

Original article

The Megalonychidae (Xenarthra, Tardigrada) from the late Miocene of Entre Ríos Province, Argentina, with remarks on their systematics and biogeography[☆]

Les Megalonychidae (Xenarthra, Tardigrada) du Miocène supérieur de la province de Entre Ríos, Argentine, avec commentaires sur leur systématique et biogéographie

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Abstract

Megalonychidae are known from the Deseadan of Argentina and Bolivia to the present, represented by the tree sloth *Choloepus* Illiger. The principal fossil records of this clade are those from the Quaternary of Central America and the Antilles (e.g., *Megalocnus* Leidy, *Acratocnus* Anthony) and North America (e.g., *Megalonyx* Harlan, *Pliometanastes* Hirschfeld and Webb). From the Quaternary of South America, Megalonychidae are recorded in Peru (*Diabolootherium* Pujos, De Iuliis, Argot and Werdelin) and Brazil (e.g., *Ahytherium* Cartelle, De Iuliis and Pujos, *Australonyx* De Iuliis, Pujos and Cartelle). In Argentina they also have been recorded in the Santa Cruz Formation (early-middle Miocene) on the coast of Santa Cruz Province (*Eucholaeops* Ameghino), Arroyo Chasicó Formation (*Protomegalonyx* Kraglievich), Río Negro Formation, in the “conglomerado osífero” (ossiferous conglomerate) or “Mesopotamiense” (late Miocene) at the base of Ituzaingó Formation, Entre Ríos Province, and Pleistocene of Buenos Aires Province. Several authors have studied the Megalonychidae from the “conglomerado osífero”, but no systematic revision of the group has been undertaken beyond the original naming of species. Taking into account that a broad range of individual variation has been observed in the Megalonychidae from the Pleistocene of North America and the West Indies, and that a similar range probably existed among the megalonychids from the “conglomerado osífero”, then the number of valid species might be lower than previously proposed. Thus, the valid species recovered from the “conglomerado osífero” are *Ortotherium laticurvatum* Ameghino, *Pliomorphus mutilatus* Ameghino, *Amphiocnus paranense* Kraglievich, *Protomegalonyx doellojuradoi* Kraglievich, *Pr. Praecursor* Kraglievich, *Megalonychops primigenius* Kraglievich, and *Paranabradys vucetichae* Scillato-Yané. However, the establishment of synonymies, as well as the generic and specific assignation of the specimens is not an easy task, due to the peculiar taphonomical context of this stratigraphic unit.

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Keywords: Ground sloth; “Conglomerado osífero”; Mesopotamic region; Taxonomy; Biogeography

Résumé

Les Megalonychidae sont reconnus depuis le Déséadien d'Argentine et de Bolivie et sont représentés de nos jours par le paresseux arboricole *Choloepus* Illiger. Les principaux registres fossiles de ce clade proviennent du Quaternaire d'Amérique centrale et des Antilles (e.g., *Megalocnus* Leidy, *Acratocnus* Anthony) ainsi que d'Amérique du Nord (e.g., *Megalonyx* Harlan, *Pliometanastes* Hirschfeld et Webb). Pour le Quaternaire sud-américain, les mégalonychidés sont signalés au Pérou (*Diabolootherium* Pujos, De Iuliis, Argot et Werdelin) et au Brésil (e.g., *Ahytherium* Cartelle, De Iuliis et Pujos, *Australonyx* De Iuliis, Pujos et Cartelle). En Argentine des membres de ce clade sont signalés dans la Formation Santa Cruz (Miocène inférieur et moyen) sur la côte de la Province de Santa Cruz (*Eucholaeops* Ameghino), dans la Formation Arroyo Chasicó (*Protomegalonyx* Kraglievich), dans la Formation Río Negro, dans le « conglomerado osífero » (conglomérat à ossements) et le « Mesopotamiense » (Miocène supérieur) de la base de la Formation Ituzaingó, Province de Entre Ríos, ainsi que du Pléistocène de la province de Buenos Aires. De nombreux auteurs ont étudié les mégalonychidés provenant du « conglomerado osífero » mais aucune révision systématique n'a été réalisée depuis la détermination originale des espèces. Tenant compte de l'importante variabilité individuelle observée chez les

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Megalonychidae d'Amérique du Nord ainsi que des Antilles, et en admettant de telles variations pour les mégalonychidés provenant du « conglomerado osífero », le nombre d'espèces valides doit être inférieur à celui proposé jusqu'à présent. Ainsi, les espèces considérées valides provenant du « conglomerado osífero » sont : *Ortotherium laticurvatum* Ameghino, *Pliomorphus mutilatus* Ameghino, *Amphiocnus paranense* Kraglievich, *Protomegalonyx doellojuradoi* Kraglievich, *Pr. praecursor* Kraglievich, *Megalonychops primigenius* Kraglievich et *Paranabradys vucetichae* Scillato-Yané. Il est certain que la mise en place de synonymies ainsi que la détermination générique et spécifique des spécimens est loin d'être simple à cause du contexte particulier de cette unité stratigraphique.

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Mots clés : Paresseux géant ; « Conglomerado osífero » ; Région Mésopotamique ; Taxonomie ; Biogéographie

1. Introduction

Within xenarthrans, sloths and ground sloths are considered members of Tardigrada (sensu Latham and Davies, 1795) or Phyllophaga or Folivora (see further discussion on the use of these terms in Delsuc et al., 2001; Fariña and Vizcaíno, 2003; McKenna et al., 2006). They constitute one of the characteristic mammalian groups for the Cenozoic of South America. Since the Deseadan (late Oligocene), Tardigrada become abundant in the fossil record, represented by several lineages (e.g., Megatheriidae, Nothrotheriidae, Megalonychidae, and Mylodontidae; Gaudin, 2004; Vizcaíno, 2009) that are especially diversified during the Miocene-Pliocene.

Megalonychidae are known from the Deseadan of Argentinean Patagonia (*Deseadognathus* Carlini and Scillato-Yané, 2004) and Bolivia (Pujos and De Iuliis, 2007) to the present, represented by the extant sloth *Choloepus* Illiger, 1811 (White and MacPhee, 2001; Gaudin, 2004; Carlini and Scillato-Yané, 2004). 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; Matthew and Paula Couto, 1959; White and MacPhee, 2001) and North America (e.g., *Megalonyx* Harlan, 1825; *Pliometanastes* Hirschfeld and Webb, 1968; Hirschfeld and Webb, 1968; White and MacPhee, 2001). From the Quaternary of South America, Megalonychidae were recorded in Peru (*Diaboloherium* Pujos, De Iuliis, Argot and Werdelin, 2007) and Brazil (*Ahytherium* Cartelle, De Iuliis and Pujos, 2008; *Australonyx* De Iuliis, Pujos and Cartelle, 2009) (Pujos et al., 2007; Cartelle et al., 2008; De Iuliis et al., 2009). In Argentina, besides the record of *Deseadognathus*, Megalonychidae were recorded in the Santa Cruz Formation (early-middle Miocene) on the coast of Santa Cruz Province (*Eucholaeops* Ameghino, 1887; Scott, 1903–1904; Scillato-Yané, 1986; Tauber, 1997; Bargo et al., 2009), the Arroyo Chasicó Formation (*Protomegalonyx chasicensis* Scillato-Yané, 1977; see Brandoni, 2009, Scillato-Yané 1977), the Río Negro Formation (Scillato-Yané et al., 1976), in the “conglomerado osífero” (ossiferous conglomerate) or “Mesopotamiense” within the Ituzaingó Formation, Entre Ríos Province Carlini et al., 2000; Cione et al., 2000; Brandoni, 2008, among others, and from the Pleistocene of Buenos Aires Province (Kraglievich, 1930a).

At the end of the 19th century, and during the 20th century, several authors studied the Megalonychidae from the “conglomerado osífero” (e.g., Ameghino, 1885, 1891;

Kraglievich, 1922, 1923a, 1923b, 1923c, 1925, 1926a, 1926b; Bordas, 1942; Scillato-Yané, 1980), but a systematic revision of the group was not performed beyond the original naming of species. Many of these fossil sloths have been excluded from other researchers' studies, due to the fragmentary nature of their remains. The most recent contributions on these megalonychids are those of Cione et al. (2000), Carlini et al. (2000), and Brandoni (2008, 2009, 2010), which commented on the different genera: *Ortotherium* Ameghino, 1885, *Pliomorphus* Ameghino, 1885, *Menillaus* Ameghino, 1891, *Amphiocnus* Kraglievich, 1922, *Protomegalonyx* Kraglievich, 1925, *Megalonychops* Kraglievich, 1926a, and *Paranabradys* Scillato-Yané, 1980. Despite these contributions, the taxonomic status of several species from the Cenozoic of Argentina, first described and named in the late 19th century, has not been addressed.

The Ituzaingó Formation (De Alba, 1953) extends from the city of Ituzaingó (Corrientes Province), where the type profile 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 mentioned unit in Entre Ríos Province, particularly from a basal level, informally known as “Mesopotamiense” or “conglomerado osífero” (Frenguelli, 1920). This unit outcrops discontinuously along the Paraná River cliffs and many streams, from the vicinity of Paraná to the locality of Hernandarias, in the north. Prospecting is currently focused on the following fossil-bearing localities: Toma Vieja (S 31° 42' 11", W 60° 28' 06", in the vicinity of Paraná), Villa Urquiza (S 31° 38' 42.5", W 60° 22' 50.5"), and La Celina (S 31° 37' 37", W 60° 20' 04") (Fig. 1A). The “conglomerado osífero” is clearly visible in places where the discordance between the underlying Paraná Formation, marine in origin (Bravard, 1858), and the sandy-clayey and conglomerate levels of the Ituzaingó Formation, becomes evident (Fig. 1B; 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 list of fossil vertebrates recorded in the “conglomerado osífero” of the Ituzaingó Formation and, based on the stratigraphic relationships between the different fossil beds, proposed greater affinity of the “conglomerado osífero” with the

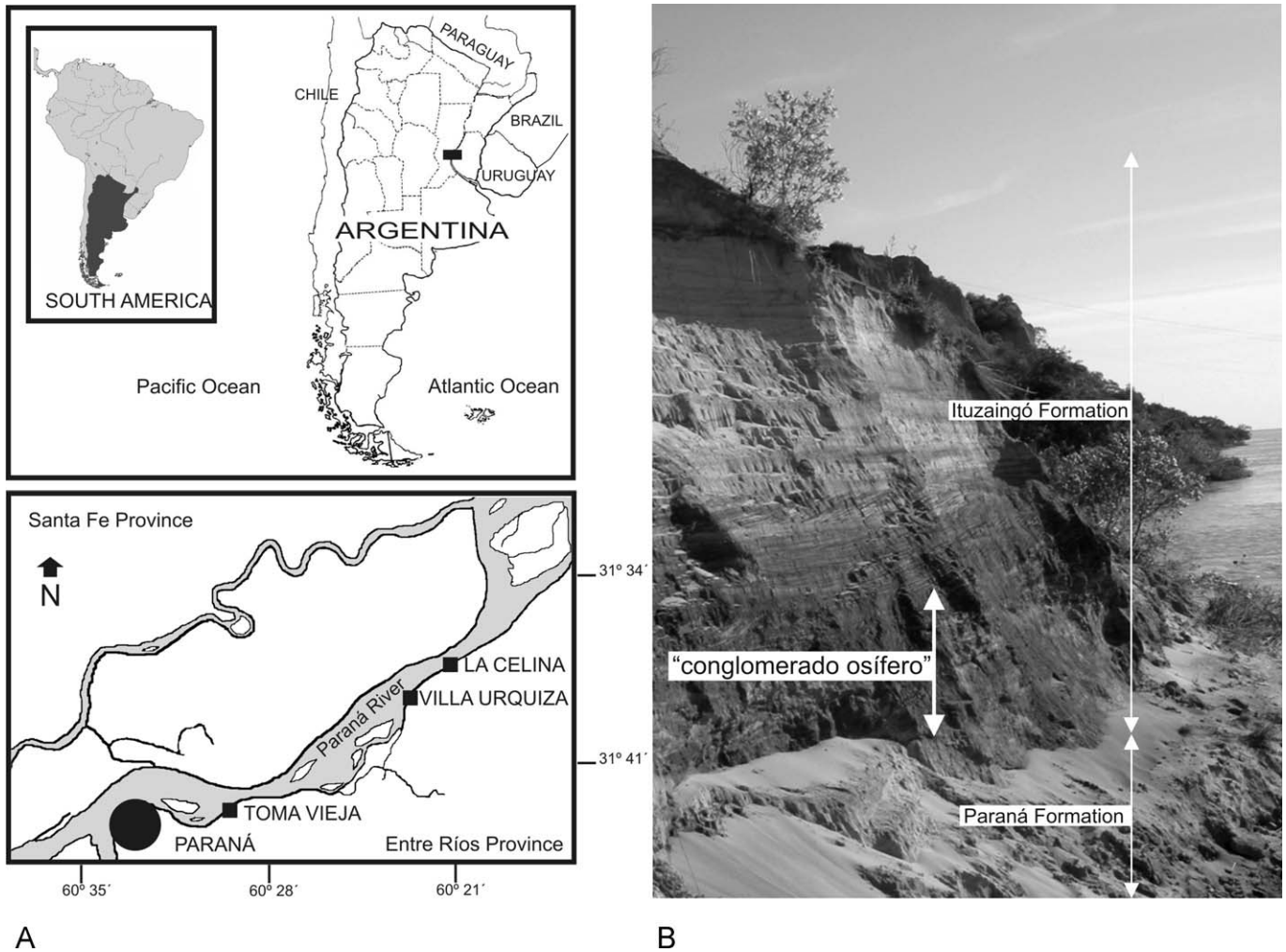


Fig. 1. A. Geographic location of the main exposures (black squares) of the “conglomerado osífero”, Entre Ríos Province, Argentina. B. Photograph of the Paraná River cliffs at the locality of Toma Vieja.

Huayquerian (late Miocene) of the Pampean region and northwestern of Argentina, correlating it with the Tortonian. On the other hand, a closer relationship between the “conglomerado osífero” and the Arroyo Chasicó Formation (early late Miocene of Buenos Aires Province, Argentina) faunal assemblages should not be discarded (Brandoni, 2009).

The aim of this contribution is: (i) to clarify the systematics of the Megalonychidae from the “conglomerado osífero” of Entre Ríos Province, Argentina, (ii) to amend the diagnoses of some genera and species, (iii) to illustrate the type specimen of each species (Table 1), and (iv) to discuss biochronological and, paleobiogeographical aspects of the Megalonychidae from the late Miocene of Argentina.

2. Systematic paleontology

Institutional abbreviations: FCP: Museo de Paleontología, Mineralogía y Arqueología, Firmat, Argentina; MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MAS: Museo de Ciencias Naturales y Antropológicas “Profesor Antonio Serrano”, Paraná, Argen-

tina; MLP: Museo de La Plata, Facultad de Ciencias Naturales y Museo, La Plata, Argentina; MNP: Museo de Nueva Palmira “Lucas Roselli”, Departamento Colonia, Uruguay.

XENARTHRA Cope, 1889

TARDIGRADA Latham and Davies in Forster, 1795

MEGALONYCHIDAE Gervais, 1855

Genus *Ortotherium* Ameghino, 1885

Type species: *Ortotherium laticurvatum* Ameghino, 1885.

Referred species: *O. robustum* Ameghino, 1891, *O. schlosseri* Ameghino, 1891, *O. seneum* Ameghino, 1891, *O. brevirostrum* Bordas, 1942, and *O. scrofum* Bordas, 1942.

Remarks: *Ortotherium* was the first named megalonychid genus from the “conglomerado osífero” (Ameghino, 1885). Kraglievich (1923a) considered *Menilaus affinis* Ameghino, 1891 congeneric with *Pliomorphus*, and that *O. seneum* should be included within *Amphiocnus*. Brandoni (2010) stated that *Menilaus* and *Amphiocnus* (in part) are congeneric with *Ortotherium* (see below). Ameghino (1885) described *O. laticurvatum* on an incomplete left dentary lacking teeth, and provided several measurements of the type material, but did

Table 1
Type specimens of the species mentioned in the text.

| Species | Type specimen |
|-------------------------------------|--------------------|
| <i>Ortotherium laticurvatum</i> | MLP M 62 (cast) |
| <i>O. schlosseri</i> | MACN Pv 13319 |
| <i>O. seneum</i> | MACN Pv 8886 |
| <i>O. scrofum</i> | MACN Pv 13657 |
| <i>O. brevirostrum</i> | MACN Pv 13656 |
| <i>O. robustum</i> | MACN A 5837 |
| <i>Menilaus affinis</i> | MACN Pv 13318 |
| <i>Pliomorphus mutilatus</i> | MLP M 55 (cast) |
| <i>Pl. ameghinoi</i> | MACN Pv 5000 |
| <i>Pl. ameghinoi gracilis</i> | MACN Pv 4999 |
| <i>Pl. gracilis</i> | MACN Pv 2954 |
| <i>Pl. robustus</i> | MACN A 4997 |
| <i>Amphiocnus paranense</i> | MLP 54-X-11-2 |
| <i>Torcetia paranense</i> | MLP 56-IV-26-1 |
| <i>Protomegalonyx doellojuradoi</i> | MACN Pv 4949 |
| <i>Pr. praecursor</i> | MACN Pv 4970 |
| <i>Megalonychops primigenius</i> | MACN Pv 10689 |
| <i>Paranabradys vucetichae</i> | MLP 41-XII-13-2003 |

not figure it. Ameghino (1889: pl. 71, figs. 12, 12a) figured a molariform assigned to *O. laticurvatum*, but later (Ameghino, 1891) referred it to *Promegatherium parvulum* Ameghino, 1891 (Megatheriidae, Megatheriinae). Ameghino (1891) described *O. robustum*, based on a small portion of a right mandible without molariforms (Ameghino, 1891: fig. 30), *O. schlosseri* on an incomplete left dentary with molariforms (Ameghino, 1891: fig. 31), and *O. seneum* on a right dentary that preserves the caniniform and two molariforms (Ameghino, 1891: fig. 32). In addition, Ameghino (1891) erected *Menilaus affinis*, based on a portion of a left dentary (Ameghino, 1891: fig. 34; see below). Brandoni (2010) performed a systematic review of the genus.

Ortotherium laticurvatum Ameghino, 1885

Fig. 2A–J

Holotype: Incomplete left dentary lacking teeth (Fig. 2A, B). The holotype has not been found in the collections of MACN, where it should have probably been housed originally. Nevertheless, a cast of the type (MLP M 62) is deposited in the Vertebrate Paleontology Division of MLP (Mones, 1986).

Referred material: MACN Pv 13319 (type of *O. schlosseri*), incomplete right dentary only preserving m1 and m3 (Fig. 2C, D); MACN Pv 8886 (type of *O. seneum* and *A. seneum* (Ameghino, 1891)), incomplete left dentary with fragmentary caniniform, m1 and m2 (Fig. 2E, F); MACN Pv 13657 (type of *O. scrofum*), mandibular symphysis with left caniniform and m1 (Brandoni, 2010, incorrectly indicated right caniniform and m1) (Fig. 2G, H); MACN Pv 13318 (type of *M. affinis*), incomplete left dentary (Fig. 2I, J).

Remarks: Brandoni (2010) considered that *O. laticurvatum* is the only valid species of the genus, with *O. schlosseri*, *O. seneum*, *O. scrofum*, *A. seneum*, and *M. affinis* being junior synonyms of *O. laticurvatum*. Further, “*Ortotherium*” *brevirostrum* (based on MACN-13656; Fig. 2K, L) is not congeneric with *O. laticurvatum*, and *O. robustum* (based on MACN A-5837; Fig. 2M, N) is a *nomen vanum* (Brandoni, 2010).

Genus *Pliomorphus* Ameghino, 1885

Type species: *Pliomorphus mutilatus* Ameghino, 1885.

Referred species: *Pl. robustus* Ameghino, 1885, *Pl. ameghinoi* Kraglievich 1923b, *Pl. ameghinoi gracilis* Kraglievich, 1923b, and *Pl. brevis* Kraglievich, 1923b.

Remarks: Ameghino (1885) described *Pl. mutilatus* on a maxillar fragment that preserves the caniniform and the first molariform (Ameghino, 1889: pl. 70, figs. 1, 1a); he also described *Pl. robustus* on an isolated caniniform. Kraglievich (1923a) considered *Menilaus affinis* congeneric with *Pliomorphus* (but see Brandoni, 2010). Kraglievich (1923b) described *Pl. ameghinoi* and *Pl. ameghinoi gracilis* on nearly complete skulls without teeth (Kraglievich, 1923b: figs. 1–3, 4.1 and fig. 5, respectively), and *Pl. brevis* on a posterior portion of a skull. Besides the Argentinean record, *Pliomorphus* was reported from Camacho Formation in Uruguay (Perea, 1998) and from the Solimões Formation in the Acre Region, Brazil (Cozzuol, 2006: appendix A; Latrubesse et al., 2010: table 2), both late Miocene in age. Given that *Pl. mutilatus* is herein considered as the only valid species for the genus (see below), an amended diagnosis is presented.

Diagnosis: as for the type and only species by monotypy.

Pliomorphus mutilatus Ameghino, 1885

Fig. 3A–H

1923. *Pliomorphus ameghinoi* Kraglievich, figs. 1–3, 4.1.

1923. *Pliomorphus ameghinoi gracilis* Kraglievich, fig. 5.

1923. *Pliomorphus brevis* Kraglievich.

Holotype: A right maxillar fragment with caniniform and first molariform (Fig. 3A, B). The holotype is missing. MLP M 55 is a cast of the original remains (Mones, 1986).

Referred material: MACN Pv 5000 (type of *Pl. ameghinoi*), a skull lacking teeth (Fig. 3C, D); MACN Pv 4999 (type of *Pl. ameghinoi gracilis*), a near complete skull without teeth (Fig. 3E, F); MACN Pv 2954 (type of *Pl. brevis*), a posterior portion of skull (Fig. 3G, H). Other cranial remains (e.g., MACN Pv 4996, MACN Pv 4997, FCP-V-M-050) that were referred to different species of *Pliomorphus* (see Kraglievich, 1923b; Brandoni, 2008) are similar to those of *Pl. mutilatus*.

Diagnosis: Larger than *Eucholaeops* spp. and smaller than *Megalonyx jeffersonii* (Desmarest, 1822), *Ahytherium aureum*, and *Megalocnus rodens* Leidy, 1868. As in *Eucholaeops* sp. skull low and elongated (lower than *Megalocnus rodens*, *A. aureum*, and *Megalonyx jeffersonii*). Rostrum slender and elongated (shorter, wider, and higher in *A. aureum*). As in *Eucholaeops* sp., anterior part of the palate nearly flat (concave in *Megalocnus rodens* and *A. aureum*). Ascending ramus of the jugal well developed slender in *Megalocnus rodens* and *Eucholaeops*; more robust in *A. aureum*.

Remarks: Kraglievich (1923b) provided a complete description of the type specimens of *Pl. ameghinoi*, *Pl. ameghinoi gracilis*, and *Pl. brevis*. In addition, the author referred to *Pl. mutilatus* a complete femur recorded in the “conglomerado ósifero” (see below). The species of *Pliomorphus* were based on cranial remains that allowed some comparisons among them. As was mentioned by Kraglievich

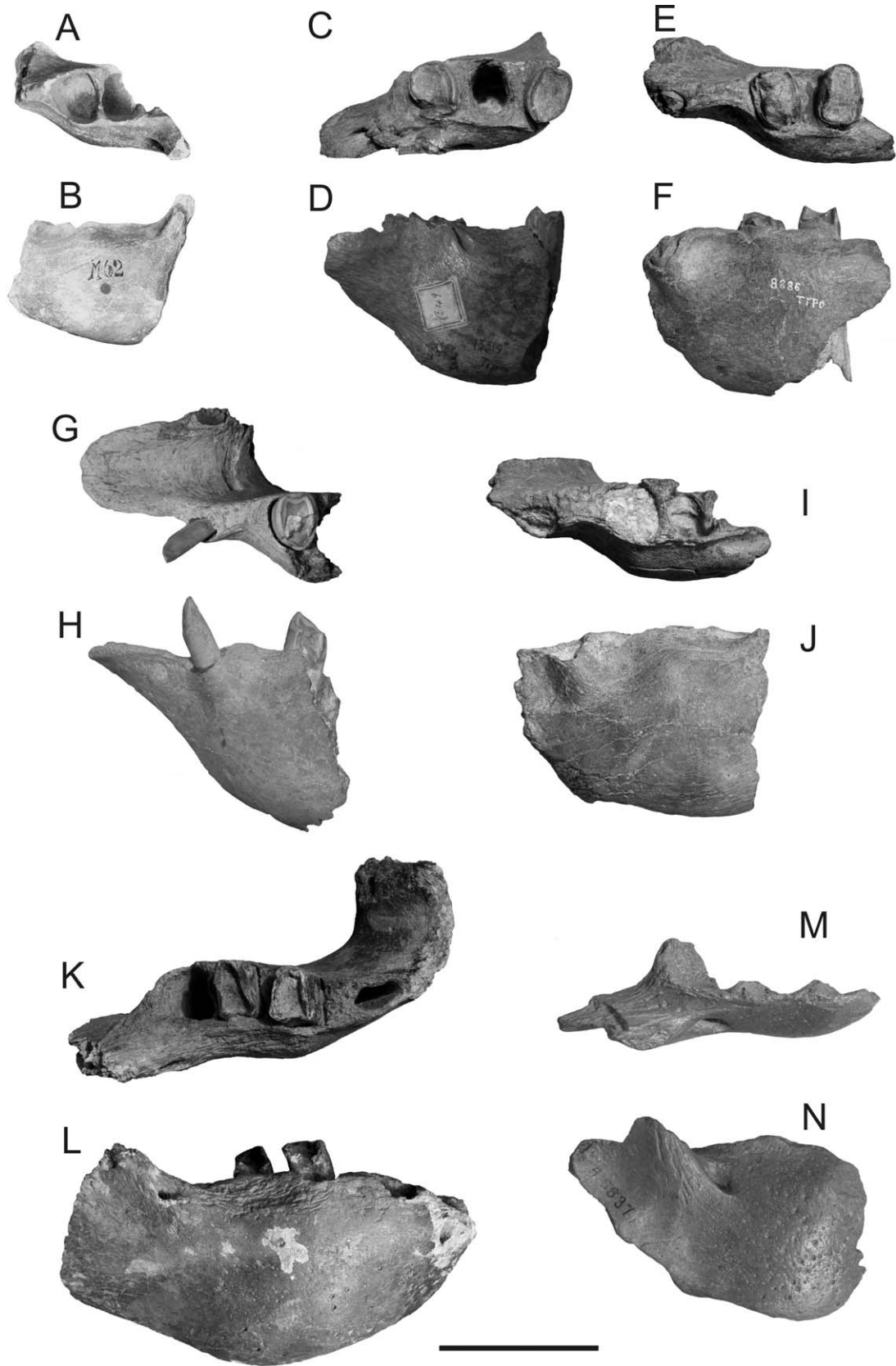


Fig. 2. A–J. *Ortotherium laticurvatum*. A, B, MLP M 62 (cast of the type of *O. laticurvatum*), partial left dentary; C, D, MACN Pv 13319 (type of *O. schlosseri*), partial right dentary; E, F, MACN Pv 8886 (type of *O. seneum* and *A. seneum*), partial left dentary; G, H, MACN Pv 13657 (type of *O. scrofum*) mandibular symphysis with left caniniform and m1; I, J, MACN Pv 13318 (type of *Menilaus affinis*), partial left dentary. K, L. MACN-13656 (type of “*Ortotherium*” *brevirostrum*), partial right dentary. M, N. MACN A-5837 (type of *O. robustum*), partial right dentary. A, C, E, G, I, K, M, occlusal view; B, D, F, H, J, L, N, lateral view. Scale bar: 50 mm.

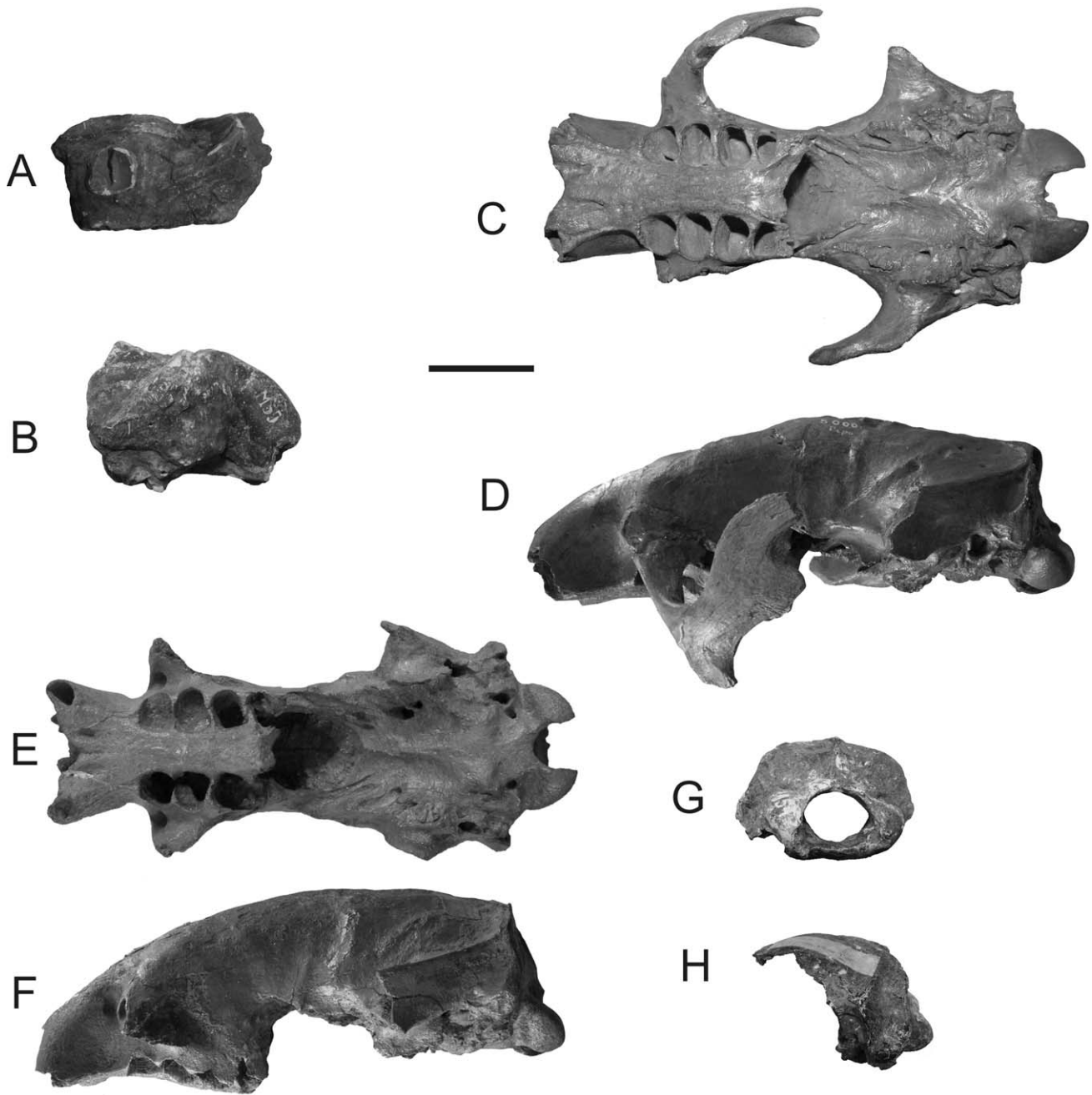


Fig. 3. *Pliomorphus mutilatus*. A, B: MLP M 55 (cast of the type of *Pl. mutilatus*), right maxillar fragment; C, D: MACN Pv 5000 (type of *Pl. ameghinoi*), nearly complete skull; E, F: MACN Pv 4999 (type of *Pl. ameghinoi gracilis*), nearly complete skull; G, H: MACN Pv 2954 (type of *Pl. brevis*), occipital fragment. A, C, E, palatal view; G, posterior view; B, D, F, lateral view. Scale bar: 50 mm.

(1923b), *Pl. ameghinoi* and *Pl. ameghinoi gracilis* are very similar and only differ in the slightly smaller size of *Pl. ameghinoi gracilis* (Kraglievich, 1923b: p. 50; Table 2). The few differences mentioned by Kraglievich (1923b) (e.g., size, shape of the parietal and occipital regions) are within the range of individual variability considered for other Megalonychidae. Furthermore, the type specimens of these species (MACN Pv 4999 and MACN Pv 5000) allow comparisons with the type specimens of *Pl. mutilatus* and *Pl. brevis*. As was mentioned, Kraglievich (1923b) determined *Pl. brevis* on the basis of the posterior part of a skull that mainly differs from

Pl. ameghinoi and *Pl. ameghinoi gracilis* on its smaller size (Table 2). As in the case for *Pl. ameghinoi* and *Pl. ameghinoi gracilis*, the differences between the skulls and the occipital area of *Pl. brevis* are among the mentioned range of variability, so there is no feature that permits a specific separation among the species of *Pliomorphus* determined by Kraglievich (1923b) i.e., *Pl. ameghinoi*, *Pl. ameghinoi gracilis*, and *Pl. brevis*. The comparison between the mentioned skulls and the type specimen of *Pl. mutilatus* indicates that these remains are very similar in size (Table 2) and shape (Fig. 3A–H), and a specific distinction would not be justified.

Table 2

Measurements (in mm) of the specimens referred to *Pliomorphus mutilatus*.

| Specimen | Diastema length | Anterior palatal width | Palatal width at M1 level | M1 length | Molariform tooth row length | Internal condyles width | External condyles width | Height at the occipital plane |
|---|-----------------|------------------------|---------------------------|-----------|-----------------------------|-------------------------|-------------------------|-------------------------------|
| MLP M 55 (cast type of <i>Pl. mutilatus</i>) | 43 | – | – | 12 | – | – | – | – |
| MACN Pv 5000 (type of <i>Pl. ameghinoi</i>) | 37 | 43 | 22 | 14 | 65 | 21 | 69 | 71 |
| MACN Pv 4999 (type of <i>Pl. ameghinoi gracilis</i>) | 33 | 42 | 20 | 13 | 62 | 25 | 68 | 75 |
| MACN Pv 2954 (type of <i>Pl. brevis</i>) | – | – | – | – | – | 25 | 65 | 65 |

Genus *Amphiocnus* Kraglievich, 1922**Type species:** *Amphiocnus paranense* Kraglievich, 1922.**Referred species:** *A. seneum* (Ameghino, 1891).

Remarks: *A. paranense* was determined on a distal portion of a left femur (Kraglievich, 1922: figs. 1, 2). Kraglievich considered that *Ortotherium seneum* must be attributed to *Amphiocnus* and determined *A. seneum*. Brandoni (2010) considered that *A. seneum* is not valid and must be considered (as *O. seneum*) as a junior synonym of *O. laicurvatum*.

Amphiocnus paranense Kraglievich, 1922

Fig. 4A, B

Holotype: MLP 54-X-11-2, distal portion of a left femur (Fig. 4A, B).

Remarks: Given that *A. seneum* is considered as not valid (Brandoni, 2010), *A. paranense* is the only valid species of the genus. *Amphiocnus paranense* has as main characters the connection among the distal facets of the femur forming a continuous articular area, and the projection of the epicondyles, specially the lateral epicondyle (Kraglievich, 1922: fig. 2; Brandoni, 2009: fig. 4.6). The connection among the distal facets is also present in most Santacrucian sloths (e.g., *Hapalops* Ameghino, 1887, *Planops* Ameghino, 1887), Quaternary Mylodontidae (e.g., *Scelidotherium* Owen, 1839, *Glossotherium* Owen, 1839), and some Megatheriinae (e.g., *Megathericulus patagonicus* Ameghino, 1904).

Genus *Torcellia* Kraglievich, 1923**Type species:** *Torcellia paranense* Kraglievich, 1923c.

Remarks: *T. paranense* is the only known species for the genus and was based on a complete right femur (Kraglievich, 1923c: figs. 1, 2).

Torcellia paranense Kraglievich, 1923

Fig. 4C, D

Holotype: MLP 56-IV-26-1, complete right femur (Fig. 4C, D).**Referred material:** MAS 1372, complete left femur (Brandoni, 2008: figs. 3.F, G).

Remarks: Brandoni (2008) considered that this species has diagnostic characters on its femur; however, due to the taphonomical characteristics of the unit, it is nearly impossible to refer femoral remains to other genera or species based on cranial and mandibular remains (e.g., *Ortotherium*, *Pliomorphus*). *Torcellia paranense* is characterized by a marked neck connecting the humeral head and the diaphysis, fovea capitis included within the humeral head, great trochanter distal to

proximal plane of the humeral head, and distal articular facets (condyloid facets and patellar facet) separated.

Genus *Protomegalonyx* Kraglievich, 1925**Type species:** *Protomegalonyx doellojuradoi* Kraglievich, 1925.**Referred species:** *Pr. praecursor* Kraglievich, 1925 and *Pr. chasicoensis* Scillato-Yané, 1977.

Remarks: Kraglievich (1925) determined *Pr. doellojuradoi* on a left femur (Kraglievich, 1926b: figs. 5, 6) and *Pr. praecursor* Kraglievich also on a left femur (Kraglievich, 1926b: figs. 7, 8). Scillato-Yané (1977) named *Pr. chasicoensis* from the Arroyo Chasicó Formation (early late Miocene), Buenos Aires Province, Argentina, and added important information on the nomenclature for the species of this genus. Brandoni (2009) gave the anatomic differences among the species of *Protomegalonyx*. Cozzuol (2006: appendix A) reported the presence of cf. *Protomegalonyx* from the late Miocene of Acre Region, Brazil.

Protomegalonyx doellojuradoi Kraglievich, 1925

Fig. 4E, F

Holotype: MACN Pv 4949, left femur (Fig. 4E, F).

Remarks: Kraglievich (1926b) described the femur of *Pr. doellojuradoi* and considered a closer relationship between *Pr. doellojuradoi* and *Megalonyx jeffersoni*. The femur of *Pr. doellojuradoi* presents a well developed greater trochanter and a conical and relatively reduced lesser trochanter.

Protomegalonyx praecursor Kraglievich, 1925

Fig. 4G, H

Holotype: MACN Pv 4970, left femur (Fig. 4G, H).

Remarks: Kraglievich (1926b) described the femur of *Pr. praecursor* indicating the differences between this species and *Pr. doellojuradoi*. *Protomegalonyx praecursor* differs from *Pr. doellojuradoi* by its smaller size, the size of the trochanteric fossa, and the more proximal position of the proximal margin of the greater trochanter.

Genus *Megalonychops* Kraglievich, 1926**Type species:** *Megalonychops primigenius* Kraglievich, 1926a.**Referred species:** *M. fontanai* Kraglievich, 1926a and *M. carlesi* Kraglievich, 1930a.

Remarks: Kraglievich (1926a) described *M. primigenius* on a proximal portion of a left humerus (Kraglievich, 1926a: figs. 5–7). Other species that were described are *M. fontanai* from the Camacho Formation (late Miocene) of Uruguay and *M. carlesi* from the Pleistocene of Buenos Aires Province,

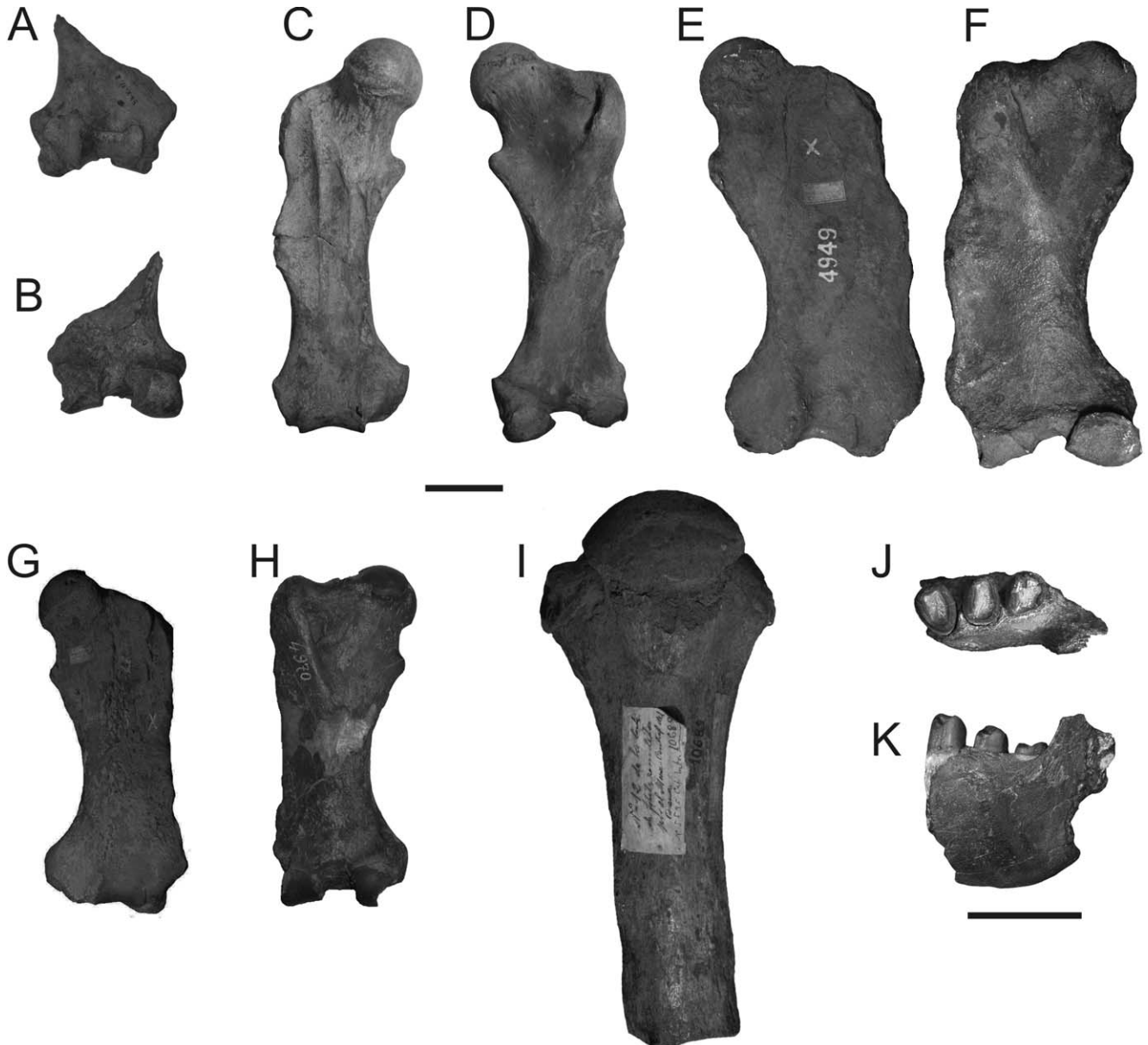


Fig. 4. A, B. *Amphiocnus paranense* (MLP 54-X-1-12), distal end of a left femur. C, D. *Torcellia paranense* (MLP 56-IV-26-1), right femur. E, F. *Protomegalonyx doellojuradoi* (MACN Pv 4949), left femur. G, H. *Pr. praecursor* (MACN Pv 4970), left femur. I. *Megalonychops primigenius* (MACN Pv 10689), proximal half of a left humerus. J, K. *Paranabradys vucetichae* (MLP 41-XII-13-2003), partial left dentary. A, C, E, G, I, anterior view; B, D, F, H, I, posterior view; J, occlusal view; K, lateral view. Scale bar: 50 mm.

Argentina (Kraglievich, 1930a). *Gilsoralesia* Roselli, 1976, also from the Camacho Formation, was determined on the basis of postcranial remains (Roselli, 1976), but Perea (1998) considered that *Gilsoralesia* is a junior synonym of *Megalonychops*.

Megalonychops primigenius Kraglievich, 1926

Fig. 4I

Holotype: MACN Pv 10689, proximal half of a left humerus (Fig. 4I).

Referred material: MNP-322 (type of *Gilsoralesia bayoi* Roselli, 1976), right tibia and a portion of fibula (Perea, 1998).

Remarks: *Gilsoralesia bayoi* was determined on the basis of a right tibia and a portion of fibula recovered from Camacho

Formation (Roselli, 1976). Perea (1998) considered that the type of *G. bayoi* could be referred to *M. primigenius*, being *G. bayoi* a junior synonym of *M. primigenius*. The only remarkable feature of the humerus of *M. primigenius* is its great size, being similar to some specimens of *Megatherium americanum* Cuvier, 1796 (Megatheriidae, Megatheriinae) (Cione et al., 2000).

Genus *Paranabradys* Scillato-Yané, 1980

Type species: *Paranabradys vucetichae* Scillato-Yané, 1980.

Remarks: *Paranabradys vucetichae* is the only known species for the genus and was based on a left dentary (Scillato-Yané, 1980: pl. 1).

Paranabradys vucetichae Scillato-Yané, 1980

Fig. 4J, K

Holotype: MLP 41-XII-13-2003, left dentary that preserves the molariforms (Fig. 4J, K).

Remarks: Although *O. laticurvatum* and *Pa. vucetichae* are nearly similar in size, *Pa. vucetichae* differs from *O. laticurvatum* in the posterior position of the anterior margin of the coronoid process with respect to the posterior edge of m3 (Brandoni, 2010).

3. Discussion

Traditionally, Megalonychidae was subdivided in several subfamilies (e.g., Ortotheriinae, Megalocninae, Megalonychinae, Choloepodinae, Ocnopodinae; see Kraglievich 1923b; Hoffstetter, 1954; Mones, 1986; McKenna and Bell, 1997; White and MacPhee, 2001; Cartelle et al., 2008). Nevertheless, not all of these groups are accepted because they are not defined on the basis of synapomorphies or, at least, would not have diagnostic characters (Carlini and Scillato-Yané, 2004, for Ortotheriinae). Megalonychidae from the “conglomerado osífero” have been mainly excluded from recent cladistic analyses (see Carlini and Scillato-Yané, 2004; Gaudin, 2004; Pujos et al., 2007; White and MacPhee, 2001) because most the species were defined on the basis of fragmentary remains (White and MacPhee, 2001; Gaudin, 2004; Carlini and Scillato-Yané, 2004; Pujos et al., 2007). Given this situation, it is preferable to maintain the “conglomerado osífero” megalonychids as Megalonychidae without assigning them to particular clades (i.e., Ortotheriinae, Megalocninae or Megalonychinae).

A broad range of individual variation has been observed in Megalonychidae from the Pleistocene of Central America and the West Indies (MacPhee et al., 2000; White and MacPhee, 2001). The probably similar range of variability in the megalonychids from the “conglomerado osífero” suggests that many previously named species are invalid, although the establishment of synonymies, as well as the generic and specific assignation of the specimens is not an easy task, due to the peculiar taphonomical context of this unit (i.e., unassociated remains). In this sense, taking into account the present state of knowledge, it is not possible to elucidate synonymies of taxa based on postcranial remains (*A. paranense*, *T. paranense*, *Pr. doellojuradoi*, *Pr. praecursor*, *M. primigenius*) with those determined on cranial ones (*O. laticurvatum*, *Pl. mutilatus*, *Pa. vucetichae*).

In the case of *Ortotherium*, the morphological differences observed in the type specimens of *O. 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 specimens, making *O. schlosseri*, *O. seneum*, *O. scrofum*, and *Menilaus affinis* synonyms of *O. laticurvatum* (see Brandoni, 2010). Also, *O. laticurvatum* and “*Ortotherium*” *brevirostrum* are not sister species and should not be placed in the same genus, and *O. robustum* is considered a *nomen vanum* (Brandoni, 2010). MACN Pv 8916, a dentary referred to *Ortotherium* sp. (Brandoni, 2010: fig. 3A–C), has only a single particular feature: the posterolateral

opening of the mandibular canal on the lateral side of the horizontal ramus. Although this character is not common among Megalonychidae, the presence of this character does not seem sufficient to justify a specific distinction. Instead, it is more appropriately interpreted, given the otherwise strong similarity of this specimen to other *Ortotherium* remains, as reflecting a wide degree of variation in this genus.

Ameghino (1885) described two species of *Pliomorphus*: *Pl. mutilatus* and *Pl. robustus*. *Pl. mutilatus* was based on a maxillar fragment that preserves the caniniform and the first molariform and *Pl. robustus* was based on an isolated caniniform. Neither of the type material of these species was found in the revised vertebrate paleontology collections; nevertheless, a cast of the type material of *Pl. mutilatus* (MLP M 55) is housed at Museo de La Plata. Kraglievich (1923b) described *Pl. ameghinoi*, *Pl. ameghinoi gracilis*, and *Pl. brevis*, and referred a complete femur to *Pl. mutilatus*. Kraglievich (1923b) mentioned some anatomic differences among *Pl. mutilatus*, *Pl. ameghinoi*, *Pl. ameghinoi gracilis*, and *Pl. brevis*. However, most, if not all, of the differences are related to the body size of the specimens. Given that the differences noted by Kraglievich (1923b) are in the range of individual variability considered for other Megalonychidae (e.g., *Ortotherium*, *Acratocnus*), the specific distinction among the mentioned species would not be justified, with *Pl. ameghinoi*, *Pl. ameghinoi gracilis*, and *Pl. brevis* being junior synonyms of *Pl. mutilatus*. Also, *Pl. robustus* must be considered a *nomen dubium* because its holotype (MACN A 4997, an isolated caniniform) probably does not have diagnostic characters. Finally, the assignation of an isolated femur (MACN Pv 4977) to *Pl. mutilatus* (see Kraglievich, 1923b) is not justified because the element was not associated with any of the mentioned cranial remains.

Amphiocnus paranense is an endemic species from the “conglomerado osífero” and is only known for distal femora remains. Taking into account the morphology of the femur of *A. paranense*, Kraglievich (1922) considered *Amphiocnus* as a precursor of, or closer to, *Megalocnus* from Central America. However, there is not sufficient available information to confirm the idea proposed by Kraglievich. On the other hand, as for other postcranial remains, the assignment of MLP 54-X-11-2 (type of *A. paranense*) to some of the species described on cranial remains is almost impossible.

Torcellia paranense is also endemic from the “conglomerado osífero” and was described on postcranial remains. At least two complete femora have been referred to *Torcellia paranense* (see Brandoni, 2008). The features present on those remains are clearly different from those observed in femora referred to other species of Megalonychidae (*Pr. doellojuradoi*, *Pr. praecursor*, *T. paranense*, and *A. paranense*; Brandoni, 2009). Then, the validity of *T. paranense* seems to be unquestionable.

The recognition of two species of *Protomegalonyx* from the “conglomerado osífero” seems to be appropriate because they differ significantly in body size and in other features (Brandoni, 2009). As mentioned, a third species, *Pr. chasicóensis*, was described from the Arroyo Chasicó Formation (Scillato-Yané,

1977; Brandoni, 2009). *Protomegalonyx chasicoensis* is smaller than the species from the “conglomerado osífero” and has other features that distinguish it from *Pr. doellojuradoi* and *Pr. praecursor* (see Scillato-Yané, 1977; Brandoni, 2009). Kraglievich (1926b) considered that *Protomegalonyx* may be the antecessor of *Megalonyx* from North America; although this hypothesis could be correct, the available information on *Protomegalonyx* is insufficient to test this hypothesis.

Megalonychops primigenius was based on a proximal fragment of humerus. Roselli (1976) determined *G. bayoi* on the basis of a right tibia and a portion of fibula from the late Miocene of Uruguay. Although there are no homologous remains to compare *M. primigenius* with *G. bayoi*, Perea (1998) considered *G. bayoi* as a junior synonym of *M. primigenius*. Perea (1998) justified his opinion on the basis of size proportions between humeral and tibial lengths observed in *Megalonychops* and other Megalonychidae. Although Perea's (1998) hypothesis may be correct, the lack of homologous remains renders this opinion tentative. Cione et al. (2000) indicated that *M. primigenius* is similar in size to *Megatherium americanum* (Megatheriidae, Megatheriinae). *Megatherium americanum* is not present at the “conglomerado osífero” (Brandoni and Scillato-Yané, 2007) but *Pyramiodontherium*, another genus of large sized Megatheriinae, is present (Brandoni and Carlini, 2009). For the “conglomerado osífero”, *Pyramiodontherium* sp. is represented by a nearly complete humerus lacking its proximal portion. The diaphysis of the humerus of *Megalonychops primigenius* and *Pyramiodontherium* sp. are similar, but a thorough comparison is not possible to perform because the remains are incomplete and do not preserve homologous portions. From the late Miocene of Uruguay, Kraglievich (1930a) described *Megalonychops fontanai* based on a distal humerus, which is similar in shape to that of *M. primigenius*. Taking into account the available information, the systematics of *Megalonychops* is not clear; however, at least for the moment is not possible to consider *M. primigenius* as not valid.

Paranabradys vucetichae is an endemic species from the “conglomerado osífero” and is distinct from other species based on mandibular remains (i.e., *O. laticurvatum*; Scillato-Yané, 1980; Brandoni, 2010).

Finally, *Diodomus copei* Ameghino, 1885 (based on MLP M 60, a fragment of mandibular symphysis) was considered as a probable Megalonychidae (Cione et al., 2000), but judging by the shape of the anterior wall of the alveolus of the first teeth, it is probable that the specimen corresponds to an undetermined Megatheriinae rather than a Megalonychidae.

As noted above, most, if not all of the discussed species are endemic to the “conglomerado osífero” and the late Miocene of Uruguay, and are based on fragmentary and dissociated remains. As the species were determined on nonhomologous remains (e.g., skulls, dentaries, femora), the assignment of new materials to each species is difficult to justify. In addition, the absence of Megalonychidae in many late Miocene units (e.g., Andalhuala Formation, Argentina, which yields complete and associated remains of other ground sloths, such as Megatheriinae) precludes comparisons with more complete specimens.

In the case of Megatheriinae from the “conglomerado osífero”, comparison and assignment of some remains were possible (Brandoni, 2006; Brandoni and Scillato-Yané, 2007; Brandoni and Carlini, 2009) given that the Tertiary record of this clade is abundant and comprises nearly complete specimens (Carlini et al., 2002; De Iuliis et al., 2004, 2008; Brandoni and De Iuliis, 2007).

Thus, taking into account that most of the species of Megalonychidae are endemic from the “conglomerado osífero”, 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. Nevertheless, the determination of the valid genera and species seems to be useful for inferring some chronological and biogeographical relations for the late Miocene of Argentina.

Besides the record from the “conglomerado osífero”, late Miocene-Pliocene Megalonychidae were recovered from the Arroyo Chasicó Formation (early late Miocene), Buenos Aires Province, and the Río Negro Formation (Scillato-Yané et al., 1976). Based on the presence of *Protomegalonyx*, among other tardigrades, in the “conglomerado osífero” and the Arroyo Chasicó Formation, Brandoni (2009) considered that the relationship between these units was closer than that considered in previous contributions, in which the “conglomerado osífero” was mainly related to the Huayquerian (late Miocene) of the Pampean Region and northwestern of Argentina (Cione et al., 2000). Nevertheless, the presence of similar ground sloth taxa, as well as other fossil mammals (e.g., *Cardiatherium Ameghino*, 1883 [Rodentia, Hydrochoeridae]; Deschamps et al., 2007) in the “conglomerado osífero” and the Arroyo Chasicó Formation suggests a similar age for deposition of the mentioned units (Brandoni, 2009), as well as similar paleoenvironmental conditions (fluvial environments with closed forest and some opened areas; Carlini et al., 2000; Cione et al., 2000; Deschamps et al., 2007; Zárate et al., 2007). This similarity may reflect a paleogeographic connection between both areas after the development of the Paranean Sea, during the late Miocene.

In summary, the genera of Megalonychidae recovered from the “conglomerado osífero” are *Ortotherium*, *Pliomorphus*, *Amphiocnus*, *Protomegalonyx*, *Megalonychops*, and *Paranabradys*. In addition, the Megatheriidae Megatheriinae from this unit are currently represented by four monospecific genera: *Promegatherium* Ameghino, 1883, *Eomegatherium* (Kraglievich, 1926a), *Pliomegatherium* Kraglievich, 1930b, and *Pyramiodontherium* (Rovereto, 1914) (Brandoni, 2006; Brandoni and Scillato-Yané, 2007; Brandoni and Carlini, 2009). Nothrotheriidae are represented by *Pronothrotherium* Ameghino, 1907 and *Neohapalops* Kraglievich, 1923a (Cione et al., 2000). Finally, Mylodontidae from the “conglomerado osífero” (*Ranculus* Ameghino, 1891, *Strabossodon* Ameghino, 1891, *Octomyodon*, Ameghino, 1904, *Promylodon* Ameghino, 1904, *Prolestodon* Kraglievich, 1932 and *Megabradys* Scillato-Yané, 1981) have not been studied since their original determination, but judging from the individual

variation present in other ground sloths (e.g., *Megalonychidae*, *Megatheriinae*) it is probably that this clade includes fewer species than considered in previous contributions.

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