

The smallest and most ancient representative of the genus *Megatherium* Cuvier, 1796 (Xenarthra, Tardigrada, Megatheriidae), from the Pliocene of the Bolivian Altiplano

Pierre-Antoine SAINT-ANDRÉ

Laboratoire de Paléontologie, Muséum national d'Histoire naturelle,
8 rue Buffon, F-75231 Paris cedex 05 (France)

Gerardo DE IULIIS

Department of Zoology, University of Toronto, 25 Harbord Street,
Toronto, Ontario, M5S 3G5 (Canada)
Faculty of Community Services and Health Sciences,
George Brown College, 200 King Street East,
Toronto, Ontario, M5A 1J5 (Canada)
gerry@zoo.utoronto.ca

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ABSTRACT

A new species of *Megatherium* Cuvier, 1796, *M. altiplanicum* n. sp., from the Montehermosan (Pliocene) of the north central Altiplano of Bolivia is described. It represents the earliest and smallest species of its genus and is the sister species of *Megatherium americanum* Cuvier, 1796 based on the following synapomorphies: very deep horizontal ramus of the dentary, prominent torsion of the femoral diaphysis, relatively concave medial and lateral femoral margins, and reduced patellar trochlea. The premaxillae are derived in being fused to each other and the maxilla, and relatively robust, features shared with *M. americanum* and *M. tarijense* Gervais & Ameghino, 1880, but those of *M. americanum* are more robust and quadrangular. In size, the new species resembles *Eremotherium sefvei* De Iuliis & Saint-André, 1997, but in the latter the femoral diaphysis is moderately twisted, the femoral margins are more nearly rectilinear, and the patellar trochlea unreduced. The presence of the new species in the Montehermosan suggests that the genus *Megatherium* had emerged by the beginning of the Pliocene, and that the most recent common ancestor of the clade (including also *M. americanum* and *M. tarijense*), predates the Pliocene. *Megatherium* was apparently adapted to a temperate climate, as opposed to the more tropical range occupied by *Eremotherium* Spillmann, 1948. The discovery of the new species possibly indicates broad ecological similarity between the Pliocene Altiplano and the Argentinian lowlands, and that the clade may have originated on the Altiplano.

KEY WORDS

Xenarthra,
Megatheriidae,
Megatherium,
Pliocene,
Bolivia,
Montehermosan,
new species.

RÉSUMÉ

Le plus petit et le plus ancien représentant du genre Megatherium Cuvier, 1796 (Xenarthra, Tardigrada, Megatheriidae), du Pliocène de l'Altiplano bolivien.

Une nouvelle espèce de *Megatherium* Cuvier, 1796, *M. altiplanicum* n. sp., datant du Montehermoséen (Pliocène) et venant du centre-nord de l'Altiplano de Bolivie est décrite ci-après. Cette espèce représente la plus ancienne et la plus petite des espèces de son genre et, selon les caractères synapomorphiques suivants, serait l'espèce sœur de *Megatherium americanum* Cuvier, 1796 : un rameau mandibulaire horizontal très profond, une diaphyse fémorale présentant une torsion proéminente, des marges fémorales médianes et latérales relativement concaves et un trochléaire patellin réduit. La fusion des prémaxillaires entre eux et avec la maxillaire, indicatif d'un caractère dérivé, ainsi que la robustesse relative de ceux-ci, sont caractéristiques également de *M. americanum* et de *M. tarijense* Gervais & Ameghino, 1880, bien que les prémaxillaires de *M. americanum* soient plus robustes et quadrangulaires. Cette nouvelle espèce ressemble à *Eremotherium sefvei* De Iuliis & Saint-André, 1997 en taille mais ce dernier a une diaphyse fémorale modérément tordue, des marges fémorales presque rectilignes et un trochléaire patellin qui n'est pas réduit. La présence de cette nouvelle espèce datant du Montehermoséen suggère que le genre *Megatherium* émergea dès la début du Pliocène et que l'ancêtre commun le plus récent de ce clade (incluant *M. americanum* et *M. tarijense*) précède le Pliocène. Apparemment, *Megatherium* était adapté à un climat tempéré, contrairement à *Eremotherium* Spillmann, 1948 qui lui, se retrouve en régions plus tropicales. La découverte de cette nouvelle espèce indique la possibilité de similarités écologiques entre l'Altiplano du Pliocène et les basses terres de l'Argentine et que le clade est peut-être originaire de l'Altiplano.

MOTS CLÉS

Xenarthra,
Megatheriidae,
Megatherium,
Pliocène,
Bolivie,
Montehermoséen,
nouvelle espèce.

INTRODUCTION

The genus *Megatherium* is known mainly from the giant ground sloth *M. americanum* described by Cuvier (1796). *M. gallardoi* Ameghino & Kraglievich, 1921 is a second large species, but is poorly known. Other species of the genus, such as *M. medinae* Philippi, 1893, *M. istilarti* Kraglievich, 1925 and *M. tarijense* Gervais & Ameghino, 1880 (see Boule & Thévenin 1920), are smaller, although still large mammals. All these species are of Pleistocene age. The discovery of a small species of *Megatherium* from the Pliocene of the Bolivian Altiplano is important phylogenetically and paleoecologically.

In discussing the Ayo Ayo (Bolivia) fauna, Hoffstetter *et al.* (1971) reported the discovery from Pliocene beds of a megatheriine species that is more similar to *Megatherium* than to the intertropical genus *Eremotherium* Spillmann, 1948

and, with a femur 390 mm in length, smaller in size than other species traditionally assigned to *Megatherium*. Other remains from Pomata (Bolivia) were assigned to this species. Hoffstetter (1986) believed that it was possibly ancestral to *Megatherium*.

The new species *Megatherium altiplanicum* n. sp. is based on remains from Ayo Ayo-Viscachani and Pomata. It is the smallest and earliest species of its genus. This combination of size and age reflects the increase of body size over time, which is one of the more important evolutionary trends among megatheriines. The medial length of the femur is comparable to that of *Eremotherium sefvei* De Iuliis & Saint-André, 1997, a small species from the Bolivian Pleistocene. However, the lateral femoral length is shorter than the medial, whereas this condition is reversed in *E. sefvei*. These species are clearly distinguished on the forms of the femoral diaphysis and the patellar trochlea

(*cf. infra*). *M. altiplanicum* n. sp. is considerably smaller than the supposed Montehermosan species *M. gaudryi* Moreno, 1888 from the Monte Hermoso region of Buenos Aires Province, Argentina. Its systematic position with respect to several other poorly known taxa, such as *Promegatherium* Ameghino, 1883 and *M. antiquum* Ameghino, 1885 is unclear. Better collections of these taxa, with precise stratigraphic controls, are required before such questions may be addressed.

ABBREVIATIONS

- IFEA Institut français d'Études andines, Lima;
- 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 (MNHN is followed by AYO or POM, denoting that the specimen is from Ayo Ayo or Pomata, respectively);
- MNHN BOL Museo Nacional de Historia Natural, La Paz;
- ROM Royal Ontario Museum, Toronto;
- M upper molariform;
- m lower molariform.

SYSTEMATICS

Infraorder TARDIGRADA

Latham & Davies *in* Forster, 1795

Family MEGATHERIIDAE Gray, 1821

Subfamily MEGATHERIINAE Gray, 1821

Genus *Megatherium* Cuvier, 1796

Megatherium altiplanicum n. sp.

HYPODIGM. — Holotype (MNHN AYO 101); this specimen preserves the palate, including both alveolar series, the maxillae anteriorly to the anterior root of the zygomatic arch; the horizontal ramus, angular process and part of the condyle of the left dentary; fragments of the horizontal and ascending rami, with parts of the coronoid process and condyle, of the left dentary; the atlas; two consecutive thoracic vertebrae and the neural arch of the next thoracic vertebra; the neural arches of three lumbar vertebrae; four consecutive caudal vertebrae; the proximal part of the right ulna; the left femur.

TYPE LOCALITY. — The type specimen was recovered from near Ayo Ayo, Departamento La Paz, 17°05'S, 68°00'W, a village on the Altiplano. The fossiliferous locality is approximately 1 km south of Ayo Ayo.



FIG. 1. — Map showing the geographical positions of the Ayo Ayo-Viscachani and Pomata localities yielding remains of *Megatherium altiplanicum* n. sp. 1, Ayo Ayo; 2, Viscachani; 3, Pomata.

TYPE STRATA. — The Ayo Ayo-Viscachani fossiliferous locality (Fig. 1) lies in the upper part of the Umala Formation.

ETYMOLOGY. — *altiplanicum*: neoformed Latin adjective (*altiplanicus*, *-a*, *-um*) meaning "relative to the Altiplano, from the Altiplano", commemorating that the holotype and referred specimens derive from the Bolivian Altiplano.

REFERRED SPECIMENS. — From Ayo Ayo: Departamento La Paz, 17°05'S, 68°00'W: distal end of a left femur (MNHN AYO 105); right cuneiform (MNHN AYO 150); left radius (MNHN AYO 203); premaxillae of a juvenile individual (MNHN AYO 230); proximal half of a right ulna (MNHN BOL V 3304); right navicular (MNHN BOL V 3312).

From Viscachani: Departamento La Paz, approximately 17°09'S, 68°50'W: distal part of a left humerus (MNHN BOL V 3338).

From Pomata: Departamento Oruro, 18°20'S, 67°55'W: atlas (MNHN POM 57); posterior part of a right dentary, including angular process and condyle (MNHN BOL V 3294).

Epochs	Years (Ma)	South American Land Mammal Age	North Central Altiplano				
Pleistocene	0.5	Lujanian	Ulloma Fm				
		Ensenadan					
	1.5	Marplatan					
1.6							
Pliocene	2.5	Chapadmalalan			Toba Ayo Ayo B Umala Fm		
	2.8						
	Miocene	5.3	Huayquerian	Toba 76 Pomata Fm			
		5.4					
6							
Miocene	12	Chasicoan	Rosa Pata Fm	Tortora Group			

FIG. 2. — Diagram showing chronostratigraphy of South American Land Mammal Ages and position of the Pomata (A), and Ayo Ayo-Viscachani (B) localities (modified after Marshall & Sempéré 1991).

Fossils in MNHN were collected by Robert Hoffstetter in 1976. The type specimen was recovered from an area sufficiently restricted in size to permit its attribution to a single individual. Fossils in MNHN BOL were collected during collaborative field seasons between this institution and IFEA.

DIAGNOSIS. — Much smaller than *M. americanum*, and smaller also than *M. medinae* and *M. tarijense*. Ventral bulge of dentary relatively as deep as in *M. americanum*. Premaxillae firmly fused to each other and to maxillae, but less robust than in *M. americanum*. Palate narrows anterior to M1. Angular process distinct and more pointed than in *M. americanum*; posterior part of the symphysis extends to the plane passing through m1. Femur twisted, with greater trochanter lying posterior to the plane passing through

the head and distal condyles, lateral margin forming a sigmoid curve, and patellar trochlea reduced to the lateral half of the distal end of the femur, but apparently not to the degree as occurs in *M. americanum*.

GEOLOGY

The Umala Formation is bounded by the Toba 76 and Ayo Ayo volcanic tuffs, which lie at its base and top, respectively (Fig. 2). Radiometric analyses of various minerals (i.e. biotite, sanidine) date the Toba 76 tuff at approximately 5.4 Ma, and the Ayo Ayo tuff at approximately 2.8 Ma, which indicate that the Umala Formation is of early and middle Pliocene age, according to the

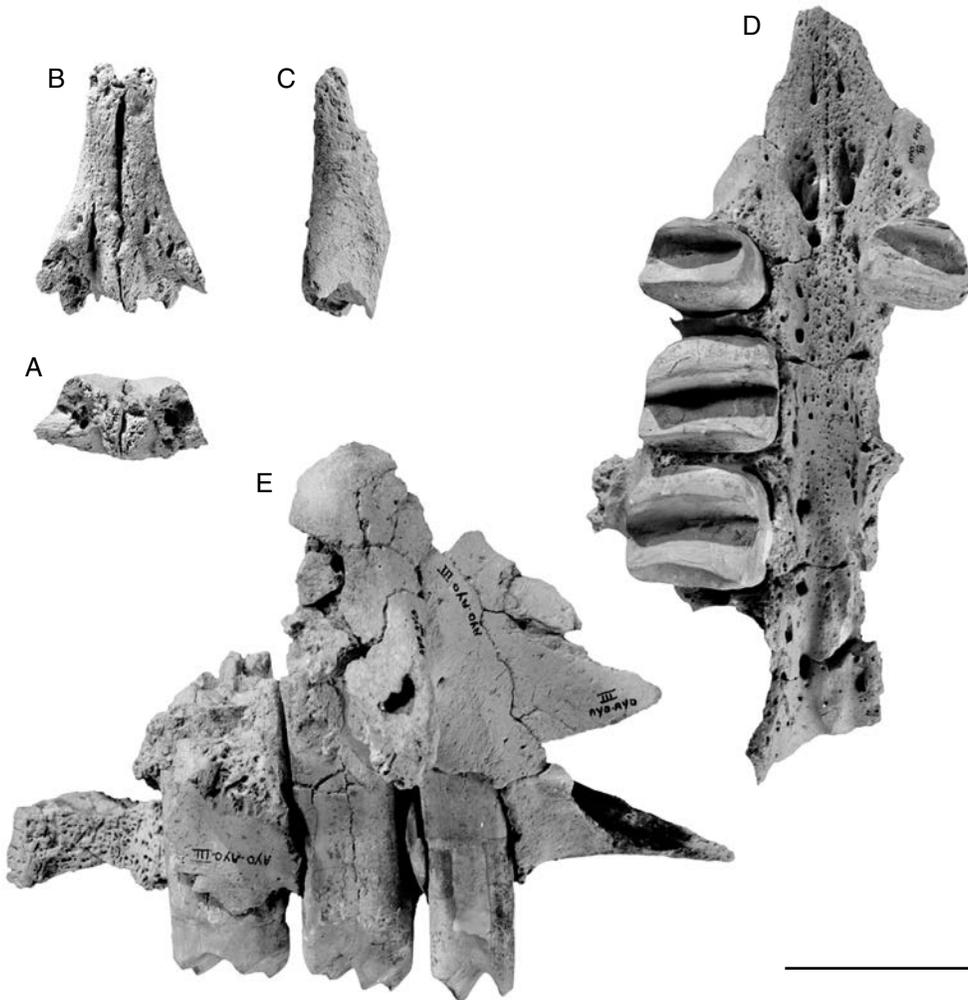


FIG. 3. — Skull remains of *Megatherium altiplanicum* n. sp.; **A-C**, premaxillae of a juvenile individual (MNHN AYO 230); **A**, proximal view; **B**, ventral view; **C**, left lateral view; **D, E**, partial premaxillae and maxillae, holotype (MNHN AYO 101); **D**, occlusal view; **E**, right lateral view. Scale bar: 5 cm.

chronology of Marshall *et al.* (1992). *M. altiplanicum* n. sp. belongs to the Montehermosan Land Mammal Age.

The Pomata fossiliferous deposits (Fig. 1) were initially referred to the Mauri Formation by Paz *et al.* (1966), but they are probably unrelated stratigraphically and ecologically to the Mauri Formation from the Oligocene and Miocene of the western Cordillera and western Altiplano. The Pomata locality lies above the conglomeratic facies of the Rosa Pata Formation, which is of

Huayquerian age (“Conglomerado Pomata” of Marshall & Sempéré 1992), and above a volcanic tuff which probably represents a horizontal extension of the Toba 76 from the base of the Umala Formation.

DESCRIPTION

Skull

The type skull material (Fig. 3) preserves the maxillae and premaxillae incompletely, and the right M1-M3 and left M1. Measurements are

TABLE 1. — Measurements (mm) of skull and mandible of *Megatherium altiplanicum* n. sp., holotype (MNHN AYO 101).

Minimum palatal width	
Between L and R M1	28.9
Between L and R M2	24.0
Between L and R M3	28.2
Between L and R M4	30.0
Midline palatal length, level of M1 to choanae	143.0
Maximum height horizontal ramus of dentary	145.0
Toothrow length between M1-M3	94.7
Lower toothrow length, alveolar	143.6
Maximum length and width of molariforms	
M1	31.6; 29.1
M2	30.9; 36.4
M3	31.6; 35.0
m1	27.3; c. 34
m2	32.7; 34.0
m3	32.4; 30.0
m4	32.7; 25.5

given in Table 1. Laterally the right maxilla includes the anterior root of the zygomatic arch to the level of the buccal wall of the M1 alveolus. A smaller portion of the left maxilla is preserved to the level of the anterior root of the arch.

Premaxilla. The width across the premaxillae posteroventrally is comparable to the palatal interalveolar width (i.e. less than the width across the molariforms), which reflects the narrowed maxillae anterior to M1. Two large palatine fissures lie between and anterior to the M1s, approximately at the level where the palate narrows. The premaxillae are fused firmly to the maxillae. Their anterior portions are missing as they are broken a short distance anterior to the palatine fissures in MNHN AYO 101. Based on the preserved proximal portions, the premaxillae do not narrow abruptly anteriorly, which is also the condition in *M. americanum*, but not in *Eremotherium laurillardii* (Lund, 1842) and probably most other megatheriines (De Iuliis 1994).

The complete premaxillae of a juvenile individual (MNHN AYO 230; Fig. 3A, B) are unfused along their contact in the sagittal plane. In ventral view, each premaxilla is triangular, somewhat elongated, and the anterior extremity is almost imperceptibly widened. The distal, subterminal sagittal margins of the premaxillae are separated

by a very flattened elliptical space. Anteriorly narrow, they widen progressively posteriorly, apparently following a constant radial curve. They are not rectangular, in contrast to the condition in adult individuals of *M. americanum*. The triangular condition, however, occurs in juvenile of the latter species (e.g., MACN 2830).

In *M. altiplanicum* n. sp. the ventral margin of the premaxilla is nearly flat in lateral view. The anterior third of the dorsal margin is dorsoventrally narrow; the central third rises at an angle of nearly 20°; the posterior third inclines slightly posteriorly. The dorsal surface bears a very obtuse angle between the posterior third and anterior two thirds. The posterior margin of the articulated premaxillae is trapezoidal, with base ventral. The posterior surface of each premaxilla bears three processes, which were probably received by corresponding depressions in the maxilla. A ventromedial process joins that from the other premaxilla to form a ventrosagittal protuberance. A second process lies ventrolaterally. A third lies at the posterior extremity of the dorsolateral margin of the premaxilla.

Maxilla. In *M. altiplanicum* n. sp. the anterior margin of the anterior zygomatic root is level with a transverse plane passing through the middle of M1, as occurs in *E. laurillardii* (Cartelle & De Iuliis 1995), although it may lie opposite the septum between M1 and M2 in the latter; in *Megatheridium annectens* Cabrera, 1928, it reaches the mesial surface of M1. The root lies more posteriorly in *M. americanum*, in which its position varies from the septum between M1 and M2 to the distal part of M2. Apparently, the position is similar in *M. medinae*.

In ventral view the antemolariform region of the maxillar palate more closely resembles that in *E. laurillardii*, *M. medinae* and *M. gallardoii*, although to a lesser degree in the latter due to the brevity of this region, than in *M. americanum* (Ameghino & Kraglievich 1921; Cabrera 1928; Hoffstetter 1952). In the first two species and *M. altiplanicum* n. sp., the antemolariform part of the maxillar palate is nearly as wide as the interalveolar width. Its lateral margins, between M1 and the premaxillae, are formed by « deux

arêtes latérales qui se placent respectivement dans le prolongement de l'axe de chaque série dentaire », a condition considered primitive by Hoffstetter (1952: 60). In *M. americanum* and *M. parodii* Hoffstetter, 1949, as well as in *Plesiomegatherium halmyronomum* Cabrera, 1928, the antemolariform width of the maxillar palate is nearly equal to that between the buccal margins of the toothrows.

In *M. altiplanicum* n. sp., the palate is narrow between the toothrows, and its width is less than the transverse width of M1-M3, which is more similar to the condition in *M. americanum*, *M. medinae*, and *Pyramiodontherium bergi* (Moreno & Mercerat, 1891) than in *E. laurillardii*, *Plesiomegatherium halmyronomum* Cabrera, 1928 and *Megatheridium annectens*. In these last three, the palate width is about equal to or wider than the width of the largest molariform.

The palatine fissures lie between the premaxillo-maxillary suture, approximately at the level where the premaxillae begin to narrow. Each fissure forms a shallow depression; its floor is pierced by a posterolateral foramen and a smaller, more anterior foramen.

Upper dentition. The upper molariforms (Fig. 3D, E) resemble those of other megatheriines. They are prismatic, quadrangular in section with width slightly exceeding length, and bear two transverse crests separated by a transverse, V-shaped valley.

M1 is less triangular in cross section than that of *M. medinae* and *M. gallardoii* (judging from the alveoli in the latter; Ameghino & Kraglievich 1921). Indeed, it resembles the M1 of *M. americanum* (as illustrated, for example, by Owen 1856), which is nearly trapezoidal in section, with a wider distal surface and a slightly rounded mesial surface. However, the shape of M1 varies between nearly trapezoidal to triangular in both *M. americanum* and *E. laurillardii*. The distal transverse crest is wider than the mesial, and its distal wear facet is considerably more prominent than the mesial facet of the mesial crest.

The mesial crest of M2 is slightly shorter transversely than the distal crest. The mesial wear facet

of the mesial crest is more prominent than the distal facet of the distal crest. This also occurs in M3. The transverse crests of this molariform are nearly equal in transverse width. The crests of M2 and M3 are nearly rectilinear, but slightly convex mesially.

Dentary. The dentary of *M. altiplanicum* n. sp. is incompletely known. The holotype (Figs 4; 5) preserves a right horizontal ramus, including right and left symphyseal regions as far as the mesial wall of the left m1 alveolus; a medial fragment of the right condyle; the right angular process; a lateral fragment of the alveolar region of the left horizontal ramus, including part of the anterior margin of the ascending ramus; a fragment of the ventral margin of the left horizontal ramus; and part of the left coronoid process, including the condyle.

The symphysis ends posteriorly at the level of the distal margin of m1. As in all megatheriines, the symphysis forms a trough-like spout. In dorsal view the lateral margins of the spout are parallel and extend anteriorly from the lingual half of the mesial margin of the m1 alveolus; this morphology reflects a narrowing of the lateral margin of the horizontal ramus. Further, the anterior margin of the spout is not rectilinear, but bears a distinct median notch. In lateral view, the dorsal margin of the spout continues anteriorly from the alveolar margin, but is not rectilinear. Its proximal two fifths are concave, its distal three fifths slightly convex. A mental foramen, representing the anterior emergence of the mandibular canal, lies on the lateral surface of the central part of the spout. The canal continues posteriorly within the lingual wall of the dentary. It emerges posteriorly, facing anteriorly and dorsally, between m4 and the anterior margin of the ascending ramus.

The ventral margin of the dentary of *M. altiplanicum* n. sp. bulges prominently, with maximum depth occurring beneath m3. The depth of the dentary relative to the toothrow length is nearly equal to that of *M. americanum*, in which depth exceeds that of all other megatheriines (Kraglievich 1930; Hoffstetter 1952; Cartelle 1992) due to increased hypsodonty. The ventral

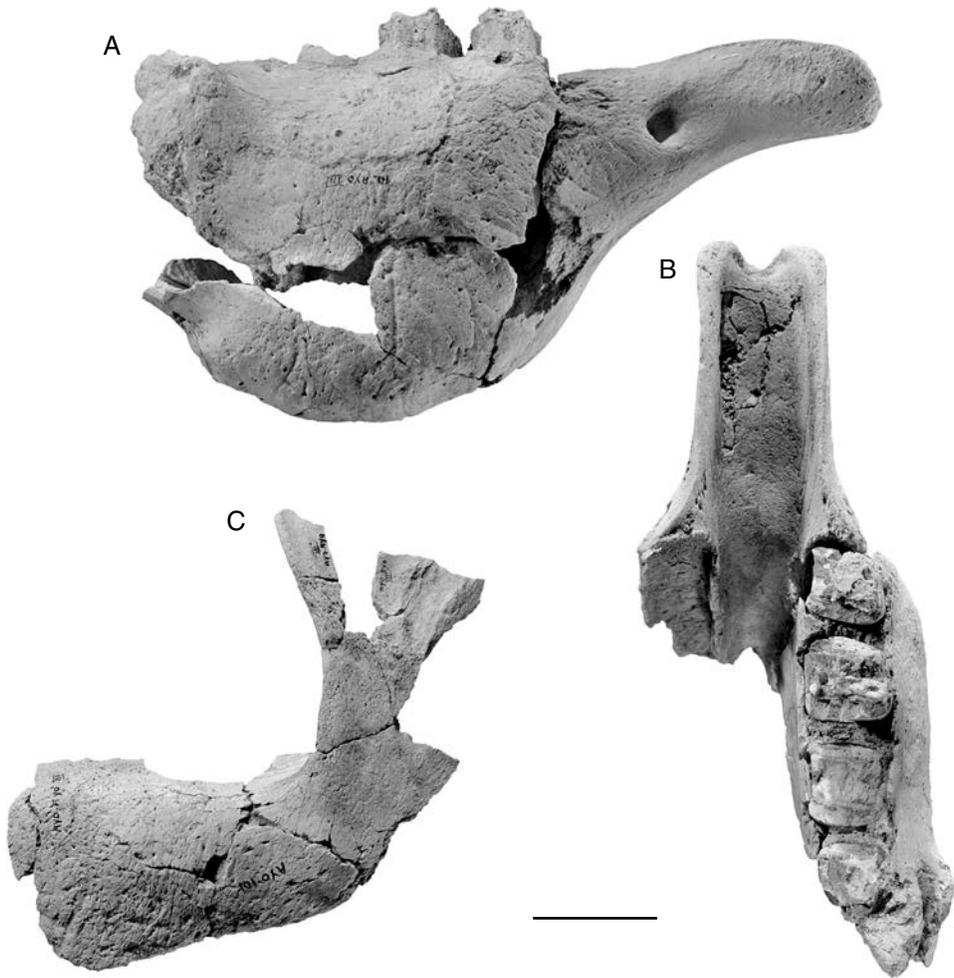


FIG. 4. — Dentary of *Megatherium altiplanicum* n. sp., holotype (MNHN AYO 101), partial right and left dentaries; **A**, right lateral view; **B**, occlusal view; **C**, left lateral view. Scale bar: 5 cm.

margin of the dentary of *M. lundi seijoi* (Kraglievich 1931: figs 1, 2) is more gently curved between the anterior extremity of the spout and apex of the mandibular bulge. MNHN AYO 101 (Fig. 5A, B) reveals that the angular process of *M. altiplanicum* n. sp. is more prominent, with dorsal and ventral margins nearly parallel, than the relatively short and stout process of *M. americanum*. The medial surface of the angular region bears a well-developed fossa for insertion of the medial pterygoid muscle. A

low convexity, lying parallel to the posteroventral margin of the angular process, reflects the depth of the fossa.

The post-molariform part of the dentary is more completely preserved in MNHN BOL V 3294 (Fig. 5C, D). It also indicates that the angular process and insertion for the medial pterygoid were more prominent and deeper, respectively, than in *M. americanum*. The anterior margin of the ascending ramus rises almost vertically lateral to the distal part of m4, and in lateral view covers

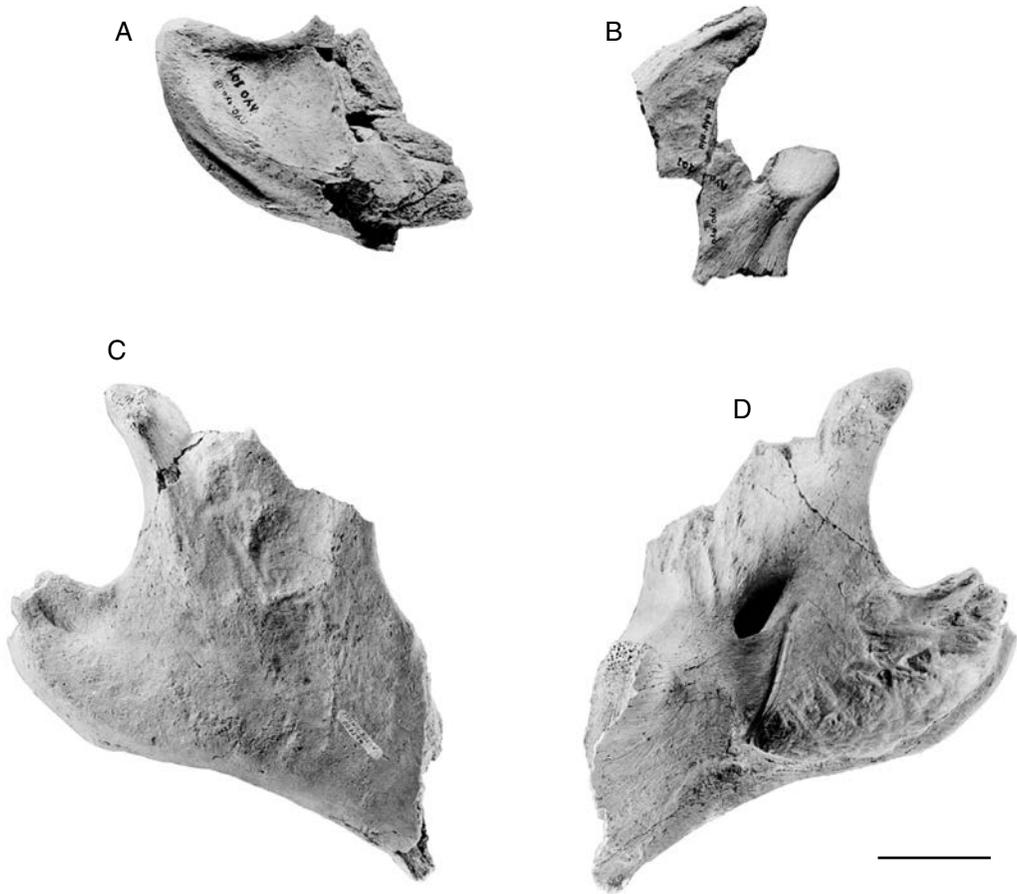


FIG. 5. — Posterior part of dentary of *Megatherium altiplanicum* n. sp., lateral views of **A**, right angular process and **B**, left condyle and coronoid process of holotype (MNHN AYO 101); and **C**, lateral and **D**, medial views of right angular region and condyle of MNHN BOL 3294. Scale bar: 5 cm.

part of this tooth, as occurs in *M. americanum*, *M. medinae* and *M. sundti* Philippi, 1893. In *E. laurillardii*, however, the anterior margin inclines slightly posteriorly and most of m4 is visible in lateral view (Hoffstetter 1952).

The condyle resembles that of *M. americanum*. Its articular surface is transversely elongated and convex. Its medial half is rounded, approximately semicircular, and its lateral half is nearly elliptical and connected to the lateral surface of the ascending ramus by a poorly defined crest.

Lower dentition. All molariforms (Fig. 4A, B) are broken below the level of the alveolar mar-

gins, although parts of m1 and m2 are preserved above the margins. The molariforms are quadrangular in section. The transverse axis of m1 lies obliquely, from mesiolingual to distobuccal, to the longitudinal axis of the dentary. m2 is mesiodistally shorter buccally than lingually, and its mesial surface is parallel to the distal surface of m1. The mesial and distal surfaces of m3 are slightly convex, and more nearly perpendicular to the longitudinal axis of the horizontal ramus than those of m1 and m2. The mesial surface of m4 is shorter than the distal surface of m3, and slightly more convex. Its buccal and lingual surfaces con-

verge distally. The distal surface of m4 of MNHN AYO 101 has suffered considerable damage, but the alveolar wall of m4 of MNHN BOL V 3294 is very rounded. As in *M. lundi seijoi* (Kraglievich 1931), m1 and m2 are implanted obliquely in the dentary, and incline posteriorly, but m4 is vertical.

Axial Skeleton

Atlas. The atlas of the holotype, missing only a part of the right wing, differs in minor details from that of *M. americanum*. Measurements are given in Table 2. In anterior or posterior view the neural canal is clearly more compressed dorsoventrally than in the Pleistocene species, and the ventral arch is proportionately much wider mediolaterally but shorter anteroposteriorly. Its neural surface bears the *fovea dentis* along its median length. In *E. laurillardii* the *fovea* varies between occupying the whole length and the posterior two thirds of the ventral arch. The ventral tubercle is poorly developed. In anterior view, the anterior articular facets curve more strongly toward the mid-line. The second intervertebral foramen, normally for the passage of blood vessels and the second cervical or spinal nerve, may be formed between the atlas anteriorly and the axis posteriorly. This occurs in MNHN AYO 101. In posterodorsal view of the atlas, this passage forms a smooth, transverse trough between the root of the dorsal arch and the anteromedial wall of the facet for the axis. The trough leads medially into the neural canal; laterally it is bounded by the medial margin of the transverse foramen. However, a second condition may occur, as in MNHN POM 57, where the trough is enclosed by an osseous bridge between the posterodorsal margin of the dorsal arch and the dorsomedial margin of the facet for the axis. This short, transverse canal is similar to the trough in arrangement, probably included the structures that passed between the intervertebral foramen, and creates two additional foramina: one opening medially, and the second opening laterally dorsal to the transverse foramen.

Two other foramina are present in *M. altiplanicum* n. sp. The intervertebral foramen (= lateral

vertebral foramen) is a short, transverse canal, which passes into the neural canal. The alar foramen passes dorsoventrally through the anteromedial part of the wing. Whereas the alar and transverse foramina (although better described as canals) become confluent within the lateral mass of the atlas and emerge ventrally upon the atlantal fossa through a common opening in *M. americanum*, they remain separated in *M. altiplanicum* n. sp. Hoffstetter (1952) stated that the atlas of *E. laurillardii* bore the normal four foramina: the alar, transverse, and the anterior and posterior intervertebrals, and apparently considered this as being the normal condition in this species and *M. americanum*. However, the presence of the posterior intervertebral is variable in *E. laurillardii* (cf. ROM 4219) and *M. altiplanicum* n. sp., and presumably also in *M. americanum*. Such variation apparently also occurs in *Megalonyx*, and in some specimens the foramen is present only on one side (McDonald 1977).

The wing is proportionately much larger than in *M. americanum*. Its dorsal surface bears a well-defined fossa or depression (probably for insertion of the *recti capitis* muscles) that extends anterior to the anterior intervertebral foramen to reach the level of the anterior margin of the dorsal arch. In *M. americanum* it does not extend beyond the foramen. Further, the wing in *M. altiplanicum* n. sp. is distinctly defined anteriorly by an emargination, produced by a lateral prolongation of the dorsolateral margin of the anterior articular facet, between the wing and the facet. In *M. americanum* the margin of the wing curves without interruption into the dorsolateral margin of the articular facet.

As in *M. americanum* and other ground sloths, the atlas bears three separate articular facets for the axis: two lateral; the third, median and ventral, articulates with the *dens* of the axis. The lateral facets are contiguous ventrally with that for the *dens* in *E. laurillardii* and *E. eomigrans* De Iuliis & Cartelle, 1999; this condition is apomorphic for *Eremotherium* (Cartelle 1992; De Iuliis & Cartelle 1999).

Thoracic vertebrae. The holotype preserves two consecutive thoracic vertebrae and the dorsal arch

of the following vertebra. A parapophyseal articular surface lies on the anterior surface of the base of the dorsal arch of all preserved vertebrae. Their centra lack *foveae costales*. Thus the ribs of the two complete vertebrae articulate only with the parapophyses (i.e. they are syncephalic ribs). In *M. americanum* this condition occurs only for the last thoracic. This suggests that the complete vertebrae and the dorsal arch belong to the most posterior part of the thoracic series, and that in *M. altiplanicum* n. sp. vertebrae other than the final thoracic bear syncephalic ribs.

The second complete thoracic vertebra bears secondary or xenarthral postzygapophyses. The dorsal arch that follows bears parapophyses, and is therefore a thoracic vertebra. Further, it bears xenarthral pre- and postzygapophyses. The xenarthral condition thus is present in the posterior two of the three thoracic vertebrae.

Lumbar vertebrae. Two consecutive arches of MNHN AYO 101 are very similar to those of the lumbar vertebrae of *M. americanum*. They bear xenarthral pre- and postzygapophyses. The anterior of the two arches bears the intratransversary foramen characteristic of the lumbar vertebrae of Xenarthra; the second arch is damaged and does not permit recognition of the foramen. A distorted neural arch preserves its right postzygapophysis, which articulates with the prezygapophysis of the anterior of the two arches.

Caudal vertebrae. The four consecutive vertebrae of the holotype resemble, based on the shape of their prominent transverse processes, caudal vertebrae 1 to 6 of *M. americanum*. A poorly defined tubercle lies sagittally on the anterior margin of the neural arch, anterior to the neural spine, of the first of this series, and resembles in size and position those on caudal vertebrae 1 and 2 of *M. americanum*. The tubercle is absent in the second vertebra of the series. Therefore, the vertebrae of the holotype are probably caudal vertebrae 2 to 5.

Humerus. Only the distal end of a left humerus (MNHN BOL 3338; Table 2) is known for *M. altiplanicum* n. sp. It is smaller than that in *M. americanum*, and the epicondyles are less expanded and prominent relative to the trochlear surface.

Radius. The left radius (MNHN AYO 203; Fig. 6; Table 2) of *M. altiplanicum* n. sp. is smaller than but morphologically similar to that of *M. americanum*. It is also more gracile because its epiphyses are smaller compared to its length. Further, in anterior or posterior views the diaphysis is apparently narrower due to a shorter and less prominent lateral crest, which served largely for the insertion of the *pronator teres*. The crest is widest within the proximal subterminal quarter of the radius; it lies further distally in *M. americanum*. There is a pronounced angle between the diaphyseal portions proximal and distal to the crest in *M. americanum* and *M. altiplanicum* n. sp., whereas in *E. laurillardii*, *M. tarijense* (FMNH P14216) and *M. medinae* the angle between these portions is less abrupt.

In *M. altiplanicum* n. sp. the diaphysis is markedly constricted mediolaterally between the crest and the distal end of the radius, and the lateral and medial margins of this part of the diaphysis are subparallel, as occurs in *M. americanum*. In *E. laurillardii*, and apparently other megatheriines, the crest lies more distally still, near the midlength of the radius. Further, the diaphysis is constricted slightly just distal to the crest, but gradually widens distally.

The bicipital tuberosity lies more proximally in *M. altiplanicum* n. sp. and *M. americanum* than in *E. laurillardii*. In *M. americanum* it lies on the medial surface of the radius, in the same transverse plane as the lateral crest, whereas the tuberosity lies more posteriorly, approximately on the medioposterior radial surface in *M. altiplanicum* n. sp.

Ulna. The proximal part of the right ulna of MNHN AYO 101 is preserved (Table 2). It is smaller than that of *M. americanum* and varies morphologically in minor ways. The olecranon process is relatively smaller. The anconeal process is more prominent and distinct. Its margins meet in an acute angle, whereas in *M. americanum* they form an obtuse angle.

Cuneiform. The cuneiform of megatheriines articulates with the pisiform palmolaterally and the unciform distally. MNHN AYO 150 strongly resembles that of *M. americanum*, but the facet



FIG. 6. — Right radius of *Megatherium altiplanicum* n. sp. (MNHN AYO 203); **A**, anterior view; **B**, posterior view; **C**, lateral view; **D**, medial view. Scale bar: 10 cm.

for the unciform is relatively larger, and that for the pisiform smaller (*c.* 30% of the maximum width of the cuneiform, as compared to 38% in *M. americanum*). However, it is worth noting that Cartelle (1992) reported considerable variation in the shapes and relative sizes of the articular surfaces in *E. laurillardii*.

Femur. The medial length of the femur (Table 2) of the holotype (Fig. 7) is nearly identical to that of the small species *Eremotherium sefvei* from the Pleistocene of Ulloma, Bolivia (387 mm; De Iuliis & Saint-André 1997), which was probably very similar in body size (*cf. infra*) to *M. altiplanicum* n. sp.

The femur of *M. altiplanicum* n. sp. is smaller than but similar to that of *M. americanum*. As in the latter, the greater trochanter projects markedly posteriorly to the plane that passes through the

head and the distal condyles, so that the bone exhibits strong vertical torsion. In lateral view its lateral margin is sigmoidal. This feature is also present in *M. americanum* (Hoffstetter 1952) and *M. gallardoii* (MACN 5002), but absent in *Eremotherium*, *M. istilarti* and *M. medinae* (Kraglievich 1925a; Hoffstetter 1952). The last two species, therefore, are not properly considered *Megatherium* sensu Hoffstetter (1952). As noted by De Iuliis & Saint-André (1997), torsion of the femur is apparently due to a posterior displacement of the greater trochanter: manipulation of the elements of the hind limb that set the head, greater trochanter, and medial distal condyle in the same plane requires that the long axis of the pes be oriented markedly anteromedially; whereas the pes is oriented anteroposteriorly when the head and distal condyles lie in the same plane.



FIG. 7. — Left femur of *Megatherium altiplanicum* n. sp., holotype (MNHN AYO 101); **A**, anterior view; **B**, lateral view; **C**, distal view. Scale bar: 10 cm.

The greater trochanter rises slightly above the crest between the head and greater trochanter. The diameter of the neck is smaller than the maximum diameter of the head, as in *M. americanum*. The notch for the round ligament is widely triangular, as in *M. americanum* and *E. laurillardii*. It is narrow and elongated in *E. sefvei* and *Pyramiodontherium bergi* (MLP 2-66).

The femur of *M. altiplanicum* n. sp. is relatively narrower than that of *M. americanum*. As in the

latter, the proximal and distal extremities are markedly expanded transversely, the epicondyles prominent, and the lateral and medial margins notably concave, whereas they are more nearly rectilinear in *E. laurillardii*. In *M. medinae* the lateral margin is nearly rectilinear, a morphology diagnostic for the species (Casamiquela & Sepulveda 1974). The less concave margins are probably plesiomorphic states.

The form of the medial condyle is diagnostic for *M. altiplanicum* n. sp. It extends anterolaterally

toward and approaches closely the patellar trochlea. These articular surfaces are in proximity in most megatheriines, but this is due to a medially expanded patellar trochlea (e.g., *E. laurillardii*), which is plesiomorphic. The patellar trochlea of *M. altiplanicum* n. sp. is not medially expanded and thus resembles those of *M. americanum* and *M. gallardoi*. In these latter species, the medial articular surface and patellar trochlea are widely separated, particularly in *M. gallardoi* (Kraglievich 1925b). Further, the trochlea does not project anteriorly in *M. altiplanicum* n. sp. and *M. americanum*, but does so in *E. laurillardii* and *E. sefvei*.

The patellar trochlea is contiguous with the articular surface of the lateral condyle, as in all megatheriines. In *M. altiplanicum* n. sp., these surfaces are separated by a faint ridge. A similar ridge occurs in some specimens of *M. americanum*; a very weak, barely perceptible demarcation may be present in *E. laurillardii* (De Iuliis 1996).

Navicular. A right navicular (MNHN BOL V 3312) from Ayo Ayo is referred to *M. altiplanicum* n. sp. It is smaller than that of *M. americanum* and the medial half of the astragalar facet is less concave. This part of the facet is larger than the lateral, convex half, whereas they are subequal in *M. americanum*. The facets on the anterior surface are arranged as in *M. americanum*, but the dorsomedial facet is relatively smaller, and the ventral margin of the ventral facet is nearly rectilinear, compared to the convex margin in the Pleistocene species. As with the carpals, Cartelle (1992) reported considerable variation in the shapes and sizes of the articular surfaces of the tarsals in *E. laurillardii*.

DISCUSSION

The holotype of *M. altiplanicum* n. sp. represents an adult individual, which had thus attained its definitive size. Two methods for estimating mass suggest that the mass of *M. altiplanicum* n. sp. may have been approximately between one quarter to one third that of *M. americanum*. Fariña *et al.* (1998) calculated a mass of 6 000 kg

for *M. americanum* based on values obtained from numerous allometric regressions of the dentition, and cranial and postcranial elements. However, these authors obtained a more conservative estimate of 4 000 kg by removing the effect of femur width (which clearly produces a disproportionately high mass estimate in megatheres), a value more similar to the mass obtained by other authors (Casinos 1996). Using the allometric equation obtained by Janis (1990) based on the lower molar toothrow length of extant ungulates gives a mass of 5 500 kg for *M. americanum* and 1 746 kg for *M. altiplanicum* n. sp.

A second method for estimating mass, that of assuming geometric similitude between *M. americanum* and *M. altiplanicum* n. sp., results in a lower estimate. Using the specimen measured by Fariña *et al.* (1998) and a mass of 4 000 kg for *M. americanum* produces a mass of 977 kg for *M. altiplanicum* n. sp.; a mass of 6 000 kg for *M. americanum* produces a mass of 1 465 kg for *M. altiplanicum* n. sp.

This species is thus considerably smaller than *M. americanum* and *M. gallardoi*, and appreciably smaller also than *M. medinae*, *M. istilarti*, *M. gaudryi* and *M. tarijense* (see Fig. 8). Indeed, it is one of the two smallest post-Miocene megatheriines, the other being *Eremotherium sefvei* from the Quaternary of Ulloma, Bolivia (De Iuliis & Saint-André 1997).

The toothrow of *M. altiplanicum* n. sp. (see Fig. 9) is approximately one-third shorter than those of *M. medinae* and *M. tarijense*; these last two species are similar in size (Casamiquela & Sepulveda 1974). Also, the mandibular toothrow of *M. lundii sejoii* (see Kraglievich 1931) is 39% longer than that of *M. altiplanicum* n. sp.

The anterior root of the zygomatic arch lies opposite M1, a position characteristic of the brevirostral (but see De Iuliis 1996) condition described by Cabrera (1928) based on the antemolariform length of the maxilla in some megatheriines. In brevirostral megatheriines, the length between the mesial alveolar wall of M1 and the anterior extremity of the maxilla is just below 17% of the condylomaxillary length, whereas in longirostral megatheriines this ratio is approximately 20%. In

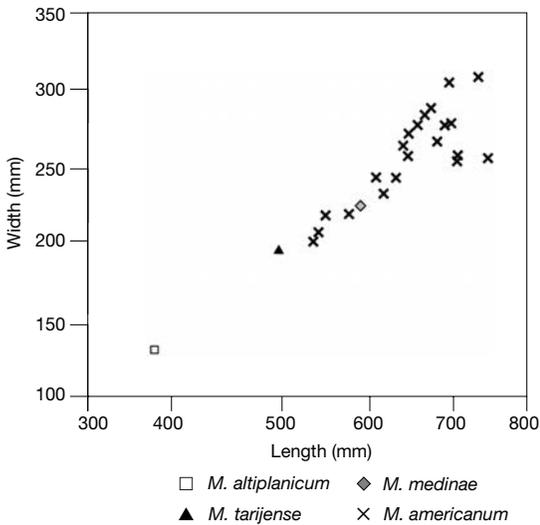


FIG. 8. — Plot of maximum length and midshaft width of the femora of selected *Megatherium* species. Data for *M. americanum* Cuvier, 1796, *M. medinae* Philippi, 1893 and *M. tarijense* Gervais & Ameghino, 1880 from De Iuliis (1996).

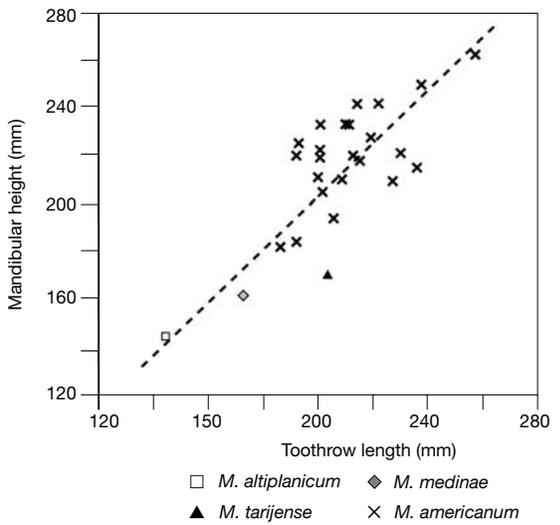


FIG. 9. — Plot of tooththrow length and maximum mandibular height of selected *Megatherium* species. Dashed line represents a slope of 1. Data for *M. americanum* Cuvier, 1796, *M. medinae* Philippi, 1893 and *M. tarijense* Gervais & Ameghino, 1880 from De Iuliis (1996).

the former group, the anterior root of the zygomatic arch lies opposite the middle or distal part of M1, while in the latter it lies at the level of M2. Cabrera (1928) and Paula Couto (1979) stated that divergence of brevisrostral and longirostral megatheriines, represented respectively by *Megatheridium* and *Plesiomegatherium*, had occurred by the late Miocene. However, a difference of 3% in the ratio of antemolariform maxillary length to condylomaxillary length lies within the range of individual variation in *Eremotherium laurillardii* (De Iuliis 1996). The position of the anterior root of the zygomatic arch lies more posteriorly (i.e. approximately opposite M2) in most megatheriines. However, the polarity of this character is equivocal, but it is worth noting that the root lies in the more posterior position in *Megathericulus*, which is probably the sister taxon to all other megatheriines, based on its highly mesiodistally compressed molariforms (De Iuliis 1994).

The palatal morphology of *M. altiplanicum* n. sp. resembles that of *M. medinae* and *E. laurillardii* in that the prealveolar width is nearly equal to the

interalveolar width, whereas in *M. americanum* the prealveolar portion is wider than the interalveolar width. Also, the interalveolar width is narrower than the width of the largest molariform in *M. altiplanicum* n. sp., *M. americanum*, *M. medinae* and *Pyramiodontherium bergi*, whereas it is equal to or wider than the widest molariform in *E. laurillardii*, *Megatheridium annectens*, and *Plesiomegatherium halmyrononum* (Cabrera 1928; Hoffstetter 1952).

The femur is strongly twisted in *M. americanum* and *M. altiplanicum* n. sp., as is clearly indicated by the markedly sigmoidal curve of the lateral femoral margin. Hoffstetter (1952) considered this feature characteristic of *Megatherium*. The femur is more nearly flat and its lateral margin nearly rectilinear in *Eremotherium*, *Plesiomegatherium* and *M. medinae*. This morphology is generalized and plesiomorphic for megatheriines, as compared to a femur that is strongly twisted and relatively constricted at its middle (see De Iuliis & Saint-André 1997).

Casamiquela & Sepulveda (1974) considered *Eremotherium* to be merely a subgenus of

TABLE 2. — Measurements (mm) of postrcranial elements of *Megatherium altiplanicum* n. sp.

Atlas (holotype, MNHN AYO 101)	
Maximum dorsoventral height	56.5
Sagittal length of neural canal	24.0
Maximum dorsoventral height of neural canal	37.5
Maximum transverse width of neural canal	41.0
Dorsoventral height of glenoid fossa	40.0
Maximum length of wing	69.5
Width of wing, from neural canal to lateral margin	54.0
Humerus (MNHN BOL V 3338)	
Maximum distal width	107.2
Width of distal articular surface	70.6
Radius (MNHN AYO 203)	
Maximum length	395.0
Maximum proximal diameter	52.5
Minimum proximal diameter	46.2
Maximum distal diameter	99.4
Minimum distal diameter	61.2
Shaft width at level of lateral crest	67.0
Minimum transverse shaft width	42.0
Minimum anteroposterior shaft thickness	27.4
Ulna (MNHN BOL V 3304)	
Olecranon process width	119.0
Olecranon process length, tuberosity to anconeal process	88.6
Width of articular surface of trochlea	103.5
Femur (holotype, MNHN AYO 101)	
Lateral length	379.0
Medial length	387.5
Proximal width	203.1
Minimum shaft width	135.0
Maximum diameter of head	94.0
Maximum width between distal tuberosities	196.5
Maximum width between condyles	140.0
Width of patellar trochlea	52.5
Maximum width of medial condyle	64.5
Maximum width of lateral condyle and patellar trochlea	77.0
Depth of medial condyle	85.0

Megatherium, with *M. medinae* being a transitional form between primitive species of *Eremotherium* sensu Hoffstetter (1952) and the more derived species of *Megatherium* sensu Hoffstetter (1952). Although this view is probably an oversimplification (De Iuliis 1996), the well-marked femoral torsion of *M. altiplanicum* n. sp. avoids misidentification with *M. medinae*, which possesses the plesiomorphic femoral morphology (Kraglievich 1931; Hoffstetter 1986).

M. medinae is occasionally referred to as the genus or subgenus *Pseudomegatherium* Kraglievich, 1931 ("false *Megatherium*"); e.g., by Hoffstetter (1986), who stated that at least two as yet undescribed species could possibly be referred to *Pseudomegatherium*, one from the Pleistocene of Peru, the other from the Quaternary of Ecuador. Casamiquela & Sepulveda (1974), followed by Hoffstetter (1986) and Marshall & Salinas (1991), synonymized *M. sundti* with *M. medinae*. However, a femur of an immature individual (PIU M4530) from Ulloma, Bolivia, bears strong resemblance to that of *M. americanum*, except that the patellar trochlea is expanded medially. This medial expansion occurs in all other megatheriines for which the femur is known, except in *M. americanum* and *M. altiplanicum* n. sp. (De Iuliis & Saint-André 1997). Femur PIU M4530 differs sufficiently in general morphology from that of *M. medinae* to suggest that it belongs to a distinct species. De Iuliis & Saint-André (1997) noted that PIU M4530 probably belonged to *M. sundti*, described from Ulloma by Philippi (1893), and thus considered this species to be valid. It is worth noting here that Hoffstetter (1986: 224) reported the presence of two megatheriine species from Plio-Pleistocene high Andean mammalian faunas as "*M. sundti* = synonym of *M. americanum* Cuvier?" However, this passage is misprinted from Hoffstetter's manuscript for this article, and should read: "*M. sundti* Phil. = synonym of *M. (Pseudomegatherium) medinae* Phil.; *M. americanum* Cuvier?" (Hoffstetter pers. comm. 1991).

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships among megatheriines are not clearly understood, largely because most described taxa are known only from fragmentary remains. De Iuliis (1996) presented a strict consensus tree that recognized only a basal megathere clade (*Megathericulus* and *Plesiomegatherium*) and an unresolved crown group of eight taxa. Among the megatheriines discussed above, only *Eremotherium laurillardi*,

Megatherium americanum, *M. medinae* and *M. altiplanicum* n. sp. are reasonably well known. The following characters permit a preliminary analysis of phylogenetic relationships among these four megatheriines.

1. DEPTH OF THE HORIZONTAL RAMUS OF THE DENTARY

The depth of the horizontal ramus of the dentary is important for determination of the evolutionary relationships among megatheriines (Kraglievich 1930). The relative increase in depth of the jaw reflects increased hypsodonty; the index of mandibular height to toothrow length multiplied by 100 provides a measure of hypsodonty (Zetti 1964; De Iuliis 1996). In *Eremotherium laurillardii*, the values for this index range between 66-83% and in *M. americanum* between 92-112%. The values for *M. medinae* are intermediate between these. The value in *M. altiplanicum* n. sp. is 101%, well within the range for *M. americanum*. De Iuliis (1996) ordered these states as follows:

- Index between 66-83%: plesiomorphic (0)
- Index between 83-92%: apomorphic (1)
- Index between 92-112%: apomorphic (2).

2. SHAPE OF THE PREMAXILLA

De Iuliis (1994) demonstrated that the small, triangular, and plate-like premaxillae of *E. laurillardii* are plesiomorphic (state 0), whereas the elongated, quadrangular, and robust premaxillae of *M. americanum* are derived (state 1). The premaxillae of *M. altiplanicum* n. sp. resemble those of *M. americanum*, but are somewhat less robust. Those of *M. medinae* have not been recovered.

3. SUTURAL ATTACHMENT OF THE PREMAXILLAE

In *E. laurillardii* the premaxillae are only loosely attached to each other and to the maxillae, so that they are rarely recovered *in situ*. This condition is plesiomorphic (De Iuliis 1994, 1996). The premaxillae of *M. americanum* are, in contrast, strongly fused to each other and to the maxillae, and are almost always recovered *in situ* in adult individuals. They are sometimes broken, but small portions of their posterior ends are pre-

served. Strongly fused premaxillae are derived (De Iuliis 1994, 1996). The premaxillae of *M. altiplanicum* n. sp. are fused to each other and to the maxillae. As stated above, the premaxillae of *M. medinae* are unknown, but the maxillae bear deep articular pockets anterolaterally for the premaxillae that are similar to those of *E. laurillardii*. These observations indicate that the premaxillae of *M. medinae* were only weakly sutured to the maxillae, and probably each other, as occurs in *E. laurillardii*.

4. TORSION OF THE FEMUR

The femoral diaphyseal shaft of megatheriines is twisted so that the greater trochanter lies posterior to a plane passing through the head of the femur and its distal condyles. The angle of torsion may be measured by placing the femur on a table with the head, greater trochanter, and lateral epicondyle in contact with the surface of the table. This raises the distomedial part of the bone (De Iuliis & Saint-André 1997). The angle is taken at the intersection between the surface of the table, and a line passing through the antero-posterior midpoints of the medial and lateral condyles and extended to the table.

The femur of *E. laurillardii* is moderately twisted, with values rarely surpassing 40°. The femur of *M. medinae* is similar, but in *M. americanum* it is markedly twisted. The greater trochanter projects more strongly posteriorly, and the angle of torsion is almost always greater than 40° (De Iuliis 1996; De Iuliis & Saint-André 1997). The morphology of the lateral margin of the femur is correlated with the degree of torsion. In *E. laurillardii*, the margin is nearly rectilinear. Hoffstetter (1952) stated that this character was also linked to the presence of a diagonal crest-like protuberance extending from the greater trochanter to the medial entepicondyle on the posterior and nearly flat surface of the femur, as occurs also in *M. medinae*, *Paramegatherium incognitum* (which we regard as of questionable validity), and probably *M. istilarti*. In *M. americanum*, the lateral margin of the femur is strongly sigmoidal (see De Iuliis & Saint-André 1997: fig. 6). De Iuliis (1996) noted that the moderately twisted femur

with a nearly rectilinear lateral margin characteristic of *E. laurillardi* is plesiomorphic (state 0); the strongly twisted femur with a sigmoidal lateral margin of *M. americanum* derived (state 1). *M. medinae* resembles *E. laurillardi*; *M. altiplanicum* n. sp. resembles *M. americanum*.

5. SHAPE OF THE MEDIAL AND LATERAL FEMORAL MARGINS

In *M. americanum* and *M. altiplanicum* n. sp. the middle part of the diaphysis is relatively more constricted than in *E. laurillardi* and *M. medinae*. The medial and lateral femoral margins in the first two species therefore are more concave, the femur is more robust, and the proximal and distal ends appear more prominent. In *E. laurillardi* and *M. medinae*, the diaphysis is relatively less constricted and the medial and lateral margins are more nearly parallel. This condition, also present in most other megatheriines, is plesiomorphic (state 0), that characteristic of *M. americanum* and *M. altiplanicum* n. sp. is apomorphic (state 1; De Iuliis 1996; De Iuliis & Saint-André 1997).

6. DEVELOPMENT OF THE PATELLAR TROCHLEA

In *E. laurillardi* and *M. medinae* the patellar trochlea is well-developed and extends medially past the sagittal plane on the anterior surface of the femur. This morphology occurs in nearly all other sloths, and De Iuliis (1996) and De Iuliis & Saint-André (1997) have shown that this condition is plesiomorphic (state 0). The exceptions are *M. americanum*, *M. istilarti* (see Kraglievich 1925b) and *M. altiplanicum* n. sp., in which the trochlear facet is reduced and restricted to the middle lateral quarter of the anterior surface of the femur. This condition is derived (state 1).

This brief analysis suggests that *M. americanum*, *M. altiplanicum* n. sp., and *M. medinae* form a clade, based on increased depth of the horizontal ramus of the dentary and relatively robust premaxillae that are fused to each other and the maxillae. Within this clade, *M. americanum* and *M. altiplanicum* n. sp. are sister species, based on the following synapomorphies: a further increase in depth of the dentary (Character 1, state 2),

pronounced torsion of the femur, a femur with a relatively constricted diaphysis and widened proximal and distal ends, and reduction of the patellar trochlea. We consider it more prudent, pending a thorough and comprehensive phylogenetic analysis, to maintain the genus *Megatherium* as it has been used traditionally (i.e. including *M. medinae*), rather than formally recognize other possible generic names, such as *Pseudomegatherium*. However, in order to emphasize the sister species relationship between *M. americanum* and *M. altiplanicum* n. sp., we assign the subgeneric name *Megatherium* to this clade, as it contains the type species of the genus (cf. ICZN 1999: art. 44.1).

ECOLOGICAL CONSIDERATIONS AND CONCLUSIONS

The presence of *M. altiplanicum* n. sp. in the Montehermosan of Bolivia indicates that a megatheriine closely related to *M. americanum* has existed at least since the early Pliocene. *M. altiplanicum* n. sp. differs considerably from *M. medinae*, first described by Philippi (1893) from northern Chile, but to which have also been referred remains from the Quaternary of Bolivia (e.g., by Casamiquela & Sepulveda 1974; Marshall & Salinas 1991). *M. medinae* is less derived than *M. altiplanicum* n. sp. with respect to *M. americanum*. It does not belong to *Megatherium* sensu Hoffstetter (1952), but rather to the subgenus *Pseudomegatherium*, according to this author. Indeed, Hoffstetter (1986) followed Kraglievich (1931) who proposed *Pseudomegatherium* for *M. medinae*. However, until a more comprehensive phylogenetic analysis is possible, we prefer to retain this species in *Megatherium*.

Casamiquela & Sepulveda (1974) suggested that *M. medinae* is closely related to *M. tarijense* and *M. lundii*. Further, they synonymized *M. sundti*, erected on damaged skulls from Ulloma by Philippi (1893), with *M. medinae*. Consequently, these remains from the base of the Ulloma Formation, Bolivia (i.e. early Lujanian) were referred to *M. medinae*. However, the remains (PIU M4530) dis-

cussed above of an immature individual, suggest that *M. medinae* (with its plesiomorphic femur) does not occur in Ulloma. Probably, remains from this region represent the species that Philippi (1893) described as *M. sundti*.

It is apparent from the altitudinal and geographic distribution of *Megatherium* sensu Hoffstetter (1952) (i.e. with a strongly twisted femur) that this genus was able to inhabit temperate lowlands (*M. americanum* is known extensively from the Quaternary pampas of Argentina), as well as high altitudes as is indicated by the presence of *M. altiplanicum* n. sp. at Ayo Ayo-Viscachani during the Pliocene and *M. sundti* at Ulloma during the Pleistocene.

In Chile, *M. medinae* is known from Chiu-Chiu (situated above 2 000 m) and in the western part of the lowland Tamarugal Pampa. Casamiquela & Sepulveda (1974) suggested that the occurrence of this species at such low altitude as the Pampa was possibly caused by *post-mortem* transport. Various undescribed remains from central and southern Peru apparently belong to a closely related form. Hoffstetter (1986) considered these remains to represent two species, distinguished on the basis of size, and referred them to *Pseudomegatherium* based on the presence of a relatively flat femur. Fragmented remains from the Puninian fauna of Ecuador were doubtfully assigned to this taxon, which is rare or absent in the northern Andes (Hoffstetter 1986).

Thus, the *Megatherium* species with a less twisted femur apparently represent a series of Quaternary forms of uncertain monophyly that were adapted to a high-altitude habitat in the central Andes. Importantly, increase in the depth of the dentary indicates that *M. medinae* (and perhaps other species from the central Andes) is more closely related to *M. americanum* and *M. altiplanicum* n. sp. than to *E. laurillardii*. The latter, also of Quaternary age, extended from southern Brazil to the southeastern United States (Cartelle & De Iuliis 1995). It is therefore generally considered to have been adapted to tropical regions, as well as a warm and dry climate. It is widespread east and west of the Andes and enters some Andean valleys, but is always found at low altitudes (Hoffstetter

1986). In contrast, *Megatherium* occurs in higher latitudes (at low altitudes), and thus is probably characteristic of more temperate climates. The presence of *M. altiplanicum* n. sp. in early and middle Pliocene sediments possibly indicates a broad ecological similarity between the Pliocene Altiplano, on the one hand, and the Pleistocene Altiplano and Argentinian lowlands, on the other. As the oldest record of the genus occurs on the Altiplano, it seems reasonable to assume that *M. altiplanicum* n. sp. evolved on the Altiplano and subsequently spread onto the central South American lowlands. Movement toward lower altitudes may have resulted from glaciations that, from at least 2.8 Ma (Patapatani Glaciation), occurred in the central Andes. However, the possibility exists that it immigrated to the Altiplano due to an ecological vacuum created by a massive extinction (*cf. infra*). Such an extinction might have been caused by the catastrophic deposition of the volcanic tuff termed Toba 76 or possibly by a more global climatic change.

The megatheriine reported, along with a mylodontid, from Member 6 of the Mauri Formation (Huayquerian) by Marshall *et al.* (1983) remains undescribed, and is not reported by Marshall & Sempéré (1992), who mention instead the presence of a mylodontid and a megalonychid. In any event, the presence of *M. altiplanicum* n. sp. in the Montehermosan of the Altiplano is of itself of great paleobiogeographic interest because it is the earliest certain species of its genus (Montehermosan megatheriines from Argentina have usually been referred to *Plesiomegatherium*, although doubtfully in some cases, as is indicated by “*?Plesiomegatherium*” in the faunal list for the Argentinian Montehermosan given by Marshall *et al.* 1983). *M. medinae*, considered Pliocene by earlier workers, was assigned to the Pleistocene by Casamiquela & Sepulveda (1974); remains from the base of the Ulloma Formation are Lujanian (Marshall & Salinas 1991) and probably belong to *M. sundti*. This indicates that the most recent common ancestor of *M. americanum*, *M. altiplanicum* n. sp., and *M. medinae* is at least early Pliocene and possibly older. The very early presence of a

Megatherium species that possesses a femur with prominent torsion on the Bolivian Altiplano indicates that the *M. altiplanicum* n. sp.-*M. americanum* clade (subgenus *Megatherium*) originated either on the Altiplano or in a region from which remains are unknown or undescribed, and that the emergence of the genus *Megatherium* (including *M. medinae*) probably dates to near the beginning of the Pliocene.

An evolution on the Altiplano would cast doubt on some of the minor conclusions drawn by Marshall & Sempéré (1992), such as that there is no paleontological data that supports the hypothesis of an endemic Altiplano-Puna fauna, and that this region was not a site of significant *in situ* evolution. These authors postulated that recurrent deposition of ash sheets during the Miocene and Pliocene resulted in repetitive and massive regional extinctions on the Altiplano-Puna, each followed by the reestablishment of faunas of low diversification through immigration from surrounding lowland areas.

However, it is possible that *M. altiplanicum* n. sp. evolved *in situ* from a form more hypsodont than, for example, *Eremotherium*. Such a postulated form, ancestral to the species of *Megatherium* possessing a prominently twisted femur, probably resembled the Pleistocene *M. medinae*, which was apparently restricted to high elevations in the Chilean (and possibly the Peruvian and Ecuadorian) Andes.

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