The pes of *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (Mammalia, Xenarthra, Phyllophaga): the most complete pes of a Tertiary Megatheriinae

Diego BRANDONI
Centro de Investigación Científica y de Transferencia Tecnológica a la Producción (CICYTTP),
Materi y España, 3105 Diamante, Entre Ríos (Argentina)
and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)
diegobrandoni@yahoo.com

Alfredo A. CARLINI
Departamento Científico de 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 (UNLP),
calle 122 y 60, 1900 La Plata (Argentina)
and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)

François PUJOS
Institut français d'Études andines, Casilla 18-1217, av. Arequipa 4595, Lima 18 (Peru)
and Département Histoire de la Terre, Muséum national d'Histoire naturelle, UMR 5143 du CNRS,
case postale 38, 8 rue Buffon, F-75231 Paris cedex (France)

Gustavo J. SCILLATO-YANÉ
Departamento Científico de Paleontología de Vertebrados,
Museo de La Plata, Paseo del Bosque s/n°, 1900 La Plata (Argentina)
and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)

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ABSTRACT
The aim of this paper is to enlarge the description of the only known complete pes of a Tertiary megatherine and make comparisons with those of other members of the subfamily. The complete pes of the type specimen of *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66) was found at the informally named "Araucanense" *s.l.* levels of Bajo de Andalhuala, Catamarca Province (late Miocene-Pliocene), Argentina. The elements of the pes show the general characters of other megatherines. However, the astragalar depression is not as deep as in *Megatherium americanum* Cuvier, 1796; the calcaneum is more slender than *Eremotherium laurillardi* (Lund, 1842); the navicular has two facets to articulate with the ectocuneiform; there are

seven separate tarsal elements (calcaneum, astragalus, navicular, entocuneiform, mesocuneiform, ectocuneiform, and cuboid) while in other megatherines, usually the mesocuneiform and the entocuneiform are fused into a single element termed the mesoentocuneiform complex; the third digit is formed only by the proximal phalanx fused with the second phalanx, and digit IV, unlike Quaternary megatherines, has three phalanges. The presence of separated entocuneiform and mesocuneiform and three phalanges in the digit IV, are interpreted as plesiomorphic condition of the characters present in the Plio-Pleistocene genera. The plesiomorphic character states observed here could be useful to solve the megatherine polytomy proposed by De Iuliis (1996), and indicate more precisely the way the states of the characters were changed.

KEY WORDS
Mammalia,
Xenarthra,
Megatheriinae,
Pyramiodontherium bergi,
Tertiary,
pes,
morphology.

RÉSUMÉ

Le pied de Pyramiodontherium bergi *(Moreno & Mercerat, 1891) (Mammalia, Xenarthra, Phyllophaga) : le pied le plus complet d'un Megatheriinae tertiaire.*

Ce travail se propose de compléter la description du seul pied complet de mégathère tertiaire connu et ainsi de pouvoir réaliser des comparaisons avec ceux des autres membres de la sous-famille. Le pied complet de l'holotype de *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66) provient du niveau « Araucanense » *s.l.* de Bajo de Andalhuala, Province de Catamarca (Miocène supérieur-Pliocène), Argentine. Les éléments du pied présentent la structure habituellement rencontrée chez les mégathères. Cependant, la dépression astragalienne est moins profonde que chez *Megatherium americanum* Cuvier, 1796 et le calcanéum est moins gracile que chez *Eremotherium laurillardi* (Lund, 1842). Le naviculaire présente deux facettes articulaires pour l'ectocunéiforme. Le pied est constitué de sept éléments (calcanéum, astragale, naviculaire, entocunéiforme, mésocunéiforme, ectocunéiforme et cuboïde) alors que chez les autres mégathères dont le pied est connu, mésocunéiforme et entocunéiforme sont fusionnés en un seul élément, dénommé complexe méso-entocunéiforme. Le troisième doigt n'est constitué que de deux phalanges, la phalange proximale résultant de la fusion de deux phalanges. Contrairement à tous les mégathères quaternaires, le doigt IV de *P. bergi* possède trois phalanges. La présence d'un entocunéiforme et d'un mésocunéiforme séparés ainsi que de trois phalanges pour le doigt IV chez le genre plio-pléistocène est considérée ici comme étant la condition primitive. Les états de caractères plésiomorphes présents ici pourraient aider à résoudre la polytomie des mégathères proposée par De Iuliis (1996) ainsi qu'à appréhender leurs différents changements.

MOTS CLÉS
Mammalia,
Xenarthra,
Megatheriinae,
Pyramiodontherium bergi,
Tertiaire,
pied,
morphologie.

INTRODUCTION

Quaternary Megatheriinae are among the best known of all extinct South American xenarthrans. Paradoxically, the most ancient Megatheriinae from the middle Miocene and Pliocene have remained largely unknown because of the relative scarceness of the material. Relying only on published accounts, there is strong uncertainty concerning the taxonomic validity, anatomical characterization, and phylogenetic relationships of the described taxa.

The oldest records of Megatheriinae date back as far as the middle Miocene, and include the genera of the "Friasian" interval, represented by three successive faunas: Colloncuran, Laventan and Mayoan (see Scillato-Yané & Carlini 1998, for a discussion of the use and extension of the term "Friasian" to include the three faunas included here). These genera are: 1) *Megathericulus* Ameghino, 1904 (including *M. patagonicus* Ameghino, 1904 and *M. primaevus* Cabrera, 1939, both from the Colloncuran [middle Miocene] of Patagonia); 2) a Megatheriinae indet. from the Laventan (middle Miocene) of Colombia described by Hirschfeld (1985: 47-49) and probably closely related to *Eomegatherium nanum* (Burmeister, 1892) (= *Promegatherium* for Hirschfeld 1985); and 3) *Eomegatherium* Kraglievich, 1926 (including both *E. andinum* Kraglievich, 1930 and *E. cabrerai* Kraglievich, 1930 from the Mayoan [middle Miocene] of Patagonia). Despite Hirschfeld's (1985) claim that *Megathericulus primaevus*, a taxon based on an astragalus found in sediments attributed to the Santacrucian (lower Miocene) (Cabrera 1939), is the oldest record of the subfamily Megatheriinae, we now know that these fossil-bearing sediments are somewhat younger and of Colloncuran age (Bondesio *et al.* 1980). We see then that old mistakes in the systematic identification and chronology of the oldest Megatheriinae persist to the present. Likewise, the general panorama of late Miocene and Pliocene megathere evolution has not been fully clarified, despite numerous papers on the subject such as the contributions of Cabrera (1928) and De Iuliis (1996). Elements of the megatherine pes have been described by several authors, mainly Owen (1860), Roth (1911), Cabrera (1929), Paula Couto (1978), Cartelle (1992), De Iuliis (1996), and Pujos & Salas (2004). Except for the contributions of Roth (1911) and De Iuliis (1996), the remaining papers concern mainly Quaternary species of *Megatherium* and *Eremotherium*. Both, Roth (1911) and De Iuliis (1996) described briefly some bones of the pes of *Pyramiodontherium bergi* (Moreno & Mercerat, 1891), and paid special attention to the astragalus and calcaneum of this "Araucanian" or late Miocene-Pliocene species.

The aim of this paper is to extend the description of the only known complete pes of a Tertiary megatherine, that of *P. bergi*, to include elements that have been less well studied, and to make more detailed and extensive comparisons with the same elements in other members of the family. The complete pes of the holotype of *P. bergi* (MLP 2-66) is housed in the collection of Departamento Científico de Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina. It was recovered from informally named "Araucanense" *s.l.* levels at Bajo de Andalhuala in Catamarca Province, Argentina, of presumed late Miocene-Pliocene age (see Carlini *et al.* 2002). According to Moreno & Mercerat (1891) the remains were collected by Methfessel and staff of the Museo de La Plata during archaeological and paleontological explorations in Catamarca Province at the end of the 19th century.

ABBREVIATIONS

FMNH	Field Museum of Natural History, Chicago;
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires;
MLP	Museo de La Plata, La Plata;
MNHN	Muséum national d'Histoire naturelle, Paris;
MUSM	Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima;
ROM	Royal Ontario Museum, Toronto;
UNA	Universidad de la Ingenieria, Lima.

SYSTEMATICS

Order XENARTHRA Cope, 1889
Suborder PHYLLOPHAGA Owen, 1842
Superfamily MEGATHERIOIDEA Gray, 1821
Family MEGATHERIIDAE Gray, 1821
Subfamily MEGATHERIINAE Gray, 1821
Genus *Megatherium* Cuvier, 1796

Pyramiodontherium bergi
(Moreno & Mercerat, 1891)

Megatherium burmeisteri Moreno & Mercerat, 1891: 229.

TABLE 1. — Specimens used for comparison.

Specimen No.	Taxon	Locality and age
MLP 91-IX-7-18	*Megathericulus patagonicus*	Santa Cruz Province, Argentina. Middle Miocene
MACN 4941	*Megatherium*? *antiquum*	Entre Ríos Province, Argentina. Late Miocene
MACN 4983	*Megatherium*? *antiquum*	Entre Ríos Province, Argentina. Late Miocene
MACN 4992	*Eomegatherium nanum*	Entre Ríos Province, Argentina. Late Miocene
MLP 99-XI-1-1	*Pliomegatherium*	Entre Ríos Province, Argentina. Late Miocene
MACN 13218	*Pliomegatherium*	Entre Ríos Province, Argentina. Late Miocene
MLP 68-III-14-1	*Plesiomegatherium* sp.	La Rioja Province, Argentina. Pliocene
MLP 2-29	*Megatherium americanum*	Buenos Aires Province, Argentina. Pleistocene
MNHN PAM 295	*Megatherium americanum*	Buenos Aires Province, Argentina. Pleistocene
ROM 21928	*Eremotherium laurillardi*	La Carolina, Ecuador and Daytona Beach, Florida, USA
ROM 21932		
ROM 22003		
ROM 22013		
ROM 22014		
ROM 30768		
FMNH P14216	*Megatherium tarijense*	Tarija Valley, near Padcaya, Bolivia. Pleistocene
MNHN TAR 269	*Megatherium tarijense*	Tarija Valley, near Padcaya, Bolivia. Pleistocene
MUSM 15	*Megatherium urbinai*	Sacaco, Arequipa Department, Peru. Pleistocene
UNA V2642	*Megatherium urbinai*	Tres Ventanas Cave, Peru. Pleistocene

Megatherium bergi Moreno & Mercerat, 1891: 231.

Pyramiodontherium dubium Rovereto, 1914: 89.

Pyramiodontherium bergi – Cabrera 1928: 344.

MATERIAL EXAMINED. — MLP 2-66 (holotype). In addition to the remains described and illustrated in Roth (1911), De Iuliis (1996), and Carlini *et al.* (2002), the following well preserved material is here described: left and right astragali, left calcaneum, right navicular, left and right cuboids, left and right ectocuneiforms, left and right mesocuneiforms, left and right entocuneiforms, right metatarsal III, left metatarsal IV, right metatarsal V, phalanx 1+2 of left and right digit III, left and right ungual phalanx, and phalanx 1 and 2 of right digit IV. Comparison specimens listed in Table 1.

COMPARATIVE DESCRIPTION

The foot bones of *P. bergi* (Fig. 1) are described in anatomical position during locomotion. As in the other megatherines, the pes has undergone torsion, resulting in a deviation of its axis with respect to the horizontal. Consequently, pedal elements are inclined along a dorsolateral-ventromedial major axis.

Astragalus

The astragalus of *P. bergi* (Fig. 2A-D), partially described by Roth (1911), has the typical shape for the subfamily Megatheriinae. It is massive, with a well developed central odontoid process in dorsomedial view, and a navicular facet in anterior view.

As in other megatherines, the fibular facet in *P. bergi* is divided into two portions, an anteroposteriorly elongate dorsal division that joins the discoid facet, and a ventral portion with a rather circular surface that is slightly extended ventrally. This latter division has well defined margins anteriorly. A similar morphology is also seen in MLP 68-III-14-1, but in this specimen the ventral portion is oval with the long axis perpendicular to the anteroposterior axis of the fibular facet, and the dorsal portion is reduced. In MACN 4992 the ventral portion of the fibular facet is similar in shape to that of *P. bergi*, although in some specimens of *M. americanum* (MLP 2-29), the ventral portion of the facet is semilunar in shape and in general more depressed. On the basis of his observations on *E. laurillardi*, De Iuliis (1996) states that the shape of the fibular facet may have intraspecific variation. In addition, he outlines the well defined margins and a bilobate facet in *M. americanum* (MNHN P1871).

The troclea tali is composed of two portions: a lateral, wide, discoid portion, and another semicylindrical, positioned in the middle of the for-

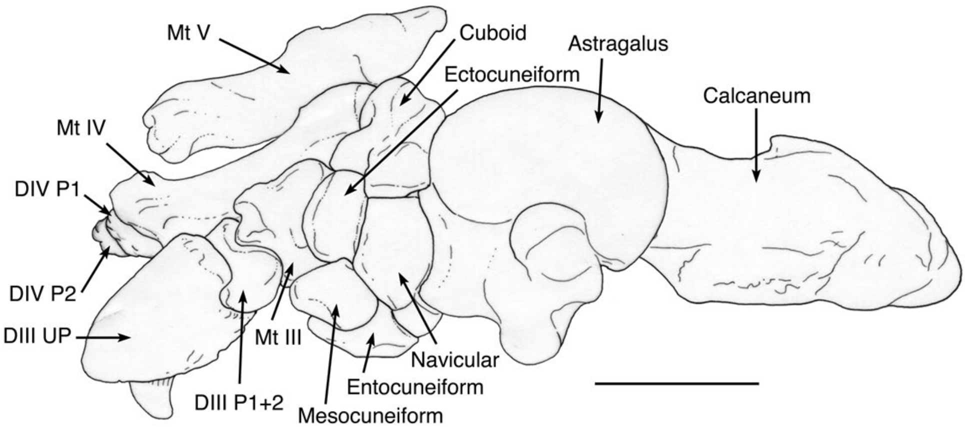


FIG. 1. — Dorsolateral view of a compose pes of *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66). Abbreviations: **DIII P1+2**, digit III, phalange 1+2; **DIII UP**, digit III, ungueal phalange; **DIV P1**, digit IV, phalange 1; **DIV P2**, digit IV, phalange 2; **Mt III, IV, V**, metatarsals III, IV, V. Scale bar: 100 mm.

mer. Both portions correspond to the discoid facet and the odontoid process of De Iuliis (1996). The dorsal part of this process has a semi-cylindrical facet termed the odontoid facet, and this feature is related to the torsion of the pes, as verified in several large-sized tardigrades.

In *P. bergi* the odontoid process (middle portion) is peg-shaped as in *Megathericulus patagonicus*, although in the latter, it is anteriorly inclined in dorsal view. Specimens MACN 4992, MACN 13218, and MLP 99-XI-1-1 are similar to *P. bergi* in the shape of the odontoid process, the facet, and its inclination. In distal view the odontoid process is somewhat compressed in the contact with the discoid facet. The angle between the odontoid and discoid facets is nearly straight in *P. bergi* and MLP 68-III-14-1, whereas it is obtuse in the remaining members of the subfamily. De Iuliis (1996) states that the compression of the odontoid process in *P. bergi* results from deformation, but there seems to be no deformation as in both astragali the shape of the odontoid process is the same. In addition, this author states that the odontoid process of *P. bergi* is as extended as in *E. laurillardi*.

In distal view the width of the discoid and odontoid facets is similar in *M. americanum* and *M. urbinai*. In *P. bergi* and MLP 68-III-14-1 the odontoid facet is larger than the discoid facet, and in *M. tarijense* the discoid facet is wider.

In *M. americanum* and MACN 4941 the odontoid process is dome-shaped, with the largest width at the contact with the discoid facet. In *P. bergi*, the proximal-distal width of the odontoid facet represents one third of the width of the discoid facet in medial view. In MLP 68-III-14-1 the middle facet is larger, occupying half the width of the discoid facet.

In *P. bergi*, a prominent portion of non-articular bone projects anteroventrally from the odontoid process. De Iuliis (1996) termed this portion the odontoid tuberosity. This tuberosity is present, although less developed in MACN 4941, MACN 4992, MLP 68-III-14-1, as well as in *M. patagonicus*. In *M. americanum* the odontoid tuberosity is somewhat less prominent than in the aforementioned specimens.

In some species (e.g., *M. patagonicus*) a small oval facet for articulation with a sesamoid can be seen between the odontoid tuberosity and the posteromedial portion of the odontoid facet. In *P. bergi*, this facet is absent.

The facet for the navicular on the anteriormost part of the astragalus is approximately oval, with the main axis oriented dorsolateral-ventromedially. The facet has two surfaces, a concave dorsolateral portion termed the astragalar depression and another ventromedial convex portion. The astragalar depression is deeper in *M. americanum* than in *P. bergi*, but similar to *P. bergi* in MACN 4941, MACN 4992, MACN 13218, MLP 99-XI-1-1, and MLP 68-III-14-1.

In *P. bergi*, the dorsomedial half of the navicular facet is positioned dorsally with respect to the plane of the discoid facet (Fig. 3A). This situation is similar in *M. patagonicus* (MLP 68-III-14-1, MACN 4992, MACN 13218, MLP 99-XI-1-1, and MACN 4941). By contrast, in *M. americanum* the dorsomedial part of the navicular facet is at the same level with discoid facet. At the other extreme, in *E. laurillardi* and *M. urbinai* the dorsal margin projects by one third over the discoid facet. The navicular facet in *M. tarijense* displays an intermediate position between *M. americanum* and *M. urbinai*.

In dorsomedial view the odontoid facet is semicylindrical in section and the projection of the base exceeds the navicular facet in *P. bergi* (Fig. 3B) as in all other Tertiary astragali. In *M. americanum* this plane cuts the navicular facet whereas in MLP 68-III-14-1 the plane scarcely cuts the facet.

The cuboid facet appears on the external side of the astragalus where it is slightly differentiated from the convex portion of the navicular facet. The cuboid facet is convex and subtriangular to pyriform in shape.

There are two facets for articulation with the calcaneum; the smaller sustentacular facet and the ectal facet. These two facets are separated by a deep and wide non-articular bony canal, the sulcus tali. A similar arrangement can be verified in most megatherines except one specimen of *M. americanum* (Kraglievich 1926), one specimen of *E. laurillardi* (ROM 22006 in De Iuliis 1996 and Pujos 2001 pers. obs.), one specimen of *M. urbinai* (UNA V2642 in Pujos & Salas 2004) in which these facets are fused, and in *M. tarijense* (MNHN TAR 269 Pujos 2002 pers. obs.) where they are partially fused. In MLP 68-III-14-1, the bony canal is deep but narrow due to the large size of the ectal facet.

The sustentacular facet is continuous with the cuboid facet but is separated from the ventral portion of the navicular facet. It is almost planar or flat and subtriangular in shape. The ectal facet is oval in shape, with the main axis anterolateral to posteromedial, parallel to the sulcus tali. The ectal facet is concave along the main axis and convex along the other axis. In dorsolateral view the distance between the ectal and the discoid facets is greater than in *M. americanum*, whereas in MLP 68-III-14-1, MACN 4941, MACN 4992, MACN 13218, MLP 99-XI-1-1, although separated, the distance is shorter.

Calcaneum

The calcaneum of *P. bergi* (Fig. 2E, F) is shaped as in other megatherines, although somewhat more gracile than in *M. americanum* and *E. laurillardi* and both more compressed and elongated posteriorly behind the articular end. The calcaneum has three articular facets on its anterior end; two articulate with the astragalus and one with the cuboid. The largest facet articulates with the ectal facet of the astragalus. This facet is also the most dorsal and is oval in shape with the main axis oriented anterolateral to posteromedially, parallel to the sulcus calcanei (placed ventrally to the facet). The facet is convex along the main axis, medially concave along the secondary axis, and flat laterally. A second facet articulates with the sustentacular facet of the astragalus. This facet is relatively quadrangular to pentagonal in outline, planar, and is separated from the former by the sulcus calcanei. The third or cuboid facet is smaller, positioned lateroventrally with respect to the sustentacular facet, and semicircular to oval in shape. In *P. bergi*, this facet and the sustentacular facet are not in contact. The sulcus calcanei, separating the ectal and sustentacular facets, runs transversally and of uniform width throughout its full extent. Finally, it should be noted that the calcaneum of MLP 68-III-14-1 is more robust and shorter than that of the type of *P. bergi*.

Navicular

The navicular (Fig. 4A-C) is oval to subrectangular in shape (distal view), antero-posteriorly compressed with the main axis oriented dorsolateral

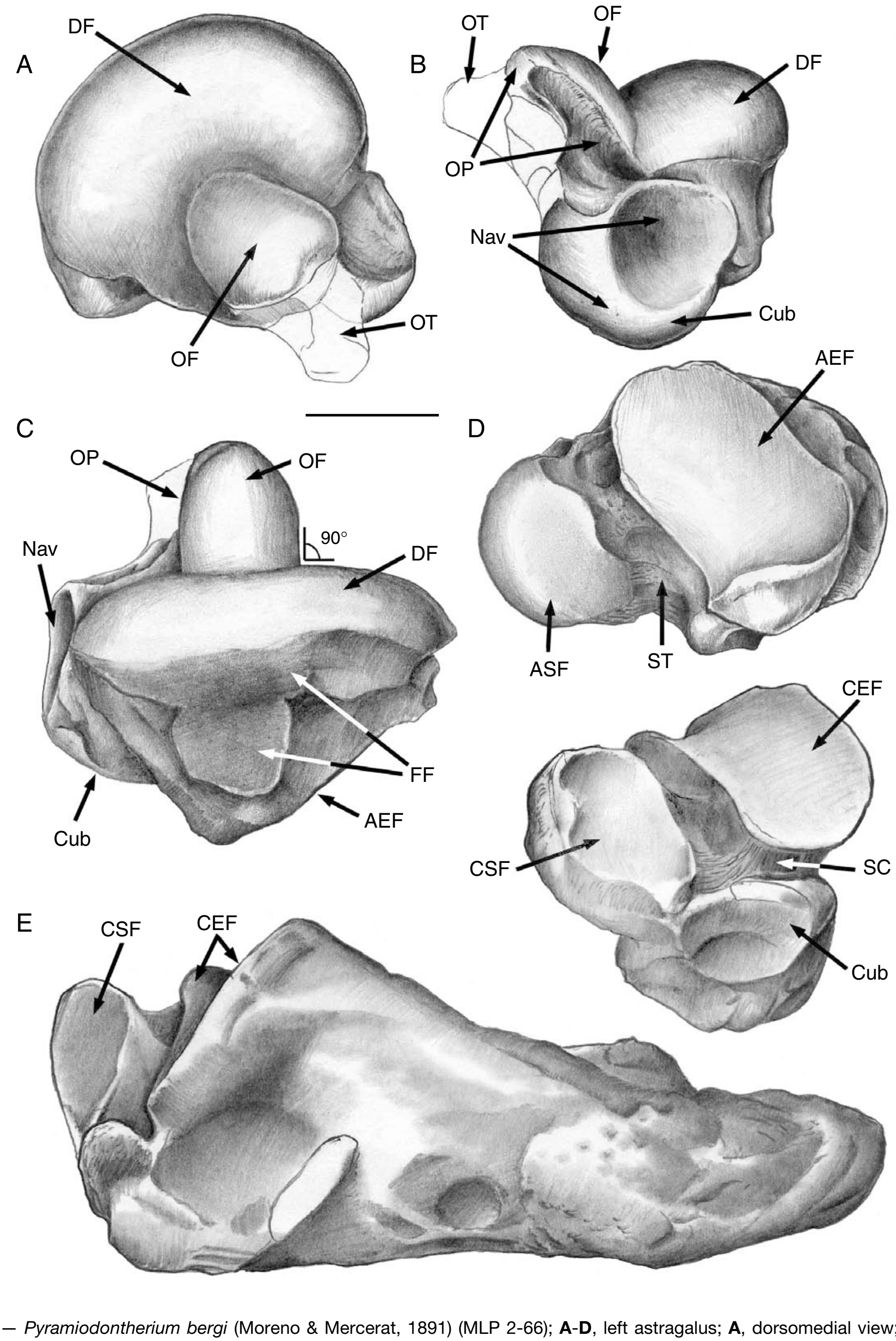


FIG. 2. — *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66); **A**-**D**, left astragalus; **A**, dorsomedial view; **B**, anteromedial view; **C**, fibular view; **D**, ventral view; **E**, **F**, left calcaneum; **E**, specular lateral view; **F**, specular distal view. Abbreviations: **AEF**, astragalar ectal facet; **ASF**, astragalar sustentacular facet; **CEF**, calcaneal ectal facet; **CSF**, calcaneal sustentacular facet; **Cub**, cuboid; **DF**, discoid facet; **FF**, fibular facet; **Nav**, navicular; **OF**, odontoid facet; **OP**, odontoid process; **OT**, odontoid tuberosity; **SC**, sulcus calcanei; **ST**, sulcus tali. Scale bar: 50 mm.

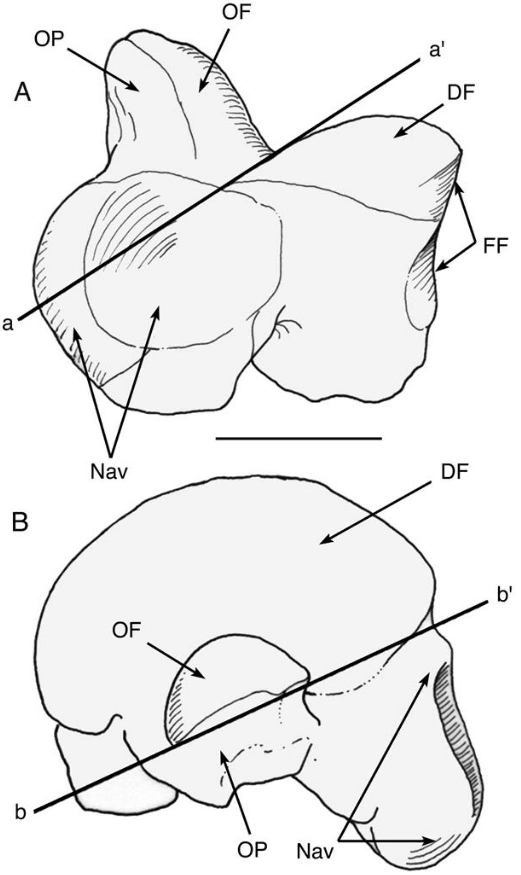


FIG. 3. — Astragalus of *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66); **A**, anterior view; **B**, dorsolateral view. **a-a' line**, projection of the plane of the discoid facet; **b-b' line**, projection of the plane of the base of the odontoid facet. Abbreviations: **DF**, discoid facet; **FF**, fibular facet; **Nav**, navicular; **OF**, odontoid facet; **OP**, odontoid process. Scale bar: 50 mm.

to ventromedially. In MLP 2-66 a portion of the dorsolateral half is missing.

The astragalar facet is located on the proximal surface, and may be differentiated into dorsolateral and ventromedial halves. The dorsolateral half is more or less circular and is formed by a condylar projection that fits into the circular depression of the astragalus (facie articular navicularis). This projection is not as well developed as in *Megatherium americanum*. The ventromedial half is relatively oval, concave along its main axes and articulates with the condylar portion of the astragalus. Both halves are similar in size, as in *M. americanum*. In *M. altiplanicum* from the Pliocene of Bolivia, the medial part of the facet is larger than the lateral part (Saint-André & De Iuliis 2001).

On the distal surface the navicular is convex along its main axes. On this aspect there are three articular facets. Ventrally there are two ectocuneiform facets, the smallest is subtriangular and ventromedial with respect to the other which is larger, quadrangular to trapezoidal, and positioned dorsolaterally.

Dorsomedially to the aforementioned facets there is a large facet that articulates with the internal meso- and entocuneiforms. This large facet is oval, elongate along the main axis of the navicular, but broken on its central part. This facet joins dorsally with the square ectocuneiform facet, being a rebound on the border (as in MACN 4983). In *M. americanum*, the ectocuneiform facets are fused and the internal cuneiform facet is smaller than the facet for the ectocuneiform.

A cuboid facet lies on the ventrolateral portion of the navicular. It is elongate along the dorsolateral-ventromedial axis. This facet has two different portions, one dorsolateral and other ventral. The dorsolateral portion contacts with the dorsal portion (condylar projection) of the navicular facet proximally, and the dorsal (square) ectocuneiform facet distally, in both cases in an approximately right angle. The lower portion of the cuboid facet contacts with the ventral portion of the astragalar facet posteriorly, and anteriorly is separated from the ventral ectocuneiform facet by a non-articulate furrow. In *M. americanum* the cuboid facet is located in a single plane, as may be seen on the navicular facet of the cuboid.

Cuboid

The cuboid (Fig. 4D-H) is irregular in shape, more or less cubic, massive, and supports two complex articular surfaces separated by non-articulating bone. On the posteromedial surface there are facets for the calcaneum, astragalus, navicular, and ectocuneiform. On the anteroventral surface of the bone, there are facets for metatarsals III, IV, and V. The dorsal surface of the cuboid is rugose, relatively flat, and devoid of articular facets. The ventral portion is more irregular, with some plantar projections, and a posterolaterally projecting crest that reaches the dorsal surface. A deep dorsoventral furrow occupies the medial side of the cuboid and separates the articular areas.

The calcaneal facet is posterolateral, square, with the dorsomedial half concave, and the ventrolateral convex. The astragalar facet is posteromedial, and contacts the calcaneal facet forming a straight angle between them. It is approximately oval with the main axis dorsolateral to ventromedial and concave in both main axes.

The navicular facet is placed medially in front of the astragalar facet. The latter is subdivided into two different planes corresponding to those developed for the lateral facet of the navicular. The navicular facet is dorsoventrally elongate and narrow; the posterior margin contacts the astragalar facet and the anterior margin contacts the ectocuneiform facet.

The small and semicircular ectocuneiform facet contacts the navicular facet posteriorly and the medial furrow anteriorly. This facet is absent in *M. americanum*, occasionally present in *E. laurillardi* (Cartelle 1992) and always present in *M. tarijense* (Pujos & Salas 2004).

The facet for metatarsal IV has two portions, each plane almost perpendicular to the other. The posterior portion is elongate along the dorsolateral-ventromedial axis, and the more anterior and dorsal plane is oval in shape, and placed on an anterior laminar projection of the cuboid. In *M. americanum* the angle between these two portions is wider.

The metatarsal V facet is next to the most elongate portion of the Mt IV facet, in a straight angle. It is almost triangular with a ventral apex, convex in both axis.

On the anteromedial end of the cuboid, supported medially by the laminar projection, there is a small oval facet for metatarsal III that is extended dorsoventrally. This facet is present in *M. americanum*, but *M. tarijense* has no articulation between the cuboid and metatarsal III.

Mesocuneiform

The mesocuneiform (Fig. 4I) is trapezoidal in medial view. It has three articular facets, two lateral facets, one proximal for the navicular, another distal for metatarsal III, and one ventral facet (on a slightly inclined plane) for the entocuneiform. The navicular facet is oval but has a downward projection that is continuous with the ascending lateral proximal entocuneiform facet. Both these facets form a continuous, dorsoventrally-oriented functional surface. The Mt III facet is circular and articulates with the medial proximal facet of metatarsal III. The two lateral mesocuneiform facets, equal in size, are separated by a fragment of non-articulating bone, also similar in size. The entocuneiform facet contacts the navicular facet and is separated from the Mt III facet. It is the largest of the articular facets and is oval to triangular in shape.

Entocuneiform

The entocuneiform (Fig. 4I) is rectangular in medial view, larger than the mesocuneiform, and has two articular facets: one lateral and the other dorsal, which articulate with the navicular and the mesocuneiform, respectively, and are in contact proximally. The navicular facet is oval and is continuous upward with the descending portion of the mesocuneiform lateral proximal facet. The mesocuneiform facet is placed located almost horizontally and perpendicular to the lateral facet. It is larger and matches in shape with the mesocuneiform ventral facet. On the internal lateral surface there is a fragment of non-articulating bone that bears a semilunar depression of flat bottom that divides the bone in two parts, one principal and other reminiscent of a plantar tuberosity.

In *P. bergi* there is no fusion of the meso- and entocuneiform, termed the mesoentocuneiform complex by De Iuliis (1996). In megatherines (e.g., *Megatherium* sp., *Eremotherium* sp.) that have this complex, it is triangular (or pentagonal) with the apex anteriorly directed. The proximal surface has an elongate navicular facet, and the distal surface displays a small oval Mt III facet dorsolaterally.

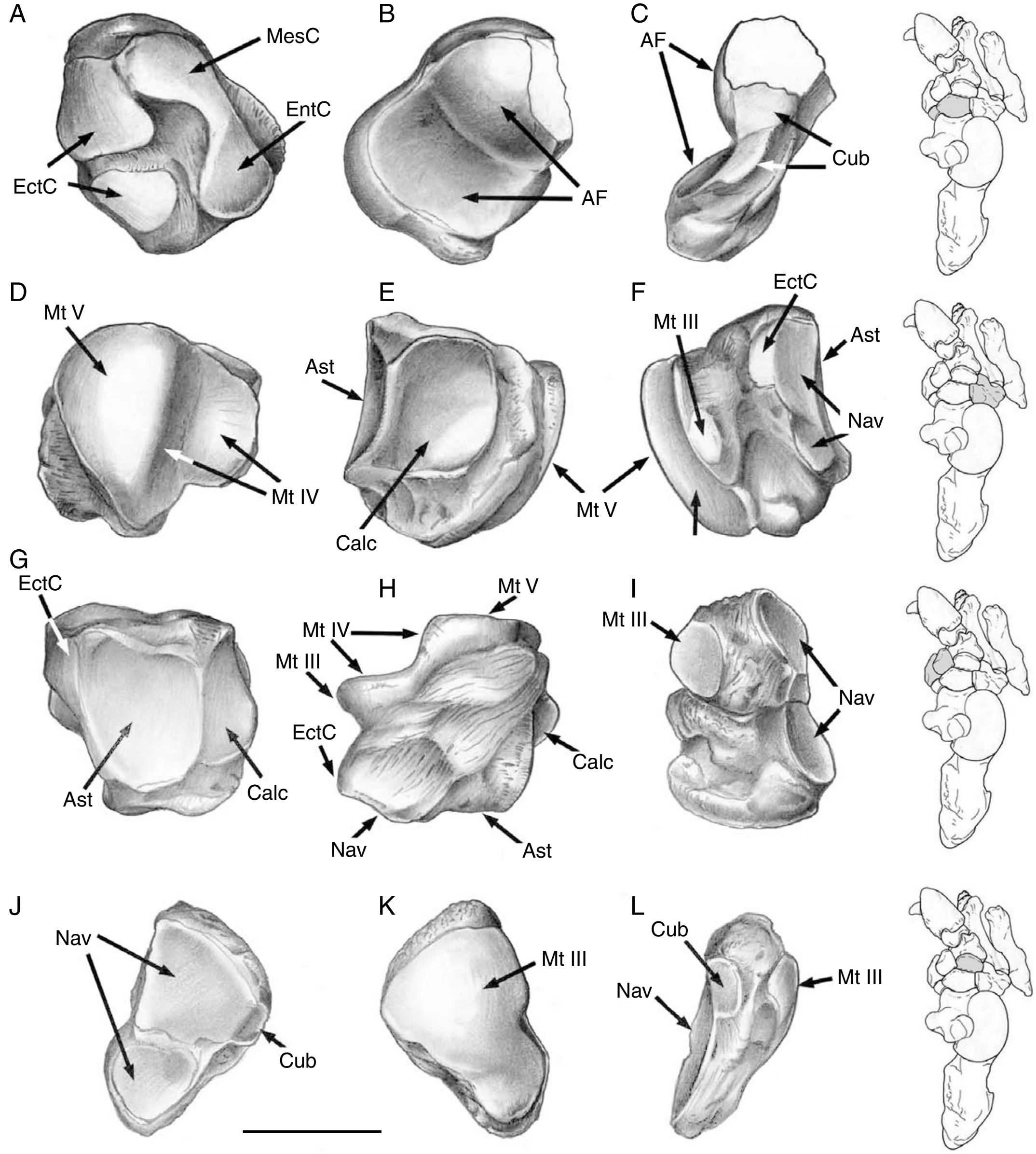


FIG. 4. — *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66); **A**-**C**, right navicular; **A**, proximal view; **B**, distal view; **C**, lateral view; **D**-**H**, right cuboid; **D**, posteromedial view; **E**, posterolateral view; **F**, proximal view; **G**, proximolateral view; **H**, dorsolateral view; **I**, right mesocuneiform and entocuneiform, lateral view; **J**-**L**, right ectocuneiform; **J**, proximal view; **K**, distal view; **L**, lateral view. Abbreviations: **Ast**, astragalus; **AF**, astragalar facet; **Calc**, calcaneum; **Cub**, cuboid; **EctC**, ectocuneiform; **EntC**, entocuneiform; **MesC**, mesocuneiform; **Mt III, IV, V**, metatarsals III, IV, V; **Nav**, navicular. Scale bar: 50 mm.

Ectocuneiform

The ectocuneiform (Fig. 4J-L) is triangular with its base dorsolateral, apex ventromedial, and elongate in its main axis. It is anteroposteriorly compressed, convex anteriorly, and diminishes in thickness dorsolaterally-ventromedially. It is more gracile, elongate and tapered than in other genera (i.e. *Megathericulus* and *Megatherium*).

The proximal and distal surfaces of the ectocuneiform are almost entirely articular, with two main areas (proximal and distal) that follow the triangular shape of the ectocuneiform, and are separated by non-articular bone. Proximally, two navicular articular facets are developed: one laterodorsal facet that is subtrapezoidal to square, and another ventromedial facet that is subtriangular. Both facets fit in shape and size with their counterparts developed on the distal surface of the navicular. Also like those of the navicular, they are separated by a transverse fringe of non-articular bone. At the same level, the laterodorsal facet is continuous ventrally with a subrectangular facet and their articular planes meet in a 120° angle. The subrectangular facet articulates with the small semicircular cuboid facet, which is absent in *M. americanum* and *M. urbinai*, and present in *M. tarijense*. Most of the distal surface of the ectocuneiform is occupied by a facet for Mt III that is approximately triangular and convex, although it has a small furrow near the ventromedial apex. In other genera (i.e. *Megatherium*), the distal facet is completely convex. In *M. urbinai*, the ectocuneiform articulates with metatarsals III and IV (Pujos & Salas 2004). There is no articulation between the ectocuneiform and the internal cuneiforms in *P. bergi*. In *M. urbinai* (MUSM 15) and *M. tarijense* (FMNH P14216), the ectocuneiform articulates with the mesoentocuneiform complex and a similar articulation is also present in some specimens of *M. americanum* (e.g., MNHN PAN 295).

Metatarsal III

In *P. bergi*, the metatarsal III (Fig. 5A-E) is anteroposteriorly very compressed compared to metatarsals IV and V. The posterior portion is strongly compressed transversally, while in other megatheres (i.e. *E. laurillardi*), this portion is shorter (Paula Couto 1978).

The ectocuneiform facet is posteromedial, almost triangular with ventral apex, and concave along both axes. A small mesocuneiform facet, oval in shape, occupies the proximomedial side of the metatarsal III. This facet contacts posteriorly with the ectocuneiform facet in straight angle.

The facet for metatarsal IV is lateral, oval in shape, and extended dorsoventrally. The surface is undulate, markedly concave anteriorly, and convex posteriorly. The articular surface is nearly parallel to the ectocuneiform facet. A small accessory Mt IV facet appears on the dorsolateral surface of the metatarsal III.

Between the facets for ectocuneiform and Mt IV, there is a posterolateral projection that supports an oval cuboid facet.

On the distal surface a crest articulates with phalanx 1+2 of digit III. It is slightly concave dorsoventrally, it narrows ventrally becoming also more acute, and is inclined along a dorsolateral to ventromedial axis. We conclude that this crest is almost entirely articular because in the middle of its dorsoventral extent (on the deepest part of the concavity) there is a small non-articulating area that fits with the corresponding phalanx 1+2 of digit III. An elongate internal surface continues beyond the crest to complete the articulation. In *M. americanum* the crest is interrupted and continues medially as an independent small oval facet. The ventromedial end of the keel has an articular facet probably for a sesamoid. On the most ventrolateral portion of metatarsal III there is a plantar prominence.

Metatarsal IV

Metatarsal IV (Fig. 5F-I) is long and not as compressed as metatarsal III. The diaphysis is triangular in section with lateral apex, whereas in *M. americanum* the section is subtriangular to oval. The proximal portion is laterally compressed and dorsoventrally expanded.

Three articular facets appear on the proximal epiphysis, an anteromedial facet for Mt III, a

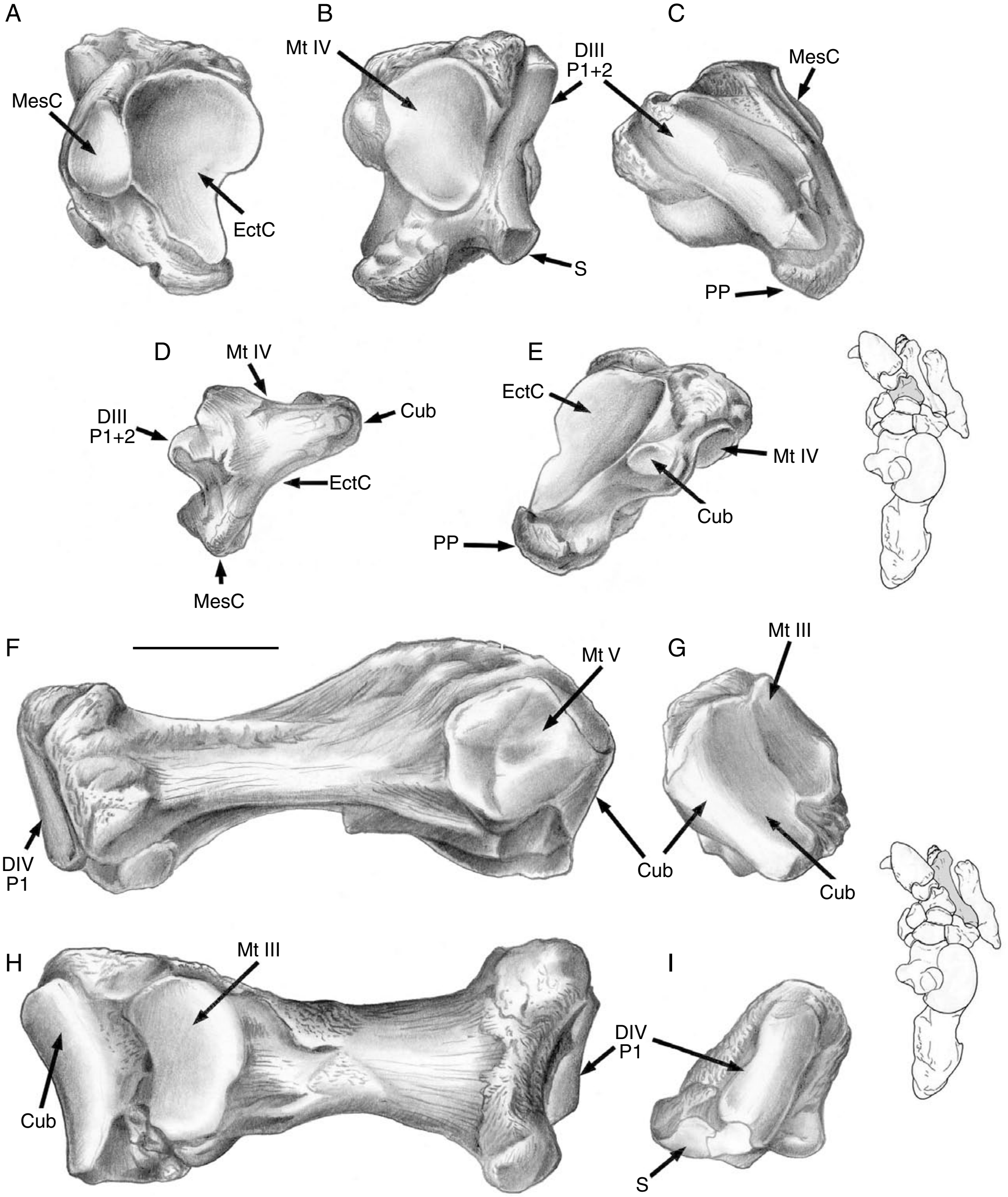


FIG. 5. — *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66); **A**-**E**, right metatarsal III; **A**, posteromedial view; **B**, lateral view; **C**, distal view; **D**, dorsolateral view; **E**, posterolateral view; **F**-**I**, left metatarsal IV; **F**, ventrolateral view; **G**, proximal view; **H**, dorsolateral view; **I**, distal view. Abbreviations: **Cub**, cuboid; **DIII P1+2**, digit III phalanx 1+2; **DIV P1**, digit IV phalanx 1; **EctC**, ectocuneiform; **MesC**, mesocuneiform; **Mt III, IV, V**, metatarsals III, IV, V; **PP**, process plantar; **S**, sesamoid bone. Scale bar: 50 mm.

posteromedial facet for the cuboid, and a lateral facet for Mt V. The facet for Mt III is oval, dorsoventrally extended, anteroposteriorly convex at the anterior part, and concave in both directions posteriorly. This facet is separated posteriorly from the cuboid facet. The cuboid facet is rectangular, dorsoventrally extended, and its anterior two-thirds is dorsoventrally concave and occupies the medial side. The posterior third is proximal in position.

The metatarsal V facet is located on the external side of the proximal epiphysis. This facet is pentagonal, with a central depression and a small extension that is continuous with the posterior portion of the cuboid facet.

The distal epiphysis is triangular with laterodorsal apex and tripod-like base. The facet for the proximal phalanx of digit IV is crested, as that for metatarsal III, but less acute in section, and narrowing ventrally. Ventromesially there is a small, and convex subcircular facet for a sesamoid. This facet was first mentioned by Cabrera (1929) when describing the pes of *Megatherium*. This same extension is present in *E. laurillardi*, but no sesamoid bone can be seen (De Iuliis 1996). Occasionally there occurs ankylosis between Mt IV and Mt III in *E. laurillardi* (Paula Couto 1978; Cartelle 1992).

Metatarsal V

Metatarsal V (Fig. 6A-C) is slightly longer than metatarsal IV but depressed dorsoplantarly with the lateral margin expanded and dorsoventrally compressed (especially the proximal two thirds). The distal portion is almost isodiametric. The medial side has two contiguous articular facets that are inclined dorsomedially. The anteriormost facet for Mt IV is pentagonal, relatively flat, and continuous posteriorly with the cuboid facet. The cuboid facet is concave and triangular with ventral base and anterior apex. The posterior end of metatarsal V is prominent and point-shaped in *P. bergi*, while in *M. americanum* it is blunted. The distal surface has a small oval, convex facet elongated along the dorsolateral-ventromedial axis for a nodular vestigial phalanx.

Digit III

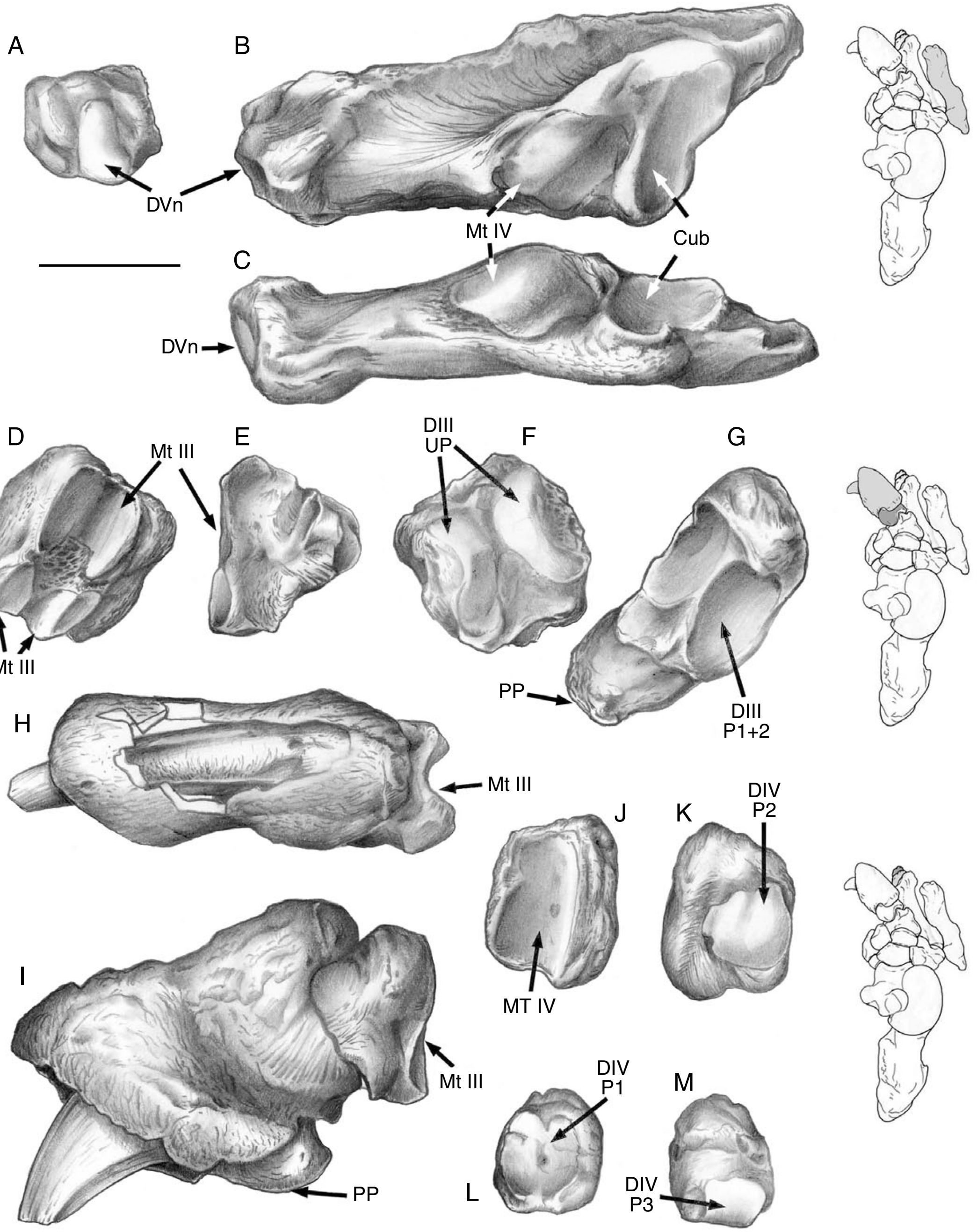
Digit III is the only posterior clawed digit in Megatheriinae. It is composed of a single proximal bone (fused phalanxes 1+2 according to Cartelle 1992) (Fig. 6D-F), and a strong ungual phalanx that is claw-shaped (Fig. 6G-I).

The proximal surface of the phalanx 1+2 bears a wide facet for metatarsal III. This facet is canal-shaped and elongated along the dorsolateral-ventromedial axis. Non-articular bone subdivides it into two parts. Distally it bears a trocleated surface that is transversely elongate and bears an incomplete non-articular bony area. The phalanx is obliquely oriented and consequently the ungual phalanx is deviated ventromedially.

The ungual phalanx articulates with the proximal phalanx (1+2) by a deeply depressed surface divided into two oval parts. This surface is oriented obliquely to the sagittal plane, very well developed, relatively short and robust, and higher than wide (especially the distal portion). Proximally it bears a crown-like expansion that would have covered the base of a large corneal claw. The central bone is also short and high, triangular in section, and projects beyond the bone that sheathed it on the proximal two-thirds of the phalanx.

Digit IV

Unlike other megatherines that have only two phalanxes, digit IV of *P. bergi* has three phalanxes. Phalanx 1 (Fig. 6J, K) is anteroposteriorly compressed and elongate along the dorsoventral axis. The proximal surface for the Mt IV facet is well developed and almost entirely articular. This facet is elongate and strongly concave transversely. The distal surface bears a dorsoventrally convex bilobate facet. The second phalanx articulates on this facet. Phalanx 2 (Fig. 6L, M) is smaller and more anteroposteriorly compressed than phalanx 1. The proximal facet is bilobate, somewhat circular, and concave on both directions. A small almost circular facet on the distal surface must have articulated with a third, probably vestigial phalanx.


A
B
DVn
Mt IV
Cub
C
DVn
D
Mt III
E
DIII
UP
F
G
Mt III
PP
DIII
P1+2
H
Mt III
J
K
DIV
P2
MT IV
I
Mt III
DIV
P1
M
PP
L
DIV
P3

DISCUSSION

The pes of *P. bergi* displays typical characters of the subfamily, i.e. astragalus and calcaneum strongly developed, three digits (III to V) of which the third is the only one clawed. Two of the characters (number of phalanxes and tarsal bones morphology) are intermediate between the condition observed in primitive megatherioids (i.e. *Hapalops*) and that found in Quaternary species of Megatheriinae (e.g., *M. americanum* and *E. laurillardi*).

The number of tarsal elements of the megatherine pes has been discussed and debated since the first half of the 19th century. Cuvier (1834-1836), Owen (1859), and Burmeister (1865), thought that *Megatherium* had only six elements, but did not explain the reason for the reduction, whether by loss or fusion of elements (see discussion in Cabrera 1929). Cabrera (1929) thought there were seven tarsal elements in *Megatherium*, as the mesocuneiform and ectocuneiform appear separated in some specimens (MLP 2-29, MLP 2-30, and MLP 27-VII-1-1 assigned to *Megatherium*). In addition, he stated that the fusion of the internal distal tarsal elements into a single bone occurred with advancing age. On the other hand, Cabrera reported that one falciform extratarsal bone, or sesamoid, articulated with the entocuneiform in these same specimens. Cabrera further speculated that the falciform element substituted for the absence of a distal phalanx on digit I and provided a supporting point during bipedalism. Cartelle (1992) stated that the falciform is part of the meso-entocuneiform complex in *E. laurillardi*. In turn, De Iuliis (1996) proposed that "there is some evidence that the falciform as identified by Cabrera (1929) may occasionally fuse with the mesocuneiform and entocuneiform into a single element". In general the ventromedial surface of the complex, represented by the portion corresponding to the entocuneiform, ends in a blunt projection. However, in *M. tarijense* FMNH P14216 this complex is ventromedially extended by an elongate tapered process that may represent the fusion of the falciform (De Iuliis 1996).

Primitive Megatherioidea (e.g., *Hapalops*) had seven separate tarsal elements (calcaneum, astragalus, navicular, entocuneiform, mesocuneiform, ectocuneiform, and cuboid) (Scott 1903-1905). This situation, similar to that of *P. bergi*, is probably a primitive condition seen in other mammals, and the fusion of different bones into a complex is the derived and most common condition among Quaternary megatheres.

In the pes of *P. bergi* there is no falciform articulating with the entocuneiform, nor is there any facet on the bone that suggests the presence of this bone. The absence of a falciform element that would act as supporting point for the pes (as believed by Cabrera 1929) suggests that *P. bergi* may not have reached a degree of bipedalism attributed to other megatherines (Casamiquela 1974; Aramayo & Manera de Bianco 1987). However, some specimens of *M. americanum* lack a falciform, and it is difficult to imagine conspecifics with less proficient bipedalism.

As in all other megatherines, *P. bergi* has only three digits (III to V) on the pes. It shows no vestige of more internal digits nor articular facets on the corresponding tarsal elements. Some authors (see below) consider that in *Megatherium* vestiges of digits I and II may have fused to different elements. Cabrera (1929) reported vestiges of Mt II, Scott (1913) observed that the pes had only three functional digits and that the first and second are reduced to vestiges, and Cartelle (1992) believed

FIG. 6. — *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) (MLP 2-66); **A**-**C**, right metatarsal V; **A**, distal view; **B**, dorsomedial view; **C**, dorsal view; **D**-**F**, left digit III 1+2 phalanx; **D**, proximal view; **E**, medial view; **F**, distal view; **G**, right digit III ungueal phalanx, proximal view; **H**, **I**, right digit III ungueal and 1+2 phalanxes; **H**, dorsolateral view; **I**, dorsomedial view; **J**, **K**, right digit IV phalanx 1; **J**, proximal view; **K**, distal view; **L**, **M**, right digit IV phalanx 2; **L**, proximal view; **M**, distal view. Abbreviations: **Cub**, cuboid; **DIII P1+2**, digit III, phalanx 1+2; **DIII UP**, digit III, ungueal phalanx; **DIV P1**, digit IV, phalanx 1; **DIV P2**, digit IV, phalanx 2; **DIV P3**, digit IV, phalanx 3; **DVn**, digit V, nodular; **Mt III**, **IV**, metatarsal III, IV; **PP**, process plantar. Scale bar: 50 mm.

that remnants of Mt II may be fused to the mesocuneiform to form part of a mesoentocuneiform complex.

The third digit has only two phalanxes. The proximal phalanx results from the fusion of two phalanxes and it is the most primitive condition known for megatherines. Unlike all Quaternary megatherines, digit IV of *P. bergi* has three phalanxes. This situation, unique among species of the subfamily, is the primitive mammalian condition (and it could be present in other Tertiary megatherines). On the navicular of *P. bergi* and one specimen from Paraná assigned to "*Megatherium antiquum*" Ameghino, 1885 (MACN 4983), there are two articular facets for the ectocuneiform. However, these two facets are fused in a single facet in the naviculars of Quaternary species.

Most of Quaternary megatherines species are well known, and particularly those of *Megatherium*, both in their morphological and phylogenetical aspects (see Cartelle 1992; De Iuliis 1994, 1996; Saint-André & De Iuliis 2001; Pujos & Salas 2004). Saint-André & De Iuliis (2001) indicate that *M. americanum* and *M. altiplanicum* are sister species and the most specialized species of *Megatherium*. Pujos & Salas (2004) postulate that the small sized *Megatherium* species, *M. urbinai*, is more similar to (*M. medinae*, *M. elenense*, and *M. tarijense*) than (*M. americanum* + *M. altiplanicum*). Among the Tertiary species, the relationships are more difficult to establish, because the scarceness and fragmentary condition of the remains (especially post cranial material). The genus *Pyramiodontherium* is represented only by two species *P. bergi* and *P. brevirostrum* Carlini, Brandoni, Scillato-Yané & Pujos, 2002 (Carlini *et al.* 2002), both from the "Araucanense" (late Miocene-Pliocene) of Catamarca Province; this genus is also present in the "Conglomerado osífero" Ituzaingó Formation (late Miocene), Entre Ríos Province, Argentina (Carlini *et al.* 2001; Brandoni *et al.* 2001). The remains assigned to *Pyramiodontherium* found in the "Conglomerado osífero" could be more closely related to those assigned to "*M. antiquum*" than with the medium sized species of *Pliomegatherium* Kraglievich, 1930.

In summary, the pes of *P. bergi* is more specialized with respect to that of *Megathericulus patagonicus*, and its morphology fits better with that assumed to be present in Upper Tertiary megatherines. The plesiomorphic states of characters observed here may help to resolve the polytomy proposed by De Iuliis (1996) and offer a more precise knowledge of the way characters states were transformed during the evolution of the group.

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