

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

ALFREDO A. CARLINI, La Plata; DIEGO BRANDONI, Diamante & RODOLFO SÁNCHEZ, Urumaco

with 2 figures and 2 tables

CARLINI, A.A.; BRANDONI, D. & SÁNCHEZ, R. 2008. Additions to the knowledge of *Urumaquia robusta* (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco Formation (Late Miocene), Estado Falcón, Venezuela. – *Paläontologische Zeitschrift* 82 (2): 153–162, 2 figs., 2 tabs., Stuttgart, 30. 6. 2008.

Abstract: We describe new remains of *Urumaquia robusta* CARLINI, BRANDONI & SÁNCHEZ, 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

Kurzfassung: Neue Funde von *Urumaquia robusta* CARLINI, BRANDONI & SÁNCHEZ, 2006 werden vorgestellt, die erheblich zum Verständnis der Art beitragen und eine präzisere Diskussion der Verwandtschaftsverhältnisse zu anderen Vertretern der südamerikanischen Megatheriinae erlauben. Das hierin beschriebene neue Material (Ulna, Phalange, Femura, Patella, Tibia, Astragalus, Navikulare, Metatarsalia IV–V) deutet auf nähere Verwandtschaft zu den Taxa *Pyramiodontherium* und *Megatheriops rectidens* hin. Dies wird unterstützt durch morphologische Ähnlichkeit der Ulna (Länge, Gracilität), des Femurs (generelle Morphologie, Form des medialen Randes) und des Astragalus (Winkel zwischen der Diskoidal- und Odontoidfacette). Tatsächlich handelt es sich bei der Ausprägung des medialen Femurrandes um eine Synapomorphie von *Urumaquia*, *Pyramiodontherium* und *Megatheriops*. Allerdings sind die phylogenetischen Verwandtschaftsverhältnisse, trotz Zunahme von Informationen über tertiäre Taxa, bisher nur teilweise verstanden.

Schlüsselwörter: Megatheriinae • *Urumaquia robusta* • Urumaco Formation • Venezuela • Postcranialelemente

Introduction

For several years, Tertiary xenarthrans from Venezuela were known through a few formally described species, particularly *Urumacotherium garciai* BOCQUENTIN-VILLANUEVA, 1984, from the Urumaco Formation (Late

Miocene) (see BOCQUENTIN-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 (SÁNCHEZ-VILLAGRA et al. 2004) and

Addresses of the authors: Alfredo A. Carlini, Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Straße 4, CH-8006 Zürich, Switzerland, and Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. CONICET, and Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; e-mail <acarlini@fnym.unlp.edu.ar>. – Diego Brandoni, Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y de Transferencia Tecnológica a la Producción (CICYTTP), Materi y España, 3105 Diamante, Entre Ríos, Argentina. CONICET; e-mail <diegobrandoni@yahoo.com>. – Rodolfo Sánchez, Museo Paleontológico de la Alcaldía de Urumaco, Falcón, Venezuela.

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 & KRAGLIEVICH, 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

Xenarthra COPE, 1889
Phyllophaga OWEN, 1842
Megatherioidea GRAY, 1821
Megatheriidae GRAY, 1821
Megatheriinae GRAY, 1821

Urumaquia robusta CARLINI, BRANDONI & SÁNCHEZ, 2006

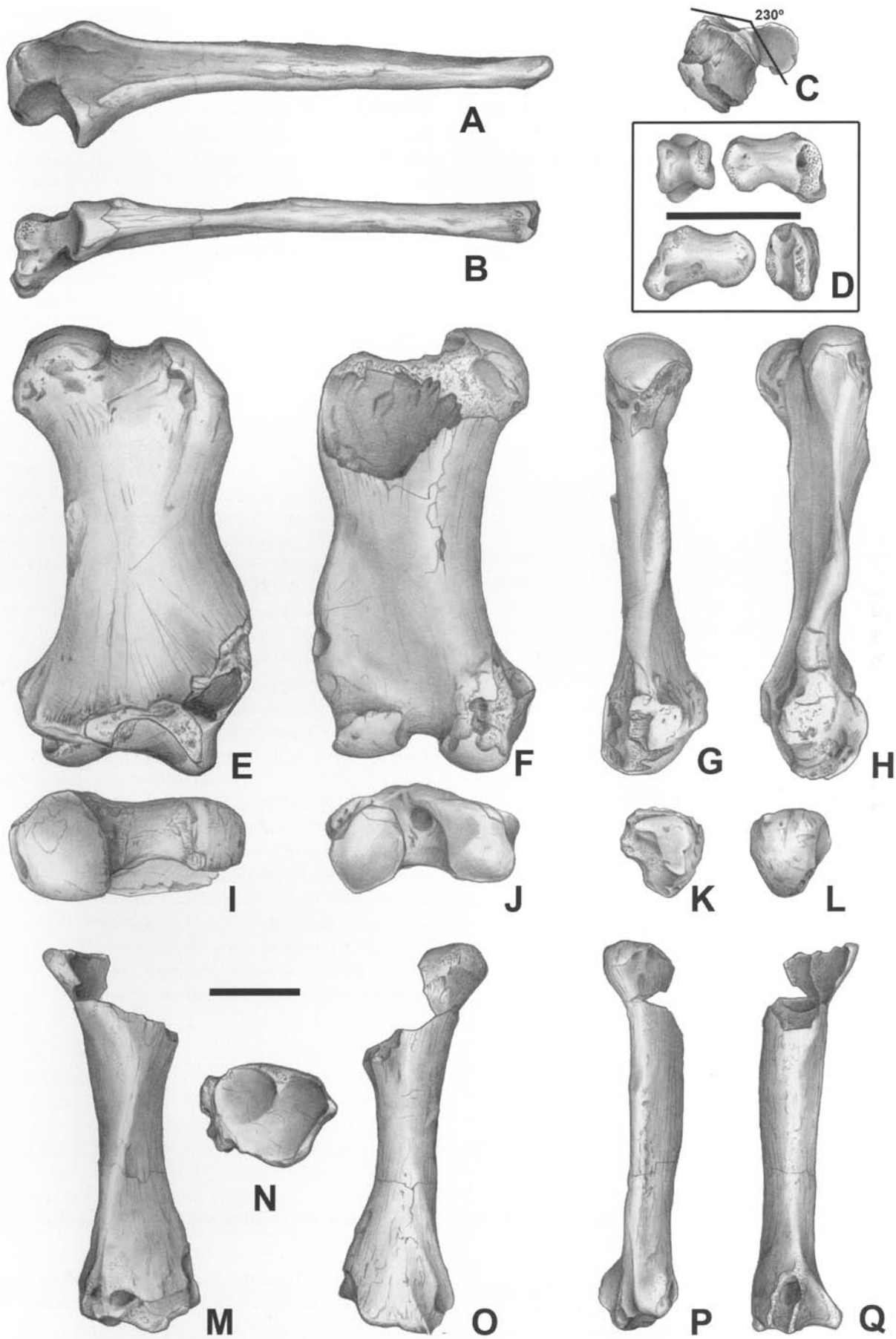
Figs. 1–2

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 *Anisodontherium halmyronomum* (CABRERA, 1928), *Megathericulus* AMEGHINO, 1904, *Eomegatherium* KRAGLIEVICH, 1926, *Pliomegatherium* KRAGLIEVICH, 1930, *Promegatherium* AMEGHINO, 1883, and *Eremotherium sefvei* DE IULIIS & SAINT-ANDRÉ, 1997; comparable to *Pyramiodontherium* and some species of *Megatherium* (*M. medinae* PHILLIPPI, 1893; *M. lundi* GERVAIS & AMEGHINO, 1880; *M. tarijense* GERVAIS & AMEGHINO, 1880; and *M. urbinai* PUJOS & SALAS, 2004), smaller than *Megatherium americanum* CUVIER, 1796 and *Megatherium gallardoii* AMEGHINO & KRAGLIEVICH, 1921; *Eremotherium laurillardii* (LUND, 1842) and *Eremotherium eomigrans* DE IULIIS & CARTELLE, 1999. Ulna gracile and slender, much longer than those of other megatheriines (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 digit III 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.



por 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 *Eremotherium*). The angle between the odontoid and discoid facets in the astragalus is approximately 100° (90° in *Pyramiodontherium bergi* and *P. scillatoyanei*, between 100° and 120° in *Megatherium* and *Eremotherium laurillardii*). 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. laurillardii* and *Megatherium urbinai*, only one third is dorsal to this plane. Humerus with a prominent deltopectoral crest, as in *Megathericulus*, *Pyramiodontherium* and *Megatheriops*, (virtually absent in *Megatherium* and *Eremotherium*). 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 megatheriine (e.g. in *Megatheriops*, *Megatherium* and *Eremotherium*); 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 megatheriines, and similar to FMNH P14511, the distal epiphysis is not widened, whereas the diaphysis continues narrowing up to the distal end. As in other megatheriines, 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 megatheriines) (Fig. 1D), and a strong ungual phalanx that is claw-shaped. The proximal surface of the phalanx 1+2 seems to be more elongate than in other megatheriines (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 *Eremotherium* 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 155 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 Megatheriinae (e.g. *Megatherium americanum*, *Pyramiodontherium bergi*) (Figs. 1G–H). In *P. bergi* this torsion is approximately 40° between the proximal and distal epiphysal axes; in *M. americanum* it varies between 31° and 57°; in *Eremotherium laurillardii* 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. scillatoyanei* (MLP 68-III-14-1), and not as in *P. brevisrostrum* (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 *Eremotherium laurillardii*, *Eremotherium sefvei* (DE IULIIS & SAINT ANDRÉ 1997: figs. 4 and 5, respectively), *Eremotherium 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 megatheriines, 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 *Megathericulus patagonicus* AMEGHINO, 1904 (MLP 92-XI-15-2), and *Megathericulus primae-vus* 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 brevisrostrum*.

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. laurillardii*, 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

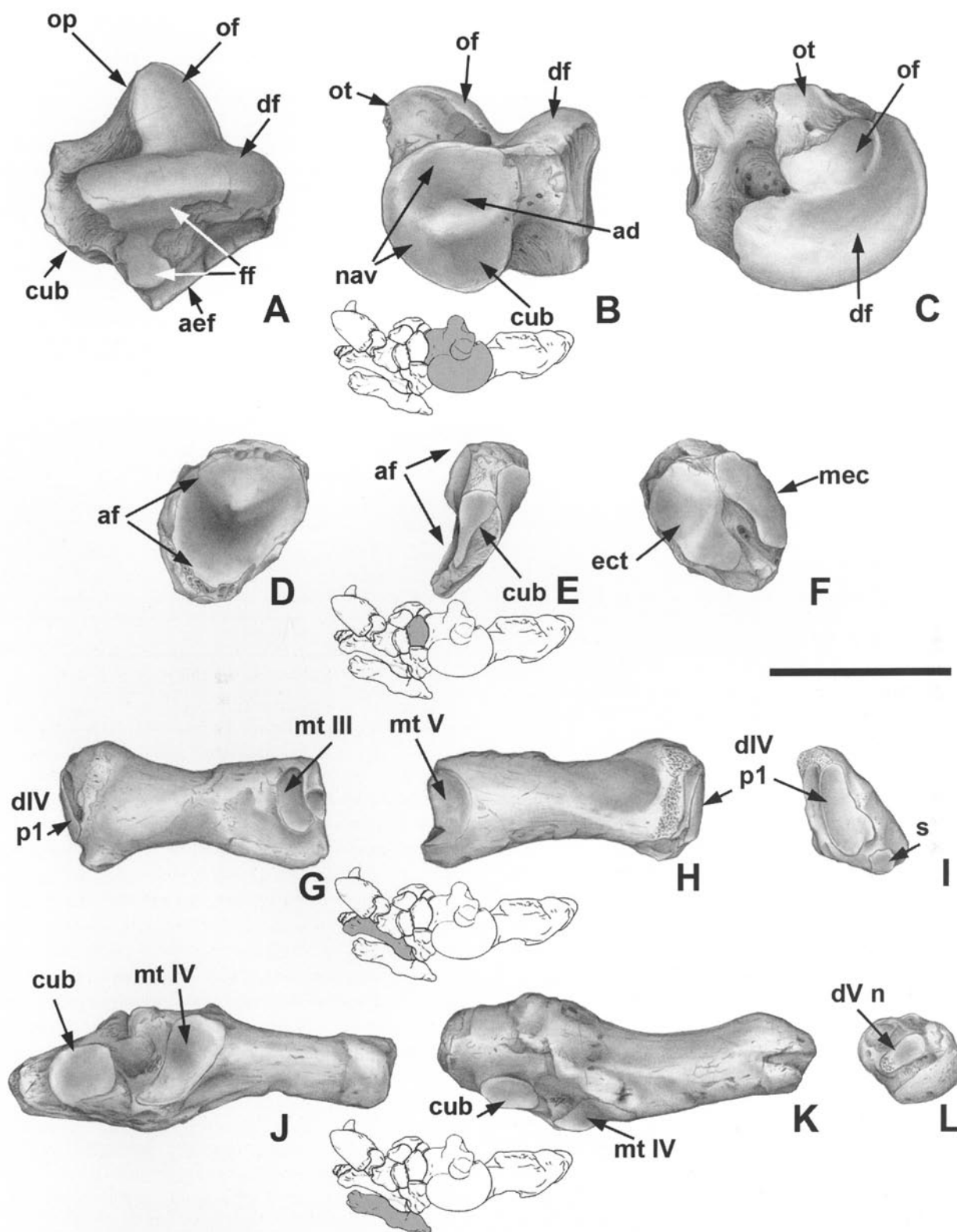


Fig. 2. *Urumaquia robusta* (AMU-CURS 169). **A–C:** Left astragalus. **D–F:** Right navicular. **G–I:** Right metatarsal IV. **J–L:** Left metatarsal V. – **A,** dorsolateral view; **B,** anterior view; **C,** dorsomedial view; **D,** proximal view; **E,** lateral view; **F,** distal view; **G,** medial 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; **dIV 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 IULIIS (1996).

Taxon	Specimen	Length (L)	Proximal width	Distal width	Diaphysis medial width
<i>Pyramiodontherium scillatoyanei</i>	MLP 68-III-14-1	473	263	257	155
<i>Pyramiodontherium bergi</i>	MLP 2-66	515	305	280	190
<i>Pyramiodontherium brevirostrum</i>	MLP 31-XI-12-25	580	300	285	180
<i>Pyramiodontherium</i> sp.	MLP 31-XI-12-26	482	230	245	166
<i>Pyramiodontherium</i> sp.	MACN Pv-2817	597	360	350	210
<i>Megatherium</i>	Sta. Rosa (Tastil)	565	310	320	250
<i>Megatherium lundii</i>	(Museo de Salto)	570	325	310	200
<i>Megatherium lundii</i>	MLP 2-30	575	299	312	211
<i>Megatherium lundii</i>	MLP 2-31	605	328	344	220
<i>Megatherium tarijense</i> *	FMNH P 14216	528	273	266	200
<i>Megatherium americanum</i> *	MLP 2-207	735	431	403	260
<i>Megatherium americanum</i> *	MLP 2-29	759	459	473	311
<i>Megatherium americanum</i> *	MLP sala9	712	392	409	270
<i>Megatherium americanum</i> *	MLP 44-XII-28-1	660	390	390	285
<i>Megatherium americanum</i>	CC 1008	620	350	330	220
<i>Urumaquia robusta</i>	AMU-CURS 169	500	230	250	160
<i>Urumaquia robusta</i>	AMU-CURS 176	475	225	248	140

partial proximal portion (AMU-CURS 176). The tibia of *Urumaquia robusta* is long, as in other Tertiary megatheriines, 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 megatheriines. The two shallow tendinous grooves for the digital flexors, limited by three crests, are well distinguishable (Figs. 1O–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 *Megathericulus 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 megatheriines, 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* (BURMEISTER 1891) (MACN Pv-4992), the ventral portion of the fibular facet is rather circular and more oval, with the long axis perpendicular to the discoid facet with a reduced dorsal portion (see BRANDONI et al. 2004). In the oldest well-known Megatheriinae, *Megathericulus 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

Tab. 2. Tibia measurements in mm. * from DE IULIIS (1996).

Taxon	Specimen	Length (L)	Proximal width	Distal width	Diaphysis medial width	Tibia L / Femur L
<i>Megathericulus patagonicus</i>	MLP 91-IX-7-18	270	120 aprox	150	55	
<i>Pyramiodontherium bergi</i>	MLP 2-66 L	514	230	222	87	0.99
<i>Pyramiodontherium bergi</i>	MLP 2-66 R		220	210	90	
<i>Pyramiodontherium brevirostrum</i>	MLP 31-XI-25	500	210	170		0.86
<i>Pyramiodontherium scillatoyanei</i>	MLP 68-III-14-1	472	215	205	81	0.99
<i>Pyramiodontherium</i>	MLP 31-XI-12-26 L	425	195	150		0.88
<i>Pyramiodontherium</i>	MLP 31-XI-12-26 R	435	180	160		
<i>Megatherium lundi</i>	MLP 2-30	446	246	222	81	0.77
<i>Megatherium lundi</i>	MLP 2-31	445	235	245	97	0.73
<i>Megatherium lundi</i>	(Museo de Salto)	450	245	235	89	0.79
<i>Megatherium</i>	Sta Rosa (Tastil)	510	265	247	97	0.9
<i>Megatherium americanum</i> *	MLP 2-207	560	360		115	0.76
<i>Megatherium americanum</i> *	MLP 2-29	620	355	305	141	0.81
<i>Megatherium americanum</i> *	MLP 2-79	539	342		123	
<i>Megatherium americanum</i> *	MLP sala9	568	330	290	100	0.79
<i>Megatherium americanum</i> *	MLP 44-XII-28-1	550	302	290	120	0.83
<i>Megatherium americanum</i> *	MACN Pv-10147	475	275		112	
<i>Megatherium tarijense</i> *	FMNH P 14216	408	214	202	85	0.77
<i>Urumaquia robusta</i>	MCN 91-72v (type)			167		
<i>Urumaquia robusta</i>	AMU-CURS 169	440		130	69	0.88

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 astragal depression (see Fig. 2B), is more circular in section than that of *P. bergi* (see BRANDONI et al. 2004). The astragal 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 *Megathericulus 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 astragal 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 instead three, 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 subtriangular 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 dorsomedially. The anteriormost facet for Mt IV is subtriangular, with a ventroposterior apex, relatively flat, and not continuous posteriorly with the cuboid facet (Figs. J–K). The cuboid facet is slightly concave and squared. The posterior end of metatarsal V is not prominent and point-shaped, as in *P. bergi*. The distal surface (Fig. 2L) has a very small oval and convex, elongated facet along the dorsolateral-ventromedial axis for a nodular vestigial phalanx, the latter smaller than that of *P. bergi*.

Discussion

The most ancient records of the subfamily Megatheriinae are as old as the Middle Miocene of Patagonia (Argentina), and include the genera of the “Friasian” lapse (sensu lato), represented in South America by three successive faunas, the Colloncuran, Laventan and Mayoan faunas. HIRSCHFELD (1985) reported megatheriine 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 megatheri-

ines 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* KRAGLIEVICH, 1930, *Eo. cabrerai*), both also recorded in the Mayoan of Patagonia (KRAGLIEVICH 1930; SCILLATO-YANÉ et al. 1993; BRANDONI & CARLINI 2004). Thus, Megatheriinae 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, CANDELA & 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 pasado” (“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 I” of CANDELA & 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 *Pyramiodontherium* 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*, *Pyramiodontherium* 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 Megatheriinae in northern South America began with some taxon closely related to the primitive Patagonian megatheriines (*Megathericulus*, *Eomegatherium*), which then further diverged into a group (*Urumaquia*) related to the clade *Pyramiodontherium-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 eljebe* 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 Pampatheriidae (*Holmesina* SIMPSON, 1930; see SCILLATO-YANÉ et al. 2005) and Glyptodontinae (*Glyptotherium* OSBORN, 1903; see CARLINI et al. 2008).

Acknowledgments

We wish to thank to H. Moreno and O. Aguilera from MCN for their assistance and permission to study the collections under their care; to O. Aguilera for his hospitality and assistance during the work of AAC in Venezuela; to C. Sánchez for help and camaraderie in the field; to M. Reguero (MLP) and A. Kramarz (MACN) for allowing us access to the collection of their respective institutions; to M.R. Sánchez-Villagra for the review of an early and final version of the ms, which improved our manuscript; to the Alcaldía de Urumaco for permission to study the fossils of AMU-CURS; to the two anonymous reviewers for their valuable comments and suggestions; to C. Deschamps for the English translation of the manuscript. Illustrations are the work of J. Gonzalez. The work of AAC in Venezuela was supported by PICT-R 0074 G3 and N514 UNLP (to AAC), and PIP 2731 (to M. Merani and AAC). This work was supported by the University of Zürich. We wish to especially thank M.R. Sánchez-Villagra and O. Aguilera for inviting us to contribute to this special volume.

References

- AGUILERA, O. 2004. Tesoros Paleontológicos de Venezuela: Urumaco, Patrimonio Natural de la Humanidad. – 148 p., Caracas (Ed. Arte).
- AMEGHINO, F. 1883. Sobre una nueva colección de mamíferos recogidos por el Profesor Pedro Scalabrini en las barrancas del Paraná. – *Boletín de la Academia Nacional de Ciencias de Córdoba* **5**: 257–306.
- AMEGHINO, F. 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. – *Anales de la Sociedad Científica Argentina* **58**: 225–291.
- AMEGHINO, C. & KRAGLIEVICH, L. 1921. Descripción del “*Megatherium gallardoi*” C. Amegh. descubierto en el Pampeano inferior de la ciudad de Buenos Aires. – *Anales del Museo Nacional de Historia Natural de Buenos Aires* **31**: 134–156.
- BOCQUENTIN-VILLANUEVA, J. 1984. Un nuevo representante de la subfamilia Preprotheriinae (Mammalia, Edentata) proveniente del Mioceno de Venezuela. – III. Congreso Latinoamericano de Paleontología Memorias, Oaxtepec, México: 516–523.
- BRANDONI, D. 2006. Los Megatheriinae (Xenarthra, Tardigrada, Megatheriidae) Terciarios de la Argentina. Sistemática, Evolución y Biogeografía. – 292 p., Ph. D. Dissertation, Universidad de La Plata, Argentina (unpublished).
- BRANDONI, D. & CARLINI, A.A. 2004. Nuevos restos de Megatheriinae (Xenarthra, Phyllophaga, Megatheriidae) en el “Mayoense” (Mioceno Medio) de Santa Cruz. XX Jornadas Argentinas de Paleontología de Vertebrados, La Plata, 2004. – *Ameghiniana* **41** (Suplemento): 37R.
- BRANDONI, D.; CARLINI, A.A.; PUJOS, F. & SCILLATO-YANÉ, G.J. 2004. The pes of *Pyramiodontherium bergi* (MORENO & MERCERAT, 1891) (Xenarthra, Phyllophaga): the most complete pes of a Tertiary Megatheriinae. – *Geodiversitas* **26**: 643–659.
- BURMEISTER, H. 1891. Continuación a las adiciones al examen crítico de los mamíferos terciarios. – *Anales del Museo Nacional de Buenos Aires* **3**: 401–461.
- CABRERA, A. 1928. Sobre algunos megaterios pliocenos. – *Revista del Museo de La Plata* **31**: 339–352.
- CABRERA, A. 1939. Un nuevo representante Santacrusense de la familia Megatheriidae. – *Notas del Museo de La Plata, Paleontología* **4**: 475–483.
- CANDELA, A.M. & MORRONE, J.J. 2003. Biogeografía de puercoespines neotropicales (Rodentia: Hystricognathi): Integrando datos fósiles y actuales a través de un enfoque panbiogeográfico. – *Ameghiniana* **40**: 351–378.
- CARLINI, A.A.; BRANDONI, D. & SÁNCHEZ R. 2006a. First megatheriines (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco (Late Miocene) and Codore (Pliocene) Formations, Estado Falcón, Venezuela. – *Journal of Systematic Palaeontology* **4**: 269–278.
- CARLINI, A.A.; BRANDONI, D.; SCILLATO-YANÉ, G.J. & PUJOS, F. 2002. Una nueva especie de megaterino (Xenarthra, Megatheriidae) del Mioceno Tardío-Plioceno de Catamarca, Argentina. – *Ameghiniana* **39**: 367–377.
- CARLINI, A.A.; SCILLATO-YANÉ, G.J. & BRANDONI, D. 2005. New Xenarthra Tardigrades of Venezuela, outstanding diversity at low latitudes. – Abstract de la Reunión en Homenaje a R. Pascual, Julio, 2005. – *Ameghiniana* **42** (Suplemento): 80R.
- CARLINI, A.A.; SCILLATO-YANÉ, G.J. & SÁNCHEZ R. 2006b. New Mylodontoidea (Xenarthra, Phyllophaga) from the Middle Miocene-Pliocene of Venezuela. – *Journal of Systematic Palaeontology* **4**: 255–267.
- CARLINI, A.A.; ZURITA, A.E. & AGUILERA, O. 2008. North American Glyptodontines (Xenarthra, Mammalia) in the Upper Pleistocene of northern South America. – *Paläontologische Zeitschrift* **82** (2): 125–138.
- CASAMIQUELA, R. & SEPÚLVEDA, F. 1974. Catalogación crítica de algunos vertebrados fósiles Chilenos. III. Los megatherioideos. Sobre *Megatherium medinae* PHILIPPI. – *Ameghiniana* **11**: 97–123.
- COPE, E. 1889. The Edentata of North America. – *American Naturalist* **23**: 657–664.
- CUVIER, G. 1796. Notice sur le squelette d’une très grande espèce de quadrupède inconnue jusqu’à présent trouvé au Paraguay et déposé au cabinet d’histoire naturelle de Madrid. – *Magasin Encyclopédique: ou Journal des Sciences, des Lettres et des Arts* **1**: 303–310.
- DE IULIIS, G. 1996. A systematic review of the Megatheriinae (Mammalia: Xenarthra: Megatheriidae). – 781 p., Ph.D. Dissertation, University of Toronto, Canada (unpublished).
- DE IULIIS, G. 2006. On the taxonomic status of *Megatherium sundti* PHILIPPI, 1893 (Mammalia: Xenarthra: Megatheriidae). – *Ameghiniana* **43**: 161–169.
- DE IULIIS, G. & CARTELLE, C. 1999. A new giant megatheriine ground sloth (Mammalia: Xenarthra: Megatheriidae) from the Late Blancan to Early Irvingtonian of Florida. – *Zoological Journal of the Linnean Society* **127**: 495–515.
- DE IULIIS, G. & SAINT-ANDRÉ, P.A. 1997. *Eremotherium sefvei* nov. sp. (Mammalia: Xenarthra: Megatheriidae) from the Pleistocene of Ulloma, Bolivia. – *Geobios* **30**: 453–461.
- DE IULIIS, G.; RÉ, G.H. & VIZCAÍNO, S.F. 2004. The Toro Negro Megatheriine (Mammalia, Xenarthra): a new species of *Pyramiodontherium* and a review of *Plesiomegatherium*. – *Journal of Vertebrate Paleontology* **24** (1): 214–227.
- GERVAIS, H. & AMEGHINO, F. 1880. Los mamíferos fósiles de la América del Sud. – 225 p., Paris and Buenos Aires (Ignon Hermanos).

- GRAY, J.E. 1821. Catalogue of carnivorous, pachydermatous, and edentate Mammalia in the British Museum. – 398 p., London (British Museum).
- HIRSCHFELD, S.E. 1985. Ground sloths from the Friasian La Venta fauna, with additions to the Pre-Friasian Coyaima fauna of Colombia, South America. – University of California Publications, Geological Sciences **128**:1–91.
- KRAGLIEVICH, L. 1926. Notas sobre gravígrados de Sud América. – Anales del Museo Nacional de Historia Natural de Buenos Aires **34**: 21–36.
- KRAGLIEVICH, L. 1930. La formación friaseana del Río Frías, Río Fénix, Laguna Blanca, etc. y su fauna de mamíferos. – Physis, Revista de la Sociedad Argentina de Ciencias Naturales **10**: 127–161.
- LINARES, O. 2004. Nuevos restos del género *Lestodon* GERVAIS, 1855 (Xenarthra, Tardigrada, Mylodontidae), del Mioceno Tardío y Plioceno Temprano de Urumaco (Venezuela), con descripción de dos nuevas especies. – Paleobiología Neotropical **2**: 1–14 (<http://www.paleobio.labbb.usb.ve/revista.html>).
- LUND, P.W. 1842. Blik paa Brasiliens dyreverden for sidste jordomvaeltning. Fjerde afhandling: fortsaettelse af pattedyrene. – Det kongelige Danske Videnskaberne Selskabs Skrifter; Naturvidenskabelige og matematisk Afhandlinger **9**: 137–208.
- MINISTERIO DE ENERGÍA Y MINAS. 1997. Léxico estratigráfico de Venezuela (Tercera Edición). – Boletín de Geología **12**: 818 p.
- OSBORN, H.F. 1903. *Glyptotherium texanum*, a new glyptodont, from the lower Pleistocene of Texas. – Bulletin of the American Museum of Natural History **19**: 491–494.
- OWEN, R. 1842. Description of the skeleton of an extinct gigantic sloth, *Mylodon robustus*, OWEN, with observations on the osteology, natural affinities, and probable habits of the megatherioid quadruped in general. – 176 p., London (R. & J. Taylor).
- PHILIPPI, R.A. 1893. Vorläufige Nachricht über fossile Säugethierknochen von Ulloma, Bolivia. – Zeitschrift der Deutschen Geologischen Gesellschaft **45**: 87–96.
- PUJOS, F. 2006. *Megatherium celendinense* sp. nov. from the Pleistocene of the Peruvian Andes and the phylogenetic relationships of Megatheriines. – Palaeontology **49**: 285–306.
- PUJOS, F. & SALAS, R. 2004. A new species of *Megatherium* (Mammalia: Xenarthra: Megatheriidae) from the Pleistocene of Sacaco and Tres Ventanas, Peru. – Palaeontology **47**: 579–604.
- ROVERETO, C. 1914. Los estratos araucanos y sus fósiles. – Anales del Museo de Historia Natural **25**: 1–247.
- SAINT-ANDRÉ, P.A. & DE IULIIS, G. 2001. The smallest and most ancient representative of the genus *Megatherium* CUVIER, 1796 (Xenarthra, Tardigrada, Megatheriidae), from the Pliocene of the Bolivian Altiplano. – Geodiversitas **23**: 625–645.
- SÁNCHEZ-VILLAGRA, M.R.; ASHER, R.J.; RINCÓN, A.D.; CARLINI, A.A. & PURDY, R.W. 2004. New faunal reports for the Cerro La Cruz locality (Lower Miocene), north-western Venezuela. – In: SÁNCHEZ-VILLAGRA, M.R. & CLACK, J.A., eds., Fossils of the Miocene Castillo Formation, Venezuela: Contributions in Neotropical Palaeontology. – Special Papers in Palaeontology **71**: 105–112.
- SCILLATO-YANÉ, G.J.; CARLINI, A.A. & VIZCAÍNO, S.F. 1993. Los Xenarthra (Mammalia, Edentata) del Mioceno medio Argentina. – X. Jornadas Argentinas de Paleontología Vertebrados, La Plata 1993. – Ameghiniana **30** (3): 352.
- SCILLATO-YANÉ, G.J.; CARLINI, A.A.; TONNI, E.P. & NORIEGA, J.I. 2005. Palaeobiogeography of the late Pleistocene pampatheres of South America. – In: RABASSA, J. & CARLINI, A.A., eds., Quaternary Paleontology and Biostratigraphy of Southern South America. – Journal of South American Earth Sciences **20**: 131–138.
- SIMPSON, G.G. 1930 *Holmesina septentrionalis*, an edentate from the Pleistocene of Florida. – American Museum Novitates **442**: 1–10.
- SIMPSON, G.G. 1947. A Miocene glyptodont from Venezuela. – American Museum Novitates **1368**: 1–10.
- SPILLMANN, F. 1948. Beiträge zur Kenntnis eines neuen gravigraden Riesensteppentieres (*Eremotherium carolinense* gen. et spec. nov), seines Lebensraumes und seiner Lebensweise. – Palaeobiologica **8**: 231–279.
- WOODBURNE, M.O.; CIONE, A.L. & TONNI, E.P. 2006. Central American Provincialism and The Great American Biotic Interchange. – In: CARRANZA-CASTAÑEDA, O. & LINDSAY, E.H., eds., Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange. – Universidad Nacional Autónoma de México, Instituto de Geología and Centro de Geociencias, Publicación Especial **4**: 73–101.

Manuskripteingang / manuscript received 20. 12. 2006;
 Manuskriptannahme / manuscript accepted 15. 3. 2008