A NEW SPECIES OF *MEGATHERIUM* (MAMMALIA: XENARTHRA: MEGATHERIIDAE) FROM THE PLEISTOCENE OF SACACO AND TRES VENTANAS, PERU

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ABSTRACT. *Megatherium urbinai* sp. nov. is a new megatheriine ground sloth from Pleistocene beds of the Sacaco area and Tres Ventanas Cave, Peru. This new species is referred to the genus *Megatherium* based primarily on humeral, femoral, and astragalar morphology. It is characterized by various features, such as a strongly reduced metacarpal-carpal-complex (MCC) and a reduced, oval scaphoid facet of the MCC located at the medial extremity of the bone that does not contact without the McII facet. The distal side of the unciform bears an undivided articular surface for the metacarpals III–V. The lateral femoral margin is nearly rectilinear and the tibia and fibula do not fuse distally. The astragalus is oriented more medially, the navicular is in a medial position, the ectocuneiform articulates with MtIII–IV, and the MtIV is more inclined laterally than in *M. tarijense* and *M. americanum*. *M. urbinai* is one of the smallest *Megatherium* species known along with *M. altiplanicum*. It has the most marked torsion of the pes for the genus. It extends the palaeogeographic distribution of the genus in South America. It is phylogenetically close to other Andean megatheriines and is less specialised than *M. tarijense*, and does not belong to the clade constituted by [*M. altiplanicum* + *M. americanum*].

KEY WORDS: Sacaco, Tres Ventanas, Peru, Late Pleistocene, Megatheriidae, systematics, locomotor mode.

THE subfamily Megatheriinae is known from sediments of Late Miocene (*Megathericulus patagonicus* Ameghino, 1904) to Late Pleistocene age in South America [*M. americanum* Cuvier, 1796 and *E. laurillardi* (Lund, 1842)] and of Late Pliocene (*Eremotherium eomigrans* De Iuliis and Cartelle, 1999) to Late Pleistocene age (*E. laurillardi*) in North America (Cartelle and De Iuliis 1995; De Iuliis 1996; De Iuliis and Cartelle, 1999).

The discovery over the past two centuries of many megatheriine specimens in South America has resulted in the naming of a multitude of taxa. Recently, the descriptions of *Eremotherium laurillardi* by Cartelle (1992) and Cartelle and De Iuliis (1995), as well as the systematic review by De Iuliis (1996), have provided a welcome revision of the systematics of the subfamily. In addition, these works have allowed an evaluation of intraspecific variation in ground sloths. This was made possible by the large collections of megatheriine remains collected in Florida (Daytona Beach, USA) and Jacobina (Bahia, Brazil). In view of the wide degree of individual variation observed in *E. laurillardi* remains of Santa Elena, Ecuador and Daytona Beach (De Iuliis 1996; F. Pujos, pers. obs. 2001), as well as from Jacobina (Cartelle 1992; De Iuliis 1996), and the apparent degree of variation in *Megatherium americanum* (De Iuliis 1996), few of the published *Megatherium* species are probably valid.

As most *Megatherium* species are poorly known, it is difficult to estimate the intraspecific variation as well as the validity of most of its species. Detailed anatomical descriptions are desirable to estimate the range of the intra and interspecific variations in Megatheriinae in particular and in other ground sloths in general. Only two megatheriine ground sloths have been described in detail, *E. laurillardi* (Cartelle 1992; Cartelle and De Iuliis 1995; De Iuliis 1996) and *M. americanum* (Owen 1851, 1855, 1856, 1858, 1860). *M. altiplanicum*, from the Pliocene of Bolivia, has been well described but is poorly known (St-André and De Iuliis 2001). The absence of detailed anatomical descriptions for most species seriously hampers our knowledge of the evolutionary history of ground sloths.

TEXT-FIG. 1. Map of Peru indicating the Sacaco area, Tres Ventanas cave, and Peruvian Pleistocene sites yielding megatheriine remains. Scale bar represents 100 km.

The Sacaco-Lomas area has yielded various vertebrate remains. Muizon (1981) reported a diverse Miocene–Pliocene marine vertebrate fauna. A Quaternary mammalian fauna included an Equidae specimen (Hoffstetter 1968). In 1983, Muizon recovered a juvenile mandible of *Glossotherium* sp. (MNHN-PRU9) from the same Pleistocene levels.

A field campaign in the Sacaco-Lomas area (Text-fig. 1) in February–March 2000 recovered a new Pleistocene mammalian fauna at Aguada de Lomas, Sacaco 1, and Sacaco 2 (Pujos and Salas 2002). Sacaco 2 yielded various remains, including MUSM 15, considered the holotype of *M. urbinai* and associated with fragmentary bones of *Equus* (*Amerhippus*) cf. *santa-elenae* (Equidae: Equinae), *Stegomastodon* sp. (Gomphotheridae: Anancinae), and a juvenile mandible of *Calomys* sp. (Muridae: Sigmodontinae).

A second specimen, UNA V2642, recovered from Cave Number 2 at Tres Ventanas (Text-fig. 1), is assigned to *M. urbinai* and helps complete its diagnosis. The Tres Ventanas remains, collected by F. Engel (UNA), were associated with a humerus and fragmentary bones of a juvenile specimen of *Scelidodon* cf. *chiliensis* (Mylodontidae: Scelidotheriinae), a common scelidotheriine of the Peruvian coast (Pujos 2000). The fossil-bearing deposit is located under a horizon that preserves evidence of human activity and dates to 6080 years BP (Engel 1970). Hoffstetter (1970, 1986) identified the ground sloth as *Megatherium* sp. The results of C14 dating (older than 40,000 years BP, Engel 1970) do not permit an estimation of the age of the fossil bearing horizon.

This new species differs significantly from all Megatheriinae previously discovered in Peru (Text-fig. 1), which are listed below by locality:

Talara tar-pits. *Eremotherium* sp. (Lemon and Churcher 1961; Hoffstetter 1970; Marshall *et al.* 1984), 14,000 years BP (Churcher 1966; Ortlieb and Macharé 1989). A re-examination of the material from Talara, housed at ROM, reveals the existence of four functional digits and an MCC composed of the trapezium and McI. Another medium-sized Megatheriinae from Talara clearly belongs to the genus *Megatherium* and is assigned to the poorly known Ecuadorian species *M. elenense* (Hoffstetter 1949, 1952; De Iuliis 1996; F. Pujos, pers. obs. 2001).

Pampa de los Fósiles area (near Trujillo). The few megatheriine remains were referred to cf. *Eremotherium* by Marshall *et al.* (1984) and Megatheriidae by Pujos (2000). They are between 26,000 and 15,000 ybp (Falguères *et al.* 1994) in age and referable to *E. laurillardi* (F. Pujos, pers. obs. 2001).

Santa Rosa cave (near Celendín). This site has yielded a new large *Megatherium* species regarded as a probable new genus of Megatheriinae (Pujos 2001).

Other fragmentary megatheriine remains are recorded in Cuzco (Cuzco Department), Azángaro and Llali (Puno Department), Ayacucho (Hoffstetter 1970, 1986, Ayacucho Department), Cerro de Pasco (Pasco Department), Yantac (Junin Department), and Piura (Piura Department, R. Salas, pers. obs. 2000).

The existence of a new *Megatherium* species in Peru is based on detailed anatomical descriptions of MUSM 15 and UNA V2642 and comparison with other *Megatherium* species, and includes a consideration of intraspecific variation. This paper also re-evaluates diagnostic characters for Pleistocene megatheriines, suggests additional characters, proposes a functional interpretation of the locomotor apparatus of the genus *Megatherium*, and considers the degree of specialization of the three well-known *Megatherium* species (*M. americanum*, *M. altiplanicum*, and *M. tarijense*).

METHODS

The remains of the new *Megatherium* species are compared to those of *M. americanum* and *M. tarijense*, of which the manus and pes are particularly well known, and to isolated elements of *M. altiplanicum*, *M. elenense*, *M. medinae*, and *M. sundti*. Diagnostic characters for *M. urbinai* sp. nov. and other *Megatherium* species are proposed. The pelvic and pectoral girdle of MUSM 15 are not included in the detailed descriptions because they are poorly preserved.

Institutional abbreviations. CIZA, Centro de Investigación de Zonas Aridas, Universidad Nacional Agraria, Lima, Peru; EPN, Escuela Politécnica Nacional, Quito, Ecuador; FMNH, Field Museum of Natural History, Chicago, USA; IFEA, Institut Français d'Etudes Andines, Lima, Peru; INC, Instituto Nacional de la Cultura del Perú, Lima, Peru; LPVUCH, Laboratorio de Paleontología de Vertebrados de la Universidad de Cayetano Herredia, Lima, Peru; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum national d'Histoire naturelle, Paris, France; MUSM, Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima, Peru; PIU, Palaeontological Institute of Uppsala, Uppsala, Sweden; ROM, Royal Ontario Museum, Toronto, Canada; SGO, Museo Nacional de Historia Natural, Santiago, Chile; UNA, Universidad Nacional Agraria, Lima, Peru; UNI, Universidad Nacional de la Ingeniería, Lima, Peru.

Osteological abbreviations. L, left; M and m, upper and lower molariform teeth, respectively; Mc, metacarpal; MCC, metacarpal-carpal-complex (see De Iuliis and Cartelle 1993); MEC, mesocuneiform-entocuneiform-complex (see De Iuliis 1996); Mt, metatarsal; P, phalanx; P(1–2), fused first and second phalange; R, right.

SYSTEMATIC PALAEONTOLOGY

Order XENARTHRA Cope, 1889

Suborder TARDIGRADA Latham and Davies, *in* Forster 1795

Superfamily MEGATHERIOIDEA Gray, 1821

Family MEGATHERIIDAE Owen, 1843

Subfamily MEGATHERIINAE Gill, 1872

Type genus. Megatherium Cuvier, 1796

Other genera. Megathericulus Ameghino, 1904; *Plesiomegatherium* Roth, 1911; *Pyramiodontherium* Rovereto, 1914; *Megatheriops* Ameghino, 1921; *Megatheridium* Cabrera, 1928; *Pliomegatherium* Kraglievich, 1930; *Eremotherium* Spillmann, 1948.

Genus MEGATHERIUM Cuvier, 1796

Type species. Megatherium americanum Cuvier, 1796.

Distribution of the genus. Early and middle Pliocene (Montehermosan) to late Pleistocene (Lujanian) deposits in South America.

Diagnosis. Medium-sized to large Megatheriinae, tooth rows subparallel as in *Megatheriops*, *Megathericulus*, *Pyramiodontherium*, and *Plesiomegatherium* (curved in *Eremotherium*); dental formula 5/4 M, all teeth are molariform and quadrangular in occlusal view (compressed anteroposteriorly in *Megathericulus* and *Plesiomegatherium*); together, L and R premaxillae are Y-shaped (*M. americanum*) or X-shaped (*M. tarijense*) (V-shaped in *Eremotherium* or juveniles of *M. americanum* and *M. altiplanicum*), premolari-form portion of maxilla short (long in *Eremotherium* and Mio-Pliocene Megatheriinae); V-shaped post-palatine notch (U-shaped in *Eremotherium* and *Megathericulus*), high or very high degree of hypsodonty, poorly developed ectotympanic (well developed in *Eremotherium*), anterior base of coronoid process anterior to m4; posterior extremity of mandibular symphysis posterior to m1 as in *Eremotherium*, *Pyramiodontherium*, *Megatheriops* (anterior to m1 in *Plesiomegatherium*); facets for atlanto-axial joint separate (fused in *Eremotherium*); deltopectoral crest reduced (well marked in *Eremotherium*, very strong in *Megatheriops*); musculospiral groove and area of attachment of brachialis anticus muscle reduced (developed in *Eremotherium*); manus with II–V functional digits (digits III–V in *E. laurillardi* and I–V in *E. eomigrans*); digits II–IV clawed; MCC formed by fusion of first digit and trapezium (by trapezium, trapezoid, and McI–II in *E. laurillardi* and, at least, by trapezium, McI, and occasionally trapezoid in *E. eomigrans*); fusion of first and second phalanges of third digit of manus; McIII Y-shaped, with a large medial limb, or I-shaped (with a small medial limb in *Eremotherium*); distal epiphysis of tibia slightly compressed anteroposteriorly (highly compressed in *Eremotherium*); discoid and ectal facets of astragalus in contact in dorsolateral view (separated in *Eremotherium*).

Megatherium urbinai sp. nov.

Text-figures 2, 3A–C, 4A–K, O, 5, 6A, 7A–D, F–H, K–L, N–O; Table 1

Derivation of name. In honour of Mario Urbina (UPCH), who found the specimen from Sacaco.

Holotype. MUSM 15, a partial skeleton including fragments of the skull, hyoid apparatus, and mandible (with two teeth), three sacral vertebrae, the 12 posterior caudal vertebrae, a hemal arch, several ribs, distal epiphysis of R and L humeri, proximal epiphysis of R radius, L radius, R and L ulnae, R and L scaphoids, L cuneiform (medial side damaged), L pisiform, L trapezoid (medial side damaged), L unciform, R magnum, R and L palmar sesamoids, L MCC, L McII–V and R IV-V, L P1-II (dorsal portion absent), L P3-II (dorsal half of the articulation absent), L P(1–2)-III, R and L P3-III, L P1-IV, R and L P2-IV, R and L P3-IV, R and L proximal P-V, R femur (most of medial surface

missing), L patella, R tibia-fibula, distal half of L tibia-fibula, one ossified meniscus of the knee joint, R and L cyamellae, R and L astragali, R calcaneum, R and L cuboids, L navicular, R ectocuneiform, L MEC, L MtIII, R MtIV, R and L P(1–2)-III, L P3-III, and one sesamoid (fabella?).

Referred specimen. UNA V2642, a partial skeleton including the coronoid process of the L dentary, proximal end of a stylohyal, a sacral vertebra, a caudal vertebra, a sternebra, several portions of ribs, R ulna (distal half), L scaphoid, R and L lunars, R and L cuneiforms, R and L pisiforms, L unciform, L magnum, R and L trapezoids, L MCC, L McII–V, R McV, R P1-II, R P2-II, R and L P(1–2)-III, L proximal P-V, L distal P-V, a palmar sesamoid, R patella, R calcaneum, R astragalus, R cuboid, R and L naviculars, R MEC, R MtIII–IV–V, phalanges R P3-III, R distal P-V. Three claws and a coprolite of the same specimen were discovered by Engel (1970 and pers. comm. 2001). This material is currently under study but is not within the scope of this paper.

Type locality. Site 'Sacaco 2' (S-15°30'36·3'–W-74°45'17'), elevation 100 m, north Sacaco, Arequipa Department, Peru (Text-fig. 1).

Other locality. Tres Ventanas Cave, 70 km east-south-east of Lima, elevation 4000 m (Text-fig. 1).

Stratigraphic occurrence. Quaternary deposits of Sacaco overlying the Pisco Formation (Miocene–Pliocene) (Muizon 1981; Marocco and Muizon 1988) and Tres Ventanas cave, of Peruvian Andes (Engel 1970).

Age. Pleistocene according to the geological map (Caldas Vidal 1978) for the specimen from Sacaco and Pleistocene, older than 40,000 ybp, according to Engel (1970), for the specimen from Tres Ventanas.

Diagnosis. Medium-sized, gracile, Pleistocene megatheriine; MCC proportionately less massive and more elongated transversely than in *M. americanum* and *M. tarijense*; scaphoid facet of MCC reduced, oval-shaped; it lies at medial edge of the bone and does not contact McII facet; articular facets for McIII–V of unciform convex and contiguous, but without the prominent crests that delimit the articulations in *M. americanum*, *M. tarijense*, and *M. elenense*; lateral surface of femoral diaphysis nearly rectilinear; greater trochanter intermediate between *M. americanum*, *M. altiplanicum*, and *M. sundti* (high) and *M. tarijense* and *M. medinae* (low); tibia and fibula slender, rectilinear without distal ankylosis (curved with partial distal ankylosis in *M. tarijense*, complete ankylosis in *M. americanum*); discoid facet of tibia ante-roposteriorly directed (anterolaterally to posteromedially directed in *M. tarijense* and *M. americanum*); discoid facet of astragalus shorter than in *M. tarijense*; one-third of navicular facet lies above the discoid facet (the two facets are at same level in *M. americanum*, the position is intermediate in *M. tarijense* and *M. medinae*); ectocuneiform articulated with MtIII–IV (only with MtIII in other *Megatherium* species) and MtIV highly twisted about its long axis.

DESCRIPTION

General characteristics. The axial skeleton (exclusive of the tail), scapula, clavicle, humeri, and femur of the new megathere are heavily weathered. The size of the coastal specimen of *Megatherium urbinai* sp. nov. (MUSM 15), based on the available limb elements, is 5 per cent greater than that of *M. altiplanicum* (St-André and De Iuliis 2001) and 15 per cent greater than that of *E. sefvei* (the smallest post-Miocene Megatheriinae species, known by a single femur from Bolivia; De Iuliis and St-André 1997); and smaller than all the other Pleistocene Megatheriinae (Appendix): *M. tarijense* and *M. sundti* (10 per cent greater), *M. elenense* (20 per cent greater), *M. medinae* (25 per cent greater), *E. eomigrans* and *M. americanum* (35 per cent greater), and *E. laurillardi* (40 per cent greater). *M. americanum* is generally much more massive than the other *Megatherium* species. The size of the Andean specimen of *M. urbinai* sp. nov. (UNA V2642) is 18 per cent greater than that of MUSM 15. This magnitude of intraspecific variation agrees well with that suggested for *E. laurillardi* (Cartelle and De Iuliis 1995; De Iuliis 1996) and *M. americanum* (De Iuliis 1996).

Skull, hyoid apparatus and mandible. The skull (nasal, supraoccipital, and temporal) and hyoid (posterior part of the basi-thyrohyal and probably one of the two anterolateral articulations for the ceratohyals) remains of MUSM 15 are very fragmentary and therefore not diagnostically informative (Text-fig. 2A). The mandible is represented by the

anterior portion of the spout, the lateral surfaces of right and left dentaries, two m (MUSM 15, Text-fig. 2B), and a portion of the left coronoid process (UNA V2642). The coronoid process is well developed dorsally as in other Megatheriinae. The lateral sides of the mandible indicate the existence of four molariforms, as is typical of megatheriines.

Post-cranial elements

Vertebrae and ribs. In *Megatherium* the three articular facets between the atlas and the axis are independent, contrary to the condition in *Eremotherium* (De Iuliis 1996; De Iuliis and Cartelle 1999). A partial cervical vertebra (UNA V2642) and three sacral vertebrae are preserved (MUSM 15). Generally, the megatheriine vertebral formula is seven cervical, 16 thoracic, three lumbar, five sacral, and 17 or 18 caudal (De Iuliis 1996). The fifth and last sacral vertebra of *Pyramiodontherium bergi* (MLP 2–66) is partially unfused according to Roth (1911). However, as the pelvis of the latter specimen is now lost, Roth's observation cannot be verified. The tail of MUSM 15 is known from the last 12 caudal vertebrae (Text-fig. 2T). The most anterior complete vertebra of this series apparently corresponds to the seventh caudal vertebra of *M. americanum*, based on Owen's (1855, pl. 17) illustrations. Part of the sixth caudal vertebra is also preserved, as is the hemal arch between the twelfth and thirteenth vertebrae. The last caudal vertebra is 'cloverleaf-shaped'. This individual did not possess hemal arches between the thirteenth and eighteenth caudal vertebrae which is usual in Megatheriinae. The thirteenth and fourteenth caudal vertebrae preserve a pathological fusion of their neural processes. Pathologies of the axial skeleton are common in ground sloths (Ferigolo 1983, 1987; McDonald 1989). Several ribs are present for the specimens but are not diagnostic. The vertebrae are not diagnostic except for the atlanto-axial joint.

Forelimb. The scapula and clavicle of MUSM 15 are too fragmentary to be informative. They are not preserved in UNA V2642.

Humerus. Only the distal epiphysis and the distal part of the diaphysis of both humeri are preserved (MUSM 15, Text-fig. 2C–D). The deltopectoral ridge (Stock 1925; Hirschfeld 1971, 1985; De Iuliis 1996, 2001) on the anterior surface, is not very prominent. The musculospiral groove, which might represent 'un vestige de la gouttière de torsion' (Hoffstetter 1952, p. 64) and the origin of the brachialis anticus muscle (Hirschfeld 1985), are moderately developed. The distal epiphysis of the humerus is stocky and the lateral epicondyle is short and well developed laterally.

Ulna. The proximal epiphysis expands transversely (Text-fig. 2E–F) and the elongated and slender olecranon process is reduced as in all Megatheriinae (De Iuliis 1996). The proximal articular surface is composed of two humeral facets: the large trochlear notch and the small facet for the humeral capitulum. Distal to the latter lies the small and almost flat facet for the head of the radius. In lateral view the diaphysis is rectilinear and transversely compressed, as in all megatheriines. The distal epiphysis is massive and does not contact the carpus.

Radius. The head is circular and the facet for the humerus is concave and shallow. In posterior (or anterior) view the lateral and medial sides of the shaft are slightly concave (Text-fig. 2G–H). The radius widens distally. The distal epiphysis is oriented markedly posteriorly and the styloid process is prominent. The anterior side of the distal epiphysis bears three grooves for the passage of tendons of muscles of the antebrachium. The medial groove (medial to the styloid process) is for the abductor pollicis longus, the central one for the extensor digitorum communis, and the lateral one for the extensor digitorum lateralis. The distal epiphysis bears two facets: a medial one for the scaphoid and a lateral one for the lunar.

Scaphoid. The morphology of the scaphoid of *Megatherium* and *Eremotherium* is similar to that of other ground sloths. Owen (1858) thought that it was a 'scapho-trapezium' but the trapezium is actually fused to McI (De Iuliis and Cartelle 1993). The scaphoid was described in detail by De Iuliis and Cartelle (1993) in *M. americanum* and *E. laurillardi*. The MCC of *Megatherium* and *Eremotherium* are different and so is the corresponding morphology of the scaphoid. In *M. urbinai* (MUSM 15 and UNA V2642), as in all the *Megatherium* species, the scaphoid is triangular in proximal view and usually bears seven articular surfaces (Text-figs 3A–E, 4A). It articulates proximally and dorsally with the radius, by way of a wide, convex (dorsopalmarly and transversely) facet for the radius.

Distomedially the scaphoid bears, at the extremity of its medial process, a small, circular facet for the MCC. The distal surface bears an articular facet for the trapezoid, two for the magnum, and an accessory facet for the lunar (Text-fig. 4A). The principal facet for the magnum, which lies dorsally, is pedestalled and dorsopalmarly elongated. It is rectangular (MUSM 15, Text-fig. 4A) or oval (UNA V2642) and bordered laterally by the small accessory facet for the
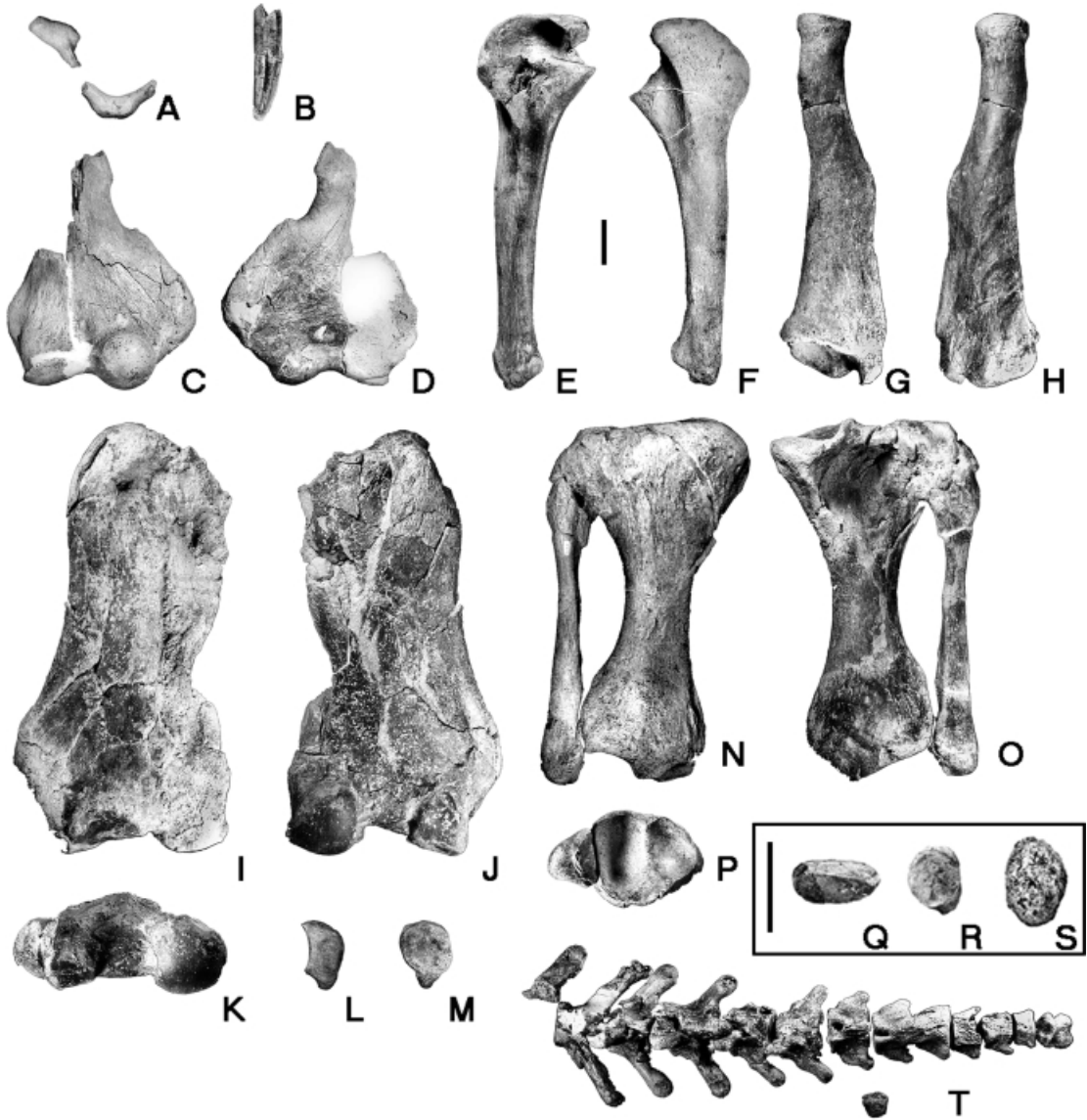
TEXT-FIG. 2. Photographs of selected elements of *Megatherium urbinai* sp. nov., holotype MUSM 15. A, posterior part of the basi-thyrohyal and probably one of the two anterolateral articulations for the ceratohyals in ventral view. B, lower right molariform tooth in lateral view. C–D, distal portion of left humerus in anterior and posterior views, respectively. E–F, right ulna in anterior and posterior views, respectively. G–H, left radius in posterior and anterior views, respectively. I–K, right femur in anterior, posterior, and distal views, respectively. L–M, right patella in lateral and posterior views. N–P, right tibia-fibula in anterior, posterior, and distal views, respectively. Q, lunula in posterior view. R, cyamella in anterodistal view. S, sesamoid bone (fabella?). T, caudal vertebrae in dorsal view and hemal arch in lateral view. Scale bar represents 50 mm.

lunar and medially by the large, triangular trapezoidal facet. The small and circular second facet for the magnum lies palmarly to the principal magnum facet and is separated from it by a deep transverse groove. Laterally the scaphoid bears the crescentic and dorsopalmarly elongated principal facet for the lunar. In proximal view the lateral surface, and thus the facet it carries, is sigmoid.
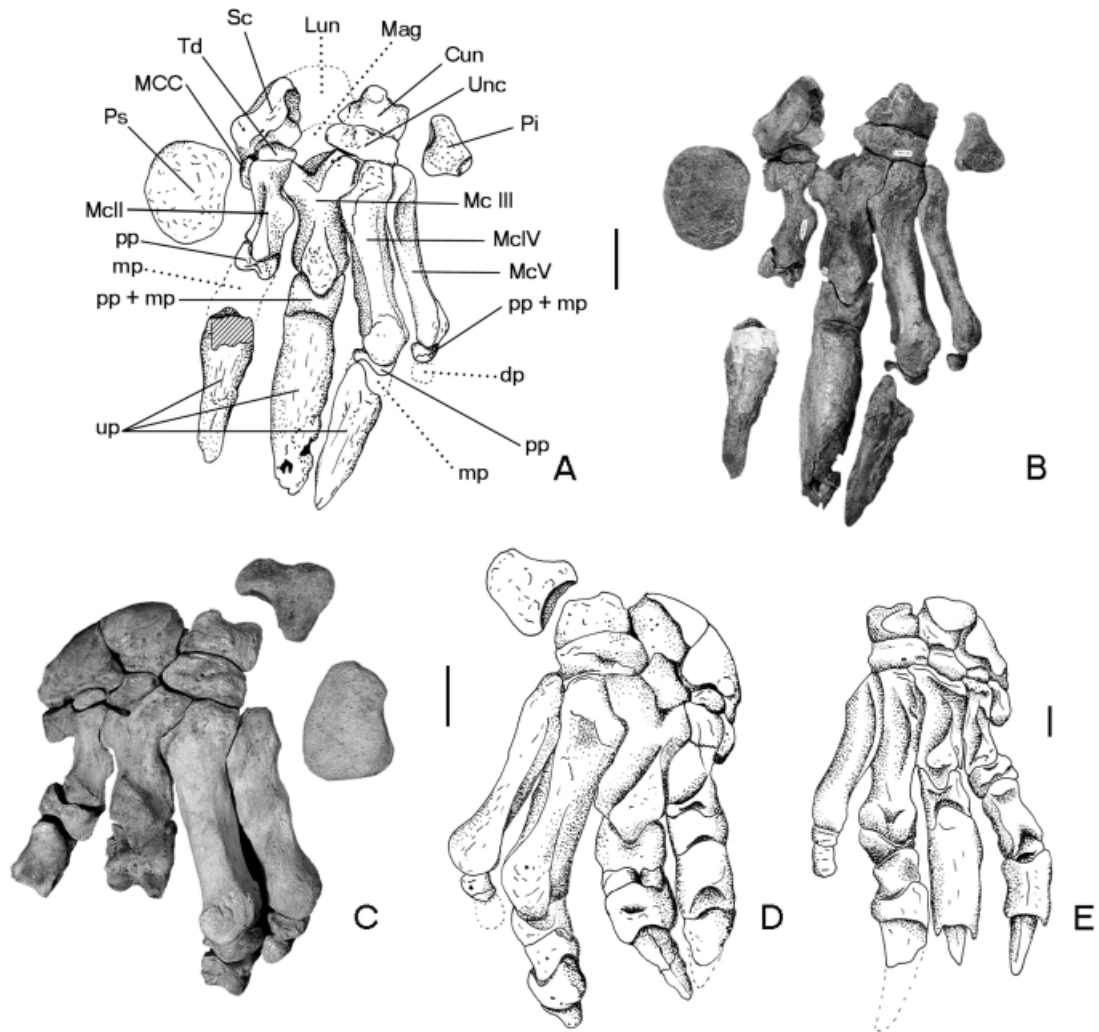
TEXT-FIG. 3. Dorsal views of A–B, right manus of *M. urbinai* sp. nov., holotype MUSM 15, Sacaco, Peru. C, left manus of *M. urbinai* sp. nov., UNA V2642, Tres Ventanas cave, Peru. D, right manus of *M. tarijense*, FMNH P14216; Tarija Formation, Tarija, Bolivia. E, right manus of *M. americanum*, redrawn from Owen 1858. Abbreviations: Cun, cuneiform; dp, distal phalanx; Lun, lunar; Mag, magnum; MCC, metacarpal-carpal-complex; Mc II–III–IV–V, metacarpals 2–3–4–5; mp, middle phalanx; pp + mp, fused proximal and middle phalanges; Pi, pisiform; pp, proximal phalanx; Ps, palmar sesamoid; Sc, scaphoid; Td, trapezoid; Unc, unciform; up, ungual phalanx. Scale bar represents 5 cm.

Lunar. The lunar is similar in all *Megatherium* species. It presents five articulations (Text-figs 3C, 4B). In UNA V2642 the proximal surface is almost entirely covered by the facet for the radius. On the distal surface a dorsopalmar crest separates the facets for the magnum and the unciform (Text-fig. 4B). The dorsal halves of these two facets are convex dorsopalmarly, the medial halves concave. The principal facet for the scaphoid, lightly concave proximodistally, lies on the proximal half of the medial surface. The second small facet for the scaphoid is contiguous with the dorsomedial portion of the facet for the magnum. The deep facet for the cuneiform is contiguous medially with the facet for the unciform and is oriented in the same direction. Its transverse diameter is greater dorsally than palmarly (Text-fig. 4B).

Cuneiform. The distomedial extremity of the cuneiform is missing in MUSM 15 (Text-fig 4C). The cuneiform is rectangular in proximal and dorsal views (Text-figs 3A–C, 4C). The ulna and cuneiform do not articulate in MUSM 15 but do so in UNA V2642. The cuneiform bears three or four articular surfaces. The oval articular facet for the unciform, covering the distal surface, is dorsopalmarly and transversely concave, and mediopalmarly bordered by the lunar facet (Text-fig. 3A–C). The latter is dorsopalmarly extended, occupies the proximomedial angle of the palmar surface, and is dorsally bordered by a deep proximodistal groove. The pisiform facet is located on the proximolateral angle of the palmar surface. It is oval, convex, and proximolaterally to distomedially oriented. The pisiform facet is considerably larger in UNA V2642 than in MUSM 15. The lunar facet is transversely extended and is contiguous with the palmar margin of the cuneiform facet.

Pisiform. The triangular pisiform is located on the palmar surface of the cuneiform, for which it bears an oval and concave articular surface (Text-figs 3A–C, 4D).

MCC. The MCC is rectangular in dorsomedial view. The McII facet (Text-fig. 4J) is quadrangular and dorsopalmarly elongated. The dorsal part of this facet is flat and larger than the palmar part which is palmarly inclined. A small facet for the trapezoid is present proximally and is contiguous laterally with the McII facet (Text-fig. 4J). The scaphoid facet is reduced, oval, and located at the extremity of the bone. It does not contact the facet for McII (Text-fig. 4K). The only difference between the two MCC. of *M. urbinai* is the greater width of the scaphoid facet in UNA V2642.

Trapezoid. The trapezoid is triangular in shape in proximal view (Text-fig. 4E), especially in UNA V2642. It is compressed proximodistally and bears four articular facets (Text-fig. 3A–C). A large portion of the palmar surface is missing in MUSM 15 (Text-fig. 4E). In dorsal view the trapezoid of *M. urbinai* is heavily compressed. The proximal surface, destined entirely for articulation with the scaphoid, is dorsopalmarly concave and transversely convex. As in other *Megatherium* species, in *M. urbinai* the rectangular facet for the magnum is flat, dorsopalmarly elongated, and entirely covers the lateral surface. The distal surface bears a large triangular, dorsopalmarly and transversely convex facet for McII and a small concave facet for the MCC (Text-fig. 4E).

Unciform. Because it is proximodistally compressed and medially bevelled, the unciform appears rectangular in dorsal view (Text-fig. 3A–C). It is considerably more compressed transversely in UNA V2642 than in MUSM 15. The cuneiform facet, which lies on the centre of the proximal surface, is transversely extended and deeply concave dorsopalmarly. The small, flat, and oval lunar facet lies medially and is contiguous with medial third of the cuneiform facet. The distal surface bears the facets for McIII–V and the magnum (Text-fig. 4F). The magnum facet is dorsolaterally to mediopalmarly inclined. Its lower portion is separated from the McIII facet by a deep, wide groove. The McIII facet occupies the medial half of the distal surface. The McIII–V facets are gently convex, contiguous, and are not defined by crests (Text-figs 3A–C, 4F).

Magnum. As in other *Megatherium* species, the magnum is the most complex carpal bone with respect to shape and articular facets. It bears seven articular surfaces that occupy nearly all of the lateral, distal, medial, and proximal surfaces (Text-figs 3C, 4G–I). Its distal part extends into the deeply recessed proximal surface of McIII (Text-fig. 3A–C). The lunar facet (Text-fig. 4G, I) is dorsopalmarly rectangular, dorsally concave, and palmarly convex. The unciform facet, lying between the lunar and McIII facets, is approximately triangular (Text-fig. 4G–H). A deep notch separates the palmar parts of the McIII and unciform facets (Text-fig. 4I). Two scaphoid facets are located proximomedially. The rectangular dorsal facet is larger, and separated from the palmar facet by a deep groove. The palmar scaphoid facet is rounded, inclined palmarly, and close to the lunar facet. The dorsal scaphoid and McIII facets are separated by two small but dorsopalmarly wide facets. The proximal facet is for the trapezoid, the distal for McII (Text-fig. 4G–H).

McII. McII is the shortest of the metacarpals (Text-fig. 3A–C). The proximal epiphysis articulates medially with the MCC, proximally with the trapezoid, proximolaterally with the magnum, and laterally with McIII. The trapezoid facet is deep and larger dorsally than palmarly (triangular in shape in proximal view). The MCC facet, in the shape of a 'figure-8', is deep, oval, elongated dorsopalmarly, and overhung by the dorsomedial portion of the proximal epiphysis. This facet is more inclined palmarly in UNA V2642 than in MUSM 15. The McIII facet is well developed distally. Its proximal half is convex dorsopalmarly and its distal half is concave proximodistally. The medial tuberosity (perhaps for ligamentous attachment with the MCC; De Iuliis 1996) of the proximal epiphysis is well developed. As in other *Megatherium* species, McII of *M. urbinai* bears a distal articulation that is convex dorsopalmarly for the first phalanx. A difference between the two *M. urbinai* specimens is the orientation of the distal epiphysis: it is much more medially oriented in UNA V2642 than in MUSM 15.
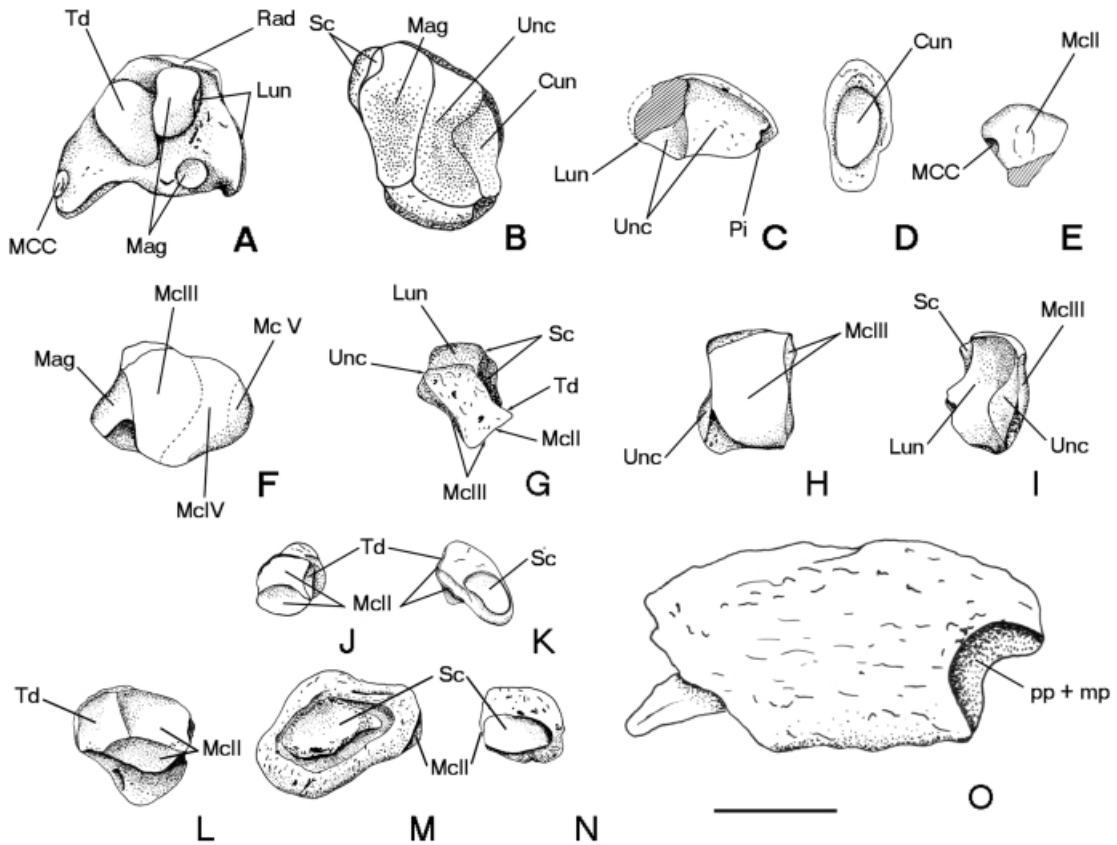
TEXT-FIG. 4. Manus elements of *M. urbinai* sp. nov., *M. americanum*, and *M. tarijense*. A–K, O, *M. urbinai* sp. nov., holotype MUSM 15 except for B, UNA V2642, showing articular surfaces for other elements. A, distolateral view of left scaphoid (dorsal towards top, medial towards left). B, distal view of left lunar (dorsal towards top, medial towards left). C, distal view of left cuneiform (dorsal towards top, medial towards left). D, dorsal view of left pisiform (proximal towards top, lateral towards right). E, distal view of left trapezoid (dorsal towards top, medial towards left). F, distal view of left unciform (dorsal towards top, medial towards left). G–I, dorsal (distal towards top, medial towards left), distomedial (dorsal towards top, medial towards right), and lateral (dorsal towards top, proximal towards left) views of right magnum, respectively. J–K, left MCC in lateral (dorsal towards top, proximal towards right) and proximal (dorsal towards top, medial towards left) views, respectively. O, medial view of right ungual phalanx of digit III (dorsal towards top, proximal towards right). L–M, right MCC of *M. americanum*, MNHN PAM 294, in lateral (dorsal towards top, proximal towards right) and proximal (dorsal towards top, medial towards right) views, respectively. N, left MCC of *M. tarijense*, FMNH P14216, in proximal (dorsal towards top, medial towards left) view. Abbreviations: Cun, cuneiform; Td, trapezoid; Lun, lunar; Mag, magnum; MCC, metacarpal-carpal-complex; Mc II–III–IV–V, metacarpals 2–3–4–5; pp + mp, fused proximal and middle phalanges; Pi, pisiform; Rad, radius; Sc, scaphoid; Td, trapezoid; Unc, unciform. Scale bar represents 50 mm.

McIII. The proximal epiphysis of McIII articulates medially with McII, proximally with the magnum, proximolaterally with the unciform, and laterally with McIV (Text-fig. 3A–C). The magnum facet is very deep, oval, extended dorsopalmarly, and bordered medially and laterally by the McII and unciform facets. The magnum facet is separated from the unciform and McII facets by high crests. The unciform facet is narrow and dorsopalmarly rectangular. Its dorsal half is concave transversely. Its palmar half is concave transversely and bordered distally by the long McIV facet. The McII facet is reduced, crescentic, and concave dorsopalmarly. The McIV facet is elongated proximodistally and concave dorsopalmarly. The proximal epiphysis is Y-shaped in dorsal view (Text-fig. 3A–C). The distal epiphysis

bears three surfaces for articulation with the proximal phalanx (fused first and second phalanges), the central portion of which forms a rounded keel.

McIV. McIV is the largest of the metacarpals (Text-fig. 3A–C). The proximal epiphysis articulates proximomedially with McIII, proximolaterally with the unciform, and laterally with McV. The McIII facet is broader than the unciform facet and inclined proximomedially. All the proximal facets are deeply concave. The diaphysis is long and robust. In distal view the phalangeal surface is inclined dorsomedially to lateropalmarly. The keel of the distal epiphysis bears two palmar processes. The palmar portion of the distal epiphysis bears a sesamoid facet in both specimens.

McV. McV is long and slender (Text-fig. 3A–C). The proximal epiphysis articulates with McIV proximomedially and the unciform proximally. The facets for these elements are contiguous and slightly concave. McV of UNA V2642 is pathological. The center of the diaphysis bears an osteoarthritic swelling that may be the result of a fracture.

Phalanges. In *Megatherium* the second and fourth digits have three phalanges (Text-fig. 3A–C). The third digit of MUSM 15 bears two phalanges (the first and second are fused). The fifth bears two rudimentary phalanges. The first phalanx of the fourth digit is very compressed proximodistally. Only the ungual phalanges of digits III–V are clawed. The ungual of the third digit is the most massive (Text-fig. 4O). In distal view the central part of the ungual (which in life supported the horny claw) of the second digit is flat on MUSM 15. The ungual phalanx of the fourth digit is triangular.

Palmar sesamoid of falciform. The sesamoid, located between McII–IV (Cabrera 1929), is nearly circular and transversely extended (Text-fig. 3A–C). Its palmar side is convex and the central part of the dorsal side is concave transversely for the metacarpals.

Hindlimb

Femur. The femur of MUSM 15 is flat (Text-fig. 2I–K) and compressed anteroposteriorly as in all Megatheriinae. The head and medial surface are missing in MUSM 15. The femur is moderately robust. As the diaphysis is highly distorted, it is impossible to estimate with accuracy its degree of torsion. The lateral side is slightly curved (Text-fig. 2I–J). The greater trochanter is moderately developed, which reflects the slight curvature of the lateral side of the diaphysis. The medial condyle is poorly developed and the entepicondyle is rounded. The distal epiphysis is flattened anteroposteriorly (Text-fig. 2K). The lateral condyle is extended anteroposteriorly and strongly convex. The patellar trochlea is nearly flat and contiguous distolaterally with the lateral condyle.

Patella. The anteroposterior diameter of the patella of MUSM 15 is short compared to the specimen from Celendín (MUSM 157) and may be related to the development of the ligaments and the age of the specimens (Text-fig. 2L–M). The posterior surface bears the femoral facet, which is longer than wide in MUSM 15 and wider than long in UNA V2642. The apex is slender and central.

Tibia-fibula. The right tibia and fibula of MUSM 15 are complete but highly flattened anteroposteriorly. They are fused proximally (Text-fig. 2N–O) as in all Megatheriinae. The proximal surface is badly crushed. The medial femoral facet is highly concave, oval, and anteroposteriorly expanded. The lateral femoral facet is convex, narrow, and elongated in the same direction as the medial facet. The facets are separated by the deep intercondylar area, which is perforated by several arterial foramina. The anterior and posterior intercondylar areas of the tibia, which served for attachment of meniscal ligaments, are not prominent. The tibia and fibula of MUSM 15 are rectilinear (Fig 2N–O). The tibia and fibula are unfused distally. The medial malleolus is short and developed posteriorly. The lateral malleolus is truncated by the presence of the triangular fibular facet. The articular facet for the astragalus occupies the entire distal surface of the tibia (Text-fig. 2P). It is composed of the rounded anteromedial portion for the odontoid process and the oval lateral portion for the discoid surface of the astragalus. The discoid facet is oriented anteroposteriorly and not anterolaterally to posteromedially, in contrast to the condition in other *Megatherium* species. Posteriorly, the medial half of the distal epiphysis bears the origin of the semimembranosus muscle (Text-fig. 2O). This attachment area is similar to that described in the Scelidotheriinae by McDonald (1987). The fibula is slender, with a rectilinear diaphysis. Its distal epiphysis is well developed anteroposteriorly (Text-fig. 2N–O). Two crests, probably for the origin of the extensor muscles, are located on its medial border.
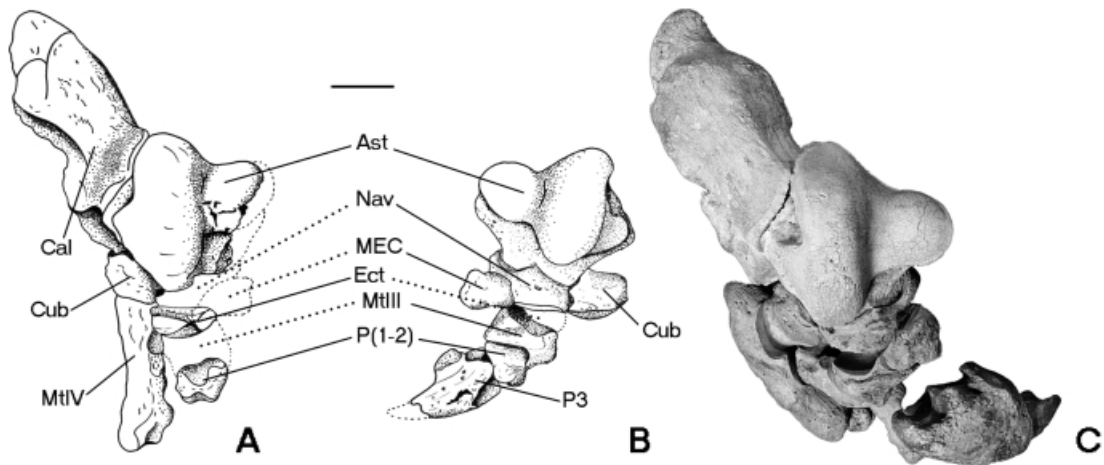
TEXT-FIG. 5. Dorsal view of pes of *M. urbinai* sp. nov: A–B, MUSM 15, holotype from Sacaco, right pes (posterior towards top, medial towards right) and left pes (posterior towards top, medial towards left), respectively. C, UNA V2642, right pes (posterior towards top, medial towards right). Abbreviations: Ast, astragalus; Cal, calcaneum; Cub, cuboid; Ect, ectocuneiform; MEC, mesocuneiform-entocuneiform-complex; Mt III–IV, metatarsals 3–4; Nav, navicular; P (1–2), fused proximal and middle phalanges; P3, distal ungual phalanx. Scale bar represents 50 mm.

Sesamoids of the knee joint. Three sesamoid bones for the knee joint were recovered (Text-fig. 2Q–S). Recently, sesamoid bones and ossified menisci of the knee joint have been discovered in position in a skeleton of *Thalassocnus natans* (Salas *et al.* 2002). Those of *M. urbinai* sp. nov. are described based on the sesamoids of *Megatherium americanum*, described by Pearson and Davin (1921). The lunula is a crescentic wedge with concave proximal and distal articular facets (Text-fig. 2Q). It is probably located in the anterior femoro-tibial articulation. The cyamella is button-shaped and bears a single articular facet (Text-fig. 2R). This sesamoid is generally located on the posterior margin of the lateral femoral facet of the tibia. A third sesamoid without articular facet has been recovered (Text-fig. 2S). It could be the fabella, a femoral sesamoid located posteriorly to the femoral condyles.

The elements of the pes are described with reference to their orientation in the pedolateral stance, following McDonald (1987).

Astragalus. The trochlea tali includes the medial (odontoid) and discoid facets (Text-figs 5A–C, 6A). The odontoid facet is short, bulky, and supported by the prominently raised odontoid process (Text-fig. 6A). The odontoid process is much bulkier in MUSM 15 than in UNA V2642. In both specimens the discoid facet is elongated anteroposteriorly and convex in dorsolateral view. The triangular fibular facet is contiguous with the distal half of the lateral margin of the discoid facet. The caput tali supports the dorsolaterally to medioplantarly oriented navicular facet, which is concave proximally and convex distally (Text-fig. 6A). The small, convex cuboid facet lies along the distomedial part of the navicular facet and appears continuous with it. Distally the astragalus bears two calcaneal articulations that are generally separated in Megatheriinae. The small and elongated sustentacular facet appears as an extension of the cuboid facet. The sustentacular and ectal facets are separated by the broad and deep sulcus tali in MUSM 15 (Text-fig. 6A). In UNA V2642 the calcaneal facets are partially fused. In MUSM 15 the ectal facet and sulcus tali are oriented approximately posteromedially to anterolaterally. The sustentacular facet bears a double convexity. The ectal facet is concave anteroposteriorly and convex transversely. In distal view the lengths of discoid and odontoid facets are equal in both specimens of *M. urbinai*. One third of the dorsomedial portion of the navicular facet is located above the level of the discoid facet in MUSM 15 (15 per cent in UNA V2642). The angle between the discoid and odontoid facet is 108 degrees in MUSM 15 and 115 degrees in UNA V2642.

Calcaneum. The calcaneum of Megatheriinae is elongated and 'shell-shaped' (Text-fig. 5A–C). The plantar portion of the anterior epiphysis is absent in MUSM 15. The tuber calcanei is short and tuberous. The diaphysis is bulky and constricted by two prominent sulci: one medial for the flexor hallucis longus muscle and one lateral for the peroneus muscle. The anterior surface bears the dorsal ectal facet, the medial sustentacular facet, and the plantar cuboid facet.
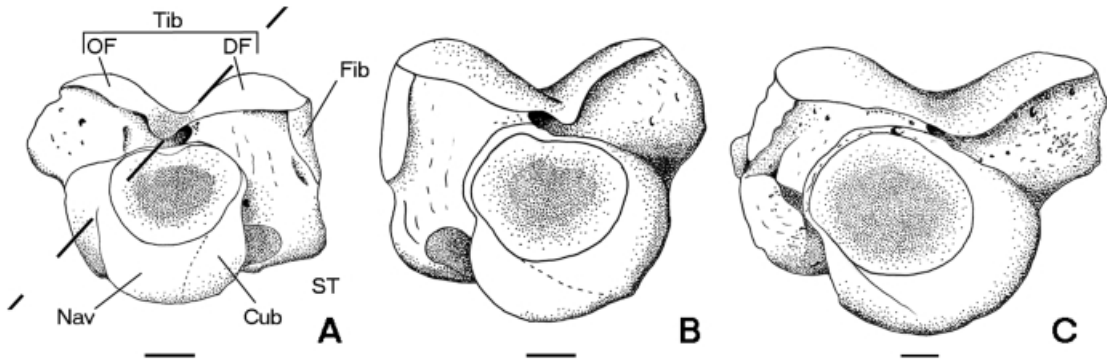
TEXT-FIG. 6. Astragalus in anterior view of A, *M. urbinai* sp. nov., holotype MUSM 15 (dorsal towards top, lateral towards right); B, *M. tarijense*, FMNH P14216 (dorsal towards top, lateral towards left); C, *M. americanum*, MNHN PAM 295 (dorsal towards top, lateral towards left). Abbreviations: Cub, cuboid; DF, discoid facet; Fib, fibula; Nav, navicular; OF, odontoid facet; ST, sulcus tali; Tib, tibia. Dashed line represents the plane of the discoid facet. Scale bar represents 20 mm.

The ectal facet is elongated dorsomedially to lateroplantarly. The ectal and sustentacular facets are separated by the sulcus calcanei in MUSM 15 but not in UNA V2642. The sustentacular facet is elongated dorsoplantarly and continues transversely to the lateral surface. This facet, rounded as in other Pleistocene megatheriines, is bordered plantarly by the cuboid facet.

Cuboid. The cuboid is compressed anteroposteriorly (Text-fig. 7A). Its lateral surface bears the contiguous and convex MtIV–V facets (Text-fig. 7A–B). The MtV facet occupies the dorsoposterior half and the MtIV facet the anterior half of the lateral surface. The posteromedial surface presents, posteriorly to anteriorly, the contiguous calcaneal, astragalar, and navicular facets (Text-fig. 7A). The latter is flat and occupies the mediodorsal corner. The large astragalar facet is concave and the calcaneal facet is an elongated, dorsoplantarly oriented strip. The dorsal third of the calcaneal facet is weakly concave; its plantar two-thirds are strongly convex. A deep notch limits the anteriomedial surface dorsoplantarly and separates the navicular and MtIV facets.

Navicular. The navicular is rectangular and compressed anteroposteriorly (Text-fig. 7C–E). The long axis extends dorsolaterally to medioplantarly (Text-fig. 7D–E). The astragalar facet occupies the entire posterior surface. Its dorsolateral half is a convex condylar tuberosity and its medioplantar half is concave in both directions. The badly damaged dorsal part of the lateral surface preserves the cuboid facet. Both cuneiform facets are lightly convex and U-shaped. The ectocuneiform facet is triangular and contiguous medially with the rectangular MEC facet.

Ectocuneiform. The ectocuneiform is compressed anteroposteriorly and triangular in anterior view (Text-fig. 7F–H). The navicular facet is concave in both directions and occupies the entire posterior surface (Text-fig. 7G). The anterior surface bears the MtIII-IV facets (Text-fig. 7H), which are convex in both directions. An MEC facet occupies the dorsomedial corner of the navicular facet. It is contiguous medially with the MtIII facet (Text-fig. 7F–G). In MUSM 15 the MEC facet of the medial side overhangs a deep dorsoplantar groove.

MEC. The MEC is triangular, with its apex oriented medially (Text-fig. 7K–L). The sigmoid navicular facet occupies the entire anterolateral surface. The dorsolateral corner of the anterolateral surface is occupied by the reduced ectocuneiform facet in MUSM 15. This facet is prolonged on the anterior surface by the MtIII facet, which is generally flat and crescentic. The MEC of UNA V2642 bears a different arrangement: the ectocuneiform facet is absent and the MtIII facet is oval and separated from the navicular facet. The medial portion of the MEC is tuberous and bears several vascular foramina in both specimens.

MtIII. MtIII is extremely short and only the lateral half of the posterior epiphysis is developed anteriorly (Text-fig. 5B). MtIII of MUSM 15 is distorted and the dorsal portion of its lateral surface is not preserved. The triangular and concave ectocuneiform facet occupies nearly all the posteromedial articular surface. This facet is much more medial in UNA
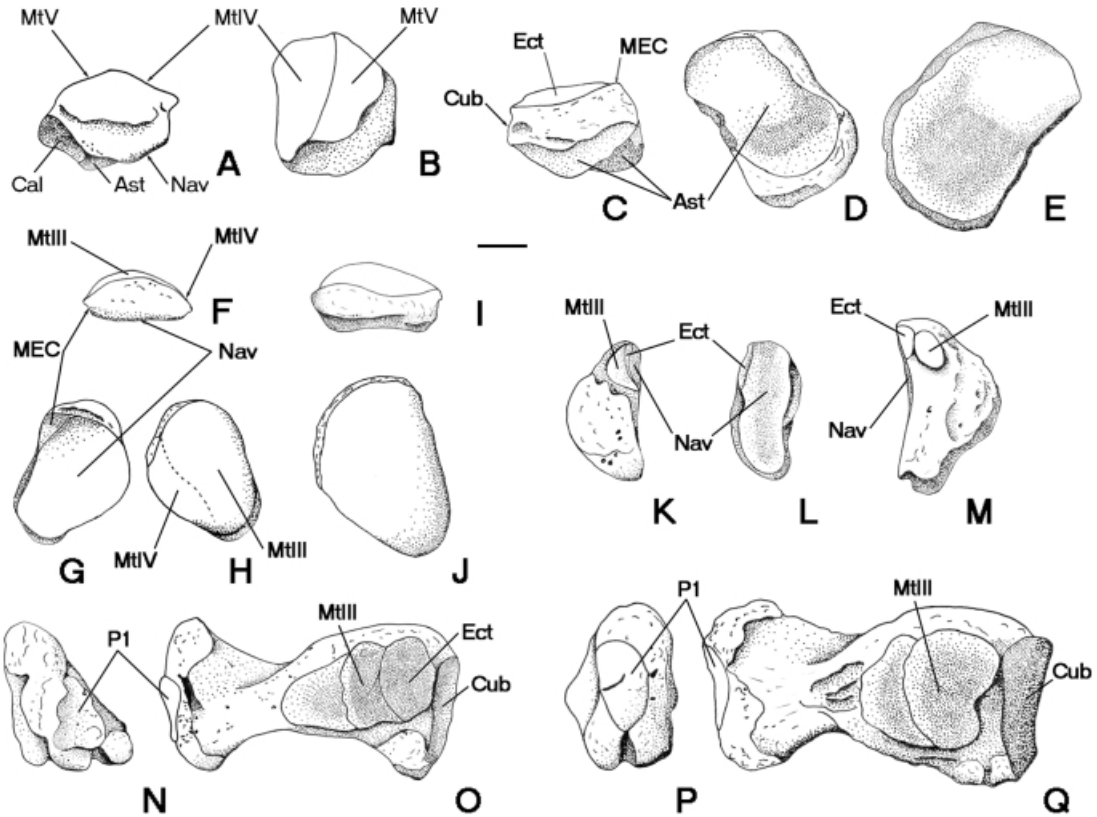
TEXT-FIG. 7. Pes elements of *M. urbinai* sp. nov., holotype MUSM 15 from Sacaco, and *M. tarijense*, FMNH P14216. *M. urbinai* sp. nov.: A–B, left cuboid in dorsal (anterior towards top, medial towards right) and anterolateral (dorsal towards top, anteromedial towards left) views, respectively. C–D, left navicular in dorsolateral (anterior towards top, dorsomedial towards right) and posterior (dorsal towards top, medial towards right) views, respectively. F–H, right ectocuneiform in dorsomedial (anterior towards top, dorsolateral towards right), posterior (dorsal towards top, lateral towards right), and anterior (dorsal towards top, lateral towards left) views, respectively. K–L, left MEC in anterior (dorsal towards top, posterior towards right) and anterolateral (dorsal towards top, lateroposterior towards right) views, respectively. N–O, right Mt IV in anterior (dorsal towards top, medial towards right) and medial (dorsal towards top, posterior towards right) views. *M. tarijense*: E, right navicular in posterior (dorsal towards top, lateral towards right) view. I–J, right ectocuneiform in dorsomedial (anterior towards top, dorsolateral towards right) and anterior (dorsal towards top, lateral towards left) views, respectively. M, right MEC in anterior (dorsal towards top, posterior towards left) view. P–Q, right Mt IV in anterior (dorsal towards top, medial towards right) and medial (dorsal towards top, posterior towards right) views, respectively. Abbreviations: Ast, astragalus; Cal, calcaneum; Cub, cuboid; Ect, ectocuneiform; MEC, mesocuneiform-entocuneiform-complex; Mt III–IV–V, metatarsals 3–4–5; Nav, navicular; P1, proximal phalanx. Scale bar represents 20 mm.

V2642 than in MUSM 15. The medial edge of the MEC facet is contiguous with the central part of the ectocuneiform facet, without anterior contact with the phalangeal facet. The MtIV facet is roughly oval with long axis oriented dorsoplantarly. MtIII is strongly twisted and inclined laterally. The U-shaped phalangeal facet lies centrally. The distal side bears two dorsal (central and medial) and three plantar (lateral, central, and medial) tuberosities. These tuberosities allow a tightly interlocking articulation with the phalanx.

MtIV. MtIV is elongated and its diaphysis is strongly twisted (Text-fig. 7N–O). The cuboid facet is regularly concave, oval, and oriented dorsolaterally to medioplantarly in both specimens. In MUSM 15 a double facet occupies the

posterior portion of the medial diaphyseal surface (Text-fig. 7O). This large facet is formed by fusion of two oval and concave facets. The posterior one corresponds to that for the ectocuneiform and the anterior one for MtIII. In UNA V2642 the facet for the ectocuneiform is smaller than in MUSM 15. The MtV facet is oval, convex in both directions, and borders the lateral side of the cuboid facet. A large and powerful plantar process supports the posterior epiphysis. The distal epiphysis is strongly twisted (25 degrees with regard to the dorsoplantar axis) in MUSM 15 and the distal plantar process is trifid (Text-fig. 7N). The diaphysis is also twisted in UNA V2642 but the plantar portion of the distal epiphysis is bifid.

Phalanges. In Megatheriinae the first and second phalanges of the third digit are ankylosed (Text-fig. 5B) and only the third posterior digit is clawed (Text-fig. 5B–C). The fourth and fifth digits possess extremely reduced proximal and distal phalanges. As in *M. americanum*, the claw of the third digit of *M. urbinai* is shorter and the plantar process more developed than in *M. tarijense*.

COMPARISON AND DISCUSSION

In the following discussion character polarity is evaluated on the basis of the condition in *Hapalops*, a genus commonly regarded as a generalized Tardigrada. Except for *Eremotherium eomigrans* (first megatheriine ground sloth known in North America from the end of the Pliocene; De Iuliis and Cartelle 1999), all the pre-Pleistocene Megatheriinae were discovered in Argentina: *Promegatherium* Ameghino, 1885; *Megathericulus* Ameghino, 1904; *Plesiomegatherium* Roth, 1911; *Pyramiodontherium* Rovereto, 1914; *Megatheriops* Ameghino, 1921; *Paramegatherium* Kraglievich, 1925; *Megatheridium* Cabrera, 1928, and *Pliomegatherium* Kraglievich, 1930; and in the upper Miocene (Friasian) of Colombia: Megatheriinae gen. and sp. indet. (Hirschfeld 1971, 1985; Hirschfeld and Marshall 1976).

McKenna and Bell (1997) and De Iuliis (1996) considered *Paramegatherium* a junior synonym of *Megatherium*. The type of *Megatheriops* (MACN 2818, skull and humeri) is clearly distinct from *Pyramiodontherium* (De Iuliis 1996; F. Pujos, pers. obs. 2000; contra McKenna and Bell 1997). Two genera, the temperate *Megatherium* Cuvier 1796 and the intertropical *Eremotherium* Spillmann, 1948, are currently recognized in the South American Plio-Pleistocene. The Pleistocene genus *Perezfontanatherium* Roselli, 1976 is probably a junior synonym of *Eremotherium laurillardi* or *Megatherium americanum*.

The genus *Megatherium* is typically from the Plio-Pleistocene of the lower and middle latitudes of South America. The best known species are *M. americanum* Cuvier, 1796 (southern South America) and *M. tarijense* Gervais and Ameghino, 1880 (Bolivian Altiplano, Tarija Formation). *M. elenense* Hoffstetter, 1949 (Santa Elena Peninsula, Ecuador, in Hoffstetter 1949, 1952; and Talara Tar Pits, northern Peru, De Iuliis 1996) may be valid but its remains are fragmentary. *M. medinae* Philippi, 1893 (from Pampa del Tamaragual, Tarapacá Province, Chile) is known from several skulls, mandibles and some postcranial elements (Philippi 1893; Casamiquela and Sepulveda 1974; Marshall and Salinas 1991). Following Casamiquela and Sepulveda (1974), Marshall and Salinas (1991) synonymized *M. sundti* Philippi, 1893 (incomplete mandible from Ulloma, Bolivia) with *M. medinae*. *M. tarijense* and *M. medinae* were considered as possibly conspecific because they are similar in size and geographical provenance, and apparently possess no easily distinguishable differences. We follow De Iuliis (1996) in considering *M. sundti* Philippi, 1893 (Ulloma, Bolivia) and *M. nazarrei* Kraglievich, 1925 (Neuquén Province, Argentina) as probably valid but unfortunately are known so far only from an incomplete mandible and scanty remains of one individual, respectively. Werdelin (1991) followed Hoffstetter (1963) in considering *M. tarijense* a junior synonym of *M. americanum*. The re-examination of FMNH P14216 of *M. tarijense*, however, clearly reveals differences between it and *M. americanum*. New material is necessary to confirm the validity of all the *Megatherium* species except *M. americanum*, *M. tarijense*, *M. altiplanicum*, and the new Peruvian taxon presented below.

To date, both *Megatherium* and *Eremotherium* are known from Peru (Lisson 1912; Hoffstetter 1970, 1986; Marshall *et al.* 1984) but often from poor remains that have not been properly described. The remains of *M. urbinai* provide the opportunity for the first detailed description of a Peruvian Megathere.

In *M. urbinai* (MUSM 15) the degree of hypsodonty (estimated with depth of the horizontal ramus of the dentary and/or depth of the molariforms) is similar to that of *M. tarijense* and less than that of *M. americanum* (MNHN mounted specimen) and *M. altiplanicum* (St-André and De Iuliis 2001). The

dectopectoral ridge of the humerus of MUSM 15 (Text-fig. 2C) is fragmentary but not particularly prominent, as also occurs in other *Megatherium* species (derived state, character 8 of De Iuliis 1996). It is more prominent in *Eremotherium laurillardi* (ROM 19756 and ROM 22101) and especially so in *Megatheriops rectidens*. *Hapalops* (Scott 1903), *Planops* (Hoffstetter 1961), and *Megatheriops* (MACN 2818) possess a strong crest, which is clearly the plesiomorphic condition. The musculospiral groove and the origin of the brachialis anticus muscle of the humerus of *M. urbinai* (Text-fig. 2C–D) are similar to those of *M. americanum* (MNHN AC7013, MLP 2–72, and MLP 2–79) and *M. tarijense* (FMNH P14216). The supracondylar notch is deeper and the proximal area of attachment more rugose in *E. laurillardi* (ROM 22098 and ROM 22099), but practically absent in *M. sundti* (PIU M4530 in De Iuliis 1996, fig. 67D). In *M. urbinai* the distal epiphysis of the humerus is bulky and the ectepicondyle is short (Text-fig. 2C–D), contrary to the conditions in *E. laurillardi*.

The radius and the ulna of *M. urbinai* (Text-fig. 2E–H) are relatively elongated and slender as in all the Megatheriinae (De Iuliis 1996). The prominence of the olecranon process of the ulna varies among *Megatherium* species. The olecranon process is bulky in *M. americanum* but elongated and slender in *M. tarijense* and *M. urbinai* (Text-fig. 2E–F). The ulnar diaphysis of *M. urbinai* (MUSM 15 and UNA V2642) is rectilinear as in all Megatheriinae. On the other hand, the diaphysis of the ulna is posteriorly bent in the primitive sloth *Hapalops longipes* (Scott, 1903). The lateral and medial sides of the shaft of the radius are slightly concave in *M. urbinai* (Text-fig. 2G–H) as in *M. americanum* (MLP 28-31-6-2), *M. tarijense* (FMNH P14216), and *M. altiplanicum* (St-André and De Iuliis 2001). They are parallel in *E. laurillardi* (ROM 22107 and 22106). The proximal half of the diaphysis of *M. elenense* (EPN V 159 in Hoffstetter 1949, fig. 9) and *M. altiplanicum* (St-André and De Iuliis 2001, fig. 6) is much more slender than in other *Megatherium* species and resembles that of *E. laurillardi*. The radius of *M. altiplanicum* is extremely slender and highly similar to that of *M. elenense*. In these, particularly *M. elenense*, the transverse diameter of the distal half of the radius is clearly less than in *M. urbinai* (Text-fig. 2G–H). The distal epiphysis of the radius is, as in *M. altiplanicum*, oriented posteriorly to a greater degree than in *E. laurillardi*, *M. tarijense*, and *M. americanum*. The styloid process of *M. urbinai* is slightly shorter than in *M. tarijense* and *M. altiplanicum*. In *M. tarijense* (FMNH P14216) the central and, especially, medial grooves for the passage of tendons of muscles of the forearm are less deep than in *M. urbinai* (Text-fig. 2H).

The manus of the two specimens of *M. urbinai* are practically complete and identical (Text-fig. 3A–C). They show the same general morphology as that known for *M. tarijense* (Text-fig. 3D) and *M. americanum* (Text-fig. 3E), namely four complete and functional digits (II–V) and an MCC composed of the trapezium and McI (De Iuliis and Cartelle 1993; Cartelle and De Iuliis 1995; De Iuliis 1996). The manus of the tropical genus *Eremotherium* has two morphologies. In *E. laurillardi* it includes three complete and functional digits (III–V), and an MCC composed of the trapezium, trapezoid, and McI–II (Cartelle 1992; De Iuliis and Cartelle 1993), which represents, in Megatheriinae, the most derived state. In *E. eomigrans* the manus has five complete and functional digits (I–V), and an MCC composed of the trapezium and McI, and occasionally the trapezoid as well (De Iuliis and Cartelle 1999), which suggests that 'digital reduction was acquired independently in *E. laurillardi* and *M. americanum*' (De Iuliis and Cartelle 1999, p. 512). The genus *Megatherium* presents an intermediate state between the five functional digits of *E. eomigrans* (a probable plesiomorphic state for the subfamily) and the three functional digits of *E. laurillardi* (most derived state). It is difficult to observe the contacts between the carpals and/or metacarpals for *M. tarijense* (FMNH P14216) because the elements of the manus are glued together (F. Pujos, pers. obs. 2001). The proximal carpal row, scaphoid, lunar, pisiform, cuneiform, and magnum are not diagnostic because they are subject to considerable intraspecific variation. For example, in four adult specimens of *E. laurillardi* from the same site of Daytona Beach (ROM 21885, 21887, 27318, and 37050) the size of the scaphoid changes by approximately 30 per cent and the position and form of the articular facets change as well (MCC and trapezoid facets are contiguous in ROM 21885, separate in ROM 21887; in distal view the lateral facet for the lunar is sigmoid in ROM 27318 and ROM 37050, convex in ROM 21887). The general morphology of this bone varies as well (transversely expanded in ROM 27318 and ROM 37050, proximodistally expanded in ROM 21887 and ROM 21885). The other carpals, such as the lunar and magnum, show similar ranges of variation. A similar range occurs in *M. tarijense* (FMNH P14216), some specimens of *M. americanum* (such as MNHN PAM 294), and *M. urbinai*. However, diagnostic characters

are present on the MCC (and on the trapezoid in relation with the morphology of the MCC), McII–III, the unciform, and the ungual phalanges. Unfortunately, manus elements are not preserved in older Megatheriinae (*Pyramiodontherium* MLP 2-66, *Megathericulus* MLP 2-203, *Megatheriops* MACN 2818, *Plesiomegatherium* MACN 2895 and MLP 26-IV-10–1) to shed possible light on the most primitive megatheriine condition, as the Pleistocene forms are highly specialized compared to other ground sloths.

The principal lunar surface of the scaphoid is crescentic, as in *M. americanum* (MNHN PAM 294). This surface is rounded in *M. tarijense* (FMNH P14216) and *M. elenense* (Hoffstetter 1949, fig. 10). In the scaphoid of *M. americanum* the palmar facet for the magnum and the principal lateral facet for the lunar may be palmarly fused (MNHN PAM 294) or unfused (MLP 2-29; De Iuliis and Cartelle 1993, fig. 3). The MCC facet of the scaphoid is more reduced in *M. urbinai* (particularly in MUSM 15) than in *M. tarijense* and *M. americanum*. The lunars of *M. urbinai* (UNA V2642), *M. tarijense* (FMNH P14216), and *M. americanum* (MNHN PAM 294) are very similar. The facets located on the distal surface of the lunar (for the magnum and unciform) are deeper in *M. americanum* than in *M. urbinai*. In MUSM 15, as in all Megatheriinae according to Hoffstetter (1952) and De Iuliis (1996), the ulna and cuneiform do not form an articular contact. However, a specimen of *M. americanum* (MNHN PAM 294) and one of *M. urbinai* (UNA V2642) shows a slight contact between the two bones. Except for this very occasional ulna-cuneiform articulation, the megatheriine cuneiform generally bears three articulations only for the unciform, the lunar, and the pisiform. In *M. urbinai* and *M. americanum* the proximal and distal sides of the cuneiform are parallel, contrary to the condition in *M. tarijense* where they converge and join medially.

Compared to *E. laurillardi*, the MCC of *Megatherium* is smaller and less complexly shaped. In *M. urbinai* (Fig. 4J–K) the MCC is less massive than that of *M. tarijense* (Text-fig. 4N; De Iuliis and Cartelle 1993, fig. 5) and, especially, that of *M. americanum* (Text-fig. 4L–M; Owen 1858, fig. 22). The MCC of *M. urbinai* is rectangular in dorsomedial view, as in *M. americanum*, but square in *M. tarijense*. The morphology of the McII facet of the MCC is similar in *M. urbinai* and *M. tarijense* (Text-fig. 4K, N). The trapezoid facet of the MCC is reduced and contiguous laterally with the McII facet in *M. urbinai* (Text-fig. 4J–K) and *M. tarijense*, but in *M. americanum* (Text–fig. 4L) the position and shape of the three facets are clearly distinct. In the latter the trapezoid facet is much more prominent than in *M. tarijense* and *M. urbinai*, and the palmar part of the McII facet is completely palmar and located between the dorsal part of the McII facet and the trapezoid facet (Text-fig. 4J–N). The maximal dorsopalmar length of the MCC occurs laterally in *M. urbinai* and medially in *M. americanum* (Text-fig. 4M). In *M. americanum* and *M. tarijense* (Text-fig. 4M–N) the facet for the scaphoid is large, in contrast to that in *M. urbinai*, especially MUSM 15 (Text-fig. 4K). This facet contacts the McII facet in *M. tarijense* (Text-fig. 4N), but not in *M. americanum* (Text-fig. 4M). The MCC is a small element but its morphology apparently varies little, and thus seems diagnostically useful in differentiating *Megatherium* species. The trapezoid in *M. tarijense* (FMNH P14216) and particularly *M. urbinai* are more proximodistally compressed than in *M. americanum*. This species presents a reduced surface for the McII and a well-developed MCC facet, in contrast to *M. urbinai* and *M. tarijense*. The morphology of the medial surface of the trapezoid of *M. americanum* is related to the proximal development of the MCC. Moreover, the McII facet of the trapezoid of *M. americanum* is not triangular but deformed by the large MCC facet, in contrast to the condition in *M. urbinai* and *M. tarijense*. In *M. urbinai* the central crest of the anterior McIII facet of the magnum is convex as in *M. tarijense*. In *M. americanum* this crest is clearly sigmoid owing to the absence of the proximomedial branch of McIII (Text-fig. 3E). The unciform is diagnostic in Megatheriinae according to De Iuliis (1996). The marked proximodistal compression of the unciform and the relatively large facet for the McV are the diagnostic features of *E. laurillardi* (De Iuliis 1996). The McV facet of *M. urbinai* (Text-fig. 4F) is less laterally oriented than in *M. tarijense*, *M. elenense* (ROM 10404), and *M. americanum*. In these species the metacarpal facets are separated from one another by prominent dorsopalmar crests. The absence of crests between the metacarpal facets of the unciform is autapomorphic in *M. urbinai* (Text-fig. 4F).

The magnum of *M. urbinai* is very similar to that of *M. tarijense* (FMNH P14216) and *M. americanum* (MNHN PAM 294), although it is more massive in the latter. In *M. urbinai* the distal crest located at the

center of the McIII facet of the magnum is rectilinear. The same condition occurs in *M. tarijense* (FMNH P14216) but not in *M. americanum* (MNHN PAM 294), in which it is sigmoid owing to, as noted above, the absence of a proximomedial branch on McIII (Text-fig. 3E).

The MCC facet of McII differs in *M. americanum* in comparison with that of *M. urbinai*, *M. tarijense*, and *M. elenense* (ROM 3779) because it is related to the morphology of the trapezoid and the MCC (see above descriptions for MCC and trapezoid). The dorsal portion of the proximal epiphysis of McII overhangs the MCC in *M. urbinai* and *M. americanum* but not in *M. tarijense*. The medial tuberosity of McII is more prominent and the diaphysis is less curved in *M. urbinai* and *M. tarijense* than in *M. americanum* (Text-fig. 3A–E). The lateral facet for McIII on McII presents a prominent, central, and dorsopalmar crest that is developed and projects laterally in *M. americanum*. This crest is absent in *M. urbinai* and *M. tarijense*. McIII shows the same development in *M. urbinai* (MUSM 15), *M. americanum* (MNHN PAM 294), and *M. tarijense* (FMNH P14216). It is shorter and more robust in *E. laurillardi* (Hoffstetter 1952; De Iuliis 1996). The McIII of *M. urbinai* (MUSM 15 and UNA V2642) and *M. tarijense* (FMNH P14216) (Text-fig. 3A–D) are Y-shaped as occurs in *Hapalops* (Scott 1903) and the Friasian mylodontid *Pseudoprepotherium* (Hirschfeld 1985). This corresponds to the plesiomorphic state. An I-shaped McIII is clearly autapomorphic in *M. americanum* (Text-fig. 3E). *Eremotherium* shows a partial reduction of the posteromedial branch of the McIII, and thus is intermediate between the conditions of *M. urbinai* and *M. americanum*. The McII facet of McIII is less concave in *M. urbinai* than in *M. americanum*, *M. tarijense*, and *M. elenense*. Therefore, Mcs II–III of *M. americanum* fit tightly together (Text-fig. 3E). They diverge distally in *M. urbinai* (Text-fig. 3A–C), *M. tarijense* (Text-fig. 3D), and apparently *M. elenense* (ROM 3779 and ROM 35033). In these three species the distal epiphysis bears three articular surfaces, of which the central surface is well developed dorsally and palmarly. In *M. americanum* the lateral surface and the palmar part of the central surface are absent. In this species the dorsal processes of the distal and proximal epiphyses, which were probably in contact with the ground, are more medially located compared to the other *Megatherium* species. The diaphysis of McIV is less robust than in *E. laurillardi* (ROM 27306, 37578, and 28856). The proximal epiphysis is generally similar in all *Megatherium* species. It is, however, more developed transversely (rectangular) in *M. urbinai* and *M. tarijense* than in *M. americanum* (square). The dorsal part of the distal epiphysis bears one tuberosity as in *M. tarijense* and not two as in *M. americanum*. The distal epiphysis of McIV of *M. urbinai* bears one sesamoid facet as in all *Megatherium* species, rather than two as in *E. laurillardi*.

McV of *M. urbinai* is much less robust than in *E. laurillardi* (ROM 31452, 30792, and 27321) and less bulky in *M. urbinai* and *M. tarijense* than in *M. americanum* (Text-fig. 3A–E). In the latter the distal epiphysis is more developed laterally than in the other *Megatherium* species. *M. urbinai* bears well-developed anterior ungual phalanges (Text-fig. 4O), as in *M. americanum*. *M. tarijense* is the first Pleistocene megatheriine known to present strong reduction of the anterior claws (and an expansion of the posterior claws). By outgroup comparison, the presence of large anterior claws is probably plesiomorphic for megatheriines. Short claws are, therefore, probably autapomorphic in *M. tarijense*.

M. urbinai is the only *Megatherium* species in which the McIII–V facets of the unciform are convex and joined to one another without demarcation. This suggests that *M. urbinai* was probably capable of increased transverse digital motion than other species for locomotion, defense or acquisition of food. Toledo (1996) and Bargo *et al.* (2000) considered, as have various other authors, that the manus and pes of sloths were twisted inward and that, therefore, these animals walked on their lateral digits, the characteristic pedolateral stance of hind foot (McDonald 1987) of many large Gravigrada. It is clear that Megatheriinae were capable of quadrupedal and bipedal movements (Pujos *et al.* 2002). They possess graviportal adaptations that are clearly distinct from those of other gravigrades such as elephants. The Megatheriinae trackways from Argentina (Aramayo and Manera de Bianco 1996) confirm both types of locomotory modes, with bipedality being more frequent. Digging habits, clearly present in other Gravigrada such as *Scelidotherium* and *Glossotherium* (Vizcaíno *et al.* 2001), seem unlikely in *Megatherium* (Bargo *et al.* 2000). The position of the manus with the ground during locomotion is uncertain in Megatheriinae. The trackways (Aramayo and Manera de Bianco 1996, fig. 2) reveal contact with the ground of at least the lateral faces of digits IV–V of the manus and digits III–V of the pes and suggest an anteater model. A possible locomotory mode which includes knuckle-walking as in gorillas is considered

by Tito and De Iuliis (2001). However, a morphofunctional analysis of Megatheriinae is beyond the scope of this work.

Notable metric and morphological variation in the femur of *E. laurillari* were noted by Cartelle (1992), Cartelle and De Iuliis (1995), and De Iuliis (1996). Similar variations are conceivable in *Megatherium* species, as such variation clearly occurs in the manus elements. The robustness of the femur (character 9 of De Iuliis 1996) of *M. urbinai* (Text-fig. 2I–K) is intermediate between that of primitive ground sloths, such as *Hapalops*, and that of the highly specialized *M. americanum*. The degree of torsion of the femoral diaphysis of *M. urbinai* is less than that of *M. americanum* and *M. altiplanicum*. The lateral femoral margin is less concave (Text-fig. 2I–J) than in *M. americanum* (MNHN PAM 296), *M. sundti* (juvenile, PIU M4530; De Iuliis 1996, fig. 103B–D), and *M. altiplanicum* (St-André and De Iuliis 2001, fig. 7A), but more concave than in *M. tarijense* (FMNH P14216), *M. medinae* (SGO PV231 in Casamiquela and Sepulveda 1974, pp. 111–113), and *E. laurillardi*. We agree with St-André and De Iuliis (2001, p. 637, character 5) that the 'less concave margins are probably plesiomorphic states'. The condition of this character in *M. urbinai* is less specialized than in [*M. americanum* + *M. altiplanicum*]. *M. sundti* is poorly known but its peculiar femoral morphology (De Iuliis 1996, fig. 103B) is distinct from that of other Megatheriinae. The medial condyle is clearly distinct in *M. urbinai* but less prominent than typical of *M. americanum* and *M. altiplanicum*. The entepicondyle is rounded and not extended anteroposteriorly as in *M. tarijense*. In the latter and *M. altiplanicum* (St-André and De Iuliis 2001, fig. 7C) the anterior part of the medial condyle is extended laterally, which results in the closing of the groove between the medial condyle and the patellar trochlea. In *M. urbinai* more than 2 cm separate these articular surfaces (Text-fig. 2K). This character is considered diagnostic with respect to the variations in *E. laurillardi* and *M. americanum*. The development of the patellar trochlea is an informative character in Megatheriinae. It is well developed in *M. urbinai*, resembling that of *M. medinae*, *M. tarijense*, and *M. sundti*. The trochlea is much more reduced in *M. americanum* and *M. altiplanicum* (St-André and De Iuliis 2001, p. 602, character 6). The markedly mediolaterally expanded trochlea of *E. laurillardi* is clearly plesiomorphic (De Iuliis and St-André 1997).

The patella is highly variable in size and morphology in *E. laurillardi* (ROM 21989, 21990, 21991, 21992, 21993, and 21998). The same range of variation is observable in patellae of *M. americanum* (MNHN mounted specimen and Kraglievich 1925, fig. 1). The patella is wider than high in *E. laurillardi*, contrary to the general condition in *Megatherium*. In *M. urbinai* the femoral facet (Text-fig. 2M) is longer than wide in MUSM 15, as in *M. tarijense*, and some specimens of *M. americanum* (MNHN, mounted skeleton). The reverse occurs in UNA V2642. The apex is slender and central in both specimens of *M. urbinai*, bulky and central in *E. laurillardi* (ROM material) and *M. americanum* (MNHN mounted skeleton; Owen 1860, fig. 38-2), and it is bulky and located medially in *M. tarijense* (FMNH P14216).

The intercondylar area of the tibia is wider in *M. urbinai* than in *M. tarijense* (FMNH P14216), as is the case for the intercondylar fossa of the femur. The lateral articular surface is 'contiguous with small, approximately semicircular facets for articulation with sesamoid elements' (De Iuliis 1996, p. 302). These surfaces are not visible on MUSM 15 because of damage. The tibia and fibula of *M. urbinai* are rectilinear (Text-fig. 2N–O) and not curved as in *M. americanum* and *M. tarijense*. The distal epiphysis of the tibia and fibula are unfused, contrary to the partial and complete ankylosis in *M. tarijense* and *M. americanum*, respectively (Text-fig. 2N–P). Partial or complete ankylosis is derived [there is no ankylosis in *Hapalops* (Scott 1903) or most other sloths].

In *M. urbinai* the discoid facet of the tibia is oriented anteroposteriorly (Text-fig. 2P) and not anterolaterally to posteromedially as in *M. tarijense* and *M. americanum*. In the last two the posterior portion of the discoid facet is located posterior to the odontoid facet, but not in MUSM 15 (Text-fig. 2P). Therefore, the odontoid facet is reduced and slightly more anterior in *M. tarijense* and *M. americanum* (MNHN AC7036) than in *M. urbinai*. This condition may be autapomorphic in *M. urbinai* based on the condition in *Hapalops longipes* and other Megatheriinae. The distal epiphysis of the tibia is more compressed anteroposteriorly in *Megatherium* than in *Eremotherium*. It is also more compressed in *M. urbinai* and *M. tarijense* than in *M. americanum*. The tibia of *M. medinae* (SGO PV231 in De Iuliis 1996, fig. 108A) and *M. sundti* (SGO PV298 in De Iuliis 1996, fig. 108B) are poorly preserved, but apparently morphologically closer to those of *M. urbinai* and *M. tarijense* than to that of *M. americanum*. The crural

index (CI = [length of the tibia/length of femur] × 100; Coombs, 1983; De Iuliis, 1996) is less than 0·9 as in all the *Megatherium* species.

The morphology of the megatheriine pes is complex due to the pedolateral stance (Text-fig. 5). In Pleistocene Megatheriinae MtI–II are absent and the two medial cuneiforms are fused to form an MEC. The re-examination of the navicular, cuboid, ectocuneiform, and MtIII of the Pliocene genus *Pyramio-dontherium bergi* (MLP 2-66) shows the absence of fusion between the entocuneiform and mesocunei-form, in contrast to the condition in Plio-Pleistocene megatheriine genera. *Megatherium* and *Eremotherium* are derived ground sloths that probably walked at least on the lateroplantar surface of the calcaneum and the lateral surface of the MtV. Only the pes of *M. americanum* and *M. tarijense* are well known.

The megatheriines have a derived astragalus with a medially well-developed odontoid process (Text-figs 5–6). The astragalus of the Miocene form *Megathericulus* is morphologically intermediate between the plesiomorphic condition in Santacrucian forms (such as hapalopsines) and Pleistocene Megatheriinae. There are many differences between the astragali of *Megatherium* and *Eremotherium*. The most important is the distance between discoid and ectal facets in dorsolateral view. This distance is considerably reduced in *Megatherium* compared to *Eremotherium* (Text-fig. 5C) and clearly separates the genera. The astragalus of *M. urbinai* closely resembles those of *M. tarijense* (FMNH P14216) and *M. medinae* (Casamiquela and Sepulveda 1974, figs 8–9). In distal view the width of the discoid and odontoid facets are equal in *M. urbinai* (Text-fig. 6A) as in *M. americanum* (Text-fig. 6C, MNHN PAM 295) and *M. elenense* (ROM 2698), but not *M. tarijense* (Text-fig. 6B, FMNH P14216), in which the discoid facet is much wider. A diagnostic character of the astragalus is the position of the dorsomedial portion of the navicular facet with respect to the plane of the discoid facet (character 11 of De Iuliis 1996; Text-fig. 6). In *M. urbinai* one-third of the navicular facet extends above the plane discoid facet (Text-fig. 6A), but in *M. americanum* the facets are nearly at the same level (Text-fig. 6C). The condition in *M. tarijense* (Text-fig. 6B) and *M. medinae* is intermediate between that of *M. americanum* and *M. urbinai*. *M. americanum* represents the most derived state and *M. urbinai* the most plesiomorphic state for *Megatherium*. In *M. urbinai* the condition is closer to the most primitive megatheriine condition present in *Megathericulus* (50 per cent of the navicular facet lies dorsal to the plane of the discoid facet; De Iuliis 1996). The angle between the discoid and odontoid facets is similar in *M. urbinai*, *M. tarijense*, *M. medinae*, and *M. elenense*, falling within the range of variation of *M. americanum* (110–115 degrees; De Iuliis 1996, p. 338).

Generally in Megatheriinae the sustentacular and ectal facets are separated, as in Nothrotheriidae. The two facets between the astragalus and calcaneum are completely fused in one specimen of *M. americanum* (Kraglievich, 1926), one specimen of *E. laurillardi* (ROM 22006 in De Iuliis 1996, p. 354 and F. Pujos, pers. obs. 2001) and partially fused in *M. tarijense* (MNHN TAR 1269). This character state is rarely observed. One specimen from Celendín (northern Peruvian Andes; Pujos 2001) presents the same augmentation of the surface of the ectal facet but without fusion with the sustentacular facet. The ectal and sustentacular facets are fused in one of the two specimens of *M. urbinai* (UNA V2642). The augmentation of the surface of the ectal facet (with occasional fusion between ectal and sustentacular facets) is considered as possibly informative for megatheriine relationships. The calcanea of Mega-theriinae are extremely similar, except for the augmentation of the ectal facet (see above for the astragalus).

The cuboid of *M. americanum* (MNHN PAM 295) bears an MtIII facet that is inclined anteriorly and extended dorsoplantarly. The mounted MNHN skeleton of *M. americanum* bears an MtIII facet, but the specimen described by Owen (1860) lacks it. The cuboid of *E. laurillardi* occasionally bears an MtIII facet (Cartelle 1992). The cuboid of *M. tarijense* does not bear an MtIII facet but does possess an ectocuneiform facet. In *M. urbinai* and *M. elenense* the angle between astragalar and calcaneal facets is approximately 45 degrees. It is nearly 90 degrees in *M. tarijense* and *M. americanum*. The calcaneal facet occupies the dorsal two-thirds of the posteromedial surface in *M. americanum* (MNHN PAM 295), the plantar two-thirds in *M. elenense* (ROM 2686), *M. tarijense* (FMNH P14216) and one of the two specimens of *M. urbinai* (UNA V2642), and all of the plantar surface in the holotype of *M. urbinai* (MUSM 15).

The navicular is similar in all *Megatherium* species. The navicular of *M. urbinai* bears a single cuboidal facet (Text-fig. 7C), whereas that of *E. laurillardi* bears two (De Iuliis, 1996).

In *M. americanum* (MNHN PAM 295, Text-fig. 6E), *M. tarijense* (FMNH P14216), and *M. elenense* (ROM without catalogue number) only one metatarsal facet (for MtIII) is present on the ectocuneiform, but two (for MtIII and IV) are present in *M. urbinai* (Text-fig. 3H) because the bone is more laterally inclined. An articulation between the MEC and the ectocuneiform is present in *M. urbinai* (MUSM 15, Text-fig. 7K–L) and in *M. tarijense* (FMNH P14216, Text-fig. 7M), but not in *M. americanum*. *M. elenense* bears an MEC facet that does not contact the MtIII facet. In *M. urbinai* (UNA V2642) the MEC does not bear an ectocuneiform facet, as is also the case in *M. americanum* (MNHN PAM 295 and Owen 1860, fig. 40). In *M. tarijense* the ectocuneiform (Text-fig. 7M) and MtIII facets of the MEC are circular and contact each other. In *M. elenense* (ROM 10423 and 10422) the ectocuneiform facet is reduced, as in *M. urbinai*, but does not contact the MtIII facet. In the latter species the MtIII facet is located at the centre of the dorsal part of the anterior surface. The contact between the MEC and MtIII is more medial in MUSM 15 and the contact between the MEC and the ectocuneiform is much more reduced in this specimen of *M. urbinai* than in *M. tarijense*.

This difference between the two *M. urbinai* specimens seems insufficient to justify recognition of MUSM 15 and UNA V2642 as distinct species. With the discovery of new specimens of this species, this character (contact between the MEC and ectocuneiform) could be reconsidered.

MtIII of *M. urbinai* is variable, as in *E. laurillardi* (ROM 27334, 21957, and 28862) and *M. elenense* (ROM 2682 and 3784). ROM 3784 is much more compressed transversely than ROM 2682 and the ectocuneiform facet is medial in the former and posteromedial in the latter. Except for the development of the facet for the MEC, MtIII is similar in all *Megatherium* species.

The tripod-shape of the distal plantar process of MtIV of *M. urbinai* MUSM 15 (Text-fig. 7C) is absent in UNA V2642, *M. tarijense* (Text-fig. 7P), *M. elenense* and, generally, *M. americanum* (but present in MNHN PAM 295). This character is apparently variable in *Megatherium*. The existence in *M. urbinai* of an articulation between the ectocuneiform and MtIV (Text-fig. 3O) is unique among Megatheriinae and is considered autapomorphic. The degree of diaphyseal torsion of MtIV is greater in *M. urbinai* than in *M. tarijense* and, generally, *M. americanum* (Text-fig. 3N–Q). The morphology of the tibial-astragalar articulation and the position and morphology of the tarsal bones suggest a higher degree of torsion of the feet compared to other *Megatherium* species.

In summary, *M. urbinai* is more similar to *M. medinae*, *M. elenense*, and *M. tarijense* than *M. americanum* and *M. altiplanicum*. Various characteristics of *M. urbinai* indicate than it is somewhat less specialized than *M. tarijense* and much less so than *M. americanum* and *M. altiplanicum*. The morphology of the manus suggests that it participated in locomotion (i.e. it was not exclusively bipedal). The high torsion of the feet may be related to more quadrupedal stance. The clade constituted by [*M. americanum* + *M. altiplanicum*] is clearly more specialized than the other *Megatherium* species known (St-André and De Iuliis 2001). The phylogenetic relationships among the Megatheriinae are unclear and the single cladistic analysis of this subfamily (De Iuliis 1996) results in a large polytomy.

Both specimens from Sacaco and Tres Ventanas are included in the same new species because they share several autapomorphies, while the few differences they exhibit may easily be ascribed to intra-specific variation. The description of a second *Megatherium* species from Peru and a phylogenetic analysis of the subfamily Megatheriinae is in progress.

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APPENDIX

Measurements of *Megatherium urbinai*, MUSM 15 from Sacaco and UNA V2642 from Tres Ventanas, in mm. AP, anteroposterior; BL, body length; dist., distal; DL/MPl, dorsolateral/medioplantar; DM/LPl, dorsomedial/lateroplantar; DPa, dorsopalmar; (e), estimate; L, length; max., maximal; McII–III–IV–V, metacarpals 2–3–4–5; MCC, metacarpal-carpal-complex; MEC, mesocuneiform-entocuneiform-complex; MH, maximal height; MtIII-IV-V, metatarsals 3–4–5; min., minimal; P, phalanx; P(1-2), fused first and second phalange; PD, proximo-distal; prox., proximal; T, transversal; —, non-measurable.

Measurements	UNA V2642	MUSM 15
CAUDAL VERTEBRAE		
No. 7 diameters (BL × T × MH)	—	46 × 41 × 25
No. 8 diameters (BL × T × MH)	—	27 × 46 × 33
No. 9 diameters (BL × T × MH)	—	34 × — × —
No. 10 diameters (BL × T × MH)	—	39 × 59 × —
No. 11 diameters (BL × T × MH)	—	41(e) × — × —
No. 12 diameters (BL × T × MH)	—	47(e) × 72 × —
No. 13 diameters (BL × T × MH)	—	51 × 90 × —
No. 14 diameters (BL × T × MH)	—	53 × 108 × —
No. 15 diameters (BL × T × MH)	—	54 × 117 × —
No. 16 diameters (BL × T × MH)	—	57 × 142 × 90
No. 17 diameters (BL × T × MH)	—	58 × 155(e) × —
No. 18 diameters (BL × T × MH)	—	56 × 168 × —
FORELIMB		
Humerus, distal epiphysis, T diameter	—	202
Radius, L	—	410
Radial head diameters (T × AP)	—	60 × 58
Distal epiphysis diameters (T × AP)	—	112 × 71
Ulna, L	—	444
Olecranon diameters (T × AP)	—	127 × 162
Distal epiphysis diameters (T × AP)	—	49 × 69
Scaphoid diameters (T × AP × DPa)	101 × 55 × 75	78 × 49 × 60
Lunar diameters (T × AP × DPa)	63 × 65 × 68	—
Cuneiform diameters (T × AP × DPa)	77 × 55(e) × 46	— × 40(e) × 35
Pisiform diameters (T × AP × DPa)	36 × 86(e) × 80	26 × 52 × 44
MCC diameters (T × AP × DPa)	52 × 37 × 28	22·5 × 26 × 19·5
Trapezoid diameters (T × AP × DPa)	36 × 23(e) × 43	36 × 25(e) × 36,5
Magnum diameters (T × AP × DPa)	51(e) × 55(e) × 68	42 × 36 × 56(e)
Unciform diameters (T × AP × DPa)	82 × 47 × 62	66 × 35·5 × 53(e)
Palmar sesamoid diameters (T × AP × DPa)	107 × 83 × 28(e)	87 × 71 × 19
Mc II diameters		
(L × DPa prox. × DPa dist. × T prox. × T.dist.)	102 × 50 × 63 × 43 × 42	86 × 43 × 53 × 38 × 32
Mc III diameters		
(L × DPa prox. × DPa dist. × T prox. × T. dist.)	144 × 65 × 86 × 85(e) × 58	120 × 50 × 67 × 69 × 50
Mc IV diameters		
(L × DPa prox. × DPa dist. × T prox. × T. dist.)	212(e) × 65 × 100 × 77 × 57	170 × 45 × 79 × 58 × 45
Mc V diameters		
(L × DPa prox. × DPa dist. × T prox. × T. dist.)	194(e) × 51 × 62 × 54 × 51	155 × 35 × 46 × 36 × 34
P 1 II diameters (L × DPa prox. × DPa dist. × T)	47 × 66 × 49(e) × 48	26 × — × — × 38(e)
P 2 II diameters (L × DPa prox. × DPa dist. × T)	76 × 44 × 30 × 45	—
P 3 II diameters (L × DPa × T)	—	139(e) × 47(e) × 39(e)
P (1−2) III diameters (L × DPa prox. × DPa dist. × T)	71 × 73 × 46 × 65(e)	66 × 53 × 40 × 44
P 3 III diameters (L × DPa × T)	—	179 × 80(e) × 49(e)
P 1 IV diameters (L × DPa prox. × DPa dist. × T)	30 × 51 × — × 50	23 × — × — × 40
P 2 IV diameters (L × DPa prox. × DPa dist. × T)	42 × 51 × 36(e) × 45	41 × 42(e) × 38(e) × 36

P 3 IV diameters (L × DPa × T)	—	139 × 44 × 39
P prox. V diameters (L × DPa prox. × DPa dist. × T)	31 × 35 × 28(e) × 38	20(e) × 27 × 20 × 22
P dist. V diameters (L × DPa prox. × DPa dist. × T)	31 × 30 × — × 25	—

HINDLIMB		
Femur, L(e)	—	460 < L < 480
L of the lateral face	—	448
Midshaft diameters (T × AP)	—	— × 38(e)
Distal epiphysis diameters (T × AP)	—	230(e) × 78(e)
Patella, L	102	76
Body diameters (T × AP)	77 × 67	58 × 38
Tibia, L	—	342
Proximal epiphysis, AP diameter	—	70
Midshaft diameters (T × AP)	—	64 × 51
Distal epiphysis, diameters (T × AP)	—	127 × 104
Fibula, midshaft diameters (T × AP)	—	23 × 24
Distal epiphysis, diameters (T × AP)	—	48(e) × 62
Tibiofibula, T diameters (prox. × dist.)	—	165(e) × 210(e)
Ossified meniscus of the knee joint (T × PD)	48 × 25	—
Cyamella (T × AP)	35(e) × 23	—
Astragalus diameters (T × AP)	150(e) × 151(e)	129 × 115
Calcaneum diameters (T × AP × DPl)	122 × 288 × 119	115(e) × 226 × 91(e)
Cuboid diameters (DL/MPl × DM/LPl × AP)	80 × 60 × 53	61 × 34 × 53(e)
Navicular diameters		
(DL/MPl × DM/LPl × AP max. × AP min.)	105 × 75 × 47 × 42(e)	79 × 48 × 38(e) × 23(e)
Ectocuneiform diameters (DL/MPl × DM/LPl × AP)	—	63 × 45 × 18
MEC diameters (DL/MPl × DM/LPl × AP)	71 × 43 × 33	58 × 30 × 28
Mt III diameters (DL/MPl × DM/LPl × L)	57 × 85 × 64(e)	50 × 66 × 50(e)
Mt IV diameters (DL/MPl prox. × DL/MPl dist. × DM/MPl prox. × DM/LPl dist. × L)	76 × 76 × 48 × 46 × 160(e)	32 × 40 × 59 × 56 × 124
Mt V diameters (DL/MPl prox. × DL/MPl dist. × DM/MPl prox. × DM/LPl dist. × L)	53 × 61 × — × 51(e) × 181	—
P (1–2) III diameters (DL/MPl prox. × DL/MPl dist. × DM/MPl prox. × DM/LPl dist. × L)	—	— × — × 40 × 22(e) × 31
P 3 III diameters (DL/MPl × DM/LPl × L)	57 × 90(e) × 160(e)	44(e) × 58 × 91(e)