A NEW GENUS OF MEGALONYCHIDAE (MAMMALIA, XENARTHRA) FROM THE LATE MIOCENE OF ARGENTINA

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ABSTRACT – The present report describes a new genus of Megalonychidae from the Late Miocene of Entre Ríos Province, Argentina, based on a detailed reanalysis of the remains on which “*Ortotherium*” *brevirostrum* (Xenarthra, Tardigrada, Megalonychidae) was originally described. “*O.*” *brevirostrum* differs from *O. laticurvatum* (type species of the genus) and *Ortotherium* sp. in: (i) absence of a markedly concavity on the lateral wall of the dentary in “*O.*” *brevirostrum*, (ii) convexity of the ventral margin of the dentary, (iii) angle between the anterior margin of the coronoid process and the alveolar plane, (iv) length of the diastema, (v) outline of the alveolus of the caniniform, (vi) outline of the molariforms, and (vii) presence of apicobasal grooves extending on the lingual and vestibular surfaces of the molariforms (m1 and m2) in “*O.*” *brevirostrum*. The presence of these differences suggests that *O. laticurvatum* and “*O.*” *brevirostrum* should not be in the same genus. In addition, “*O.*” *brevirostrum* cannot be accommodated within an existing genus; hence the determination of a new genus of Megalonychidae is justified. The new taxon shows some features (e.g. shape of the alveolus of the caniniform, presence of apicobasal grooves in the molariforms) that are present in some genera of Megalonychidae from the Pleistocene of Central America and Antilles (i.e. *Neocnus* and *Parocnus*). This similarity could imply that the genera from the Pleistocene of Central America and Antilles and the new taxon are related.

Key words: Tardigrada, South America, Central America, ground sloths, diversity.

RESUMO – O presente trabalho descreve um novo gênero de Megalonychidae do Mioceno superior da Província de Entre Ríos, Argentina, resultado de uma nova análise detalhada dos restos “*Ortotherium*” *brevirostrum* (Xenarthra, Tardigrada, Megalonychidae) originalmente descritos. “*O.*” *brevirostrum* difere de *O. laticurvatum* (espécie tipo do gênero) e *O.* sp. em: (i) a ausência de uma acentuada concavidade da parede lateral do dentário em “*O.*” *brevirostrum*, (ii) convexidade da margem ventral do dentário, (iii) ângulo entre a linha alveolar margem anterior do processo coronoide, (iv) comprimento do diastema, (v) um contorno alveolar do caniniforme, (vi) contorno dos molariformes, e (vii) presença de sulcos apicobasal que se prolongam sobre os lados lingual e labial dos molariformes (m1 e m2) em “*O.*” *brevirostrum*. A presença destas diferenças sugere que *O. laticurvatum* e “*O.*” *brevirostrum* não deveriam estar no mesmo gênero. Além disso, “*O.*” *brevirostrum* não pode pertencer a este gênero, logo a determinação de um novo gênero de Megalonychidae é justificada. O novo táxon mostra algumas características (por exemplo, a forma dos alvéolos com formato caniniforme e a presença de sulcos apicobasal nos molariformes) que estão presentes em alguns gêneros de Megalonychidae do Pleistoceno da América Central e Antilhas (i.e. *Neocnus* e *Parocnus*). Essas semelhanças poderiam indicar que os gêneros do Pleistoceno da América Central e Antilhas e o novo táxon estão relacionados.

Palavras-chave: Tardigrada, América do Sul, América Central, preguiças, diversidade.

INTRODUCTION

The clade Megalonychidae (Xenarthra, Tardigrada) is known from the Oligocene of Santa Cruz Province, Argentina (i.e. *Deseadognathus* Carlini & Scillato-Yané, 2004) and Bolivia (Pujos & De Iuliis, 2007) as well as from the present, represented by the extant sloth *Choloepus* Illiger, 1811 (see White & MacPhee, 2001; Gaudin, 2004; but see Carlini & Scillato-Yané, 2004 for the systematic allocation of the other extant sloth, i.e. *Bradypus* Linnaeus, 1758). Although the most important fossil records of this clade are those from the Quaternary of Central America and the Antilles (e.g. *Megalocnus* Leidy, 1868, *Acratocnus* Anthony, 1916,

Parocnus Miller, 1929, *Neocnus* Arredondo, 1961, *Paulocnus* Hooijer, 1962; see Matthew & Paula Couto, 1959; White & MacPhee, 2001) and North America (e.g. *Megalonyx* Harlan, 1825, *Pliometanastes* Hirschfeld & Webb, 1968; see Hirschfeld & Webb, 1968; White & MacPhee, 2001; McDonald *et al.*, 2013a), in South America the clade is mainly recorded from the Neogene and Quaternary of Argentina (see below), the Quaternary of Brazil (i.e. *Ahytherium* Cartelle, De Iuliis & Pujos, 2008; *Australonyx* De Iuliis, Pujos & Cartelle, 2009), the Pleistocene of Peru (i.e. *Diaboloherium* Pujos, De Iuliis, Argot & Werdelin, 2007; see Pujos *et al.*, 2007; Shockey *et al.*, 2009; see also Pujos *et al.*, 2011 for the systematic allocation of *Diaboloherium*), and the Pleistocene of Venezuela (i.e.

Megistonyx oreobios McDonald, Rincón & Gaudin, 2013; see McDonald *et al.*, 2013b). In Argentina, besides the record of *Deseadognathus riggsi* Carlini & Scillato-Yané, 2004, from the Deseado Formation, Megalonychidae were recorded from the Santa Cruz Formation (late Early Miocene) of Santa Cruz Province (*i.e.* *Eucholoeops* Ameghino, 1887; Scott, 1903-1904; Scillato-Yané, 1986; Tauber, 1997; Bargo *et al.*, 2009), the Arroyo Chasicó Formation (Late Miocene) of Buenos Aires Province (*i.e.* *Protomegalonyx chasicoensis* Scillato-Yané, 1977; see Scillato-Yané, 1977; Brandoni, 2009), the Río Negro Formation (Scillato-Yané *et al.*, 1976), the “Conglomerado osífero” (ossiferous conglomerate) or “Mesopotamiense” (Late Miocene) within the Ituzaingó Formation, Entre Ríos Province (Carlini *et al.*, 2000; Cione *et al.*, 2000; Brandoni, 2010, 2011, 2013a), and from the Pleistocene of Buenos Aires Province (Kraglievich, 1930).

Several authors have studied the Megalonychidae from the “Conglomerado osífero” (*e.g.* Ameghino, 1883, 1885, 1891a; Kraglievich, 1922, 1923a, b, c, 1925, 1926a, b; Bordas, 1942; Scillato-Yané, 1980); however, these ground sloths were not usually considered in recent studies due in large part to the poor preservation and fragmentary nature of their remains (Brandoni, 2010). The most recent contributions on Megalonychidae from the “Conglomerado osífero” are those by Brandoni (2008, 2010, 2011) who actualized systematic aspects of *Ortotherium* Ameghino, 1885, *Pliomorphus* Ameghino, 1885, *Menilais* Ameghino, 1891, *Amphiocnus* Kraglievich, 1922, *Protomegalonyx* Kraglievich, 1925, *Megalonychops* Kraglievich, 1926, and *Paranabradys* Scillato-Yané 1980.

With respect to *Ortotherium*, several species were erected by Florentino Ameghino at the end of the 19th century: *O. laticurvatum* Ameghino, 1885, *O. robustum* Ameghino 1891, *O. schlosseri* Ameghino, 1891, and *O. seneum* Ameghino, 1891 (see Ameghino, 1891a). In addition, Bordas (1942) described *O. scrofum* Bordas, 1942, and *O. brevirostrum* Bordas, 1942 (Cione *et al.*, 2000; Carlini *et al.*, 2000; Brandoni 2010, 2011, 2013a). Brandoni (2010) considered *O. laticurvatum* as the only valid species for the genus, with *O. schlosseri*, *O. seneum*, *O. scrofum*, being junior synonyms of *O. laticurvatum*. In addition, Brandoni (2010) considered “*Ortotherium*” *brevirostrum* not congeneric with *O. laticurvatum* suggesting that “*Ortotherium*” *brevirostrum* may be the type species of a new genus; however, Brandoni (2010) did not nominate such a genus.

The present report describes a new genus of Megalonychidae based on a detailed reanalysis of the remains on which “*Ortotherium*” *brevirostrum* was originally described.

Institutional abbreviations. MACN Pv, Colección Paleontología Vertebrados del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

Other abbreviations. c, caniniform; Ma, millions of years ago; m1-m3, lower molariform 1-3; po, posterolateral opening of mandibular canal.

GEOLOGICAL SETTING

In Entre Ríos Province, Argentina, remains of fossil vertebrates were collected from the lower levels of the Ituzaingó Formation, particularly from a basal level, informally known as “Mesopotamiense” or “Conglomerado osífero” (Frenguelli, 1920); recently these levels were considered as the lower member of the Ituzaingó Formation (Brunetto *et al.*, 2013). The Ituzaingó Formation extends from the city of Ituzaingó in Corrientes Province where the type profile was originally described, to the north of Paraná, the capital of Entre Ríos Province (Figure 1A). The “Mesopotamiense” outcrops discontinuously from cliffs along the Paraná River, from the vicinity of the city of Paraná to the locality of Hernandarias (Figure 1B). The “Mesopotamiense” (Figure 2) is clearly visible in places where the discordance between the underlying Paraná Formation, marine in origin, and the sandy-clayey and conglomerate levels of the Ituzaingó Formation becomes evident. 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. Cione *et al.* (2000) referred the “Conglomerado osífero” to the Huayquerian (Late Miocene) of the South America Stage/Age system. Recently, Brandoni (2013b) analyzed a complete and updated list of fossil continental mammals recorded in the “Mesopotamiense” and proposed an affinity of the “Mesopotamiense” with the Chasicóan fauna of Buenos Aires Province, and considered that the beginning of the deposition of the “Mesopotamiense” begins in the early Late Miocene (*i.e.* Tortonian Stage/Age, Gradstein *et al.*, 2012).

SYSTEMATIC PALEONTOLOGY

Superorder XENARTHRA Cope, 1889

Order TARDIGRADA Latham & Davies in Forster, 1795

Family MEGALONYCHIDAE Gervais, 1855

Mesopotamocnus gen. nov.

1885 *Ortotherium* in part. Ameghino, p. 111-113.

Type species. *Mesopotamocnus brevirostrum* (Bordas, 1942) comb. nov.

Derivation of name. *Mesopotam*, from its geographic provenance: Mesopotamia (from Greek meaning between rivers; *ocnus* from latinized Greek meaning slowness).

Geographic and stratigraphic provenances. In the vicinity of the city of Paraná, Entre Ríos Province (Argentina; Figure 1B) within the “Conglomerado osífero” or “Mesopotamiense” (lower member of Ituzaingó Formation, see Brunetto *et al.*, 2013; Figure 2). Tortonian Stage/Age (Late Miocene) (Cione *et al.*, 2000; Brandoni, 2010, 2011, 2013b).

Diagnosis. Larger than *Deseadognathus*, slightly larger than *Eucholoeops*, similar in size to *Ortotherium* and

Figure 1. Map of the Itzaingó Formation and the “Mesopotamiense”. **A**, location of the Itzaingó Formation at Mesopotamia, Argentina (dark grey areas); **B**, principal localities where the “Conglomerado osífero” is exposed (grey circles) (modified from Brunetto *et al.*, 2013).

Figure 2. Generalized stratigraphic profile of the area of Paraná, Entre Ríos Province, Argentina (modified from Aceñolaza, 1976; Brandoni, 2006).

Paranabradys, and smaller than *Megalonyx*, and *Megalocnus*. Posterolateral opening of mandibular canal on lateral margin of base of coronoid process, as in *Eucholoeops*, *Paranabradys*, and *Megalocnus*. As in *Ortotherium*, anterior margin of the coronoid process lateral to midpoint of m3, more anterior than in *Eucholoeops* and *Paranabradys*, and more posterior than in *Megalocnus*, *Megalonyx*, and *Pliometanastes*. As in *Ortotherium*, posterior margin of mandibular symphysis ventromedial to c-m1 diastema; slightly anterior to the plane of the m1 in *Parocnus* and *Deseadognathus*, ventromedial to m1-m2 interval in *Megalocnus*; ventromedial to the caniniform in *Megalonyx* and *Pliometanastes*. As in *Parocnus*, alveolus of caniniform meniscoid in cross-section; subcircular in *Ortotherium*; larger and more oval in *Megalonyx*; larger and meniscoid in *Megalocnus*; subtriangular in *Deseadognathus* and *Eucholoeops*; m1 trapezoidal in cross-section; subrectangular in *Megalonyx* and *Megalocnus*. m2 trapezoidal in cross-section, and m3 suboval in cross-section; m2 subtrapezoidal and m3 nearly oval in *Megalonyx* and *Megalocnus*. As in some specimens of *Neocnus*, m1 and m2 with apicobasal grooves extending on their lingual and vestibular surfaces. Occlusal surface of m1 and m2 with two crests (lophids) along the mesial and distal edge of each tooth.

Mesopotamocnus brevirostrum (Bordas, 1942)
comb. nov.
(Figures 3A-C)

1942 *Ortotherium brevirostrum* Bordas, pl. 2, p.176.

Holotype. MACN Pv 13656, type of *Ortotherium brevirostrum* Bordas, 1942, incomplete right dentary that preserves the m1 and m2.

Geographic and stratigraphic provenances. In the vicinity of the city of Paraná, Entre Ríos Province (Argentina; Figure 1B) within the “Conglomerado osífero” or “Mesopotamiense” (lower member of Ituzaingó Formation, see Brunetto *et al.*, 2013; Figure 2). Tortonian Stage/Age (Late Miocene) (Cione *et al.*, 2000; Brandoni, 2010, 2011, 2013b).

Diagnosis. As for the genus by monotypy.

Description. MACN Pv 13656 is an almost complete right dentary that preserves the m1 and m2, although it is missing the angular process, condyloid process, caniniform, and m3. The preserved length is 115 mm, and maximum depth (at the level m2-m3) is 55 mm, being similar in size to most of the specimens referred to *Ortotherium* and *Paranabradys* (see Brandoni, 2010, tab. 1).

The ventral margin of the dentary is very convex both transversely and anteroposteriorly; whereas in *Ortotherium laticurvatum* and *Ortotherium* sp. (see Brandoni, 2010), it is anteroposteriorly less convex; and in *Eucholoeops* sp. it is nearly straight anterior to the m3 (Bargo *et al.*, 2009, fig. 2F). As in the specimens referred to *Ortotherium*, *Eucholoeops fronto* Ameghino, 1891 (see Ameghino, 1891b), and *Megalocnus rodens* Leidy, 1868, among others, the dorsoventral height of the horizontal ramus decreases anteriorly to m3.

In *Mesopotamocnus brevirostrum* comb. nov., the posterolateral opening of the mandibular canal is at the base of the coronoid process, almost at the same level of the alveolar series, and faces nearly laterally (Figure 3A). In *Megalonyx jeffersonii* Desmarest, 1822, and *Paranabradys vucetichae* Scillato-Yané, 1980 (see Scillato-Yané, 1980, fig. 1.1), the position of the opening resembles *M. brevirostrum* comb. nov.. In *Ortotherium* sp., *Acratocnus odontrigonus* Anthony, 1916, and *Neocnus dousman* MacPhee, White & Woods, 2000, the posterolateral opening of the mandibular canal is on the lateral side of the horizontal ramus (Anthony, 1926, pl. XXXVIII; MacPhee *et al.*, 2000, figs. 8B, 12B; Brandoni, 2010, fig. 3A).

As in *Ortotherium*, in *Mesopotamocnus brevirostrum* comb. nov. the anterior margin of the coronoid process is lateral to the midpoint of m3 (Figures 3A-C). In *Paranabradys vucetichae* (see Scillato-Yané, 1980, fig. 1.1) and *Eucholoeops* sp. (Bargo *et al.*, 2009, fig. 2F), it is posterior to m3, so that the entire tooth is visible in lateral view. In *Megalonyx jeffersonii*, *Megalocnus rodens*, *Parocnus browni* (Matthew, 1931), and *Pliometanastes protistus* Hirschfeld & Webb, 1968, it is lateral to m3, obscuring it in lateral view (see Gaudin, 2004, character 40). In *Mesopotamocnus brevirostrum* comb. nov., the anterior margin of the coronoid process forms a 136° angle with the alveolar plane; whereas the angle is 107° in *Ortotherium* sp. (Brandoni, 2010).

In occlusal view at tooth row level (Figure 3B), the lateral wall of the horizontal ramus is markedly convex, without the concave dorsal portion (*i.e.* the buccinator fossa) between the caniniform and the first molariform that is present in most Megalonychidae, including *Ortotherium laticurvatum*, *Megalocnus rodens* (see Matthew & Paula Couto, 1959, pl. 8), *Parocnus* spp. (see Matthew & Paula Couto, 1959, pl. 30), *Megalonyx jeffersonii* (see Stock, 1925, pl. 17) and *Pliometanastes protistus* (see Hirschfeld & Webb, 1968, fig. 14). Although the left dentary is not preserved, its preserved portion suggests that the margin of the mandibular symphysis seems to be U-shaped (Figure 3B). As in *Ortotherium laticurvatum*, the posterior margin of the mandibular symphysis of *Mesopotamocnus brevirostrum* comb. nov. is located ventromedial to the c-m1 diastema (Figure 3B); whereas in *Parocnus browni* and *Deseadognathus riggsi*, the symphysis is slightly anterior to the m1 (Mathew & Paula Couto, 1959, fig. 2C; Carlini & Scillato-Yané, 2004, fig. 2D); it is ventromedial to the m1-m2 septum in *Megalocnus rodens* (see Mathew & Paula Couto, 1959, fig. 1C), and in *Megalonyx jeffersonii* and *Pliometanastes protistus* (see Hirschfeld & Webb, 1968, fig. 14) reaches the plane of the middle of the caniniform.

The lower dental series of the Megalonychidae comprises four teeth; a diastema is present between the first tooth (generally termed caniniform) and the rest of the teeth (molariforms). The lower dental tooth row of *Mesopotamocnus brevirostrum* comb. nov. is 65 mm in length, the outline of the caniniform alveolus is oval to meniscoid, with its mesiodistal length twice as long as the vestibulolingual width (length, 12 mm; width 7 mm), and the main axis nearly aligned to the tooth row (Figure 3B). In *Ortotherium laticurvatum*,

Figure 3. Right dentary of *Mesopotamocnus brevirostrum* (Bordas, 1942) comb. nov. (MACN Pv 13656). **A**, lateral view; **B**, occlusal view; **C**, medial view. **Abbreviations:** c, caniniform; m1-m3, lower molariform 1-3; po, posterolateral opening of mandibular canal. Scale bar = 50 mm.

the caniniform is subcircular in cross-section; in *Megalonyx jeffersonii* is ovate, often with a marked posteromedial bulge. In *Parocnus browni* (see Mathew & Paula Couto, 1959, fig. 2C and pl. 30), the outline of the alveolus is similar to that of *Mesopotamocnus brevirostrum* comb. nov. In *Megalocnus rodens*, it is meniscoid in outline with its major axis nearly oblique respect the tooth row (Matthew & Paula Couto, 1959, pl. 9). In *Deseadognathus riggsi* and *Eucholoeops fronto* it is subtriangular in section. The diastema is relatively short (8.6 mm) compared with the diastema of *Ortotherium* (15-20 mm; Brandoni, 2010).

The m1 is rectangular to trapezoidal in section (lingual length, 9 mm; vestibular length 12 mm; width, 18 mm). The occlusal surface is formed by two crests (lophids) along the mesial and distal edge of the tooth; these crests are lingually connected (Figures 3B,C). As in some specimens of *Neocnus* (see McAfee, 2011), this tooth has apicobasal grooves extending on their lingual and vestibular surfaces (Figures 3A-C); with the lingual groove deeper than the vestibular one. In *Ortotherium laticurvatum*, the m1 is subtriangular in section and with rounded edges; in *Megalocnus rodens*, the m1 is subrectangular in section, and in *Parocnus browni* the section is similar to that of *Mesopotamocnus brevirostrum* comb. nov..

The m2 also presents a trapezoidal outline (lingual length, 8 mm; vestibular length 11.5 mm; width, 15 mm). As in the m1, the m2 has the vestibulolingual lophids and the apicobasal grooves on lingual and vestibular surfaces (Figures 3B,C). In *Ortotherium laticurvatum*, the m2 is oval to trapezoidal, with the long axis oriented transversely relative to the sagittal plane. In *Megalocnus rodens* and *Parocnus browni*, the m2 is subtriangular in section and with rounded edges.

The alveolus of the m3 is suboval in outline with the long axis anteroposteriorly inclined with respect to the sagittal plane (length, 14 mm; width, 18 mm). The interalveolar septa separating the alveoli of the three molariforms are not very thin (Figure 3A); the septa are thin in *Ortotherium*.

DISCUSSION

“*Ortotherium*” *brevirostrum* was originally described as a Nothrotheriinae, a group that was included in Megalonychidae (see Bordas, 1942, p. 174,176); however, the genus *Ortotherium* is currently considered as a Megalonychidae, without assignment to a particular clade (e.g. Ortotheriinae, Megalocninae or Megalonychinae) (see Brandoni, 2011). In addition, most of the genera and species that were traditionally viewed as nothrotheres are considered members of Nothrotheriinae (e.g. *Nothrotherium* Lydekker, 1889, *Nothropus* Burmeister, 1882, *Pronothrotherium* Ameghino, 1907, *Nothrotheriops* Hoffstetter, 1954, *Mionothropus* De Iuliis, Gaudin & Vicars, 2011) or as basal Megatherioidea (e.g. *Hapalops* Ameghino, 1887, *Schismotherium* Ameghino, 1887, *Xyophorus* Ameghino, 1887, *Pelecypodon* Ameghino, 1891) (Gaudin, 2004; De Iuliis *et al.*, 2011; Pujos *et al.*, 2011).

“*Ortotherium*” *brevirostrum* differs from *Ortotherium laticurvatum* (Figures 4A,B) and *Ortotherium* sp. (Figures

Figure 4. Dentaries of *Ortotherium* Ameghino, 1885. **A-B**, left dentary of *Ortotherium laticurvatum* Ameghino, 1885 (MLP M 62, cast of type of *O. laticurvatum*); **C,D**, left dentary of *Ortotherium* sp. (MACN Pv 8916). **A,C**, lateral view; **B,D**, occlusal view. **Abbreviations:** c, caniniform; m1-m3, lower molariform 1-3; po, posterolateral opening of mandibular canal. Scale bar = 50 mm

4C,D) in several features: (i) absence of a markedly concavity on the lateral wall of the dentary in “*O.*” *brevirostrum*, (ii) convexity of the ventral margin of the dentary, (iii) angle between the anterior margin of the coronoid process and the alveolar plane, (iv) length of the diastema, (v) outline of the alveolus of the caniniform, (vi) outline of the molariforms, and (vii) presence of apicobasal grooves extending on the lingual and vestibular surfaces of the molariforms in

“*O.*” *brevirostrum*. As noted by Brandoni (2010), the presence of these differences suggests that *O. laticurvatum* and “*O.*” *brevirostrum* should not be in the same genus. In addition, and based on currently available evidence, “*O.*” *brevirostrum* cannot be accommodated within an existing genus, hence the determination of a new genus of Megalonychidae (*Mesopotamocnus* nov. gen.) is justified. It is important to remark that given the present state of knowledge, it is not possible to elucidate synonymies between the Megalonychidae from the “Mesopotamiense” based on postcranial remains to those determined on cranial ones. Thus, it is not possible to refer MACN Pv 13656 (type of *M. brevirostrum* comb. nov.) to any of the genera and species described on postcranial remains (e.g. *Torcellia*, *Protomegalonyx*, *Amphiocnus*).

Mesopotamocnus brevirostrum comb. nov. shows features that clearly resemble those of megalonychids (e.g. presence of a relatively robust caniniform, presence of diastema between c1 and m1); however, the presence of apicobasal grooves on the lingual and vestibular surfaces of the molariforms (m1 and m2) it is not common among Megalonychidae, apicobasal grooves are present in the molariforms of some specimens of *Neocnus* (McAfee, 2011), but resembles the morphology of the molariforms of Nothrotheriidae (see De Iuliis *et al.*,

2011). According to De Iuliis *et al.* (2011), the presence of apicobasal grooves on molariform teeth is a synapomorphy of Nothrotheriidae (represented by *Thalassocnus* Muizon & McDonald, 1995, *Mionothropus*, *Pronothrotherium*, *Nothrotherium*, and *Nothrotheriops* in the analysis performed by De Iuliis *et al.*, 2011). In addition, this feature is also present in the Nothrotheriinae “*Xyophorus*” *bondesioi* Scillato-Yané, 1979, and “*Xyophorus*” *villarroeli* Saint-André, 1996 (Brandoni, 2014).

In most Megalonychidae, the caniniform is relatively robust and it is separated from the molariforms by a diastema. In *Diabolotherium nordenskioldi* (Kraglievich, 1926), originally described as a Megalonychidae from the Pleistocene of Peru, the alveolus of the first lower tooth resembles that of the Megatheriinae and the diastema is absent (see Kraglievich, 1926b; Pujos *et al.*, 2007, fig. 6B; Shockey, 2009, fig. 4.1). However, recently and based on the shape of the teeth, Pujos *et al.* (2011) considered that *Diabolotherium* is neither a nothrotheriid nor a megalonychid. In some Nothrotheriinae (e.g. *Pronothrotherium typicum* Ameghino, 1907, *Mionothropus cartellei* De Iuliis, Gaudin & Vicars, 2011) and some basal megatherioids (e.g. *Hapalops*), the caniniform is reduced, subcircular or suboval in outline, and separated from the molariforms by a diastema. As was

Figure 5. Cladograms showing relationships among Megalonychidae. **A**, modified from White & MacPhee (2001); **B**, modified from Gaudin (2004).

indicated, in *Mesopotamocnus brevirostrum* comb. nov. the alveolus of the caniniform is oval to meniscoid in outline, with anteroposterior length twice that of the vestibulolingual width, resembling the condition of some Megalonychidae from Central America (see below).

Mesopotamocnus brevirostrum comb. nov. shows some features (e.g. shape of the alveolus of the caniniform, presence of apicobasal grooves in the molariforms) that are present in some genera of Megalonychidae recorded from the Pleistocene of Central America and Antilles. *M. brevirostrum* comb. nov. shares with *Neocnus* the shape of molariforms (presence of apicobasal grooves) and with *Parocnus* the shape of the alveolus of the caniniform. This similarity could imply that the genera from the Pleistocene of Central America and Antilles and *M. brevirostrum* comb. nov. are related.

Currently, based on cladistic analyses, *Parocnus* is considered the sister group to *Megalocnus* (White & MacPhee, 2001; Gaudin, 2004). White & MacPhee (2001) proposed a diphyletic origin for the Antillean megalonychids, with the clade Megalocninae formed by *Megalocnus* and *Parocnus* and the clade Choloepodinae represented by *Choloepus*, *Acratocnus*, *Paulocnus*, and *Neocnus* (Figure 5A). On the other hand, Gaudin (2004) proposed a close relationship between the extant *Choloepus* and the Antillean Megalonychidae with a clade formed by *Parocnus*, *Megalocnus*, *Acratocnus*, *Choloepus* and *Neocnus* (Figure 5B). Whether *Mesopotamocnus brevirostrum* comb. nov. is the sister group to Megalocninae (*sensu* White & MacPhee, 2001) or it is related to Choloepodinae (*sensu* White & MacPhee, 2001) cannot be tested with the available information since it is necessary to have more complete specimens of *M. brevirostrum* comb. nov. It is important to remark that in the early 19th Century, Kraglievich (1923b) had already considered a close relationship between the Megalonychidae from the Neogene of Entre Ríos Province, Argentina, with those from the Pleistocene of Central America and Antilles (e.g. *Megalocnus*).

Finally, given that most of the species of Megalonychidae from the “Mesopotamiense” are endemic, the taphonomical context of the unit (e.g. fragmented and disassociated remains), and the absence of well-preserved megalonychid remains in other coeval units of South America, a systematic review of the species in a cladistic and evolutionary context is difficult to perform (see Brandoni, 2011). Nevertheless, the study of the genera and species recorded in the Late Miocene of Argentina could be useful for inferring some chronological and biogeographical relations for the Cenozoic of South America and Central America and Antilles.

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