Journal of Systematic Palaeontology **4** (3): 269–278
doi:10.1017/S1477201906001878 Printed in the United Kingdom
Issued 11 August 2006

First Megatheriines (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco (Late Miocene) and Codore (Pliocene) Formations, Estado Falcón, Venezuela

Alfredo A. Carlini
Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina and Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina

Diego Brandoni
Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y de Transferencia Tecnológica a la Producción (CICyTTP-CONICET), Materi y España, 3105 Diamante, Entre Ríos, Argentina

Rodolfo Sánchez
Museo Paleontológico de la Alcaldía de Urumaco, Falcón, Venezuela

SYNOPSIS Two new genera and species of Megatheriinae are described from the Neogene of Venezuela: *Urumaquia robusta* gen. et sp. nov. from the Urumaco Formation (Late Miocene) and *Proeremotherium eljebe* gen. et sp. nov. from the Codore Formation (Pliocene). These represent only the second Tertiary record of the subfamily at low latitudes in South America. The anatomical features of *Urumaquia robusta* suggest that the levels of the Urumaco Formation bearing the fauna here studied may not be correlated with the Laventan SALMA, but with Chasicoan–Huayquerian SALMAs.

KEY WORDS New taxa, Mio–Pliocene, ground sloths, Venezuela, South America

Contents

Introduction

The Quaternary ground sloths Megatheriinae are amongst the best known South American fossil mammals, with *Megatherium americanum* Cuvier, 1796, the first fossil mammal to be described from that continent (Hoffstetter 1982). By contrast, Megatheriinae from earlier deposits remain relatively poorly investigated, in part because of the fragmentary nature of their fossil record. There remains much uncertainty about the validity of many of these taxa and about their anatomy and phylogenetic relationships.

The oldest records of Megatheriinae date back to the Middle Miocene and come from the 'Friasian' interval (see Scillato-Yané & Carlini 1998) with its three successive faunas, the Colloncuran, Laventan and Mayoan. Table 1 provides a summary of the temporal and geographical distribution of all South American Megatheriinae described to date. This shows that the Megatheriinae are rare in low

Table 1 Distribution of Tertiary Megatheriinae in South America.

Taxon	Age	Location	Reference
Megathericulus patagonicus Ameghino, 1904	Middle Miocene; Colloncuran	Patagonia	Carlini *et al.* (2002*a*)
Megathericulus primaevus Cabrera, 1939	Middle Miocene; Colloncuran	Patagonia	Carlini *et al.* (2002*a*)
Megatheriinae indet.	Middle Miocene; Laventan	Colombia	Hirschfeld (1985)
Eomegatherium andinum Kraglievich, 1930	Middle Miocene; Mayoan	Patagonia	Kraglievich (1930)
Eomegatherium cabrerai Kraglievich, 1930	Middle Miocene; Mayoan	Patagonia	Kraglievich (1930)
Plesiomegatherium halmyronomum Cabrera, 1928	Late Miocene; Chasicoan	Buenos Aires Province, Argentina	Cabrera (1928)
Megatheriops rectidens (Rovereto, 1914)	Late Miocene; Huayquerian	Mendoza Province, Argentina	Rovereto (1914)
Promegatherium smaltatum Ameghino, 1883	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Carlini *et al.* (2001, 2002*a*)
Promegatherium remulsum Ameghino, 1886	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Ameghino (1886)
Promegatherium parvulum Ameghino, 1889	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Carlini *et al.* (2001, 2002*a*)
Pliomegatherium lelongi Kraglievich, 1930	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Carlini *et al.* (2001, 2002*a*)
Pliomegatherium paranensis Kraglievich, 1930	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Carlini *et al.* (2001, 2002*a*)
Eomegatherium nanum (Burmeister, 1891)	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Kraglievich, (1926); Carlini *et al.* (2001, 2002*a*)
Pyramiodontherium sp.	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Carlini *et al.* (2001, 2002*a*)
'*Megatherium*' *antiquum* Ameghino, 1885	Late Miocene–Pliocene; Ituzaingó Formation	Entre Ríos Province, Argentina	Ameghino (1885)
Pyramiodontherium bergi (Moreno & Mercerat, 1891)	Late Miocene; Huayquerian	Catamarca Province, Argentina	Cabrera, (1928); Carlini *et al.* (2002*a*)
Pyramiodontherium brevirostrum Carlini *et al.*, 2002*a*	Late Miocene; Huayquerian	Catamarca Province, Argentina	Carlini *et al.* (2002*a*)
Pyramiodontherium scillatoyanei De Iuliis *et al.*, 2004	Late Pliocene	La Rioja Province, Argentina	De Iuliis *et al.* (2004)
Megatherium istilarti Kraglievich, 1925	Pliocene; 'Irenense'	Buenos Aires Province, Argentina	Kraglievich (1925)
Megatheridium annectens Cabrera, 1928	Pliocene; 'Rionegrense'	Buenos Aires Province, Argentina	Cabrera (1928)
Plesiomegatherium hansmeyeri Roth, 1911	Pliocene?	?Jujuy Province, Argentina	Rovereto (1914); Cabrera (1928); De Iuliis *et al.* (2004)
Megatherium altiplanicum Saint-André & De Iuliis, 2001	Pliocene	Bolivia	Saint-André & De Iuliis (2001)
Eremotherium eomigrans De Iuliis & Cartelle, 1999	Pliocene; Late Blancan to Early Irvingtonian	Florida, North America	De Iuliis & Cartelle (1999)
Plesiomegatherium. sp.	Pliocene, Codore Formation	Urumaco, Venezuela	Linares (2004)
Megatheriine indet.	Middle Miocene	Quebrada Honda, Bolivia	Carlini *et al.* (2002*b*)

latitudes. Consequently, the new material described here significantly increases our knowledge of megatheriine diversity in northern South America.

Abbreviations used

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; **MCL**, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Brazil; **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 America Land Mammal Age; **UCMP**, Museum of Paleontology, University of California, Berkeley, USA.

Systematic palaeontology

XENARTHRA Cope, 1889

PHYLLOPHAGA Owen, 1842

MEGATHERIOIDEA Gray, 1821

MEGATHERIIDAE Gray, 1821

MEGATHERIINAE Gray, 1821

Genus ***URUMAQUIA*** nov.

Etymology. *Urumaquia*, from Urumaco, its geographical provenance.

Type species. *Urumaquia robusta* gen. et sp. nov.

Distribution. Urumaco, Estado Falcón, Venezuela; Urumaco Formation, Late Miocene (Ministerio de Energía y Minas 1997; Aguilera 2004).

Diagnosis. A middle to large-sized Megatheriinae, larger than *Plesiomegatherium halmyronomum*, *Megathericulus*, *Eomegatherium*, *Pliomegatherium*, *Promegatherium* 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*a*) and smaller than *Megatherium americanum* Cuvier, 1796 and *Megatherium gallardoi* Ameghino & Kraglievich, 1921; *Eremotherium laurillardi* (Lund 1842) and *E. eomigrans*. Tibia distally very thick, with the diaphysis curved and shallow grooves for the foot extensor tendons (shallower than in *Megatherium* and *Eremotherium*). The angle between the odontoid and discoid facets is approximately 100° (90° in *Py. bergi* and *Py. scillatoyanei*, between 100° and 120° in *Megatherium* and *Eremotherium laurillardi*). Nearly one half of the navicular facet is dorsal with respect to the plane of the discoid facet (cf. *Pyramiodontherium* spp., *E. laurillardi* and *Megatherium urbinai*, where 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 dorsoventrally convex, entirely articular and inclined along a dorsolateral to ventromedial axis.

Urumaquia robusta sp. nov. (Fig. 1)

Etymology. *Robusta*, in reference to its general robustness.

Holotype. MCN 91-72v, left astragalus (with the odontoid process broken at its base) and left distal tibia.

Type locality. As for genus.

Referred material. MCN 74-72v (in part, not the fragment of a distal humerus), right metatarsal III and MCN 5-72v, left humerus of a juvenile specimen, without epiphyses.

Occurrence. As for genus.

Diagnosis. As for genus.

Description

Tibia (Figs 1A & B)

The distal epiphysis is thick, without the strong differences in diameter between epiphysis and distal diaphysis observed in most other megatheriines. The small preserved portion of the diaphysis shows a marked curvature of the axis. The tendinous impressions of the foot extensors are slightly marked and the medial malleolus projects slightly medially, but less so than in *Pyramiodontherium* species (Carlini *et al*. 2002*a*). The astragalar facet of the tibia has a wide facet for the odontoid process as in *Py. brevirostrum* (MLP 31-XI-12-25) and *Py. scillatoyanei* (MLP 68-III-14-1) (similar to most of the Quaternary taxa) and relatively wider than that of *Py. bergi* (MLP 2-66). The discoid facet is similar in development to *Pyramiodontherium* species. 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 *Py. brevirostrum* and 87° in *Py. bergi*. These particular features for a distal tibia of a Megatheriinae could be interpreted as pathological. However, there is neither evidence suggesting any kind of fracture and posterior welding, nor alterations of the articular surfaces that would indicate illness. Hence, we think that this morphology is normal for the species.

Astragalus (Figs 1C & D; Table 2)

This has the typical shape for Megatheriinae (see De Iuliis 1996; Brandoni *et al*. 2004). It is massive, with a well-developed central odontoid process in dorsomedial view and a navicular facet in anterior view. As in other megatheriines, the fibular facet is divided into two main areas, an anteroposteriorly elongated dorsal portion (that joins the discoid facet dorsally) and a ventral facet with a rounded surface slightly extended ventrally. A similar form can be observed in *Py. bergi* (MLP 2-66) and in *Py. scillatoyanei* (MLP 68-III-14-1). In the former, and also in *Eomegatherium nanum* (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 and 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*

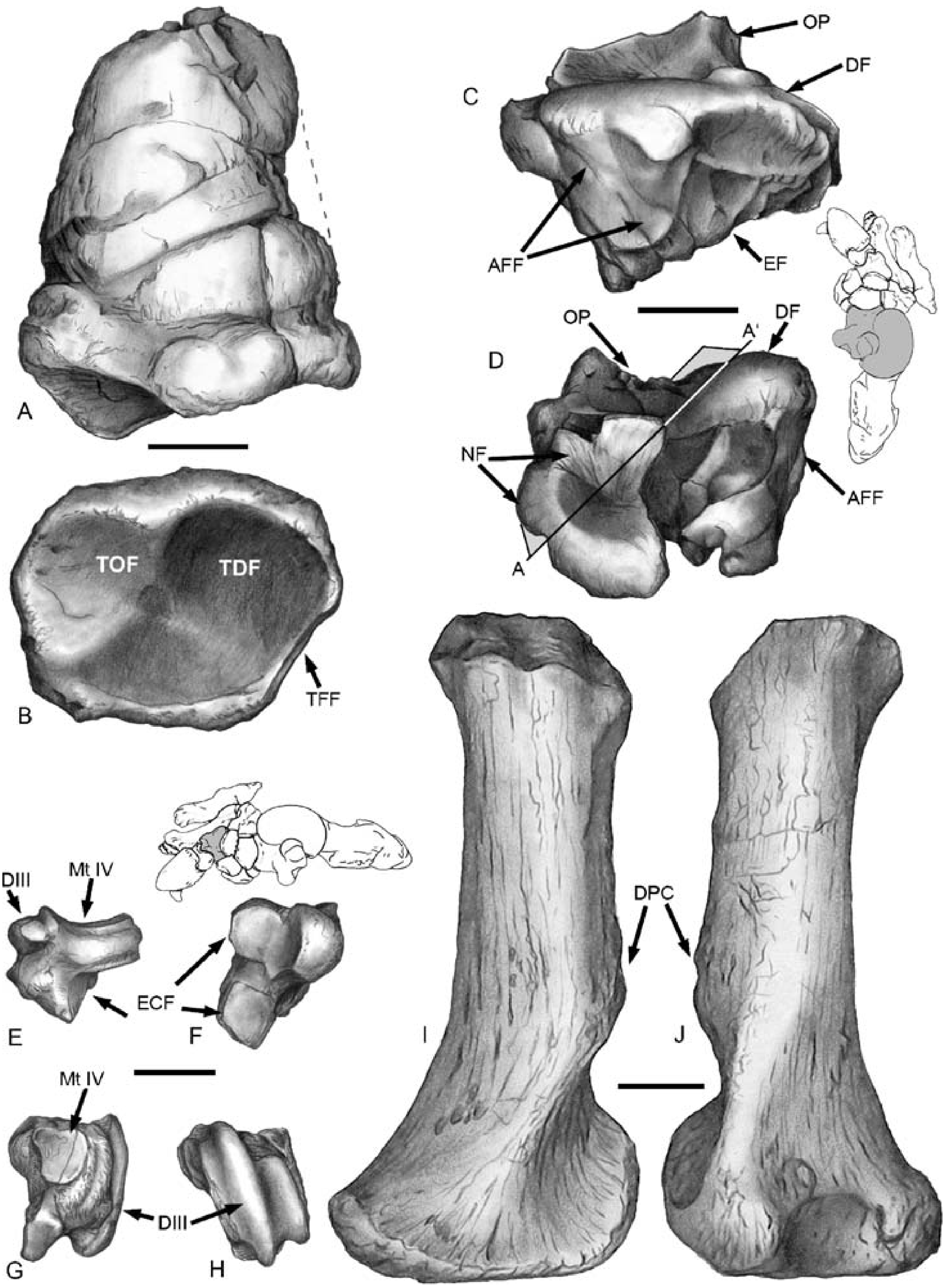

Figure 1 *Urumaquia robusta* gen. et sp. nov. **A**, **B**, left tibia (MCN 91-72): A, anterior view; B, distal view. **C**, **D**, left astragalus (MCN 91-72)**:** C, fibular view; D, anteromedial view (note that this bone is shown in a slightly more dorso-medial view in the reconstruction than in Pujos & Salas (2004*a*) and De Iuliis *et al.* (2004), affecting the apparent position of plane A–A′). **E–H**, right metatarsal III (MCN 74-72): E, dorsolateral view; F, posterolateral view; G, lateral view; H, distal view. **I**, **J**, left humerus (MCN 5-72): I, anterior view; J, posterior view. In the reconstruction the grey area represents the projection of the A–A′ plane. Abbreviations: AFF, astragalar fibular facet; D III, digit III; DF, discoid facet; DPC, deltopectoral crest; ECF, ectocuneiform facet; EF, astragalar ectal facet; Mt IV, metatarsal IV; NF: navicular facet; OP: odontoid process. TDF, tibial discoid facet; TFF, tibial fibular facet; TOF, tibial odontoid facet. A–A′, projection line of the plane of the discoid facet. Scale bars = 50 mm.

Table 2 Measurements of astragali in Megatheriines.

Taxon	Specimen	Length	Width
Urumaquia robusta	MCN 91-72	175	144†
Megathericulus patagonicus	MLP 91-IX-7-18	99	103
Megathericulus patagonicus	MLP 92-XI-15-2	95	100
Eomegatherium nanum	MACN-Pv-4992	130	130
Pyramiodontherium scillatoyanei	MLP 68-III-14-1	155	141
Pyramiodontherium bergi	MLP 2-66	175	162
Megatherium lundi	MLP 2-30	182	165
Megatherium lundi	MLP 2-31	195	185
Megatherium americanum	MLP 2-207	218	225
Megatherium americanum	MLP 44-XII-28-1	240	209
Megatherium americanum	MLP 2-29	245	230

† Incomplete.

Table 3 Measurements of humeri of Megatheriines.

Taxon	Specimen	Total Length	Distal Width
Urumaquia robusta	MCN 5-72v	384	175
Megatheriops rectidens	MACN-Pv-2818	482	183
Pyramiodontherium bergi	MACN-Pv-2654	555	190
Pyramiodontherium scillatoyanei	MLP 68-III-141	595	188
Megatherium gallardoi†	MACN-Pv-5002	787	368
Megatherium americanum†	MLP 28-III-16-2	721	316
Megatherium americanum†	MLP 41-II-28-1	710	340
Megatherium tarijense†	FMNH P14216	527	219
Eremotherium laurillardi†	MCL 849	782	346
Eremotherium laurillardi†	MCL 860	739	307
Eremotherium laurillardi†	MCL 861	781	317

† From De Iuliis (1996).

robusta only the base of the odontoid process, with the odontoid facet, is preserved. The angle between the odontoid and discoid facets is approximately 100°, whereas it is nearly 90° in *Py. bergi* and *Py. scillatoyanei* and more obtuse in the remaining members of the Megatheriinae. The facet for the navicular, on the anterior-most part of the astragalus, has its major axis orientated dorsolaterally to ventromedially. The concave dorsolateral portion of the navicular facet, termed the astragalar depression, is similar but more circular than those of *Py. bergi* (see Brandoni *et al*. 2004). The astragalar depression is deeper in *M. americanum* than in *U. robusta*, *Py. bergi*, *Py. scillatoyanei* and *Eo. nanum*. 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., *E. 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 as the discoid facet plane (Fig. 1D). There are two facets for articulation with the calcaneum, the reduced sustentacular facet and the large ectal facet, separated by a deep and wide non-articular bony canal, the *sulcus tali*.

Metatarsal III (Fig. 1E-H)

In megatheriines, metatarsal III is short compared to metatarsals IV–V. In *U. robusta*, the posterior half is not strongly transversely compressed as in *Py. bergi* (see Brandoni *et al*. 2004), whereas in other megatheres (e.g. *E. laurillardi*), this portion is shorter (Paula Couto 1978). The ectocuneiform facet is posteromedially orientated and divided into two subcircular areas. The small mesocuneiform facet is subtriangular with the apex pointed dorsally and with a strong plantar concavity. It occupies the medial face of metatarsal III and articulates with the mesocuneiform or with the meso-entocuneiform complex (if present: Brandoni *et al*. 2004). The facet for metatarsal IV is lateral, oval in shape and dorsoventrally extended. The surface undulates slightly and is nearly parallel to the proximal surface of the ectocuneiform facet. In *Py. bergi*, between the ectocuneiform and metatarsal IV facets, there is a posterolateral projection that supports an oval cuboid facet (Brandoni *et al*. 2004: fig. 5 d-e). In *Urumaquia robusta* this projection is broad and more robust than in other megatheriines, without a facet for the cuboid. On the distal surface a carinate articulation (to digit III) is slightly dorsoventrally convex and inclined along the dorsolateral to ventromedial axis. This crest is entirely articular, in contrast to the situation in *Py. bergi, E. laurillardi* and *Megatherium americanum,* where the medial part is not articular. An elongated internal surface continues beyond the crest to complete the articulation. On the most ventrolateral portion of metatarsal III there is a plantar tuberosity, less developed than in *Py. bergi*.

Humerus (Figs 1I & J; Table 3)

The humerus referred here to *Urumaquia robusta* belongs to a juvenile specimen since the epiphyses are not fused and have been lost. It has the general shape of those of other Tertiary megatheriines and, as in some megalonychids, planopines and nothrotheres, it is relatively elongated and slender. The entepicondylar foramen (present in megalonychids) is absent. Distally the humerus is wide but compressed anteroposteriorly and its posterior surface is almost flat. Perhaps due to its immaturity, the proximal third of the diaphysis is subtrapezoidal in section and the two distal thirds seems to be more compressed than in Quaternary species. In *Py. scillatoyanei* (MLP 68-III-14-1) the cross-section of the proximal third is less depressed and is irregular in shape, while the distal third is subtrapezoidal in shape with the angles more rounded. In *Py. brevirostrum* (MLP 31-XI-12-25) only the proximal epiphysis of the right humerus is preserved; its head is well developed and clearly separated from the tuberosities, which are at an angle of 115° to each other (Carlini *et al*. 2002*a*: fig. 4); the cross-section of the diaphysis immediately below the tuberosities is subtrapezoidal. In *U. robusta*, the deltopectoral crest is well developed as in other Tertiary megatheriines (e.g. *Megathericulus patagonicus* MLP 91-IX-7-18, *Megatheriops rectidens* MACN Pv-2818, *Py. scillatoyanei* MLP 68-III-14-1). It is formed by the pectoral crest and laterally by the deltoid crest, which join approximately at the distal third of the diaphysis. As in *Megathericulus patagonicus* (see De Iuliis 2003: plate 3 [N.B. the caption for this plate is that of his plate 4 and that shown in plate 3 belongs to plate 6]), the deltopectoral crest in *U. robusta* seems to be more lateral than in most other megatheriines. In Pleistocene megatheriines (*Megatherium* and *Eremotherium*), the deltopectoral crest is less developed, being reduced to a prominence located at the centre of the diaphysis (in anterior view). The humerus UCMP 41115 of an undetermined megatheriine from the Miocene of La Venta, Colombia (Hirschfeld 1985: fig. 33), also has a developed deltopectoral crest, although less lateral and more proximally placed at the diaphysis.

Genus ***PROEREMOTHERIUM*** gen. nov.

Type species. *Proeremotherium eljebe* gen. et sp. nov. No other species known.

Etymology. From 'pro', before and 'eremotherium', genus of Quaternary Megatheriinae of intertropical distribution.

Diagnosis. A middle-sized megatheriine, similar in size to *Plesiomegatherium halmyronomum*, larger than most species of *Megathericulus*, *Eomegatherium*, *Pliomegatherium*, *Promegatherium* and *Eremotherium sefvei*; a little smaller than the species of *Pyramiodontherium* and some species of *Megatherium* (*M. medinae*, *M. lundi*, *M. tarijense* and *M. urbinai*) and much smaller than *Megatherium americanum*, *Megatherium gallardoi, Eremotherium laurillardi* and *E. eomigrans*. Skull roof slightly convex in the middle third and anterior portion of the maxillary strongly triangular in shape; post-orbital apophysis absent. Occipital condyles placed in a plane very close to the palatal plane; ventral margin of the zygomatic process of squamosal almost at the height of the dorsal part of the occipital condyle; the palatal roof and the margin of the alveolar series are at the same level; the palatal notch located at the level of the anterior half of M4; the palatal width slightly larger than the width of the largest alveolus. Dental series are lingually convex and labially straight.

Occurrence. 1.5 km Northwest of Cerro Chiguaje, Urumaco, Estado Falcón, Venezuela; middle member, 'El Jebe', of the Codore Formation, Pliocene (Ministerio de Energía y Minas 1997; Aguilera 2004).

Remarks. *Proeremotherium* is closely related to *Eremotherium*, a Quaternary megatheriine genus distributed almost exclusively at low latitudes of South, Central and North America (Cartelle & De Iuliis 1995; Pujos & Salas 2004*a*), but is distinguished by its size, by the triangular shape of the predental part of its rostrum and by its lower condyles (see Table 4).

Proeremotherium eljebe sp. nov. (Fig. 2)

Etymology. In reference to its stratigraphic provenance.

Holotype. AMU-CURS 126, well preserved skull without jugals, premaxillae, right M1, M4-M5 and left M2-5.

Occurrence. As for genus.

Diagnosis. As for genus.

Description. The skull of *Proeremotherium eljebe* is 460 mm in total length. It is a low skull, elongated and slender. In lateral view, the upper portion of the skull is slightly convex in its middle third and slightly concave at the sagital midline of the parietals, similar to *E. eomigrans* (De Iuliis & Cartelle 1999: figs 3a & 4a), but in contrast to *Pyramiodontherium*, *Megatheriops* and *Megatherium,* where the dorsal shape of the skull is sigmoid and there is a marked depression located at the level of the naso-frontal suture.

In dorsal view (Fig. 2A), the top of the skull has strong sagittal crests forming a laterally concave arch. The crests converge along the skull midline for the first half of its total length, then diverge anteriorly to end over the zygomatic root of the maxilla. The surface delimited by the crests is even and there is no post-orbital apophysis, somewhat like the arrangement in some Santacrucian tardigrades (e.g. *Planops, Prepotherium* and *Hapalops*) and probably *Megathericulus*. In front of the zygomatic roots of the maxilla the rostrum has a strongly triangular shape, which is not observed in any other genus. As in *Eremotherium*, and unlike *Megatherium, Pyramiodontherium*, and *Plesiomegatherium halmyronomum*, the occipital condyles are placed in a plane very close to the palatal plane (Fig. 2*b*, Table 4). The difference between these planes reaches its maximum in *M. americanum* and *M. gallardoi* (see Ameghino & Kraglievich 1921; De Iuliis 1996; Bargo 2001; Pujos & Salas 2004*a*, *b*).

In lateral view (Fig. 2*b*), the zygomatic root of the maxilla is short, located at the level of the boundary of M1–M2 to M2–M3, in a low position to the infraorbital foramen, 22 mm above the alveolar margin. This root position is similar to that of most megatheriines, although the foramen is closer with respect to the alveolar margin than in other megatheriines (i.e. *Py. bergi* $\approx$ 60 mm, *Py. brevirostrum* $\approx$ 70 mm, *Pl. hansmeyeri* $\approx$ 38 mm, *Pl. halmyronomum* $\approx$ 40 mm). In

Table 4 Measurements of skulls in Megatheriines.

Taxon	Specimen	M1OCL	OCH	OPTH	TL
Proeremotherium eljebe	AMU-CURS 126	416	39	128	169
Megatheriops rectidens†	MACN-Pv-2818	365	119	117	173
Pyramiodontherium bergi	MLP 2-66	420	122	78	200
Plesiomegatherium halmyronomum	MLP 26-IV-10-1	355	100	80	132
Megatherium gallardoi†	MACN-Pv-5002	625	230	125	240
Megatherium americanum†	MACN-Pv-1000	466	194	97	
Megatherium americanum†	MLP 2-64	571	211	139	239
Eremotherium laurillardi†	MCL 1700/01	534	112	170	214
Eremotherium laurillardi†	MCL 170101	523	110	174	214

M1OCL, M1 to occipipital condyle linear distance; **OCH**, palatal plane to middle line occipital condyle distance; **OPTH**, middle line occipital condyle to skull roof distance; **TL**; toothrow length; †From De Iuliis (1996).

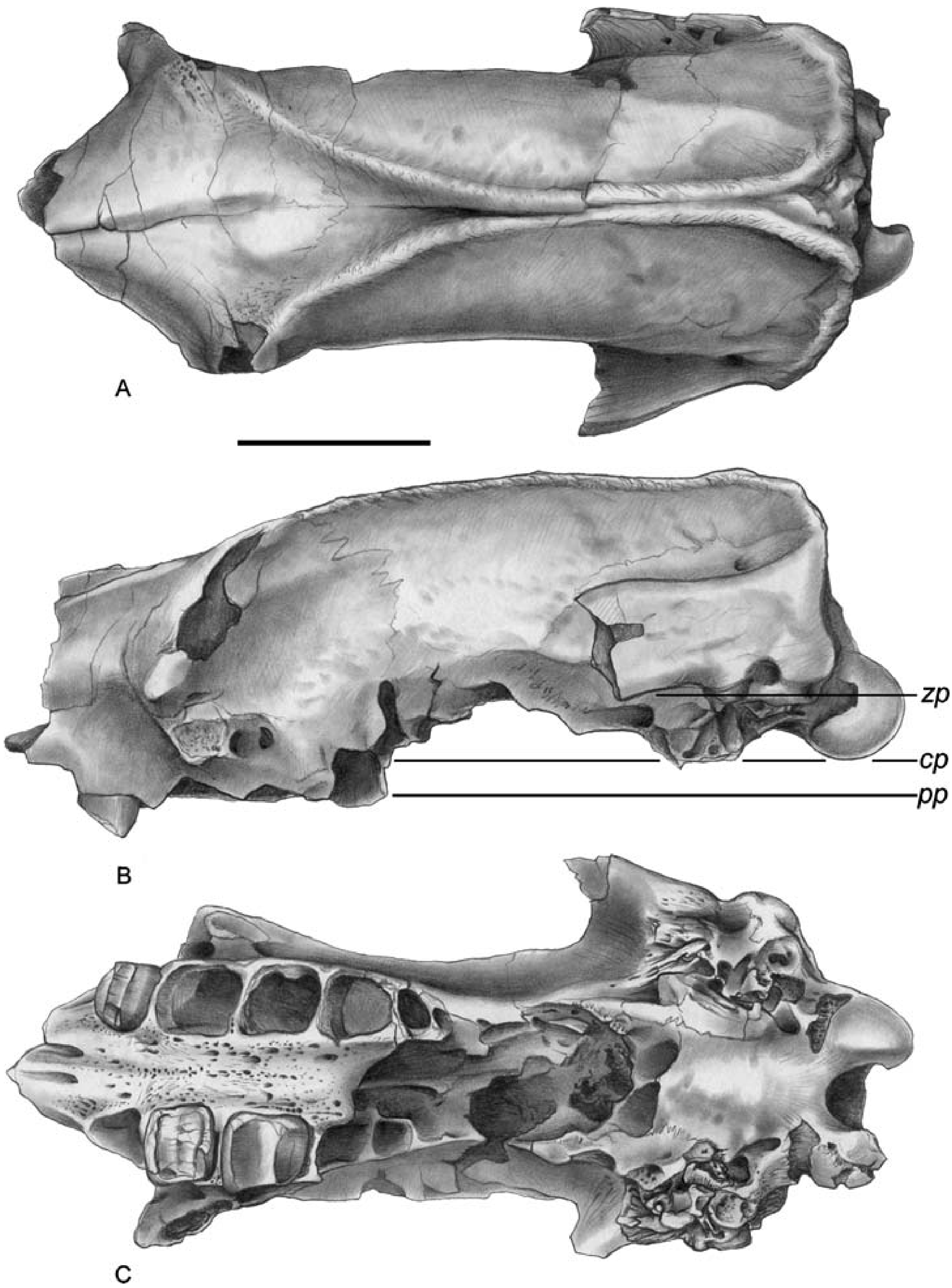

Figure 2 *Proeremotherium eljebe* gen. et sp. nov. **A–C**, skull of the holotype (AMU-CURS 126): A, dorsal view; B, left lateral view; C, palatal view. Abbreviations: *cp*, condylar plane; *pp*, palatal plane; *zp*, zygomatic plane. Scale bar = 100 mm.

Megathericulus patagonicus, the foramen is located slightly more posteriorly than it is in *Pr. eljebe*, where it is level with the middle part of M2 and half of M3. The squamosal zygomatic root is high and laminar and its ventral margin is almost at the height of the dorsal part of the condyle (Fig. 2B). This arrangement is similar to that seen in *E. eomigrans* and *E. laurilliardi* but unlike that of some species of *Megatherium* (e.g. *M. americanum* and *M. gallardoi*) in which the ventral margin is lower (without reaching the middle of the condyle).

In palatal view (Fig. 2C), the predentary region seems to be short and narrow and bears two asymmetric palatine foramina, which continue anteriorly as a pair of furrows. The anterior part of the maxillae is broken and the contact with the premaxillae is not visible. The lateral margins of the rostrum are roughly parallel (and may even be convergent distally), whereas in *Py. brevirostrum*, *Py. bergi* and *Megathericulus patagonicus,* after a predentary constriction, the palate expands like a spatula. An analogous morphology occurs in species of *Planops* and *Hapalops* (see Scott 1903–05; Hoffstetter 1961). Generally, the palate is strikingly flat (especially the predentary portion). In addition, the palatal roof and the margin of the alveolar series lie in the same plane, as they do in *Megathericulus patagonicus*, *Pl. halmyronomum*, *Eo. andinum* and *E. laurillardi*. In other megatheriines (e.g. *Megatheriops rectidens*, *Py. bergi* and *M. americanum*), the palatal roof is concave and the alveolar and palatal planes do not coincide. In *Pl. hansmeyeri* the palatal roof is not completely preserved, but in medial view the planes are not coincidental. In *Pr. eljebe*, the palatal notch is placed level with the anterior half of M4, while in *Megatheriops rectidens* it is level with the interalveolear limit of M4–M5 and in *Megathericulus*, *Pyramiodontherium* and *Eremotherium*, it is level with or posterior to M5. In *Pr. eljebe* the palatal width is slightly larger than the width of the largest alveolus, as in *Pl. halmyronomum*, *Megatheridium annectens* (Cabrera 1928: pl. 1, fig. b), *E. laurillardi* and *E. eomigrans*. In *Megathericulus patagonicus*, the palatal width between the tooth rows is slightly less than the width of the largest alveolus, because the molariforms are extremely wide. In *Megatherium americanum*, *Megatherium altiplanicum* (Saint-André & De Iuliis 2001: fig. 3d), *Py. bergi*, *Py. brevirostrum* (Carlini *et al.* 2002*a*: figs 1a & b) and *Megatheriops rectidens*, the distance between the dental series is less than the width of the largest molariform.

In Megatheriinae the upper dental series is formed by five molariforms and the lower by four. In both series, molariforms are closely spaced, without diastema and the distance between them is constant. This contrasts with the arrangement in other sloths (e.g. some Nothrotheriinae, Planopinae and Megalonychidae) where a diastema may appear between the first tooth (generally termed caniniform) and the rest, referred to as molariforms. In most Megatheriinae, the molariforms are quadrangular in section (square, rectangular, or trapezoid) with well-marked corners (for examples of Megatheriinae with molariforms that are not square see De Iuliis *et al*. 2004). Two well-developed transversal crests separated by a 'V'-shaped valley are present on the occlusal surface of each molariform tooth (except M5). The upper dental series are 169 mm long (almost 36.7% of the total preserved skull length), lingually convex and labially straight. In *Py. bergi* and *Megathericulus patagonicus* the dental series converge slightly to the anterior and are lingually slightly concave and labially convex. Generally the upper molariforms of *Pr. eljebe* are sub-squared as in *Megatheriops rectidens*, *Megatherium americanum* and other advanced megatheriines, but unlike *Megathericulus patagonicus*, where the upper molariforms must have been rectangular, to judge from the alveolar morphology. The left M1 and the right M2–3 and the alveoli of the left M2–5 and right M1, M4–5 are preserved in the Venezuelan specimen. M1–4 are essentially as wide as long and M5 is wider than long. M1 and M4 are trapezoidal in shape and M2–3 are subquadrangular. M5 is markedly rectangular, with the anterior side of the alveolus being slightly convex and the posterior concave.

Remarks. Linares (2004) initially referred the holotype of *Proeremotherium eljebe* to *Plesiomegatherium s.l.* (sic).

Discussion

The new species reported here represent the first Tertiary Megatheriinae from Venezuela and the second record of this clade at low latitudes in South America (the first being the specimens from the middle Miocene of La Venta, Colombia described by Hirschfeld (1985) and McDonald (1997)). The megatheriine remains from La Venta illustrated by Hirschfeld (1985: fig. 33) probably represent two different taxa, comparable to *Megathericulus* (cf. *M. patagonicus*) and *Eomegatherium* (cf. *E. cabrerai*) both from the Mayoan of the Argentine Patagonia. Consequently, during the middle Miocene megatheriines were probably distributed through most of western South America.

The two new genera and species from the Late Miocene–Pliocene of Venezuela, each show a set of uniquely distinctive features. *Urumaquia robusta* is similar in size to, and even larger than, the species of *Pyramiodontherium*, *Megatheriops* and '*Megatherium*' *antiquum,* from the Late Miocene–Pliocene of Argentina but is more robust (see Tables 2, 3). Furthermore, some characters of the astragalus (location of the navicular facet with respect to the plane of the discoid facet, relationship between the ventral portion of the fibular and ectal facet) suggest this taxon is more derived than those found in the Middle Miocene of Argentina and, very probably, those of the Middle Miocene of La Venta, Colombia, where smaller and more gracile megatheriines than *Urumaquia robusta* are recorded. These differences suggest that the Late Miocene levels of the Urumaco Formation bearing the megatheriines are not correlated with the Middle Miocene Laventan SALMA but more probably correlate with the Chasicoan–Huayquerian SALMAs. Clearly the biochronology developed for the southern part of South America has to be refined to incorporate the new data from Venezuela. Many examples show that faunas are much more stable at low latitudes (e.g. McKenna 1956; Carlini *et al.* 1997) retaining taxa with evolutionary stages interpreted as primitive in faunas of high latitudes.

In summary, *Eremotherium* has three valid species, *E. eomigrans* (with a temporal range from 2.1 to 1.1 Ma, probably extending to 2.5 Ma), *E. sefvei* and *E. laurillardi*. *Eremotherium eomigrans* is the first Megatheriinae to have entered North America after the formation of the Panama Isthmus (De Iuliis & Cartelle 1999). Regarding the relationships between the species of *Eremotherium*, De Iuliis & Cartelle (1999) stated that *E. eomigrans* and *E. laurillardi* formed an ancestor-descendant sequence. No ancestral forms of *Eremotherium* are yet known and *Proeremotherium eljebe* shows many of the expected characters for an ancestor, something that should be tested in a phylogenetic analysis.

Acknowledgements

We wish to thank A. Mercader, M. López and A. Pulgar at the CIAAP and M. Arispe, C. Silvera and E. Nóbrega at the MCN, for their assistance and permission to study the collections under their care; C. Villalba and A. Pulgar for help and camaraderie in the field; Dr O. Aguilera for his hospitality and assistance during the work of A. A. Carlini in Venezuela; Drs M. Reguero (MLP) and A. Kramarz (MACN) for allowing us access to the collection of their respective institutions; Dr G. J. Scillato-Yané, M. R. Sánchez-Villagra and A. Smith for the critical review of the manuscript which certainly improved it. We also thank the two reviewers, Dr F. Pujos and Dr G. De Iuliis, for their valuable comments and suggestions and Dr C. Deschamps for the English translation of the manuscript. Illustrations are the work of J. Gonzalez. The work of A. A. Carlini in Venezuela was supported by the Committee for Research and Exploration of the National Geographic Society (Grant 7600-04 to M. R. Sánchez-Villagra) and PICT-R 0074 G3 (to A. A. Carlini). Finally, we wish especially to thank M. R. Sánchez-Villagra for inviting us to study this wonderful Xenarthran fauna in Venezuela.

References

Aguilera, O. 2004. *Tesoros paleontológicos de Venezuela: Urumaco patrimonio natural de la Humanidad*. Universidad Nacional Experimental Francisco de Miranda. Ed. Arte: Coro, Venezuela, 148 pp.

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.

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.

— 1885. Nuevos restos de mamíferos fósiles Oligocenos recogidos por el Profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la ciudad de Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* **8**: 5–207.

— 1886. Contribuciones al conocimiento de los mamíferos fósiles de los terrenos terciarios antiguos del Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* **9**: 5–228.

— 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas Academia Nacional Ciencias Córdoba* **6**: 1–1027.

— 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina* **58**: 225–291.

Bargo, M. S. 2001. The ground sloth *Megatherium americanum*: skull shape, bite forces, and diet. *Acta Palaeontologica Polonica* **46**: 173–192.

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 la adición 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.

— 1939. Un nuevo representante Santacrusense de la Familia Megatheriidae. *Notas del Museo de La Plata, Paleontología* **4**: 475–483.

Carlini, A. A., Vizcaíno, S. F. & Scillato-Yané, G. J. 1997. Armored Xenarthrans: a unique taxonomic and ecologic assemblage. Pp. 213–226 *in* R. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn (eds) *Vertebrate Paleontology on the Neotropics. The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press: Washington and London.

—, Scillato-Yané, G. J., Noriega, J. I. & Aceñolaza, F. 2001. Perezosos terrestres (Xenarthra, Tardigrada) del "Mesopotamiense" (Fm. Ituzaingó, Mioceno tardío-Plioceno) de la Provincia de Entre Ríos, Argentina. *Studia Geologica Salmanticensia* **36**: 13–27.

—, Brandoni, D., Scillato-Yané, G. J. & Pujos, F. 2002*a*. Una nueva especie de megaterino (Xenarthra, Megatheriidae) del Mioceno tardío-Plioceno de Catamarca, Argentina. *Ameghiniana* **39**: 367–377.

—, Scillato-Yané, G. J. & Brandoni, D. 2002*b*. Un nuevo tardígrado (Mammalia, Xenarthra) del Mioceno Medio de Quebrada Honda, Bolivia: el más antiguo Megatheriinae? *VIII Congreso Argentino de Paleontología y Bioestratigrafía*. **Resúmenes: 98**. Corrientes, Octubre 2002, Argentina.

Cartelle, C. & De Iuliis, G. 1995. *Eremotherium laurillardi*: the panamerican Late Pleistocene Megatheriid sloth. *Journal of Vertebrate Paleontology* **15**: 830–841.

Cope, 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)*. Unpublished PhD Thesis: University of Toronto, Canada, 781 pp.

— 2003. Toward a morphofunctional understanding of the humerus of Megatheriinae: the identity and homology of some diaphyseal humeral features (Mammalia, Xenarthra, Megatheriidae). *Senckenbergiana Biologica* **83**: 68–78.

— & 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.

— & Saint-André, P. A. 1997. *Eremotherium sefvei* nov. sp. (Mammalia: Xenarthra: Megatheriidae) from the Pleistocene of Ulloma, Bolivia. *Geobios* **30**: 453–461.

—, 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**: 214–227.

Gervais, H. & Ameghino, F. 1880. *Los mamíferos fósiles de la América del Sud*. Ignon Hermanos: Paris and Buenos Aires.

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.

Hoffstetter, R. 1961. Description d'un squelette de *Planops* (Gravigrade du Miocène de Patagonie), *Mammalia* **25**: 57–96.

— 1982. Les Edentes Xenarthres, un groupe singulier de la faune Neotropicale. Pp. 385–443 *in* E. Montanaro Gallitelli (ed.) *Proceedings of the First Meeting on "Paleontology, Essentials of Historical Geology"*. STEM Mocchi Modena Press: Modena, Italy.

Gray, J. E. 1821. *Catalogue of Carnivorous, Pachydermatous, and Edentate Mammalia in the British Museum*. British Museum: London, 398 pp.

Kraglievich, L. 1925. Cuatro nuevos gravígrados de la fauna araucana chapadmalense. *Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia"* **33**: 215–235.

— 1926. Notas sobre gravígrados de Sud América. *Anales del Museo Nacional de Historia Natural de Buenos Aires* **34**: 21–36.

— 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. Bioestratigrafía de la fauna de mamíferos de las Formaciones Socorro, Urumaco y Codore (Mioceno Medio–Plioceno Temprano) de la región de Urumaco, Falcón, Venezuela. *Paleobiología Neotropical* **1**: 1–26.

Lund, P. W. 1842. Blik paa Brasiliens dyreverden for sidste jordomvaeltning. Fjerde afhandling: fortsaettelse af pattedyrene. *Detkongelige Danske Videnscavernes Selskabs Skrifter; Naturvidenskabelige og mathematisk Afhandlinger* **9**: 137–208.

McDonald, H. G. 1997. Xenarthrans: Pilosans. Pp. 233–245 *in* R. F. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn (eds) *Vertebrate Paleontology* *of the Neotropics. The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press: Washington and London.

McKenna, M. C. 1956. Survival of primitive notoungulates and condylarths into the Miocene of Colombia. *American Journal of Science* **254**: 736–743.

Ministerio de Energía y Minas. 1997. *Léxico estratigráfico de Venezuela* (Tercera Edición). Ministerio de Energía y Minas, Boletín de Geología, **12**, 818 pp.

Moreno, F. P. & Mercerat, A. 1891. Exploración arqueológica de la Provincia de Catamarca: paleontología. *Revista del Museo de La Plata* **1**: 222–236.

Owen, 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*. R. & J. Taylor, London.

Paula Couto, C. de. 1978. Mamíferos fósseis do Pleistoceno do Espírito Santo. *Anais da Academia Brasileira de Ciências* **50**: 365–379.

Philippi, R. A. 1893. Vorläufige nachricht über fossile säugethierknochen von Ulloma, Bolivia. *Zeitschrift der deutschen geologischen Gesellschaft* **45**: 87–96.

Pujos, F. & Salas, R. 2004*a*. A new species of *Megatherium* (Mammalia: Xenarthra: Megatheriidae) from the Pleistocene of Sacaco and Tres Ventanas, Peru. *Palaeontology* **47**: 579–604.

— & — 2004*b*. A systematic reassessment and paleogeographic review of fossil Xenarthra from Peru. *Bulletin Institute Francaise Etudes Andines* **33**: 331–377.

Roth, S. 1911. Un Nuevo Género de la Familia 'Megatheridae'. *Revista del Museo de La Plata* **18**: 7–21.

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.

Scillato-Yané, G. J. & Carlini, A. A. 1998. Nuevos Xenarthra del Friasense (Mioceno medio) de Argentina, *Studia Geologica Salmanticensia* **34**: 43–67.

Scott, W. B. 1903–1905. Mammalia of the Santa Cruz Beds. Part 1: Edentata. *Reports of the Princeton University to Patagonia* **5**: 1–364.