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# *Anisodontherium* from the Late Miocene of north-western Argentina

DIEGO BRANDONI, JAIME E. POWELL, and OSVALDO E. GONZÁLEZ



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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

Xenarthrans 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 *Vermilingua* and Tardigrada. While both of the latter two taxa pursue either terrestrial or arboreal lifestyles, *Vermilingua* (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

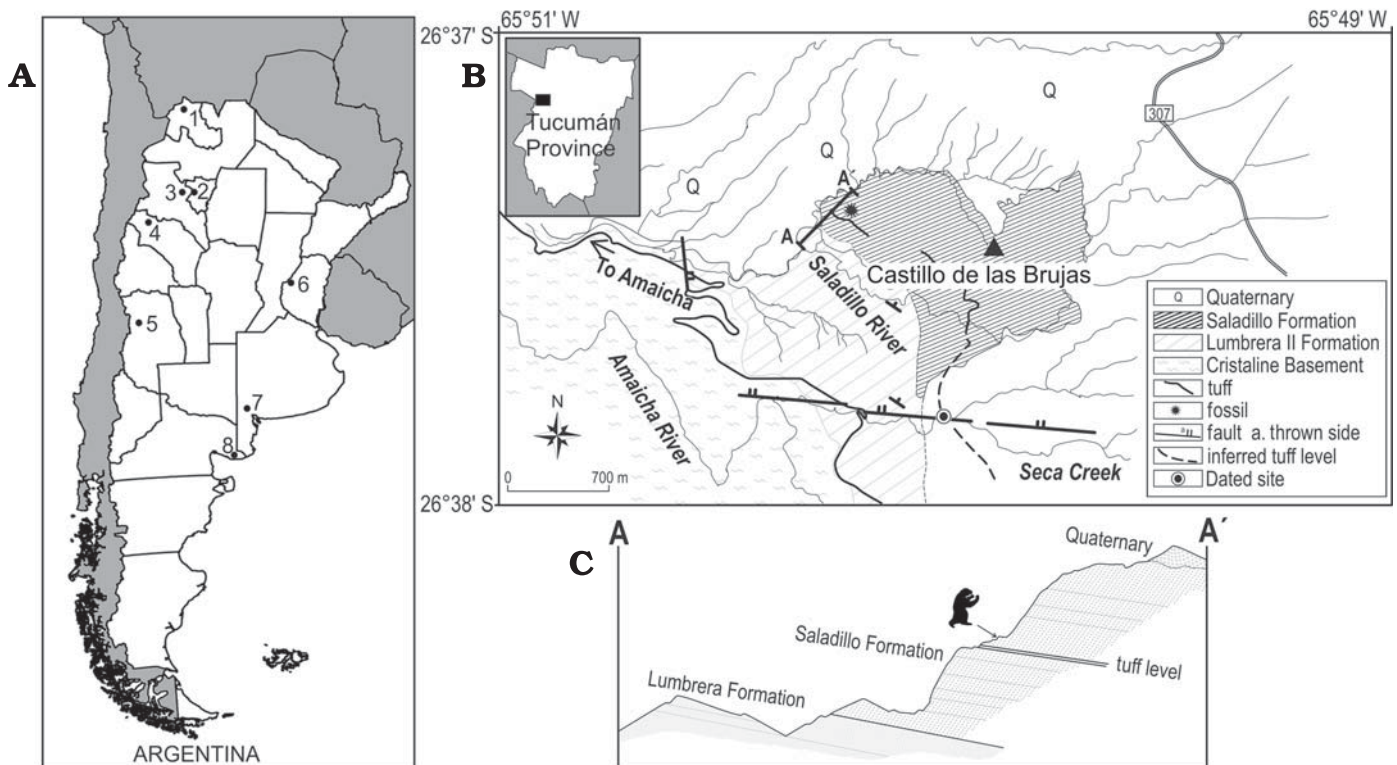


Fig. 1. **A.** Map of Argentina showing the distribution of fossil Megatheriinae during the Late Miocene–Pliocene. 1, Abra Pampa (Jujuy Province); 2, Saladillo Formation (Tucumán Province); 3, Andalhuala and Corral Quemado formations (Catamarca Province); 4, Toro Negro Formation (La Rioja Province); 5, Huayquerías de San Carlos (Mendoza Province); 6, “conglomerado osífero”, Ituzaingó Formation (Entre Ríos Province); 7, Arroyo Chasicó Formation (Buenos Aires Province); 8, Río Negro Formation (Río Negro Province). **B.** Geologic map of Cerro Castillo de las Brujas area (Tucumán Province). **C.** Schematic profile of the sequence indicating the position of the fossiliferous level and the dated tuff.

dearth of studies. Overall, the list of valid megatheriine genera from the Middle Miocene–Pliocene of Argentina currently comprises *Megathericulus* Ameghino, 1904, *Eomegatherium* Kraglievich, 1926, *Promegatherium* Ameghino, 1883, *Megatheridium* Cabrera, 1928, *Pliomegatherium* Kraglievich, 1930, *Megatheriops* C. Ameghino and Kraglievich, 1921, *Plesiomegatherium* Roth, 1911, *Megatheridium* Cabrera, 1928, *Pyramiodontherium* Rovereto, 1914, and *Anisodontherium* Brandoni and De Iuliis, 2007.

In terms of species, Megatheriinae were represented in Argentina during the Late Miocene–Pliocene by *Pyramiodontherium bergi* (Moreno and Mercerat, 1891) from the provinces of Catamarca and Tucumán; *Pyramiodontherium brevisrostrum* Carlini, Brandoni, Scillato-Yané, and Pujos, 2002, from Catamarca Province; *Pyramiodontherium scillatoyanei* De Iuliis, Ré and Vizcaíno, 2004, from La Rioja Province; *Plesiomegatherium hansmeyeri* Roth, 1911, from Jujuy Province (but see Brandoni and De Iuliis 2007); *Megatheriops rectidens* (Rovereto, 1914) from Mendoza Province; *Promegatherium smaltatum* Ameghino, 1883, *Pliomegatherium lelongi* Kraglievich, 1926, *Eomegatherium nanum* (Burmeister, 1891) and *Pyramiodontherium* 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; Rodríguez 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 Andalhuala 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 megatheriine 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 megatheriine 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, Hipsodonty 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. The unit was locally dated based on a 30 cm thick tuff level located 3 m below the fossil remains (Fig. 1C), indicating a K/Ar age of  $10 \pm 0.3$  Ma (Late Miocene) (González et al. 2000).

## 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).

*Geographic and stratigraphic range.*—Bank of the Arroyo Chasicó, near Chasicó Lagoon, Buenos Aires Province, Argentina (Fig. 1A), Arroyo Chasicó Formation (Upper Miocene). Cerro Castillo de Las Brujas, Tucumán Province, Argentina (Fig. 1A), Saladillo Formation (Upper Miocene) (Fig. 1A).

*Anisodontherium* sp.

Figs. 2, 3A.

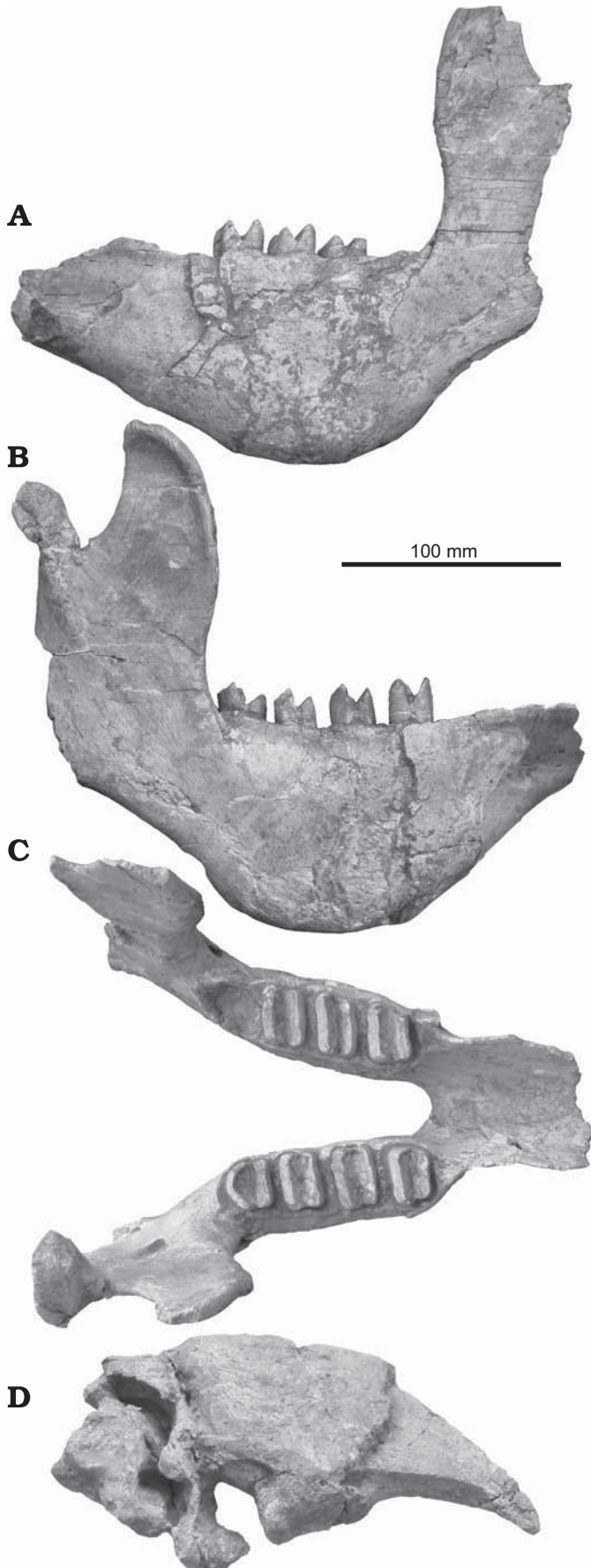
*Referred material.*—PVL 6425, a nearly complete mandible lacking both angular processes and the left articular condyle (Fig. 2A–C); and digit III of the manus (Fig. 2D). Cerro Castillo de Las Brujas ( $26^{\circ} 38' 07.26''\text{S}$ ,  $65^{\circ} 50' 53.04''\text{W}$ ), Tucumán Province, Argentina, 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 *Plesiomegatherium hansmeyerii* (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*, *Megathericulus patagonicus* Ameghino, 1904 (see De Iuliis et al. 2008: fig. 2D), *Eomegatherium andinum* Kraglievich, 1930, *Pliomegatherium lelongi* (see Brandoni 2006: figs. 3.2, 4), *Eremotherium laurillardii* (Lund, 1842), and *Megatherium tarijense* 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 *Megatherium* 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 halmyronomum* (see Brandoni and De Iuliis 2007: fig. 3A) and probably also *Megathericulus 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 eomigrans* De Iuliis and Cartelle, 1999 (see De Iuliis and Cartelle 1999: fig. 4B), *Plesiomegatherium hansmeyeri*, *Megatheriops rectidens*, *Pyramiodontherium 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 halmyronomum*, the position of this opening is not observable owing to the poor state of preservation of this part of the dentary. The condition in *Megathericulus patagonicus* resembles that of PVL 6425, whereas in other megatheriines, such as *Pliomegatherium*, *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 halmyronomum* (see Brandoni and De Iuliis 2007: fig. 3B), *Megathericulus 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 laurillardii*, it reaches approximately to a point halfway along m1. It is even farther posterior, reaching the plane of the alveolar septum between

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 brevisrostrum* (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. americanum* and *M. gallardoi* (see Brandoni et al. 2008: fig. 2D), although in *M. americanum* 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. americanum*. 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 andinum* (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, megatheriine 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

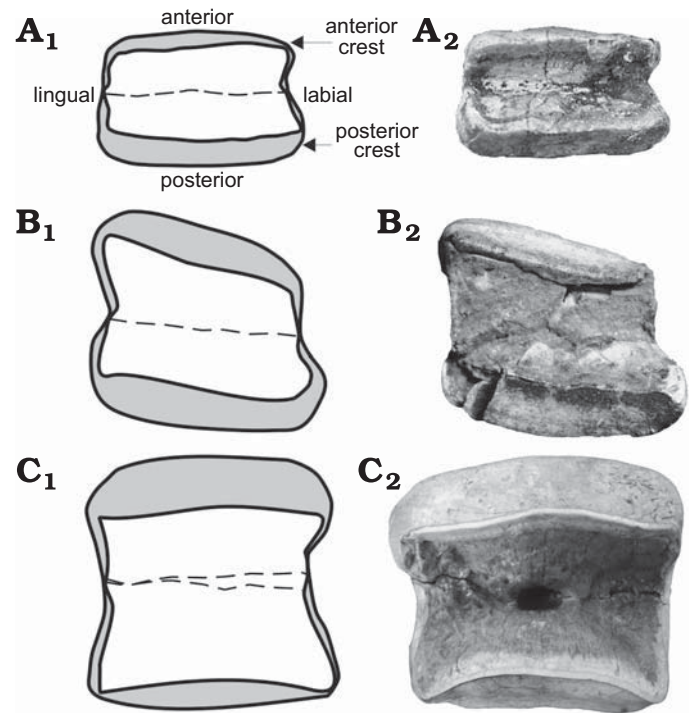


Fig. 3. Lower molariforms of megatheriines in occlusal view. **A.** *Anisodontherium* sp. (PVL 6425), Cerro Castillo de Las Brujas, Tucumán Province, Argentina. Saladillo Formation (Upper Miocene). **B.** *Pyramiodontherium* Rovereto, 1914 (MLP 31-XI-12-25), Bajo de Andalhuala, Catamarca Province, Andalhuala Formation (Upper Miocene). **C.** *Megatherium* Cuvier, 1796 (CICYTTP-PV-M-2-356), Entre Ríos Province, Tezanos Pinto Formation (Upper Pleistocene). Explanatory drawings (A<sub>1</sub>–C<sub>1</sub>), photographs (A<sub>2</sub>–C<sub>2</sub>).

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 megatheriines 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 and De Iuliis 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 megatheriines from Argentina, the HI ranges from 75–113 (Table 2), whereas among Quaternary megatheriines 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).

|                 | Tooth | Length/width |
|-----------------|-------|--------------|
| Left tooth row  | m1    | 18/27        |
|                 | m2    | 19/28        |
|                 | m3    | 17/26        |
|                 | m4    | 19/22        |
| Right tooth row | m1    | 19/28        |
|                 | m2    | 18/28        |
|                 | m3    | 17/27        |

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.

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

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 megatheriine and a mesotheriine (Mammalia, Notoungulata) from the Saladillo Formation, with the megatheriine 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 megatheriine 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., *Megathericulus*, *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 megatheriine 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 *Megathericulus* and *Eomegatherium andinum* 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 megatheriine 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 Kraglievich (1931, 1934) mentioned the presence of a megatheriine based on cranial remains recovered from Tiopunco (Tucumán Province), which were referred to *Pyramiodontherium* by Kraglievich (1931) and Brandoni and Carlini (2009). The presence of *Anisodontherium* in Tucumán Province therefore increases both the

species and genus diversity of megatheriines 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 megatheriine. At  $10 \pm 0.3$  Ma, the age estimate for this layer is consistent with another estimate of  $10.7 \pm 1.7$  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 (Bondesio 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 (Bondesio et al. 1980; Deschamps et al. 2007, 2009; Verzi 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. halmyronomum* 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 (Bondesio 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 (Verzi 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 megatheriines 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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