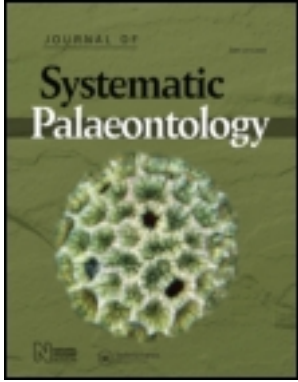


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## Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tjsp20>

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François Pujos<sup>ab</sup>, Rodolfo Salas-Gismondi<sup>c</sup>, Guillaume Baby<sup>d</sup>, Patrice Baby<sup>de</sup>, Cyrille Goillot<sup>de</sup>, Julia Tejada<sup>c</sup> & Pierre-Oliver Antoine<sup>f</sup>

<sup>a</sup> Departamento de Paleontología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET-Mendoza, Avda. Ruiz Leal s/n, Parque Gral. San Martín, Mendoza, Argentina, 5500

<sup>b</sup> Institut Français d'Etudes Andines (IFEA), Casilla 18-1217, Av. Arequipa 4595, Lima 18, Perú

<sup>c</sup> Departamento de Paleontología de Vertebrados, Museo de Historia Natural-UNMSM, Lima, Perú

<sup>d</sup> Université de Toulouse; UPS (SVT-OMP), LMTG, 14 Avenue Édouard Belin, F-31400, Toulouse, France

<sup>e</sup> CNRS, LMTG, F-31400 Toulouse, France and IRD, LMTG, F-31400, Toulouse, France

<sup>f</sup> Institut des Sciences de l'Évolution (CNRS-UMR 5554), CC064, Université Montpellier 2, Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France

Published online: 25 Mar 2013.

To cite this article: François Pujos, Rodolfo Salas-Gismondi, Guillaume Baby, Patrice Baby, Cyrille Goillot, Julia Tejada & Pierre-Oliver Antoine (2013) Implication of the presence of Megathericulus (Xenarthra: Tardigrada: Megatheriidae) in the Laventan of Peruvian Amazonia, *Journal of Systematic Palaeontology*, 11:8, 973-991, DOI: [10.1080/14772019.2012.743488](https://doi.org/10.1080/14772019.2012.743488)

To link to this article: <http://dx.doi.org/10.1080/14772019.2012.743488>

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## Implication of the presence of *Megathericulus* (Xenarthra: Tardigrada: Megatheriidae) in the Laventan of Peruvian Amazonia

François Pujos<sup>a,b,\*</sup>, Rodolfo Salas-Gismondi<sup>c</sup>, Guillaume Baby<sup>d</sup>, Patrice Baby<sup>d,e</sup>, Cyrille Goillot<sup>d,e</sup>, Julia Tejada<sup>c</sup> and Pierre-Oliver Antoine<sup>f</sup>

<sup>a</sup>Departamento de Paleontología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET-Mendoza, Avda. Ruiz Leal s/n, Parque Gral. San Martín 5500, Mendoza, Argentina; <sup>b</sup>Institut Français d'Études Andines (IFEA), Casilla 18-1217, Av. Arequipa 4595, Lima 18, Perú; <sup>c</sup>Departamento de Paleontología de Vertebrados, Museo de Historia Natural-UNMSM, Lima, Perú; <sup>d</sup>Université de Toulouse; UPS (SVT-OMP), LMTG, 14 Avenue Édouard Belin, F-31400, Toulouse, France; <sup>e</sup>CNRS, LMTG, F-31400 Toulouse, France and IRD, LMTG, F-31400, Toulouse, France; <sup>f</sup>Institut des Sciences de l'Évolution (CNRS-UMR 5554), CC064, Université Montpellier 2, Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France

(Received 22 February 2011; accepted 29 April 2012; first published online 25 March 2013)

Middle Miocene remains of giant megatheriine ground sloths (Tardigrada: Megatherioidea) are scarce and generally located in southern South America. The discovery of a well-preserved edentulous dentary of *Megathericulus* sp. from the Middle Miocene (Laventan South American Land Mammal Age - SALMA; 13.5–11.8 Ma) of the Amazonian Peru increases our knowledge of this genus, which had previously been recognized in Argentina. A preliminary revision of the earliest Megatheriinae allowed clustering the four middle Miocene species within the genus *Megathericulus* Ameghino: *M. patagonicus* Ameghino, *M. primaevus* Cabrera, *M. andinum* (Kraglievich), and *M. cabrerai* (Kraglievich). This small-sized genus is mainly characterized by a lateral depression that borders m1, a posterior external opening of the mandibular canal anterior to the base of the ascending ramus that opens anteriorly or anterodorsally, the base of the symphysis located anteriorly to the m1, important anteroposterior compression of the teeth, elongation of the region of the maxilla anterior to the M1, humerus elongated and gracile, patellar trochlea of femur contiguous with medial and lateral articular facets for tibia, strongly developed odontoid tuberosity, and astragalus with prominent odontoid process. The genus *Eomegatherium* Kraglievich is therefore restricted to the Huayquerian SALMA of Argentina and represented by a single species, *E. nanum* Burmeister. Megatheriinae constitute the first clade of Tardigrada in which the caniniform tooth has been secondarily modified into a molariform tooth. Three molariform patterns can be observed during megatheriine evolution in relation to tooth compression and loph or lophid orientation. Middle Miocene Megatheriinae occur only in the westernmost part of South America. These giant ground sloths might have dispersed latitudinally from Colombia/Patagonian Argentina before colonizing eastern areas of Andean South America (Bolivia, Venezuela, north, and east of Argentina) during the late Miocene and early Pliocene.

**Keywords:** Tardigrada; Megatheriinae; *Megathericulus patagonicus*; middle Miocene; Western Amazonia

### Introduction

Xenarthrans constitute one of the most peculiar and characteristic clades of South American mammals. This clade clusters three groups with fossil and recent representatives: sloths (Tardigrada or Phyllophaga, Vizcaino & Fariña 2003), armoured Xenarthra or armadillos (Cingulata), and anteaters (Vermilingua). According to Gaudin (2004) and Gaudin & McDonald (2008), Megatheriidae and Nothrotheriidae are sister groups and form the clade Megatheria; Megatheriidae include Megatheriinae and *Planops* Ameghino, 1887. The latter genus, from the Santacrucian South American Land Mammal Age (SALMA) of Argentina, is also considered by some authors as typifying a distinct non-megatheriid megatherioid subfamily (i.e. Planopsinae; De Iuliis 1994). Megatheriinae

are considered among the largest continental mammals to have populated America during the Neogene period (Fariña *et al.* 1998). Their climax occurred during the middle Pleistocene–early Holocene epochs (Ensenadan–Lujanian SALMA, Fariña *et al.* 1998) with the tropical form *Eremotherium laurillardii* (Lund, 1842) and the Pampean ‘temperate’ species *Megatherium* (*Megatherium*) *americanum* Cuvier, 1796. Megatheres colonized all of South America, from Pampean areas of Argentina (Cuvier 1796), to the Bolivian Altiplano (St-André & De Iuliis 2001; De Iuliis *et al.* 2009), Amazonia (Pujos & Salas 2004; Cozzuol 2006), Colombia (Hirschfield 1985), and Venezuela (Carlini *et al.* 2006). *Eremotherium* Spillmann, 1948 (i.e. *E. eomigrans*, De Iuliis & Cartelle, 1999) migrated to North America after the Isthmus of Panama formed by the early Pliocene, c. 4 Ma (De Iuliis 2004). All megatheriine species

\*Corresponding author. Email: fpujos@mendoza-conicet.gov.ar

disappeared during the Pleistocene–Holocene transition, as part of the megafauna extinction (e.g. Barnosky *et al.* 2004).

Megatheriinae were abundant during Pliocene and, especially, Pleistocene epochs, while pre-Pliocene remains of the clade are relatively scarce (De Iuliis 1996; Brandoni 2006a). The Megatheriinae first occur during the middle Miocene (Friasian, Colloncuran, Laventan, and early Mayoan SALMAs) in Argentinian Patagonia, with *Megathericulus* Ameghino, 1904 and *Eomegatherium* Kraglievich, 1930 and in Colombia with a megatheriine of uncertain affinities (Hirschfeld 1985).

*Megathericulus* was originally represented by *M. patagonicus* Ameghino, 1904 and *M. primaevus* Cabrera, 1939. *Megathericulus patagonicus* is primarily based on the anterior part of a skull including nasals and edentulous maxillae (MACN A-11151, Fig. 4) and an astragalus (which belong to the same individual; Ameghino 1904) from the Patagonian locality of Laguna Blanca (Chubut Province), early middle Miocene in age (Friasian, *sensu* Ameghino 1904). De Iuliis *et al.* (2008) recently extended the knowledge of this genus with the description of a badly preserved hemimandible (Fig. 5E, F) and several postcranial elements from the same geographical area (e.g. humerus MLP 91-IX-7–18 and tibia MLP 91-IX-15–2 considered Mayoan in age). Cabrera (1939) described a second species, *M. primaevus*, from the middle Miocene (Colloncuran) of Argentina, based on several postcranial elements including a tibia, an incomplete femur, and an astragalus (MLP 39-VI-24–1) collected in Neuquén Province.

According to Brandoni (2006a), who recently revised the Argentinian megatheriines, the coeval counterpart of *Megathericulus* is *Eomegatherium*, which is represented by three species and is currently only known from Argentina: *E. andinum* Kraglievich, 1930, *E. nanum* (Burmeister, 1891), and *E. cabrerai* Kraglievich, 1930. *Eomegatherium nanum* is represented by a single dentary (MACN Pv-4993, considered as the holotype by Brandoni 2006a) and an astragalus (MACN 4992), *E. andinum* by cranial and mandibular fragments (MLP 2–204, Fig. 5C, D), and *E. cabrerai* by skull fragments (badly preserved and impossible to compare with other Miocene taxa), an anterior epiphysis of ulna, and a fragmentary astragalus (MLP 2–206; see Brandoni 2006a, fig. 7C–E). *Eomegatherium andinum* and *E. cabrerai* occur in the late middle–early late Miocene of Patagonia (Mayoan), whereas *E. nanum* is known from the late Miocene of Entre Ríos Province, Argentina (Ituzaingó Fm., Huayquerian; Cione *et al.* 2000; Brandoni 2005; see Fig. 8). The discrepancies between Mayoan and Huayquerian species of *Eomegatherium* are so obvious that the generic assignment of these species will be considered in the Discussion of the present study.

Hirschfeld (1985) described a well-preserved Laventan ground sloth assemblage from the Colombian site of La Venta that included several Megatheriinae, but this author did not suggest any generic identification. While postcranial

remains clearly correspond to a member of the subfamily, the two teeth numbered UCMP 39595 and 39596 do not show the usual megatheriine pattern and may belong instead to the clade Planopsinae (see discussion below for more details).

Several other megatheriine genera appeared in the Argentinian territory during the Late Miocene: *Anisodontherium halmyronomum* (see Brandoni & De Iuliis 2007) from the Chasicóan SALMA of the Chasicó Fm., separated from *Plesiomegatherium* Roth, 1911 by Brandoni & De Iuliis (2007); *Megatheriops rectidens* (Rovereto, 1914) from the Huayquerian of Mendoza Province; *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) and *P. brevirostrum* Carlini *et al.*, 2002 from the Huayquerian of Catamarca Province; the Huayquerian forms from the Ituzaingó Fm. of Entre Ríos Province (*Eomegatherium nanum* but also *Pyramiodontherium* sp. Rovereto, 1914, *Promegatherium smaltatum* Ameghino, 1883 and *Pliomegatherium lelongi* Kraglievich, 1930; Brandoni 2005), and *Urumaquia robusta* Carlini *et al.*, 2006 from the ‘late Miocene’ of Venezuela.

Phylogenetic affinities of Megatheriinae with other Megatherioidea are relatively well understood (Gaudin 2004), but primitive cranial, mandibular and dental conditions, as well as the possible geographical origin and dispersion of the clade, are poorly constrained (De Iuliis 1996; Pujos 2006; Fig. 7).

The new Peruvian specimen described here provides fundamental information on the primitive megatheriine condition, mainly in relation to the anteroposterior compression of the teeth, the maximum height of the mandible and the possible presence of longitudinal grooves, but also to the position of the posterior external opening of the mandibular canal, the concavity of the dorsal margin of the horizontal ramus, the position of the base of the symphysis in relation to m1, and the development of the posterior ascending ramus. Furthermore, it bridges a considerable gap in the Miocene geographical distribution of the clade. It will help to correlate the earliest members of the clade from Argentinian Patagonia with specimens from northern areas of the continent, such as Peru, Colombia, and Venezuela.

The aims of the present work are: (1) to describe the oldest well-preserved megatheriine dentary; (2) to obtain new information on mandibular condition and dental patterns in Mio-Pliocene megatheriine ground sloths; (3) to evaluate the co-occurrence of two distinct genera (i.e. *Megathericulus* and *Eomegatherium*) during the Middle Miocene in South America; and (4) to present a palaeogeographical overview and a putative dispersal scenario of Megatheriinae in South America from the Colloncuran up to the Montehermosan SALMA.

The following orientations will be used to describe and compare teeth and mandibles: anterior/posterior and lateral/medial for descriptions of the mandible;

mesial/distal and vestibular/lingual for tooth descriptions. For the South American Land Mammal Ages, we follow Croft (2007).

### Institutional abbreviations

**AMU-CURS:** Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; **CICYTTP-CONICET:** Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Entre Ríos, Argentina; **FMNH:** Field Museum of Natural History, Chicago, Illinois, USA; **GET:** Géosciences Environnement Toulouse, Université Paul-Sabatier, Observatoire Midi-Pyrénées, Toulouse, France; **GHUNLPAM:** Cátedra de Geología Histórica de la Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de La Pampa, Santa Rosa, Argentina; **IMBECU:** Instituto de Medicina y Biología Experimental de Cuyo, CCT-CONICET-Mendoza, Mendoza, Argentina; **IRD:** Institut pour la Recherche et le Développement, France; **MACN:** Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; **MLP:** Museo de La Plata, La Plata, Argentina; **MNHN:** Muséum national d’Histoire naturelle, Paris, France; **MUSM:** Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; **ROM:** Royal Ontario Museum, Toronto, Ontario, Canada; **UCMP:** Museum of Paleontology, University of California, Berkeley, California, USA; **UF:** Florida Museum of Natural History, Gainesville, Florida, USA; **UNLPAM:** Universidad Nacional de La Pampa, Facultad de Ciencias Exactas y Naturales, La Pampa, Argentina.

### Other abbreviations

**DM,** depth of the mandible; **Fm.,** Formation; **HI,** hypsodonty index; **LTR,** length of the tooth row; **m-,** lower molariform teeth; **Mc,** metacarpal; **NALMA,** North American Land Mammal ‘Age’; **peomc,** posterior external opening of the mandibular canal; **SALMA,** South American Land Mammal Age (following the scheme proposed by Croft 2007).

### Considered specimens and taxa

Pre-Pleistocene Megatheriinae are uncommon, especially outside Argentina, and mandibular remains are scarce. The Middle Miocene specimen MUSM 1564 will be mainly compared with previously described dentaries of *Megathericulus patagonicus* (MLP 91-IX-7–18, Mayoan; De Iuliis *et al.* 2008; Fig. 5E, F), *Eomegatherium nanum* (MACN Pv-4995, Huayquerian; Burmeister, 1891; Fig. 5A, B), *Eomegatherium andinum* (MLP 2–204, Mayoan;

Kraglievich 1930; Fig. 5C, D), *Anisodontherium halmyronomum* (MLP 30-XII-10–21, Chasicosan; Brandoni & De Iuliis 2007), *Megatheriops rectidens* (MACN 2818, Huayquerian; Rovereto 1914), *Pliomegatherium lelongi* (MACN Pv-13213, MACN Pv-5269, Huayquerian; Brandoni 2006b), and *Pyramiodontherium bergi* (MLP 2–66, Huayquerian; Moreno & Mercerat 1891; Cabrera 1928).

Partial skulls of *Megathericulus patagonicus* (MACN A-11151, maxilla of the oldest well-preserved megatheriine skull; Kraglievich 1930; Ameghino 1904; Bondesio *et al.* 1980; Fig. 4), as well as isolated teeth from the Laventan of La Venta (Colombia, UCMP 39595 and 39596; Hirschfeld 1985; Fig. 6D–F) and from the Huayquerian of La Pampa Province of Argentina (GHUNLPAM 8010; Fig. 6A–C), are included in the present study and discussed.

Cranio-mandibular morphology of the Colloncuran *Megathericulus primaevus* from Colloncuran (MLP 39-VI-24–1) is unknown, whereas skull fragments of the Mayoan *Eomegatherium cabrerai* from Mayoan (MLP 2–206) are definitively not informative (see Brandoni 2006a for more information). Postcranial elements (i.e. ulna and astragalus) of *M. patagonicus* and *E. cabrerai* will be considered to estimate affinities between these two taxa.

Astragali of *Megathericulus patagonicus* (MACN A-11151), *Eomegatherium cabrerai* (MLP 2–206), and *Eomegatherium nanum* (MACN 4992) are also compared for inferring affiliations of these species within these two genera.

Pre-Montehermosan Megatheriinae are the main focus of the present study, but other well-known pre-Pleistocene forms, such as *Proeremotherium eljebe* Carlini *et al.*, 2006 (AMU-CURS 126, Pliocene of Codore Fm., Venezuela; Carlini *et al.* 2006), *Eremotherium eomigrans* (UF 124233, Late Blancan–Early Irvingtonian NALMA; De Iuliis & Cartelle 1999), and *Megatherium (Megatherium) altiplanicum* (MNHN AYO 101, Montehermosan; St-André & De Iuliis, 2001), are also considered.

### Systematic palaeontology

Superorder **Xenarthra** Cope, 1889

Order **Tardigrada** Latham & Davies (in Forster), 1795

Superfamily **Megatherioidea** Gray, 1821

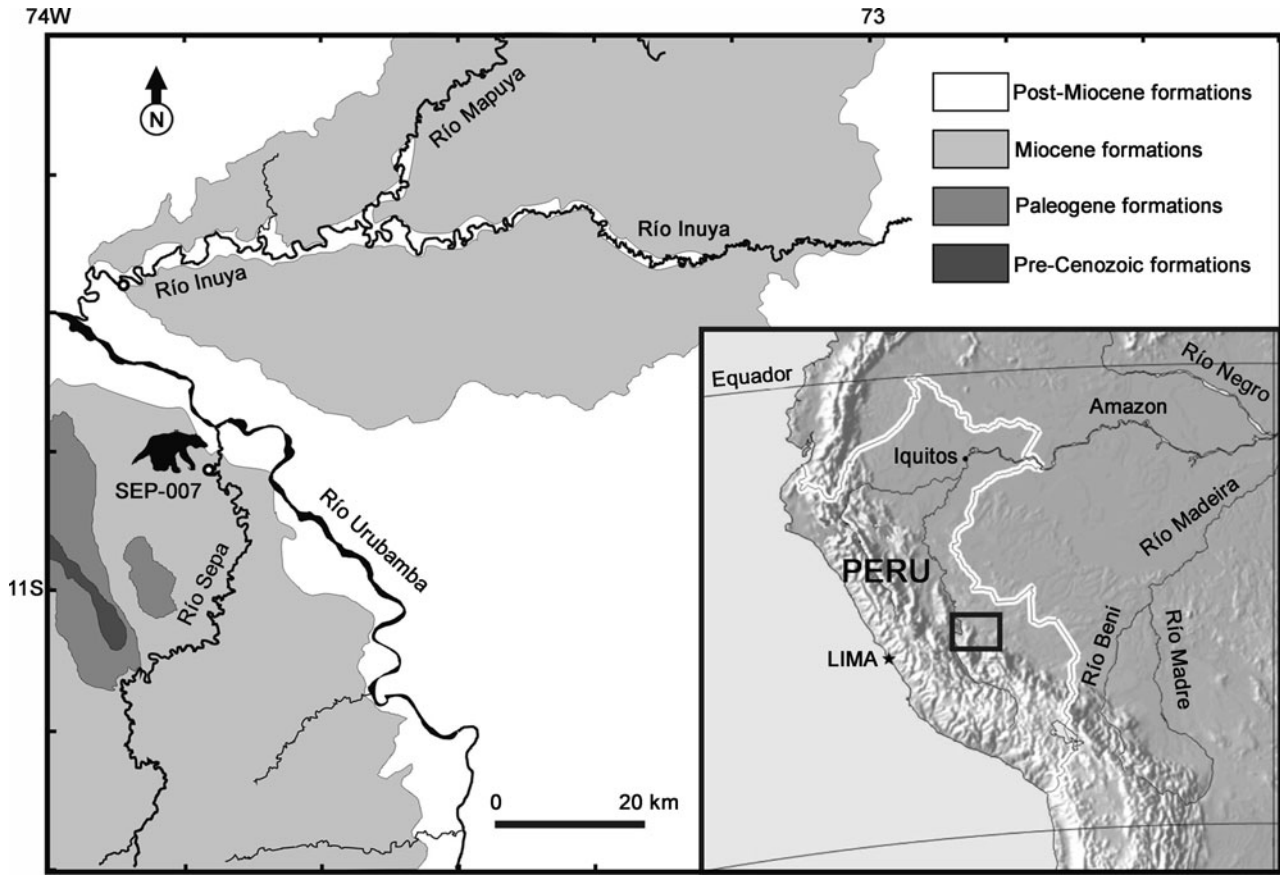
Family **Megatheriidae** Gray, 1821

Subfamily **Megatheriinae** Gray, 1821

Genus ***Megathericulus*** Ameghino, 1904

**Type species.** *Megathericulus patagonicus* Ameghino, 1904. Holotype: MACN A-11151, anterior portion of the skull (Fig. 4) and right astragalus from the Friasian of Laguna Blanca (Chubut Province, Argentina; Ameghino 1904).

**Other species.** *Megathericulus primaevus* Cabrera, 1939. Holotype: MLP 39-VI-24–1, several postcranial



**Figure 1.** Map showing the Middle Miocene locality SEP 007 in Amazonian Peru, where the specimen MUSM 1564 of the giant Laventan SALMA ground sloth *Megathericus* sp. was found.

elements (ribs, partial right radius, right Mc III, fragments of right femur, tibia, calcaneum, and right astragalus) from the Colloncuran of Cañadón Ftamichi (Neuquén Province; Cabrera 1939).

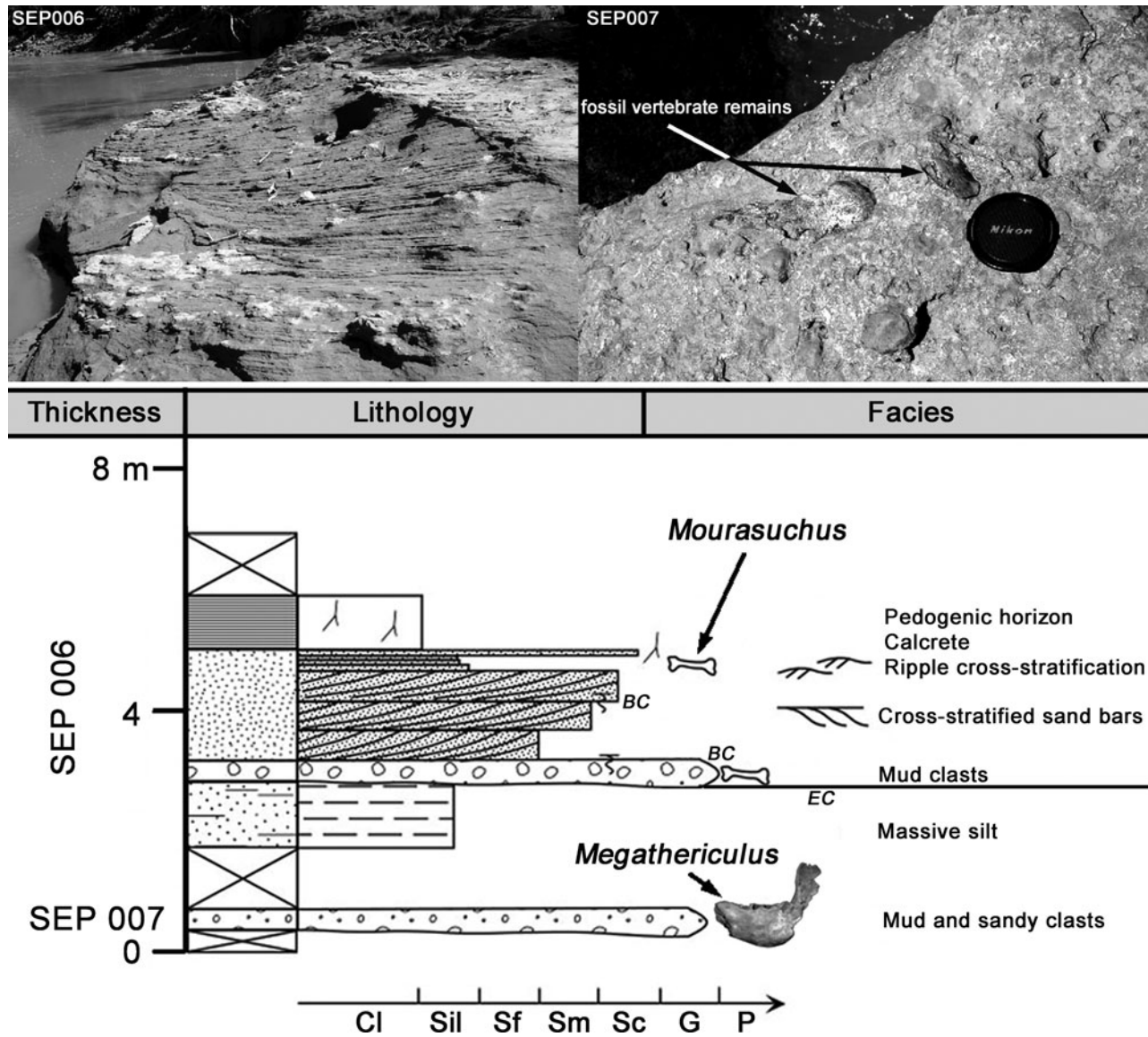
**Diagnosis.** (Modified from De Iuliis 1996; Brandoni 2006a; De Iuliis *et al.* 2008.) Small-sized megatheriine ground sloth (half the size of *Megatheriops* and *Pyramiodontherium*); dorsal margin of the horizontal ramus concave, as in *Anisodontherium*; lateral depression that borders m1; posterior external opening of the mandibular canal anterior at the base of the ascending ramus that opens anteriorly or anterodorsally; posteriorly inclined ascending ramus of the mandible which forms an obtuse angle with the horizontal ramus ( $100\text{--}130^\circ$ ); in dorsal view, base of the symphysis located anteriorly to m1, as in *Anisodontherium*; m4 anterior to the ascending ramus; ventral border of the pre dental region is poorly inclined; important antero-posterior compression of the teeth; region of the maxilla anterior to the M1 elongated (approximately as long as the molariform tooth row), with lateral edges diverging anteriorly; prominent median V-shaped notch between premaxillo-maxillary articular surfaces; humerus elongated and gracile; prominent and laterally positioned deltopec-

toral crest on anterior surface of humerus; musculospiral groove extends along lateral surface of deltopectoral crest onto posterior surface of humerus; patellar trochlea of femur contiguous with medial and lateral articular facets for tibia; astragalus with prominent odontoid process.

### **Megathericus** sp.

**Material.** MUSM 1564, well-preserved right edentulous dentary (Fig. 3).

**Locality, horizon and age.** The SEP-007 locality is a small island cropping out from Río Sepa, a left-bank tributary of Río Urubamba, south-eastern Peru, during the dry season (Fig. 1). This area is part of the Fitzcarrald Arch, the uplift from which the Ucayali and Madre de Dios basins split less than 4 Ma ago (Espurt *et al.* 2007). The stratigraphical section encompassing both SEP-007 and the adjacent locality SEP-006 exposes some typical tidal deposits of the Miocene Ipururo Formation (Fig. 2), comparable to the outcrops of the Ríos Inuya-Mapuya area *c.* 50 km to the north-east, as described by Espurt *et al.* (2010). The Ipururo sedimentation could have occurred under a tidally controlled environment in a complex



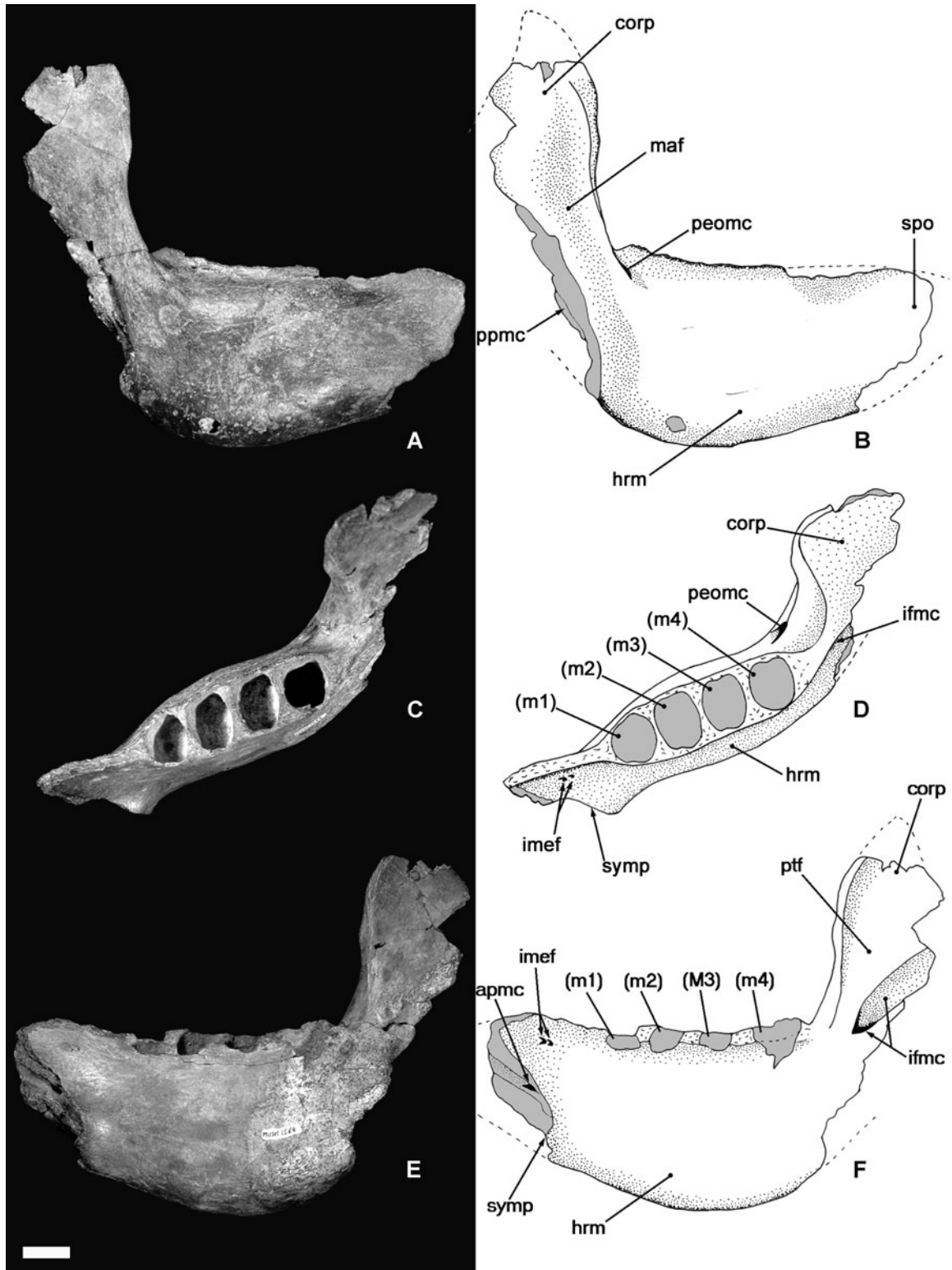
**Figure 2.** Top, photographs of SEP 006 (left) and SEP 007 (right) outcrops from which Laventan SALMA fossil vertebrates were recovered on Río Sepa (Amazonian Peru). Bottom, lithological succession of SEP 006 and SEP 007. Abbreviations: BC, bioturbated contact; EC, erosional contact.

mega-wetland connected to the Caribbean Sea, as suggested by Hoorn *et al.* (2010a, b). The depositional environment was controlled by Andean tectonic evolution and orogenic loading in the Amazonian foreland basin (Roddaz *et al.* 2010). The edentulous megatheriine mandible MUSM 1564 (Fig. 3) was discovered in July 2007 during a field mission organized by a Franco-Peruvian team (IRD, MUSM, and GET). It was unearthed *in situ* in a channel-shaped conglomerate with sandstone and mudstone clasts and a high concentration of fish and turtle remains. As a vertebrate-yielding locality, SEP-007 is part of the Fitzcarrald local fauna, referred to the late Middle Miocene Laven-

tan (13.5–11.8 Ma; Antoine *et al.* 2007; Salas-Gismondi *et al.* 2007; Negri *et al.* 2010; Goillot *et al.* 2011).

### Comparative description

MUSM 1564 is a right edentulous dentary in which the four dental alveoli are preserved (Fig. 3). The anterior extremity of the 'spout' (as the pre-dentary region of ground sloths is commonly called), the apex of the coronoid process, and the angular process are not preserved. The specimen belongs to an adult, as in occlusal view m1 is barely separated from



**Figure 3.** Photographs (left) and drawings (right) of right dentary of *Megathericulus* sp. (MUSM 1564) from the late Middle Miocene Laventan SALMA of Amazonian Peru Amazon in lateral (A, B, anterior towards right), occlusal (C, D, anterior towards left), and medial (E, F, anterior towards left) views. Abbreviations: apmc, anterior portion of the mandibular canal; corp, coronoid process; hrms, horizontal ramus of the mandible; ifmc, internal foramen of the mandibular canal; imef, internal mental foramina; maf, masseteric fossa; (m1)–(m4), alveoli of the four lower molariform teeth; peomc, posterior external opening of the mandibular canal; ppmc, posterior portion of the mandibular canal; ptf, pterygoid fossa; spo, ‘spout’; symp, symphysis. Scale bar = 2 cm.

**Table 1.** Measurements (in mm) of the right dentary of *Megathericulus* sp. from Laventan SALMA of Peruvian Amazon (MUSM 1564) and m2 or m3 megatheriine molariform tooth from Huayquerian SALMA of Argentinean Cerro Azul Formation, La Pampa Province, Argentina (GHUNLPAM 8010).

Taxa and specimen	Measurements (mm)
<b><i>Megathericulus</i> sp. (MUSM 1564)</b>	
Diameters of m1 alveoli (MD × VL)	18 × 20.2
Diameters of m2 alveoli (MD × VL)	17.1 × 23.2
Diameters of m3 alveoli (MD × VL)	18.1 × 22.3
Diameters of m4 alveoli (MD × VL)	20.9 × 18.8
Length of the toothrow (= LTR)	84.6
Maximum height of the ramus (at m3 = DM)	78.1
Maximum width of the ramus (at m3)	38.2
<b>Megatheriinae indet. (GHUNLPAM 8010)</b>	
Diameters of isolated m2 or m3 (MD × VL)	~16 × ~21.2

Abbreviations: DM, depth of the mandible; VL, vestibulolingual (or transverse); LTR, length of the tooth row (from mesial margin of the m1 alveolus to vestibular margin of the m4 alveolus); MD, mesiodistal; VL, vestibulolingual.

the dorsolateral edge of the ramus (De Iuliis 1996; Cartelle & De Iuliis 2006).

The tooth row reveals the existence of four molariform teeth without diastema (Fig. 3C, D). The tooth row (84.6 mm; Table 1) is larger than in the specimen of

*Megathericulus patagonicus* figured by De Iuliis *et al.* (2008;  $\sim 70 \pm 2$  mm) and smaller than in *Eomegatherium andinum* ( $\sim 97 \pm 2$  mm) and *Anisodontherium halmyronomum* (115 mm). The size of megatheriines has increased considerably since the Huayquerian period, as shown by the tooth row length of *Pyramiodontherium bergi* and *Megatheriops rectidens* (189 and 165 mm, respectively; Table 2). Similarly, the Huayquerian *E. nanum* is considerably larger than Middle Miocene *Eomegatherium andinum*. In *E. nanum*, the m2–m4 length is 116 mm according to Brandoni (2006a).

In occlusal view (Fig. 3C, D), the preserved portion of the rostrum suggests a shovel-shaped ‘spout’, thus differing from most other Megatheriinae. The posterior lateral border of the spout is slightly oblique to the axis of the dental series, indicating that the spout was probably expanded anteriorly, a condition that is present in *Eomegatherium andinum* (MLP 2–204) and *Pyramiodontherium bergi*. This condition contrasts with that observed in most megatheriines, in which the spout is long with parallel edges. The external mental foramen is always present in sloths. In Megatheriidae and Nothrotheriidae, it is usually located at the level of the symphysis mid-length. Most of the ‘spout’ of MUSM 1564 is broken and the mental foramen is not preserved. We infer that the opening was located a few millimetres beyond the most anterior preserved portion of the spout since, in

**Table 2.** Hypsodonty index of megatheriine ground sloths (terminology and some *Megatherium-Eremotherium* data after Bargo *et al.* 2006).

Taxa	Specimen numbers	LTR	DM	HI (min–max)
<b>Laventan SALMA (Middle Miocene)</b>				
<i>Megathericulus</i> sp.	MUSM 1564	84.6	78.1	0.92
<b>Chasicoan SALMA (Late Miocene)</b>				
<i>Anisodontherium halmyronomum</i>	MLP 30-XII-10–21	115	123	1.07
<b>Huayquerian SALMA (Late Miocene)</b>				
<i>Megatheriops rectidens</i>	MACN 2818	165	145	0.88
<i>Pyramiodontherium bergi</i>	MLP 2–66	189	154	0.81
<i>Pliomegatherium lelongi</i>	MACN 13213	144	103	0.72
<b>Montehermosan SALMA (Late Miocene–Early Pliocene)</b>				
<i>Megatherium (M.) altiplanicum</i>	MNHN AYO 101	143.6	145.0	1.01
<b>Late Blancan–Early Irvingtonian NALMA (Late Pliocene–Early Pleistocene)</b>				
<i>Eremotherium eomigrans</i>	UF 121737	215	169	0.78
<b>Ensenadan–Lujanian SALMA (Late Pleistocene–Early Holocene)</b>				
<i>Megatherium (M.) americanum</i>	22 specimens	213	215.7	1.02 (0.89–1.14)
<i>Megatherium (P.) medinae</i>	4 specimens	148.8	134.3	0.90 (0.81–0.94)
<i>Megatherium (P.) tarijense</i>	2 specimens	178	154.5	0.87 (0.82–0.92)
<i>Megatherium (P.) elenense</i>	4 specimens	113.3	85	0.75 (0.72–0.77)
<i>Eremotherium laurillardii</i>	17 specimens	178.5	145.6	0.77 (0.73–0.83)

Abbreviations: LTR, length of the tooth row; DM, depth of the mandible; HI, Hypsodonty Index (mandibular height (at the level of the third tooth)/tooth row length).



this position, a thin wall of bone separates the mandibular canal from the lateral surface of the spout.

The anteroposterior axis of the dental series is rectilinear, and the anteriormost tooth (m1) is not shifted laterally, as occurs in most Mylodontidae and Megalonychidae. The position and shape of the anteriormost tooth alveolus of MUSM 1564 indicates that this tooth was not caniniform-shaped (Fig. 3C–F). In dorsal view, the lateral wall of the horizontal ramus is convex and the medial wall roughly flat and rectilinear, as commonly observed in this subfamily (Fig. 3C, D). The maximum thickness of the ramus is located between m2 and m3 (Table 1).

The hypsodonty index (HI) is the ratio of depth of the mandible (DM) to the length of the tooth row (LTR). The HI of the Amazonian specimen is 0.92, an average value for Megatheriinae, i.e. comparable to that of *Megatheriops rectidens* (0.88), slightly higher than in *Pyramiodontherium bergi* (0.81), and lower than in *Megatherium (M.) altiplanicum* and *Anisodontherium halmyronomum* (1.01 and 1.07, respectively; Table 2). Unfortunately, it was impossible to calculate the HI for *Megathericulus patagonicus* (see De Iuliis *et al.* 2008).

In lateral view (Fig. 3A, B), the ventral edge of the horizontal ramus is strongly convex, indicating very hypsodont teeth, as in other Megatheriinae. Interestingly, the maximum height of the horizontal ramus is located at the level of m3–m4, which could represent the plesiomorphic condition; in most derived forms, such as species of *Megatherium*, the deepest area of the mandible is located more anteriorly. Unfortunately, the ventral margin of the mandible is not preserved in *M. andinum* and *E. patagonicus* (Fig. 5D, F). In lateral view, the dorsal margin of the horizontal ramus is slightly concave (Fig. 3A, B), as in *A. halmyronomum* (see Brandoni & De Iuliis 2007) and *E. andinum* MLP 2–204 (Fig. 5D), whereas it is rectilinear as in *Megatheriops*, *Pyramiodontherium*, and *Pliomegath-erium*. A gentle lateral depression borders the alveolus of m1 anteriorly (Fig. 3A, B).

The posterior external opening of the mandibular canal ('posterolateral external opening'; De Iuliis *et al.* 2008) is located at the anterior base of the ascending ramus; it opens anteriorly and it is visible both dorsally and laterally (Fig. 3A–D), as in *Megathericulus patagonicus* (Fig. 5E, F; De Iuliis *et al.* 2008). In *Eomegath-erium andinum*, it opens anterodorsally. At the same time, the ascending ramus is more posteriorly inclined in the latter than in the Amazonian dentary (Fig. 5D). In *E. nanum*, it also opens more dorsally and is laterally displaced (Fig. 5A, B; Brandoni & De Iuliis 2007). In MUSM 1564, this aperture is oval and located at the posterior half of the alveolus for m4, while it is posterior to this alveolus in *M. patagonicus* (Fig. 5E, F; De Iuliis *et al.* 2008).

In dorsal view, the ascending ramus is posterolateral to m4. The anterior border of the ascending ramus and the dorsal border of the horizontal ramus form an ante-

rior angle of *c.* 100° (Fig. 3A, B, E, F), as in *Anisodontherium halmyronomum* and *Eremotherium eomigrans*. This angle is *c.* 80–90° in *Megatheriops rectidens* and *Megatherium (M.) altiplanicum*, while it is *c.* 120–130° in Middle Miocene Patagonian specimens of *Eomegath-erium andinum* (MLP 2–204, Fig. 5D) and of *Megathericulus patagonicus* (Fig. 5F). In *Eomegath-erium nanum* (Fig. 5B), the ascending rami of the mandibles is not preserved.

The base of the anterior border of the ascending ramus is concave and smooth in its anterior part, whilst higher it is convex and rough, which corresponds to the insertion of the *temporalis* muscle (see Bargo 2001). A portion of the posterior border of the coronoid process is preserved; allowing the assumption of a dorsal extension of the coronoid process (Fig. 3C, D) and the characteristic megatheriine configuration of the ascending ramus.

The medial surface of the horizontal ramus is flattened dorsoventrally and is slightly anteroposteriorly convex. In dorsal view, the base of the symphysis is rough and located 14 mm in front of the m1 alveolus (Fig. 3C, D), as in *Anisodontherium*, *Eomegath-erium nanum*, *E. andinum*, and *Megathericulus patagonicus* (Fig. 5C, E for the last two species). In *Pyramiodontherium bergi* and *Pliomegath-erium lelongi*, the symphysis is located at the level of the posterior border of m1. In lateral view, the 'spout' of the mandible is not complete but some of the premental region is observable. Its ventral border is poorly inclined, as seems to be typical in *Megathericulus* (Figs 3A, B, E, F, 5F) and in contrast with what occurs in later taxa like *Pyramiodontherium* and *Pliomegath-erium*. Two internal mental foramina are located 21 mm anteriorly to the alveolus on the medial side of the alveolus of m1 (Fig. 3C–F), at the level of the base of the tooth row. This character, highly variable in sloths, cannot be considered as diagnostic. As most of the 'spout' is broken, the anterior portion of the single mandibular canal is visible in medial view (Fig. 3E, F). On the same view, the internal foramen of the mandibular canal is widely open posterodorsally and located posteriorly to the alveolus of m4, as in other Megatheriinae (Fig. 3E, F).

The four molariform alveoli are preserved and m2–m3 show an important anteroposterior compression of the teeth, comparable to what is observed in *Anisodontherium halmyronomum* and *Megathericulus patagonicus* (Figs 3C, D, 5C, E). In most derived forms, the teeth are less anteroposteriorly compressed (e.g. *Pyramiodontherium* and *Megath-eriops*). In occlusal view, the molariform shaft of MUSM 1564 is rectilinear and vertical. The lower molariform alveoli suggest that the teeth were bilophodont.

The m1 is trapezoidal in cross section, with a posterior half wider than the anterior one (22 and 17 mm, respectively; Fig. 3C, D). The anterior wall of the alveolus is convex anteriorly, while the posterior loph is convex posteriorly. The presence of two lophs is also suggested by two lingual and vestibular longitudinal grooves. The

labial longitudinal groove is deeper than the lingual one. In occlusal view, m1 is 6 mm apart from the lateral margin of the dentary.

The m2 is much more compressed anteroposteriorly than m1 (Table 1) and therefore more rectangular-shaped. As for m1, its anterior and posterior lophs are anteriorly and posteriorly convex, respectively. The posterior loph is extended lingually and the vestibular side of the alveolus of m2 is parallel to the tooth row sagittal axis. Lingual and vestibular longitudinal grooves are also present on m2.

The m3 is practically identical to m2, i.e. it is bilophodont with lingual and vestibular longitudinal grooves.

Finally, m4 is more rounded and less compressed anteroposteriorly than other molariform teeth. In contrast to m1–m3, only a vestibular longitudinal groove is present on this tooth. The m4 is located at the base of the ascending ramus.

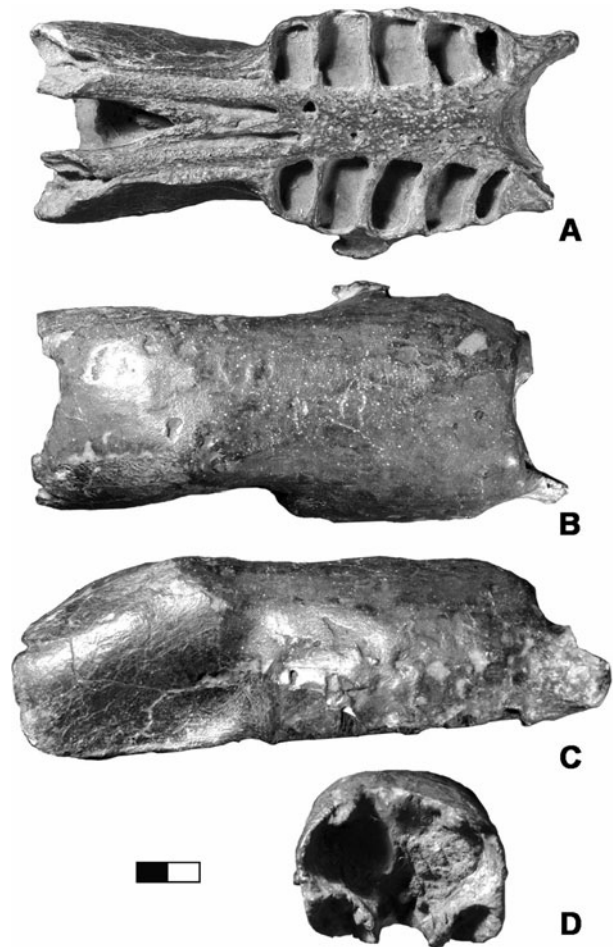
## Discussion

### *Megathericulus*, *Eomegatherium* and the primitive condition in Megatheriinae

MUSM 1564 from the Laventan of Amazonia shows affinities with *Eomegatherium* and *Megathericulus*, the earliest conspicuous megatheriines, also Middle Miocene in age. Before the discovery of the Peruvian specimen, Middle Miocene Megatheriinae were exclusively located in Argentina (*Megathericulus patagonicus*, *M. primaevus*, *E. andinum*, and *E. cabrerai*) and Colombia (unidentified taxon; Hirschfeld 1985; Fig. 8). Middle Miocene megatheriines are small-sized and usually represented by fragmentary remains (see De Iuliis 1996; Brandoni 2006a; De Iuliis *et al.* 2008).

Thanks to the good preservation of MUSM 1564, and especially taking into account that it was discovered in Amazonia, this specimen provides important information on the clade's origin and on plesiomorphic cranio-mandibular conditions of megatheriines. This Laventan specimen is younger than the Colloncuran *Megathericulus* species from Patagonia (De Iuliis *et al.* 2008; Fig. 8), and it is at the same time coeval with Colombian forms from La Venta (Hirschfeld 1985; Fig. 6D–F), and older than *Eomegatherium nanum*, *E. cabrerai*, and *Anisodontherium halmyronomum* from the Mayoan Chasicuan and Huayquerian of Argentina (Fig. 8).

MUSM 1564 is similar in size to the specimen of *Megathericulus patagonicus* described by De Iuliis *et al.* (2008), slightly smaller than *Eomegatherium andinum* and *Anisodontherium halmyronomum*, and considerably smaller than *Megatheriops rectidens* and *Pyramiodontherium bergi*, as is attested by the length of the tooth row (Table 2). MUSM 1564 has four lower quadrangular to oval molariform teeth (plesiomorphic condition in sloths; Engelmann 1987), suggesting a 5/4M dental formula (typical at order level), which is confirmed by the oldest megatheriine

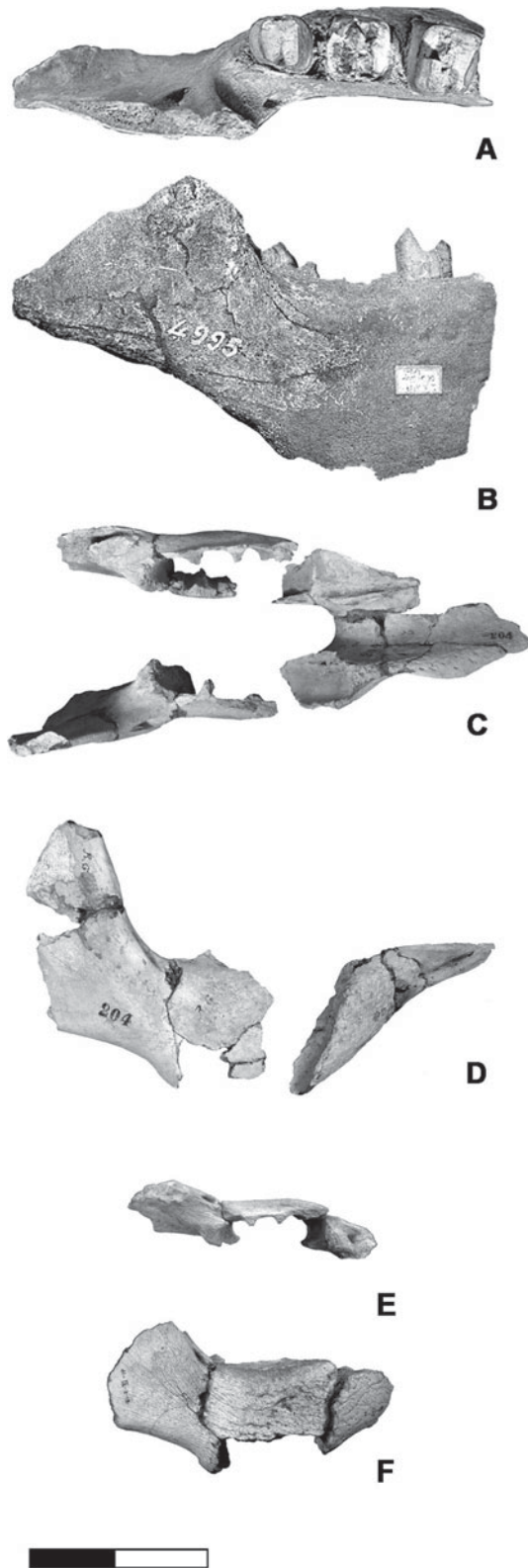


**Figure 4.** Photographs of the anterior portion of the skull of the holotype of *Megathericulus patagonicus* (MACN A-11151) from the early Middle Miocene Friasian SALMA of Laguna Blanca (Chubut Province, Argentina) in occlusal (A, anterior towards left), dorsal (B, anterior towards left), left lateral (C, anterior towards left), and anterior (D, dorsal towards top) views. Scale bar = 2 cm.

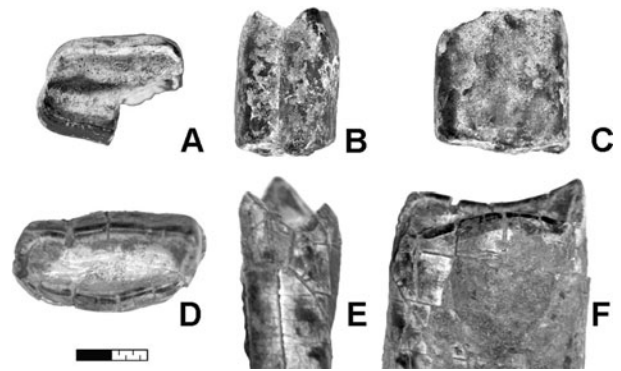
maxilla (Fig. 4A). The m1 is trapezoidal, while m2–m3 are rectangular and anteroposteriorly compressed (especially m2–m3); m4 is more rounded (Fig. 3C, D). Miocene Planopsinae and Nothrotheriidae retain a small caniniform tooth. The shape of the maxilla and of the dentary of the earliest ‘true megatheriine sloth’ *Megathericulus* confirm that it is the first clade of sloths in which the caniniform tooth has been secondarily modified into a molariform tooth (Fig. 4).

The observation of this new Peruvian specimen and a detailed revision of all members of the subfamily allow identification of three successive molariform morphologies throughout megatheriine evolution, especially in relation to the anteroposterior compression of the teeth:

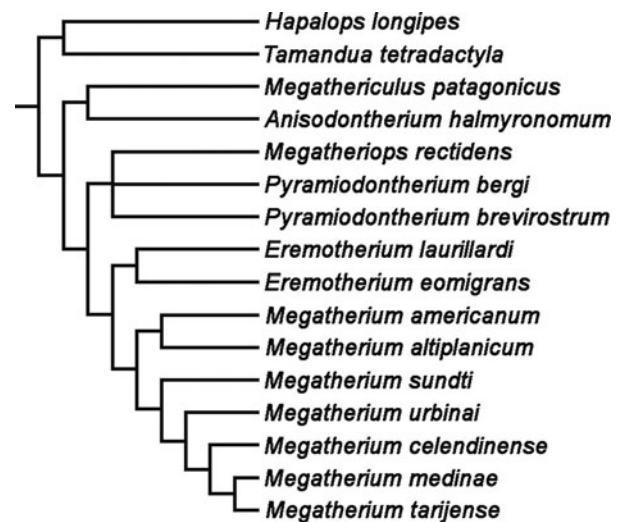
1. In the pre-Huayquerian species *Megathericulus patagonicus*, *Anisodontherium halmyronomum*, and



**Figure 5.** Photographs of mandibular remains of some Miocene Patagonian Megatheriinae: *Eomegatherium nanum* (MACN 4995, **A, B**), *E. andinum* (MLP 2-204, **C, D**), and *Megathericulus patagonicus* (MLP 91-IX-7-18, **E, F**) in occlusal (**A, C, E**) and lateral (**B, D, F**, the last reversed from the original) views (anterior towards right). Scale bar = 10 cm.



**Figure 6.** **A–C**, left m2 or m3 of a small-sized representative of Megatheriinae (GHUNLPAM 8010) from the Late Miocene of the Cerro Azul Formation (La Pampa Province, Argentina) in occlusal (mesial towards top), vestibular (mesial towards left), and mesial (dorsal towards top) views, respectively. **D–F**, isolated molariform tooth of cf. *Planops* (UCMP 39596) from the Laventan SALMA of La Venta (Colombia) (previously identified as a Megatheriinae by Hirschfeld 1985) in occlusal (distal towards top), labial or vestibular (distal towards left), and mesial (dorsal towards top) views, respectively. Scale bar = 1 cm.



**Figure 7.** Megatheriine phylogenetic relationships (adapted from Pujos 2006). Originally referred to as *Plesiomegatherium halmyronomum* (e.g. Pujos 2006), this species is now identified as *Anisodontherium halmyronomum* according to Brandoni & De Iuliis (2007).

*Eomegatherium andinum*, the molariforms are compressed anteroposteriorly and the lophes or lophids are perfectly perpendicular to the anteroposterior axis of the tooth row.

2. In the Huayquerian and Montehermosan *Pyramiodontherium bergi*, *P. brevirostrum*, *Megatheriops rectidens*, *Eomegatherium nanum*, *Urumaquia robusta*, and possibly *Pliomegatherium lelongi* (only badly preserved teeth available), the molariforms do not show any anteroposterior compression and lophes/lophids are not perpendicular to the

anteroposterior axis of the tooth row. Instead, they are extended mesiolingually to distovestibularly.

3. In post-Montehermosan genera, such as *Proeremotherium*, *Eremotherium*, and *Megatherium*, molariforms are not compressed anteroposteriorly and lophids or lophids are perfectly perpendicular to the anteroposterior axis of the tooth row.

Comparison between maxilla and mandible of *Megathericulus* suggests that, as in all members of the clade, the anteroposterior compression of the teeth is more marked in upper than in lower teeth (Figs 3, 4).

Bargo *et al.* (2009) recently described the existence of cusps and cuspids on molariform teeth in the Santacrucian megalonychid *Eucholoeops* Ameghino, 1887. The presence of cuspids is not clear in the oldest known megatheriine teeth from the Chasican (i.e. *Anisodontherium*; Brandoni & De Iuliis 2007). Hirschfeld (1985) thought that two teeth from Laventan levels of La Venta (Fig. 6D–F) belonged to a megatheriine. Even though postcranial elements from this locality (UCMP 41115) are characteristic of the subfamily, the teeth described by Hirschfeld (1985, fig. 33) do not correspond to the megatheriine pattern because they are oval in shape, strongly compressed anteroposteriorly, and they bear cusp(id)s (Fig. 6D–F). This morphology does not correspond to the oldest known Chasican megatheriine teeth of *Anisodontherium*, and the general shape is distinct from what can be deduced from the alveoli of ascertained Middle Miocene Megatheriinae (including MUSM 1564). An unpublished isolated tooth from the Huayquerian of Cerro Azul Fm. of La Pampa Province, Argentina (GHUNLPAM 8010; Cerdeño & Montalvo 2001) has dimensions (Table 1) and a general shape similar to the lower m2–m3 alveoli of *Megathericulus* sp. from SEP-007 (Fig. 6A–C). This isolated tooth confirms the differences between the plesiomorphic megatheriine model and the ‘planopsine pattern’ of the isolated teeth from La Venta (Fig. 6): GHUNLPAM 8010 bears two transversal lophids (Fig. 6A–C); the anterior lophid is convex mesially, while the distal lophid is convex posteriorly; lophids are separated by a deep transversal valley that opens lingually and vestibularly, and cuspids are not identifiable. The dental features of UCMP 39595 (Fig. 6D–F) could correspond to the Middle Miocene megatherioid of uncertain affinities *Planops* (e.g. *P. martini*; Hoffstetter 1961).

In lateral view, the dorsal margin of the horizontal ramus of MUSM 1564 is concave, as in *Anisodontherium* and *Eomegatherium andinum* (Fig. 3A, B, E, F), whereas it is rectilinear in *Megatheriops*, *Pyramiodontherium*, and *Pliomegatherium*. The lateral depression that borders the alveolus of m1 anteriorly in MUSM 1564 is interpreted as a primitive condition among Megatheriinae. It is absent in most derived forms while it occurs in Oligocene sloths, such as *Pseudoglyptodon* Engelmann, 1987, *Octodontotherium* Ameghino, 1895, and *Orophodon* Ameghino, 1895 and it

seems to be related to the presence of a caniniform tooth. It is not observable in *Anisodontherium* Brandoni & De Iuliis, 2007. Early Middle Miocene Megatheriinae may have retained this dorsolateral fossa, inherited from their hypothetical ancestor, in which the anteriormost tooth was caniniform. This condition is considered to be plesiomorphic in Tardigrada (Engelmann 1987; Pujos & De Iuliis 2007).

In MUSM 1564, the posterolateral border of the ‘spout’ is wide and convex, as in *Megatheriops* and *Anisodontherium* from the Late Miocene, and not rectilinear as in *Megatherium (Megatherium) altiplanicum* St-André & De Iuliis, 2001 and in MLP 91-IX-7–18, referred to *Megathericulus patagonicus* (Fig. 5E).

Hypsodonty is a good marker of dietary preferences in ungulates (Simpson 1951, 1953). Bargo *et al.* (2006) recently estimated the degree of hypsodonty in sloths by calculating the HI of six Pliocene–Pleistocene Megatheriinae: two *Eremotherium* species (*E. laurillardi* and *E. eomigrans*) and four *Megatherium* species (*M. (M.) americanum*, *M. (M.) altiplanicum*, *M. (P.) tarijense*, and *M. (P.) medinae*). We have extended the HI estimation to all megatheriine species from which well-preserved mandible remains are available (Table 2). It can be observed that the HI is quite variable at subfamily level. Megatheriinae have a relatively high HI in comparison with other tardigrades, with the exception of *Pliomegatherium* (0.72) and some Pleistocene species, such as *E. laurillardi* and *M. (P.) elenense* (0.72 and 0.75, respectively). MUSM 1564 (*Megathericulus* sp.) and *Megatheriops* exhibit similar HI (0.92 and 0.88, respectively), i.e. slightly higher than *Pyramiodontherium bergi* (0.81) and lower than *M. (M.) altiplanicum* and *Anisodontherium* (1.01 and 1.07, respectively). Pleistocene species referred to *Megatherium (Megatherium)* show more hypsodonty (HI average ranging between 1.01 and 1.02) than species of *M. (Pseudomegatherium)*, with an HI ranging between 0.75 and 0.90.

Bargo & Vizcaino (2008, p. 192) suggested that *M. (M.) americanum* “was probably the most selective feeder, with a prehensile lip very thick and strong, and more developed than in the narrow-muzzled mylodontids”. Like most megaherbivores and omnivores, *Megatherium* has a well-developed cranio-mandibular musculature. The strong mandibular muscle insertions present in MUSM 1564 (*Megathericulus* sp.) suggests that the earliest members of the clade had already a strong insertion for the masseter and temporal muscles (Fig. 3).

In MUSM 1564, the posterior external opening of the mandibular canal (peomc) is located anteriorly to the base of the ascending ramus; it opens anteriorly and is visible dorsally and laterally, as in *Megathericulus patagonicus* (Fig. 3A–D; see De Iuliis *et al.* 2008). In *Eomegatherium andinum*, it opens anterodorsally; it is laterally displaced and opens dorsally in *E. nanum* (see Brandoni & Scillato-Yané 2007). Indeed, an anterior opening of this peomc

appears to be a primitive trait; a dorsal opening, as it is observable in most recent forms (e.g. *Megatherium* and *Eremotherium*), represents the derived condition. However, in MUSM 1564, the peomc is at the same level as m4 (Fig. 3A–D), while it is more posterior in *Megathericulus patagonicus* (Fig. 5E–F).

An important character of the mandible is the anterior angle between ascending and horizontal rami (or the posterior inclination of the ascending ramus; Figs 3A, B, E, F, 5B, D). In MUSM 1564, *Anisodontherium halmyronomum*, and *Eremotherium eomigrans*, this angle is *c.* 100°; in *Megatheriops* and *M. (M.) altiplanicum*, it is more acute (80–90°) while the angle ranges from 120 to 130° in the Middle Miocene *Megathericulus patagonicus* and *Eomegatherium andinum*. These data suggest that in Megatheriinae, the plesiomorphic condition is an obtuse angle between the anterior border of the ascending ramus and the horizontal ramus (100–130°), and the derived state an acute to right angle (80–90°), maybe in relation to a crown height increase.

In MUSM 1564, the maximum height of the horizontal ramus is located at the level of m3 (Fig. 3A, B, E, F). In relation to the preservation of the specimens, it is impossible to estimate the location of the maximum height of the mandible in *Megathericulus patagonicus* (Fig. 5F), *Eomegatherium andinum* (Fig. 5D), and *E. nanum* (Fig. 5B). MUSM 1564 exhibits the most primitive condition known for the subfamily (see Pujos 2006); it may also be autapomorphic for the concerned taxon, but more information on primitive megatheriine mandibles is necessary to confirm this.

In dorsal view, the base of the symphysis is closely located to the anterior alveolus for m1 in *Megathericulus patagonicus* (Fig. 5E, F), *Eomegatherium andinum* (Fig. 5C, D), and *Anisodontherium halmyronomum* (MLP 30-XII-10–21, Brandoni & De Iuliis 2007, fig. 3B). In *Pyramiodontherium bergi* (MLP 2–66) and *Pliomegatherium lelongi* (MACN 13213), the symphysis is located at the same level as the posterior border of m1. It seems that Colloncuran to Chasicosan SALMA Megatheriinae exhibit the plesiomorphic condition (i.e. base of the symphysis anterior to m1; see Pujos 2006, character 7) and Huayquerian forms the derived condition (i.e. base of the symphysis and m1 at the same level).

Finally, the inclination of the ventral border in lateral view of the predental region (i.e. the ‘spout’) changes in megatheriine ground sloths. In MUSM 1564, the ‘spout’ is poorly inclined as in *Megathericulus patagonicus* (plesiomorphic, Fig. 5F); this inclination increases for most derived forms since Mayoan times.

According to the most recent revision of Argentinian Megatheriinae performed by Brandoni (2006a), *Eomegatherium* includes three species: *E. andinum*, *E. cabrerai*, and *E. nanum*. *Eomegatherium andinum* (Fig. 5C, D) and *E. cabrerai* are Mayoan, and *E. nanum* (Fig. 5A, B) is Huay-

querian in age (Fig. 8). Brandoni (2006a) considered that only the postcranial skeleton yields diagnostic features in the latter species, due to the bad preservation of cranial elements. This author also mentioned that it is difficult to justify that the species *nanum* and *andinum* are congeneric given the differences between their mandibular anatomies (Brandoni 2006a). Finally, the youngest species of the genus is *E. nanum* from the Huayquerian ‘conglomerado osífero’ or ‘Mesopotamiense’ of Entre Ríos Province, Argentina (Brandoni 2006a). *Eomegatherium nanum* is middle-sized and its teeth are not compressed anteroposteriorly, neither of which corresponds to the pattern of the two Mayoan species mentioned above nor to the generic definition as presented by Brandoni (2006a). Indeed, dentaries of *E. andinum* and *E. nanum* are radically different (Fig. 5A–D) and it is highly debatable whether they belong or not to the same genus as suggested by Brandoni (2006a).

Cranial remains of *E. cabrerai* are so fragmentary that it is impossible to use them for a detailed comparison, but the postcranial elements (i.e. proximal epiphysis of the ulna and astragalus) are comparable. The length of the olecranon of the ulna is similar in *M. patagonicus* and *E. cabrerai*. De Iuliis *et al.* (2008, p. 182) noted that the proximolateral facets of the ulna (for humeral and radial articulations) in *M. patagonicus* MLP 91-IX-7–18 face nearly laterally rather than anteriorly, a character considered diagnostic at genus level by these authors. A similar condition is observable in *E. cabrerai* MLP 2–206 and reinforces the affinity between the two species. Although the astragalus of *M. primaevus* is much smaller than that of *M. patagonicus*, they share a similar general morphology, with the astragalus of both bearing a sesamoid facet (the probable plesiomorphic condition in sloths) and a prominent odontoid process though smaller than in the Late Pliocene genus *Pyramiodontherium* (De Iuliis *et al.* 2008). The dentaries of *M. patagonicus* and *E. nanum* are clearly different but their astragali exhibit some similarities. However, in anterior view, they differ in the position of the navicular facet with respect to the main axis of the discoid facet, a character considered as diagnostic for the subfamily by De Iuliis (1996, character 11) and Pujos (2006, character 27). In *M. patagonicus* the navicular facet is well dorsal to the discoid facet (De Iuliis *et al.* 2008), but it is ventral in *E. nanum* and *E. cabrerai*. Finally, the astragalus of *E. cabrerai* differs slightly from that of *M. patagonicus* but also from that of *E. nanum*, especially in the morphology of the odontoid facet for the tibia, which is less convex than in other taxa. A major character not reported in the literature consists of the exposure of the articular facet for the cuboid in anterior view. In *E. nanum*, this facet is particularly visible, in contrast to the condition in *M. patagonicus*, *M. primaevus*, and *E. cabrerai*. Given these considerations, the inclusion of these three species within *Eomegatherium* as commonly accepted in the literature is extremely doubtful. Cranial and postcranial characters suggest that *E. nanum* is clearly different from

*E. andinum* and *E. cabrerai*. As the last two species exhibit greater resemblances with *Megathericulus patagonicus* and *M. primaevus* and as they are coeval (i.e. Late Miocene for *E. nanum* and Middle Miocene for the three other species), it seems more appropriate, pending the discovery of new specimens, to include the species *cabrerai* and *andinum* within *Megathericulus*.

Finally, *Anisodontherium halmyronomum* (Chasicuan; Brandoni & De Iuliis 2007) also shows some affinities with the Peruvian specimen studied here, but MUSM 1564 does not correspond to the former because *Anisodontherium* exhibits: (1) a larger size; (2) a higher HI; (3) a more important anteroposterior compression of molariform teeth; (4) an m4 without vestibular, but with lingual longitudinal groove; (5) an m1 triangular and not trapezoidal in shape; and (6) a lateral wall of the dentary rectilinear and not convex in occlusal view.

MUSM 1564 is represented by a single edentulous hemimandible, which presents affinities with *Eomegatherium* and *Megathericulus*. As a consequence, its taxonomic referral is difficult. In fact, MUSM 1564 appears to be closely related to both *Megathericulus patagonicus* (MLP 91-IX-7-18, Fig. 5E, F) and *Eomegatherium andinum* (MLP 2-204, Fig. 5C, D). The Peruvian specimen cannot be compared with other Middle Miocene megatheriines because *M. primaevus* is only represented by postcranial remains (Cabrera 1939) and skull fragments of *E. cabrerai* are badly preserved and not informative (Kraglievich 1930; Brandoni 2006a).

The anteroposterior compression of the teeth is slightly less pronounced in MUSM 1564 than in MLP 91-IX-7-18. This compression is clearly visible on the latter (Fig. 5C) but also on the holotype of *M. patagonicus* (maxilla MACN A-11151; Fig. 4A). The strong anteroposterior compression of the teeth in *Megathericulus* and in *Eomegatherium andinum* (it is absent in *E. nanum*; Fig. 5A), is still less developed than in some Nothrotheriidae, such as *Pronothrotherium typicum* Ameghino, 1907 (FMNH P14467) from the Huayquerian–Montehermosan SALMA of North-Western Argentina (De Iuliis *et al.* 2011). In *M. patagonicus*, the dorsolateral border of the horizontal ramus is flat in anterior view, and not convex as in MUSM 1564 and *Eomegatherium*. The posterior opening of the mandibular canal is anterior, as in *M. patagonicus* (De Iuliis *et al.* 2008); it is generally more dorsal in most derived forms. In lateral and dorsal views, however, this opening is more posterior in *M. patagonicus* than in MUSM 1564. The latter is also very close to what occurs in *Eomegatherium andinum* (MLP 2-204; Fig. 5C, D). Finally, in the present specimen, the posterior external opening of the mandibular canal is more anterior than in *M. patagonicus* (Fig. 3A–D).

The position and orientation of the posterior external opening of the mandibular canal, the location of the base of the symphysis in relation to m1, the inclination of the ventral border of the premental region, and the anteropos-

terior compression of the teeth all suggest that MUSM 1564 is closely related to *Megathericulus patagonicus*. However, it is not possible to make an identification at species level because *Megathericulus primaevus* is only represented by postcranial remains and thus can not be compared with the Peruvian specimen. For this reason, and pending new discoveries, we refer to MUSM 1564 as documenting *Megathericulus* sp. *M. primaevus* is considered to be a valid species, even though the synonymy between both species cannot be discarded. On the other hand, MUSM 1564 shares with *Eomegatherium andinum* a similar shape of the dorsal margin of the horizontal ramus and position of the base of the symphysis in relation to the m1.

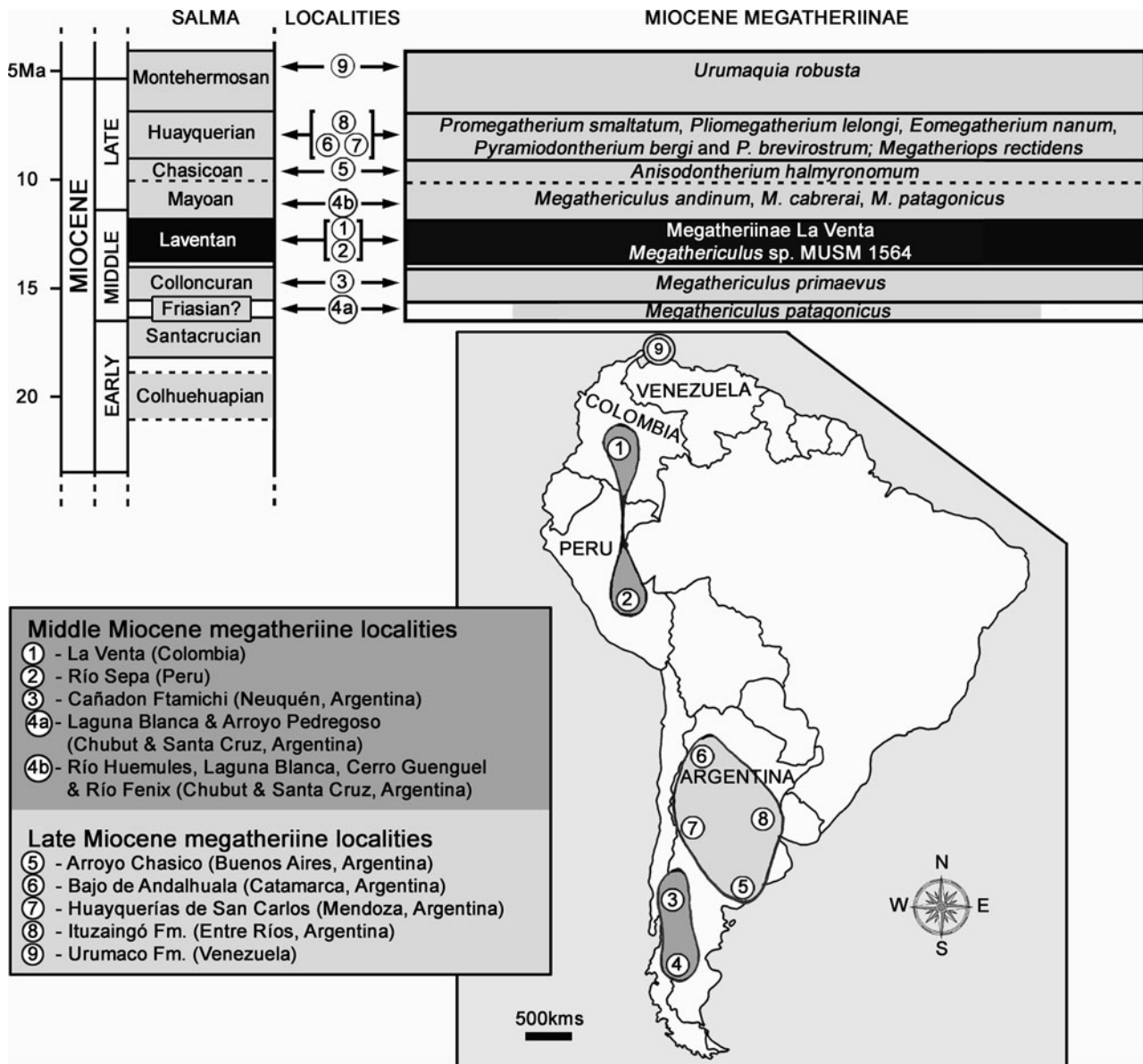
Mandibles of *E. andinum* and of *M. patagonicus* are not well preserved. They share a similar position of the base of the symphysis in relation to m1 and the anterior angle between ascending and horizontal rami, but they also present subtle differences.

During the last few decades, two important Late Pleistocene faunas have been discovered in Daytona Beach Bonehead (Florida, USA; Cartelle & De Iuliis 1995; De Iuliis 1996) and Toca das Onças (Jacobina, Bahia, Brazil; Cartelle & Bohórquez 1982; Cartelle 1992). They allowed Cartelle & De Iuliis (2006) to determine important intraspecific variation in the Pan-American ground sloth *Eremotherium laurillardii*. Their work definitively changed our understanding of intraspecific variation in Megatheriinae, but more widely in Megatherioidea. Considering the existence of (1) noticeable intraspecific variations in the megatheriine *Eremotherium laurillardii* (see Cartelle & De Iuliis 2006); (2) subtle differences between mandibles of *M. patagonicus* and *E. andinum* (see comments mentioned above); (3) significant differences between Mayoan and Huayquerian representatives of *Eomegatherium* (also see previous comments) especially on astragalus; and (4) affinities of MUSM 1564 with the latter genera, we suggest that *E. cabrerai* and *E. andinum* are referred to the genus *Megathericulus*. Consequently, we consider that a single megatheriine genus existed during the Middle Miocene (Colloncuran–Mayoan interval); this statement will have to be confirmed when new Miocene megatheriine remains are discovered and all members of the clade Megatheriinae are revised in detail; so far, *Megathericulus* includes the following species: *M. patagonicus*, *M. primaevus*, *M. cabrerai*, and *M. andinum*.

On the other hand, *Eomegatherium* is a valid monotypic genus represented by the Huayquerian *E. nanum*, which is clearly distinct from other Megatheriinae (see Brandoni 2006a for further details on diagnostic characters).

### Palaeobiogeographical origin of Megatheriinae

From the Middle Miocene period up to the Recent Lujanian SALMA, Megatheriinae have occupied all of South



**Figure 8.** Geographical and biostratigraphical position of Miocene megatheriine remains (South American Land Mammal Ages after Croft 2007) (top); main Middle Miocene megatheriine localities after Brandoni (2006a) including the controversial age of the Ituzaingó fauna (bottom).

America, from the Patagonian steppes to the Andes (De Iuliis 1996; Pujos 2008; Shockey *et al.* 2009) (Fig. 8). They also colonized North America after the emergence of the Isthmus of Panama (De Iuliis & Cartelle 1999). Two genera populated the Americas during the Pleistocene–Holocene period, the ‘temperate’ *Megatherium* in the southern half of South America, and the ‘tropical’ *Eremotherium* in the northern half of the continent and North America (De Iuliis 1996; Pujos 2008). Pre-Pleistocene forms are scarce and mainly restricted to Argentina, usually in relation to the extensive development of palaeontological research in South America.

According to De Iuliis (1996) and Carlini *et al.* (2006, table 1; 2008), only five pre-Pleistocene Megatheriinae represented by relatively abundant remains have been found outside Argentina:

- ‘Megatheriinae indet.’ from the Laventan of Colombia (Hirschfeld 1985);
- *Megatherium (Megatherium) altiplanicum* from the Montehermosan of Bolivia (St-André & De Iuliis 2001);
- the North American *Eremotherium eomigrans* from the late Blancan–early Irvingtonian of Florida (De Iuliis & Cartelle 1999);

- the Venezuelan species *Urumaquia robusta* and *Proeremotherium eljebe* from the Late Miocene of Urumaco Fm. and the Pliocene of Codore Fm., respectively (Carlini *et al.* 2006, 2008).

Of note, the Middle Miocene sloth from Quebrada Honda (Bolivia), which has been briefly presented by Carlini *et al.* (2002) as a ‘Megatheriine indet.’, belongs to another clade of Megatherioidea (Pujos *et al.* 2011) and it has therefore not been considered in the present work on Megatheriinae.

Before the discovery of the Peruvian specimen from Río Sepa, Middle Miocene giant megatheriine ground sloths were mainly located in the southern part of the continent and in the Colombian locality of La Venta. The oldest genus of Megatheriinae, *Megathericulus*, is present in the Argentinian Provinces of Neuquén (Cañadón Ftamichi), Chubut (Laguna Blanca, Arroyo Pedregoso and Río Huemules), and Santa Cruz (Estratos de Guenguel and Río Fénix). The discovery of *Megathericulus* in Laventan levels of Peruvian Amazonia considerably extends the geographical range of this primitive genus beyond the Argentinian border. All Middle Miocene Megatheriinae are located close to the Andes, in the westernmost part of the South American continent. Late Miocene Megatheriinae are more diverse, with at least six genera occupying the northern half of Argentina (*Anisodontherium*, *Pyramiodontherium*, *Megatheriops*, *Promegatherium*, *Pliomegatherium*, and *Eomegatherium*) in the provinces of Buenos Aires, Mendoza, Catamarca, and Entre Ríos; *Urumaquia* is located in northern Venezuela (Fig. 8).

Southern South America is usually considered the cradle of most Tardigrada clades, including Megatheriinae, but new discoveries of primitive Miocene megatheriine forms in Colombia (Hirschfeld 1985), Venezuela (Carlini *et al.* 2006), and now Peru, as well as in the Early Pliocene of Bolivia (St-André & De Iuliis 2001), require that alternative scenarios be considered.

The western part of the Peru–Chile desert (coastal Andes and western central depression) was arid throughout the Neogene period (Evenstar *et al.* 2005), while the Atacama Desert (one of the major hyperarid deserts of the world) originated at 14 Ma during global climate desiccation (Hartley & Chong 2002). Recent climate and topography of South America differ from those of the Middle Miocene: modelling results suggest a 1000–4000 m topographic Andean uplift between ~10.3 Ma (Mayoan SALMA) and 6.8 Ma (Montehermosan SALMA), i.e. when the Altiplano rose to its current elevation (Garzzone *et al.* 2006; Sepulchre *et al.* 2009). The effect of such local topographic changes on local environment was emphasized by concomitant global climate deterioration, with a noticeable shift from humid and warm conditions during the Middle Miocene Climatic Optimum (MMCO) to drier and colder conditions in the Late Miocene (Zachos *et al.* 2008; Hoorn *et al.* 2010b).

The first occurrence of Megatheriinae (Middle Miocene) coincided with the MMCO, during which warm conditions were notably recorded on the Pacific coast of South America (Tsuchi 2002) and in Western Amazonia (e.g. Antoine *et al.* 2006). Drastic environmental alteration during the Late Miocene then led to a significant change in faunal composition (e.g. Negri *et al.* 2010). The latter was particularly noticeable in America (Cerling *et al.* 1997).

Pujos (2008) proposed that Pleistocene–Holocene *Megatherium* species may have used the Andes as a ‘dispersal route’ to reach northern areas of the Pacific coast. Comparable circumstances could explain the palaeobiogeographical distribution of the oldest forms, as well as the presence of *Megathericulus* in both Patagonia and Peru during the same period. Accordingly, emergence and dispersal of the clade in western South America could have been enhanced by the existence of arid regions on the Pacific coast and lower elevation of the Andes by that time. An alternate route would consist in the eastern Andean piedmont (also termed the Sub-Andean Zone) and the ‘western Amazonian corridor’, as hypothesized by Antoine *et al.* (2007) and Croft (2007) for Middle Miocene native ungulates and caviomorph rodents.

The recent and unexpected discovery of diverse Miocene mammal faunas, including megatheriine sloths, in northernmost South America (Carlini *et al.* 2006) and in western Amazonia (Antoine *et al.* 2007; Goillot *et al.* 2011), suggests that the early evolutionary history of Megatheriinae is still far from being well constrained, and that efforts should be made to address this issue during the next few years.

## Conclusions

1. *Megathericulus* is a small-sized representative of Megatheriinae; its mandible is mainly characterized by a lateral depression which borders m1 and a posterior external opening of the mandibular canal anterior to the base of the ascending ramus which opens anteriorly or anterodorsally; the ascending ramus of the mandible is posteriorly inclined; in dorsal view the base of the symphysis is located anteriorly to the m1; the m4 is anterior to the ascending ramus; the ventral border of the predental region is poorly inclined; and important anteroposterior compression of the teeth is present.
2. *Megathericulus* is considered to be the only Middle Miocene megatheriine genus; it includes specimen MUSM 1564 and four species: *M. patagonicus* (oldest member of the clade) from the Friasian of Chubut and Santa Cruz Provinces, Argentina; *M. primaevus* from the Colloncuran of Neuquén Province, Argentina; and *M. cabrerai* and *M. andinum* from the Mayoan of Chubut and Santa Cruz Provinces, Argentina.



3. *Eomegatherium* is restricted to the type and only species, *E. nanum*, from the Huayquerian of Entre Ríos Province, Argentina.
4. The megatheriine dentary MUSM 1564 from Río Sepa, Peruvian Amazonia, discovered in the Ipururo Fm. of the Fitzcarrald Arch (Laventan [13.5–11.8 Ma]), is identified as *Megathericulus* sp.; this specimen shows affinities with *M. patagonicus* and, supposedly, with *M. andinum*.
5. The revision of the earliest megatheriine genera, especially the Middle to Late Miocene *Megathericulus* species and *Anisodontherium halmyronomum*, suggests the following plesiomorphic mandibular condition for this clade: small- to medium-sized; in lateral view, dorsal margin of the horizontal ramus concave; presence of a lateral depression that borders m1 anteriorly; posterior lateral opening of the mandibular canal anterior to the base of the ascending ramus and opens anteriorly; ascending ramus of the mandible posteriorly inclined (anterior angle of *c.* 100/130° between the horizontal ramus and the anterior border of the ascending ramus); in dorsal view, base of the symphysis located anteriorly to the m1; in lateral view, ventral border of the anterior region of the mandible (i.e. the ‘spout’) poorly inclined; 5/4 molariform teeth compressed anteroposteriorly, consisting of two transversal lophes (or lophids), and anteroposterior compression more pronounced on upper than on lower molariform teeth.
6. Megatheriinae is the first clade of Tardigrada in which the caniniform tooth were secondarily modified into a molariform tooth; all later members of Tardigrada show a similar pattern.
7. Three successive molariform patterns can be observed in megatheriine evolution:
  - presence of an anteroposterior compression of the teeth and lophes or lophids perfectly perpendicular to the anteroposterior axis of the tooth row (pre-Huayquerian times);
  - absence of an anteroposterior compression of the teeth, and lophes or lophids not perpendicular to the anteroposterior axis of the tooth row but extended mesiolingually to distovestibularly (Huayquerian and Montehermosan times);
  - absence of anteroposterior compression of the teeth, and lophes or lophids perfectly perpendicular to the anteroposterior axis of the tooth row (post-Montehermosan times).
8. Isolated molariform teeth from La Venta (Laventan of Colombia) previously referred to a representative of Megatheriinae by Hirschfeld (1985) are related to the clade Planopsinae; however, the presence of Megatheriinae in La Venta remains unquestionable as it has been confirmed by postcranial specimens.

9. The primitive megatheriine genus *Megathericulus* is now recorded in the Middle Miocene of both Argentina (provinces of Buenos Aires, Catamarca, Mendoza and Entre Ríos) and Peruvian Amazonia.

## Acknowledgements

We thank the following colleagues for facilitating access to fossil collections under their care: B. Simpson (FMNH), A. Kramarz (MACN), M. Reguero and S. Bargo (MLP), C. Argot, C. de Muizon, and P. Tassy (MNHN), and N. Valencia (MUSM). Special thanks to D. Brandoni (CICYTTP-CONICET) for information on Middle Miocene Megatheriinae from Argentina, C. I. Montalvo (UNLPAM) who allowed us to mention and present the GHUNLPAM 8010 specimen from La Pampa, and G. De Iuliis (ROM) for pictures of La Venta specimens. M. Superina (IMBECU, CCT-CONICET-Mendoza) improved linguistic aspects of the text. We thank C. de Muizon and an anonymous reviewer for their interesting comments and suggestions which helped improve the manuscript. This research project was possible thanks to the IRD-Perupetro S.A. research agreement, and supported by IRD (UR 154), French INSU-CNRS programmes DyETI (*Dynamique et Evolution de la Terre Interne*) and ECLIPSE II (*Evolution néogène du Bassin amazonien occidental et biodiversité: relations avec la géodynamique andine*), and post doctoral fellowships of the IFEA (2003–2006) and CONICET (2008–2010) for one of us (F.P.).

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