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Anisodontherium from the Late Miocene of north-western Argentina

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The fossil record of Megatheriinae (Tardigrada, Megatheriidae) in Argentina extends from the Colloncuran (Middle Miocene of Patagonia) to the Lujanian (Late Pleistocene–Early Holocene of the Pampean region). In the Late Miocene of north-western Argentina, Megatheriinae is represented by just three species belonging to a single genus, Pyramiodontherium. Here, we describe a partial mandible and the phalanges of a third digit of the manus recovered from the Saladillo Formation (Upper Miocene) of Tucumán Province, and assign them to Anisodontherium sp. Anisodontherium is primarily characterized by mesiodistally compressed molariforms, an anterior margin of the coronoid process located posterior to m4, and a posterior margin of the mandibular symphysis located anterior to m1. While these features can also be observed in A. halmyronomum from the Arroyo Chasicó Formation (Buenos Aires Province, Pampean region), Anisodontherium sp. is smaller and more slender than the former. The shape of each molariform of Anisodontherium affects the total length of the molariform tooth row, and thus the interpretation of some characters used in cladistic and paleobiological analyses. The material described here adds to the knowledge of the mandibular and dental anatomy of early megatheriines. In addition, the occurrence of Anisodontherium in Tucumán Province provides the first record of this genus outside the Pampean region, and increases the diversity of megatheriines during the Late Miocene–Pliocene of north-western Argentina.

Key words: Xenarthra, Megatheriinae, Anisodontherium, ground sloths, diversity, Upper Miocene, Argentina.

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Introduction

Xenarths are characterized by a particular suite of skeletal modifications setting them apart from all other placental mammals (McDonald 2003). Molecular evidence indicates that they represent one of the four major mammalian clades (Delsuc et al. 2001, 2002; Madsen et al. 2001; Murphy et al. 2001; Moller-Krull et al. 2007; Delsuc and Douzery 2008; Prasad et al. 2008). Xenarthra, including fossil species, consist of two major clades: Cingulata (armadillos, pampatheres, and glyptodonts), characterized by the development of bony dermal armor and an omnivorous, carnivorous or herbivorous diet (see Vizcaíno 2009); and Pilosa, in turn comprising Vermilinguia and Tardigrada. While both of the latter two taxa pursue either terrestrial or arboreal lifestyles, Vermilinguia (anteaters) show marked adaptations to myrmecophagy, whereas Tardigrada (sloths and ground sloths) are generally herbivorous (see McDonald and De Iuliis 2008; Vizcaíno 2009; Brandoni et al. 2010).

The Tardigrada (sensu Latham and Davies 1795) constitute one of the characteristic mammalian groups of the Cenozoic of South America. After the Deseadan (Late Oligocene), tardigrades become abundant in the fossil record and are represented by several lineages, such as Megatheriidae, Nothrotheriidae, Megalonychidae, and Mylodontidae (Gaudin 2004, McDonald and De Iuliis 2008), which became especially diversified during the Late Miocene–Pleistocene.

The fossil record of Megatheriinae (Tardigrada, Megatheriidae) in Argentina extends from the Colloncuran (Middle Miocene of Patagonia) to the Lujanian (Late Pleistocene–Early Holocene of the Pampean region), when the clade was represented primarily by Megatherium americanum Cuvier, 1796. Although recent efforts (e.g., Carlini et al. 2002; De Iuliis et al. 2004, 2008; Brandoni 2006; Brandoni and De Iuliis 2007; Brandoni and Scillato-Yané 2007; Brandoni and Carlini 2009) have increased our knowledge of the older (Middle Miocene–Pliocene) megatheriines of Argentina, the often fragmentary nature of their remains has resulted in a relative...

In terms of species, Megatheriinae were represented in Argentina during the Late Miocene–Pliocene by *Pyramidodontherium bergi* (Moreno and Mercerat, 1891) from the provinces of Catamarca and Tucumán; *Pyramidodontherium brevirostrum* Carlini, Brandoni, Scillato-Yané, and Pujos, 2002, from Catamarca Province; *Pyramidodontherium scillatoyanei* De Iuliis, Ré and Vizcaíno, 2004, from La Rioja Province; *Plesiomegatherium hansmeyeri* Roth, 1911, from Jujuy Province (but see Brandoni and Carlini 2009); *Megatheriops rectidens* (Rovereto, 1914) from Mendoza Province; *Promegatherium smaltatum* Ameghino, 1883, *Pliomegatherium elongis* Kraglievich, 1926, *Eomegatherium nanum* (Burmeister, 1891) and *Pyramidodontherium* sp. (see Brandoni and Carlini 2009) from Entre Ríos Province; *Megatheridium annectens* Cabrera 1928 from Río Negro Province; and *Anisodontherium halmyronomum* (Cabrera, 1928) from Buenos Aires Province (Fig. 1A).

The fossil mammals from the Late Miocene–Pliocene beds of north-western Argentina have been intensely studied (see e.g., Moreno and Mercerat 1891; Rovereto 1914; Kraglievich 1934; Tauber 2005; Rodriguez Brizuela and Tauber 2006; Candela et al. 2007; Nasif et al. 2007). In the provinces of Catamarca and Tucumán, most of these fossils were found in the Andalhuála and Corral Quemado formations, which are among the most fossiliferous formations of the Late Miocene–Pliocene of Argentina (see Moreno and Mercerat 1891; Ameghino 1919; Riggs and Patterson 1939; Cabrera 1944; Castellanos 1946; Marshall and Patterson 1981). In the Province of Tucumán, fossil mammals have also been reported from the locality of Tiopunco (Ameghino 1919; Esteban and Abdala 1993), the Saladillo Formation (Powell and González 1997) and the India Muerta Formation (Babot and Ortiz 2008), with both Tiopunco (Ameghino 1919; Kraglievich 1934; Brandoni and Carlini 2009) and the Saladillo Formation (Powell and González 1997) having yielded remains of megatheriines.

The presence of a megatherine from the Saladillo Formation is based on several remains, including a mandible, vertebrae and fragments of a radius and ulna, which, though mentioned by Powell and González (1997), have so far neither been described nor figured. Among this material, a nearly complete mandible stands out as preserving several taxonomically important features commonly used in megatherine sys-
tematics. Here, we describe and compare these mandibular remains, as well as an associated digit III of the manus, and discuss their systematic, biogeographic and biochronological implications.

Institutional abbreviations.—CICYTTP-PV, Colección de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; MACN Pv, Colección Paleontología Vertebrados del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; PVL, Paleontología Vertebrados Lillo, Facultad de Ciencias e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina.

Other abbreviations.—HI, Hypsodonty Index; Ma, millions of years ago; m1−m4, lower molariform 1−4; SALMA, South American Land Mammal Age.

Geological setting

The fossils were found in strata assigned to the Saladillo Formation (= Hiladas del Saladillo, Peirano 1946), exposed near the area of Cerro Castillo de Las Brujas, Tucumán Province (Fig. 1B). The Saladillo Formation, which represents the basal unit of the Subgroup Santa María (Neogene), is separated from the underlying Eocene Lumbrera Formation by a paraconformity (Vergani et al. 1991), and in several places in turn overlain by the Upper Miocene San José Formation. At Cerro Castillo de Las Brujas, the lowermost levels of the Saladillo Formation consist of fluvial deposits of pink, red, brown and occasionally gray sandstone (ranging from fine to coarse), siltstone, and, albeit rarely, claystone. Rounded pumice clasts indicating the beginning of important volcanic activity are present close to the bone-bearing level, with the latter being located 28.40 m above the base of the formation.

Other rock units are present, including a 30 cm thick tuff level, with the latter being located 3 m below the fossil remains (Fig. 1C), indicating a K/Ar age of 10±0.3 Ma (Late Miocene) (González et al. 2000). The unit was locally dated based on a 30 cm thick tuff level, with the latter being located 28.40 m above the base of the formation.

Systematic paleontology

Xenarthra Cope, 1889
Tardigrada Latham and Davies in Forster, 1795
Megatheriidae Gray, 1821
Megatheriinae Gray, 1821
Genus Anisodontherium Brandoni and De Iuliis, 2007
Type species: Anisodontherium halmyronomum (Cabrera, 1928); Bank of the Arroyo Chasicó, near Chasicó Lagoon, Buenos Aires Province, Argentina, Arroyo Chasicó Formation (Upper Miocene).

Anisodontherium sp.

Referred material.—PVL 6425, a nearly complete mandible lacking both angular processes and the left articular condyle (Fig. 2A−C); and digit III of the manus (Fig. 2D), Cerro Castillo de Las Brujas (26° 38’ 07.26’S, 65° 50’ 53.04”W), Tucumán Province, Argentina, Saladillo Formation (Upper Miocene) (Fig. 1B).

Emended diagnosis (modified from Brandoni and De Iuliis 2007).—Low, elongated skull; palate flattened; lateral walls of rostrum rectilinear and parallel; short tooth row; anterior margin of coronoid process sigmoid; posterior margin of mandibular symphysis located anterior to m1 and rounded; both dentaries well separated; posterolateral opening of mandibular canal located at the base of the coronoid process, nearly on the alveolar plane; anterolateral opening of mandibular canal located anterior to posterior margin of mandibular symphysis; m4 anterior to anterior margin of coronoid process; lower molariforms small and mesiodistally compressed (especially m2 and m3); molariforms with a markedly deep, V-shaped valley between the transverse crests, particularly on m1; hard dentine, especially that of the anterior wall of each molariform, not well developed; anterior transverse crest of molariforms without a well-developed wear facet.

Description.—In lateral view (Fig. 2A, B), the ventral margin of the dentary is generally convex, but ascends posterior to the base of the m4 alveolus, thus forming a notch between the level of the alveolus and the angular process. In this PVL 6425 closely resembles Anisodontherium halmyronomum (see Brandoni and De Iuliis 2007: fig. 3A) and Plesiomega−therium hansommayeri (see Roth 1911: fig. 1), although the ventral bulge is more marked in those species.

While the angular processes of PVL 6425 are incompletely preserved, their broken bases suggest a ventral position, as also seen in Anisodontherium halmyronomum (see Brandoni and De Iuliis 2007: fig. 3A), Megatheriops rectidens, Megathericus patagonicus Ameghino, 1904 (see De Iuliis et al. 2008: fig. 2D), Eomegatherium andinum Kraglievich, 1930, Pliomegatherium lelongi (see Brandoni 2006: figs. 3.2, 4), Erenotherium laurillardii (Lund, 1842), and Megatherium tarjense Gervais and Ameghino, 1880 (see De Iuliis et al. 2009: fig. 2C); by contrast, the angular processes are more dorsally positioned in some species of Megatherium Cuvier, 1796, such as M. americanum and M. gallardoi Ameghino and Kraglievich, 1921 (see Brandoni et al. 2008: fig. 2C).

The anterior margin of the coronoid process is sigmoid in lateral view (Fig. 2A, B), with the ventral part being concave
and the dorsal part convex. The posterior margin of the coronoid process is concave. The highest point of the coronoid process is located 135 mm, and the articular condyle 100 mm above the alveolar plane. In *Eremotherium* Spillmann, 1948, the articular condyle is relatively low, whereas in *Mega−therium* it occupies a more dorsal position (De Iuliis and Cartelle 1999).

In PVL 6425, m4 lies anterior to the anterior margin of the coronoid process and is entirely visible in lateral view (Fig. 2B), as is the case in *Anisodontherium halmyronomonum* (see Brandoni and De Iuliis 2007: fig. 3A) and probably also *Megathericus patagonicus* (see De Iuliis et al. 2008: fig. 2C, D) and *Eomegatherium andinum*. In other megatheriines, m4 is located more posteriorly with respect to the coronoid process, although there is some variation in its exact position: in *Pliomegatherium lelongi*, the distal margin of m4 nearly coincides with the plane of the anterior margin of the coronoid process (Brandoni 2006: figs. 3.1–4); by contrast, in *Eremotherium comigrans* De Iuliis and Cartelle, 1999 (see De Iuliis and Cartelle 1999: fig. 4B), *Plesiomega−therium hansmeyeri*, *Megatheriops rectidens*, *Pyramiodon−therium bergi*, and *Pyramiodontherium brevirostrum* (see Carlini et al. 2002: fig. 2), only the mesial half of m4 is visible in lateral view; finally, m4 is located entirely posterior to the anterior margin of the coronoid process and hidden from lateral view in several specimens of *Megatherium americanum*.

The posterolateral opening of the mandibular canal lies at the base of the coronoid process, almost reaching the alveolar plane (Fig. 2A, B). In *Anisodontherium halmyronomonum*, the position of this opening is not observable owing to the poor state of preservation of this part of the dentary. The condition in *Megathericus patagonicus* resembles that of PVL 6425, whereas in other megatheriines, such as *Pliomega−therium*, *Megatheriops*, *Pyramiodontherium*, *Megatherium*, and *Eremotherium*, the foramen is located dorsally, medial to the base of the coronoid process, and usually opposite m4. As in *Pyramiodontherium* and *Megatheriops*, the antero−lateral opening of the mandibular canal is situated anterior to the posterior margin of the mandibular symphysis.

In occlusal view (Fig. 2C), the posterior margin of the mandibular symphysis is located ventromedial and anterior to the level of m1, as in *Anisodontherium halmyronomonum* (see Brandoni and De Iuliis 2007: fig. 3B), *Megathericus patagonicus* (see De Iuliis et al. 2008: fig. 2C), *Eomegatherium andinum*, and *E. nanum* (see Kraglievich 1930: fig. 5A). The position of the posterior margin of the mandibular symphysis in other megatheriines varies: in *Pyramiodontherium bergi* and *Eremotherium laurillardi*, it reaches approximately to a point halfway along m1. It is even farther posterior, reaching the plane of the alveolar septum between

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Fig. 2. Megatheriine *Anisodontherium* sp. (PVL 6425), Cerro Castillo de Las Brujas, Tucumán Province, Argentina. Saladillo Formation (Upper Miocene). A–C. Mandible in left lateral (A), right lateral (B), and occlusal (C) views. D. Digit III of the manus in lateral view.
m1 and m2, in Plesiomegatherium hansmeyeri (see Roth 1911: fig. 1), Pyramiodontherium brevirostrum (see Carlini et al. 2002: fig. 2), Megatherium altiplanicum Saint-André and De Iuliis, 2001 (see Saint-André and De Iuliis 2001: fig. 4B), and M. tarijense (see De Iuliis et al. 2009: fig. 2D). Finally, the posterior margin of the mandibular symphysis generally reaches to a point halfway along the m2 in M. americanaum and M. gallardoi (see Brandoni et al. 2008: fig. 2D), although in M. americanaum it occasionally also lies at the level of the m1/m2 alveolar septum. In PVL 6425, the posterior margin of the symphysis is rounded and the dentaries are well separated. By contrast, the dentaries approach each other more closely at the level of the symphysis and form a nearly V-shaped outline in dorsal view in Megatherium altiplanicum, M. gallardoi, M. tarijense, and most specimens of M. americanaum. In Anisodontherium sp., the articular condyle is nearly oval in outline, while being subcircular in M. tarijense (see De Iuliis et al. 2009: fig. 2D).

The most notable feature of the dentition of PVL 6425, and especially m2 and m3, is the mesiodistally compressed, rather than isodiametric (length and width being almost equal) shape of the molariforms (Figs. 2C, 3A; Table 1). This mesiodistal compression also occurs in Anisodontherium halmyronomum (see Brandoni and De Iuliis 2007: fig. 3B, D), Megathericulus patagonicus and Eomegatherium andinus (note that no teeth have so far been described for the latter two species; however, their form can be inferred from their alveoli). By contrast, in Pyramiodontherium, Megatheridium, Megatheriops, Pliomegatherium, Megatherium, Eremotherium, and Plesiomegatherium hansmeyeri the molariforms are isodiametric, albeit differently shaped. In occlusal view, megatherine molariforms have two crests of hard dentine separated by a deep valley excavated in the soft dentine (Fig. 3). Unlike Pyramiodontherium and Megatherium (Fig. 3B and 3C, respectively), Anisodontherium sp. lacks well-developed hard dentine, especially along the anterior wall of the molariforms, as well as wear facets on the anterior transverse crests (Fig. 3A).

In PVL 6425, m1 has a nearly trapezoidal outline in occlusal view, whereas m2 and m3 are clearly rectangular, and the margins of m4 (the smallest) are flat anteriorly and convex posteriorly. In Anisodontherium halmyronomum the shape of the molariforms is similar to those of PVL 6425, whereas in Pyramiodontherium bergi the anterior and posterior crests of m1 and m2 are oriented obliquely with respect to the anteroposterior axis, giving those teeth a more trapezoidal outline (Fig. 3B). By contrast, all of the molariforms of Megatherium and Eremotherium are nearly squared (Fig. 3C). In addition, the molariforms, and particularly m1, of Anisodontherium sp. and A. halmyronomum possess a deep V-shaped valley between the transverse crests (Fig. 2A, B). While present, this valley is generally shallower in other taxa, such as Pyramiodontherium, Megatheriops, and Megatherium.

In taxa showing mesiodistal compression of the molariforms, the molariform tooth row is relatively shorter than in megatherines with isodiametric cheek teeth. This has implications for the Hypsodonty Index (HI), calculated as the greatest height of the mandibular ramus/length of the molariform tooth row × 100, which has been used as an indicator of hypsodonty of the molariforms in sloths (see Zetti 1964; Bargo et al. 2006; Brandoni et al. 2007; Fields 2009). For PVL 6425, the HI is nearly 99 (taking into account an average of the measurements of both dentaries), compared to a value of 103–107 in Anisodontherium halmyronomum. In other Tertiary megatherines from Argentina, the HI ranges from 75–113 (Table 2), whereas among Quaternary megatherines the HI is greatest in Megatherium americanum, in which it varies between 92 and 112 (Saint-André and De Iuliis 2001). However, as was noted by De Iuliis et al. (2004)

Table 1. Measurements (in mm) of the molariforms of Anisodontherium sp. (PVL 6425).

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Length/width</th>
</tr>
</thead>
<tbody>
<tr>
<td>m1</td>
<td>18/27</td>
</tr>
<tr>
<td>m2</td>
<td>19/28</td>
</tr>
<tr>
<td>m3</td>
<td>17/26</td>
</tr>
<tr>
<td>m4</td>
<td>19/22</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Length/width</th>
</tr>
</thead>
<tbody>
<tr>
<td>m1</td>
<td>19/28</td>
</tr>
<tr>
<td>m2</td>
<td>18/28</td>
</tr>
<tr>
<td>m3</td>
<td>17/27</td>
</tr>
</tbody>
</table>
Table 2. Measurements (in mm) of the mandibles of Tertiary megatheriines from Argentina. Abbreviations: MTRL, molariform tooth row length; HMR, height of the mandibular ramus; HI, Hypsodonty Index.

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen number</th>
<th>MTRL</th>
<th>HMR</th>
<th>HI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anisodontherium sp.</td>
<td>PVL 6425 left</td>
<td>92</td>
<td>90</td>
<td>98</td>
</tr>
<tr>
<td>Anisodontherium sp.</td>
<td>PVL 6425 right</td>
<td>94</td>
<td>95</td>
<td>101</td>
</tr>
<tr>
<td>Anisodontherium halmyronomum</td>
<td>MLP-30-XII-10-21 left</td>
<td>115</td>
<td>123</td>
<td>107</td>
</tr>
<tr>
<td>Anisodontherium halmyronomum</td>
<td>MLP-30-XII-10-21 right</td>
<td>112</td>
<td>115</td>
<td>103</td>
</tr>
<tr>
<td>Pyramiodontherium bregi</td>
<td>MLP 2-66</td>
<td>195</td>
<td>150</td>
<td>77</td>
</tr>
<tr>
<td>Pyramiodontherium brevirostrum</td>
<td>MLP 31-XI-12-25</td>
<td>188</td>
<td>160</td>
<td>85</td>
</tr>
<tr>
<td>Pyramiodontherium sp.</td>
<td>MLP 31-XI-12-26</td>
<td>166</td>
<td>145</td>
<td>87</td>
</tr>
<tr>
<td>Megatheriops rectidens</td>
<td>MACN Pv-2818</td>
<td>168</td>
<td>148</td>
<td>88</td>
</tr>
<tr>
<td>Pliomegatherium lelongi</td>
<td>MACN Pv-13213</td>
<td>135</td>
<td>102</td>
<td>75</td>
</tr>
<tr>
<td>Megatheridium annectens</td>
<td>MACN Pv-2833</td>
<td>146</td>
<td>165</td>
<td>113</td>
</tr>
</tbody>
</table>

and Brandoni and De Iuliis (2007), HI values for Anisodontherium and M. americanum are not directly comparable (see below).

Digit III is composed of a proximal phalanx (fusion of phalanges 1+2) and a strong, claw-shaped ungual phalanx (Fig. 2D). The proximal surface of the phalanx (1+2) bears a wide facet for Mc III, which is elongated along the dorsolateral-ventromedial axis. The well-developed and relatively short and robust ungual phalanx is higher than wide, particularly in its distal portion, and oriented obliquely to the sagittal plane. It articulates with the proximal phalanx (1+2) along a deeply depressed surface, which is divided into two oval parts.

Discussion

Powell and González (1997) mentioned the presence of a megatherine and a mesotherine (Mammalia, Notoungulata) from the Saladillo Formation, with the megatherine being represented by a mandible, vertebrae, and fragments of a radius and ulna. In addition, a digit and a scapula were also part of the recovered specimen. However, only the mandible and the digit show features consistent with the morphology of Megatheriinae, whereas the other bones cannot clearly be assigned to this group of ground sloths (DB personal observation). Thus, for the moment, we have chosen to restrict our description to the former two elements.

"Plesiomegatherium" halmyronomum was described by Cabrera (1928) based on a skull recovered from the Arroyo Chasicó Formation (specimen MLP 26-IV-10-1), in southwestern Buenos Aires Province, Argentina. Later, Cattoi (1966) referred a mandible (MLP 30-XII-10-21) from the same formation to this species. More recently, Brandoni and De Iuliis (2007) considered P. hansmeyeri (the type species of Plesiomegatherium) from Jujuy Province and "P." halmyronomum to be sufficiently different to warrant the erection of the new genus Anisodontherium for the megatherine originally described by Cabrera (1928).

PVL 6425 resembles the mandible of Anisodontherium halmyronomum (MLP 30-XII-10-21) in the shape of the molariforms (mesiodistally compressed), the position of the anterior margin of the coronoid process (posterior with respect to m4), and the position of the posterior margin of the symphysis (anterior with respect to m1), thus justifying its referral to this genus. However, PVL 6425 is smaller and more slender than A. halmyronomum, and further differs from the latter in the convexity of the ventral margin of the dentary (ventral bulge less pronounced). These differences might signal the existence of a new species of Anisodontherium in the Late Miocene of Tucumán Province. However, given the broad range of individual variation observed in other Megatheriinae (e.g., Pliomegatherium, Megatherium, Eremotherium), as well as the incompleteness of PVL 6425, we prefer to describe the latter as Anisodontherium sp. New discoveries of more complete and better preserved material resembling PVL 6425 will be necessary before a new species can be reliably diagnosed.

During the course of their evolution, the body size of megatheriines and, as a result, the size of their molariforms generally increased. However, in the molariforms this process did not occur evenly, with the relative increase in the anteroposterior length of these teeth generally exceeding that in their labiolingual width (Kraglievich 1930). Thus, while the molariforms of earlier megatheriines are usually rectangular in occlusal view, those of Quaternary megatheriines are nearly squared (isodiametric). This increase in the anteroposterior length of the molariforms necessarily led to a relative increase in the length of the molariform tooth row, which in turn resulted in Quaternary megatheriines (e.g., Megatherium, Eremotherium) generally possessing a relatively longer tooth row than taxa from the Middle and Late Miocene (e.g., Megathericus, Anisodontherium).

At least three features commonly used in megatheriine systematics and paleobiological analyses are closely related to the length of the molariform tooth row: the Hypsodonty Index, the position of the anterior margin of the coronoid process, and the position of the posterior margin of the mandibular symphysis.

The Hypsodonty Index has been used in megatheriine systematics and cladistics (see Saint-André and De Iuliis 2001;
Pujos 2006; Brandoni and De Iuliis 2007; Brandoni et al. 2008), as well as paleobiological studies of ground sloths (see Bargo et al. 2006; Fields 2009). In particular, it is one of the characters proposed to separate Megatherium from Eremotherium (see Saint-André and De Iuliis 2001), as well as M. americanum from M. gallardoi (see Brandoni et al. 2008). In addition, the differences between the HI of Megatherium americanum and Eremotherium laurillardi have been related to paleoenvironmental aspects, with M. americanum (high HI) linked to open grassland, and Eremotherium laurillardi (low HI) to closed forest habitats (Bargo et al. 2006). However, unlike in those previous studies, the HI values for Anisodontherium cannot be directly compared to those of most megatherine genera, such as Megatherium, since the relatively shorter molariform tooth row in Anisodontherium exaggerates its hypsodonty. In addition, with just two specimens of Anisodontherium described, the available sample is too small, and there is insufficient paleoenvironmental information for the Arroyo Chasicó and Saladillo formations to speculate whether the HI may reflect paleoenvironmental conditions.

As noted above, in Anisodontherium the anterior edge of m1 is posterior to the posterior margin of the symphysis, and the posterior edge of m4 is anterior to the anterior margin of the coronoid process. Thus, the molariform tooth row lies entirely between the posterior margin of the mandibular symphysis and the anterior margin of the coronoid process, as is also the case in Megathericus and Eomegatherium andinus from the Colloncuran–Mayoan of Argentina. By contrast, the molariform tooth row extends beyond those mandibular features in Megatherium americanum and Eremotherium laurillardi, owing to the presence of squared molariforms. The position of the posterior margin of the mandibular symphysis and the anterior margin of the coronoid process relative to the tooth row has been used in cladistic analyses of Megatheriinae (Pujos 2006). However, given that these characters seem closely related to the length of the molariform tooth row, and thus the shape of the molariforms, it seems likely that the latter might have an influence on the way these features are scored and interpreted in cladistic and paleobiological analyses.

Thus far only three valid megatherine species, all assigned to a single genus, have been described from the Late Miocene–Pliocene of north-western Argentina, including Pyramiodontherium bergi and P. brevirostrum, both of which were recovered from Bajo de Andalhuala in the Valle de Santa María, south of Chiquimil (Catamarca Province) (see Cabrera 1928; Carlini et al. 2002), as well as P. scillatoyanei from the Upper Miocene–Lower Pliocene lower member of the Toro Negro Formation of La Rioja Province (De Iuliis et al. 2004). In addition, Ameghino (1919) and Kragliévich (1931, 1934) mentioned the presence of a megatherine based on cranial remains recovered from Tiopunco (Tucumán Province), which were referred to Pyramiodontherium by Kragliévich (1931) and Brandoni and Carlini (2009). The presence of Anisodontherium in Tucumán Province therefore increases both the species and genus diversity of megatherines in the Late Miocene of north-western Argentina.

While previous workers suggested an Eocene (Bossi and Palma 1982) or Paleocene–Early Miocene (Bossi and Muruaga 2009) age of the Saladillo Formation, these estimates were mainly based on stratigraphic interpretations, and are not supported by radiometric dating or fossil evidence. The tuff level dated by González et al. (2000) is located just 3 m below the fossiliferous level which yielded the megatherine. At 10 ± 0.3 Ma, the age estimate for this layer is consistent with an another estimate of 10.7±1.7 Ma for the age of a second tuff layer exposed at Campo del Arenal, 42 km west of Cerro Castillo de Las Brujas (Grier and Dallmeyer 1990). Together, these results strongly indicate a Late Miocene age for the lowermost levels of the Saladillo Formation.

In addition to the record from the Saladillo Formation, Anisodontherium has been recovered from the Arroyo Chasicó Formation (Buenos Aires Province), traditionally divided into the basal Vivero Member and the overlying Las Barrancas Member (Bondeśio et al. 1980). This subdivision was based on lithological features and paleontological evidence, and was followed by several authors who studied fossil vertebrates from the Chasicó Lagoon area (Bondeśio et al. 1980; Deschamps et al. 2007, 2009; Verzì et al. 2008, among others). However, Zárate et al. (2007) suggested that the lithofacies identified in the Arroyo Chasicó Formation may not support its differentiation into two members. While the precise provenance of the holotype of A. halmyronium is unknown, Cattoi (1966) indicated that the mandible MLP 30-XII-10-21 was recovered from the Vivero Member.

While the fauna recovered from the Arroyo Chasicó Formation was originally interpreted to represent the early Late Miocene Chasicóan SALMA (Bondeśio et al. 1980; Deschamps et al. 2007), more recent studies suggested that at least part of the faunal assemblage should be assigned to the Late Chasicóan or possibly Early Huayquerian SALMA, indicating a Late Miocene age (Verzì et al. 2008). Zárate et al. (2007) interpreted lithofacies 1 at the base of the formation as the result of a period of sedimentation occurring around 9.23 Ma. However, since the lower boundary of the formation is not exposed, the beginning of sedimentation probably exceeds 10 Ma (Schultz et al. 2004; Zárate et al. 2007). Thus, the presence of Anisodontherium in the lowermost levels of both the Saladillo and the Arroyo Chasicó formations seems to confirm the radiometric age estimates. Nevertheless, the correlation of the two units remains to be corroborated by new discoveries of better preserved specimens and additional radiometric data.

In summary, the specimen described here increases our knowledge of the mandibular anatomy of early megatherines and represents the first record of Anisodontherium outside the Pampean region, Argentina. In addition, the presence of Anisodontherium in Tucumán Province increases the diversity of Megatheriinae in the Late Miocene–Pliocene of north-western Argentina.

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