A review of Pliomegatherium Kraglievich, 1930 (Xenarthra: Phyllophaga: Megatheriidae)

2006 (4)

Diego Brandoni, Diamante

With 3 figures

Brandoni, D. (2006): A review of Pliomegatherium Kraglievich, 1930 (Xenarthra: Phyllophaga: Megatheriidae). - N. Jb. Geol. Paläont. Mh., 2006: 212-224; Stuttgart.

Abstract: Eight species of Megatheriinae have been recognized from the "Conglomerado osifero" of the Ituzaingó Formation (late Miocene - Pliocene) of Argentina, but the validity of some of these taxa is doubtful. The taxonomic status of one of them, Pliomegatherium, is assessed based on restudy of the material on which the species were originally based. The morphological differences observed in the type specimens of Pliomegatherium lelongi and Pl. paranensis do not justify their specific separation. Thus Pl. paranensis is considered as a synonym of Pl. lelongi.

Key words: Pliomegatherium, Megatheriinae, systematics, upper Miocene, Pliocene, Argentina.

Zusammenfassung: Acht Arten von Megatheriinae wurden bisher aus dem "Conglomerado osífero" der Ituzaingó-Formation (Ober-Miozän – Pliozän) Argentiniens beschrieben, doch erscheint die Gültigkeit einiger dieser Taxa fragwürdig. Der taxonomische Status der Gattung Pliomegatherium wurde anhand des Typusmaterials der Arten nachuntersucht. Die morphologischen Unterschiede zwischen den Typusexemplaren von Pliomegatherium lelongi und Pl. paranensis lassen keine Trennung dieser Arten zu. Pl. paranensis stellt demnach ein Synonym von Pl. lelongi dar.

Schlüsselwörter: Pliomegatherium, Megatheriinae, Systematik, Ober-Miozän, Pliozän, Argentinien.

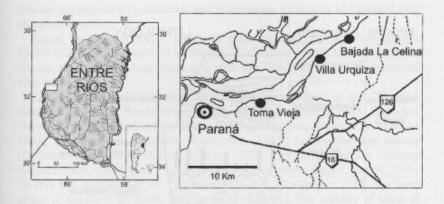


Fig. 1. Geographic location of the main exposures of the "Conglomerado osífero" of the Ituzaingó Formation.

1. Introduction

The subfamily Megatheriinae, typified by Megatherium Cuvier, 1796, has in the Argentine Republic a Friasian (middle Miocene) to Lujanian (late Pleistocene – early Holocene) biochron. Its highest diversity is recorded in the "Conglomerado osífero", the bone-rich conglomerate of the Ituzaingó Formation (upper Miocene – Pliocene) of Entre Ríos Province. Compared with the better known Quaternary Megatheriinae (Cartelle 1992; De Iuliis 1996; Saint-André & De Iuliis 2001; Pujos & Salas 2004), the relatively few megatheriine remains from the Tertiary of Argentina have not been adequately described. Recent work has advanced our understanding of several of these Tertiary megatheriines (Carlini et al. 2002; De Iuliis et al. 2004). Despite these efforts, the taxonomic status and phylogenetic relationships among several small and medium-sized species from the Tertiary of Argentina, first described and named around the turn of the last century, have been largely neglected.

The "Conglomerado osífero", formerly known as "Mesopotamiense", outcrops along the banks of the Paraná river, between Paraná City upstream as far north as Hernandarias town. Among the most prospected localities are La Celina (S 31° 38' 37", W 60° 23' 04"), Toma Vieja (S 31° 42' 11", W 60°

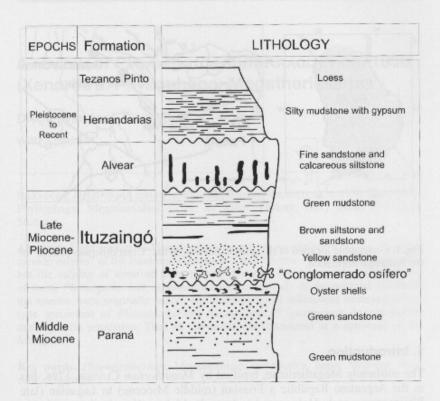


Fig. 2. Stratigraphic profile of the area of Paraná, Entre Ríos Province.

28' 06") and Villa Urquiza (S 31° 38' 42.5", W 60° 22' 50.5"), all in Entre Ríos Province (Fig. 1). The unconformity between the underlying marine Paraná Formation (Bravard 1858) and the sandy-clay and gravel levels of the Ituzaingó Formation (DE ALBA 1953) is clearly distinguishable at all three localities (Fig. 2). The "Conglomerado osífero" is variable in thickness and is characterized by levels of quartz gravels and clay clasts with numerous isolated fragments of bones and teeth of both continental and marine vertebrates. The vertebrate remains have characteristic fossilization and are

heavily impregnated by siliceous and ferruginous infiltrates and stained with manganese oxide.

Based on the vertebrate taxa and their biostratigraphic relationships, CIONE et al. (2000) proposed a correlation of this unit with the Huayquerian SALMA elsewhere in Argentina, and with the Tortonian of the international time scale.

The seven described species of megatheriines found in the "Conglomerado osífero" are *Promegatherium smaltatum* Ameghino, 1883; *Promegatherium remulsum* Ameghino, 1886; *Promegatherium parvulum* Ameghino, 1891; *Megatherium antiquum* Ameghino, 1885; *Eomegatherium nanum* (Burmeister, 1891) Kraglievich, 1926; *Pliomegatherium lelongi* Kraglievich, 1930, and *Pliomegatherium paranensis* Kraglievich, 1930. To this list, one species of *Pyramiodontherium* Rovereto, 1914, has been added (Carlini et al. 2000; Brandoni et al. 2001). The validity of some of these taxa (e.g., *Pr. remulsum, Pr. parvulum*, and *M. antiquum*) is doubtful, as they are generally based on very fragmentary material, which prevents the identification of morphological characters that might be used to establish their specific validity. On the other hand, the degree of individual variation attributed to this group (De Iuliis 1996; Cartelle & De Iuliis 1999; Pujos & Salas 2004) has not been considered in previous work on some of the aforementioned species.

In this paper, the taxonomic status of species of *Pliomegatherium* is assessed based on restudy and redescription of the original material on which the species were originally based. Finally, the possible phylogenetic relationships of this genus to other genera of Megatheriinae are discussed.

Institutional abbreviations: MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. MLP: Museo de La Plata, La Plata, Argentina.

2. Taxonomic history

Kraglevich (1930: 153, figs. 5.b, 6.b) created the genus and species *Pliomegatherium lelongi* on the basis of a right mandibular ramus (MACN Pv-13213) without molariform teeth. In the same paper he erected *Pliomegatherium paranensis* based on a fragmentary right mandibular ramus (MACN Pv-5269) with ml and m2. Mones (1986) cited this species as *Pliomegatherium paranense*. The specimen label for MACN Pv-5269 reads "*Pliomegatherium caissoi*", and written on the bone surface appears the binomen "*Pliomegatherium caixoi*". This last binomen "in Schedule" has never been formally used. Hoffstetter (1958), without further explanation, considered *Pliomegatherium* a synonym of *Promegatherium*. Kraglevich

(1930) gave no diagnosis for his new genus *Pliomegatherium*, and only *Pliomegatherium lelongi* was illustrated.

3. Systematic paleontology

Order Xenarthra Cope, 1889
Suborder Phyllophaga Owen, 1842
Superfamily Megatherioidea Gray, 1821
Family Megatheriidae Gray, 1821
Subfamily Megatheriinae Gray, 1821

Genus Pliomegatherium Kraglievich, 1930

Type species: Pliomegatherium lelongi Kraglievich, 1930.

Diagnosis and comparisons: Small to medium sized Megatheriinae. Similar in linear dimensions to Plesiomegatherium hansmeyeri ROTH, 1911, "Plesiomegatherium" halmyronomum Cabrera, 1928, and Eomegatherium nanum (Burmeister, 1891) Kraglievich, 1926, but larger than Megathericulus patagonicus Ameghino, 1904 and Eomegatherium andinum Kraglievich, 1930; smaller than Megatheriops rectidens (ROVERETO 1914), Pyramiodontherium bergi (MORENO & MERCERAT, 1891) Cabrera, 1928, Pyramiodontherium brevirostrum Carlini, Brandoni, SCILLATO-YANE & PUJOS, 2002, and Pyramiodontherium scillatoyanei DE IULIIS, RÉ & VIZCAÍNO, 2004; and much smaller than Megatherium americanum, Eremotherium laurillardi (LUND 1842), and Eremotherium eomigrans DE IULIIS & CARTELLE, 1999. Proximally, mandibular symphysis ends near the level of the middle of the alveolus of m1. In Megathericulus patagonicus and Eomegatherium andinum the symphysis ends in front of the ml, whereas in Pyramiodontherium brevirostrum and Megatherium altiplanicum SAINT-ANDRÉ & DE IULIIS, 2001, at level of the interalveolar septum between m1 and m2. Horizontal ramus and angular process low as in Eremotherium laurillardi and E. eomigrans. Alveolus of m4 lies anterior to the anterior margin of the ascending ramus, but not to the degree seen in Megathericulus patagonicus and Eomegatherium andinum, and in contrast to the more posterior position in Pyramiodontherium bergi, Megatheriops rectidens, Eremotherium laurillardi and Megatherium americanum, among others. As in most

Fig. 3. Pliomegatherium lelongi Kraglievich, 1930. Right hemimandible MACN Pv-13213: 1 – dorsal view; 2 – lateral view. Right hemimandible MACN Pv-5269: 3 – dorsal view; 4 – lateral view. Astragalus MLP 99-XI-1-1: 5 – dorsolateral view; 6 – anterior view. Scale bar 10 cm.

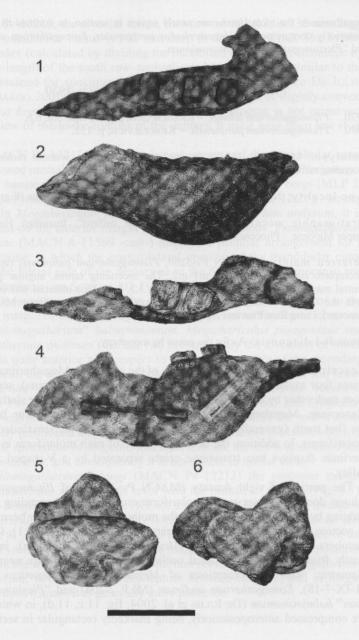


Fig. 3 (Legend see p. 216)

megatheriines, the molariforms are nearly square in section, in contrast to anteroposteriorly compressed in Megathericulus patagonicus, Eomegatherium andinum and "Plesiomegatherium" halmyronomum.

Pliomegatherium lelongi Kraglievich, 1930

Fig. 3

1930 Pliomegatherium lelongi. - Kraglievich, p. 153, figs. 5.b, 6.b.

1930 Pliomegatherium paranensis. - Kraglievich, p. 155.

Holotype: MACN Pv-13213: incomplete right dentary, without molariforms, ascending ramus and angular process (Fig. 3.1, 3.2).

Type locality: North of Paraná City, Entre Ríos Province, Argentina (Fig. 1).

Stratigraphic occurrence: "Conglomerado osífero", Ituzaingó Formation (upper Miocene - Pliocene) (Fig. 2).

Referred material: MACN Pv-5269, *Pliomegatherium paranensis* (holotype) incomplete right dentary with m1-m2. The ascending ramus, angular process, ventral margin and m3-m4 are missing (Fig. 3.3, 3.4). This material was collected from the "Conglomerado osifero" of the Ituzaingó Formation (upper Miocene – Pliocene), Entre Ríos Province, Argentina.

Emended diagnosis: As for the genus by monotypy.

Description: The lower dental series of the subfamily Megatheriinae comprises four molariforms in a continuous row (without diastema), separated from each other by evenly spaced short diastemata, unlike other sloths (e.g., Planopinae, Megalonychiidae) in which a diastema may occur between the first tooth (generally termed the caniniform) and the remainder of the molariforms. In addition, the occlusal surface of each molariform in Megatheriinae displays two transverse crests separated by a V-shaped incised valley.

The portion of right dentary (MACN Pv-13213) of *Pliomegatherium lelongi* does not preserve the molariform crowns or the ascending ramus. Judging by the shape of the alveoli, the molariforms would have been square in section, except for ml which appears subtrapezoidal (Fig. 3.1). In most members of the subfamily (e.g., *Megatherium*, *Eremotherium*), independently from their cross-sectional outline, the molariforms are nearly isodiametric, with the exceptions of *Megathericulus patagonicus* (MLP 91-IX-7-18), *Eomegatherium andinum* (MLP 2-204) and "*Plesiomegatherium*" halmyronomum (DE IULIIS et al. 2004, fig. 11.c, 11.d), in which they are compressed anteroposteriorly, being markedly rectangular in section. In

MACN Pv-13213, the alveolar series, between ml and m2, is 135 mm long, and the mandibular ramus is 102 mm deep at the level of m2. The hypsodonty index (calculated by dividing the maximum depth of the mandible by alveolar length of the tooth row, multiplicated by 100) is 75, similar to the value obtained for specimens of *Eremotherium laurillardi* (see De Iuliis 1996; Bargo 2001). The lower contour of the mandible is slightly convex, similar to *Eremotherium laurillardi*. The angular process is not preserved, but in view of the lower contour of the dentary, it must have been low (Fig. 3.2).

In MACN Pv-13213, the posterolateral opening of the mandibular canal is positioned medially with respect to the ascending ramus as in *Plesiomega-therium hansmeyeri* (MACN Pv-2895), *Pyramiodontherium bergi* (MLP 2-66) and *Pyramiodontherium brevirostrum* (MLP 31-XI-12-25), among others. In *Megathericulus patagonicus* and *Eomegatherium andinum*, it is positioned on the anterior margin of the ascending ramus. *Promegatherium smaltatum* (MACN A-11560 -cast-) displays a peculiar arrangement for a megatheriine, in which the posterolateral opening of the mandibular canal lies on the lateral side of the dentary as in the Santacrucian Planopinae and Nothrotheriinae (see Scott 1903-1904; DE IULIIS 1994).

In *Pliomegatherium lelongi* the alveolus of m4 is placed anterior to the anterior margin of the ascending ramus, although not to the degree observed in "*Plesiomegatherium*" halmyronomum, Megathericulus patagonicus and Eomegatherium andinum (the last two preserve only the alveolus) in which the m4 is quite anterior with respect to the anterior margin of the ascending ramus, with the result that it is visible in entirety in lateral view. In *Plesiomegatherium hansmeyeri* (MACN Pv-2895), Megatheriops rectidens (MACN Pv-2818), Pyramiodontherium bergi (MLP 2-66) and Eremotherium eomigrans (DE IULIIS & CARTELLE 1999, fig. 4.b) the m4 is more posteriorly positioned and only the anterior half of the m4 is visible laterally. In several specimens of Megatherium americanum, the m4 is positioned still more posteriorly, and consequently it is not visible in lateral view.

In Pliomegatherium lelongi (MACN Pv-13213) the posterior margin of the mandibular symphysis is level with the middle of the m1 (Fig. 3.1), while in Eomegatherium nanum (Kraglievich 1930, fig. 5.a), Eo. andinum, Megathericulus patagonicus and "Plesiomegatherium" halmyronomum (De Iuliis et al. 2004, fig. 11.c, 11.d), it is in front of the anterior surface of the m1. In Pyramiodontherium bergi, this margin is a little behind or posterior to the middle of m1; in Pyramiodontherium brevirostrum and Megatherium altiplanicum, it is level with the septum between m1-m2; and in Mega-

therium americanum it is generally more posterior.

The specimen MACN Pv-5269 (Fig. 3.3, 3.4), originally referred to *Pliomegatherium paranensis* (Kraglievich, 1930), is represented by a fragment right dentary that preserves only m1 and m2. The dental series measures 145 mm in total length, and at the contact m1-m2 the ramus is 105 mm high. The ml is subtrapezoidal in cross-section and the m2 is a little more squared in outline. The anterior lower contour of the mandible (Fig. 3.4) is similar to that of the type specimen of *Pliomegatherium lelongi* and *Eremotherium laurillardi*. As in MACN Pv-13213, in MACN Pv-5269 the alveolus of the m4 is placed anterior to the anterior margin of the ascending ramus. The posterior margin of the mandibular symphysis of MACN Pv-5269 (Fig. 3.3) is placed in a similar position to that of MACN Pv-13213.

4. Discussion

Knowledge of the morphology and individual variation in the Megatheriinae is based mainly on the remains of two Pleistocene Megatheriinae, Megatherium americanum and Eremotherium laurillardi (Cartelle 1992; Cartelle & De Iulis 1995; De Iulis 1996; De Iulis & Cartelle 1999; Pujos & Salas 2004). The range of variation of the Quaternary species would be expected to have also been present in many Tertiary species, but the number of specimens for comparison is substantially lower and the incompleteness of the available material hampers a comprehensive analysis. Assuming the hypothesis that the intraspecific variability could have been similar in Quaternary and Tertiary Megatheriinae, the morphological differences observed in the type specimens of Pliomegatherium lelongi MACN Pv-13213 and Pliomegatherium paranensis MACN Pv-5269 do not justify the specific separation of these species, as suggested by De Iuliis (1996). Consequently, here it is proposed that Pl. lelongi and Pl. paranensis are conspecific, with Pl. paranensis being a synonym of Pl. lelongi.

Concerning the relationships between *Pliomegatherium lelongi* and other Megatheriinae, the shape of the mandible in lateral view is very similar to that observed in *Eremotherium laurillardi*; however, it is difficult to establish the relationships between these two taxa given our present state of knowledge, and the fact that they come from sediments of very different age, late Miocene (*Pliomegatherium lelongi*) and Pleistocene (*Eremotherium laurillardi*). On the other hand, the characters (e.g., location of the posterior margin of the mandibular symphysis, and of the posterolateral opening of the mandibular canal) found in the mandibular remains referred to *Pliomegatherium lelongi* suggest an intermediate evolutionary grade between the oldest megatheriines (*Megathericulus patagonicus* and *Eomegatherium andinum* Kraglievich, 1930) from the middle Miocene of Patagonia, and

the more recent taxa (Pyramiodontherium, Megatherium, and Eremotherium).

In addition to the reported mandibular remains, a left astragalus (MLP 99-XI-1-1) from the "Conglomerado osífero" may belong to Pliomegatherium lelongi. It is similar in size to those of Eomegatherium nanum and Eo. cabrerai Kraglievich, 1930, but with features that suggest a more advanced evolutionary grade than this last species. In Pliomegatherium lelongi (MLP 99-XI-1-1), the ventral portion of the fibular facet has a circular contour (Fig. 3.5), similar to that observed in Pyramiodontherium bergi (BRANDONI et al. 2004, fig. 2.c), Py. scillatoyanei (DE IULIIS et al. 2004, fig. 7.a), and in some specimens of Megatherium americanum (see Brandoni et al. 2004), and the distance that separates the fibular facet from the ectal facet is relatively larger than in Eomegatherium nanum (MACN Pv-4992), Eo. cabrerai (MLP 2-206), and Megathericulus patagonicus (MACN A-11151, MLP 91-IX-7-18, MLP 92-XI-15-2). In addition, the astragalus MLP 99-XI-1-1 has the plane of the navicular facet perpendicular to the plane of the discoid facet, while in Megathericulus patagonicus, Eomegatherium cabrerai and Eo. nanum the navicular facet is inclined slightly with respect the discoid facet. As in Eomegatherium cabrerai and Eo. nanum, the dorsomedial portion of the navicular facet is ventral, with the plane of the discoid facet intersecting approximately at the centre of the circular depression of the navicular facet (Fig. 3.6). In Megathericulus patagonicus, one-half lies dorsal to the plane of the discoid facet. In contrast, the dorsal part of the navicular facet lies at nearly the same level as the plane of the discoid facet in Megatherium americanum.

Finally, study of different unassociated materials found in the "Conglomerado osífero" of the Ituzaingó Formation suggests that the number of valid species of megatheriines may be lower than previously proposed. However, the establishment of synonymies, as well as the generic and specific assignment of the specimens is not easy, mainly because of the peculiarities of the taphonomy context of this unit.

Acknowledgements

I thank M. REGUERO (MLP) and A. KRAMARZ (MACN) for facilitating access to collection of their institutions, and G. J. SCILLATO-YANÉ for the critical review of the ms. I also acknowledge the suggestions made by the reviewers A. CARLINI and G. DE IULIIS. Finally, many thanks to C. DESCHAMPS and R. MADDEN for improving the English version of this work.

- CIONE, A. L., AZPELICUETA, M. M., BOND, M., CARLINI, A. A., CASCIOTTA, J., COZZUOL, M., DE LA FUENTE, M., GASPARINI, Z., GOIN, F. J., NORIEGA, J. I., SCILLATO-YANÉ, G. J., SOIBELZON, L., TONNI, E. P., VERZI, D. H. & VUCETICH, M. G. (2000): Miocene Vertebrates From Paraná, Eastern Argentina". – INSUGEO, Ser. Corr. Geol., 14: 191-237.
- CUVIER, G. (1796): Notice sur le squelette d'une très-grande espèce de quadrupède inconuce jusqu'à present trouvé au Paraguay, et déposé au cabinet d'histoire naturelle de Madrid. – Mag. Encycl. J. Sci. Lett. Arts, 1: 303-310; 2: 227-228.
- DE ALBA, E. (1953): Geología del Alto Paraná, en relación con los trabajos de derrocamiento entre Ituzaingó y Posadas. – Rev. Asoc. Geol. Argent., 8 (3): 129-161.
- DE IULLIS, G. (1994): Relationships of the Megatheriinae, Nothrotheriinae, and Planopsinae: some skeletal characteristics and their importance for phylogeny. – J. Vert. Paleont., 14: 577-591.
- (1996): A Systematic Review of the Megatheriinae (Mammalia: Xenarthra: Megatheriidae). – Unpublished Doctoral Thesis, University of Toronto. – 781 pp.; Toronto.
- DE ILLIIS, G. & CARTELLE, C. (1999): A new giant megatheriine ground sloth (Mammalia: Xenarthra: Megatheriidae) from the late Blancan to early Irvingtonian of Florida. – Zool. J. Linn. Soc., 127: 494-515.
- DE IULIIS, G., Ré, G. H. & VIZCAÎNO, S. F. (2004): The Toro Negro megatheriine (Mammalia: Xenarthra): a new species of *Pyramiodontherium* and a review of *Plesiomegatherium*. – J. Vert. Paleont., 24: 214-227.
- HOFFSTETTER, R. (1958): Xenarthra.. In: PIVETEAU, J. (Ed.): Traité de Paléontologie, p. 535-640.
- KRAGLIEVICH, L. (1926): Notas sobre gravígrados de Sud América. Anal. Mus. Nac. Hist. Nat. Buenos Aires, 34: 21-36.
- (1930): La formación friascana del Río Frias, Río Fénix, Laguna Blanca, etc. y su fauna de mamiferos. – Physis, Rev. Soc. Argent. Cien. Nat., 10: 127-161.
- LUND, P. W. (1842): Blik paa Brasiliens Dyreverden for Sidste Jordomvaeltning. Fjerde Afhandling: Fortsaettelse af Pattedyrene. – Detkongelige Danske Videnscavernes Selskabs Skrifter, Naturvidenskabelige og mathematisk Afhandlinger, 9: 137-208.
- Mones, A. (1986): Paleovertebrata Sudamericana. Catálogo Sistemático de los Vertebrados fósiles de América del Sur. Parte I. Lista Preliminar y Bibliográfica. – Cour. Forsch.-Inst. Senckenberg, 82: 1-625.
- MORENO, F. P. & MERCERAT, A. (1891): Exploración arqueológica de la Provincia de Catamarca: Paleontología. – Rev. Mus. La Plata, 1: 222-236.
- PUJOS, F. & SALAS, R. (2004): A new species of Megatherium (Mammalia: Xenarthra: Megatheriidae) from the Pleistocene of Sacaco and Tres Ventanas, Peru. Palaeontology, 47: 579-604.
- ROTH, S. (1911): Un nuevo género de la familia Megatheridae. Rev. Mus. La Plata, 18: 7-21.
- ROVERETO, C. (1914): Los estratos araucanos y sus fósiles. Anal. Mus. Nac. Hist. Nat. Buenos Aires, 25: 1-247.

SAINT-ANDRÉ, P. A. & DE IULIIS, G. (2001): The smallest and most ancient representative of the genus Megatherium CUVIER, 1796 (Xenarthra, Tardigrada, Megatheriidae), from the Pliocene of the Bolivian Altiplano. – Geodiversitas, 23: 625-645.

SCOTT, W. B. (1903-1904): Mammalia of the Santa Cruz Beds. Part 1: Edentata. – Rep. Princeton Univ. Patagonia, 1896-1899, 5: 1-364.

Manuscript received: July 5th, 2005. Revised version accepted by the Stuttgart editor: December 8th, 2005.

Address of the author:

DIEGO BRANDONI, Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y de Transferencia Tecnológica a la Producción (CICYTTP-CONICET), Materi y España, 3105 Diamante, Entre Ríos, Argentina; E-mail: diegobrandoni@yahoo.com