Additions to the knowledge of *Urumaquia robusta* (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco Formation (Late Miocene), Estado Falcón, Venezuela

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with 2 figures and 2 tables

CARLINI, A.A.; BRANDONI, D. & SANCHEZ, R. 2008. Additions to the knowledge of *Urumaquia robusta* CARLINI, BRANDONI & SANCHEZ, 2006, which significantly improve the knowledge of the species and allow a more precise discussion about the relationships with the rest of the South American Megatheriinae. The new remains (ulna, phalanx, femora, patella, tibia, astragalus, navicular, metatarsals IV-V) described here suggest close affinities of this taxon with the species of *Pyramiodontherium* and with *Megatheriops rectidens*, based on morphological similarities of the ulna (length, gracility), femur (general morphology, shape of the medial margin), and astragalus (angle between the discoidal and odontoid facets). In fact, the shape of femoral medial margin is a shared derived character among *Urumaquia, Pyramiodontherium* and *Megatheriops*. However, and despite the increasing information concerning Tertiary species, their phylogenetic relationships are only partially understood.

Keywords: Megatheriinae • *Urumaquia robusta* • Urumaco Formation • Venezuela • postcranial bones

**Introduction**

For several years, Tertiary xenarthrans from Venezuela were known through a few formally described species, particularly *Urumacotherium garciai* BOCUENTIN-VILLANUEVA, 1984, from the Urumaco Formation (Late Miocene) (see BOCUENTIN-VILLANUEVA 1984) and *Asterostemma venezolensis* SIMPSON, 1947, from the Santa Ines Formation (Middle? Miocene) (see SIMPSON 1947). Recent papers mentioned indeterminate Megatherioidea from Middle Miocene sediments of the Castillo Formation (SANCHEZ-VILLAGRA et al. 2004) and...
new Mylodontidae from the Urumaco and Codore formations (Late Miocene – Pliocene), Estado Falcón (Linares 2004). More recently, we reported part of the large diversity of tardigrades we are identifying in three successive Tertiary formations, the Socorro, Urumaco, and Codore formations, cropping out in the Estado Falcón, which encompass a temporal lapse from the Middle Miocene to the Pliocene (Carlini et al. 2005, 2006a, b). Among them, we described the first Megatheriinae from the Tertiary of Venezuela (Carlini et al. 2006a), represented by two new genera and species from the Late Miocene – Pliocene. For the Urumaco Formation (Late Miocene) we described Urumaquia robusta Carlini, Brandoni & Sánchez, 2006, based on few but significant remains (see Carlini et al. 2006 a) that have been collected in the Urumaco outcrops in the 1970's by a collaborative fieldwork between Venezuelan colleagues and Harvard University (USA).

Brief overviews of the megatheriine remains of the upper Tertiary of South America and their geographic and temporal distribution (Carlini et al. 2002, 2006a) show that the Tertiary findings were not frequent at low latitudes. More precisely, the new taxa we described in 2006 did not only extend the knowledge of megatheriine diversity in South America, but also led us to speculate about the moment of differentiation of Megatherium Cuvier, 1796, and Eremotherium Spillmann, 1948, both genera with maximum diversity in the Pleistocene. Urumaquia robusta is similar in size, and even larger, than the Upper Miocene-Pliocene Argentinean species of the genera Pyramiodontherium Rovereto, 1914, and Megatheriops C. Ameghino & Kragleivich, 1921. Some features present in the few materials known so far (location of the navicular facet with respect to the plane of the discoidal facet, and relationship between the ventral portion of the fibular facet and the ectal facet of the astragalus), suggested the possibility that U. robusta represents a taxon with an anatomy more derived than that of taxa found in the Middle Miocene of Argentina. The taxa recorded in the Middle Miocene of La Venta, Colombia, most probably were the smallest and most gracile Megatheriinae at the time (see Hirschfeld 1985; Carlini et al. 2006a), being more plesiomorphic than those of Venezuela. Fortunately, in fieldwork carried out during 2005 and 2006, we found more material that can undoubtedly be assigned to Urumaquia robusta (that could not be included in the original study). In fact, among the new remains, we found homologous specimens to those of the type specimen (distal tibia and astragalus), which significantly improve the knowledge of the species and allow a discussion of the affinities of the Venezuelan species with the rest of the South American Megatheriinae.

Abbreviations used in the text: AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; FMNH, Field Museum of Natural History, Chicago, USA; MACN, Colección de Paleontología de Vertebrados del Museo Argentino de Ciencias Naturales, “Bernardino Rivadavia”, Buenos Aires, Argentina; MCN, Museo de Ciencias, Caracas, Venezuela; MLP, Colección de Paleontología de Vertebrados del Museo de Ciencias Naturales de La Plata, La Plata, Argentina; SALMA, South American Land Mammal Age.

**Systematic paleontology**

Xeurathra COPE, 1889
Phyllophaga OWEN, 1842
Megatherioidae GRAY, 1821
Megatheriidae GRAY, 1821
Megatheriinae GRAY, 1821

**Urumaquia robusta** Carlini, Brandoni & Sánchez, 2006

Figs. 1–2

**Newly referred material:** AMU-CURS 169: right phalanx 1+2 D III (manus), complete left and poorly preserved right femora, right patella, almost complete left tibia, left astragalus, left and right navicular, right metatarsal IV, left metatarsal V; AMU-CURS 176: medial half of the right tibial proximal epiphysis, and complete but crushed right femur; AMU-CURS 179: almost complete left ulna.

**Distribution:** Urumaco, Estado Falcón, Venezuela; Urumaco Formation, Late Miocene (MINISTERIO DE ENERGÍA Y MINAS 1997; Aguilera 2004).

**Revised diagnosis:** A middle- to large-sized Megatheriinae, larger than Anisodontotherium halymoronorum (Cabrera, 1928), Megathericulus Ameghino, 1904, Eomegatherium Kragleivich, 1926, Pliomegatherium Kragleivich, 1930, Promegatherium Ameghino, 1883, and Eremotherium sefuei De Iulius & Saint-An-dre, 1997; comparable to Pyramiodontherium and some species of Megatherium (M. medinae Phillipps, 1893; M. lundi Gervais & Ameghino, 1880; M. tarijense Gervais & Ameghino, 1880; and M. urbinai Pujo & Salas, 2004), smaller than Megatherium americum Cuvier, 1796 and Megatherium gallardoi Ameghino & Kragleivich, 1921; Eremotherium lauri-lardi (Lund, 1842) and Eremotherium eomigrans De Iulius & Cartelle, 1999. Ulna gracile and slender, much longer than those of other megatherines (e.g. in Megatheriops, Megatherium and Eremotherium). Femur similar to that of Pyramiodontherium, with a slight torsion of the diaphysis of about 22°; the trochanter ma-

**Fig. 1. Urumaquia robusta** (AMU-CURS 179). A–C: Left ulna. Urumaquia robusta (AMU CURS 169). D: Right distal phalanx 1+2 (manus). E–J: Left femur. K–L: Right patella. M–Q: Left tibia. – A, lateral view; B, anterior view; C, proximal view; D, distal, medial, lateral, and proximal views; E, anterior view; F, posterior view; G, medial view; H, lateral view; I, proximal view; J, distal view; K, femoral view; L, anterior view; M, anterior view; N, distal view; O, posterior view; P, medial view; Q, lateral view. – Scale bar = 100 mm.
Urumaquia robusta (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco Formation
major proportionally less developed than in Pyramiodontherium, and with the medial margin of the diaphysis concave. Tibia distally very thick, and with shallow grooves for the foot extensor tendons (shallower than in Megatherium and Ereotherium). The angle between the odontoid and discoid facets in the astragalus is approximately 100° (90° in Pyramiodontherium bergi and P. scillatoyanai, between 100° and 120° in Megatherium and Ereotherium laurillardi). The astragalar depression is deep and conical with a very sharp apex. Nearly one half of the navicular facet is dorsal with respect to the plane of the discoid facet, whereas in Pyramiodontherium spp., E. laurillardi and Megatherium urbinai, only one third is dorsal to this plane. Humerus with a prominent deltoid crest, as in Megathericus, Pyramiodontherium and Megatheriops, (virtually absent in Megatherium and Ereotherium). Metatarsal III with two subcircular areas forming the ectocuneiform facet. Distal surface to digit III slightly convex dorsoventrally, entirely articular and inclined along a dorsolateral to ventromedial axis.

Description
Ulna: The ulna (AMU-CURS 179) (600 mm length) is very gracile and proportionally much longer than those of any other megatherine (e.g. in Megatheriops, Megatherium and Ereotherium); it is straight, thinning toward the distal end and thickening proximally (being always gracile) toward a massive but short olecranon process (Figs. 1A–C). Unlike most megatherines, and similar to FMNH P14511, the distal epiphysis is not widened, whereas the diaphysis continues narrowing up to the distal end. As in other megatherines, it has a proximal facet for the humerus divided into two areas (one for the condyle and another for the trochlea), that form an angle of about 230°, and another proximal facet for the radius.

Digit III P 1+2 (manus): Digit III is the strongest anterior clawed digit in Megatheriinae. It is composed of a single proximal bone (fused phalanges 1+2?), as has been proposed for the other megatherini (Fig. 1D), and a strong ungual phalanx which is claw-shaped. The proximal surface of the phalanx 1+2 seems to be more elongate than in other megatherines (e.g. Megatherium), and bears a wide facet for metacarpal III. This facet is canal-shaped and elongated along the dorsolateral-ventromedial axis. A small, transverse, non-articular distinct ridge-like bone subdivides it into two areas, the upper one is concave and oval in section (in Megatherium and Ereotherium the ridge-like non articular bone is more developed). The distal surface bears an asymmetric trochlea and an incomplete vertical non-articular bony area between the semicircular condyles. The phalanx is slightly oriented medially and, consequently, the ungual phalanx is deviated ventromedially.

Femur: The femur of Urumaquia robusta (AMU-CURS 169) is morphologically similar to that of the species of Pyramiodontherium (Figs. 1E-J). Its total length is 500 mm and the minimum transverse diameter at the middle of the diaphysis is 135 mm (see Tab. 1); it is transversally expanded both in the proximal and distal portions. The torsion of the diaphysis is clearly less (approx. 22°) than in the other species of Megatheriniinae (e.g. Megatherium americanum, Pyramiodontherium bergi) (Figs. 1G–H). In P. bergi this torsion is approximately 40° between the proximal and distal epiphysial axes; in M. americanum it varies between 31° and 57°; in Ereotherium laurillardi between 10° and 41° (DE IULIIS 1996; DE IULIIS et al. 2004). The articular surface of the femoral head is clearly defined proximally by a distinctive neck, as in P. scillatoyanai (MLP 68-III-14-1), and not as in P. brevirostrum (MLP 31-XI-12-25). The trochanter major is proportionally less developed than those of the Pyramiodontherium spp., where it is more outward extended. As in the species of Pyramiodontherium, Megatherium americanum and M. sundti PHILIPPI, 1893 (DE IULIIS 2006: fig. 2C), the medial margin of the diaphysis is concave in Urumaquia robusta (Figs. 1E–F), whereas in Ereotherium laurillardi, Ereotherium sefvei (DE IULIIS & SAINT ANDRÉ 1997: figs. 4 and 5, respectively), Ereotherium eomigrans (DE IULIIS & CARTELLE 1999: fig. 5a), and Megatherium medinae (CASAMIQUELA & SEPÚLVEDA 1974: fig. 6) both the lateral and medial margins are subparallel. In Urumaquia robusta, and as in most megatherines, the patellar facet is separated from the internal condyle and continuous with the external condyle, forming a single articular surface (Figs. 1E, J), whereas in Megathericus patagonicus AMEGHINO, 1904 (MLP 92-XI-15-2), and Megathericus primaeus CABRERA, 1939 (MLP 39-VI-24-1), it is connected with both condyles. In U. robusta the patellar facet is more developed than in Pyramiodontherium bergi, and contrary to Megatherium americanum, it is widely continuous with the lateral condyle. However, the limits of the patellar facet are indicated by a slight difference in the level with the end of the condylar area (Fig. 1J). The ectepicondyle is massive, although not as much as in Pyramiodontherium brevirostrum.

Patella: Associated with the remains AMU-CURS 169 there is an almost complete right patella, which has the medial third of the articular surface partially eroded (Figs. 1K–L). It is subtriangular, with the apex toward the tibia and a wide proximal base. The external surface is rugose, and the femoral facet is almost flat and asymmetrical, displaced laterally. It is similar to that of some specimens of E. laurillardi, although there seems to be a large variability in shape and size in the patellae of the latter species.

Tibia: Two remains of tibiae of two different specimens are known besides the type specimen (MCN 91-72v); one (AMU-CURS 169) is almost complete, but lacks the external portion of the proximal epiphysis (Figs. 1M–Q), the other one is represented only by the
Fig. 2. *Urumaquia robusta* (AMU-CURS 169). A–C: Left astragalus. D–F: Right navicular. G–I: Right metatarsal IV. J–L: Left metatarsal V. — A, dorsolateral view; B, anterior view; C, dorsomedial view; D, proximal view; E, lateral view; F, distal view; G, medial view; H, lateral view; I, distal view; J, medial view; K, dorsal view; L, distal view. — Abbreviations: *ad*, astragalar depression; *aef*, astragalar ectal facet; *af*, astragalar facet; *cub*, cuboid facet; *df*, discoid facet; *dlIV p1*, digit IV phalanx 1; *dV n*, digit V, nodular facet; *ect*, ectocuneiform facet; *ff*, fibular facet; *mec*, meso-entocuneiform complex facet; *mt III*, metatarsal III facet; *mt IV*, metatarsal IV facet; *mt V*, metatarsal V facet; *nav*, navicular facet; *of*, odontoid facet; *op*, odontoid process; *ot*, odontoid tuberosity; *s*, sesamoid facet. — Scale bar = 100 mm.
**Tab. 1. Femur measurements in mm. * from De Iulii (1996).**

<table>
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<tr>
<th>Taxon</th>
<th>Specimen</th>
<th>Length (L)</th>
<th>Proximal width</th>
<th>Distal width</th>
<th>Diaphysis medial width</th>
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<td>250</td>
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<tr>
<td><em>Megatherium lundi</em></td>
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Partial proximal portion (AMU-CURS 176). The tibia of *Urumaquia robusta* is long, as in other Tertiary megatherines, with a minimum total length of 440 mm and a minimum transverse width of the diaphysis of 65 mm (AMU-CURS 169); the relationship tibia length/femur length is similar to that of *P. brevirostrum*, and lower than in *P. bergi* and *P. scillatoyanei* (see Tab. 2). The proximal articular surface has a markedly concave internal condylar facet, which is oval in shape; the longitudinal axis is oblique, forming an angle of approximately 45° with the transverse axis. The cnemial crest of *U. robusta* (Fig. 1M) is not as marked as in *P. bergi*, but the middle section of the diaphysis is subtriangular as in this latter species; in contrast, the tibia is oval in section in several specimens of *Megatherium americanum* and *Pyramiodontherium scillatoyanei* (MLP 68-III-14-1). As in the type specimen, the distal epiphysis is thick, without the strong differences in diameter between the epiphysis and the distal diaphysis observed in most other megatherines. The two shallow tendinous grooves for the digital flexors, limited by three crests, are well distinguishable (Figs. 10-P). The astragalar facet of the tibia (Fig. 1N) has a wide facet for the odontoid process, as in *P. brevirostrum* (MLP 31-XI-12-25) and *P. scillatoyanei* (MLP 68-III-14-1) (similar to most Quaternary taxa), and is relatively wider than that of *P. bergi* (MLP 2-66). The discoid facet is similar in development to species of *Pyramiodontherium*. The angle between both facets is approximately 106°, while it is 135° in *Megathericus patagonicus* (MLP 91-IX-7-18, MLP 92-XI-15-2), 114° in *P. brevirostrum* and 87° in *P. bergi*.

**Astragalus:** The astragalus has the typical shape for Megatheriinae (see BRANDONI et al. 2004). It is massive, with a well-developed central odontoid process in dorsomedial view (Figs. 2A–C) and a navicular facet in anterior view (Fig. 2B). As in other megatherines, the fibular facet is divided into two main areas (Fig. 2A), an anteroposteriorly elongated dorsal portion (that joins the discoid facet dorsally) and a ventral facet with a rounded surface slightly extended ventrally. A similar general shape can be observed in *Pyramiodontherium bergi* (MLP 2-66) and in *P. scillatoyanei* (MLP 68-III-14-1), but in *P. scillatoyanei*, and also in *Eomegatherium nanum* (Burmester 1891) (MACN Pv-4992), the ventral portion of the fibular facet reaches the ectal facet. In the oldest well-known Megatheriinae, *Megathericus patagonicus*, the ventral part of the fibular facet reaches the ectal facet.

In *Urumaquia robusta* (AMU-CURS 169) the complete odontoid process with the odontoid facet is...
Urumaquia robusta (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco Formation

Tab. 2. Tibia measurements in mm. * from De Iuliis (1996).

<table>
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<tr>
<th>Taxon</th>
<th>Specimen</th>
<th>Length (L)</th>
<th>Proximal width</th>
<th>Distal width</th>
<th>Diaphysis medial width</th>
<th>Tibia L / Femur L</th>
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</tbody>
</table>

preserved. The angle between the odontoid and discoid facets is approximately 100° (Fig. 2B), as in the type specimen. The facet for the navicular, on the anterior-most part of the astragalus, has its major axis oriented dorsolaterally to ventromedially. The concave dorsolateral portion of the navicular facet, termed the astragalar depression (see Fig. 2B), is more circular in section than that of P. bergi (see BRANDONI et al. 2004). The astragalar depression is deep as in P. bergi, P. scillatoyanei, and Eomegatherium nanum, but conical with a very sharp, pointed apex. In U. robusta about one-half of the navicular facet is positioned dorsally with respect to the plane of the discoid facet, similar to Megathericus patagonicus. In Pyramiodontherium spp., Eremotherium laurillardi, and Megatherium urbinai, only one-third is dorsally located. In contrast, in M. americanum the top of the dorsomedial part of the navicular facet is at the same level with the discoid facet plane. There are two facets for articulation with the calcaneum, the reduced sustentacular facet and the large and concave ectal facet, separated by a deep and wide non-articular bony canal, the sulcus tali.

Navicular: The navicular (Figs. 2D–F) is oval to sub-rectangular in shape (distal view) and antero-posteriorly compressed, with the main axis oriented dorsolaterally to ventromedially (De Iuliis 1996; BRANDONI et al. 2004). The astragalar facet (Fig. 2D) is located on the proximal surface, and can be differentiated into dorsolateral and ventromedial halves. The dorsolateral half is more or less subcircular in the outer section, but is eccentrically conic resulting in a subtriangular shape; instead in P. bergi and M. americanum it is subcircular and forms a prominent condylar projection that fits into the circular depression of the astragalus. This projection is well developed, but not as in M. americanum. The ventromedial half is semilunar, concave along its main axes and articulates with the condylar portion of the astragalus. As in P. bergi and M. americanum, both halves are similar in size; in M. altiplanicum from the Pliocene of Bolivia, the medial part of the facet is larger than the lateral part (Saint-André & De Iuliis 2001).

A cuboid facet lies on the ventrolateral portion of the navicular (Fig. 2E). It is elongate along the dorsolateral-ventromedial axis. In Urumaquia robusta and Megatherium americanum the cuboid facet is located in
a single plane. In *P. bergi*, this facet has two different portions, one dorsolateral and another ventral (see BRANDONI et al. 2004).

On the distal surface, the navicular is convex along its main axes (Fig. 2E). As in *M. americanum*, there are two articular facets (Fig. 2F), ventrally the ectocuneiform facet and dorsomedially the meso-entocuneiforms facet; in *P. bergi* there are in two, because the ventral facet is divided in two (see BRANDONI et al. 2004).

**Metatarsal IV**: Metatarsal IV (Figs. 2G–I) is long and not as compressed as metatarsal III (see CARLINI et al. 2006a). The diaphysis is laterally oriented triangular in section, whereas in *M. americanum* the section is sub-triangular to oval. Proximally, two articular facets are preserved, an anteromedial facet for Mt III (Fig. 2G) and a lateral facet for Mt V (Fig. 2H). The facet for the cuboid is not preserved, because the bone is broken. The facet for Mt III is oval, dorsoventrally extended, and slightly concave in both directions. The facet for Mt V is located on the external side of the proximal epiphysis. This facet is subcircular and flat. The distal epiphysis is triangular, with a laterodorsal apex and a tripod-like base (Fig. 2I). The facet for the proximal phalanx of digit IV is crested, as that for metatarsal III, but less acute in section, and narrowing ventrally. Ventromedially there is a small and convex subcircular facet for a sesamoid.

**Metatarsal V**: Metatarsal V (Figs. 2J–L) is slightly longer than metatarsal IV, but depressed dorsoplantarly, with the lateral margin expanded and dorsoventrally compressed (especially the proximal two-thirds). The distal portion is almost isodiametric. The medial side has two continuous articular facets that are inclined dorso-

Discussion

The most ancient records of the subfamily Megatheriinae (sensu lato), represented in South America by three successive faunas, the Colloncuran, Laventan and Mayoan faunas. *Hirschfeld* (1985) reported megatherine remains from the Laventan SALMA of Colombia. Hence, for the Miocene, the fossil record suggests that the Megatheriinae were distributed at least in north-western South America and western Patagonia. The megatherines of La Venta (Colombia) have not been fully studied yet; however, in view of the few published data, there are two taxa related to *Megathericulus* (cf. *M. patagonicus*) and *Eomegatherium* (cf. *Eo. andinum* Kragliev-

Eo. *andinum* Kraglievich, 1930, *Eo. cabrerae*), both also recorded in the May-

oan of Patagonia (Kraglievich 1930; Scillato-Yané et al. 1993; Brandoni & Cardini 2004). Thus, *Mega-

theriinae* were probably distributed homogeneously along the west of the continent (Carlini et al. 2006a) in the Middle Miocene in South America, although a wider distribution encompassing the whole of South America cannot be discarded. Concerning the geographic relationship between Patagonia and La Venta, Canedla & Morrone (2003: 373) stated: “Más allá de estas incertidumbres, las similitudes faunísticas entre La Venta y las mencionadas faunas fósiles de Argentina, expresadas aquí en el trazo I, indican que ellas serían las descendientes de una biota ancestral ampliamente distribuida en el paso de“ (“These uncertainties aside, the faunistic similarities between La Venta and the faunas from Argentina mentioned above, expressed here in the ‘trazo 1’ indicate that they would be descendants from an ancestral biota of wide distribution in the past”). In this sense, most Tertiary Megatheriinae are distributed along the “trazo generalizado 1” of Canedla & Morrone (2003: fig. 7).

The information about the Megatheriinae recorded in northern South America is very scarce. Recently, Carlini et al. (2006a) described two new Megatheriinae from the Late Miocene-Pliocene of Venezuela. The new remains of *Urumaquia robusta* here described suggest closer affinities of this taxon with the species of *Pyramidodontherium* and *Megatheriops rectidens* (Rovereto 1914), based on morphological similarities of the ulna (length, gracility), femur (general morphology, shape of the medial margin), and astragalus (angle between the discoidal and odontoid facets). In fact, the shape of femoral medial margin is a shared derived character among *Urumaquia, Pyramidodontherium* and *Megatheriops*. However, and despite the increasing information concerning Tertiary species, the phylogenetic relationships among them are only partially understood (Brandoni 2006; Pujos 2006), mainly because of the absence of enough data for the analysis (Brandoni 2006).

Hence, it is very likely that the history of Mega-

theriinae in northern South America began with some taxon closely related to the primitive Patagonian mega-

therines (*Megathericulus, Eomegatherium*), which then further diverged into a group (*Urumaquia*) related to the clade *Pyramidodontherium-Megatheriops* (see Brandoni 2006; Pujos 2006), and finally gave rise to the phyletic series proposed by Carlini et al. (2006a) (i.e. *Proeremotherium-Eremotherium*). These authors considered *Proeremotherium eljebu* Carlini, Brandoni & Sánchez, 2006, as the taxon basal to *Eremotherium*, the latter representing the mainly Pleistocene megatheriine widely distributed in southern North America, Central
America, and lowlands of northern and eastern South America. It might be possible that, as in Glyptodontinae (see CARLINI et al. this volume), Megatheriinae (Proeremotherium sp.) migrated to North America after the Panama isthmus was definitively established in the Late Pliocene (ca. 2.7 Ma, see WOODBURNE et al. 2006), gave rise to Eremotherium there, and then this last genus re-entered South America some time during the Pleistocene. If so, this is another case of xenarthran cladogenetic processes in North America after the Late Pliocene, that led to taxa that re-entered South America, as in the Pampatheridae (Holmesina SIMPSON, 1930; see SCILLATO-YANE et al. 2005) and Glyptodontinae (Glyptotherium OSBORN, 1903; see CARLINI et al. 2008).

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