, 1840 and *Ocnotherium giganteum* (MCL 4228/03, MCL 4228/40), and the Lestodontini *Lestodon armatus* (MNPA-V 005773) do not have the entepicondylar foramen (Owen, 1842; Reinhardt, 1875; Stock, 1925; Kraglievich, 1934; Cartelle, 1992; Henriques, 1992). However, Pleistocene scelidotheriines differ from the above-mentioned taxa by the retention of a well-developed entepicondylar foramen in *Scelidotherium leptocephalum* (Figure 7B), *Valgipes bucklandi* (MCL 22211/89 Figure 8B, MCL 22256/01-02, MCL 4294-03), *Catonyx chiliensis* and *C. tarijensis* (see Miño-Boilini, 2015, fig. 2a). On the other hand, in *C. cuvieri* a condition similar to the mylodontines occurs (MCL 22473, MCL 22474; Figure 8C) (McDonald, 1987; Cartelle, 1992; Cartelle *et al.*, 2009).

Concerning extant xenarthrans, the two-toed sloth *Choloepus* (MCN-D 281) does not have an entepicondylar foramen, while extant armadillos and anteaters, such as *Euphractus sexcinctus* Linnaeus, 1758 (MCN-D 2757) and *Tamandua tetradactyla* Linnaeus, 1758 (MCN-D 047), have such structure (Figures 8D–F). Therefore, the occurrence of an entepicondylar foramen in cingulates suggests a relation to the primitive condition of their skeleton, while its absence in sloths suggests a derived condition of the forelimb.

The entepicondylar foramen is also absent in humans, but a bony spur on the medial side of the humerus, known as the supracondylar process, is frequently observed. The supracondylar process and its ligamentous connection are probably homologous to the arch that forms the superficial wall of the entepicondylar foramen in other mammal groups (Landry Jr., 1958), including xenarthrans.

Negri (2004) and Cartelle *et al.* (2009) interpreted the occurrence of the entepicondylar foramen in terms of evolutionary trends, especially in extinct sloths. The absence of an entepicondylar foramen in some Miocene (*e.g.*, *Thinobadistes segnis* Hay, 1919) and Pleistocene (*e.g.*, *Glossotherium robustum*, *Catonyx cuvieri*) mylodontids was considered as a derived condition. The disappearance of such a structure in other Miocene mylodontids (*e.g.*, *Pseudopreotherium venezuelanum*) could correspond to a transition stage likely related to Pleistocene taxa. Although the above-mentioned hypothesis supports an evolutionary trend towards the disappearance of the entepicondylar foramen from Miocene to Pleistocene mylodontids, in fact, the evolutionary changes of this character are not clearly understood, indicating that phylogenetic studies are necessary to elucidate this question.

It is possible that the entepicondylar foramen or simply a bony spur on the medial side of the humerus (supracondylar process) are all variations of no important meaning, since the



**Figure 8.** Humerii of Xenarthra, in anterior view, illustrating the presence/absence of an entepicondylar foramen. **A**, *Glossotherium robustum* (LGP-Q0004); **B**, *Valgipes bucklandi* (MCL 22211/89); **C**, *Catonyx cuvieri* (MCL 22473); **D**, *Choloepus* sp. (MCN-D 281); **E**, *Tamandua tetradactyla* (MCN-D 047); **F**, *Euphractus sexcinctus* (MCN-D 2757). **Abbreviations:** ef, entepicondylar foramen. Scale bars = 50 mm.

spur may be the point of fixation of a ligament that completes in this way a “tendinous” entepicondylar foramen.

*Remarks on the humeral crests.* The interpretation of the main differences between the humeri of the living and fossil xenarthrans, mostly sloths, requires a detailed analysis of the morphology of the anterior humeral face and the homology of its structures (De Iuliis, 2003), which has not been adequately explained in the literature. They have received various classifications (e.g., inner/outer ridge, medial/lateral

ridge, deltoidal tract, pectoral ridge, intermediate crest, third crest, median ridge) because their position on the humeral shaft and the musculature attachment are criteria applied to classify such structures.

The pectoral and deltoid crests (Figure 9) are well known in the literature because they are related to the attachment of homonymous muscles, which allow performing the main actions of the forelimb that correspond to the adduction and abduction of the arm, respectively. However, extinct sloths can

bear a third crest placed between the pectoral and deltoid ones, which was first described by Negri (2004), and more recently named the brachiocephalic crest (Amson *et al.*, 2015a).

Studies on the morphology and function of the humeral crests in extinct sloths are still necessary, although there have already been biomechanical studies of the limb bones to infer their locomotory abilities (Bargo *et al.*, 2000; Vizcaino *et al.*, 2003; Milne *et al.*, 2011). The functional anatomy of the forelimb for extant xenarthrans (sloths, armadillos, anteaters) is well known, which can be used as a proxy for the morphological and muscular reconstruction of extinct sloths (Mendel, 1985; Taylor, 1985), and the grooves and bone scars have proven to have a similar pattern for the origin and insertion of muscles and tendons. A complex set of muscles have their origin, insertion, or pass by the anterior face of the humeral shaft (*e.g.*, *m. deltoideus*, *m. pectoralis*, *m. biceps brachialis*), allowing the forearm to play an important role in locomotion.

The humeral crests coalesce in the anterior portion of the humeral shaft resulting in a distinct structure that still requires detailed morphological analysis. We propose to call “platform” the well-developed structure observed in mylodontid sloths and in some extinct and extant armadillos (*e.g.*, *Euphractus sexcinctus*, *Eutatus seguini* Gervais, 1873). However, megatheriids, megalonychids, and some extinct and extant armadillos (*e.g.*, *Propraopus* Ameghino, 1881, *Dasybus novemcinctus* Linnaeus, 1758) have a shelf, which, in general, bears the union of deltoid and pectoral crests (deltopectoral shelf) that corresponds to a less developed structure in comparison to mylodontids and the above-mentioned armadillos (Vizcaino *et al.*, 2003; Castro, 2009; Pitana, 2011).

*Glossotherium robustum* (*e.g.*, LGP-Q 0004) has well-developed deltoid and pectoral crests and a weak brachiocephalic crest, which coalesces with the deltoid one, resulting in a deltoid platform (Figure 9A). *Ocnotherium giganteum* (MCL 4228/03) has three well-developed crests, and *Glossotherium phoenesis* (MCL 4303/23) appears to have a similar condition.

The specimen MCN-PV 038 (Scelidotheriinae indet.) shows well-developed pectoral and deltoid crests and a less developed brachiocephalic crest (Figure 7A). The deltoid and brachiocephalic crests are contiguous on their distal portion, forming a deltoid platform. *Catonyx cuvieri* (MCL 22473, MCL 22474, MCL 22475; Figure 9C) has well-developed pectoral and deltoid crests (Cartelle *et al.*, 2009), but shows a distinct condition from that of MCN-PV 038 because the pectoral crest sometimes coalesces with the brachiocephalic crest, and both have a pectoral platform. However, two specimens (MCL 22475/01, MCL 4250/01) have the pectoral crest medioposteriorly oriented bearing a deltoid platform similar to the condition seen in the Mylodontinae. *Valgipes bucklandi* has strong deltoid and pectoral crests, which are continuous with the arch over the entepicondylar foramen, showing a deltopectoral platform; the brachiocephalic crest, when present, is weak (Figure 9B). However, two specimens (MCL 22256/01-02) have the pectoral crest coalescent

with the brachiocephalic crest, and both result in a pectoral platform. Juvenile specimens of *Valgipes bucklandi* (MCL 22255/01-02) revealed a distinct condition, because the deltoid crest is unique and strongly developed, the pectoral crest is a medially oriented rugose protuberance and the brachiocephalic crest is weak, so a platform-like in adult specimens does not occur.

De Iuliis *et al.* (2009) described a deltopectoral shelf in *Megatherium* (*Pseudomegatherium*) *tarijensis* Gervais & Ameghino, 1880 (Figure 9D), and observed that some early megatheriines (*e.g.*, *Megathericulus* Ameghino, 1904, *Megatheriopsis* Ameghino & Kraglievich, 1921) have a deltopectoral shelf. Thus, De Iuliis (2003), De Iuliis *et al.* (2008) and Carlini *et al.* (2006b) also stated that the occurrence of a prominent and laterally flared deltopectoral shelf would be a plesiomorphic feature for megatheriids, which is reduced to a prominence on the humeral shaft in later taxa (*e.g.*, *Megatherium americanum*, *Eremotherium laurillardii*).

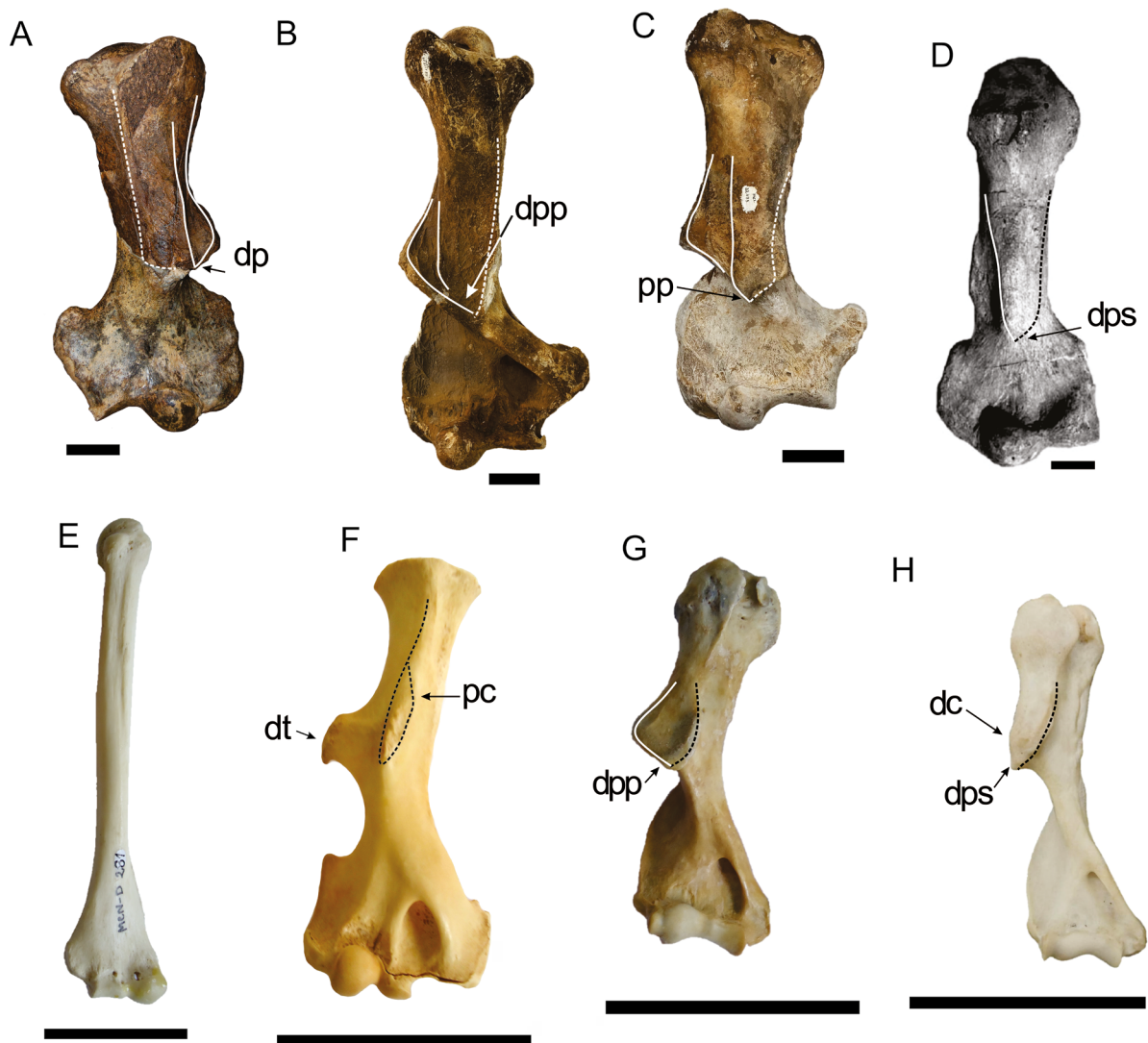
In living xenarthrans, the two-toed sloth *Choloepus* sp. does not have any kind of structure on the anterior surface of the humeral shaft (Figure 9E), except some tenuous ridges that could correspond to the deltoid crest. The anteater *Tamandua tetradactyla* has a well-developed deltoid tubercle (Taylor, 1985), but the pectoral crest is just a protuberance on the anterior face of the humeral shaft (Figure 9F). The armadillo *Euphractus sexcinctus* has a deltopectoral platform (Figure 9G); however, *Dasybus novemcinctus* has a deltopectoral shelf, and both do not have a brachiocephalic crest (Figure 9H).

Therefore, the occurrence of a humeral platform/shelf is mainly related to the degree of development of the humeral crests. The occurrence of a deltopectoral platform/shelf is related to the union of the deltoid, pectoral, and brachiocephalic crests, when it occurs, as observed in megatheriids and some scelidotheriines. In Mylodontidae, a different pattern occurs compared to the Megatheriidae, because the deltoid crest unites with the brachiocephalic crest and results in a well-developed deltoid platform.

## Radius

In this study, two complete specimens of the Mylodontidae radius were analyzed: one assigned to *Lestodon armatus* and the other to *Glossotherium robustum*. It was possible to distinguish both mainly because of their size, since *L. armatus* is considerably larger, while *G. robustum* is smaller. Both specimens have typical Mylodontinae features, such as a posterior border roughly straight in lateral view and anterior border not inflected medially in anterior view (Boscaini *et al.*, 2019a, characters 316 and 318, respectively) as observed in *Glossotherium phoenesis* (MCL 4303/05), but different from the Scelidotheriinae *Catonyx cuvieri* (MCL 22472/21) and *Valgipes bucklandi* (MCL 22211/55) here analyzed, where the posterior border is concave anteriorly in lateral view and the anterior border is inflected medially in anterior view.

Between *Glossotherium robustum* and *Lestodon armatus* there were some differences apart from the size. The former



**Figure 9.** Humeri of fossils and extant sloths, armadillo, and anteater, in anterior view, illustrating the morphology of the anterior surface of the humeral shaft. **A**, *Glossotherium robustum* (LGP-Q0004); **B**, *Valgipes bucklandi* (MCL 22211/89); **C**, *Catonyx cuvieri* (MCL 22473); **D**, *Megatherium tarijensis* [modified from De Iuliis *et al.* (2009)]; **E**, *Choloepus* sp. (MCN-D 281); **F**, *Tamandua tetradactyla* (MCN-D 047); **G**, *Euphractus sexcinctus* (MCN-D 2757); **H**, *Dasyurus novemcinctus* (MCN-D 3963). **Abbreviations:** **dc**, deltoid crest; **dp**, deltoid platform; **dpp**, deltopectoral platform; **dps**, deltopectoral shelf; **dt**, deltoid tubercle; **pc**, pectoral crest; **pp**, pectoral platform. Scale bars = 50 mm.

has a markedly straight lateral border in anterior view, while in *L. armatus* there are two contiguous concavities. The ulnar notch and the bicapital tuberosity are much more rugose in *G. robustum*, and the arrangement of the anterior crests is different. In *G. robustum*, the crest of the *m. extensor digitorum communis* is considerably more lateral than in *L. armatus*, which also has a short longitudinal ridge distolateral to the crest.

#### Femur

MCN-PV 1424 corresponds to a femur of *Glossotherium robustum*, collected in the interior portion of Rio Grande do Sul (Rincão dos Fialho, Pantano Grande). It has the distal portion and most of the shaft preserved, with some details that allow attributing this to the corresponding taxa.

The crest for the attachment of the musculature in the anterior part of the shaft is prominent, especially that of the *m. vastum medialis*, which has an enlargement in its proximal portion. Approximately in the half part of the lateral margin there is the third trochanter that is prominent and proximodistally elongate. As in *Glossotherium phoenesis*, MCN-PV 1424 presents the medial border of the shaft markedly concave, while the lateral one is straight, and the distal portion of the bone is more mediolaterally expanded than in *G. phoenesis* (MCL 4231/05).

#### Tibia and astragalus

The hindlimb bones of the ground sloths, especially the tibia and astragalus, revealed a series of morphological changes (*e.g.*, lateral rotation of the tibia, occurrence of an

odontoid process on the astragalus) compared to other groups of mammals. These modifications are mostly related to locomotor ability and the form and function of the hindlimbs of ground sloths (*e.g.*, Toledo *et al.*, 2018).

Tibiae and astragali were the elements with a considerable number of specimens therefore, in addition to the measurements, they were analyzed quantitatively. These results allowed us to separate the Rio Grande do Sul sample in two morphotypes in both bones based on size. The larger tibiae were attributed to *Lestodon armatus*, while the smaller were assigned to *Glossotherium robustum* (Figure 5); the same pattern was observed for the astragali (Figure 6). The specimens attributed to *L. armatus* were positioned closely to *O. giganteum* but far from Scelidotheriinae (*Catonyx cuiveri* and *Valgipes bucklandi*) and *Glossotherium*. The tibiae MCN-PV 1112 and MCN-PV 447 differed from the others in the lateromedial width of the middle of the shaft (smaller and larger, respectively), but they share the same characteristics with *L. armatus*. This variation suggests two extremes of sexual dimorphism (gracile and robust forms), as previously described for other mylodontids (McDonald, 2006; Boscaini *et al.*, 2019b; Varela *et al.*, 2022). The astragalus MCN-PV 5715 is proportionally smaller than the other *L. armatus*, but morphologically it is similar, and here considered as a juvenile.

Although similar in size, *Lestodon armatus* and *Ocnotherium giganteum* tibiae share some morphological similarities (general appearance and proportions of the bone and arrangement of articular facets of the distal end and distal tendinal groove patterns), but they are distinguished in the shape of the medial facet for the femur, which is much posteriorly projected in *O. giganteum*. The gap between the two proximal facets (intercondylar eminence) is smaller and the *sulcus extensorius* is deeper in *L. armatus*, than in *O. giganteum*, whereas the tibial tuberosity is more distally located in the shaft of *O. giganteum* than in *L. armatus*. Distally, the facets for the astragalus and for the fibula are positioned equally, with the same shape and the same angle between the odontoid and discoid facets. But, while in *L. armatus* the base of the odontoid process contacts entirely the medial border of the discoid facet, in *O. giganteum* only the posterior half of the facets is in contact. This arrangement gives the distal portion of the tibiae a kind of notch in this non-articular area.

*Glossotherium robustum* tibiae are morphologically very similar to those of *G. phoenesis* but are slightly larger. Although placed closely to *Catonyx cuiveri*, this latter and *G. robustum* differ greatly in morphology in all portions of the bone, mainly in the *sulcus extensorius*, which is absent in *C. cuiveri* and present in *G. robustum*. The pattern of the distal tendinal groove (three for the former and one for the latter) and the arrangement of the distal fibular facet that is anteroposteriorly expanded in *C. cuiveri* is posteromedial positioned in *G. robustum*.

The astragali morphospace maintained a similar pattern of the tibiae to *Lestodon armatus*, placing this species

near *Ocnotherium giganteum*. As in the tibia, both have similarities, mainly in the shape and proportions of the bone. Proximally, they have a similar appearance, with the angle between the discoid and odontoid facets near 90°, but in *O. giganteum* the base of the odontoid process contacts only the posterior half of the discoid facet forming a non-articular area on the anterior half, while in *L. armatus* the contact between the facets occurs entirely in the medial border of the discoid facet. The facets of the calcaneus are separated by the *sulcus tali* and have the same shape in both species. The navicular and cuboid facets are very similar in size, shape, and orientation, while the lateral fibular facet is smaller and more distally positioned in *O. giganteum* (MCL 4228/42).

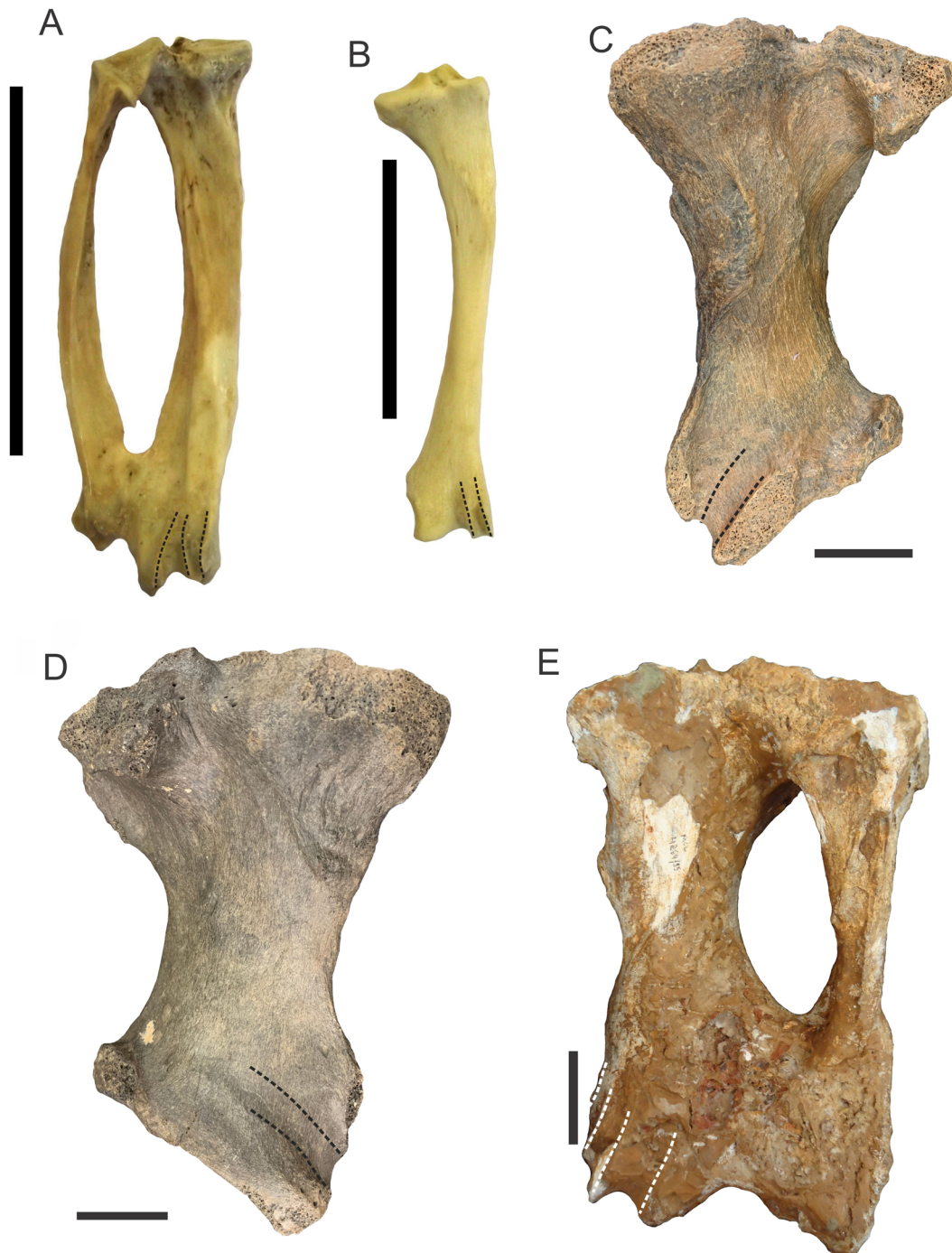
Astragali belonging to the species of the genus *Glossotherium* were closely related to each other, but although similar, they have a few differences in size. Due to the fragmentary nature of MCN-PV 5716 and MCN-PV 6603, some minor details cannot be thoroughly analyzed.

*Remarks on the distal tendinal grooves.* The distal end of the tibia has tendinal grooves (Figure 10) that are variable in number and morphology among various extinct sloths. Early mylodontids, *Pseudopreotherium confusum* and *Simomyodon uccasamamensis*, have two tendinal grooves (Hirschfeld, 1985; Saint-André *et al.*, 2010), except *Thinobadistes segnis*, which was referred as having one tendinal groove by Webb (1989) and two by Boscaini *et al.* (2019a). One tendinal groove is observed in *Glossotherium robustum* (MCN-PV 1482, MCN-PV 2388; Figures 4I–L, 10C) and in some specimens of *Lestodon armatus* from the Pleistocene of Rio Grande do Sul [MCN-PV 338, MCN-PV 438, MCN-PV 447 (Figure 10D), MCN-PV 1112]. However, some also appear to have two grooves (MCN-PV 32113), and Boscaini *et al.* (2019a) attributed two grooves to this species.

The megatheriids *Planops martini*, *Preprotherium potens* Ameghino, 1891 and *Megathericulus patagonicus* have three tendinal grooves (Hoffstetter, 1961; De Iuliis *et al.*, 2008), whereas *Urumaquia robusta* has two (Carlini *et al.*, 2006b). However, the late megatheriids *Eremotherium laurillardi* and *Megatherium americanum* have one broad, deep groove (Cantalamessa *et al.*, 2001).

The tree sloth *Choloepus* has one tendinal groove; however, the extant armadillo *Euphractus sexcinctus* has two tendinal grooves, and both are proximodistally oriented on the distal portion of the posterior tibial surface (Figures 10A, B). Meanwhile, in *Glossotherium robustum*, *Lestodon armatus* and *Valgipes bucklandi* the tendinal groove is obliquely oriented, although in the latter there are three tendinal grooves (Figures 10C–E). Thus, the occurrence of three tendinal grooves could be considered a plesiomorphic character, and two of these structures represent a transitional stage related to the derived condition that corresponds to the occurrence of one single tendinal groove (Webb, 1989; Cartelle, 1992; Negri, 2004).

Extant sloths have been analyzed to determine how anatomical modifications of their hands and feet are related to their positional behavior and locomotor ability (Mendel,



**Figure 10.** Tibiae of Mylodontidae fossils and extant sloth, armadillo and anteater, in posterior view, indicating the tendinal grooves with dotted lines. **A**, *Choloepus*; **B**, *Euphractus sexcinctus*; **C**, *Glossotherium robustum* (MCN-PV 8247); **D**, *Lestodon armatus* (MCN-PV 447); **E**, *Valgipes bucklandi* (MCL 4264/55). Scale bars = 50 mm.

1981, 1985). The hands and feet of living sloths have become virtual hooks due to suspensory behavior (Mendel, 1981, 1985). Although tree sloths and ground sloths differ greatly in size and locomotor ability, the muscular reconstruction can be correlated with extinct sloths (Naples & McAfee, 2012).

The disposition of the prime accessory flexors of the foot is similar in extant and extinct sloths. The tendons of the *m. tibialis posterior* pass through the tendinal groove, as does

probably the tendon of the *extensor hallucis longus*, so the same interpretation of the muscular disposition is consistent between extant and extinct sloths; however, for the latter the *m. tibialis posterior* probably has an oblique insertion, which differs from tree sloths.

Therefore, the decrease in the number of tendinal grooves in fossil sloths probably does not result from the loss or decrease of the flexor muscle, because the hindlimbs support



the weight of the body during locomotion, and a reduced muscle would be incompatible with this condition. Instead, it is probably related to individual variations, according to functional aspects, resulting from different adaptive solutions.

## CONCLUSIONS

A detailed anatomical postcranial study of fossil Mylodontidae from Rio Grande do Sul State revealed diagnostic characters that largely allow the attribution of the Mylodontinae material to the species *Glossotherium robustum* and *Lestodon armatus*. The Scelidotheriinae material is scarce and very fragmentary, with few characters available that did not enable a generic or specific identification. However, the presence of an entepicondylar foramen in specimen MCN-PV 038 allows to affirm the record of another Scelidotheriinae taxon that was not represented in Rio Grande do Sul or even in Brazil so far.

Folivora reveals a mosaic of postcranial features because it retains primitive traits shared with other mammals (*e.g.*, the presence of an entepicondylar foramen in the humerus) and derived characters. Although in most cases isolated and fragmentary, the materials assigned to *Lestodon armatus* have structures with specific morphological characters, such as radial crests in lateral view, the posteriormost crest almost reaching the posterior border of the radius in its proximalmost portion. In addition, the astragalar articulation of the tibiae (distal one) forms a 90° angle between the odontoid and discoid facets, resulting in the same angle of the proximal astragalar facets. The distal articulations of the astragalus (ectal and sustentacular facets) are separated by the *sulcus tali*.

The specimens assigned to *Glossotherium robustum*, also in most cases isolated and fragmentary, have typical morphological characteristics. Radial crests occupy only the anterior half of the shaft in lateral view. The angle between the proximal astragalar facets forms a 140° angle, resulting in the same angle in the distal tibial articulations; the distal portion of the astragalus bears only one facet, which is the union of the ectal and sustentacular facets; in this case, there is no *sulcus tali*.

In addition to morphologic features, the morphometric data also revealed differences between the postcranial materials of *Lestodon armatus* and *Glossotherium robustum*, indicating that the former are larger than the latter. These morphologic and morphometric data may contribute to the identification of other materials of these groups, as well as future functional analyses.

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