Rivista Italiana di Paleontologia e Stratigrafia	volume 115	no. 1	pp. 111-123	March 2009

ON THE PRESENCE OF *PYRAMIODONTHERIUM* (MAMMALIA, XENARTHRA, MEGATHERIIDAE) IN THE LATE MIOCENE OF NORTHEASTERN ARGENTINA AND ITS BIOGEOGRAPHICAL IMPLICATIONS

DIEGO BRANDONI [1] & ALFREDO A. CARLINI [2]

Received: March 25, 2008; accepted: October 8, 2008

Key words: Argentina, Biogeography, Late Miocene, Megatheriinae, *Pyramiodontherium*, Systematics.

Abstract. The biochron of the subfamily Megatheriinae, large to very large terrestrial sloths typified by *Megatherium* Cuvier, in Argentina extends from the middle Miocene of Patagonia to the late Pleistocene-early Holocene. Megatheriines reached their highest diversity in the lower levels (="conglomerado osífero", Late Miocene) of the Ituzaingó Formation in Entre Ríos Province, northeastern Argentina. Among the four megatheriines that occur in this unit, the genera *Promegatherium* Ameghino, *Eomegatherium* Kraglievich and *Pliomegatherium* Kraglievich represent relatively small to medium-sized taxa. Here we describe new material assigned to *Pyramiodontherium,* the largest of the four genera from the same bed and comparable in size to some Quaternary species of *Megatherium*. Three valid species of *Pyramiodontherium* have been recognized, all distributed mainly in northwestern Argentina, from the Late Miocene in Catamarca Province (and probably also in Tucumán Province), and the late Pliocene in La Rioja Province. The presence of this genus in northeastern Argentina extends its known paleobiogeographical distribution.

Riassunto. Il biochrono della sottofamiglia Megatheriinae, tardigradi di dimensioni anche molto grandi esemplificati da *Megatherium* Cuvier, si estende in Argentina dal Miocene Medio della Patagonia sino al tardo Pleistocene-Olocene basale. I megatheriini raggiunsero la loro diversità più pronunciata nei livelli inferiori (="conglomerado osífero", tardo Miocene) della Formazione Ituzaingó nella Provincia di Entre Ríos, nel nordest dell'Argentina. Tra le quattro forme di megatheriini che si trovano in questa unità, i generi *Promegatherium* Ameghino, *Eomegatherium* Kraglievich e *Pliomegatherium* Kraglievich rappresentano taxa di taglia da relativamente piccola a media. Si descrive qui nuovo materiale attribuito a *Pyramiodontherium,* la forma di maggiori dimensioni tra i quattro generi dello stesso strato, di taglia confrontabile con alcune specie quaternarie di *Megatherium*. Sono state riconosciute come valide tre specie di *Pyramiodontherium*, tutte presenti soprattutto nel nordovest dell'Argentina, dal tardo Miocene della Provincia di Catamarca (e probabilmente anche nella Provincia di Tucumán), e nel tardo Pliocene della Provincia di La Rioja. La documentata presenza di questo genere nel nordest dell'Argentina ne estende la distribuzione paleobiogeografica sinora nota.

Introduction

The Xenarthra are a group of mammals with an almost exclusively Neotropical distribution. They are characterized by a skeletal architecture distinct from all other placental mammals. They are further distinguished by molecular evidence supporting their position as one of the four major clades of mammals (Delsuc et al. 2001, 2002; Madsen et al. 2001; Murphy et al. 2001). Xenarthrans include three clades: 1) the Cingulata, covered with a bony dermal shell; 2) the Vermilingua, highly specialized for myrmecophagy; and 3) the Tardigrada or Phyllophaga, the arboreal and terrestrial sloths. Outside Cingulata, only a few extinct forms of Tardigrada possessed a tegument with subcutaneous osteoderms.

From the time of the earliest published records of fossil Tardigrada (see Carlini et al. 1990a, b), the diversity of this group has been highly variable in mammal assemblages. Its diversity in the lower levels (Late Miocene) of the Ituzaingó Formation (Late Miocene-Pliocene) in Entre Ríos Province is much higher than in any other mammal-bearing unit of the Late Miocene-Early Pliocene interval in Argentina (Cione et al. 2000). Sloths

1 Corresponding author. Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICYTTP-CONICET), Materi y España, 3105 Diamante, Entre Ríos, Argentina. E-mail: diegobrandoni@yahoo.com

2 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, and Palaontologisches Institut und Museum, Universitât Zürich, Karl Schmid-Strasse 4,CH-8006 Zürich, Switzerland. E-mail: acarlini@museo.fcnym.unlp.edu.ar

species in this unit have been assigned to Megatheriidae (Megatheriinae), Nothrotheriidae, Megalonychidae (Megalocninae, Megalonychinae, and "Orthotheriinae"), and Mylodontidae (Mylodontinae, Scelidotheriinae, and Octomylodontinae) (Carlini et al. 2000). In particular, the temporal range of the subfamily Megatheriinae (as typified by *Megatherium* Cuvier, 1796) in Argentina extends from the "Friasian"- Colloncuran - (Middle Miocene) to the Lujanian (late Pleistocene-early Holocene). Among the megatheriines previously identified in the lower levels of the Ituzaingó Formation, the genera *Promegatherium* Ameghino, 1883, *Eomegatherium* Kraglievich, 1926, and *Pliomegatherium* Kraglievich, 1930, are all mostly small to medium-sized sloths.

In this work we describe new material assigned to *Pyramiodontherium* Rovereto, 1914 (Megatheriinae) from the lower levels (="conglomerado osífero", see below) of Ituzaingó Formation of Entre Ríos Province. These remains are larger than those of the other genera and comparable in size to some *Megatherium* species (e.g., *M. tarijense* Gervais & Ameghino, 1880, *M. sundti* Philippi, 1893) of Quaternary age.

Institutional abbreviations: CICYTTP, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Entre Ríos, Argentina; FMNH, Field Museum of Natural History of Chicago, Chicago, USA; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MAS, Museo de Ciencias Naturales y Antropológicas Profesor Antonio Serrano, Paraná, Entre Ríos, Argentina; MLP, Museo de la Plata, La Plata, Argentina; MRVU, Museo Regional de Villa Urquiza, Villa Urquiza, Entre Ríos, Argentina; ROM, Royal Ontario Museum, Toronto, Canada; UCMP, University of California Museum of Paleontology, Berkeley, USA.

Anatomical abbreviations: ad, astragalar depression; aef, astragalar ectal facet; cub, cuboid facet; df, discoid facet; d IV, digit IV; dpc, deltopectoral crest; ff, fibular facet; mc III, metacarpal III; mc V, metacarpal V; nav, navicular facet; of, odontoid facet; op, odontoid process; ot, odontoid tuberosity; pt, patellar trochlea; s, sesamoid bone; un, unciform.

Other abbreviations: SALMA, South America Land Mammal Age; NWA, Northwestern of Argentina.

Taxonomic history of *Pyramiodontherium*

Moreno & Mercerat (1891, p. 229) provided a partial description of *Megatherium burmeisteri* Moreno & Mercerat, 1891, from Bajo de Andalhuala in Catamarca Province, based on MLP 2-66, a specimen that includes skull, mandible, and several postcranial bones. In their description, these authors argued that their new species was two-thirds of the size of *Megatherium americanum* Cuvier, 1796, and noted the oblique (with respect to the sagittal plane) arrangement of the transverse crests in the molariform teeth. In the same contribution, Moreno & Mercerat (1891, p. 231) erected a separate species *Megatherium bergi* Moreno & Mercerat, 1891, based on a partial skull (MLP 2-78) deformed by compression, but with the same provenance. Somewhat later, Lydekker (1894, pp. 76-77) argued that *Megatherium burmeisteri* and *Megatherium bergi* could not be distinguished morphologically or taxonomically from *Megatherium gaudryi* Moreno, 1888, from Monte Hermoso in Buenos Aires Province.

Roth (1911) added to our knowledge of MLP 2-66 with a description of elements of the axial and appendicular skeleton and referred *Megatherium burmeisteri* to his newly erected genus *Plesiomegatherium* Roth, 1911, as *Plesiomegatherium burmeisteri* Roth, 1911.

Rovereto (1914, p. 89) established *Pyramiodontherium dubium* Rovereto, 1914, based on MACN-Pv 8143, a juvenile right maxilla from the Valle de Santa María in Catamarca Province ("Formación Araucanense" -sic-) but allocated this species incorrectly among the megalonychids.

Carlos Ameghino (1919, pl. VII) illustrated a fragmentary skull of a large megatheriine from the Tiopunco region of Tucumán Province that he referred to *Plesiomegatherium*. In the original publication, the specimen belonged to the "Museo de Tucumán" and was catalogued number 35, however, the original material is now MACN-Pv 13764, and we refer it to *Pyramiodontherium*.

Cabrera (1928) further considered that the size and anatomical differences between *Plesiomegatherium burmeisteri* and *Plesiomegatherium hansmeyeri* Roth, 1911, were sufficient to exclude the Catamarca species (MACN-Pv 8143) from the genus and include it within *Pyramiodontherium*, following the rules of zoological nomenclature. Cabrera (1928, p. 341) pointed out that *Pyramiodontherium dubium* could not be recognized as a distinct species because the cranial material for which it was erected was fragmentary and juvenile, and did not provide diagnostic characters from the adult megatheriine material collected from the same horizon and nearly the same locality. After extensive discussion of the arguments, Cabrera (1928) concluded that *Megatherium burmeisteri*, *Megatherium bergi*, and *Pyramiodontherium dubium* represented a single species, *Pyramiodontherium bergi* (Moreno & Mercerat, 1891).

Kraglievich (1930, p. 158) described *Pyramiodontherium*? *carlesi* (sic) based on one astragalus (MACN-Pv 5300) from the "Uquian" (Uquía, Jujuy Province). However, the exact provenance, both geographic and stratigraphic, of these remains is not adequately known.

Carlini et al. (2002) erected *Pyramiodontherium brevirostrum* Carlini, Brandoni, Scillato-Yané & Pujos, 2002, for associated axial and appendicular skeletal remains (MLP 31-XI-12-25) from Bajo de Andalhuala in Catamarca Province. Shortly thereafter, De Iuliis et al.

(2004) described *Pyramiodontherium scillatoyanei* De Iuliis, Ré & Vizcaíno, 2004, based on MLP 68-III-14-1 from the lower member of the Toro Negro Formation in La Rioja Province. These remains included a humerus discussed and illustrated by Carlini et al. (2002) as *Plesiomegatherium*?, following the original designation of Ramos (1970, p. 374).

Remains representing *Pyramiodontherium* are also known from outside northwestern Argentina. A humerus from the lower levels of Ituzaingó Formation in Entre Ríos Province was referred to *Pyramiodontherium* sp. (see Carlini et al. 2000; Cione et al. 2000; Brandoni 2005; Brandoni & Scillato-Yané 2007). Kraglievich (1934) had already noted that several molariform teeth from the lower levels of Ituzaingó Formation that had served as the basis for species of *Promegatherium* and *Megatherium*, were very similar to those of *Pyramiodontherium*. In addition, most recently, Guillaume (2005) and Guillaume et al. (2005) have suggested the presence of this genus in late Miocene-Pliocene outcrops in the Valdés Peninsula of Chubut Province in Patagonia.

Geological setting and age

The Ituzaingó Formation extends from the city of Ituzaingó in Corrientes Province where the type profile

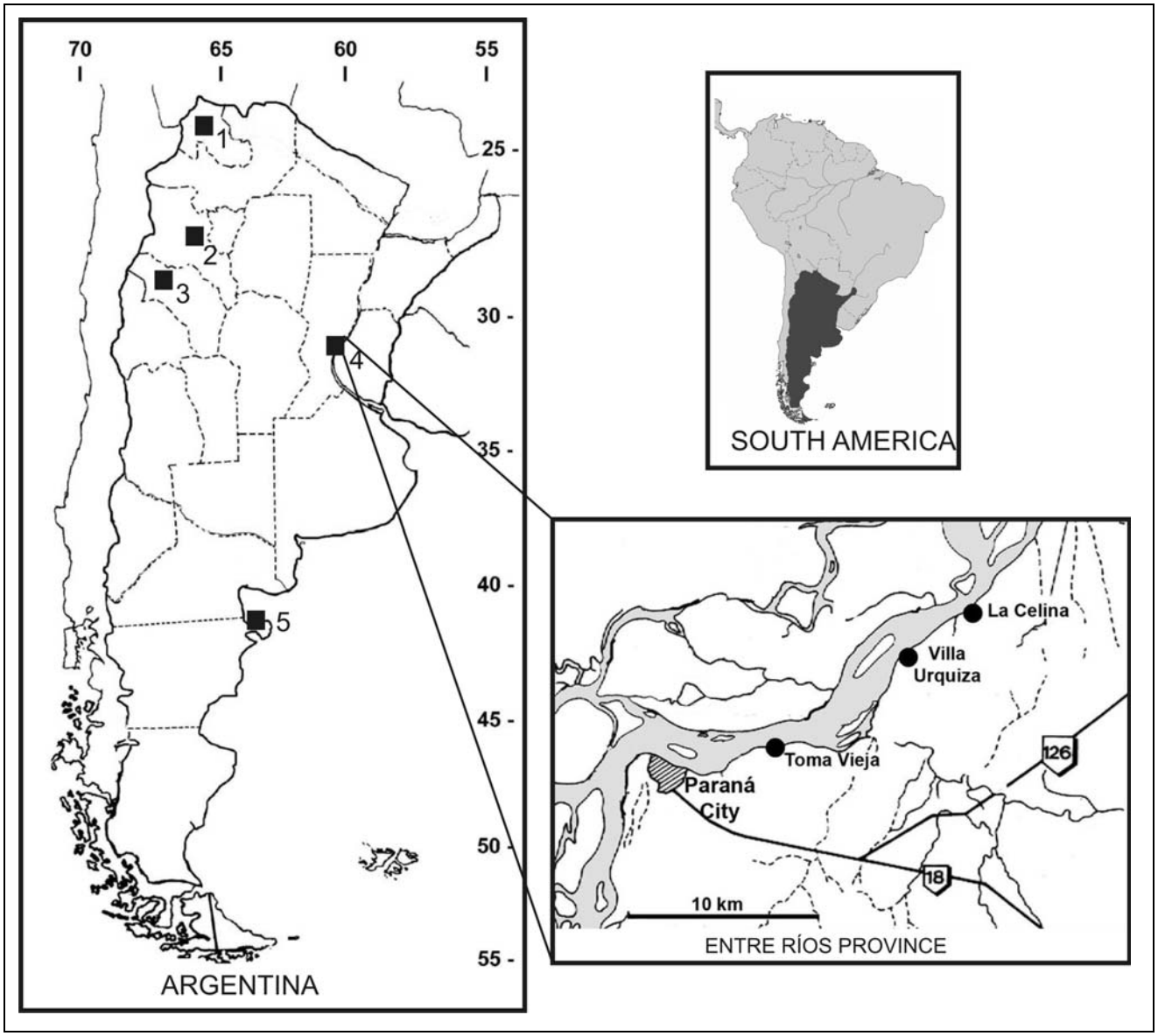

Fig. 1 - Geographic distribution of the species of *Pyramiodontherium* (black squares) and geographic location of the main exposures of the "conglomerado osífero", Entre Ríos Province, Argentina (black circles). 1, *Pyramiodontherium*? *carlesi*, Uquia, Jujuy Province; 2, *Py. scillatoyanei*, Toro Negro Formation, La Rioja, Province; 3, *Py. bergi* and *Py. brevirostrum*, Valle de Santa María, Catamarca Province; 4, *Pyramiodontherium* sp., "conglomerado osífero", Entre Ríos Province; 5, *Pyramiodontherium*?, Valdés península, Chubut Province.

was originally described (De Alba 1953), to the north of Paraná, the capital of Entre Ríos Province. Fossil vertebrates come from the lower levels of Ituzaingó Formation, particularly from a basal level informally known as the "Mesopotamian" or "conglomerado osífero" (bone-rich conglomerate, see Frenguelli 1920). The conglomerate outcrops discontinuously along the banks of the Paraná river from the vicinity of the city of Paraná upstream to Pueblo Brugo. Fossil prospecting is currently focused on the localities of "La Celina" (S 31° 37′ 37″, W 60° 20′ 04″), "Toma Vieja" (S 31° 42′ 11″, W 60° 28′ 06″), and "Villa Urquiza" (S 31° 38′ 42.5″, W 60° 22′ 50.5″) (see Fig. 1).

The "conglomerado osífero" is clearly visible at the unconformity between the underlying marine Paraná Formation (Bravard 1858) and the conglomeratic levels of the fluvial Ituzaingó Formation (Fig. 2). Of variable thickness, the conglomerate is characterized by fine quartz gravel, clay and coarse chalcedony clasts, as well as dissociated and fragmentary but abundant bones and teeth of continental and marine vertebrates.

Cione et al. (2000) presented an updated list of fossil vertebrates recorded in the "conglomerado osífero" of the Ituzaingó Formation and, based on the stratigraphic relationships between different fossil beds from the Late Miocene-Pliocene of Argentina, found greater affinity of the association with the Huayquerian, correlated with the Tortonian (11.61 to 7.25 Ma) of the international scale (Gradstein et al. 2004).

Systematic paleontology

Xenarthra Cope, 1889
Tardigrada Latham & Davies in Forster, 1795
Megatherioidea Gray, 1821
Megatheriidae Gray, 1821
Megatheriinae Gray, 1821

Pyramiodontherium sp. Rovereto, 1914
Figs 3, 4

Material: MRVU 107, right humerus without proximal epiphysis, Villa Urquiza, Entre Ríos Province. CICYTTP-Pv M-1-110, left radius without epiphyses, of a juvenile specimen, Arroyo Quebracho, Entre Ríos Province. CICYTTP-Pv M-1-109, left IV metacarpal, Arroyo El Chilcal, Entre Ríos Province. MACN-Pv 4939, distal fragment of right femur, Toma Vieja, Entre Ríos Province. MAS 1392, left astragalus, Toma Vieja, Entre Ríos Province.

Stratigraphic Occurrence: "conglomerado osífero", Ituzaingó Formation, Entre Ríos Province (Argentina). Late Miocene (Huayquerian SALMA, see Cione et al. 2000).

Anatomical description and comparisons

Humerus. The shape of humerus MRVU 107 (Figs. 3A, B) is generally similar to that of other megatheriines, but relatively elongated and more gracile, as in megalonychids and prepotheriines. As in all megatheriines, there is no entepicondylar foramen. An entepicondylar foramen is present in most megalonychids, with the exception of some taxa, as *Diabolotherium*

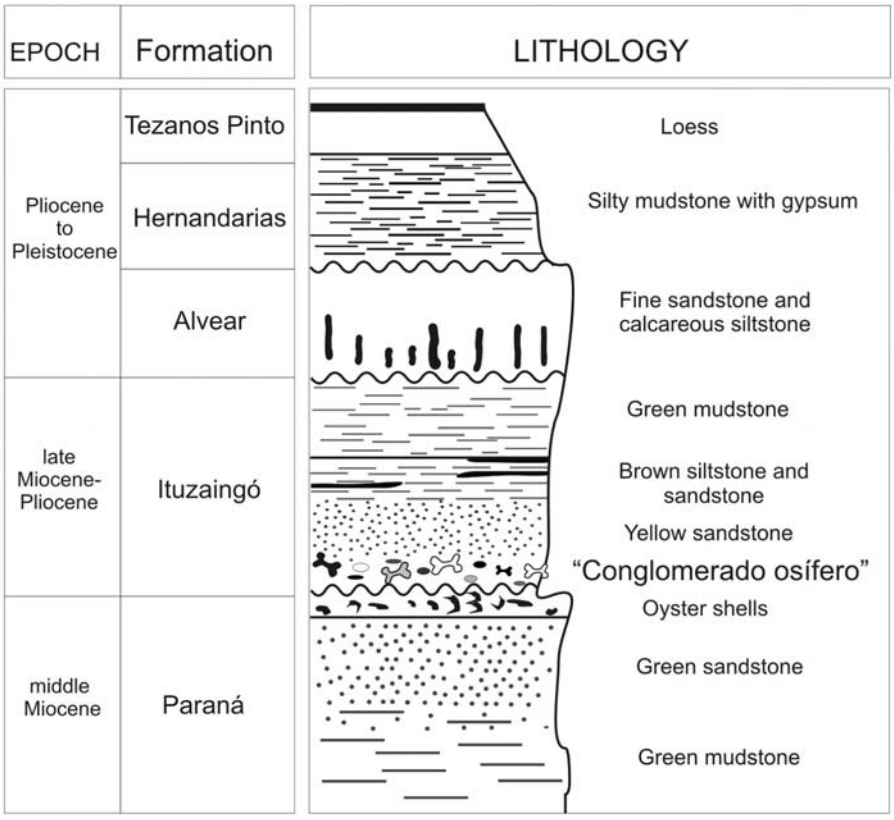

Fig. 2 - Generalized stratigraphic profile of the area of Paraná, Entre Ríos Province, Argentina (modified from Aceñolaza 1976).

Tab. 1 - Measurements (mm) of the humerus of Megatheriinae. * Measurements from De Iuliis (1996); p, preserved.

Taxon	Specimen	Length	Distal Width
Pyramiodontherium sp.	MRVU 107	580p	230
Megathericulus patagonicus	MLP 91-IX-7-18	290p	165
Megatheriops rectidens	MACN Pv-2818 right	482	183
Megatheriops rectidens	MACN Pv-2818 left	475	185
Pyramiodontherium scillatoyanei	MLP 68-III-14-1	595	195
Pyramiodontherium ? *	FMNH P14511	733	280
Megatherium gallardoi	MACN Pv-5002	795	365
*Megatherium tarijense**	FMNH P14216	527	219
Megatherium americanum *	MACN Pv-10148	738	330
Megatherium americanum *	MLP 2-72	700	350
Megatherium americanum *	MLP 2-79	695	327
Megatherium americanum *	MLP 28-III-16-2	721	316
Megatherium americanum *	MLP 41-II-28-1	710	340
Eremotherium laurillardi *	ROM 22101	791	360
Eremotherium laurillardi *	ROM 10447	814	343
Eremotherium laurillardi *	ROM 10449	806	354
Eremotherium laurillardi *	FMNH P26970	791	358
Eremotherium laurillardi *	FMNH P27080	751	341
Eremotherium laurillardi *	FMNH P27081	730	312

Pujos, De Iuliis, Argot & Werdelin, 2007, and *Parocnus* Miller, 1929. The humerus is anteroposteriorly compressed and broader in its distal third, with a flat posterior aspect and deep olecranon fossa. Although the bone is not preserved in entirety, it is 580 mm long, similar to the length of the homologous portion in specimens of *Megatherium americanum* (Tab. 1), however its distal width (230 mm) is relatively less.

As noted, the diaphysis is markedly slender, and similar in this respect to the humerus of *Nothrotheriops shastense* Sinclair, 1905. Its proximal third is subtrapezoidal in cross section (Fig. 3A, B) and the distal two thirds are more markedly flattened than in Quaternary species. In *Pyramiodontherium scillatoyanei*, the section of the proximal third of the diaphysis is more isodiametric with an irregular outline and the distal third is subtrapezoidal with more rounded angles. Only the proximal epiphysis of the right humerus is preserved in the type material of *Pyramiodontherium brevirostrum* (MLP 31-XI-12-25). Here, the humeral head is well developed and is clearly distinct from the tuberosities; the latter are arranged at an angle of 115°. The cross section of the diaphysis immediately distally to the tuberosities is also subtrapezoidal.

Another important characteristic of the humerus MRVU 107 is the presence of a well developed deltopectoral crest (Fig. 3A), which is also present in *Megathericulus patagonicus* Ameghino, 1904 (MLP 91-IX-7-18), *Megatheriops rectidens* (Rovereto, 1914) (MACN-Pv 2818) and *Pyramiodontherium scillatoyanei*. The deltopectoral crest is formed medially by the pectoral ridge and laterally by the deltoid ridge, which contact each other at approximately the distal third of the diaphysis. In the Plio-Pleistocene megatheriines (e.g., *Megatherium*, *Eremotherium* Spillmann, 1948), the deltopectoral crest is poorly developed and reduced to a triangular protuberance (De Iuliis 2003).

A well developed deltopectoral crest is also present in the humerus of the undetermined Megatheriinae FMNH P14511 from the Corral Quemado Formation (Marshall & Patterson 1981) and also UCMP 41115 from the Miocene of La Venta in Colombia (Hirschfeld 1985) (De Iuliis et al. 2004; Carlini et al. 2006).

Radius. A fragmentary left radial diaphysis (CICYTTP-Pv M-1-110) of a juvenile specimen, for which neither epiphysis is preserved, is referred tentatively to *Pyramiodontherium* sp. (Figs. 3C-D). This assignation is based on the size of the radius, which coincides with the expected size for a specimen with a humerus of such dimensions as discussed above.

Metacarpal IV. Metacarpal IV is the largest metacarpal in the Megatheriinae. In *Pyramiodontherium* sp. (Figs. 3F-J) it is relatively longer (265 mm) compared with that of other members of the subfamily. MC IV has three proximal articular facets for MC III, unciform, and MC V respectively (Figs. 3G, H, J). The facet for MC III, situated on the proximomedial aspect of MC IV, is approximately trapezoidal and concave. The articular facet for the unciform is adjacent to that for MC III medially and to that for MC V laterally; it presents a flat, dorsoventrally elongated lateral portion and a slightly concave medial aspect. The facet for MC V is situated laterally situated on the MC IV; it is approximately subtriangular with the apex directed anteriorly. The distal end of MC IV is separated from the proximal end by a long diaphysis that is compressed mediolaterally and expanded dorsoventrally. Its distal surface is wholly articular (Figs. 3F, I); bearing a large facet that

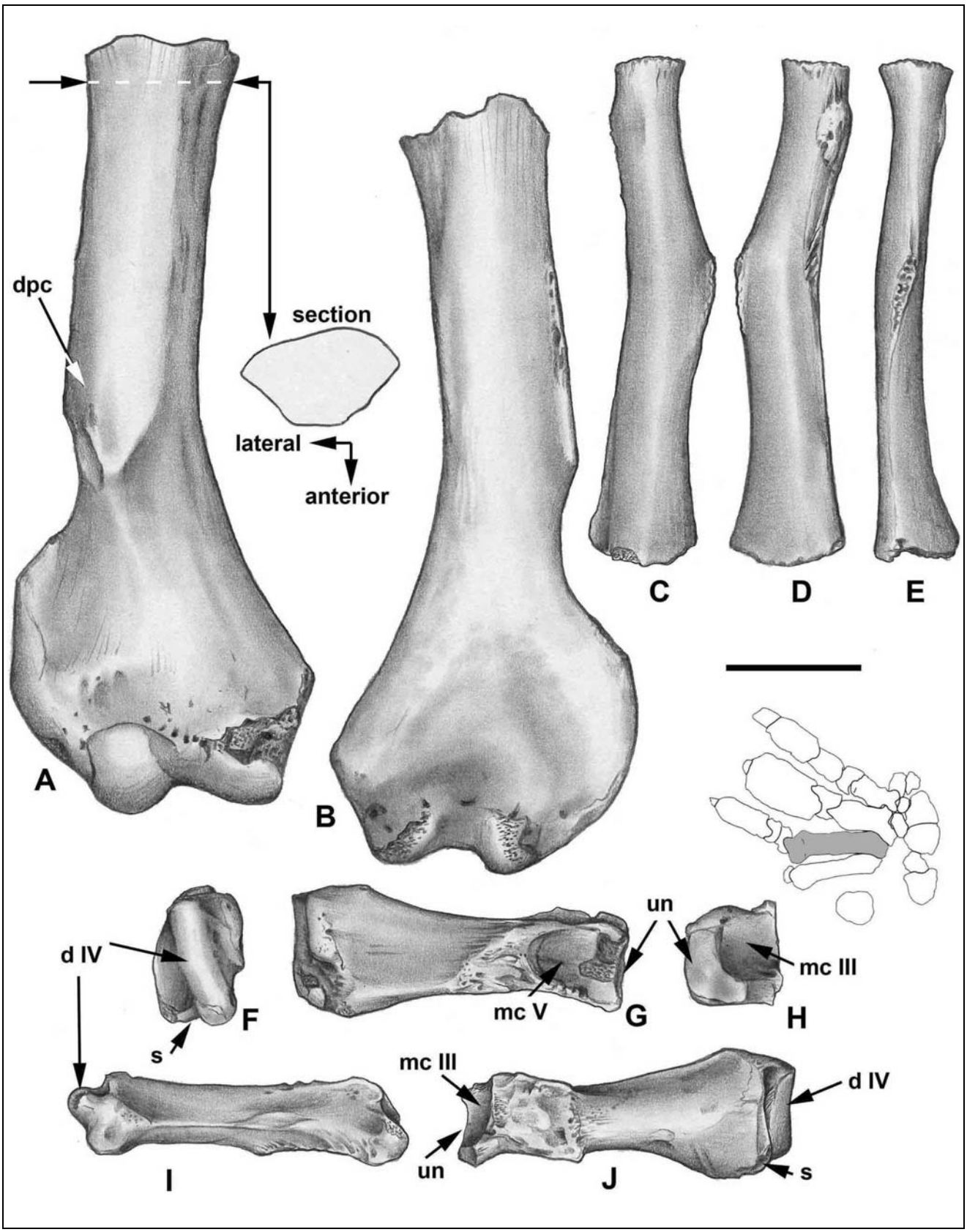

Fig. 3 - *Pyramiodontherium* sp. A, B) Right humerus (MRVU 107); C-E) left radius (CICYTTP-Pv M-1-110); F-J) left MC IV (CICYTTP M-1-109). A, anterior view; B, posterior view; C, posteromedial view; D, anterolateral view; E, medial view; F, distal view; G, lateral view; H, proximal view; I, dorsal view; J, medial view. Abbreviations: dpc, deltopectoral crest; d IV, digit IV; mc III, metacarpal III; mc V, metacarpal V; s, sesamoid bone; un, unciform. Scale bar equals 10 cm.

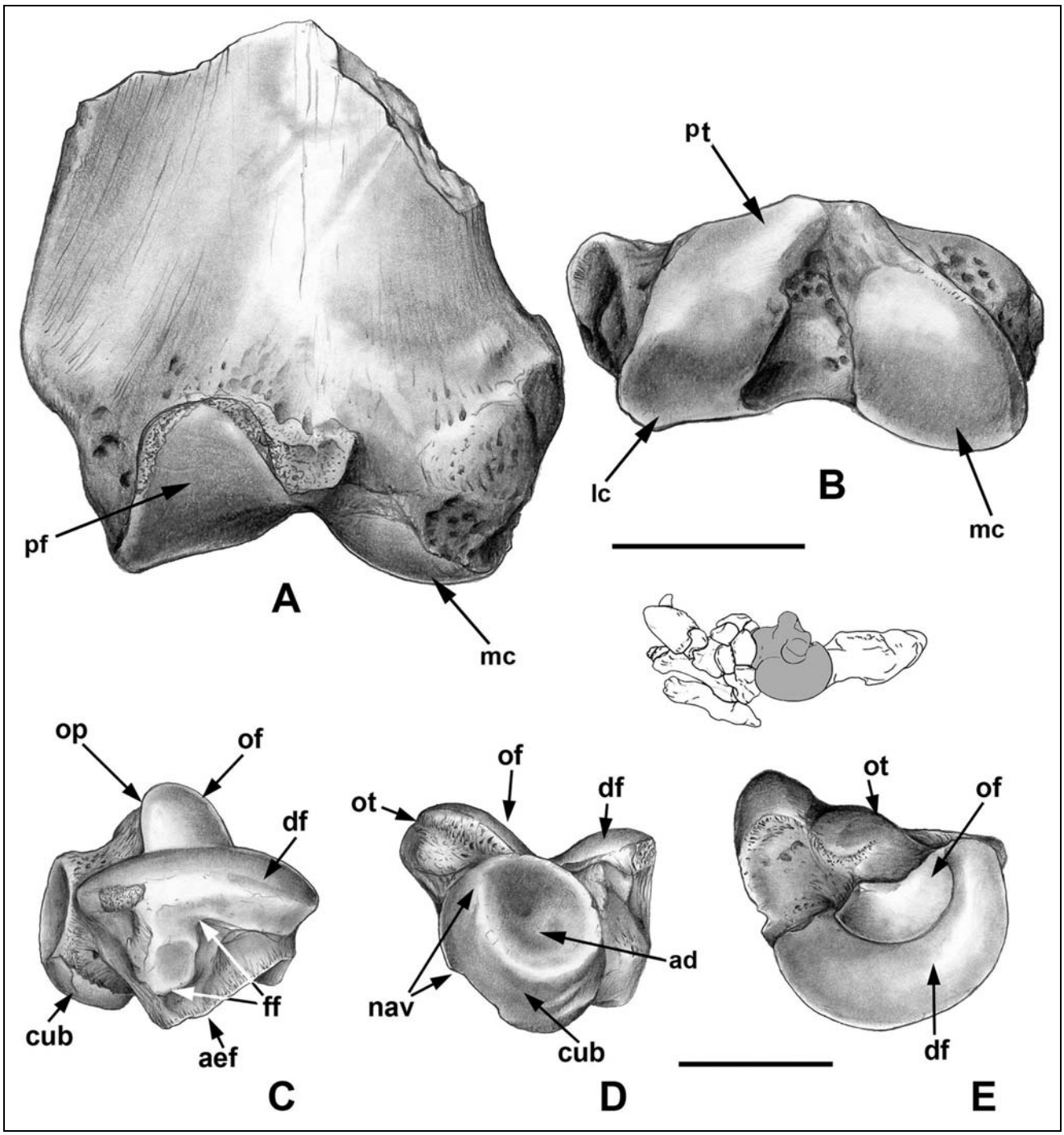

Fig. 4 - *Pyramiodontherium* sp. A, B) Right femur (MACN 4939); C-E) left astragalus (MAS 1392). A, anterior view; B, distal view; C, dorsolateral view, D, distal view, E, dorsomedial view. Abbreviations: ad, astragalar depression; aef, astragalar ectal facet; cub, cuboid facet; df, discoid facet; ff, fibular facet; nav, navicular facet; of, odontoid facet; op, odontoid process; ot, odontoid tuberosity; pt, patellar trochlea. Scale bar equals 10 cm.

articulates with the proximal phalanx 1. This facet has three surfaces: two of them are relatively flat and separated by a central dorsoventral keel. In addition, there is a small circular ventromedial circular facet for a sesamoid bone. With respect to the number of sesamoids, one or two bones may occasionally be fused to MC IV in *Eremotherium laurillardi* (Lund, 1842). Owen (1860) reported the presence of a single medial facet in *Megatherium americanum*, and a simple single facet is also the condition in *M. tarijense* (see De Iuliis 1996). The assignation of CICYTTP-Pv M-1-109 to *Pyramiodontherium* sp. is based on the size of the MC IV, which coincides with the expected size for a specimen with a humerus of such dimensions as discussed above.

Femur. MACN-Pv 4939 is the distal portion of a right femur (Figs. 4A, B). The patellar trochlea is rela-

tively flat, separated from the internal condyle and poorly differentiated from the external condyle, so that it forms a single articular surface in combination with the latter. This relationship between the patellar trochlea and the condyles is common to most megatheriines, with the exception of *Megathericulus patagonicus* (MLP 92-XI-12-2) and *Megathericulus primaevus* Cabrera, 1939 (MLP 39-VI-24-1), in which the patellar trochlea is connected to both condyles (De Iuliis et al. 2008). As in *Pyramiodontherium bergi* and *Py. brevirostrum*, the patellar trochlea is restricted to a location very close to the external condyle; thus, the medial margin of the patellar trochlea is distant from the lateral margin of the internal condyle (Fig. 4B). In *Pyramiodontherium scillatoyanei*, the patellar trochlea is better developed and differentiated from the lateral condyle as a prolongation (De Iuliis et al. 2004, fig. 6A), as occurs in *Eremotherium laurillardi* and *E. sefvei* De Iuliis & Saint André, 1997 (see De Iuliis & Saint André 1997, fig. 1a and fig. 2 respectively). In *Megatherium americanum* and *M. altiplanicum* Saint-André & De Iuliis, 2001, the patellar trochlea of the femur is extremely reduced as an anteromedial extension of the lateral condyle. In *M. altiplanicum*, these surfaces are also very close to each other, but this is due to lateral projection of the internal condyle (Saint-André & De Iuliis 2001, fig. 7c). MACN- Pv 4939 has a massive ectepicondyle, but not as large as that of *Pyramiodontherium brevirostrum*.

Species	Specimen	Length	Width
Megathericulus patagonicus	MACN A-15111	90	105
Megathericulus patagonicus	MLP 91-IX-7-18	99	103
Megathericulus patagonicus	MLP 92-XI-15-2	95	100
Megathericulus primaevus	MLP 34-VI-24-1	88	85
Eomegatherium cabrerai	MLP 2-206	-	130
Eomegatherium nanum	MACN Pv-4992	130	130
Anisodontherium halmyronomum	MLP 28-X-11-81	-	114
Pyramiodontherium scillatoyanei	MLP 68-III-14-1	155	141
Pyramiodontherium bergi	MLP 2-66 Left	175	162
Pyramiodontherium bergi	MLP 2-66 Right	172	162
Pyramiodontherium sp.	MAS 1392	167	163
Pliomegatherium lelongi	MLP 99-XI-1-1	148	148
Megatherium lundi	MLP 2-30	182	165
Megatherium lundi	MLP 2-31	195	185
Megatherium americanum	MLP 44-XII-28-1	240	209
Megatherium americanum	MLP 2-29	245	230
Megatherium americanum	MACN Pv-4412	240	209
Megatherium americanum	MACN Pv-10147	192	180
Megatherium americanum	MACN Pv-12815a	243	215
Megatherium americanum	MACN Pv-12815b	260	236
Megatherium americanum	MACN Pv-12815c	230	213
Megatherium americanum	MACN Pv-12815d	235	200
Megatherium americanum	MACN Pv-14112	190	155
Megatherium americanum	MACN Pv-14132	217	203
Megatherium americanum	MACN Pv-17573	245	228
Megatherium americanum	MACN Pv-14054	200	185
Megatherium americanum	MACN Pv-14111	240	223
Megatherium americanum	MACN Pv-17636	215	190
Megatherium americanum	MACN Pv-10633	160	155
Megatherium americanum	MACN Pv-14865	195	188
Megatherium americanum	MACN Pv-13577	222	190
Megatherium americanum	MACN Pv-10106	225	210

Tab. 2 - Measurements (mm) of the astragalus of Megatheriinae.

Astragalus. The astragalus (Figs. 4C-E) of *Pyramiodontherium* sp. (MAS 1392) has the typical shape for the subfamily Megatheriinae. This is a massive bone and bears a well-developed odontoid process at the center of the discoidal facet in dorsomedial view. It is similar in size to that of other species of the genus and larger than the other genera and species from the "conglomerado osífero" (Tab. 2). The fibular facet is divided into two portions (Fig. 4C); a dorsal anteroposteriorly elongate portion that joins the discoidal facet, and a ventral portion with a circular surface that projects perpendicular to the dorsal portion; a condition seen in *Pyramiodontherium bergi*, *Py. scillatoyanei*, and *Pliomegatherium lelongi* Kraglievich, 1930 (see Brandoni et al. 2004; De Iuliis et al. 2004; Brandoni 2006b). By contrast, in *Eomegatherium nanum* (Burmeister, 1891) the ventral portion of the fibular facet is more oval (Brandoni & Scillato-Yané 2007, fig.1.2).

The odontoid process is similar in shape to that of *Pyramiodontherium bergi* (MLP 2-66). The process bears the odontoid facet, which is somewhat compressed at the level of contact with the discoidal facet. In distal view (Fig. 4D), these facets are at nearly right angles to each other, as they are in *Py. bergi* and *Py. scillatoyanei* (MLP 68-III-14-1).

The odontoid process bears a non-articular eminence that De Iuliis (1996) designated the "odontoid tuberosity" (Fig. 4E). This tuberosity is also present in *Megathericulus patagonicus* (MACN-A 11151), *Py. scillatoyanei*, and *Eomegatherium nanum*, and is well-developed in *Py. bergi* (see Brandoni et al. 2004) and in some Mylodontinae (e.g., *Glossotherium* Owen, 1840) although to a lesser degree.

The facet for the navicular, located in the most distal portion of the astragalus (Figs. 4C, D), is approximately oval with its major axis directed dorsolateral to ventromedial; the plane of the navicular facet is slanted with respect to the plane of the discoidal facet, whereas in other megatheriines both planes are nearly perpendicular to each other. The facet for the navicular has a concave portion dorsolaterally, the astragalar depression and, a convex portion ventromedially. In MAS 1392, slightly more than one third of the facet for the navicular is above the plane of the discoidal facet (Fig. 4D) as in *Pyramiodontherium bergi* (Brandoni et al. 2004, fig. 3A), *Py. scillatoyanei* (De Iuliis et al. 2004, fig. 7B), and *Eomegatherium nanum* (Brandoni & Scillato-Yané 2007, fig. 3.1); in *Megathericulus patagonicus* the dorsomedial half of the facet for the navicular is dorsal to the plane of the discoidal facet (De Iuliis et al. 2008), while in *Megatherium americanum* this portion of the navicular facet is at the same level as the plane of the discoidal facet. In *Eremotherium laurillardi* and *Megatherium urbinai* Pujos & Salas, 2004, the condition is similar to that of *Pyramiodontherium* and *Eomegather-*

ium; whereas the condition in *M. tarijense* Gervais & Ameghino, 1880, is intermediate between those of *M. americanum* and *M. urbinai.*

There are two facets for articulation of the calcaneus: a smaller sustentacular facet and a larger ectal facet. These two facets are separated by a wide and deep sulcus tali. This sulcus is present in most megatheriines except for a specimen of *M. americanum* (Kraglievich, 1926), one specimen of *E. laurillardi* (ROM 22006 see De Iuliis 1996), and one specimen of *M. urbinai* (UNA V2642 see Pujos & Salas 2004) in which both facets are fused to each other; they are partially fused in *M. tarijense* (MNHN TAR 1269 see Pujos & Salas 2004). In *Py. scillatoyanei* this canal, although deep, is narrow due to the large size of the ectal facet.

The subtriangular and almost flat sustentacular facet is continuous with the facet for the cuboid bone and separated from the ventral portion of the facet for the navicular. The ectal facet is very developed; it is oval with the major axis oriented anterolaterally to posteromedially and parallel to sulcus tali. This facet is concave along its major axis and convex along its minor axis.

Discussion

The Megatheriinae from the "conglomerado osífero" (Northeastern of Argentina)

Previously, seven species of megatheriines have been described from the "conglomerado osífero": *Promegatherium smaltatum* Ameghino, 1883; *Promegatherium remulsum* Ameghino, 1886; *Promegatherium parvulum* Ameghino, 1891; *Megatherium antiquum* Ameghino, 1885; *Eomegatherium nanum* (Burmeister, 1891) Kraglievich, 1926; *Pliomegatherium lelongi* Kraglievich, 1930, and *Pliomegatherium paranensis* Kraglievich, 1930. However, in a recent revision, only three of these are valid: *Pr. smaltatum*, *Pl. lelongi*, and *Eo. nanum* (see Brandoni 2006b; Brandoni & Scillato-Yané 2007).

Promegatherium smaltatum, *Pliomegatherium lelongi*, and *Eomegatherium nanum* were originally based on fragmentary materials (i.e., molariforms, dentaries) that do not allow direct or complete comparisons. Nevertheless, the few diagnostic features comparable among the type and referred material (see Brandoni 2006b; Brandoni & Scillato-Yané 2007) indicate that these species are similar in size (i.e., small to medium sized megatheriines) but clearly distinguishable among themselves (Kraglievich 1930; Brandoni 2006b; Brandoni & Scillato-Yané 2007).

Taking into account the greater size of the specimens here described and the characteristics shared with other *Pyramiodontherium* species (i.e., *Py. bergi*, *Py. brevirostrum*, *Py. scillatoyanei*), there is enough justification to support the presence of *Pyramiodontherium* in the abovementioned unit and the presence of *Pyramiodontherium* in the northeastern Argentina increases its geographical distribution substantially (Fig. 1).

Many of the features present in the astragalus MAS 1392, and the femur MACN-Pv 4939, are similar to those of *Pyramiodontherium bergi*, but the humerus MRVU 107 is larger than humeri known from the late Miocene-Pliocene levels of the Northwestern Argentina (except FMNH P14511, see De Iuliis 1996; Brandoni 2006a), and has a very different proximal cross section. In this sense, the presence of a new species of *Pyramiodontherium* in the "conglomerado osífero" is a reasonable hypothesis. However, new discoveries of more complete and better preserved material homologous to those of the previously described, will be necessary in order to diagnose a new species.

The *Pyramiodontherium* species from the northwestern of Argentina

Three valid species of *Pyramiodontherium* have been described from northwestern Argentina, from the Late Miocene in Catamarca Province, the Late Pliocene in La Rioja Province, and probably also in Tucumán Province.

Pyramiodontherium bergi was the first valid species to be erected. Considering the scarce remains and studies that existed at the time, Cabrera's (1928) decision to attribute the specimens MACN-Pv 8143, MLP 2-78 and MLP 2-66 to this single species was correct. Among these materials, specimen MACN-Pv 8143 is clearly a juvenile individual (in addition to its small size, the molariforms show no signs of wear), and specimen MLP 2-78 is too deformed to be identifiable as a distinct species.

Carlini et al. (2002) recognized *Pyramiodontherium brevirostrum* on the basis of several remains. Along with other diagnostic characters, this new species was erected given the greater robustness of MLP 31-XI-12-25 (the type of *Py. brevirostrum*) compared with *Py. bergi*. Although new material of *Pyramiodontherium* from Catamarca Province suggests greater individual variation than originally considered by Carlini et al. (2002), the assignation to a species different from *Py. bergi* is still warranted.

A third valid species is *Pyramiodontherium scillatoyanei* from the lower member of the Toro Negro Formation (Upper Pliocene) of La Rioja Province, described by De Iuliis et al. (2004). The characteristics of the postcranial skeleton serve to assign this species to the genus and although the type of *Pyramiodontherium scillatoyanei* (MLP 68-III-14-1) does not preserve any cranial remains comparable with the species from Catamarca, it evidently represents a different species.

Pyramiodontherium bergi and *Py. brevirostrum* were found at Bajo de Andalhuala in the Valle de Santa María south of Chiquimil in Catamarca Province, but their stratigraphic provenance is not known with any greater precision. The type material of *Py. bergi* and *Py. brevirostrum* belongs to old collections of Museo de La Plata, from a time when the distinction between the Andalhuala Formation ("Araucanean") and Corral Quemado Formation had not yet been proposed. Given that Riggs & Patterson (1939) and Marshall & Patterson (1981) have indicated that many specimens of *Pyramiodontherium* were found in the Andalhuala Formation at the Chiquimil area and in the Corral Quemado Formation in the vicinity of Puerta de Corral Quemado; as well as the fact that Andalhuala Formation is the best represented fossiliferous unit at Bajo de Andalhuala (Chiquimil), it is probable that the type materials of *Py. bergi* and *Py. brevirostrum* are in fact from the Andalhuala Formation, rather than from Corral Quemado Formation, where collections were not made (Riggs & Patterson 1939; Marshall & Patterson 1981).

Regarding *Pyramiodontherium*? *carlesi*, the few known remains are from Uquía, in Jujuy Province, although their exact provenance is unknown. *Py.*? *carlesi* is considerably larger than the species of *Pyramiodontherium* and some of its features are similar to those of several species of *Megatherium*. Thus, its assignment to *Pyramiodontherium* is doubtful.

Relationships among the *Pyramiodontherium* species from the northwestern of Argentina

Considering only the characters that are directly comparable among the three species of *Pyramiodontherium* (NWA), there is evidently greater affinity between *Pyramiodontherium bergi* and *Py. brevirostrum* than between these species and *Py. scillatoyanei*. The morphological features observed in the type specimens of these species from Catamarca Province are sufficient to group them in a common genus, but as separate species. The depressed rostrum, convexity of maxillary walls, inclination of the molariform ridges with respect to the sagittal plane, and similarities in the morphometry of long bones support the congeneric status of these taxa (see Carlini et al. 2002). However, *Py. brevirostrum* is clearly more robust than *Py. bergi*, and both species differ in rostrum outline and section, presence of a rostral ridge in *Py. brevirostrum*, shape of the last upper molariform, and minor differences in the arrangement of upper dental series. Regarding the appendicular skeleton, they differ in degree of femoral torsion and development of the cnemial crest of the tibia (see Carlini et al. 2002).

Pujos (2006) indicates that *Py. bergi*, *Py. brevirostrum* and *Megatheriops rectidens* conform a monophyletic clade, but curiously the author did not consider *Py. scillatoyanei* in his analysis. The only unequivocal synapomorphy of the *Pyramiodontherium-Megatheriops* clade of Pujos (2006) is the moderate medial development of the patellar trochlea (character 20[1] of Pujos 2006). Pujos (2006) considered a different arrangement of the patellar trochlea and the distal condyles of the femur for *Pyramiodontherium* species (i.e., *Py. bergi*, *Py. brevirostrum*) and *Eremotherium laurillardi* and *E. eomigrans*. We consider that *Py. scillatoyanei* is very similar to these last species in this aspect and differs from *Pyramiodontherium bergi* and *Py. brevirostrum*; so that, there is no unequivocal synapomorphy that group the three species of *Pyramiodontherium* and *Megatheriops rectidens*. Furthermore, it must be emphasized that the phylogenetic analyses performed so far that have included the three species of *Pyramiodontherium* from northwest Argentina (Guillaume 2005; Brandoni 2006a, c) have not completely resolved the phylogenetic relationships among them and with *Megatheriops rectidens.* Nevertheless, the authors agree with the proximate relationship between species of *Pyramiodontherium* and *Megatheriops rectidens*. Intraspecific variation observed in the group, plus the shortage of available material of Tertiary taxa (especially from the "conglomerado osífero") makes full resolution difficult because of the relative paucity of characters applicable to the majority of taxa (Brandoni 2006a, c).

On the other hand, even if we accept a greater range of intraspecific variation, it is still not possible to assign several recently discovered remains, or MLP 2-78 and MACN-Pv 8143, to either of the two species from Catamarca Province, since this material is very fragmentary. Therefore, we suggest that MLP 2-78 and MACN-Pv 8143 be tentatively allocated as part of *Py. bergi*, following Cabrera's (1928) original proposal, until such time as their status can be discussed with benefit of additional information. It is noteworthy that a right femur (MACN-PV 2817) from the Valle de Santa María, while similar in size to *Py. bergi* and *Py. brevirostrum*, have the arrangement and shape of the patellar trochlea similar to *Py. scillatoyanei.* For this reason, the presence of *Py. scillatoyanei* in the late Miocene of Catamarca Province cannot as yet be ruled out.

Acknowledgments. We express our gratitude to Dr. A. Kramarz (MACN), Dr. M. Reguero (MLP), Drs. F. Aceñolaza and P. Aceñolaza (MRVU) and to G. Bahler (MAS), for facilitating access to collections under their care at their respective institutions. Illustrations are the work of J. González. We are grateful to R. Madden (Duke University) for his comments and corrections. This work was partially founded by PICT 2006-344 to DB; PICT-R 074/G3 and UNLP N-514 to AAC.

REFERENCES

Ameghino C. (1919) - Sobre los mamíferos fósiles del piso Araucanense de Catamarca y Tucumán. *Act. Prim. Reun. Nac. Soc. Arg. Cien. Nat. (Tucumán, 1916)*, 2: 150-153, Buenos Aires.

Ameghino F. (1883) - Sobre una nueva colección de mamíferos recogidos por el Profesor Pedro Scalabrini en las barrancas del Paraná. *Bol. Acad. Nac. Cien. Cba*, 5: 257-306, Córdoba.

Ameghino F. (1885) - Nuevos restos de mamíferos fósiles Oligocenos recogidos por el Profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la ciudad de Paraná. *Bol. Acad. Nac. Cien. Cba*, 8: 5-207, Córdoba.

Ameghino F. (1886) - Contribuciones al conocimiento de los mamíferos fósiles de los terrenos terciarios antiguos del Paraná. *Bol. Acad. Nac. Cien. Cba*, 9(1-2): 5-228, Córdoba.

Ameghino F. (1891) - Mamíferos y Aves fósiles argentinos. Especies nuevas, adiciones y correcciones. *Rev. Arg. Hist. Nat.*, 1: 240-259, Buenos Aires.

Ameghino F. (1904) - Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *An. Soc. Cien. Arg.*, 58: 225-291, Buenos Aires.

Brandoni D. (2005) - Los Megatheriinae (Xenarthra, Tardigrada) de la Formación Ituzaingó (Mioceno Superior-Plioceno) de la provincia de Entre Ríos. In: Temas de la Biodiversidad Fluvial del Litoral II, *INSUGEO*, Miscelánea, 14:27-35, Tucumán.

Brandoni D. (2006a) - Los Megatheriinae (Xenarthra, Tardigrada, Megatheridae) Terciarios de la Argentina. Sistemática, Evolución y Biogeografía. Unpublished Doctoral Thesis, Universidad Nacional de La Plata, La Plata, Argentina, 292 pp., La Plata.

Brandoni D. (2006b) - A review of *Pliomegatherium* Kraglievich, 1930 (Xenarthra: Phyllophaga: Megatheriidae). *Neues Jahr. Geol. Paläont., Monat.*, 4: 212-224, Stuttgart.

Brandoni D. (2006c) - Análisis filogenético de la subfamilia Megatheriinae (Mammalia, Xenarthra, Megatheriidae). *9º Cong. Arg. Paleont. Bioestr*, Actas: 97, Córdoba.

Brandoni D., Carlini A. A., Pujos F. & Scillato-Yané G. J. (2004) - The pes of *Pyramiodontherium bergi* (Moreno and Mercerat, 1891) (Xenarthra, Phyllophaga): the most complete pes of a Tertiary Megatheriinae. *Geodiversitas*, 26(4): 643-659, Paris.

Brandoni D. & Scillato-Yané G. J. (2007) - Los Megatheriinae (Xenarthra, Tardigrada) del Terciario de Entre Ríos, Argentina: aspectos taxonómicos y sistemáticos. *Ameghiniana*, 44(2): 427-434, Buenos Aires.

Bravard A. (1858) - Monografía de los terrenos marinos Terciarios de las cercanías del Paraná. Imprenta del Congreso de la Nación (Versión facsimilar). Buenos Aires, 1995, V XII + 1-107 pp., Buenos Aires.

Burmeister H. (1891) - Continuación a las adiciones al examen crítico de los mamíferos terciarios. *An. Mus. Nac. Bs As*, 3: 401-461, Buenos Aires.

Cabrera A. (1928) - Sobre algunos megaterios pliocenos. *Rev. Mus. La Plata*, 31: 339-352, La Plata.

Cabrera A. (1939) - Un nuevo representante Santacrucense de la Familia Megatheriidae. *Not. Mus. La Plata, Paleont.*, 4: 475-483, La Plata.

Carlini A. A., Pascual R., Reguero M., Scillato-Yané G. J., Tonni E. P. & Vizcaíno S. F. (1990a) - The first paleogene land placental mammal from Antarctica: its paleoclimatic and paleobiogeographical bearings. *IV Internat. Cong. Syst. Evol. Biol.*, Washington.

Carlini A. A., Scillato-Yané G. J. & Vizcaíno S. F. (1990b) - Un singular Paratheria del Eoceno temprano de Patagonia, Argentina. *Ameghiniana*, 26(3-4): 241, Buenos Aires.

Carlini A. A., Scillato-Yané G. J., Noriega J. I. & Aceñolaza F. (2000) - Perezosos terrestres (Xenarthra, Tardigrada) del "Mesopotamiense" (Fm. Ituzaingó, Mioceno tardío Plioceno) de la Provincia de Entre Ríos, Argentina. *Stvd. Geol. Salmant.*, 36: 13-27, Salamanca.

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(3): 367-377, Buenos Aires.

Carlini A. A., Brandoni D. & Sánchez R. (2006) - First megatheriines (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco (Late Miocene) and Codore (Pliocene) Formations, Estado Falcón, Venezuela. *J. Syst. Paleont.*, 4(3): 269-278, Cambridge.

Cione A. L., Azpelicueta M. M., Bond M., Carlini A. A., Casciotta J., Cozzuol M., De La Fuente M., Gasparini Z., Goin F. J., Noriega J. I., Scillato-Yané G. J., Soibelzon L., Tonni E. P., Verzi D. H & Vucetich M. G. (2000) - Miocene Vertebrates From Paraná, Eastern Argentina", *INSUGEO, Ser. Corr. Geol.*, 14: 191-237, Tucumán.

Cope E. D. (1889) - The Edentata of North America. *American Naturalist*, 23: 657-664, Chicago.

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. *Mag. Encyc.: J. Scien. Let. Arts*, 1(3): 303-310, Paris.

De Alba E. (1953) - Geología del Alto Paraná, en relación con los trabajos de derrocamiento entre Ituzaingó y Posadas. *Rev. Asoc. Geol. Arg.*, 8(3): 129-161, Buenos Aires.

De Iuliis G. (1996) - A Systematic Review of the Megatheriinae (Mammalia: Xenarthra: Megatheriidae). Unpublished Doctoral Thesis, University of Toronto, Toronto, 781 pp., Toronto.

De Iuliis G. (2003) - Toward a morphofunctional understanding of the humerus of Megatheriinae: the identity and homology of some diaphyseal humeral features (Mammalia, Xenarthra, Megatheriidae). *Senck. Biol.*, 83(1): 68-78, Frankfurt.

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, Lyon.

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*. *J. Vert. Paleont.*, 24(1): 214-227, Deerfield.

De Iuliis G., Brandoni D. & Scillato-Yané G. J. (2008) - New remains of *Megathericulus patagonicus* Ameghino, 1904 (Xenarthra, Megatheriidae): information on primitive features of megatheriines. *J. Vert. Paleont.*, 28(1): 181-196, Deerfield.

Delsuc F., Catzeflis F. M., Stanhope M. J. & Douzery E. J. P. (2001) - The evolution of armadillos, anteaters and sloths depicted by nuclear and mitochondrial phylogenies: implications for the status of the enigmatic fossil *Eurotamandua*. *Proc. Roy. Soc. London, B*, 268: 1605-1615, London.

Delsuc F., Scally M., Madsen O., Stanhope M. J., de Jong W. W., Catzeflis F. M., Springer M. S. & Douzery E. J. P. (2002) - Molecular phylogeny of living xenarthrans and the impact of character and taxon sampling on the placental tree rooting. *Molec. Biol. Evol.,* 19: 1656-1671, Oxford.

Frenguelli J. (1920) - Contribución al conocimiento de la geología de Entre Ríos. *Bol. Acad. Nac. Cien. Cba.*, 24: 55-256, Córdoba.

Gervais H. & Ameghino F. (1880) - Los mamíferos fósiles de la América del Sud. 225 pp., F. Savy-Ignon Hermanos, Paris-Buenos Aires.

Gradstein F. M., Ogg J. G. & Smith A. G. (2004) - A geologic time scale 2004. Cambridge University Press, Cambridge.

Gray J. E. (1821) - On the natural arrangement of vertebrose animals. *Lond. Med. Repos.* 5: 296-310, London.

Guillaume A. (2005) - Descripción de un nuevo Megatheriidae (Mammalia, Xenarthra) del Plioceno de la Provincia de Chubut, Argentina. Anatomía, Filogenia y Sistemática. Tesis de Grado de la Universidad Nacional S. J. Bosco, 192 pp., Trelew.

Guillaume A., Cladera G. A., Ortiz-Jaureguizar E., Carlini A. A. & Zimicz N. (2005) - Un nuevo Megatheriinae (Mammalia, Xenarthra, Megatheriidae) del Neógeno de Punta Quiroga (Golfo San José, Patagonia, Argentina). *Ameghiniana*, 42(4): 31R-32R, 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. *Univ. California Publ., Geol. Scien.,* 128: 1-91, Berkeley.

Kraglievich L. (1926) - Notas sobre gravígrados de Sud América. *An. Mus. Nac. Hist. Nat. Bs As*, 34: 21-36, Buenos Aires.

Kraglievich L. (1930) - La formación friaseana del Río Frías, Río Fénix, Laguna Blanca, etc. y su fauna de mamíferos. *Physis*, 10: 127-161, Buenos Aires.

Kraglievich L. (1934) - La antigüedad Pliocena de las faunas de Monte Hermoso y Chapadmalal deducida de su comparación con las que le precedieron y le sucedieron. Imprenta "El Siglo Ilustrado": 1-136, Montevideo.

Latham J. & H. Davies. (1795) - Faunula indica, 38 pp. In: Forster, J. R. - Zoologia indica. Ed. secunda, Halle a. S., London.

Lund P. W. (1842) - Blik paa Brasiliens dyreverden for sidste jordomvaeltning. Fjerde afhandling: fortsaettelse af pattedyrene. *Detk. Dan. Vidensc. Sels. Skrif.; Nat. math. Afhand.*, 9: 137-208, Copenhague.

Lydekker R. (1894) - Contributions to a knowledge of the fossil vertebrates of Argentina, 2. *An. Mus. La Plata, Paleont.*, 3: 1-118, La Plata.

Madsen O., Scally M., Douady C. J., Kao D. J., De Bry R. W, Adkins R., Amrine H. M., Stanhope M. J., de Jong W. W. & Springer M. S. (2001) - Parallel adaptative radiations in two major clades of placental mammals. *Nature*, 409: 610-614, London.

Marshall L. G. & Patterson B. (1981) - Geology and geochronology of the mammal-bearing Tertiary of the valle de Santa María and río Corral Quemado, Catamarca Province, Argentina. *Field. Geol.*, 9: 1-80, Chicago.

Miller G. S. (1929) - A second collection of mammals from caves near St. Michel, Haiti. *Smithsonian Miscell. Collec.*, 81(9): 1-30, Washington.

Moreno F. P. (1888) - Informe preliminar de los progresos del Museo de La Plata durante el primer semestre de 1888. *Bol. Mus. La Plata*, 1-35, La Plata.

Moreno F. P. & Mercerat A. (1891) - Exploración arqueológica de la Provincia de Catamarca: paleontología. *Rev. Mus. La Plata*, 1: 222-236, La Plata.

Murphy W. J., Eizirick E., Jonhson W. E., Zhang Y. P., Ryder O. A. & O' Brien S. J. (2001) - Molecular phylogenetics and the origins of placental mammals. *Nature*, 409: 614-618, London.

Owen R. (1840) - Fossil Mammalia, 4. In: Darwin C. (Ed.) - The Zoology of the voyage of H.M.S. Beagle under the command of Captain Fitzroy, N. R., during the years 1832 to 1836. Smith, Elder Co. 1(13): 81-111, London.

Owen R. (1860) - On the *Megatherium* (*Megatherium americanum* Cuvier and Blumenbach). Part IV. Bones of the anterior extremities. *Phil. Trans. Roy. Soc. London.,* 148(1): 261-278, London.

Philippi R. A. (1893) - Vorläufige Nachricht über fossile säugethierknochen von Ulloma, Bolivia. *Zeitsch. Deuts. Geol. Gesell.*, 45: 87-96, Berlin.

Pujos F. (2006) - *Megatherium celendinense* sp. nov. from the Pleistocene of Peruvian Andes and the megatheriine phylogenetic relationship. *Palaeontology*, 49(1): 285-306, London.

Pujos F. & Salas R. (2004) - A new species of *Megatherium* (Mammalia: Xenarthra: Megatheriidae) from the Pleistocene of Sacaco and Tres Ventanas, Peru. *Palaeontology*, 47(3): 579-604, London.

Pujos F., De Iuliis G., Argot C. & Werdelin L. (2007) - A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implication for sloth history. *Zool. J. Linn. Soc.*, 149: 179-235, London.

Ramos V. A. (1970) - Estratigrafía y estructura del Terciario en la Sierra de los Colorados (Provincia de La Rioja), República Argentina. *Rev. Asoc. Geol. Arg.,* 25(3): 359-382, Buenos Aires.

Riggs E. S. & Patterson B. (1939) - Stratigraphy of Late-Miocene and Pliocene deposits of the Province of Catamarca (Argentina) with notes on the faunae. *Physis*, 14: 143-162, Buenos Aires.

Roth S. (1911) - Un Nuevo Género de la Familia Megatheridae. *Rev. Mus. La Plata*, 18: 7-21, La Plata.

Rovereto C. (1914) - Los estratos araucanos y sus fósiles. *An. Mus. Nac. Hist. Nat. Bs As*, 25: 1-247, Buenos Aires.

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(4): 625-645, Paris.

Sinclair W. J. (1905) - New mammalia from the Quaternary caves of California. *Univ. California Pub., Bull. Geol.*, 4: 145-161, Berkeley.

Spillmann F. (1948) - Beiträge zur Kenntnis eines neuen gravigraden Reisensteppentieres (*Eremotherium carolinense* gen. et spec. nov), seines Lebensraumes und seiner Labensweise. *Palaeobiologica*, 8(3): 231-279, Wien.