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On the taxonomic status of *Megatherium sundti* Philippi, 1893 (Mammalia: Xenarthra: Megatheriidae)

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Abstract. Remains of a medium-sized megathere from Pleistocene deposits near Ulloma, Bolivia, suggest that the commonly accepted synonymy of *Megatherium sundti* Philippi, 1893 with *Megatherium medinae* Philippi, 1893 (Mammalia: Xenarthra: Megatheriidae) is unjustified. The strongest evidence supporting the distinction of these species is provided by their femora. In *M. medinae* the femur is plesiomorphic, bearing nearly parallel lateral and medial margins and an unreduced patellar trochlea. In *M. sundti* the femur bears strongly concave lateral and medial margins and a somewhat reduced patellar trochlea, resembling the derived condition in *Megatherium americanum* Cuvier, 1796. Less marked morphological differences in the skull, mandible, and tibia are apparently associated with these distinct femoral morphologies. The differences are clearly sufficient for recognition of *M. sundti* as a valid species, distinct from *M. medinae* and another medium-sized megathere, *Megatherium tarijense* Gervais and Ameghino, 1880, from Pleistocene deposits near Tarija, Bolivia.

Resumen. SOBRE LA POSICIÓN TAXONÓMICA DE *MEGATHERIUM SUNDTI* PHILIPPI, 1893 (MAMMALIA: XENARTHRA: MEGATHERIIDAE). El estudio de materiales atribuibles a un megaterio de tamaño mediano del Pleistoceno de depósitos cercanos a Ulloma, Bolivia, sugieren que la hipótesis comúnmente aceptada de la sinonímia de *Megatherium sundti* Philippi, 1893 con *Megatherium medinae* Philippi, 1893 (Mammalia: Xenarthra: Megatheriidae) no está justificada. El fémur provee la evidencia más fuerte para distinguir ambas especies. En *M. medinae* los márgenes lateral y medial son ligeramente cóncavos y la troclea patelar no está reducida, condiciones plesiomorfas en los fémures de megaterios. *M. sundti* tiene el margen medial y el margen lateral marcadamente cóncavo y la troclea patelar algo reducida, de manera parecida a la condición derivada presente en *Megatherium americanum* Cuvier, 1796. Diferenciaciones morfológicas sutiles en el cráneo, la mandíbula y la tibia parecen estar asociadas con las distintas morfologías femorales. Las diferencias son suficientes para reconocer a *M. sundti* como una especie válida diferente de *M. medinae*, así como de *Megatherium tarijense* Gervais y Ameghino, 1880, otro megaterio de tamaño mediano de depósitos pleistocenos cercanos a Tarija, Bolivia.

Key words. Mammalia. Megatheriidae. *Megatherium sundti*. *Megatherium medinae*. Taxonomy. Pleistocene. Bolivia.

Palabras clave. Mammalia. Megatheriidae. *Megatherium sundti*. *Megatherium medinae*. Taxonomía. Pleistoceno. Bolivia.

Introduction

Knowledge of the morphology and variation in the Megatheriinae is based mainly on the remains of the two Pleistocene giant ground sloths *Megatherium americanum* Cuvier, 1796 and *Eremotherium laurillardi* (Lund, 1842 *sensu* Cartelle and De Iuliis, 1995 *nec* Guérin and Faure, 2000). The former is known primarily from the Pleistocene of Argentina, but also from several localities in Uruguay and Tarija, Bolivia (De Iuliis, 1996). The latter is known mainly from the Pleistocene-Holocene of Brazil and southeastern USA, as well as several Central American and northern South American countries, such as Panama, El Salvador, Mexico, Venezuela, Ecuador (Cartelle, 1992; Cartelle and De Iuliis, 1995; De Iuliis, 1996), and Peru (Pujos, 2002, 2006). The giant ground sloth *Eremotherium eomigrans* De Iuliis and Cartelle, 1999 is known from remains of several individuals from the late Pliocene-early Pleistocene of Florida, USA (De Iuliis and Cartelle, 1999).

Relatively few megatheriine remains from other areas of South America, such as northwestern Argentina, Peru, Bolivia (except Tarija), and Chile, have been described (De Iuliis *et al*., 2004). Included among these are the smaller and medium-sized megatheriines. Recent work has advanced our understanding of several of these megatheriines (De Iuliis and Saint-André, 1997; Saint-André and De

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Iuliis, 2001; Carlini *et al*., 2002; De Iuliis *et al*., 2004); as well, Pujos (2002) has described two new large species from Peru. Despite these efforts the status and relationships among several medium-sized species from Chile and Bolivia, first described and named during the late 1800s, have been largely neglected. These include *Megatherium tarijense* Gervais and Ameghino, 1880, *Megatherium medinae* Philippi, 1893, and *Megatherium sundti* Philippi, 1893. The purpose of this paper is to review the status of *M. sundti* and its historical relationship to *M. medinae*. The latter has long been considered to be a valid taxon, whereas the former has usually been viewed as a synonym of the latter. *M. sundti* has recently been recognized as a valid taxon based on material that has not yet been described in the published literature. These remains are presented here and the reasons for recognition of *M. sundti* as a valid species are discussed.

Abbreviations. FMHN: Field Museum of Natural History, Chicago, USA. L: left. M: upper molariform. m: lower molariform. MNHN BOL: Museo Nacional de Historia Natural, La Paz, Bolivia. NRM: Swedish Museum of Natural History, Stockholm, Sweden. PIU: Museum of Evolution, Paleontology, Uppsala University, Uppsala, Sweden. R: right. SGO: Museo Nacional de Historia Natural, Santiago, Chile.

Taxonomic history

Philippi (1893a: 91) erected the species *Megatherium medinae* based on SGO PV 252 (formerly 1-VI-67-8), an incomplete mandible from Pampa del Tamarugal, near Pica, Tarapacá Province, Chile (Marshall and Salinas, 1991). Remains subsequently recovered elsewhere in Chile (e.g., near Santiago, Frasinetti and Azcárate, 1974; near Calama, Salinas *et al*., 1991) have been assigned to this species. Later in the same article, Philippi (1893a: 91) erected *Megatherium sundti* on SGO PV 277 (formerly 5-VI-67/2), an incomplete mandible recovered from Pleistocene deposits near Ulloma, Bolivia, "in den Uferabhängen des Rio Desaguadero."The remains were recovered from the south side of the river (Marshall and Salinas, 1991) at the base of the Ulloma Formation (Sundt, 1892). They are referable to the early part of the Lujanian South American Land Mammal Age, approximately 0.5 Mya (Salinas *et al*., 1991).

Philippi published German and Spanish versions of his descriptions. These papers are very similar with regard to the megatheres (see Marshall and Salinas, 1991), but the Spanish version (Philippi, 1893b) includes a table of measurements for M3/m3, diagrams that illustrate slightly more detail, and differences in arrangement and labeling of the figures. Most workers have cited the Spanish version for nomenclatural purposes, although the German version apparently has priority. Although more precise publication dates for these could not be determined, this opinion is based on the order that these articles are listed by Romer *et al*. (1962), Mones (1986; who also stated that the Spanish version is an abbreviated translation of the German article), and Marshall and Salinas (1991).

There are two further technical nomenclatural nuances with the name *M. medinae* that merit mention. One is that the name was first published by Ameghino (1889) under the synonymy list for *M. lundi*. Ameghino (1889) cited the name thrice in his text, and gave a cursory description of the species, stating that *M. medinae* was much more gracile and smaller than *M. americanum* based on casts that he had received from Philippi. Ameghino (1889) attributed the species to Philippi, but noted that it had not been described. Apparently, "*El nombre fue referido por el mismo Philippi a una fecha once años anterior, y a él aludió Ameghino en 1889; pero realmente no parece haber sido publicado como nombre válido antes de 1893*" (Cabrera, 1928: 341). A search for a possibly earlier mention of the name by Philippi has been in vain. Frassinetti (1982: 21) includes only the Spanish version of the article as "Philippi, R.A. 1892-1893", but the date of publication of the volume containing the article is clearly 1893. The second concern is that the species first appears in Philippi's (1893a: 91) text as "*M. Meginae*" although the relevant text is preceded by a diagram (Philippi, 1893a: fig. 5) that is labelled as "*Megatherium medinae*." Technically, *M. medinae* is a *nomen nudum*, as suggested by Casamiquela (1967). However, Casamiquela and Sepúlveda (1974) and probably all other paleontologists concerned with megatheriine ground sloths have long considered the name valid and applied it; Ameghino (1889) is apparently the sole exception. Further, and formally more important, a *nomen nudum* may be made available later for the same or a different concept. Therefore, *M. medinae* is the valid name for this species.

Philippi (1893a: 91) distinguished *M. medinae* and *M. sundti* based on the relative orientations of the upper toothrows, noting that in *M. medinae* "die beiden Zahnreihen stark divergiren, während sie bei dem *Megatherium* von Ulloma fast ganz parallel laufen". Philippi (1893a, 1893b) also examined skull remains, but made no attempt to distinguish the species based on this material. Ameghino (1904) considered *M. sundti* a synonym of *M. tarijense*. Frassinetti and Azcárate (1974:38) maintained a distinction between the species, and considered *M. sundti* to be "*un megatérido bastante más pequeño y con las líneas de ambos lados de los molares inferiores paralelas*", whereas they are divergent in *M. medinae*. This was based on Philippi's

(1893a) original description. However, the characteristic of size is doubtful, and that of the divergent tooth rows misleading. As noted by Casamiquela and Sepúlveda (1974), the divergent tooth rows in SGO PV 252 are caused by lateral deformation of the tooth bearing portion of the left ramus.

Casamiquela and Sepúlveda (1974) considered *M. sundti* a junior synonym of *M. medinae*, arguing that the differences between the skeletal remains from Tarapacá and Ulloma were due to intraspecific variation, compounded by age and poor preservation. Marshall and Salinas (1991) agreed with these conclusions. The synonymy of *M. sundti* with *M. medinae* seems reasonable, given the preservation of the material from these localities, and the scarcity of directly comparable elements. Indeed, it is difficult to distinguish between the cranial and postcranial remains from Tarapacá and Ulloma, particularly on the features discussed by Casamiquela and Sepúlveda (1974), given the remains available to these workers. However the additional material from Ulloma (PIU M4530) indicates that there are valid morphological distinctions, particularly in the femur, which suggests that *M. medinae* and *M. sundti* should be maintained.

Casamiquela and Sepúlveda (1974) considered a possible synonymy of their concept of *M. medinae* with *M. tarijense*, but appeared sceptical and deferred to Hoffstetter's (1963) opinion that *M. tarijense* was probably not distinct from *M. americanum*. Indeed, *M. tarijense* has often been viewed as questionably valid, and commonly as a synonym of *M. americanum*. Such hypotheses were reasonable, given the scarce remains of *M. tarijense* and the probable presence of *M. americanum* in the deposits of the Tarija Valley, Bolivia, from which *M. tarijense* is also known. However, a nearly complete skeleton (FMNH P14216), not described in the literature, of an individual clearly demonstrates that this species is distinct from *M. americanum*, and probably also from *M. medinae* and *M. sundti* (see De Iuliis, 1996; De Iuliis and Saint-André, 1997; Saint-André and De Iuliis, 2001). A second skull from Tarija (NRM M4890) was assigned by Werdelin (1991) to *M. americanum*, but De Iuliis (1996) referred it to *M. tarijense*.

Systematic paleontology

XENARTHRA Cope, 1889
TARDIGRADA Latham and Davies in Forster, 1795
MEGATHERIIDAE Gray, 1821
MEGATHERIINAE Gray, 1821

Megatherium Cuvier, 1796

Megatherium sundti Philippi, 1993a: 91

Holotype. SGO PV 277 (formerly 5-VI-67/2), an incomplete mandible (see Casamiquela and Sepulveda, 1974: pl. 4). Left dentary lacks anterodorsal portion of coronoid process; right dentary missing most of its posterior half; right m1-m4, L m4, and mesial half of left m1 are missing; left m2-m3 are broken at level of alveolar margins.

Type locality and age. Pleistocene deposits near Ulloma, Bolivia, "in den Uferabhängen des Rio Desaguadero" (Philippi, 1893a: 87), from the base of the Ulloma Formation (Sundt, 1892) on the south side of the river (Marshall and Salinas, 1991). Pleistocene; early part of the Lujanian Land Mammal Age, approximately 0.5 My (Salinas *et al*., 1991).

Referred material. PIU M4530: includes the partial skeleton of a single individual. The remains indicate that it was not yet adult, but may have been approaching its adult size and form. This is indicated by non-closure of several skull, and iliosacral, iliopubal, and ischiosacral sutures, but that in the long bones fusion of the epiphyses and diaphysis had apparently begun. The remains include: skull, missing ventral surface; R side, including molariforms, otherwise nearly complete; L side damaged, with partial nasal, maxilla, frontal, and isolated temporal region; horizontal rami of R and L dentaries, lacking symphyseal region; R dentary preserving base of ascending ramus and molariforms broken more or less at alveolar margins; anteroventral portion of L scapula, including glenoid fossa; nearly complete L humerus; nearly complete L pelvis; nearly complete L femur; SGO PV 273 (formerly 5-VI-67-1) - greater part of skull with dentition (see Casamiquela and Sepulveda, 1974: pl. 3, top); SGO PV 278 (formerly 5-VI-67-3) - greater part of skull with dentition; SGO PV 280 (formerly 5-VI-67-5) - greater part of zygomatic arch; SGO PV 281 (formerly 5-VI-67-6): - greater part of zygomatic arch; SGO PV 276 (formerly 5-VI-67-8) - greater part of mandible missing anterior tip of symphysis; SGO PV 285 (formerly 5-VI-67-11) -posterior part of right dentary without teeth; SGO PV 298 (formerly 6-VI-68-2)- nearly complete R tibia with proximal portion of R fibula; SGO PV 189 (formerly 13-V-69-3) - Marshall and Salinas (1991) indicated that this catalogue number includes "thirteen pieces of a foot and foreleg," although several may not belong to *Megatherium*; however, at least a L metacarpal IV (formerly SGO PV 13-V-69/2) and an incomplete unla (formerly SGO PV 13-V-69 -3/12) are diagnostic.

Age. Lujanian South American Land Mammal Age, Pleistocene (see Marshall and Salinas, 1991).
Type locality. South side of Río Desaguadero, about 40 km south of Coroco, northern Altiplano of Bolivia (see Marshall and Salinas, 1991).
Diagnosis. Medium-sized megatheriine, very similar in linear dimensions to *M. medinae* and *M. tarijense* Gervais and Ameghino, 1880, but larger than *M. altiplanicum* Saint-André and De Iuliis, 2001 and *E. sefvei* De Iuliis and Saint- André, 1997, and smaller than *M. americanum* Cuvier, 1796, *E. laurillardi* (Lund, 1842), and *E. eomigrans* De Iuliis and Cartelle, 1999; skull relatively less gracile compared to *M. medinae*, particularly in its shorter and higher rostrum; and relatively less elongated than *M. tarijense*; dorsal profile of skull less regularly sinuous than in *M. medinae* and raised prominently centrally more than in *M. tarijense*; dentary relatively compressed anteroposteriorly compared to *M. medinae*; anterior margin of coro-

noid more vertical and further forward than in *M. medinae* and covers all or much of m4 in lateral view; humerus with strong deltopectoral crest, nearly as in *M. americanum*, *E. laurillardi*, and *E. eomigrans*, compared to markedly reduced crest in *M. tarijense*. Femur robust with strongly concave medial and lateral margins and relatively expanded proximally and distally, as in *M. americanum* and *M. altiplanicum*, and in contrast to *M. medinae*, *M. tarijense*, *E. laurillardi*, *E. eomigrans*, and *E. sefvei*; tibia relatively robust, expanded proximally and distally, as in *M. americanum*, and in contrast to *M. medinae*, *M. tarijense*, *E. laurillardi*, and *E. eomigrans*.

Descriptions and discussion

Skull and mandible

The remains discussed here are from near Ulloma and Tarija, Bolivia, and the province of Tarapacá, northern Chile. The skull material from these regions is neither as abundant nor well-preserved as that for *Megatherium americanum* from Argentina and *Eremotherium laurillardi* from Brazil and the United States, except for the remains of a well-preserved and nearly complete individual from the Tarija Formation, FMNH P14216, and the less-complete juvenile from Ulloma, PIU M4530 (figure 1). As noted above, FMNH P14216 represents *M. tarijense*. The SGO remains from Chile represent *M. medinae*, whereas the SGO and PIU remains from Ulloma represent *M. sundti*.

Among the general similarities between *M. sundti* (SGO) and *M. medinae* (SGO) cited by Casamiquela and Sepúlveda (1974) are the morphology of the skull and its outline in lateral view, width of the rostrum, the length and form of the tooth rows, and the positions of the occipital condyles and anterior zygomatic roots. However, these generalities apply to many megatheriines. Although the SGO skull remains from Tarapacá and Ulloma demonstrate considerable variation (Casamiquela and Sepulveda, 1974) there are subtle differences, apparently correlated with distinct femoral morphologies, that suggest specific distinction. This assertion rests on the PIU remains from Ulloma. Differences between the Tarapacá and Ulloma (including the PIU remains)

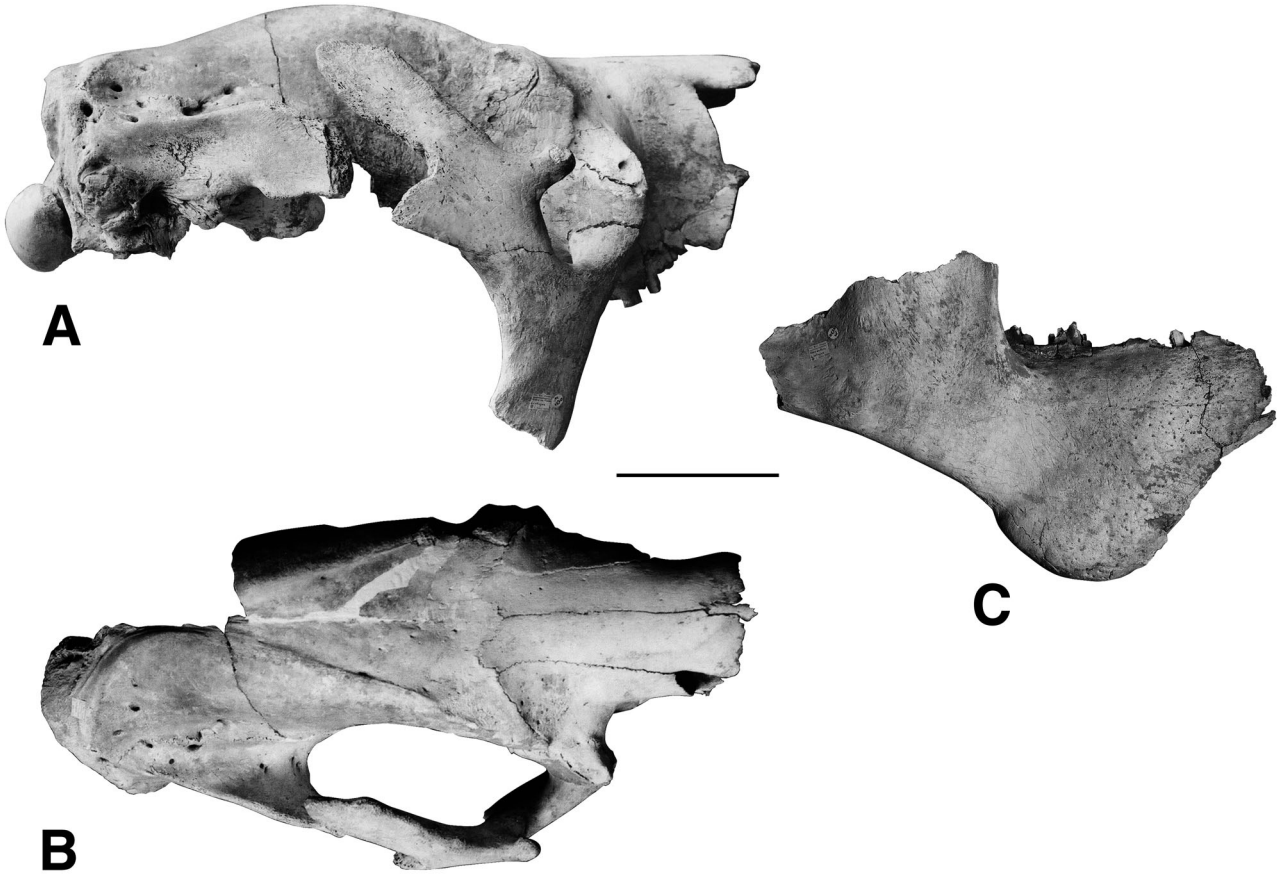

Figure 1. Cranial remains of ***Megatherium sundti*** Philippi 1893, PIU M4530. **A,** Skull in lateral view. **B,** Skull in dorsal view. **C,** Right, dentary in lateral view. Scale bars represent 100 mm / *restos craneales de* **Megatherium sundti** *Philippi 1893, PIU M4530.* ***A,*** *Cráneo en vista lateral.* ***B,*** *Cráneo en vista dorsal.* ***C,*** *Dentario derecho en vista lateral. Escala = 100 mm.*

skulls are that the rostrum is relatively elongated, slender, and more gracile in *M. medinae*, and shorter and higher in *M. sundti* (figure 1.A). The dorsal profile in the former is more regularly sinuous, with a gentle transition between cranial and rostral portions (the exaggerated domed appearance in *M. medinae* SGO PV 275 is due to improper reconstruction of the central part of its profile; see Casamiquela and Sepulveda, 1974: pl. 1), whereas that of *M. sundti* is domed or inflated centrally, just posterior to its anteroposterior midpoint. The outline is concave between the posterior part of the dome and nuchal crest. The absence of a dome in *M. sundti* SGO PV 273 reflects breakage and improper reconstruction.

In dorsal view the skull of *M. medinae* (see Casamiquela and Sepúlveda, 1974: pls. 1, 2) appears more elongated, with weaker postorbital processes and postorbital constriction, and resembles more that of *Eremotherium laurillardi* than *M. americanum*. In *M. sundti* (figures 1.A, B) the skull is relatively more robust and resembles more that of *M. americanum*. A small internasal element is wedged anteriorly between and projects beyond the nasals (figure 1.B).

The skulls of *M. medinae*, *M. sundti*, and *M. tarijense*, very similar in linear dimensions (table 1), are clearly smaller than those of *M. americanum* and *E. laurillardi*. They resemble more *M. americanum* in morphology, but they are approximately intermediate between *M. americanum* and *E. laurillardi* in proportions. The skull of *M. tarijense* resembles that of *M. sundti* in being raised centrally, but is not prominently domed and the dorsal profile is considerably flatter. In dorsal view the skull of *M. tarijense* is relatively elongated and narrow, particularly posteriorly, but the postorbital processes are larger and the postorbital constriction narrower, so that the lateral walls of the skull are markedly concave.

As in *M. americanum* the maximum width of the palate between the tooth rows is smaller than the width of the largest molariform in *M. medinae* (see Casamiquela and Sepúlveda, 1974: pls.1, 2), *M. sundti* (see Casamiquela and Sepúlveda, 1974: pl. 3), and *M. tarijense* (see De Iuliis, 1996: pl. 29). The lingual margin of the tooth rows in the SGO specimens is intermediate between those of *M. americanum* and *E. laurillardi*, in being more nearly parallel than in the latter, but diverging slightly anteriorly and posteriorly. A line drawn through the midpoints of the molariforms of each row is nearly rectilinear, as in *M. americanum*. The degree of divergence varies between and within individuals, and may be largely due to distortion. The width between the molariforms and degree of divergence of the tooth rows is somewhat greater in SGO PV 231 (*M. medinae*), the skull of an immature individual (the midline palatal suture is open). These features are to be expected in juveniles (see De Iuliis, 1996). The tooth rows of FMNH P14216 are slightly distorted, but their midpoint lines are nearly linear, with some anterior and posterior divergence. The palatal surface between the tooth rows is similar to that in *M. americanum* in being nearly flat, but more similar to that in *E. laurillardi* in being relatively smooth.

The position of the anterior zygomatic root is variable, but approximately as in *M. americanum*. Its anterior margin lies lateral to the middle or distal half of M2; its posterior margin distal to the mesial part of M3 and M4, respectively. In FMNH P14216 the position of the left and right roots are dissimilar, but fall within the range of the SGO and PIU specimens. In *E. laurillardi* the anterior margin of the root lies approximately between M1 and M2.

The mandibles of *M. sundti* (figure 1.C; Casamiquela and Sepulveda, 1974: pls. 3, 4; De Iuliis, 1996: pls. 54, 55) and *M. medinae* (see Casamiquela and Sepúlveda, 1974: pl. 5; De Iuliis, 1996: pls. 52, 53), similar in size and morphology, are not easily distinguished, but this may be due to the usually incompletely and poorly preserved remains of these species. However, variation does exist

Table 1. Measurements (mm) for elements assigned to ***Megatherium sundti*.** Abbreviations: / *Medidas de los elementos atribuidos a* **Megatherium sundti**. *Abreviaturas:* CONW-Minimal Width of Postorbital Constriction / *ancho mínimo de la constricción postorbitaria*; DW-Distal Width / *ancho distal*; L- Greatest Proximo distal Length*; L- Longitud poróximodistal mayor*; M1L-Length from mesial margin of M1 to posterior surface of occipital condyles / *longitud desde el margen mesial del M1 a la superficie posterior de los cóndilos occipitales*; MBH-Maximal Height of Mandibular Body / *altura máxima del cuerpo mandibular*; MCAH-Height between dorsal margin of Mandibular Condyle and Alveolar Margin / *altura entre el borde dorsal del cóndilo mandibular y el margen del alvéolo*; MSW-Midshaft Width / *ancho de la diáfisis*; POPW-Width across Postorbital Processes / *ancho entre los procesos postorbitales*; PW-Proximal Width / *ancho proximal*; TRL-Toothrow Length / *longitud de la hilera dentaria.*

Skull				
Specimen	M1L	TRL	POPW	CONW
SGO PV 273	404	138	163	119
PIU M4530	391	-	156	123
Dentary				
Specimen	MBH	TRL	MCAMH	
SGO PV 276	126	149	141	
SGO PV 277	138	145	122	
PIU M4530	146	154	-	
Humerus				
Specimen	L	DW		
PIU M4530	531	244		
Femur				
Specimen	L	PW	DW	MSW
PIU M4530	530	256	266	162
Tibia				
Specimen	L	PW	MSW	
SGO PV 298	468	263	92	

in shape of the ventral bulge and ventral margins of the body anterior and posterior to the ventral bulge, angle of inclination of the spout, position of the posterior end of the symphysis, and size and robustness, but the degree of variation is not particularly greater than occurs in the mandibles of *M. americanum* and *E. laurillardi*. Without larger samples, it is difficult to ascertain whether the differences between *M. sundti* and *M. medinae* are consistently diagnostic.

The qualitative impression is that the mandibles from Ulloma appear relatively more robust or compact, so that the body seems anteroposteriorly compressed. The anterior margin of the coronoid process is apparently more vertical and farther anterior in *M. sundti*, and lends to the compressed appearance. In lateral view the anterior margin covers all or most of m4 in *M. sundti* but leaves m4 largely exposed in *M. medinae*. The hypsodonty index (HI=greatest height of mandibular body/length of mandibular toothrow x 100) is a measure of hypsodonty commonly used for megatheriines (see e.g., Zetti, 1964; De Iuliis, 1996; Saint-André and De Iuliis, 2001). Mean values of HI in *M. sundti* (92) and *M. medinae* (90) are closely similar. These values are close to the low end of the range for *M. americanum* (92-112); the range for *E. laurillardi* is 66-83 (Saint-André and De Iuliis, 2001); the mean for *M. tarijense* is 87 (see De Iuliis, 1996). However, the HI value of 95 in the juvenile specimen of *M. sundti* (PIU M4530) is higher than observed in juveniles of other species. In *E. laurillardi* HI is similar in juveniles and adults; that is, there is apparently no allometric increase during ontogeny. The juveniles of *M. americanum*, on the other hand, resemble more closely the juveniles (and adults) of *E. laurillardi*; that is, they have lower HI values than adults of *M. americanum*, implying an allometric increase in HI during ontogeny. The highest HI value for a juvenile of *M. americanum* is 88 (see De Iuliis, 1996). The implication for *M. sundti* is that HI may be higher (and thus more like that of *M. americanum*) than reported here, based on the *M. americanum* model of ontogenetic development.

Humerus

The humerus of *M. sundti* (531 mm), nearly equal in length to that of *M. tarijense* (527 mm), is considerably smaller than those of *M. americanum* (626-787 mm) and *E. laurillardi* (734-878 mm; data from De Iuliis, 1996). The humerus is not known for *M. medinae*. The lateral projection of the lateral surface of the humerus projects most prominently among megatheriines in *E. laurillardi*. It is less prominent and scarred in *M. americanum*, and so the humeral shaft appears more parallel-sided. The humerus of *M. sundti* (figure 2.A) resembles that of *M. americanum*. The deltopectoral crest, on the anterior humeral surface, is similar in relative size in *M. sundti*, *M. americanum*, and *E. laurillardi*. The humerus of *M. tarijense* [as well as *M. nazarrei* (Kraglievich 1925); see De Iuliis, 1996] is apparently derived (see De Iuliis, 2001, 2003). In *M. tarijense* the deltopectoral crest is reduced and the lateral surface barely projects laterally, so its humeral diaphysis is more nearly cylindrical and the ectepicondylar notch is relatively small.

Pelvis

Pelves of *M. americanum*, *M. tarijense* (MNHN BOL A-585; see De Iuliis, 1996: pl. 91C-E), and *E. laurillardi* were available for comparison. Although the pelvis of *M. sundti* (figure 2.B) strongly resembles these, several differences may be distinguished. For example, the wing of the ilium is apparently less flared laterally. The less prominent iliac crest does not extend as far lateroventrally. It forms a regularly curved and shorter arc and the dorsal eminence just lateral to the sacral margin, so characteristic of the other taxa, is strongly reduced. The pubic tubercle is less prominent. It is not clear, however, whether these differences are diagnostic or due to the age of PIU M4530.

Femur

The femur of *M. medinae* (SGO PV 231, formerly 1-VII-67/64; see Casamiquela and Sepulveda, 1974: pl. 6) is only slightly different from that of *M. tarijense* (see De Iuliis, 1996: pl. 102). Differences include a more prominent lesser trochanter, a smaller notch on the posterior surface of the head, and a greater length. However, the smaller femur (SGO PV 185, formerly 9-V-69-1/39), though incomplete, is similar in size to that of *M. tarijense*.

The femur of PIU M4530 (figures 2.C-D) presents the strongest evidence suggesting that the megatheriine from Ulloma is specifically distinct from the *M. medinae* SGO remains from Chile and the *M. tarijense* remains from Tarija. In length the femur of *M. sundti* falls within the range for *M. medinae* and *M. tarijense*, but its shape is markedly different. The medial and lateral margins are strongly concave, and the greater trochanter and ectepicondyle are relatively prominent (figure 2.C). Its middle diaphyseal portion is markedly constricted transversely, relatively more so than in the more constricted specimens of *E. laurillardi*, and strongly resembling the condition in *M. americanum*. In *E. laurillardi* the diaphysis appears relatively constricted in the larger and presumably older individuals, due to expanded proximal and distal

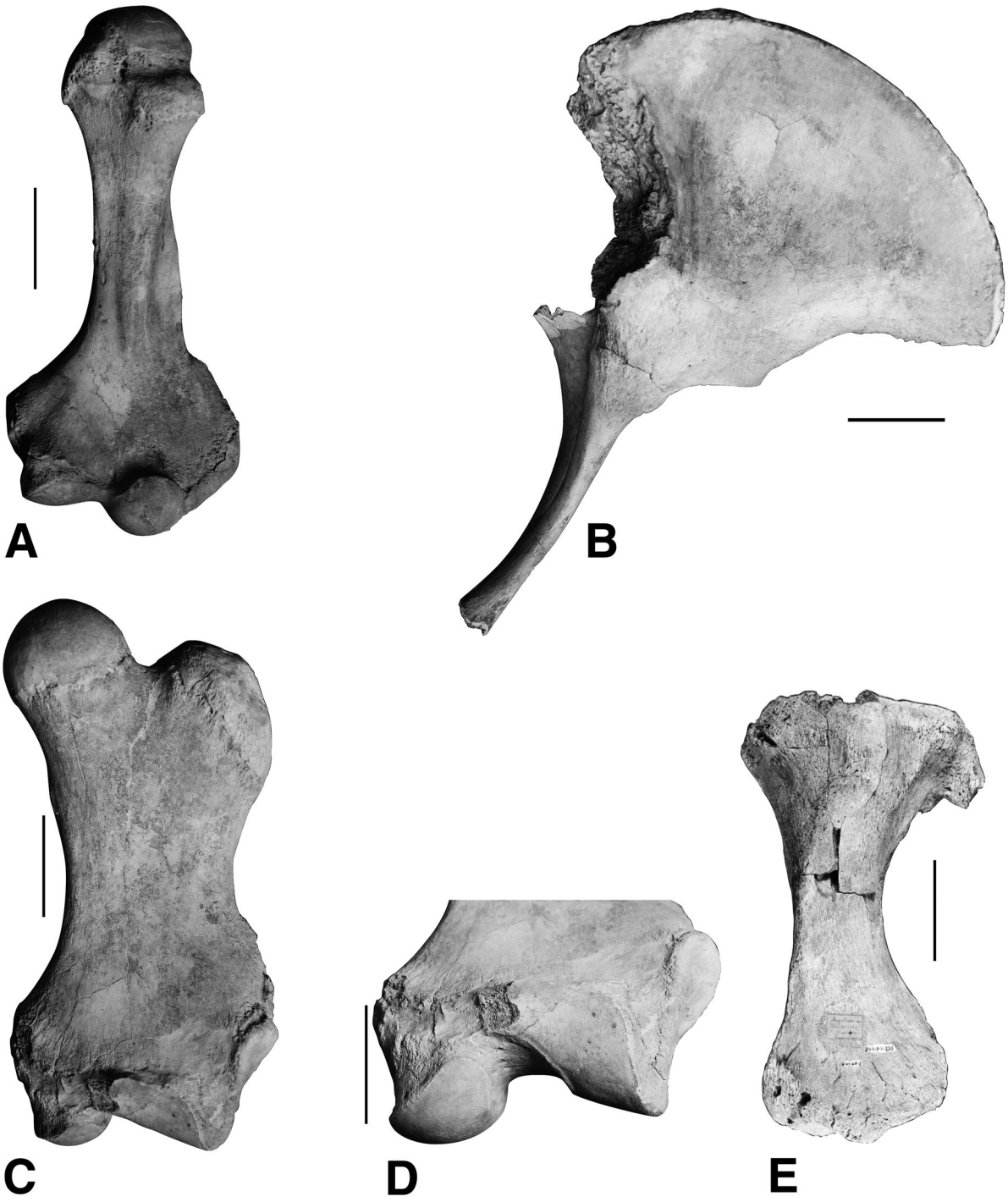

Figure 2. Postcranial remains of ***Megatherium sundti*** Philippi, 1893, PIU M4530 (A-D) and SGO PV 298 (E). **A,** Left humerus in anterior view. **B,** Left pelvis in anterior view. **C,** Left femur in anterior view. **D,** Distal end of left femur in anterodistal view. **E,** Left tibia in anterior view. Scale bars represent 100 mm / *restos postcraneales de* **Megatherium sundti** *Philippi, 1893, PIU M4530 (A-D) y SGO PV 298 (E).* ***A,*** *Húmero derecho en vista anterior.* ***B,*** *Pelvis izquierda en vista anterior.* ***C,*** *Fémur izquierdo en vista anterior.* ***D,*** *Extremo distal del fémur izquierdo en vista anterodistal.* ***E,*** *Tibia izquierda en vista anterior. Escala = 100 mm.*

epiphyseal regions, in contrast to the condition in all *M. americanum* individuals and the juvenile PIU M4530.

The patellar trochlea is medially extended and nearly flat transversely (figure 2.D), but its medial part is narrower proximodistally than in *M. medinae*, *M. tarijense*, and *E. laurillardi*. In *M. americanum* (and *M. istilarti* Kraglievich, 1925; see De Iuliis, 1996) the medial part of the trochlea is markedly reduced. In *Megatherium altiplanicum* Saint-André and De Iuliis, 2001, the small Pliocene species of the Bolivian Altiplano, the femoral diaphysis is constricted and

the patellar trochlea reduced, but not to the degree in *M. americanum* (Saint-André and De Iuliis, 2001).

Tibia-fibula

The tibia of *M. sundti* (SGO PV 298; figure 2.E) is stockier and transversely expanded proximally and distally compared to that of *M. medinae* SGO PV 231; (see De Iuliis, 1996: pl. 108A), and thus resembles more that of *M. americanum* (see De Iuliis, 1996: pl. 106). The tibiae of *M. medinae* and, particularly, *M. tarijense* (see De Iuliis, 1996: pl. 107G) are relatively gracile and elongated, resembling that of *E. laurillardi* (see De Iuliis, 1996: pl. 105). As these descriptions (except for *E. laurillardi* and *M. americanum*) are based on single specimens, the distinctions noted may be tenuous. It may, however, be significant that a stockier tibia is associated with a femur that is also transversely expanded proximally and distally in *M. americanum* and *M. sundti*. The more gracile tibia of *E. laurillardi*, *M. tarijense*, and *M. medinae* is associated with a generally less expanded femur. The fibulae of *M. sundti* and *M. medinae* are each represented only by a small, proximal portion fused to the tibia.

Conclusions

The newly described remains (PIU M4530) from Ulloma, Bolivia, show several features that are inconsistent with the view that the remains should be assigned to *M. medinae*. The PIU skull and SGO skulls from Ulloma share, in addition to provenance, similarities (e.g., relatively robust, relatively short and high rostrum, dorsal profile raised centrally) that indicate they are probably conspecific. This applies as well to the mandibles (e.g., relatively robust, a more vertical anterior margin of the coronoid process that covers much or all of m4). These skull and mandible features are only subtly different from those of the SGO material from near Pica, Chile, but their association with distinctly different femoral and tibial morphologies is evidence supporting their validity as specific characters, certainly until additional and better preserved remains are discovered. The marked differences in femora provide strong evidence for a specific distinction between the Ulloma and Pica remains. This applies equally to the differences between the Ulloma material and that from Tarija, Bolivia, discussed above as belonging to *M. tarijense*. Based on these distinctions, *M. sundti* is apparently a valid species and its distinction from *M. medinae* and *M. tarijense* should be maintained.

Saint-André and De Iuliis (2001) discussed the possible relationships among several *Megatherium* species. Their preliminary phylogenetic analysis suggested that *M. americanum* and *M. altiplanicum* are sister species and form a clade with *M. medinae*. *M. tarijense* was omitted from their discussion. Although the material discussed here is limited, the femoral morphology of *M. sundti* (e.g., markedly concave lateral and medial diaphyseal margins, transversely expanded proximally and distally, at least some medial reduction of the patellar trochlea) is strongly similar to that of *M. americanum* and *M. altiplanicum* and suggests that it may be closely related to this clade and form a monophyletic group with these species that excludes *M. medinae*. The relationships of *M. tarijense* are not discussed here, as work on this species is in progress by G. De Iuliis, G. Tito, and F. Pujos.

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