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ORIGINAL PAPER

New Remains of *Megathericulus patagonicus* Ameghino, 1904 (Xenarthra, Tardigrada) from the Serravallian (Middle Miocene) of Bolivia; Chronological and Biogeographical Implications

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Abstract In this contribution, we describe new remains (skull and humeri) of the Megatheriinae *Megathericulus patagonicus* Ameghino, 1904, recovered from the middle Miocene fossiliferous locality of Quebrada Honda, Bolivia. We also discuss the taxonomic, biogeographical, and chronological relevance of this discovery. Referral of the new specimens described here to *Megathericulus patagonicus* is based on metric and morphological similarities with the holotype and a humerus that has been referred to this species. Shared features include: 1) molariforms that are mesiodistally compressed and rectangular in outline; 2) a relatively less compressed M1 with labial and lingual margins that converge slightly mesially; 3) a very long premolariform portion of the maxillae (rostrum); 4) anteriorly divergent lateral edges of the maxillae; 5) a prominent, median V-shaped notch (apex posterior) between the articular surfaces of the maxillae and premaxillae; and 6) a long, gracile humerus with a prominent anterolaterally positioned deltopectoral crest on the anterior surface and a clearly evident lateral musculo-spiral channel. Precise geographic and stratigraphic data exist for the described remains, which are closely associated with a tuff dated at 12.2–12.5 Ma (Serravallian, middle Miocene), making it the first accurately dated specimen referred to *Megathericulus* Ameghino, 1904.

Keywords Megatheriinae · Folivora · South America · Ground sloths · ^{40}Ar/^{39}Ar dating · U-Pb dating

Introduction

At present, the fossil record of Megatheriinae (Tardigrada, Megatheriidae) extends from the middle Miocene of Patagonian Argentina to the early Holocene of Argentina and Brazil, when the subfamily was represented by *Megatherium* Cuvier, 1796, and *Eremotherium* Spillmann, 1948. Although recent efforts have increased our knowledge of older (middle to late Miocene) megatheriines of South America (e.g., Carlini et al. 2002a, 2006; De Iuliis et al. 2004, 2008; Brandoni 2006; Brandoni and De Iuliis 2007; Brandoni and Scillato-Yané 2007; Brandoni and Carlini 2009; Brandoni et al. 2012; Pujos et al. 2013), the generally fragmentary nature of the remains has resulted in a relative

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dearth of studies compared to those focusing on geologically younger species. In approximate chronological order, the list of valid megatheriine genera from the Miocene of South America currently includes: *Megathericulus* Ameghino, 1904, *Eomegatherium* Kraglievich, 1926, *Promegatherium* Ameghino, 1887, *Megatheridium* Cabrera, 1928, *Anisodontherium* Brandoni and De Iuliis, 2007, *Pliomegatherium* Kraglievich, 1930, *Megatheriops* C. Ameghino and Kraglievich, 1921, *Pyramiodontherium* Rovereto, 1914, and *Urumaquia* Carlini et al., 2006.

Among Megatheriinae, *Megathericulus* is the geologically oldest and earliest-diverging (most primitive) genus and is traditionally represented by two species: *Megathericulus patagonicus* Ameghino, 1904, and *Megathericulus primaevus* Cabrera, 1939, (but see De Iuliis et al. 2008 for a different point of view). *Megathericulus patagonicus* was described by Ameghino (1904) and was originally recorded from the lower levels of exposures near Laguna Blanca (Chubut Province, Argentina) that were referred to the middle Miocene (Kraglievich 1930; Bondesio et al. 1980; Scillato-Yané and Carlini 1998); several other remains have been recovered from the Río Mayo Formation since that time (middle Miocene of Chubut and Santa Cruz provinces, Argentina; Brandoni 2006; De Iuliis et al. 2008). *Megathericulus primaevus* was originally recorded at Cañadón Ftamichi (near Paso Flores, Neuquén Province) in levels considered to be middle Miocene in age (see Cabrera 1939; Scillato-Yané and Carlini 1998). *Megathericulus* sp. was recently recorded from the middle Miocene of Peruvian Amazonia (Pujos et al. 2013), and the genus has also been mentioned for the Collón Curá Formation (middle Miocene of Río Negro Province; Bondesio et al. 1980).

In Bolivia, Megatheriinae are represented by *Eremotherium sefvei* De Iuliis and Saint-André, 1997, from the Pleistocene of Ulloma, and by four species of *Megatherium*: *M. americanum* Cuvier, 1796, *M. tarijense* Gervais and Ameghino, 1880, *M. sundti* Phillipi, 1893, and *M. altiplanicum* Saint-André and De Iuliis, 2001. Among them, *M. altiplanicum* is recorded from the Pliocene, whereas *M. tarijense*, *M. sundti*, and *M. americanum* are recorded from the Pleistocene (Saint-André and De Iuliis 2001; De Iuliis 2006; De Iuliis et al. 2009). Apart from the study of Croft et al. (2016), which noted the presence of an indeterminate Megatheriinae from the Cerdas locality, no Miocene records of Megatheriinae from Bolivia are known with certainty. However, other types of ground sloths have been reported from the middle Miocene of Cerdas and Quebrada Honda (Carlini et al. 2002b; Croft et al. 2009; Pujos et al. 2011, 2014; Brandoni 2014).

The paleontological site of Quebrada Honda is located in southern Bolivia, near the border with Argentina, and has yielded one of the most diverse assemblages of middle Miocene continental vertebrates in South America (Croft 2007 and references therein; see also Croft et al. 2011; Engelman and Croft 2014; Cadena et al. 2015). In 2011, a well-preserved skull, associated teeth, and some postcranial remains of a megatheriine sloth were collected at Quebrada Honda through ongoing collaborative field investigations by personnel of the Universidad Autónoma Tomás Frías (Potosí, Bolivia), Case Western Reserve University (Cleveland, Ohio), and the Universidad Nacional de La Plata (Argentina). In this contribution, we provide an initial description of these remains, which will be described and illustrated in greater detail in a subsequent work, refer them to *Megathericulus patagonicus*, and discuss the taxonomic, biogeographical, and chronological relevance of this discovery. We also refer a second specimen from the same area, a nearly complete humerus, to this species.

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study. All relevant information is included in the article itself. Additional details about dating can be requested directly from P.D. Gans.

Geological Setting

Late middle Miocene vertebrate fossils from the Quebrada Honda area (ca. 21°57′ S, 65° 9′ W; Fig. 1) were first reported by Hoffstetter (1977). In the ensuing 40 years, a variety of international research teams have investigated the paleontology and geology of the site. Nonetheless, the geological formation yielding Quebrada Honda fossils has yet to be formally named, though it has been mapped as the Honda Group by the Servicio Geológico de Bolivia (GEOBOL). Its age is well constrained. MacFadden et al. (1990) published two $^{40}K/^{40}Ar$ dates for outcrops near the town of Quebrada Honda: a mean sanidine date from near the base of the formation (Unit 9) of 12.83 ± 0.7 Ma, and a mean biotite date from near the top of the formation (Unit 17) of 11.96 + 0.11. They also published two paleomagnetic profiles, one for the same outcrops and another for potentially correlative outcrops located 5–6 km to the north (see below). MacFadden et al. (1990) correlated the two basalmost local paleomagnetic zones of the Quebrada Honda outcrops – from which most fossils derive – to C5AAn and C5Ar.3r of the geomagnetic polarity time scale (GPTS), resulting in an extrapolated age of ca.13.0–12.7 Ma. This corresponds to a slightly older interval (13.2–12.9 Ma) within the Serravallian Age (13.8–11.6 Ma; Gradstein et al. 2012) based on the most recent iteration of the GPTS (Ogg 2012).

As alluded to above, other outcrops of the Honda Group in the general vicinity of the town of Quebrada Honda have also yielded vertebrate remains. These other outcrops have yet to be constrained by radioisotopic dates but are assumed to be roughly correlative based on the low stratigraphic dip of Honda Group strata and the overall similarities in mammal faunas (MacFadden et al. 1990; also pers. observ. and ongoing research). The most fossiliferous of these outcrops

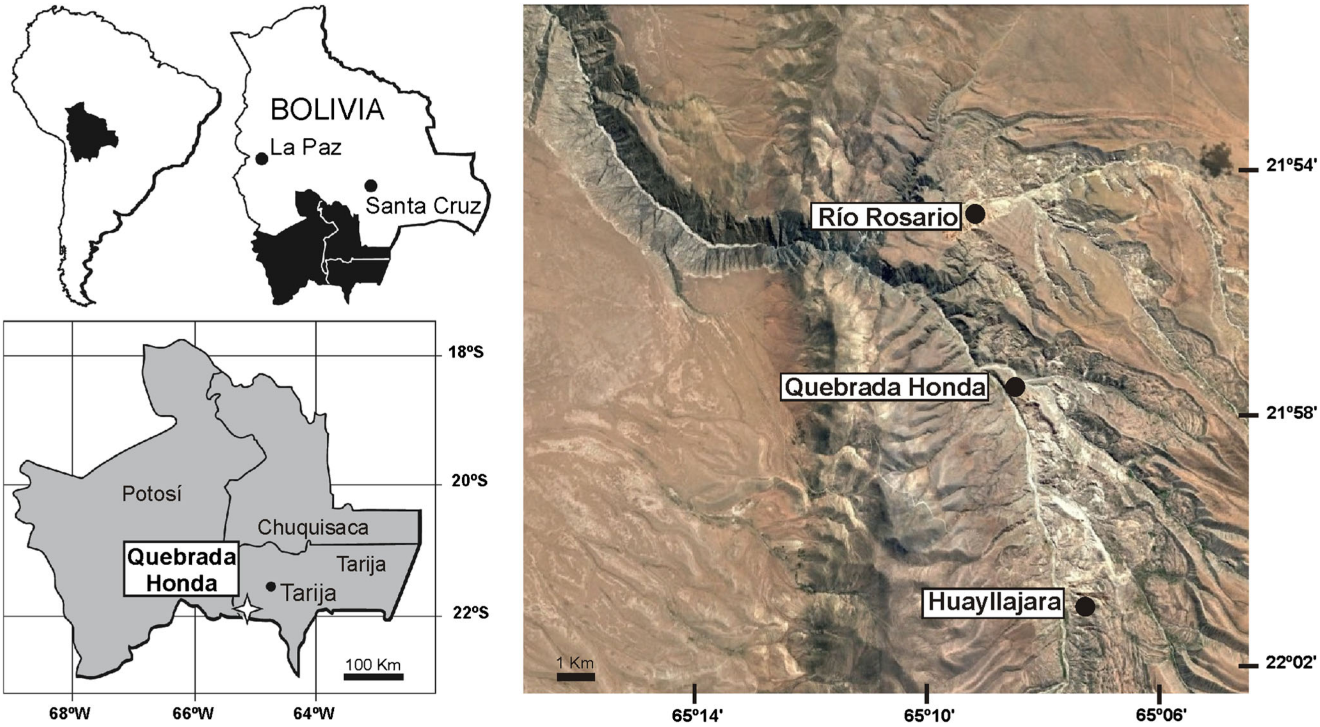

Fig. 1 Geographic context of Quebrada Honda, Bolivia

are those that have been referred to as Río Rosario (cf. MacFadden et al. 1990), which are located in the east-west trending Quebrada Rosario, roughly halfway between the towns of Quebrada Honda and Papachacra. Río Rosario outcrops are best exposed and most fossiliferous along the south side of the Quebrada Rosario, and this is where MacFadden et al. (1990) measured their second local paleomagnetic section. This section could not be precisely correlated to that of Quebrada Honda due to a lack of one-to-one correspondence between the paleomagnetic zones, but MacFadden et al. (1990) estimated the age of Río Rosario fossils at roughly 13.0–12.5 Ma. Based on Ogg (2012), this would correspond to roughly 13.2–12.8 Ma.

Fossiliferous outcrops of the Honda Group are also present on the opposite (north) side of the Quebrada Rosario. Most of the exposures are slumps that represent paleolandslides, precluding precise geological and chronological correlations with Quebrada Honda and Río Rosario outcrops. Nonetheless, some important fossils have been described from these exposures, including the holotype of the predatory marsupial (sparassodont) *Acyon myctoderos* Forasiepi et al., 2006 (see Forasiepi et al. 2006) and a partial skeleton of the same species (Engelman et al. 2015).

To emphasize the geographic distinctiveness of the Quebrada Honda and Río Rosario outcrops and their potentially (albeit slightly) different ages, Croft et al. (2011) used the terms Quebrada Honda Local Fauna and Río Rosario Local Fauna, respectively, to refer to these assemblages; these same authors reserved use of the term Quebrada Honda Fauna for the fossils of the Honda Group as a whole (i.e., of all local faunas). Engelman et al. (2015) extended this scheme by introducing the term Papachacra Local Fauna to refer to the assemblage derived from the north side (Papachacra side) of the Quebrada Rosario.

The partial megatheriine skeleton described herein (UATF-V-001414) was collected from the north side of the Quebrada Rosario (Fig. 1) and thus pertains to the Papachacra Local Fauna. It was collected at S 21°54′ 31.86″, W 65° 9′ 10.40″, ca. 8 m above the floor of the quebrada at an elevation of 3535 m. The specimen was collected in situ, as was a sample from a nearby (2 m distant) reworked ash fall tuff from the same stratigraphic level as the fossil. The tuff was analyzed at the Laboratory for Argon Geochronology at the University of California, Santa Barbara using two methods: ^{40}Ar/^{39}Ar dating of plagioclase, which yielded an estimated age of 12.32 ± 0.14 Ma, and U-Pb dating of individual zircon crystals, which yielded two populations with ages of 12.35 ± 0.15 Ma and 13.00 ± 0.15 Ma. The close concordance between the ^{40}Ar/^{39}Ar date and that of the younger population of zircons strongly suggests the sampled tuff is approximately 12.35 Ma (and that the older zircons were reworked from older tuffs in the area). This age is within the range for the entire section published by MacFadden et al. (1990) and compatible with the interpretation that the sediments containing UATF-V-001414 and the associated tuff were moved down section en masse from their original position by a paleolandslide. Thus, UATF-V-001414 likely derives from sediments stratigraphically higher than those producing the bulk of specimens from the Quebrada Honda Fauna.

The second specimen described herein, a nearly complete left humerus (UATF-V-001163), was collected in outcrops ca. 7.5 km to the south of the town of Quebrada Honda and ca. 3 km southwest of the town of Huayllajara, at S 22° 1′ 4.32″, W 65° 7′ 29.70″ (Fig. 1). These outcrops correspond to the same geological unit as those of Quebrada Honda and the Quebrada Rosario. To our knowledge, fossils have not previously been reported from this region, which we here refer to as the Huayllajara Local Fauna. Studies of the stratigraphic relationships among these areas are ongoing (including paleomagnetic and radioisotopic analyses), so the stratigraphic position of UATF-V-001163 relative to specimens from other local faunas is not known with certainty. However, it was collected in reddish-brown mudstones similar to those of the basal levels at both Quebrada Honda and the Quebrada Rosario, suggesting that it could be of similar age to most specimens from these areas (i.e., Serravallian age, ca. 13 Ma).

MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; **UATF-V**, Universidad Autónoma Tomás Frías-Vertebrate Paleontology Collection, Potosí, Bolivia.

Systematic Paleontology

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

Megathericulus Ameghino, 1904

Type species: *Megathericulus patagonicus* Ameghino, 1904.

Geographic and stratigraphic distribution: Laguna Blanca, southwestern of Chubut Province, Argentina (Río Mayo Formation, early middle Miocene); Cañadón Ftamichi, Paso Flores, Neuquén Province, Argentina (Collón Curá Formation, early middle Miocene); Río Collón Curá, Río Negro Province, Argentina (Collón Curá Formation, early middle Miocene); Cerro Guenguel, northwestern Santa Cruz Province, Argentina (Río Mayo Formation, late middle Miocene); Arroyo El Pedregoso, southwestern Chubut Province, Argentina (Río Mayo Formation, late middle Miocene); and SEP 07 locality, southeastern Peru (Ipururo Formation, middle Miocene) (see Kraglievich 1930; Bondesio et al. 1980; Scillato-Yané and Carlini 1998; De Iuliis et al. 2008; Pujos et al. 2013); Papachacra and Huayllajara local faunas, southern Bolivia (unnamed formation of the Honda Group, late middle Miocene) (this work; see below).

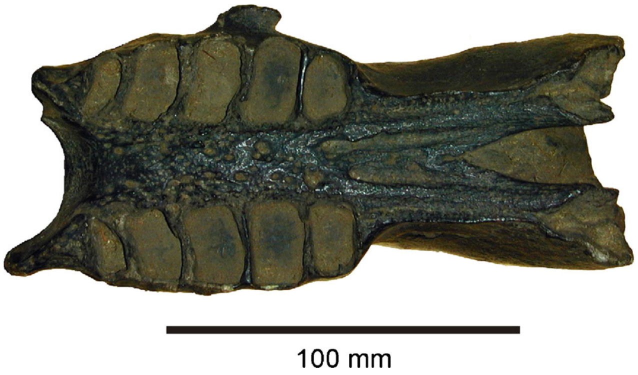

Fig. 2 *Megathericulus patagonicus* Ameghino, 1904. MACN A 11151 (holotype), anterior part of the skull in palatal view

Megathericulus patagonicus Ameghino, 1904

Holotype: MACN A 11151, anterior portion of cranium with edentulous palate (Fig. 2) and complete right astragalus.

Referred material: UATF-V-001414, nearly complete skull without mandible (Fig. 3), two isolated upper teeth (molariforms, M), nearly complete right humerus (Fig. 4a, d), and articulated but fragmentary bones of the distal forelimb; UATF-V-001414 is an adult specimen as all cranial sutures are closed and growth plates are absent in the postcranial bones. UATF-V-001163, mostly complete left humerus in three pieces (Fig. 4b, e).

Geographic and stratigraphic provenance: Unnamed formation of the Honda Group, late middle Miocene (Serravallian age), southern Bolivia (see above).

Description

The skull of UATF-V-001414 lacks jugals and premaxillae, and only the distal half of the last molariform on the left side remains in its alveolus. It measures 333 mm in total length. The preserved rostrum is quite long, despite the loss of the premaxillae.

In dorsal view (Fig. 3a), the skull is long and slender with its greatest width at the level of the zygomatic root of the maxilla and at the mastoid region. It is narrowest at the anterior level of the zygomatic root of the maxilla and increases in width anteriorly along the preserved rostrum. The skull is also narrow just anterior to the orbital wall of the zygomatic root of the maxilla; there is an interorbital constriction at the midpoint of the orbital area from where it increases in width gradually up to the squamosal zygomatic root. The temporal fossae have borders that are convex anteriorly and posteriorly and straight medially (parallel to the sagittal plane). They converge with

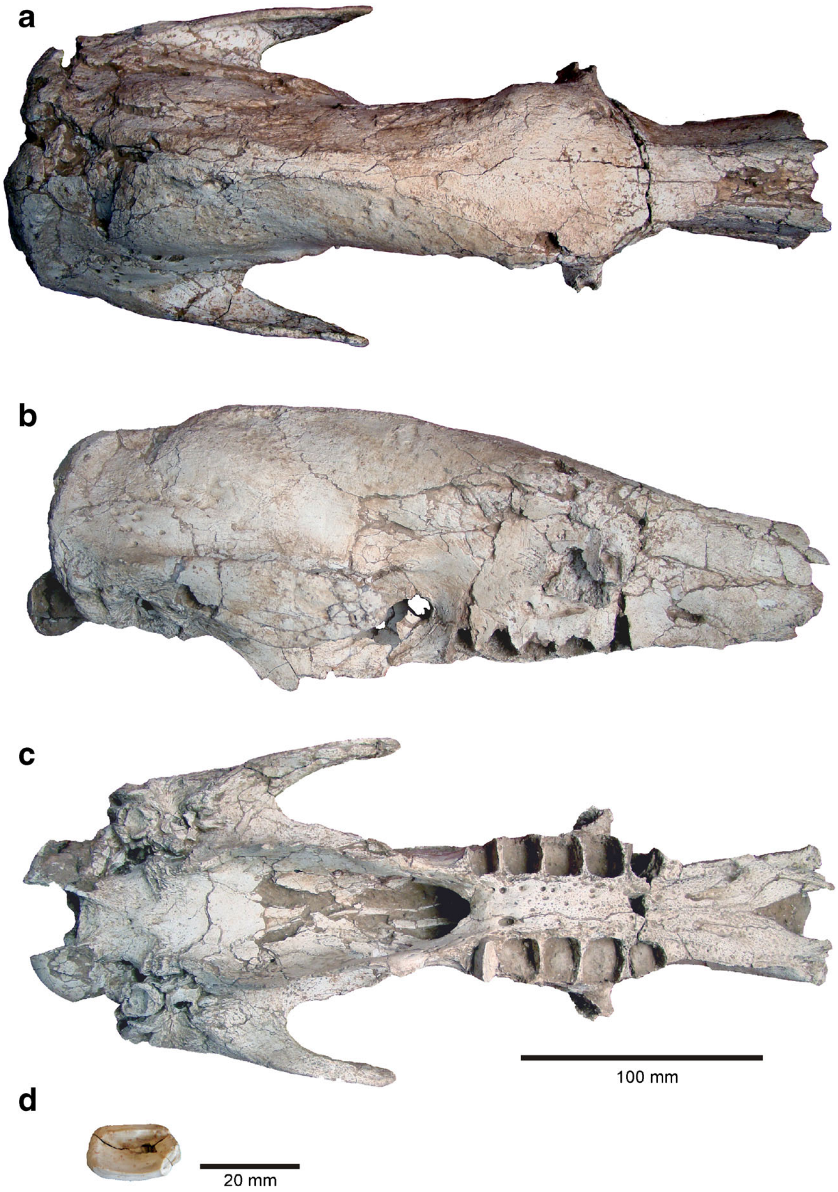

Fig. 3 *Megathericulus patagonicus* Ameghino, 1904. UATF-V-001414, nearly complete skull without mandible; **a** dorsal view; **b** lateral view; **c** palatal view; **d** molariform in occlusal view

one another near the midline of the skull roof and have a shared border that starts near the level of the interorbital constriction and extends posteriorly to the squamosal zygomatic root; although no sagittal crest is formed, the shared medial border is elevated (Fig. 3a). The postorbital processes are poorly developed. The posterior part of the skull roof is somewhat fragmented, and its unmodified anatomy cannot be discerned.

In lateral view (Fig. 3b), the skull is relatively low and conical in outline, narrowing anteriorly. The dorsal margin of the skull is slightly convex at its middle third and descends gradually anteriorly. The occipital plane is vertical and perpendicular to the rear fifth of the skull roof. The maxillary zygomatic root is anteroposteriorly short and positioned between the coronal plane of the anterior margin of the M2 and the midpoint of the M3; the infraorbital foramen is 20 mm above the alveolar margin. The squamosal zygomatic root is low, triangular, and horizontally flat. The zygomatic apophysis projects anteriorly, is flat in the sagittal plane, and has a ventral margin that is slightly convex and almost at the same level as the alveolar margin; its anterior tip reaches the same plane as the contact between the palate and pterygoids (Fig. 3b). Although the orbital region is not well preserved, some foramina and other structures can be identified. The sphenopalatine foramen is large and subcircular in outline. The sphenorbital fissure and optic foramen are positioned posterior to and slightly above the sphenopalatine foramen and are covered laterally by a bony lamina that delimits an anteroventral to posterodorsal channel. (This structure is only preserved on the right side of the specimen.) The foramen ovale is positioned at the same dorsoventral level as the sphenopalatine foramen and posterior to the sphenorbital

Fig. 4 *Megathericulus patagonicus* Ameghino, 1904. **a**,**d** UATF-V-001414, nearly complete right humerus; **b**,**e** UATF-V-001163, mostly complete left humerus in three pieces; **c**,**f** MLP 91-IX-7-18; distal portion of a left humerus. **a-c**, anterior view; d-f, posterior view

fissure + optic foramen. The occipital condyles are above the alveolar level at a distance equal to its dorsoventral height.

In palatal view (Fig. 3c), the premolariform area is long (even considering that the premaxillaries are not preserved) and narrow, and wider distally. Its preserved length is similar to the length of the toothrow and 2.5× the width between the medial walls of the M1s. Two proximal palatine foramina are present that continue anteriorly as a pair of progressively wider furrows. The anterior part of the palate ends in a V-shaped notch that points posteriorly, and its apex is positioned ca. two-fifths the distance from the anterior to posterior end of the premolariform portion of the palate. The lateral margins of the premolariform palate are straight and distally divergent. The palate is markedly flat (mainly the premolariform portion); the premolariform and molariform (alveolar toothrows) areas are at the same plane, and several vascular foramina are present in the latter. The posterior palatal notch is nearly U-shaped, and its anterior margin is at the level of the posterior wall of the M5 alveoli. At the molariform portion, the palatal width (25 mm) is slightly larger than the largest alveolus width (M2 to M4, 17–20 mm). The ventral portion of the vertical lamina of the pterygoids is lost on both sides; only the dorsal part of the pterygoids is preserved, as a thin lamina fused with the basilar plate. The occipital condyles are transversely expanded and project posteriorly beyond the level of the occipital plane. The medial margin of the occipital condyles is straight, and the external articular face is rounded. The ectotympanic is U-shaped, opens upward, and delimits the external acoustic meatus, which is circular in outline. Between the occipital condyle and the ectotympanic ring, there is a wide, subcircular, and slightly concave styloid fossa.

The upper toothrow (M1-M5) is nearly 80 mm in length. Each toothrow is slightly convex externally and nearly straight lingually (Fig. 3c). Beyond its straightness, there is maximum distance between toothrows between each anterior margin of the M1, and each posterior margin of the M5. UATF-V-001414 only preserves part of the left M5 (in its alveolus) and two isolated teeth, M2? and M3?, that are anteroposteriorly compressed (ca. 11 mm x ca. 18 mm). The labial and lingual faces have shallow vertical grooves. On the occlusal surface are two transverse lophs (anterior and posterior) separated by a V-shaped valley (Fig. 3d). The left M5 is markedly anteroposteriorly compressed (7 mm × 16 mm) but lacks obvious lophs.

The humeri of UATF-V-001414 (Fig. 4a, d) and UATF-V-001163 (Fig. 4b, e) are relatively long and gracile (Table 1). In both specimens, an entepicondylar foramen is absent, the posterior surface is flattened and bears a shallow olecranon fossa, and the distal third of the diaphysis is markedly expanded mediolaterally (especially in UATF-V-001414 with a projected entepicondyle) and compressed anteroposteriorly. The greater and lesser tuberosities are large (their mediolateral width equals that of the humeral head) and separated by a distinct groove from a terminal rounded head. A very prominent and long deltopectoral shelf is present as a raised, wide, and flattened shelf located on the anteroproximal humeral surface. This structure is formed by the pectoral crest medially and deltoid crest laterally, which meet together just distal to the middle third of the diaphysis. The musculospiral groove, for the passage of the radial nerve, curves along the lateral surface of the deltoid crest from the posterolateral surface of the humerus to the anterior surface.

Comparisons

The skull of *Megathericulus* is relatively elongated and slender, similar to that of *Pyramiodontherium*, *Megatheriops*, and the Planopinae (e.g., *Planops* Ameghino, 1887, *Prepoplanops* Carlini et al., 2013); in the Pleistocene megatheriines (e.g., *Megatherium*, *Eremotherium*), it is more robust.

The rostrum of *Megathericulus patagonicus*, as represented only by the maxilla and the nasal, is very long. De Iuliis (1996) used the "Premolariform Maxillary Length Index" (PMMLI) to evaluate the length of the rostrum anterior to M1 relative to the length of the toothrow. The PMMLI is calculated by dividing the premolariform length of the maxilla (PMML of De Iuliis 1996) by the length of the toothrow and multiplying by 100. In UATF-V-001414, the upper toothrow equals 80 mm, and the premolariform length of the maxilla equals 80 mm, resulting in PMMLI =100. The PMMLI in the type specimen of *Megathericulus patagonicus* (MACN A 11151) is ca. 100; it is 60 in *Anisodontherium halmyronomum* (Cabrera, 1928), 45–55 in *Pyramiodontherium bergi* (Moreno and Mercerat, 1891), 48 in *Megatheriops rectidens* (Rovereto, 1914), 22–27 in *Eremotherium laurillardi* (Lund, 1842), and 9–16 in *Megatherium americanum* (see De Iuliis 1996; Brandoni and De Iuliis 2007). In addition, the index of PMML/width of the rostrum at the midpoint of M1, is ca. 2 in *Megathericulus*, >1 in *Anisodontherium*, *Pyramiodontherium*, and *E. laurillardi*, and <1 in *M. americanum* and *M. tarijense*. As in UATF-V-001414, the palatal width of the type specimen of *Megathericulus patagonicus* at the level of the dental series (22–25 mm) is similar to the largest alveolus width (24 mm), because the molariforms are extremely wide (Fig. 2).

The premolariform part of the palate of *Megathericulus patagonicus* is spatula-shaped (divergent anteriorly), similar to that of *Pyramiodontherium bergi* and *Py. brevirostrum* Carlini et al., 2002a. In contrast, in species of *Megatherium* (e.g., *M. americanum*, *M. tarijense*) and *E. laurillardi*, the lateral edges of the maxillary palate are subparallel, and in *Megatheriops rectidens*, they tend to be distally convergent.

In UATF-V-001414, the posterior palatal notch is nearly U-shaped, whereas in the holotype of *Megathericulus patagonicus*, it is U-shaped; in both specimens, the anterior margin of the palatal notch is at the level of the posterior margin of M5. The distal margin of the posterior palatal notch is at the level of the posterior margin of M4 in *Megatheriops rectidens*, and in *Megatherium tarijense*, it is V-shaped, and its mesio-distal margin is at M4 level. In *E. laurillardi* and *M. americanum*, each of which is represented by several skulls, the shape and position of the posterior palatal notch has certain variability.

As mentioned previously, the skull of UATF-V-001414 is narrow in the orbital area anterior to the zygomatic root of the maxilla and increases gradually in width from the interorbital constriction to the squamosal zygomatic root; in contrast, both

Table 1 Measurements (in mm) of humeri referred to *Megathericulus patagonicus* Ameghino, 1904. * = estimated

	Total Length	Proximal Width	Diaphysis Width	Distal Width	Distal Facet Width
UATF-V-001414	*360	116	53	155	98
UATF-V-001163	ca. 382	104	64	136	91
MLP 91-IX-7-18			65	162	96

orbital walls are nearly parallel in *E. laurillardi*, *M. americanum*, and *Megatheriops rectidens*.

In UATF-V-001414, as described previously, the maxillary zygomatic root is placed between the plane of the anterior margin of the M2 and the middle of the M3; this contrasts with its position in *A. halmyronomum* and *Pyramiodontherium* spp., where it is between the M1–M2 alveolar septum and the middle part of the M3, and in *Megatheriops rectidens*, in which it lies between the middle part of the M2 and the middle of M3 (Brandoni 2006; Brandoni and De Iuliis 2007). The abundant skull remains of *E. laurillardi* and *M. americanum* suggest that the position of this root also has certain variability. In *E. laurillardi*, the root tends to be placed from the middle of M1 to the anterior part of M3, whereas in *M. americanum*, the root may extend from between the M1–M2 alveolar septum and the posterior half of M3 to between the posterior half of M2 to the M3–M4 alveolar septum (De Iuliis 1996; Brandoni and De Iuliis 2007).

In UATF-V-001414, the occipital condyles are in a horizontal plane slightly above the level of the alveolar margin; the condyles are more dorsally placed in *A. halmyronomum*, *Megatheriops rectidens*, *Py. bergi*, and *E. laurillardi*. In *Megatherium* spp. (e.g., *M. americanum*, *M. tarijense*, *M. sundti*), the condyles are even more dorsal.

The most notable feature of the dentition of UATF-V-001414, as shown by the alveoli, is that the molariforms are mesiodistally compressed (especially M2-M5) rather than isodiametric (subequal length and width). Mesiodistal compression of the molariforms also occurs in *Anisodontherium* and "*Eomegatherium" andinum*. In *Pyramiodontherium*, *Megatheridium*, *Megatheriops*, *Pliomegatherium*, *Megatherium*, and *Eremotherium*, the molariforms are isodiametric, but their cross-sections vary in shape from rectangular to trapezoidal (see Brandoni et al. 2012).

As in several pre-Pleistocene species of Megatheriinae, the humerus of *Megathericulus patagonicus* is relatively slender (Fig. 4). An index that has been used to evaluate humeral robustness is the Humerus Robustness Index (HRI), calculated as: distal transverse width/total length × 100 (Brandoni et al. 2012). In megatheriines with a robust humerus (*Megatherium*, *Eremotherium*), HRI > 40 (42 for *M. tarijense*, 45–50 for *M. americanum*, and 42–46.5 for *E. laurillardi*); in megatheriines with a slender humerus (e.g., *Pyramiodontherium*, *Megatheriops*), HRI < 40 (38 for *Megatheriops rectidens*; 33 for *Pyramiodontherium scillatoyanei* De Iuliis et al., 2004). The index cannot be precisely calculated in either specimen from the Quebrada Honda area, but HRI is estimated at ca. 43 in UATF-V-001414 based on its estimated length, and ca. 35.6 in UATF-V-001163. The high value of HRI in UATF-V-001414 is probably due to the projection of the entepicondyle.

Megatheriops rectidens and *Py. scillatoyanei* possess a raised deltopectoral shelf, whereas in larger Pleistocene species (*M. americanum*, *M. tarijense*, *E. laurillardi*), the deltopectoral shelf is reduced to an elongated, triangular ridge (De Iuliis et al. 2008). Despite obvious general similarities with megatheriines, the humeri from Quebrada Honda also resemble the long, gracile humeri of Megalonychidae and Planopinae. As in other megatheriines, the entepicondylar foramen is not present in these specimens, but unlike most megatheriines, the humeri have a very pronounced and extended deltopectoral shelf. The musculospiral groove is also clearly evident, as occurs in many other tardigrades (e.g., primitive megatheriids, megalonychids, mylodontoids) but not in most Quaternary megatheriines.

Discussion

Megathericulus was founded by Ameghino (1904) based on remains that represent the type species of *Megathericulus patagonicus* (MACN A 11151; Fig. 2). Two other species, *M. friasensis* Kraglievich, 1930, and *M. primaevus*, were later described from the middle Miocene of Patagonian Argentina, although *M. friasensis* was recovered from an area that today pertains to Chile. *Megathericulus friasensis* was erected on a fragment of skull (MLP 2–203) that probably corresponds to a Scelidotheriinae (see Kraglievich 1930; Brandoni 2006; De Iuliis et al. 2008). Similarly, the type specimen of *M. primaevus* (MLP 39-VI-24-1), which consists of an astragalus, distal part of a femur, and metacarpal III, among other bone fragments, was considered by De Iuliis et al. (2008) as having features common to several other ground sloths, indicating that it may not be appropriate to refer it to Megatheriinae.

Pujos et al. (2013) referred an edentulous dentary (MUSM 1564) to *Megathericulus* sp. from the middle Miocene of Peru and transferred *Eomegatherium andinum* Kraglievich, 1930, and *Eo. cabrerai* Kraglievich, 1930, to *Megathericulus* (as *Megathericulus andinum* and *Megathericulus cabrerai*). Regarding *Eomegatherium*, *Eo. andinum* was described based on the specimen MLP 2–204 (a fragmentary dentary without teeth and small portions of skull), and *Eo. cabrerai* was described based on MLP 2–206 (a fragment of a skull, a proximal portion of a left ulna, and a fragment of a left astragalus). Thus, the remains on which *Eo. andinum* and *Eo. cabrerai* were erected are so fragmentary that it is not possible to make precise comparisons among them and known specimens of *Megathericulus*. The few anatomical features that are comparable among the mentioned species pertain to the dentary, astragalus, and proximal portion of ulna (see Brandoni 2006; De Iuliis et al. 2008; Pujos et al. 2013); however, the dentary of *Eo. andinum* is too poorly preserved to resolve its validity or generic assignment and the astragalus fragment of *Eo. cabrerai*, although superficially similar to that of *Megathericulus patagonicus* (see Brandoni 2006; Pujos et al. 2013), also resembles that of *Eo. nanum* (Burmeister, 1891) (type species of *Eomegatherium*) in size and shape (Brandoni 2006). Thus, it is not possible to strongly establish whether *Eo. cabrerai* and *Eo. andinum* should be referred to *Eomegatherium* or *Megathericulus*. Until new, more complete remains are found that shed light on these taxa, we think it preferable to refer to *Eo. andinum* and *Eo. cabrerai* as "*Eomegatherium*" *andinum* and "*Eomegatherium*" *cabrerai* (see Bengtson 1988, for a discussion of the use of quotation marks and open nomenclature). This leaves *M. patagonicus* as the only well-characterized species of the genus.

Referral of the new specimens described here (UATF-V-001414, UATF-V-001163) to *Megathericulus patagonicus* is based on metric and morphological similarities with the holotype (MACN A 11151; Fig. 2) and a humerus that has been referred to this species (MLP 91-IX-7-18; Fig. 4c,f; see De Iuliis et al. 2008). Shared features include: 1) molariforms that are mesiodistally compressed and rectangular in outline; 2) a relatively less compressed M1 with buccal and lingual margins that converge slightly mesially; 3) a very long premolariform portion of the maxillae (rostrum); 4) anteriorly divergent lateral edges of the maxillae; 5) a prominent, median V-shaped notch (apex proximal) between the articular surfaces of the maxillae and premaxillae; and 6) a long, gracile humerus with a prominent and anterolaterally positioned deltopectoral shelf on the anterior surface and a clearly evident lateral musculo-spiral channel.

The most peculiar features of the skull of *Megathericulus patagonicus* are the length of the rostrum and the shape of the molariforms. The rostrum is very long, similar to that of Planopinae (e.g., *Planops*, *Prepoplanops*), with a high PMMLI value (ca. 100), although this value could be related to the shape of the molariforms. During the course of megatheriine evolution, both body size and molariform size generally increased (Brandoni et al. 2012). However, this size increase did not occur evenly in the molariforms, with the anteroposterior length of these teeth generally exceeding their labiolingual width (Kraglievich 1930; Brandoni et al. 2012; Pujos et al. 2013). Thus, while the molariforms of early megatheriines (e.g., *Megathericulus*, *Anisodontherium*) are usually rectangular in outline, those of Quaternary megatheriines are nearly square (i.e., more isodiametric). This increase in the anteroposterior length of each molariform resulted in an increase in the relative length of the molariform toothrow which, in turn, resulted in a relatively longer toothrow in Quaternary megatheriines (e.g., *Megatherium*, *Eremotherium*). As mentioned previously, *Megathericulus patagonicus* has a PMMLI close to 100; this high value could be the result of its anteroposteriorly compressed molariforms (shorter than the Quaternary megatheriines) combined with a long predental region of the rostrum.

The geographic and stratigraphic provenances of the type remains on which *Megathericulus* species are based are unknown (e.g., the exact geographic location of "Laguna Blanca" locality is unknown). However, accurate geographic and stratigraphic data are available for several referred specimens including MLP 91-IX-7-18, MLP 92-XI-15-2, MUSM 1564, and the specimens described herein. MLP 91-IX-7–18 was recovered from the Cerro Guenguel locality (Río Mayo Formation), where an underlying level has been dated preliminarily at ca. 11.8 Ma (^{40}Ar/^{39}Ar; Madden et al. 1997), making the fossils younger than this age (De Iuliis et al. 2008). MLP 92-XI-15-2 was recovered from the Arroyo Pedregoso locality, also from the Río Mayo Formation. At both localities, the Río Mayo Formation overlies the Arroyo Pedregoso Formation, which has been dated at 12.18 +/− 0.15 Ma (^{40}Ar/^{39}Ar from plagioclase; Dal Molin and Franchi 1996). MUSM 1564 was recovered from the SEP-007 locality in southeastern Peru (Pujos et al. 2013) and corresponds to the Fitzcarrald Local Fauna, which has been referred to the Laventan South American Land-Mammal Age (SALMA) on biostratigraphic grounds (see Tejada-Lara et al. 2015 and references therein). The Laventan SALMA corresponds to the late middle Miocene (Serravallian age; 13.5–11.8 Ma; Madden et al. 1997), but independent age constraints are lacking for the Fitzcarrald Local Fauna.

As detailed in Geological Setting, precise geographic and stratigraphic data exist for both UATF-V-001414 and UATF-V-001163. The former is closely associated with a tuff dated at 12.5–12.2 Ma, making it the first accurately dated specimen referred to *Megathericulus*. This specimen is likely older than those from the Río Mayo Formation referred to *M. patagonicus*, but this cannot be determined with certainty given that detailed stratigraphic and analytical data have not been published for radiometric dates from the Río Mayo and Arroyo Pedregoso formations. UATF-V-001163 from the Huayllajara Local Fauna may date to 13.2–12.8 Ma, like the bulk of the Quebrada Honda Fauna, but this remains to be verified through ongoing geological studies in the region. If confirmed, this specimen will represent the oldest record for *Megathericulus* and may help establish a securely dated range of up to one million years for the species in southern Bolivia.

Megathericulus shows characters that are presumably ancestral for Megatheriinae (e.g., molariforms that are mesiodistally compressed and rectangular in outline, very long rostrum, long and gracile humerus with a prominent and laterally positioned deltopectoral shelf), suggesting it is an early-diverging taxon with respect to other members of the subfamily (Brandoni 2006; Pujos 2006). Traditionally, the subfamily Megatheriinae has been considered to be the sister group of Planopinae (i.e., *Planops*, *Prepoplanops*), with both included in Megatheriidae (De Iuliis 1994; Gaudin 2004). However, a recent phylogenetic analysis by Amson et al. (2016) found the genus *Thalassocnus* Muizon and McDonald, 1995, to be the sister group of Planopinae +

Megatheriinae and thus to represent a third subfamily within Megatheriidae (Thalassocninae). Amson et al. (2016) also found Megatheriidae to be the sister taxon of Nothrotheriidae (e.g., *Nothrotherium* Lydekker, 1889, *Nothrotheriops* Hoffstetter, 1954, "*Xyophorus*" Ameghino, 1887) as in previous analyses (e.g., Gaudin 2004). An undetermined Megatheriinae (Croft et al. 2016) and "*Xyophorus*" cf. *bondesioi* (see Croft et al. 2009; Brandoni 2014) at the locality of Cerdas represent the oldest records of the subfamilies Megatheriinae and Nothrotheriinae, respectively, suggesting that both of these groups and perhaps their common ancestor may have originated and/or had their center of dispersion in low or middle latitudes of South America and later dispersed into higher and lower latitudes.

The presence of *Megathericulus patagonicus* at Quebrada Honda increases the known sloth diversity in the fauna to five species, with previously documented species including the nothrotheriids "*Xyophorus*" sp. (see discussion in Croft et al. 2009; Brandoni 2014), *Lakukullus anatisrostratus* Pujos et al., 2014, a large mylodontid known only from fragmentary remains (Takai et al. 1984; Pujos et al. 2014; unpublished material in UATF-V collections), and *Hiskatherium saintandrei* Pujos et al., 2011, of uncertain affinities within Megatherioidea. This fauna is quite distinct from the roughly contemporaneous fauna of La Venta, Colombia, in which mylodontids are abundant and include three species.

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