

PALEONTOLOGICAL NOTE

Nematherium (Xenarthra, Folivora) from the Serravallian of La Venta, Department of Huila, Colombia; chronological and biogeographical implications

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ABSTRACT. The restudy of a sloth specimen from the Honda Group (La Venta, Department of Huila, Colombia), more precisely from the upper levels of the La Victoria Formation and the lower levels of the Villavieja Formation (Serravallian, middle Miocene), suggests its assignment to *Nematherium* sp. (Mammalia, Folivora). This is the first record of *Nematherium* for Colombia, and given that until now the genus had been recorded from the Burdigalian (early Miocene) of southern South America, the record presented herein extends its geographic and chronological distribution.

Keywords: Sloths, Mylodontoidea, *Nematherium*, middle Miocene, La Victoria Formation, Villavieja Formation.

RESUMEN. *Nematherium (Xenarthra, Folivora) en el Serravallense de La Venta, Departamento de Huila, Colombia; implicancias cronológicas y biogeográficas.* El reestudio de un espécimen de perezoso del Grupo Honda (La Venta, Departamento de Huila, Colombia), más precisamente de los niveles superiores de la Formación La Victoria y de los niveles inferiores de la Formación Villavieja (Serravallense, Mioceno medio), sugiere su asignación a *Nematherium* sp. (Mammalia, Folivora). Este es el primer registro de *Nematherium* en Colombia y, dado que hasta ahora el género había sido registrado para el Burdigaliense (Mioceno temprano) en el sur de Sudamérica, el registro aquí presentado amplía su distribución geográfica y cronológica.

Palabras clave: Mylodontoidea, *Nematherium*, Mioceno medio, Formación La Victoria, Formación Villavieja.

1. Introduction

The Honda Group, represented by the La Victoria and Villavieja formations, is located in the Magdalena Valley of central Colombia and includes several fossiliferous localities (e.g., San Francisco St. Beds, El Cardon Red Beds; Madden *et al.*, 1997; Catena and Croft, 2020). The outcrops of the Honda Group have provided a rich Miocene vertebrate fauna, including fishes, reptiles, amphibians, birds, and mammals (Kay and Madden, 1997), which was the base for the recognition of the Laventan South American Land Mammal Age (SALMA) (see Madden *et al.*, 1997). Based on $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric dating (Guerrero, 1997), the age of the Honda Group ranges from ~13.5 to 11.5 Ma (Serravallian).

Regarding mammals, most of the records correspond to Sparassodonta, Didelphimorphia, Paucituberculata, Caviomorpha, Astrapotheria, Litopterna, Notoungulata, Primates, Chiroptera, and Xenarthra (Cingulata and Pilosa) (Kay and Madden, 1997; Croft, 2016; Catena and Croft, 2020). Among Pilosa, most of the remains of ground sloths (suborder

Folivora=Tardigrada=Phyllophaga) recorded in the Honda Group consist of skulls, jaws, and postcranial elements, assigned to different genera and species of the families Mylodontidae, Megalonychidae, and Megatheriidae (see Hirschfeld, 1985; McDonald, 1997; Kay and Madden, 1997; Villarroel, 1998, 2000; Rincón and McDonald, 2020).

Members of the family Mylodontidae from the Honda Group were studied by Hirschfeld (1985), McDonald (1997), Villarroel (1998), and Rincón and McDonald (2020). The subfamily Mylodontinae includes the genera *Magdalenabradys*, *Glossotheriopsis*, and *Brievabradys* (see McDonald, 1997; Villarroel, 2000; Rincón and McDonald, 2020); whereas the subfamily Scelidotheriinae is represented by cf. *Neonematherium*, *Neonematherium flabellatum*, and a large scelidotherere (see Hirschfeld, 1985; McDonald, 1997).

The aim of this contribution is to restudy an extinct sloth specimen studied by Hirschfeld (1985) from the Honda Group (La Venta, Department of Huila), Colombia (Fig. 1), which is herein assigned to the genus *Nematherium*.

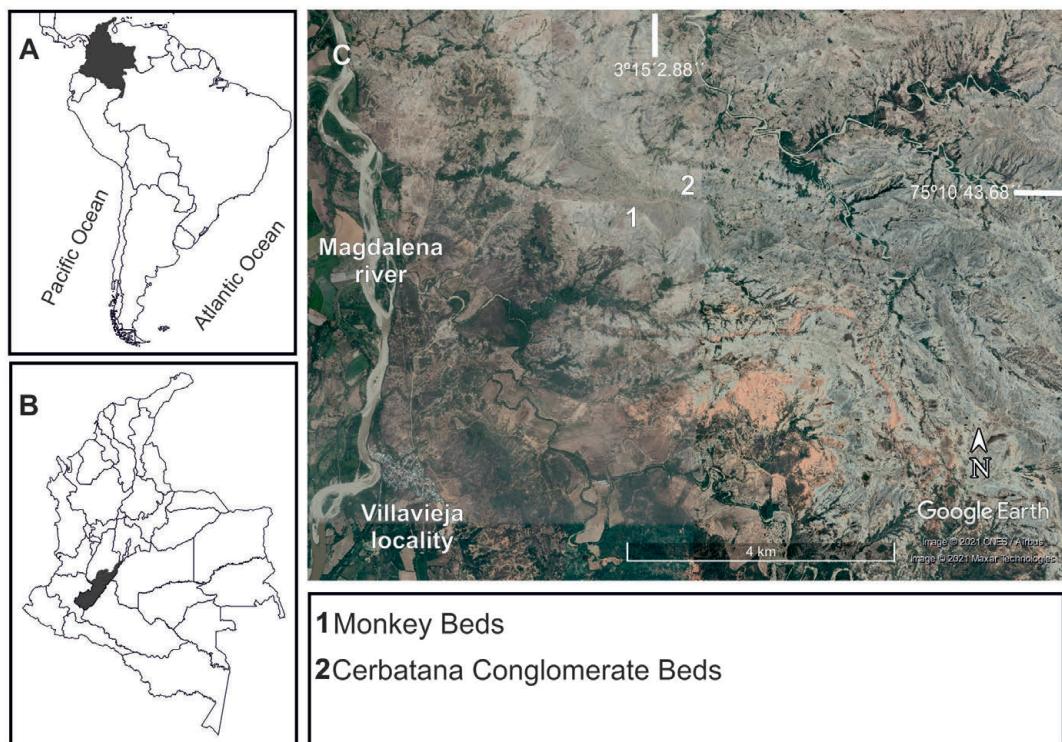


FIG. 1. Maps showing the location of the study area. **A.** Colombia, South America. **B.** Department of Huila, Colombia. **C.** Detail of La Venta area next to Villavieja locality (modified from Barasoain *et al.*, 2022).

Institutional abbreviations. **AMNH:** American Museum of Natural History, New York, USA; **CORD PV:** Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina; **MACNA:** Colección Ameghino, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MLP:** División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina; **MPEF PV:** Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MPM-PV:** Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina; **SGO PV:** Museo Nacional de Historia Natural, Santiago, Chile; **UCMP:** Museum of Paleontology, University of California, Berkeley, USA.

Anatomical abbreviations. **Mf1-5:** upper molariform 1-5.

2. Geological setting

The Honda Group (Fig. 2) is represented by the La Victoria Formation, overlain by the Villavieja Formation (Guerrero, 1997). The La Victoria Formation is mainly composed of alternating sandstone and mudstone levels. Mudstones include the most fossiliferous levels and are reddish-brown to greenish grey in color, whereas sandstones often include pebble and conglomeratic pockets. The top of this unit is characterized by the presence of clast-supported conglomerate levels. Some clastic layers of this sequence are used as regional marker levels including, from bottom to top: "Cerro Gordo Sandstone Beds", "Chunchullo Sandstone Beds", "Tatacoa Sandstone Beds", and "Cerbatana Conglomerate Beds" (Fig. 2; Guerrero, 1997; Barasoain *et al.*, 2022).

The Villavieja Formation is mainly composed of reddish to greyish mudstones, arranged into very thick levels with an occasional alternation of thin sandstone levels, which are essentially composed by volcanic litharenites. The formation is subdivided into the lower "Baraya Member", mainly composed of grey mudstones, and the upper "Cerro Colorado Member", which also includes red mudstones (Polonia Red Beds). Most part of the fossiliferous richness of this formation is restricted to the lower levels of the Baraya Member. Marker levels of the Villavieja Formation include, from bottom to top: "Monkey Beds", "Fish Beds", "Ferruginous Beds", "La Venta Red Beds", "El Cardon Red Beds", and "San Francisco Sandstone Beds" (Fig. 2). Guerrero (1997) carried

out a detailed magnetostratigraphic study together with several $^{40}\text{Ar}/^{39}\text{Ar}$ dating, concluding that the whole Honda Group sequence spans from ~13.5 to 11.5 Ma, with the limit between the La Victoria Formation and the Villavieja Formation at ~12.48 Ma.

The specimen herein studied (UCMP 39275; Fig. 3) comes from locality V-4932 which includes the levels between the Cerbatana Conglomerate Beds of the La Victoria Formation (Serravallian, middle Miocene) and the Monkey Beds of the Villavieja Formation (Serravallian, middle Miocene) (see Hirschfeld, 1985; Madden *et al.*, 1997, fig. 29.2). These levels were dated through $^{40}\text{Ar}/^{39}\text{Ar}$ in 12.649 ± 0.258 Ma (Plagioclase) and 12.486 ± 0.111 Ma (Hornblende) (Fig. 2; Guerrero, 1997; Barasoain *et al.*, 2022).

3. Materials and methods

Nematherium was erected by Ameghino (1887) based on two isolated molariforms of *N. angulatum*. Other species described during the end of the 19th Century are *N. sinuatum* (Ameghino, 1887), *N. longirostris* (Ameghino, 1891), and *N. lavagnanum* (Mercerat, 1891). Scott (1903-1904) considered valid the species *N. angulatum* (with *N. lavagnanum*, *N. sinuatum*, and *N. longirostris* as its synonyms), *N. auca* (including *Lymodon auca* and *L. perfectus*), *N. profundatum* (including *Ammotherium profundatum* and *A. aculeatum*), and *N. declivum* (on the basis of *A. declivum*). Bordas (1939) described *N. grande* based on three isolated molariforms, and Simpson (1941) defined *N. birdi* on a fragment of skull with molariforms. Finally, de Barrio *et al.* (1984) considered *N. longirostris* as a valid species. In this contribution, the taxonomic arrangement proposed by Scott (1903-1904) and Simpson (1941) is followed.

In order to identify the specimen presented herein, the following species and specimens were used for comparison: *N. profundatum*, represented by MACN A 5787, and the holotype of *Ammotherium aculeatum* (MACN A 5781) from the Santa Cruz Formation, Argentina; *N. declivum* (MACN A 5783), from the Santa Cruz Formation, Argentina; *N. auca*, represented by the holotypes of *L. auca* (MACN A 4661) and *L. perfectus* (MACN A 5786), from the Santa Cruz Formation, Argentina; *N. birdi* (AMNH 32652 holotype), from the Palomares Formation, Chile; *Analcitherium antarcticum* (MACN A 4668 holotype), from the Santa Cruz Formation, Argentina;

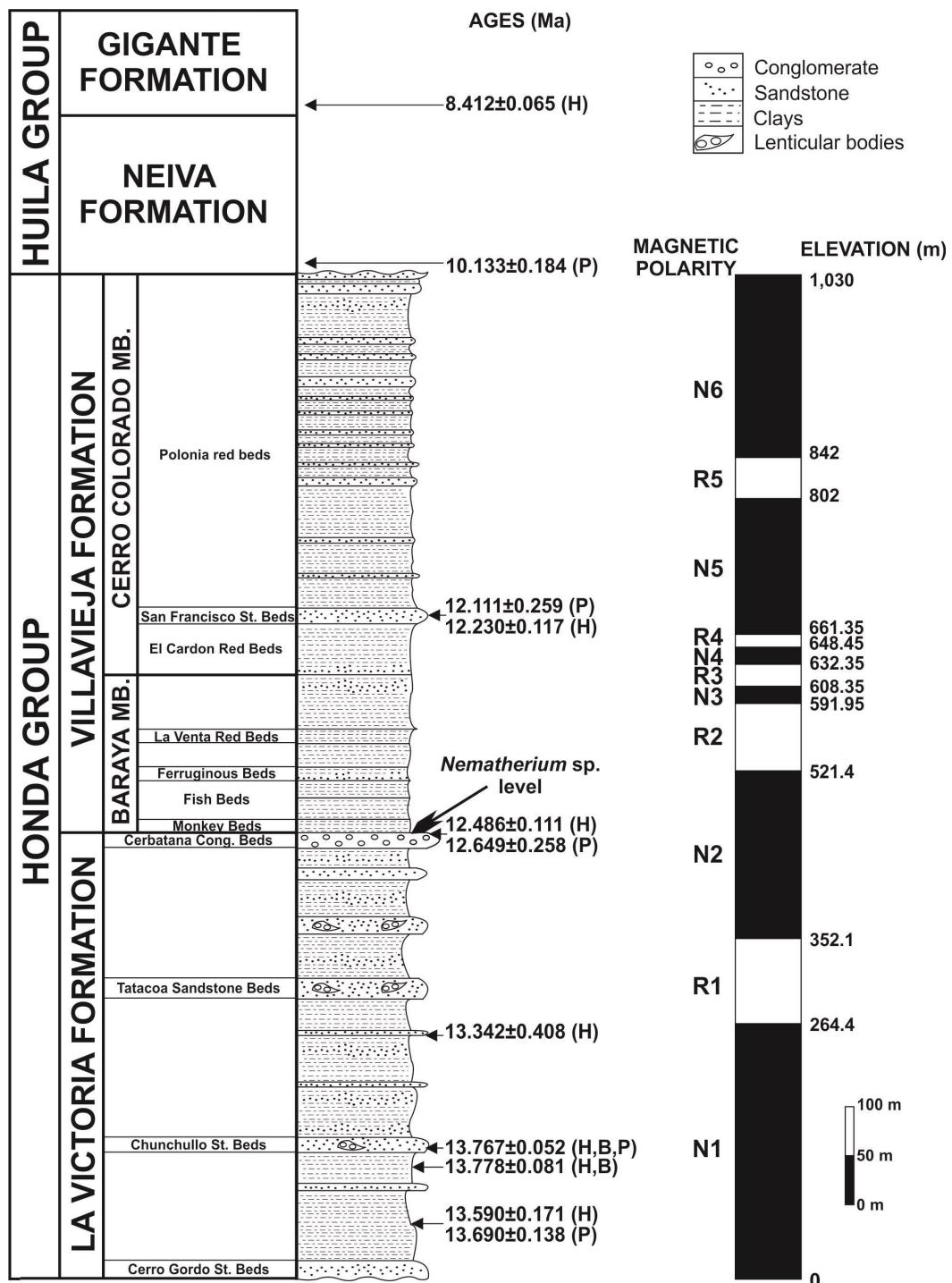


FIG. 2. Stratigraphic section of the Honda Group at the study area and ages obtained from the $^{40}\text{Ar}/^{39}\text{Ar}$ analyses of biotite (B), hornblende (H) and plagioclase (P) (modified from Guerrero, 1997; Barasoain *et al.*, 2022). Specimen of *Nematherium* sp. was recovered from upper levels of the La Victoria Formation and lower levels of the Villavieja Formation. Abbreviations: N1-N6: normal polarity intervals, R1-R5: reversed polarity intervals.

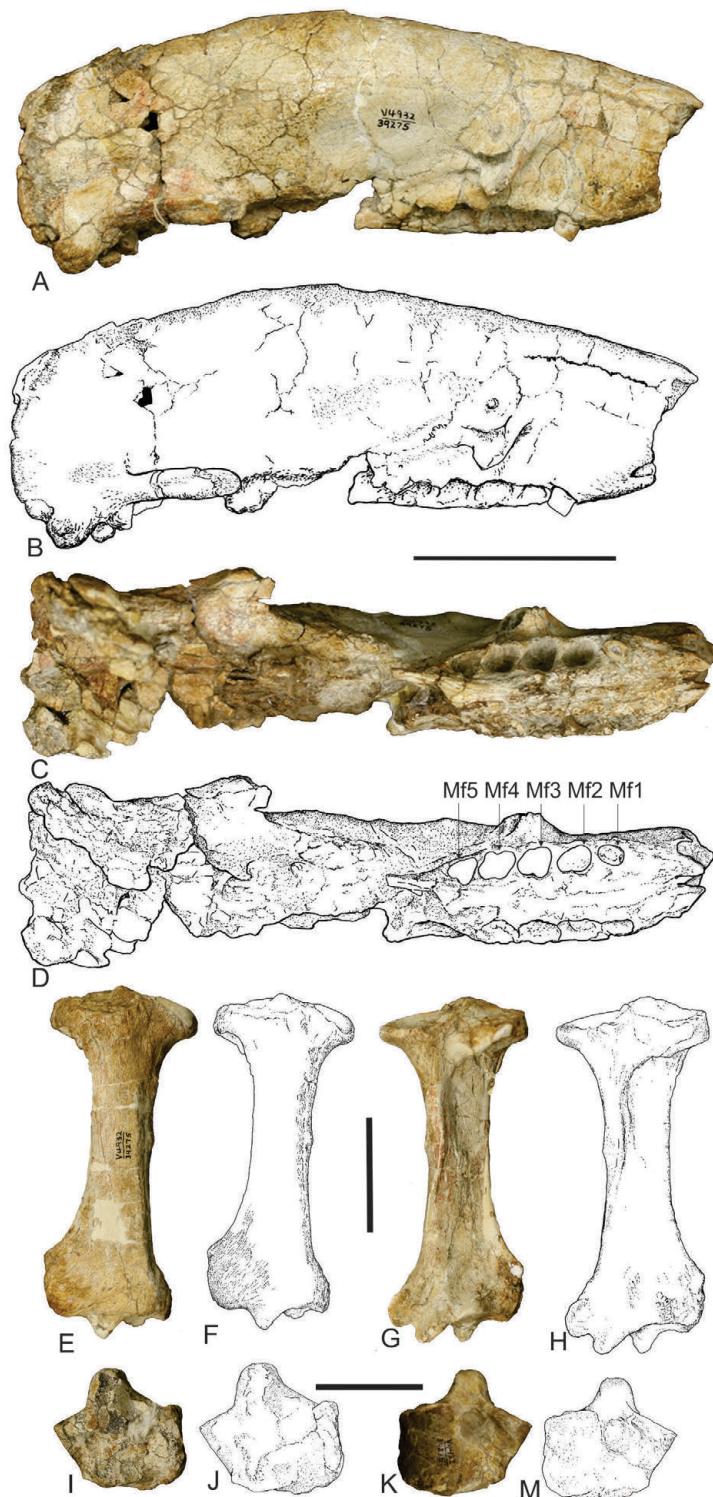


FIG. 3. *Nematherium* sp. A-B. Skull in right lateral view. C-D. Skull in palatal view. E-F. Left tibia in anterior view. G-H. Left tibia in posterior view. I-J. Right astragalus in ventral view. K-L. Right astragalus in dorsal view. Scale bar: 50 mm.

Neonematherium flabellatum (MACN A 11628 holotype), from the Tehuelche Formation, Argentina; and *Sibyllotherium guenguelianum* (MLP 90-XII-31-5 holotype), from the El Pedregoso Formation, Argentina.

4. Results

4.1. Systematic paleontology

Class Mammalia Linnaeus, 1758

Superorder Xenarthra Cope, 1889

Suborder Folivora Delsuc *et al.*, 2001

Superfamily Mylontoidea Gill, 1872

Genus *Nematherium* Ameghino, 1887

Nematherium sp.

Referred specimen. UCMP 39275, skull, right and left tibiae, and right astragalus (Fig. 3; see Hirschfeld, 1985).

Geographic and stratigraphic provenance. UCMP locality V-4932 (Railway Bridge, Department of Huila) (Fig. 1), upper levels of the La Victoria Formation and lower levels of the Villavieja Formation (see also Madden *et al.*, 1997, fig. 29.2).

5. Descriptions and comparison

The skull is complete on the right side except for the premaxilla, pterygoid, and zygomatic arch; the right Mf1 is preserved; no sutures can be seen

between the squamosal and the parietal and frontal, suggesting it is an adult specimen (Fig. 3A-D).

The skull is narrow and elongated, 225 mm long from the posterior end of the occipital condyle to the anterior end of the maxillae; nasals and maxillae are short, as in *Nematherium* spp., *Neo. flabellatum*, *S. guenguelianum*, and Quaternary Scelidotheriinae. In lateral view (Fig. 3A-B), the skull is subrectangular, as in Quaternary Scelidotheriinae, *N. profundatum*, *N. birdi*, *N. auca*, *Analcitherium antarcticum*, and *S. guenguelianum*. The skull roof at level of parietal is convex as in *N. profundatum*, *N. birdi*, *N. auca*, and *Analcitherium antarcticum*, different from *S. guenguelianum*, in which it is horizontal, while in *Neo. flabellatum* it is not preserved (the holotype described only preserved the anterior region of the skull). The margin of the palate is almost horizontal and slightly dorsal toward the predental region as in *N. profundatum*, *N. auca*, *N. birdi*, and *A. antarcticum*, different from *S. guenguelianum* and *Neo. flabellatum*, in which it is convex. The lacrimal foramen is dorsal to the Mf3 as in Quaternary Scelidotheriinae, *N. profundatum*, *N. auca*, *A. antarcticum*, and *Neo. flabellatum*. In ventral view (Fig. 3C-D) the dental series diverge anteriorly (Table 1) as in *N. profundatum*, *N. birdi*, *N. declivum*, *Neo. flabellatum*, and *S. guenguelianum*, different from Quaternary Scelidotheriinae and *A. antarcticum*, in which they are parallel. The Mf1 (Fig. 3C-D) is oval in cross section, whereas in *N. profundatum*, *N. auca*, and *A. antarcticum* it is subtriangular, in *N. birdi* and

TABLE 1. MEASUREMENTS (IN mm) OF THE PALATE OF SPECIMENS REFERRED TO *NEMATHERIUM*, *ANALCITHERIUM*, AND *NEONEMATHERIUM*.

Species	Specimen	TRL	PW Mf1	PW Mf5
<i>Nematherium</i> sp.	UCMP 39275	59	15	12
<i>N. profundatum</i>	MACN A 5787	45	19	9
<i>N. profundatum</i>	MACN A 5781	45.5	17.5	12.5
<i>N. declivum</i>	MACN A 5783	38	15.2	10
<i>N. auca</i>	MACN A 5786	56	-	-
<i>N. birdi</i>	AMNH 32652	50	-	10
<i>Analcitherium antarcticum</i>	MACN A 4668	38	13.5	10
<i>Neonematherium flabellatum</i>	MACN A 11628	*62	-	15

TRL: tooth row length; PW Mf1: palatal width at Mf1; PW Mf5: palatal width at Mf5.*: approximate.

S. guenguelianum it is reniform, and in *Neo. flabellatum* it is not preserved and the alveolus is broken. The alveolus of Mf2 (Fig. 3C-D) is subtriangular as in *N. profundatum*, *N. auca*, *N. declivum*, *N. birdi*, and *A. antarcticum*, whereas in *Neo. flabellatum* and *S. guenguelianum* it is triangular with a deep vertical lingual furrow that defines two lingual lobes. The alveolus of Mf3 (Fig. 3C-D) is subcuadrangular, different from *N. birdi*, in which it is subrectangular, and from *N. profundatum*, *N. declivum*, *N. auca*, and *A. antarcticum*, in which it is subtriangular, and from *Neo. flabellatum* and *S. guenguelianum*, in which it is subtriangular but with a lingual furrow that defines two lingual lobes. The alveolus of Mf4 (Fig. 3C-D) is subcuadrangular, while in *N. profundatum*, *N. auca*, *N. declivum*, and *A. antarcticum* it is subtriangular, in *N. birdi* it is subrectangular, in *Neo. flabellatum* it is subtriangular with a vertical lingual furrow that defines two lingual lobes, and in *S. guenguelianum* it is not preserved. The alveolus of Mf5 (Fig. 3C-D) is subtriangular as in *N. profundatum*, *N. auca*, *N. declivum*, and *N. birdi*, in *A. antarcticum* it is suboval, and in *Neo. flabellatum* it is triangular with a convex labial side.

The tibia is straight (Fig. 3E-H), similar in Quaternary Scelidotheriinae (McDonald, 1987; Miño-Boilini, 2012), with no evidence of co-ossification with the fibula as it occurs in some Pleistocene sloths and in cingulates (Toledo *et al.*, 2015). The proximal epiphysis is broad (Table 2), similar in Quaternary Scelidotheriinae, and antero-posteriorly compressed; the medial condyle is slightly below the lateral condyle. The lateral condyle is flatter than the medial condyle, being the intercondylar eminence slightly developed. The distal epiphysis is massive, similar in Quaternary Scelidotheriinae, with two deep furrows for the extensor muscles of the astragalus-tibia articulation.

TABLE 2. MEASUREMENTS (IN mm) OF THE TIBIA AND ASTRAGALUS OF THE SPECIMEN ANALYZED IN THE CURRENT STUDY.

Species	Specimen	L	PW	DW
<i>Nematherium</i> sp.	UCMP 39275 (tibia)	162	70	65
	UCMP 39275 (astragalus)	57	-	-

L: greatest proximal-distal length; PW: proximal width; DW: distal width.

The astragalus of *Nematherium* is narrow and long, with a marked trochlea, the internal facet of the calcaneus is divided into two surfaces almost perpendicular to each other, the cuboid facet is small, and the navicular facet is shallow (Scott, 1903-1904) (Fig. 3I-M).

6. Discussion and conclusions

Nematherium was described by Ameghino (1887) on the basis of *N. angulatum* (MACN A 2138: two isolated molariforms) recovered from the Santa Cruz Formation (Santa Cruz Province, Argentina). Regarding its systematic position among the suborder Folivora, there are different opinions. The genus was considered as a member of Mylodontidae Scelidotheriinae (see McDonald, 1987; McDonald and Perea, 2002; Saint-André *et al.*, 2010). Alternatively, *Nematherium* was considered a Mylodontidae, but placed into its own subfamily (*i.e.*, *Nematheriinae*, see Scillato-Yané, 1977), criterion followed by several authors (see Scillato-Yané and Carlini, 1998; Miño-Boilini, 2012; Miño-Boilini *et al.*, 2014); or with *Analcitherium*, a Scelidotheriidae Scelidotheriinae (Casali *et al.*, 2022), or as a sister taxa to other Mylodontidae (see Gaudin, 2004; Boscaíni *et al.*, 2019; Varela *et al.*, 2019). *Nematherium* is characterized by a relatively smaller overall size than other mylodontids, an elongate skull as in Scelidotheriinae, and five upper and four lower molariforms arranged in a continuous series without diastema and divergent tooth row, condyle of mandible above the tooth row level, among other features (see Scott, 1903-1904; Scillato-Yané, 1977; McDonald, 1987; Gaudin, 2004; Casali *et al.*, 2022).

The specimen UCMP 39275 was originally assigned to cf. *Neonematherium* by Hirschfeld (1985), and recently to a Scelidotheriinae indet. by Miño-Boilini and Quiñones (2020). Although Hirschfeld (1985) indicated many similarities between UCMP 39275 and the species of *Nematherium* (*e.g.*, upper dentition), she considered that the size of the specimen UCMP 39275 (larger than *N. profundatum* and slightly larger than *N. auca*) and its stratigraphic position and age justified its assignment to cf. *Neonematherium*. On the other hand, Miño-Boilini and Quiñones (2020) made a general review of Scelidotheriinae, indicating that, given the state of preservation, UCMP 39275

should be considered as a Scelidotheriinae indet. instead.

The present study of UCMP 39275 identifies similar features with those present in the species of *Nematherium* and dissimilar ones with *Neo. flabellatum*: 1) the skull roof at the level of the parietal is convex as in *N. profundatum*, *N. birdi*, and *N. auca*; 2) the palatal margin is almost horizontal and slightly dorsal toward the predental region, as in *N. profundatum*, *N. auca*, *N. birdi*, whereas in *Neo. flabellatum* is convex; 3) the alveolus of Mf2 is subtriangular in cross section as in *N. profundatum*, *N. auca*, *N. declivum*, *N. birdi*, whereas in *Neo. flabellatum* is triangular with a deep vertical lingual furrow that defines two lingual lobes; and 4) the alveolus of Mf5 is subtriangular as in *N. profundatum*, *N. auca*, *N. declivum*, and *N. birdi*, whereas in *Neo. flabellatum* is triangular with a convex labial side.

The above-mentioned similarities with the species of *Nematherium* suggest here the inclusion of UCMP 39275 in *Nematherium*; however, given such similarities are nearly present in all the species of the genus, the assignment of UCMP 39275 to *Nematherium* sp. is appropriate.

In southern South America, *Nematherium* has been recorded in the Sarmiento Formation at Gran Barranca (Chubut Province, Argentina), at some localities of the Santa Cruz and Pinturas formations (Santa Cruz Province, Argentina), and in the Cura-Mallín and the Palomares formations (Chile). In addition, Bordas (1939) reported the presence of *Nematherium grande* in the “Santacrucean beds” of Pampa del Castillo (Chubut Province, Argentina).

In Argentina, most of the well-preserved remains of *Nematherium* (e.g., *N. angulatum*, *Nematherium* sp.; see Scott, 1903-1904; Bargo *et al.*, 2012) were recovered from the Santa Cruz Formation (early-middle Miocene) at the Atlantic Coast of the Santa Cruz Province and along the Santa Cruz River (Scott, 1903-1904; Bargo *et al.*, 2012, 2019). In this sense, Marshall *et al.* (1983) considered the genus *Nematherium* as a guide fossil for the Santacrucean fauna of Argentina. Tauber (1997, 1999) reported *Nematherium* sp. based on a skull fragment (CORD PV 1223 1/5) found in level 1 near the base of the Estancia La Costa Member of the Santa Cruz Formation exposed at the Atlantic coast (Estancia La Costa locality). Bargo *et al.* (2012) reported two specimens referred to *Nematherium* sp., based on a skull (MPM-PV 3407) found in level 3 of the middle section of the Estancia La Costa Member

(Estancia La Costa locality), and on a dentary (MPM-PV 3703) found in level 5.3 (middle section of the Estancia La Costa Member) at the Puesto Estancia La Costa locality (see Matheos and Raigemborn, 2012). In the banks of the Santa Cruz River, *Nematherium* sp. is mentioned for the Yaten Huageno locality (Cuitiño *et al.*, 2016), whereas a left dentary of *N. longirostris* (MPM-PV 19326) was recovered from the Segundas Barrancas Blancas locality (Bargo *et al.*, 2019). According to Perkins *et al.* (2012) and Fleagle *et al.* (2012), the Santa Cruz Formation, along the Atlantic coast, spans the interval ~18-16 Ma, with the base of the middle section located around 16.5 Ma (Matheos and Raigemborn, 2012). According to Cuitiño *et al.* (2016), all the mammal specimens from Yaten Huageno come from levels that underlie a tuff dated at 16.88 ± 0.65 Ma, whereas levels from Segundas Barrancas Blancas vary in age from ~16.32 to 15.63 Ma.

In addition to these records from the Santa Cruz Formation, Kramarz *et al.* (2010) assigned to *Nematherium* sp. a fragment of dentary with two molariforms (MPEF PV 7289) found in the upper levels of the Sarmiento Formation (Upper Fossil Zone, 19.7-18.7 Ma) at the Gran Barranca locality (Chubut Province, Argentina).

Simpson (1941) described *N. birdi* on a fragment of palate with molariforms (AMNH 32652) from the Palomares Formation (=Santa Cruz Formation; Bostelmann *et al.*, 2013), on the east side of Laguna Blanca (Magallanes Province, Chile). Flynn *et al.* (2008) assigned to *Nematherium* cf. *angulatum* or sp. nov. a mandible (SGO PV 5560) found in the basal levels of the Cura-Mallín Formation at the Laguna del Laja area (Biobío Region, Chile). These levels were dated in ~19.8-18 Ma (Herriott, 2006) at the informal locality of Estero Correntoso.

Brandoni *et al.* (2019) reported *Nematherium* sp. from the middle section of the Pinturas Formation (Santa Cruz Province), at the localities of Portezuelo Sumich Norte, Portezuelo Sumich Sur, and Cerro de Los Monos. Radiometric ages of ~17.99 Ma near the base of the Pinturas Formation at the Estancia el Carmen locality and ~16.8 Ma in the overlaying Santa Cruz Formation at Portezuelo Sumich Norte (see Perkins *et al.*, 2012; Fleagle *et al.*, 2012) place the Pinturas Formation in the Burdigalian (20.44-15.97 Ma, Cohen *et al.* 2013; ICS, 2022).

Taking into account the above-mentioned records, Brandoni *et al.* (2019) considered that *Nematherium*

is a guide fossil for the Burdigalian in southern South America. The finding of *Nematherium* sp. in the upper levels of the La Victoria Formation and lower levels of the Villavieja Formation, in Colombia, levels that were assigned to the Serravallian, extend the geographic and chronologic distribution of the genus.

This record (*Nematherium* sp. UCMP 39275) is added to the other Mylodontidae sloths reported for the Honda Group: *Magdalenabradys*, *Glossotheriopsis*, *Brievabradys*, a large scelidotherid, and *Neonematherium flabellatum* (see Hirschfeld, 1985; McDonald, 1997; Villarroel, 2000; Rincón and McDonald, 2020).

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