

On *Megatherium gallardoi* (Mammalia, Xenarthra, Megatheriidae) and the Megatheriinae from the Ensenadan (lower to middle Pleistocene) of the Pampean region, Argentina

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ABSTRACT

The Megatheriinae (Mammalia, Xenarthra, Megatheriidae) are recorded in Argentina from the middle Miocene to the early Holocene. Only the genus *Megatherium*, comprising several species of controversial validity, is recognized for the Pleistocene of the Pampean region. *Megatherium americanum* is the best studied species and occurs frequently in sediments assigned to the Lujanian stage (*Equus (Amerhippus) neogeus* Biozone, c. 0.13-0.08 My). On the other hand, *M. gallardoi* and *M. silenum*, both from Ensenadan sediments (*Mesotherium cristatum* Biozone) of Buenos Aires Province, have been considered by some authors as synonyms of *M. americanum*. The main goal of this contribution is to complete the description of *M. gallardoi*, clarify its taxonomic status, and establish its relationships with other megatheriines. The most remarkable features of *M. gallardoi* are: premaxillae not fused to each other or to the maxillae; mandibular ramus relatively low; femur with lateral and medial diaphyseal margins markedly concave, diaphysis expanded transversely; medial reduction

KEY WORDS

Mammalia,
Megatheriidae,
Megatherium gallardoii,
Megatherium silenum,
Bonaerian,
Ensenadan,
Buenos Aires Province,
Argentina.

of the patellar trochlea; humerus and femur robust. Based on the anatomical and comparative analysis, we propose that: 1) *M. gallardoii* is a valid species; 2) specimen MACN Pv 5002 (holotype of *M. gallardoii*) is an adult individual; 3) *M. gallardoii* is related to the clade formed by *M. americanum* and *M. altiplanicum*; and 4) *M. silenum* (the other Megatheriinae known for the Ensenadan Stage of Argentina) should be considered *nomen vanum* because it lacks diagnostic features and corresponds undoubtedly to a juvenile individual.

RÉSUMÉ

Sur Megatherium gallardoii (Mammalia, Xenarthra, Megatheriidae) et les Megatheriinae de l'Ensenadéen (Pléistocène inférieur à moyen) de la région pampéenne, Argentine.

Les Megatheriinae (Mammalia, Xenarthra, Megatheriidae) sont enregistrés en Argentine depuis le Miocène moyen jusqu'à l'Holocène basal. Dans le Pléistocène de la région de la Pampa, on reconnaît uniquement *Megatherium*, lequel présente plusieurs espèces dont la validité reste controversée. *Megatherium americanum* est l'espèce la plus souvent étudiée et se retrouve fréquemment dans des sédiments assignés à l'étage Lujanien (biozone d'*Equus (Amerhippus) neogeus*, c. 0,13-0,08 Ma). D'autre part, *M. gallardoii* et *M. silenum* provenant des sédiments ensenadéens (biozone de *Mesotherium cristatum*) de la province de Buenos Aires, ont été considérés comme synonymes de *M. americanum* par quelques auteurs. Le principal objectif de cette contribution est de compléter la description de *M. gallardoii*, de clarifier son statut taxonomique et d'établir son lien avec d'autres Megatheriinae. Les caractéristiques les plus remarquables de *M. gallardoii* sont : premaxillaires non fusionnées entre eux, ni avec les maxillaires; branche horizontale de la mandibule relativement basse; bords latéraux de la diaphyse du fémur concaves; diaphyses élargies transversalement; réduction médiale de la trochlea de la rotule; humérus et fémur robustes. L'analyse comparative de l'anatomie permet de proposer que: 1) *M. gallardoii* est une espèce valide; 2) le spécimen MACN Pv 5002 (holotype de *M. gallardoii*) correspond à un individu adulte; 3) *M. gallardoii* présente des relation de parenté avec le clade formé par *M. americanum* et *M. altiplanicum*; et 4) *M. silenum* (l'autre Megatheriinae de l'étage ensenadéen argentin) doit être considéré *nomen vanum* car il manque de caractères diagnostiques et correspond sans doute à un individu juvénile.

MOTS CLÉS

Mammalia,
Megatheriidae,
Megatherium gallardoii,
Megatherium silenum,
Bonaéréen,
Ensenadéen,
province de Buenos Aires,
Argentine.

INTRODUCTION

Xenarthrans are currently distributed almost exclusively in the Neotropical region. These mammals are characterized by a particular skeletal architecture that sets them apart from all other placental mammals; furthermore, molecular evidence has indicated that they represent one of the four major mammalian clades (Delsuc *et al.*

2001, 2002; Madsen *et al.* 2001; Murphy *et al.* 2001). They comprise two clades: 1) Cingulata, with a bony dermal armor or shield; and 2) Pilosa (Vermilingua and "Tardigrada"); the Vermilingua or anteaters show marked myrmecophagous adaptations; the "Tardigrada" or sloths, both terrestrial and arboreal, some extinct forms of which showed their tegument reinforced by subcutaneous osteoderms.

The “Tardigrada” (*sensu* Latham & Davies 1795) or “Phyllophaga” or Folivora (see discussion on the use of these term in Delsuc *et al.* 2001; Fariña & Vizcaíno 2003), with a diversity comprising over 80 genera (McKenna & Bell 1997), constitute one of the characteristic mammalian groups for the Cenozoic of South America, but they also occurred in both Central America and North America. The earliest record of the clade corresponds to two isolated elements, one ungual phalanx and a fragmentary caniniform tooth, from the middle Eocene of Antarctica (Vizcaíno & Scillato-Yané 1995); on the other hand, Simpson (1948) had earlier reported the presence of a probable sloth from the middle Eocene of Patagonia. Sloths become abundant in the fossil record since the Deseadan (late Oligocene), represented by several lineages of Megatherioidea and Mylodontoidea that become especially diversified during the Miocene-Pliocene. The Megatherioidea comprise three families: Megatheriidae Gray, 1821, Megalonychidae P. Gervais, 1855 and Nothrotheriidae F. Ameghino, 1920.

Within the Megatheriidae, the Megatheriinae (giant ground sloths) have been intensively studied since the second half of the 19th century, although the first report of this subfamily dates back to the late 18th century, when the species *Megatherium americanum* Cuvier, 1796, was erected on the basis of a specimen found in 1785. The oldest recorded taxon in the group is *Megathericulus patagonicus* F. Ameghino, 1904 from the Colloncuran (middle Miocene) of Patagonia, and the most recent one is *M. americanum* from the Lujanian (*c.* 7500 RCYBP, early Holocene, Politis *et al.* 2004; Politis & Messineo 2008) of the Pampean region (Argentina). The genus *Megatherium* Cuvier, 1796 comprises numerous described species; however, the validity of some of them has been and is still being debated. In this sense, several authors have considered that *M. americanum* is the only valid Megatheriinae species for the Pleistocene of the Pampean region (De Iuliis 1996; Pujos & Salas 2004; Pujos 2006). However, other authors have indicated that this genus was more diverse in the abovementioned region (Carlini & Scillato-Yané 1999; Cione *et al.* 1999; Carlini *et al.* 2006),

and have included *M. gallardoi* C. Ameghino & Kraglievich, 1921, *M. silenum* (F. Ameghino, 1898), and *M. tarijense* H. Gervais & F. Ameghino, 1880 in the Ensenadan Stage of the Pampean region (see Carlini & Scillato-Yané 1999; Cione *et al.* 1999; Cione & Tonni 2005).

Several other species of *Megatherium* are recognized outside Argentina, including *M. altiplanicum* Saint-André & De Iuliis, 2001 (Pliocene of the Bolivian Altiplano); *M. tarijense* and *M. sundti* Philippi, 1893 (Pleistocene of Bolivia); *M. urbinai* Pujos & Salas, 2004 and *M. celendinense* Pujos, 2006 (Pleistocene of Peru); *M. medinae* Philippi, 1893 (Pleistocene of Chile) and *M. elenense* (Hoffstetter, 1949) (Santa Elena Peninsula, Ecuador).

Concerning *M. gallardoi*, Ameghino & Kraglievich (1921) described the skull of the holotype specimen (MACN Pv 5002) and stated that “en una memoria posterior nos ocuparemos del fémur, húmero y cúbito que [...] deberán considerarse como piezas típicas del *M. gallardoi*” [“In a later memoir we will concern ourselves with the femur, humerus and ulna which [...] should be considered as part of the type of *M. gallardoi*”] (1921: 136, 137); however, this promised second part was never published. De Iuliis (1996) considered *M. gallardoi* as a synonym of *M. americanum*; however, this taxon was treated as a separate, valid species in the comparisons made by Saint-André & De Iuliis (2001) for *M. altiplanicum*, and in those made by Carlini *et al.* (2006) for *Urumaquia robusta* Carlini, Brandoni & Sánchez, 2006 and *Proeremotherium eljebe* Carlini, Brandoni & Sánchez, 2006. Bargo *et al.* (2006a, b) included MACN Pv 5002 in *M. americanum*, without any clarification regarding the taxonomic status of *M. gallardoi*.

MACN Pv 5002 represents the most complete and best preserved specimen of Megatheriinae from the Ensenadan of Argentina. It is noteworthy that less than 10 remains assignable to Megatheriinae from this stage have been found in the paleontological collections examined, most of these being fragmentary. Hence the great interest in completing the description of *M. gallardoi*, which represents the main goal of this work. Additionally, a systematic review of tardigrades is fundamental, as an overestimation of diversity

TABLE 1. — Measurements of *Megatherium gallardoi* C. Ameghino & Kraglievich, 1921 (MACN Pv 5002). All measurements are in mm, except Hypsodonty Index.

Skull	total length	830
	occipital width	310
	nasal width	180
	tooth row length	229
Mandible	total length	654
	tooth row length	223
	horizontal mandibular ramus height	196
	Hypsodonty Index (HI)	87
	premolariform length	256
	m2 width	60
	m2 length	47
Humerus	m3 width	52
	m3 length	45
	total length	795
	distal width	365
Ulna	diaphysis width	137
	distal facet width	212
	total length	694
	proximal width	288
Femur	distal width	100
	total medial length	716
	total lateral length	764
	proximal width	455
	medial width	315
	distal width	458

has already been recognized for this group (see De Iuliis 1996; Pujos & Salas 2004; Brandoni 2005, 2006; Brandoni & Scillato-Yané 2007), as for other xenarthran lineages (see Duarte 1997; Soibelzon *et al.* 2006).

THE ENSENADAN STAGE

Ameghino (1881) divided the Pampean sediments into three layers: “pampeano inferior”, “pampeano superior” and “pampeano lacustre”. Later, Ameghino (1889) gave the name of “ensenadense” to those sediments that correspond to the “pampeano inferior”, and distinguished two components, “ensenadense basal” and “ensenadense cuspidal” (Ameghino 1910). Biostratigraphically, the Ensenadan Stage (lower to middle Pleistocene) is based on the *Mesotherium cristatum* Biozone (Cione & Tonni 2005; Soibelzon *et al.* 2008).

The fossils that occur in the subsoil of Buenos Aires city have long been studied (e.g., Ameghino 1881; Ameghino & Kraglievich 1921; Rusconi 1929, 1931, 1936, 1937; Scillato-Yané 1982;

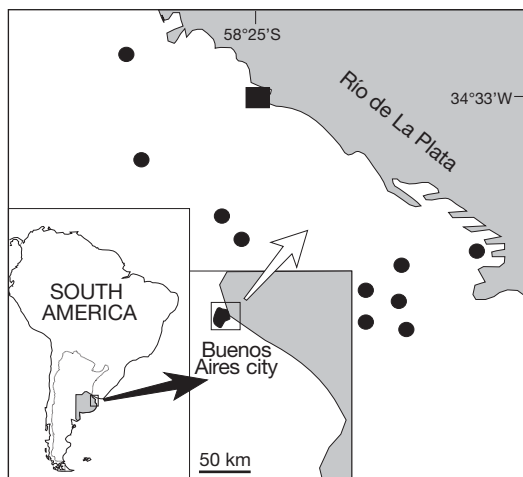


FIG. 1. — Location map: ■, provenance of fossil remains of *Megatherium gallardoi* C. Ameghino & Kraglievich, 1921 (MACN Pv 5002); ●, excavations performed in Buenos Aires city.

Soibelzon 2004; Zurita *et al.* 2005; Zurita 2007). A countless number have been collected from excavations performed in the city itself (more details in Soibelzon *et al.* 2008). MACN Pv 5002 was collected at a site that is currently part of the “Planta Potabilizadora Gral. San Martín”, Buenos Aires city, Argentina (Fig. 1). Ameghino & Kraglievich (1921) stated that the remains of *Mesotherium cristatum* Serres, 1867 were exhumed from the same provenance level of MACN Pv 5002, which removes any doubt about its assignment to the Ensenadan Stage.

ABBREVIATIONS

FMNH Field Museum of Natural History, Chicago;
 MACN Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires;
 MLP Museo de la Plata, La Plata;
 RCYBP Radio carbon years before present.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Order XENARTHRA Cope, 1889
 Family MEGATHERIIDAE Gray, 1821
 Subfamily MEGATHERIINAE Gray, 1821
 Genus *Megatherium* Cuvier, 1796

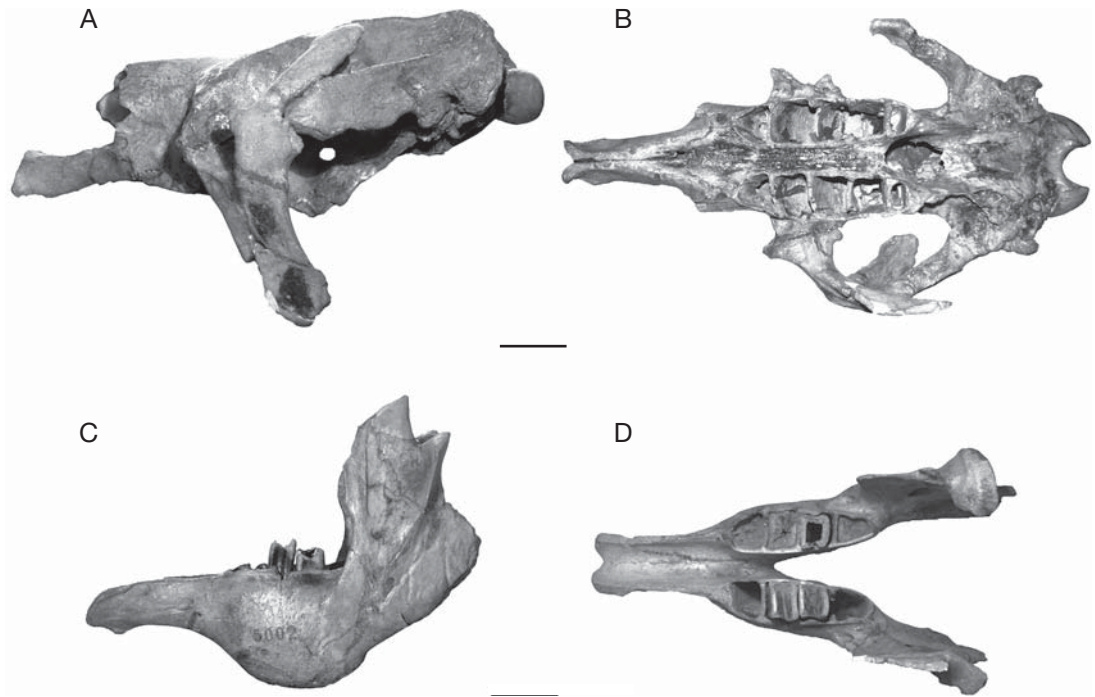


FIG. 2. — *Megatherium gallardoi* C. Ameghino & Kraglievich, 1921 (MACN Pv 5002): **A**, skull, specular lateral view; **B**, same, palatal view; **C**, mandible, lateral view; **D**, same, dorsal view. Scale bar: 100 mm.

Megatherium gallardoi

C. Ameghino & Kraglievich, 1921

HOLOTYPE. — MACN Pv 5002, partial skull (left zygomatic arch and molariforms missing), complete mandible lacking molariforms 1 and 4, right humerus, left ulna and left femur (Figs 2; 3; Tables 1; 2).

TYPE LOCALITY. — Excavations for water filters made as part of the building work of the public water supply system (34°33'23.53"S, 58°25'46.66"W, Buenos Aires, Argentina, Ameghino & Kraglievich 1921) (Fig. 1).

TYPE LEVEL. — Ensenadan Stage (lower to middle Pleistocene).

DESCRIPTION

Skull (Fig. 2; Table 1)

As mentioned above, the skull and mandible of *Megatherium gallardoi* have been thoroughly described by Ameghino & Kraglievich (1921). Among the features of the specimen MACN Pv 5002, Ameghino & Kraglievich (1921) mentioned that

the skull roof profile does not show an abrupt transition between the frontal and nasal regions (Fig. 2A), as observed in several specimens of *M. americanum*; that the temporal fossa is located entirely below the lambda-nasal plane, whereas in most specimens of *M. americanum* the dorsal portion of the temporal fossa is located above this plane; and, that the postorbital processes of the frontal bone are reduced (Fig. 2A; Ameghino & Kraglievich 1921: fig. 2).

In addition to the characters described by Ameghino & Kraglievich (1921), the premaxillae in *Megatherium gallardoi* are weakly united to the maxillae (Fig. 2B), without strong fusion between these bones that occurs in most specimens of *M. americanum* and *M. altiplanicum*. In *M. celandinense* (see Pujos 2006: fig. 3.6), *M. tarijense* and *M. sundti* the condition is similar to that of *M. gallardoi*. The premaxillae of *M. gallardoi* are not fused to each other as in the abovementioned species (Fig. 2B).

TABLE 2. — Measurements of *Megatherium gallardoi* C. Ameghino & Kraglievich, 1921 (MACN Pv 5002) and specimens referred to *M. americanum* Cuvier, 1796. All measurements are in mm, except Humerus Robustness Index (HRI). Abbreviation: p, preserved.

	<i>M. gallardoi</i>		<i>M. americanum</i>			
Humerus		MACN 7128	MACN 14686	MLP 2-34	MLP 2-106	MLP 2-28
total length	795	800	690	705	565	750
distal width	365	375	340	325	255	350
HRI	46	46.8	49.2	46	45	46.6
Ulna		MACN 6410	MACN 10629	MLP 2-110	MLP 2-115	MLP 2-28
total length	694	640	680	565	592	690
proximal width	288	230	255	195p	220	295
Femur		MACN 10110	MACN 12826	MACN 5055	MLP 45-X-27-9	MLP 2-29
total length	716	690	715	780	595	750
proximal width	455	400	420	415	330	465
medial width	315	275	300	310	232	315
distal width	458	380	405	390p	320	480

Mandible (Fig. 2C, D; Table 1)

The mandibles of *Megatherium gallardoi* and *M. americanum* appear similar in size and general morphology. However, they differ in the shape of the ventral bulge and in the ventral margins of the mandibular body, both anteriorly and posteriorly to the ventral bulge, as well as in the angle of inclination of the spout.

In this clade, the degree of hypsodonty may be evaluated through comparisons of molariform crown height, or by the height of the horizontal mandibular ramus relative to tooth row length (maximum height of mandibular ramus/tooth row length \times 100, see De Iuliis 1996; Bargo *et al.* 2006a; among others). According to this method, the values of Hypsodonty Index (HI) (Zetti 1964; De Iuliis 1996; Saint-André & De Iuliis 2001; Bargo 2001; Bargo *et al.* 2006a) obtained for MACN Pv 5002 are similar to those observed in several species of tertiary megatheriines (e.g., *Pyramiodontherium* Rovereto, 1914, *Megatheriops* C. Ameghino & Kraglievich, 1921, see Brandoni 2006). The value of HI is 87 in MACN Pv 5002, 101 in *Megatherium altiplanicum* (see Bargo *et al.* 2006a), 92-112 in *M. americanum* (see Saint-André & De Iuliis 2001), and 107 in *Anisodontherium halmyronomum* (Cabrera, 1928) (see Brandoni & De Iuliis 2007). However, as discussed by De Iuliis *et al.* (2004) and Brandoni & De Iuliis (2007), the HI value of *A. halmyronomum* is not directly comparable with others due to the

particular shape of the molariforms in this species (i.e. molariforms mesiodistally compressed and thus rectangular rather than square in cross section). The molariforms of MACN Pv 5002 are nearly rectangular in section (Fig. 2D; Table 1), though not as rectangular as in *A. halmyronomum* or *Megathericulus patagonicus*.

Humerus (Fig. 3A)

The humerus of *Megatherium gallardoi* is mostly similar to that of other megatheriines, as well as those of Megalonychidae and Preprotheriinae, in that it is relatively elongated and gracile. An entepicondylar foramen is absent as in other megatheriines. According to the general condition of sloths, the posterior surface is flattened and bears a shallow olecranon fossa, and the distal third of the diaphysis is markedly expanded mediolaterally and compressed anteroposteriorly. The humerus of MACN Pv 5002 (795 mm long) is longer than that of most specimens of *M. americanum* (Table 2; De Iuliis 1996: appendix 4C), and similar in length to several humeri of *Eremotherium laurillardii* (Lund, 1842) (730-878 mm; De Iuliis 1996: appendix 4C); whereas the humerus of *M. celendinense* (see Pujos 2006: fig. 4.F, G) is relatively shorter and more massive.

As in other Pleistocene megatheriines (*Megatherium americanum*, *M. sundti*, *Eremotherium laurillardii*), in MACN Pv 5002, the deltopectoral



FIG. 3. — **A-D**, *Megatherium gallardoi* C. Ameghino & Kraglievich, 1921 (MACN Pv 5002); **E**, *M. silenum* (Ameghino, 1898) (MLP 2-61); **A**, right humerus, anterior view; **B**, left ulna, dorsal view; **C**, left femur, anterior view; **D**, same, distal view; **E**, mandible, lateral view. Scale bar: 100 mm.

crest is reduced to an elongated triangular ridge; this structure is even more reduced in *M. celendinense* and *M. tarijense* (see Pujos 2006). Among pre-Pleistocene Megatheriinae such as *Pyramiodontherium scillatoyanei* De Iuliis, Ré & Vizcaino, 2004 (see De Iuliis *et al.* 2004: fig. 5.A, B), *Megathericulus patagonicus* and *Megatheriops rectidens* (Rovereto, 1914) (see De Iuliis 2003: figs 3 and 4.A respectively), the deltopectoral crest is strongly raised distally and deflected laterally (see De Iuliis 2003 for a discussion of the muscular and functional

implications related to size and form of the deltopectoral crest in megatheriines). The presence of a well-developed deltopectoral crest is considered to be plesiomorphic (De Iuliis 1996; Brandoni 2006; Pujos 2006).

As in other *Megatherium* species and in *E. laurillardii*, the humerus of *M. gallardoi* is markedly robust; whereas it is relatively slender in the majority of the pre-Pleistocene species (except *Eremotherium eomigrans* De Iuliis & Cartelle, 1999). An index to evaluate humeral robustness, the Humerus

Robustness Index (HRI), is calculated as: humeral distal transversal width/humeral total length \times 100 (Brandoni 2006). In those megatheriines with a robust humerus (*M. americanum*, *E. laurillardii*), HRI values are over 40; whereas in others with a slender humerus (e.g., *Pyramiodontherium*, *Megatheriops*) HRI is under 40. The value of HRI is 46 for MACN Pv 5002, 42 for *M. tarijense*, 45-50 for *M. americanum*, and 42-46.5 for *E. laurillardii* (see Brandoni 2006: table 3).

Ulna (Fig. 3B)

The ulna of MACN Pv 5002 (694 mm long) is longer than that of other *Megatherium* species (Table 2) except MACN Pv 10148, in which the ulna is almost the same length (see De Iuliis 1996). However, the general morphology of this bone resembles that of *M. americanum*. As in the latter, the diaphysis is mediolaterally compressed and tapered distally. In *Urumaquia robusta* and FMNH P14511, the ulna is very gracile and proportionally much longer than in any other Megatheriinae (e.g., *Megatheriops*, *Megatherium* and *Eremotherium* Spillmann, 1948) (see Carlini *et al.* 2008).

Femur (Fig. 3C, D)

The femur of MACN Pv 5002 is morphologically similar to that of *M. americanum*, but larger than many specimens of the latter species (Table 2; De Iuliis 1996: appendix 4F). It is 764 mm in total lateral length and 315 mm in minimum transverse diameter at the middle of the diaphysis, and is expanded transversally at both its proximal and distal portions (455 and 458 mm respectively).

The femoral head and neck are prominent, as in *E. laurillardii* and *M. americanum* (see De Iuliis & Saint-André 1997: figs 4.1 and 4.2 respectively); whereas in *M. altiplanicum* (Saint-André & De Iuliis 2001: fig. 7.A) the neck is more constricted, but not as much as in *E. sefvei* (De Iuliis & Saint-André 1997: fig. 5.1, 2). As in *Eremotherium* and other species of *Megatherium*, the greater trochanter is markedly deflected backward from the plane that passes through the distal condyles and head, so that the femur shows vertical torsion. In MACN Pv 5002, vertical torsion of the diaphysis is approximately 30°; whereas it ranges between 31 and

57° in *M. americanum* and between 10 and 41° in *Eremotherium laurillardii* (De Iuliis 1996; De Iuliis *et al.* 2004). Its lateral margin is sigmoidal in lateral view, a feature also present in *M. americanum* (De Iuliis & Saint-André 1997: fig 6.3) and *M. altiplanicum* (Saint-André & De Iuliis 2001: fig. 7.B).

The lateral and medial femoral margins are notably concave (Fig. 3C). This feature occurs in *M. americanum* (De Iuliis & Saint-André 1997: fig. 4.2), *M. altiplanicum* (Saint-André & De Iuliis 2001: fig. 7.A), *M. sundti* (De Iuliis 2006: fig. 2.C) and in the species of *Pyramiodontherium* (see Carlini *et al.* 2002; De Iuliis *et al.* 2004; Brandoni 2006); whereas in *M. medinae* (Casamiquela & Sepulveda 1974: pl. VI), *M. urbinai* (Pujos & Salas 2004: fig. 2.I, J), *Eremotherium laurillardii* (De Iuliis & Saint-André 1997: fig. 4.1) and *E. sefvei* (De Iuliis & Saint-André 1997: fig. 5.1, 2), the proximal and distal portions of the femur are less expanded transversally and the margins are nearly rectilinear and parallel.

As in most megatheriines, the patellar trochlea of *M. gallardoii* is separated from the internal condyle and continuous with the external condyle, forming a single articular surface (Fig. 3D). Whereas the patellar trochlea contacts both condyles in *Megathericulus patagonicus* F. Ameghino, 1904 (MLP 92-XI-15-2, see De Iuliis *et al.* 2008) and *Megathericulus primaevus* Cabrera, 1939 (MLP 39-VI-24-1). As in *Megatherium americanum* and *M. altiplanicum* (Saint-André & De Iuliis 2001: fig. 7.C), the patellar trochlea of the femur is extremely reduced as an anteromedial extension of the lateral condyle (Fig. 3D). Whereas in *Megatherium sundti*, *M. tarijense*, *M. medinae*, and *M. urbinai* the patellar trochlea is well developed; and is also well developed in *E. laurillardii* and *E. sefvei* (De Iuliis & Saint-André 1997: figs 1a and 2 respectively).

DISCUSSION

Ameghino & Kraglievich (1921) erected the species *Megatherium gallardoii* based on certain cranial characters that differ from those present in *M. americanum*. Additionally, they stated that “el avanzado grado de obliteración de las suturas demuestra que este cráneo debió pertenecer a un individuo adulto”

["the advanced degree of suture obliteration shows that this skull belonged to an adult individual"] (1921: 137). On the other hand, De Iuliis (1996) considered *M. gallardoi* as a synonym of *M. americanum*, judging the specimen to be a subadult individual, and that the differences mentioned by Ameghino & Kraglievich (1921) represented intraspecific variations of *M. americanum*. De Iuliis (1996) stated that his assessment of the specimen as an immature individual was supported by the presence of cranial sutures.

Cartelle & De Iuliis (2006) indicated that some cranial features permit a differentiation between immature and adult individuals of genus *Eremotherium*. MACN Pv 5002 does indeed have some persistent cranial sutures. However, the median and transverse palatal sutures are closed in MACN Pv 5002 (Fig. 2B) as in aged specimens of *Eremotherium*. Although in MACN Pv 5002 the two portions that form the zygomatic arch (the temporal process of the jugal and the zygomatic process of the temporal) are not fused (Fig. 2B), this is not uncommon in some aged individuals of *Eremotherium* (see Cartelle & De Iuliis 2006). The most manifest cranial sutures of MACN Pv 5002, namely the premaxillae-maxillae and the interpremaxillae sutures (Fig. 2B), are important in Megatheriinae systematics (see below).

Furthermore, the study of the postcranial elements (humerus, ulna and femur), whose epiphyses are completely fused to the respective diaphyses (Fig. 3A-D), leads us to consider that we are undoubtedly dealing with an adult specimen. This co-occurrence of persistent cranial sutures and fused limb bone epiphyses is known for some species of megatheriines (e.g., *Megatherium sundti*, see De Iuliis 2006), and yet in other species the sutures between diaphysis and epiphyses are retained (e.g., *Pyramiodontherium scillatoyanei*, see De Iuliis *et al.* 2004). Although the aforementioned specimens had probably not reached maturity, these are considered to be valid species by the consensus of reviewers.

As regards the fusion of the premaxillae and maxillae, in *Megatherium americanum* and *M. altiplanicum* the premaxillae are fused to each other and to the maxillae; this feature is considered as the derived state for the character (Saint-André &

De Iuliis 2001; Pujos 2006). De Iuliis (1996) considered that in MACN Pv 5002 the premaxillae are not fused to each other and only weakly to the maxilla. In his opinion this would be an indication of the subadult status of the specimen, which therefore is referred to *M. americanum*. Although in MACN Pv 5002 the premaxillae are not fused to each other and weakly to the maxilla, we believe the specimen to be an adult. Consequently, its character state for the mentioned character is different to that of *M. americanum*. As in *Megatherium medinae*, *M. celendinense*, *M. sundti*, and *M. tarijense*, *M. gallardoi* retains the plesiomorphic state for this character (premaxillae not fused to each other or to the maxillae) (see Saint-André & De Iuliis 2001: character 3; Pujos 2006: character 3).

With respect to the Hypsodonty Index, the value of HI for MACN Pv 5002 is below the low end of the range for *M. americanum*. Thus, *M. gallardoi* shows a different character state for this character than *M. americanum* (see Saint-André & De Iuliis 2001: character 1).

The postcranial elements described here support the idea that *M. gallardoi* is more closely related to *M. americanum* and *M. altiplanicum* than to the Andean lineage (i.e. *M. sundti*, *M. urbinai*, *M. celendinense*, *M. tarijense*, and *M. medinae*, see Pujos 2006). The extremely reduced femoral patellar trochlea and the presence of notably concave lateral and medial femoral margins are the derived characters (Saint-André & De Iuliis 2001; Pujos 2006) that support the abovementioned relationship.

The morphological features present in MACN Pv 5002, indicate that *Megatherium gallardoi* is a valid species. Besides, and taking into account the morphology of the premaxillae-maxillae and the Hypsodonty Index, the assignment of MACN Pv 5002 to *M. americanum* is not justified. Moreover, if would be the case, the inclusion of MACN Pv 5002 in *M. americanum* would enlarge the range of individual variation of this species, and a revision of some characters used in systematic of megatheriines should be required (i.e. premaxillae-maxillae arrangement and Hypsodonty Index).

With respect to the other Ensenadan Megatheriinae of Argentina, *M. silenum* is represented by a left dentary (MLP 2-61) that preserves all the

molariforms (Fig. 3E). Judging for the shape of the molariforms, MLP 2-61 corresponds undoubtedly to a juvenile individual. *Megatherium tarijense* is restricted to Valle de Tarija, Bolivia (De Iuliis 1996, 2006). Finally, few fragmentary specimens (e.g., MACN Pv 2896, MACN Pv 10654) could be referred to *M. americanum*.

CONCLUSIONS

Megatherium gallardoi is a valid species. The few derived characters available for evaluation in MACN Pv 5002 (e.g., markedly concave lateral and medial diaphyseal margins, transversely expanded proximally and distally, medial reduction of the patellar trochlea) suggest that *Megatherium gallardoi* might be closely related to the *M. americanum*-*M. altiplanicum* clade (Pujos 2006). However, *M. americanum* and *M. altiplanicum* have as derived characters, the presence of premaxillae-maxillae fusion and the high HI value (Saint-André & De Iuliis 2001). *Megatherium silenum* (MLP 2-61) should be considered *nomen vanum* because it lacks diagnostic features and the material used for its description corresponds undoubtedly to a juvenile individual.

Finally, the presence of *M. gallardoi* in ensenadan sediments, together with other exclusive taxa (e.g., *Glyptodon munizi* F. Ameghino, 1881, *Arctotherium angustidens* H. Gervais & F. Ameghino, 1880, and *Mesotherium cristatum*; see Soibelzon 2008) contributes to the biostratigraphic definition of this unit.

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