

## ON THE SYSTEMATICS OF *ORTOTHERIUM* AMEGHINO (XENARTHRA, TARDIGRADA, MEGALONYCHIDAE) FROM THE ‘CONGLOMERADO OSÍFERO’ (LATE MIOCENE) OF ARGENTINA

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Megalonychidae are a group of Xenarthra known from the Deseadan SALMA of Argentina (Carlini and Scillato-Yané, 2004) and Bolivia (Pujos and De Iuliis, 2007) to the present, represented by the extant sloth *Choloepus* Illiger (White and MacPhee, 2001; Gaudin, 2004; but see Carlini and Scillato-Yané, 2004). Although the principal records of Megalonychidae are those from Central and North America (e.g., Matthew and Paula Couto, 1959; Hirschfeld and Webb, 1968; White and MacPhee, 2001), in South America, Megalonychidae are common in the ‘Conglomerado osífero’ (Ossiferous Conglomerate) or ‘Mesopotamiense’ within the Ituzaingó Formation, Entre Ríos Province, Argentina (Paula Couto, 1979; Carlini et al., 2000; Cione et al., 2000).

Several authors have studied the Megalonychidae from the ‘Conglomerado osífero’ (e.g., Ameghino, 1885, 1891; Kraglievich, 1922, 1923a, 1923b, 1923c, 1925, 1926; Bordas, 1942; Scillato-Yané, 1980), but no systematic revision of the group has been performed beyond the original naming of species. Many of these fossil sloths have not been included in studies by other researchers due to the fragmentary nature of their remains. The most recent works on Megalonychidae from the ‘Conglomerado osífero’ are those by Carlini et al. (2000), Cione et al. (2000), and Brandoni (2008), which briefly commented on the different genera: *Ortotherium* Ameghino, 1885, *Pliomorphus* Ameghino, 1885, *Menilaus* Ameghino, 1891, *Amphiocnus* Kraglievich, 1922, *Protomegalonyx* Kraglievich, 1925, *Megalonychops* Kraglievich, 1926, and *Paranabradys* Scillato-Yané, 1980. Despite these contributions, the taxonomic status of several species from the Tertiary of Argentina that were first described and named in the late 19th century has not been addressed.

The dentary specimen that forms the basis for this report, from the ‘Conglomerado osífero’ of Entre Ríos Province, was briefly commented upon and illustrated by Brandoni (2008). The aim of this paper is to describe this specimen (here referred to *Ortotherium*), provide an emended diagnoses for the genus and species, and assess variation within the genus. For the purposes of this paper, I follow the systematic arrangement suggested by Gaudin (2004) (e.g., *Eucholaeops* Ameghino is considered a Megalonychidae).

**Institutional Abbreviations**—MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MLP, Museo de La Plata, Facultad de Ciencias Naturales y Museo, La Plata, Argentina.

**Anatomical Abbreviations**—c, caniniform; HRM, height of the mandibular ramus; m1–m3, molariforms 1–3; po, posterolateral opening of mandibular canal.

**Other Abbreviations**—SALMA, South American Land Mammal Age.

### GEOLOGICAL SETTING

The Ituzaingó Formation (De Alba, 1953) extends from the city of Ituzaingó (Corrientes Province), where the type pro-

file was described, to north of the city of Paraná (Entre Ríos Province). Remains of fossil vertebrates have been collected from the lower levels of the Ituzaingó Formation in Entre Ríos Province, particularly from a basal level, informally known as ‘Mesopotamiense’ or ‘Conglomerado osífero’ (Frenguelli, 1920). This unit crops out discontinuously along the Paraná River cliffs from the vicinity of Paraná to the locality of Pueblo Brujo. Prospecting is currently focused on the following fossil-bearing localities: Toma Vieja (S31°42’11”, W60°28’06”, in the vicinity of Paraná), Villa Urquiza (S31°38’42.5”, W60°22’50.5”), and La Celina (S31°37’37”, W60°20’04”) (Fig. 1).

The ‘Conglomerado osífero’ is clearly visible in places where the discordance between the underlying Paraná Formation, which is marine in origin (Bravard, 1858), and the sandy-clayey and conglomeratic levels of Ituzaingó Formation becomes evident (see Cione et al. 2000:fig. 2; Brandoni and Scillato-Yané, 2007:fig. 2). Its thickness is variable, and it is characterized by levels with fine quartz gravel, clay and chalcedony clasts, as well as abundant bones and teeth, frequently fragmented and disassociated, and mostly corresponding to continental and marine vertebrates. The type of fossilization is very characteristic; remains are well mineralized, hard, heavy, and impregnated with siliceous and ferruginous infiltrations; in addition, they are frequently stained by manganese oxide.

Cione et al. (2000) analyzed a complete and updated list of fossil vertebrates recorded in the ‘Conglomerado osífero’ of the Ituzaingó Formation and, based on the stratigraphic relationships between the different fossil beds, they proposed affinity with the Huayquerian SALMA (late Miocene), correlating it with the Tortonian.

### SYSTEMATIC PALEONTOLOGY

XENARTHRA Cope, 1889  
TARDIGRADA Latham and Davies in Forster, 1795  
MEGALONYCHIDAE Gervais, 1855  
*ORTOTHERIUM* Ameghino, 1885

*Menilaus* Ameghino, 1891.

*Amphiocnus* Kraglievich, 1923c, nec Kraglievich, 1922.

**Type Species**—*Ortotherium laticurvatum* Ameghino, 1885.

**Horizon and Locality**—In Argentina, the different species of the genus have been found in the vicinity of the city of Paraná, Entre Ríos Province (Ameghino, 1885, 1891), within the ‘Conglomerado osífero’ of Ituzaingó Formation, Huayquerian SALMA (late Miocene) (see Cione et al., 2000).

**Emended Diagnosis**—Slightly larger than *Eucholaeops* Ameghino, similar in size to *Paranabradys*, and smaller than *Megalonyx* Harlan, and *Megalocnus* Leidy. As in most Megalonychidae, mandible with diastema between c and m1, differing from *Diaboloherium nordenskioldi* (Kraglievich), which lacks a diastema. Posterolateral opening of mandibular canal on lateral margin of base of coronoid process, as in *Eucholaeops*, *Paranabradys*, and *Megalocnus*, or on lateral surface of



FIGURE 1. Geographic location of the main exposures (black squares) of the 'Conglomerado osífero,' Entre Ríos Province, Argentina.

horizontal ramus. Anterior margin of coronoid process lateral to midpoint of m3, more anterior than in *Eucholaeops* and *Paranabradys*, and more posterior than in *Megalocnus*, *Megalonyx*, and *Pliometanastes* Hirschfeld and Webb. Posterior margin of mandibular symphysis inferomedial to c–m1 diastema; inferomedial to m1/m2 interval in *Megalocnus*; inferomedial to c in *Megalonyx* and *Pliometanastes*. Alveolus of caniniform elliptical in cross-section and small relative to molariforms; larger and more oval in *Megalonyx*; larger and meniscoid in *Megalocnus*. m1 subtrapezoidal in cross-section; subrectangular in *Megalonyx* and *Megalocnus*. m2 and m3 oval in cross-section; m2 subtrapezoidal and m3 nearly oval in *Megalonyx* and *Megalocnus*.

**Remarks**—The species originally assigned to *Ortotherium* were: *O. robustum* Ameghino, 1891, *O. schlosseri* Ameghino, 1891, *O. seneum* Ameghino, 1891, *O. brevisrostrum* Bordas, 1942, and *O. scrofum* Bordas, 1942. Kraglievich (1923c) considered *Menilaus affinis* Ameghino, 1891, congeneric with *Pliomorphus*. In addition, Kraglievich (1923c) considered that *O. seneum* should be included within *Amphiocnus*. However, the evaluation of the characters present in the type specimens of these taxa do not justify the statements of Kraglievich (1923c). The morphological features observed in the specimens herein studied indicate that *Menilaus* and *Amphiocnus* (in part) are congeneric with *Ortotherium* (see below).

*ORTOTHERIUM LATICURVATUM* Ameghino, 1885 (Fig. 2)

*Ortotherium schlosseri* Ameghino, 1891:151, fig. 56 (original description).

*Ortotherium seneum* Ameghino, 1891:152, fig. 57 (original description).

*Ortotherium scrofum* Bordas, 1942:178, lamina II (original description).

*Amphiocnus seneum* (Ameghino) Kraglievich, 1923c:10 (new combination).

*Menilaus affinis* Ameghino, 1891:154, fig. 59 (original description).

**Holotype**—Incomplete left dentary (Fig. 2A–B). The holotype has not been found in the collections of MACN, where it probably was deposited originally. Nevertheless, a cast of the type (MLP M 62) is deposited in the Vertebrate Paleontology collections of MLP (Mones, 1986).

**Referred Material**—MACN Pv-13319 (type of *Ortotherium schlosseri*), incomplete right dentary only preserving m1 and m3 (Fig. 2C–D). MACN Pv-8886 (type of *Ortotherium seneum* and *Amphiocnus seneum*), incomplete left dentary with fragmentary caniniform, m1, and m2 (Fig. 2E–F). MACN Pv-13657 (type of *Ortotherium scrofum*), mandibular symphysis with right caniniform and m1 (Fig. 2G–H). MACN Pv-13318 (type of *Menilaus affinis*), incomplete left dentary (Fig. 2I–J).

**Emended Diagnosis**—Posterolateral opening of mandibular canal on lateral margin of base of coronoid process, close to level of alveolar series; on lateral surface of horizontal ramus in the new specimen herein described referred to *Ortotherium* sp.

**Remarks**—*O. laticurvatum* is the type species of the genus. Ameghino (1885) described the species and provided several measurements of the type material, but did not figure it. Ameghino (1889:pl. LXXI, figs. 12 and 12a) figured a molariform assigned to *O. laticurvatum*, but later (Ameghino, 1891) referred it to *Promegatherium parvulum* Ameghino (Megatheriidae, Megatheriinae). *Amphiocnus paranense* Kraglievich (the type and only known species of the genus) was erected on the basis of a distal femur (Kraglievich, 1922:figs. 1–2). As mentioned above, Kraglievich (1923c) believed that *O. seneum* should be included within *Amphiocnus*. Kraglievich (1923c:10) stated that “Respecto al *O. seneum*, mi opinión es que debe, con mayor verisimilitud, referirse al *phylum megalocninae* y que muy bien podría ser congénere de *Amphiocnus* . . .”. Kraglievich (1923c) justified his statement using the resemblances between the caniniform of *O. seneum* and that of *Megalocnus* from Cuba. However, the features present in MACN Pv-8886 (e.g., position of the posterior margin of mandibular symphysis, shape and size of the caniniform) clearly resemble *Ortotherium* rather than *Megalocnus*. Therefore, this specimen is assignable to *Ortotherium* and not to *Amphiocnus* as suggested by Kraglievich (1923c).

Kraglievich (1923c), without discussion, also considered *Menilaus affinis* congeneric with *Pliomorphus*. However, similarity in the shape and size of the caniniform, position of the posterior margin of the mandibular symphysis, and position of the anterior margin of the coronoid process in *O. laticurvatum* and *M. affinis* do not justify either generic or specific separation, and *M. affinis* is considered a junior synonym.

*ORTOTHERIUM*, sp. indet. (Fig. 3A–C)

**Referred Material**—MACN Pv-8916, a nearly complete left dentary, lacking part of the coronoid process, condyloid process, part of the mandibular symphysis, angular process, and teeth (Fig. 3A–C).

**Horizon and Locality**—Vicinity of Paraná city, Entre Ríos Province, Argentina, within the ‘Conglomerado osífero’ of Ituzaingó Formation, Huayquerian SALMA (late Miocene) (see Cione et al., 2000).

**Description**—MACN Pv-8916 is an almost complete left dentary that preserves an important part of the coronoid process, although it is missing the angular process, condyloid process, and teeth. It resembles other specimens referred to this genus in size (Table 1, Fig. 2A–J). The preserved length is 123 mm, and

TABLE 1. Measurements (in mm) of the mandibles of *Ortotherium* specimens cited in the text.

Specimen	c length	c width	m1 length	m1 width	m2 length	m2 width	m3 length	m3 width	HMR
MLP M 62 (cast of type of <i>O. laticurvatum</i> )	—	—	10	15	10	13	—	—	38
MACN Pv-13319 (type of <i>O. schlosseri</i> )	—	—	14	17	15	19	14	16	52
MACN Pv-8886 (type of <i>O. seneum</i> )	9	11	13	17	17	20	—	—	55
MACN Pv-13657 (type of <i>O. scrofum</i> )	9	8	14	16	—	—	—	—	52
MACN Pv-13318 (type of <i>M. affinis</i> )	11	11	15	15	15	15	—	—	60
MACN Pv-13656 (type of <i>O. brevirostrum</i> )	19	6	11	18	11	15	14	18	52
MACN Pv-8916 ( <i>Ortotherium</i> , sp. indet.)	12	11	16	18	14	15	15	15	57

**Abbreviations:** c, caniniform; **HMR**, height of the mandibular ramus; **m1–m3**, molariforms 1–3.

maximum depth (between m1 and m2) is 57 mm. The ventral margin is convex both transversely and anteroposteriorly. The posterolateral opening of the mandibular canal is on the lateral side of the horizontal ramus. Its ventral edge is 20 mm below the level of the alveoli and its posterior edge is just anterior to a plane passing anterior to the coronoid process (Fig. 3A). In contrast, in MLP M 62 (a cast of the type of *O. laticurvatum*) and MACN Pv-13319 (type of *O. schlosseri*, herein referred to

*O. laticurvatum*; Figs. 2B and D, respectively), the posterolateral opening of the mandibular canal is at the base of the coronoid process, almost at the same level as the alveolar series, oriented nearly laterally. In *Megalonyx* and MLP 41-XII-13-2003, type of *Paranabradys vucetichae* Scillato-Yané (Scillato-Yané, 1980:lamina 1.1), the position of the opening resembles the latter species. In *Acratocnus odontrigonus* Anthony, 1916, a megalonychid from the Pleistocene of Puerto Rico (Anthony, 1926:pl. XXXVIII) and

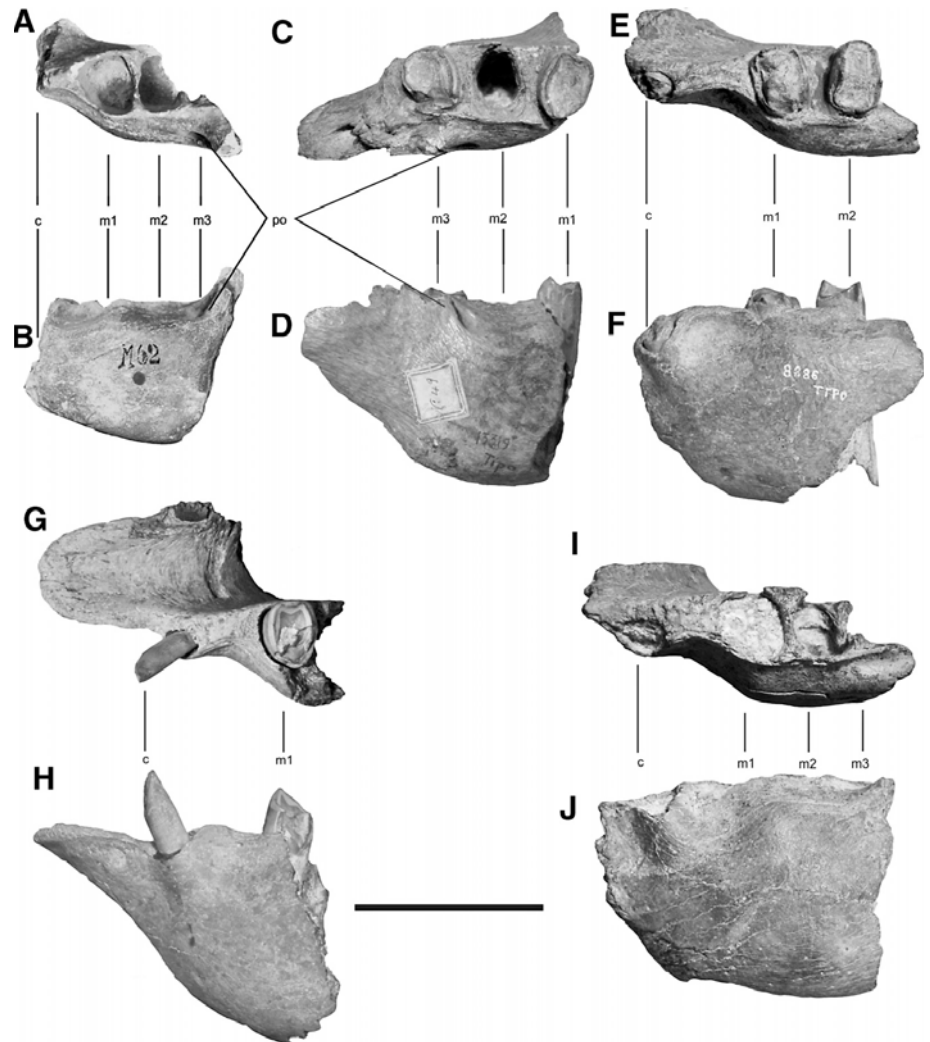


FIGURE 2. A–J, *Ortotherium laticurvatum*. A, B, MLP M 62 (cast of the type of *O. laticurvatum*); C, D, MACN Pv-13319 (type of *O. schlosseri*); E, F, MACN Pv-8886 (type of *O. seneum* and *A. seneum*); G, H, MACN Pv-13657 (type of *O. scrofum*); I, J, MACN Pv-13318 (type of *Menilauis affinis*). A, C, E, G, I, occlusal view; B, D, F, H, J, lateral view. **Abbreviations:** c, caniniform; **m1–m3**, molariforms 1–3; **po**, posterolateral opening of mandibular canal. Scale bar equals 50 mm.

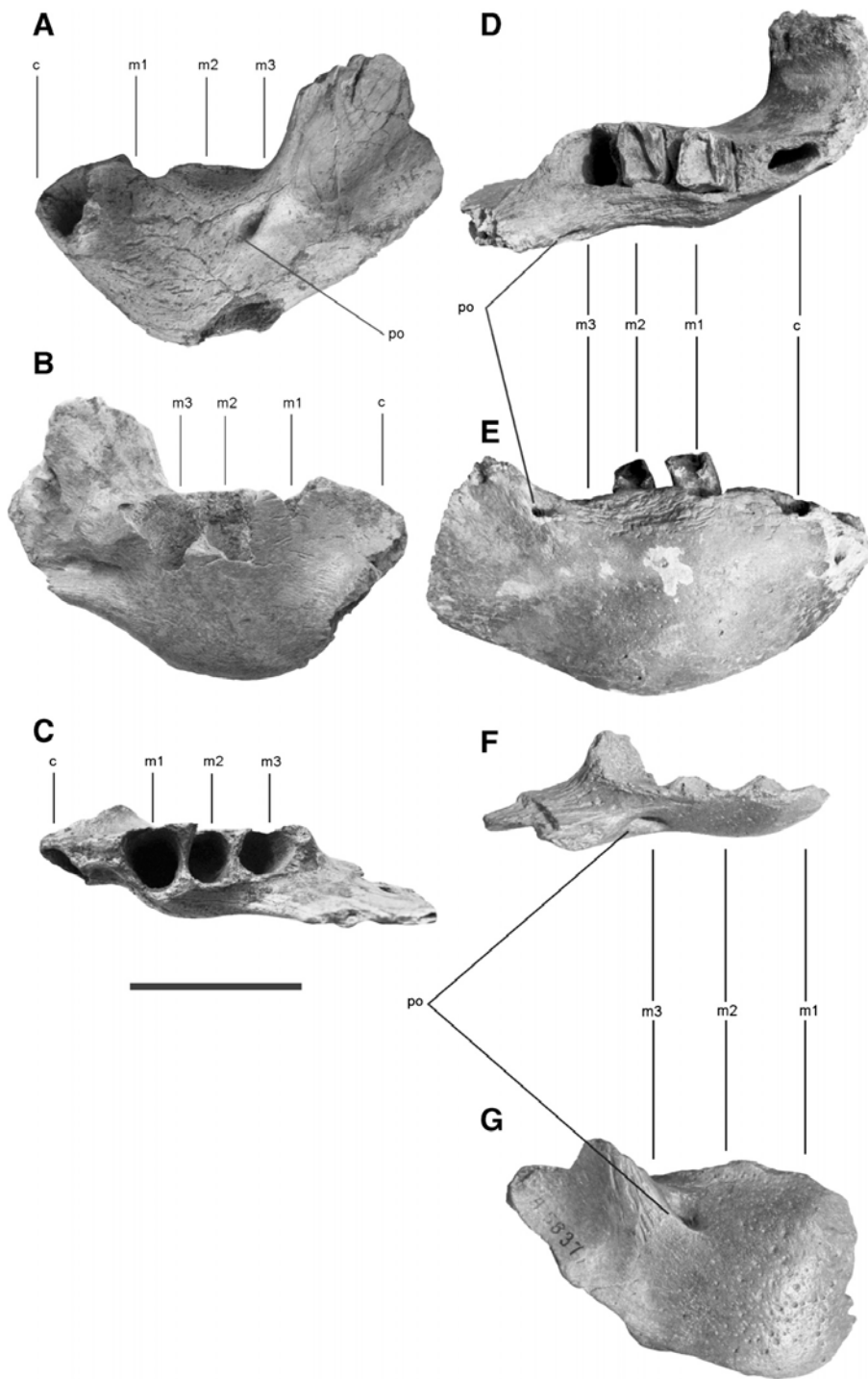


FIGURE 3. A–C, MACN Pv-8916 (*Orthotierium* sp. indet.); D, E, MACN-13656 (type of *O. brevisrostrum*); F, G, MACN A-5837 (type of *O. robustum*). A, E, G, lateral view; B, medial view; C, D, F, occlusal view. **Abbreviations:** c, caniniform; m1–m3, molariforms 1–3; po, posterolateral opening of mandibular canal. Scale bar equals 50 mm.

*Neocnus* Arreondo (MacPhee et al., 2000:fig. 12B–C), the position of the posterolateral opening of the mandibular canal resembles that of MACN Pv-8916.

In MACN Pv-8916 (Fig. 3A–C), as in MACN Pv-13319 (Fig. 2C–D) and MACN Pv-13318 (Fig. 2I–J), the anterior margin of the coronoid process is lateral to the midpoint of m3. In *P. vucetichae* (see Scillato-Yané, 1980:lamina 1.1) and *Eucholaeops*, it is posterior to m3, so that the entire tooth is visible in lateral view. In *Megalonyx*, *Megalocnus*, and *Pliometanastes*, it is lateral to m3, obscuring it in lateral view (see Gaudin, 2004:character

40). In MACN Pv-8916, the anterior margin of the coronoid process forms a  $107^\circ$  angle with the alveolar plane (Fig. 3A–B).

In occlusal view at tooththrow level, the lateral wall of the horizontal ramus is markedly convex, except for a concave dorsal portion between the caniniform and the first molariform (Fig. 3A–C). This concavity is present in most Megalonychidae, including *O. laticurvatum*, *Megalocnus rodens* Leidy (see Matthew and Paula Couto, 1959:pl. 8), *Megalonyx jeffersonni* Stock (see Stock, 1925:pl. 17), and *Pliometanastes protistus* Hirschfeld and Webb (see Hirschfeld and Webb, 1968:fig. 14). Pujos and De

Iuliis (2007) described a Megalonychidae indet. from the De-seadan SALMA of Bolivia, in which the concavity is visible (Pujos and De Iuliis, 2007:fig. 6F–G, J–K). In MACN Pv-13656 (type of *O. brevirostrum*), the concavity is absent.

The posterior margin of the mandibular symphysis of MACN Pv-8916 is located inferomedial to the c–m1 diastema (Fig. 3B–C), as in specimens referred to *O. laticurvatum* (Fig. 2A, E, G, I). In *Megalocnus*, the symphysis is inferomedial to the m1/m2 interval (Mathew and Paula Couto, 1959:fig. 1C), whereas in *Megalonyx* and *P. protistus* (Hirschfeld and Webb, 1968:fig. 14) inferomedial to c.

The lower dental series of the Megalonychidae comprises four teeth; in most species, a diastema is present between the first tooth (generally termed caniniform) and the rest of the teeth (molariforms). In *D. nordenskiöldi*, a Megalonychidae from the Pleistocene of Peru, the alveolus of the first tooth resembles that of the Megatheriinae and the diastema is absent (Pujos et al., 2007:fig. 6B).

In MACN Pv-8916, the external margin of the caniniform alveolus is subcircular, similar to that of *O. laticurvatum*. In *Megalonyx*, the caniniform is ovate, often with a marked posteromedial bulge. In *Megalocnus rodens*, it is meniscoid in cross-section (Matthew and Paula Couto, 1959:pl. 9). The internal margin of the caniniform of MACN Pv-8916 is trapezoidal and has marked edges. The alveolar length of m1–m3 is 55 mm. The alveolus of m1 is subtriangular in section with an anterior apex and rounded edges (Fig. 3C). The alveolus of m2 is oval, with the long axis oriented transversely relative to the sagittal plane (Fig. 3C). The alveolus of m3 is suboval with the long axis inclined anteroposteriorly relative to the sagittal plane (Fig. 3C). The interalveolar septa separating the alveoli of the three molariforms are very thin. In other Megalonychidae (e.g., *Megalonyx*, *Megalocnus*, *Acratocnus*), the m1 is subrectangular in cross-section, m2 is subtrapezoidal, and m3 is nearly oval.

## DISCUSSION

A broad range of individual variation has been observed in the Megalonychidae from the Pleistocene of Central America and the West Indies (MacPhee et al., 2000; White and MacPhee, 2001). If such variation is also present in the Megalonychidae from the ‘Conglomerado osífero’ of Ituzzaingó Formation, then the number of valid megalonychid species from the ‘Conglomerado osífero’ may well be lower than has been proposed previously. In this sense, the morphological differences observed in the type specimens of *Ortotherium laticurvatum*, *O. schlosseri*, *O. seneum*, *O. scrofum*, and *Menilaus affinis* do not justify the specific (and generic, in the case of *Menilaus*) distinction of these species. Consequently, here it is proposed that the aforementioned species are conspecific, making *O. schlosseri*, *O. seneum*, *O. scrofum*, and *M. affinis* synonyms of *O. laticurvatum*.

*Ortotherium brevirostrum* Bordas, based on MACN Pv-13656 (Fig. 3D–E), was originally described as a Nothrotheriinae, a subfamily included in Megalonychidae (see Bordas, 1942:174). Many species traditionally included in Nothrotheriinae are currently considered members of a distinct Nothrotheriidae (see Gaudin, 2004). Some of the features present in MACN Pv-13656 (e.g., absence of a concavity on the lateral wall of the dentary, shape of the caniniform alveolus, molariform shape, and angle between the anterior margin of the coronoid process and the alveolar plane) clearly differ from those in specimens here referred to *Ortotherium*. The presence of these differences suggests that *O. laticurvatum* and *O. brevirostrum* are not sister species and should not be in the same genus. Based on currently available evidence, *O. brevirostrum* cannot be accommodated within an existing genus, and the determination of a new genus of Megalonychidae (based on MACN Pv-13656) would be justified.

*Ortotherium robustum* Ameghino, based on very fragmentary material (MACN A-5837, a lateral wall of a right dentary; Fig. 3F–G), must be considered as nomen vanum because it does not possess any diagnostic character that would allow its determination. In addition, given that *Menilaus* is considered a synonym of *Ortotherium*, *Menilaus berroi* Kraglievich from the Tertiary of Uruguay (Kraglievich, 1932) must be referred to *Ortotherium*.

With respect to the new specimen herein described, several characters present in MACN Pv-8916 (e.g., position of posterior margin of mandibular symphysis, position of the anterior margin of the coronoid process respect to the m3) are shared with those referred to *Ortotherium*, supporting its assignation to this genus. However, the position of the posterolateral opening of the mandibular canal, on the lateral surface of the horizontal ramus, is not a common feature among the Megalonychidae from the ‘Conglomerado osífero’ for which this character may be assessed.

The new specimen of *Ortotherium* described here increases the range of intrageneric variation with respect to the position of the posterolateral opening of the mandibular canal. Thus, the position of this opening seems to be variable among the Megalonychidae. The variability of this character and its phylogenetic significance have been discussed by De Iuliis (1994), who indicated that the position of this opening could be variable among different Tardigrada (e.g., *Hapalops*). However, this character is commonly used to diagnose groups within sloths (e.g., genera and species of Megatheriinae, see De Iuliis, 1996; Pujos, 2006). The fact that some specimens within a single genus have a different position of the posterolateral opening of the mandibular canal indicates that caution should be exercised when making taxonomic decisions based on this character. Nevertheless, this character has been included in several recent phylogenetic analyses (e.g., Carlini and Scillato-Yané; 2004; Gaudin, 2004; Pujos et al., 2007).

Finally, the establishment of synonymies, as well as the generic and specific assignation of specimens from ‘Conglomerado osífero’ of Ituzzaingó Formation, is not an easy task; this is primarily due to the peculiar taphonomical context of this unit, which mainly produces disassociated and fragmentary material. New findings of better-preserved fossil material will be necessary in order to more thoroughly test the hypothesis of intraspecific variation among other taxa from Argentine Mesopotamia.

## ACKNOWLEDGMENTS

I thank M. Reguero (MLP) and A. Kramarz (MACN) for facilitating access to collections of their institutions. Reviews by anonymous reviewers, P. Holroyd, and D. Croft improved this article. This work was funded by PICT 2006-344.

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Submitted March 6, 2008; accepted September 9, 2009.