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On the status of “*Urotherium antiquum*” (Ameghino) (Xenarthra, Glyptodontidae)



À propos du statut de « *Urotherium antiquum* » (Ameghino) (Xenarthra, Glyptodontidae)

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ABSTRACT

Within the Late Neogene Glyptodontidae of the Pampean region of Argentina, “*Urotherium antiquum*” was described on the basis of some associated osteoderms of the dorsal carapace, which in addition include a partial skull and left hemimandible. The diagnostic characters are located on the exposed surface of the osteoderms of the dorsal carapace which somewhat resembles those of the Pleistocene genus *Neuryurus*. Although the relationship of “*U. antiquum*” to the remaining Glyptodontidae has never been clarified, some cladistic analyses suggest a close phylogenetic affinity with the clade composed of *Plohophorus* + (*Glyptodon* + *Doedicurus*). A careful comparison of “*U. antiquum*” to well-characterized taxa with similar stratigraphic and geographic provenance reveals that no significant skull differences are observed from *Plohophorus figuratus* Ameghino. It seems likely that the alleged ornamentation pattern that characterizes this species was produced by a taphonomic alteration of the exposed surface of the osteoderms, a process broadly distributed in glyptodonts having a “rosette” ornamentation pattern. Finally, some characters present in the osteoderms of the type specimen of “*U. antiquum*” suggest that it may be a juvenile specimen. In summary, “*U. antiquum*” should be considered a junior synonym of *P. figuratus*.

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R É S U M É

Parmi les Glyptodontidae du Néogène supérieur de la Pampa (Argentine), « *Urotherium antiquum* » est décrit sur la base d'ostéodermes associés de la carapace dorsale, qui comportent en plus une partie de crâne et une demi-mandibule gauche. Les caractères diagnostiques sont situés sur la surface exposée des ostéodermes de la carapace dorsale,

Mots clés :

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qui ressemblent un peu à ceux du genre pléistocène *Neuryurus*. Quoique la relation de « *U. antiquum* » avec les Glyptodontidae restants n'ait jamais été précisée, quelques analyses cladistiques suggèrent une proche affinité phylogénétique avec le clade composé de *Plohophorus* + (*Glyptodon* + *Doedicurus*). Une comparaison soignée de « *U. antiquum* » avec des taxons bien caractérisés de provenances stratigraphiques et géographiques similaires révèle qu'aucune différence significative au niveau du crâne n'est observée chez *Plohophorus figuratus* Ameghino. Il semble probable que le motif d'ornementation supposé qui caractérise cette espèce a été produit par une altération taphonomique de la surface exposée des ostéodermes, un processus largement répandu chez les glyptodontes présentant un motif d'ornementation « en rosette ». Finalement, quelques caractères présents chez les ostéodermes du spécimen type de « *U. antiquum* » suggèrent qu'il puisse s'agir d'un juvénile. En résumé, « *U. antiquum* » devrait être considéré comme un synonyme junior de *P. figuratus*.

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1. Introduction

Among Late Neogene Xenarthra Glyptodontidae (Cingulata) in southern South America, the genus *Urotherium* Castellanos includes several species that were widely distributed in the Pampean, northwestern and Mesopotamian regions of Argentina (Castellanos, 1948; Reguero and Candela, 2011; Reguero et al., 2007). The main characters proposed for *Urotherium* are morphological details on the exposed surface of the osteoderms of the dorsal carapace and caudal tube, which are clearly rugose and uniformly perforated by numerous small foramina (see Castellanos, 1926, 1948). Despite its poor characterization, most *Urotherium* species were considered valid and constitute part of the Neogene diversity of Glyptodontidae (but see Zurita et al., 2016). This lack of clear characterization has motivated a discussion regarding the phylogenetic affinity of the species of *Urotherium*, both in precladistic and cladistic scenarios. They have been alternatively included in the “Hoplophorinae” Lomaphorini (Hoffstetter, 1958; Mones, 1986; Pascual et al., 1966; Paula-Couto, 1979), Neuryurini (Carlini and Scillato-Yané, 1999), Doedicurinae (Castellanos, 1932), and Trachycalyptini (Castellanos, 1959); according to Hoffstetter (1958: 585) they are phylogenetically close to the “Neothoracophorini”. In recent cladistic analyses, *Urotherium* (“*U. antiquum*”) was interpreted as the sister taxon of the clade *Plohophorus* Ameghino + (*Glyptodon* Owen + *Doedicurus* Burmeister) (Fericola, 2008; Porpino et al., 2010).

However, a recent taxonomic revision of the type material of the species included in *Urotherium* (*U. simile* Castellanos, *U. simplex* Castellanos, and *U. interundatum* (Ameghino)), together with new findings, indicates that the main characters proposed for this genus are merely due to taphonomic alterations of the exposed surface of the osteoderms which likely belong to juvenile specimens of well-known species (Zurita et al., 2016). Consequently, no valid characters can be observed.

A notable exception is the only species of *Urotherium* that includes a partial skull, left hemimandible and some fragments of dorsal carapace, “*U. antiquum*” (= *Euryurus antiquus* = *Neuryurus antiquus*). This species was recognized by Ameghino (1888) in his “*Piso hermoso de la formación araucana*”, which corresponds to the Monte Hermoso

Formation (Early Pliocene, Montehermosan Stage/Age; see Tomassini et al., 2013). In fact, this is the only *Urotherium* species that has been phylogenetically analyzed (see Porpino et al., 2010).

However, a careful examination and comparison of the “*U. antiquum*” materials with well-known Late Neogene glyptodonts with the same or similar stratigraphic and geographic provenance shows some “morphological problems”. Thus, this paper aims to clarify the taxonomic status of “*U. antiquum*” and reevaluate the traditionally diagnostic characters proposed for this species.

2. Materials and methods

The chronological and biostratigraphic schemes used in this contribution follow Cione and Tonni (2005), Cione et al. (2007), and Tomassini et al. (2013). The systematics partially follows Hoffstetter (1958), Paula-Couto (1979), McKenna and Bell (1997), and Fericola (2008). The description and terminology for osteoderms mainly follows Zurita (2007) and Krmptovic et al. (2009). All the values included in tables are expressed in millimeters (mm), with an error range of 0.5 mm. Measurements smaller than 150 mm were taken with “Vernier” calipers.

Institutional abbreviations. **MACN A:** Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional de Ameghino, Buenos Aires, Argentina; **MCNC-PV:** Museo provincial de Ciencias Naturales de Córdoba; **MLP:** División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; **MMP:** Museo Municipal de Ciencias Naturales “Lorenzo Scaglia”, Mar del Plata, Argentina; **Xen,** Colección Paleontológica “Cementos Avellaneda”, Olavarría, Argentina.

Other abbreviations. **cf:** central figure; **cs:** central sulcus; **rs:** radial sulci; **rf:** radiating foramina; **pf:** peripheral figures; **Mf:** upper molariforms; **TL:** total length of skull; **TDPR:** transverse diameter of postorbital region; **LTS:** length of the tooth series; **TD1:** transverse diameter of the palate at level of M1; **TD5:** transverse diameter of the palate at level of Mf 5; **MTDZA:** maximum transverse diameter between zygomatic arches; **LP:** length of the palate.

3. Systematic palaeontology

Magnorder Xenarthra Cope, 1889

Order Cingulata Illiger, 1811

Suborder Glyptodontia Gray, 1869 (*nom. transl.* Ameghino, 1889)

Family Glyptodontidae Gray, 1869

Subfamily “Hoplophorinae” Huxley, 1864 (*nom. transl.* Weber, 1928)

Tribe “Plohophorini” Castellanos, 1932 (*nom. transl.* Hoffstetter, 1958)

Genus *Plohophorus* Ameghino, 1887

Plohophorus figuratus Ameghino, 1887

=*Urotherium antiquum* (Ameghino, 1888) Castellanos, 1926 **new synonymy**

=*Euryurus antiquus* Ameghino, 1888

=*Neuryurus antiquus* (Ameghino, 1888) Ameghino, 1889 (Fig. 2A, B, C, D, I and Fig. 3A, B, C, D, E)

Remarks on the type materials of “*U. antiquum*”. The species was originally recognized on the basis of some associated osteoderms of the dorsal carapace (Ameghino, 1888), but the type materials were not illustrated. Some years later, Lydekker (1895: 15) observed that the type material corresponds to that illustrated by Ameghino (1889, pl. 62, fig. 6). In addition to this, Ameghino (1895: 523) mentioned that the skull, left hemi mandible (see Ameghino, 1889, pl. 63, figs. 1 and 2) and the associated osteoderms of the dorsal carapace (see Ameghino, 1889, pl. 62, figs. 6 and 6a) declared by Lydekker (1895) corresponded to the same specimen. In recent times, these materials were found at the paleontological collections of the Museo Argentino de Ciencias Naturales (MACN A-229, 230, 231), corresponding to those figured by Ameghino (1889). In agreement with the proposal of Ameghino (1895), the remains belong to a single specimen.

Geographic and stratigraphic provenance (Fig. 1). Farola Monte Hermoso (S 33°58', W 61°41'), Buenos Aires Province, Argentina. Monte Hermoso Formation (Early Pliocene, Montehermosan Stage/Age; see Tomassini et al., 2013).

3.1. Taxonomic and historical background

The genus *Euryurus* was originally recognized by Gervais and Ameghino (1880). Later, Ameghino (1888: 493) recognized the species *E. antiquus* on the basis of materials (associated osteoderms of the dorsal carapace) coming from his “*Piso hermósico de la formación araucana*” (Ameghino, 1889: 842–843; pl. 62, fig. 6) that corresponds to the Monte Hermoso Formation (Early Pliocene, Montehermosan Stage/Age; see Tomassini, 2012; Tomassini et al., 2013) in the Buenos Aires Province. Several years later, the generic name was replaced by *Neuryurus* Ameghino, 1889, as the first was preoccupied by *Euryurus* Koch, 1847. Ameghino (1888) characterized the exposed surface of the osteoderms of “*E. antiquus*” as having an evident rough aspect and a large number of small foramina; in some osteoderms, it is possible to observe a poorly defined circular central figure. In 1889, Ameghino carried out the first

detailed description and illustrated the materials, which included the associated osteoderms of the dorsal carapace, a relatively well preserved skull and a left hemimandible (Ameghino, 1889: pl. 62, figs. 6 and 7; pl. 63, figs. 1 and 2). As in the original description, the species was mainly characterized by a particular morphology of the exposed surface of the osteoderms. In turn, the internal surface of the osteoderms was characterized as having fewer foramina and showing some resemblance with those observed in the Pleistocene Doedicurinae *Doedicurus* (Ameghino, 1889; pl. 62, fig. 6). The first to doubt the validity of this species was Lydekker (1895: 15; pl. 9, figs. 1–3), who interpreted the material that Ameghino identified as “*N. antiquus*” as belonging to juvenile specimens of *P. figuratus*. The taxonomic conclusion of Lydekker (1895) was based on an erroneous conception about the ontogenetic evolution of the osteoderms in glyptodonts (see Ameghino, 1895; Zurita et al., 2011). This originated a heated discussion between Lydekker (1895) and Ameghino (1895), who strongly rejected the interpretation of Lydekker. To support his position, Ameghino (1895: 523) mentioned that the associated osteoderms of the dorsal carapace (Ameghino, 1889; pl. 62, fig. 6) belong to the same specimen as the skull and hemimandible (Ameghino, 1889; pl. 63, figs. 1 and 2). Finally, Castellanos (1926) transferred “*N. antiquus*” to his Neogene genus *Urotherium* (“*U. antiquum*”) (see also Kraglievich, 1934). Since then, the taxon was considered valid by most authors (e.g. Cabrera, 1944; Castellanos, 1926; Fericola, 2008; Fericola and Porpino, 2012) and even included in cladistics analyses. A recent study concerning the diversity of Late Neogene Glyptodontidae (see Zurita et al., 2016) offers the opportunity to reevaluate the status of this species. In the following sections, we provide a justification for the new proposed synonymy.

3.2. Description and comparisons

Skull (MACN A-229) (Fig. 2A–D). Ameghino (1889, pl. 63, figs. 1 and 2) described and illustrated a partial skull and left hemimandible that he identified as “*N. antiquus*”. Only the skull was found (MACN A-229) and it lacks the right zygomatic arch. Among the recognized diversity of Montehermosan (Early Pliocene) and Chapadmalalan (Late Pliocene) Glyptodontidae of the Pampean region of Argentina, only three species have known skulls, “*U. antiquum*”, cf. *Eleutherocercus antiquus* (Doedicurinae) and *P. figuratus* (“Hoplophorinae” Plohophorini). The latter two represent the most frequently recorded taxa in Neogene strata (Zurita et al., 2014, 2016). The skull (MMP 4676) recovered from the Chapadmalal Formation was tentatively assigned by Oliva et al. (2010) to the Glyptodontinae cf. *Paraglyptodon chapadmalensis* (Ameghino), and is currently under revision; it is possible that this identification needs a correction (Zurita et al., 2016).

The morphology of the skull of “*U. antiquum*” (MACN A-229) is not concordant with that known of Doedicurinae (i.e. cf. *E. antiquus* and *Doedicurus*), excluding its inclusion in this subfamily. In fact, the morphology of the molari-forms and palate of this clade is very particular (see Zurita et al., 2014: fig. 2). Additionally comparison to MMP 4676

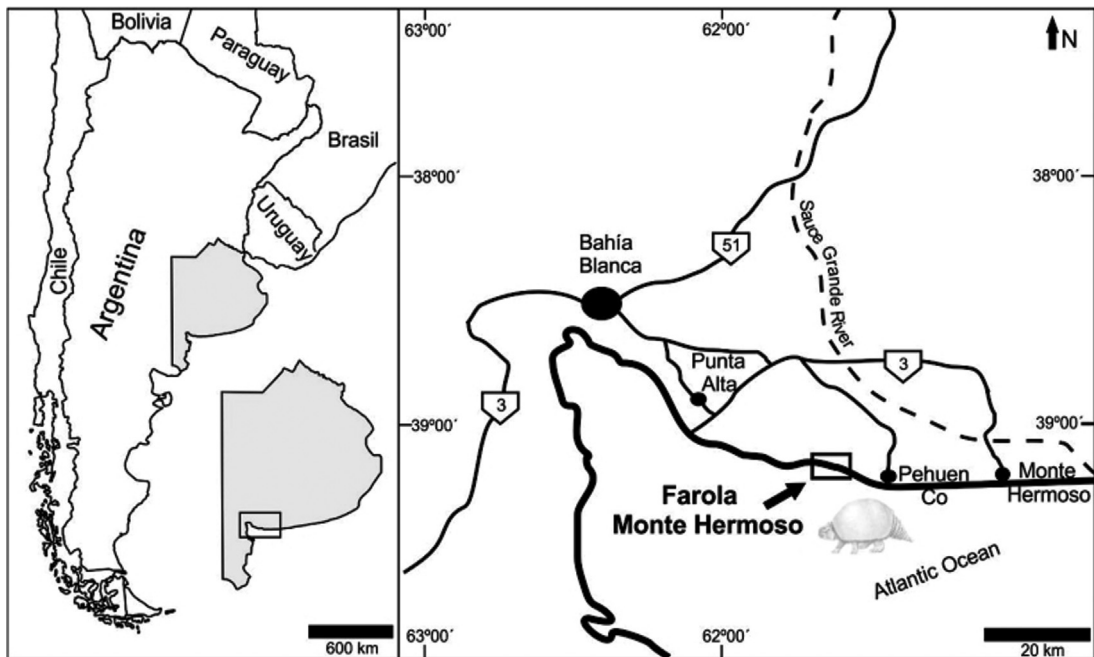


Fig. 1. Geographic location of *Urotherium antiquum* (Ameghino).

Fig. 1. Carte montrant l'emplacement de *Urotherium antiquum* (Ameghino).

shows significant differences. Thus, the discovery of new and more complete *Plohophorus* specimens (MMP 4823; Xen 72) allows a detailed comparison and, as emphasized by Lydekker (1895) MACN A-229 shows a remarkable similarity with *P. figuratus*, one of the most recorded taxa in the Montehermosan and Chapadmalalan levels. In fact, the general morphology of the skull and molariforms are almost identical.

In anterior view (Fig. 2A), it is possible to observe that the most distal borders of the narines are not preserved in MACN A-229. However, the morphology is clearly similar to that of *P. figuratus* (Fig. 2E), and also shows some resemblance to cf. *Eleutherocercus antiquus*. Furthermore, it is possible to see that the orbital notch is completely different than cf. *E. antiquus*, in which this structure is more laterally expanded, with evident bony ridges on its ventral edge.

In lateral view (Fig. 2B, F) *P. figuratus* and "*U. antiquum*" show the same dorsal profile. The occipital and parietal areas are clearly elevated with respect to the nasal region. The zygomatic arch presents the same graceful morphology in both MACN A-229 and *P. figuratus*, and completely differs from that of cf. *Eleutherocercus antiquus*, in which this structure is much more developed. The orbital notch is subelliptical and dorso-ventrally elongated, as in *P. figuratus*, and does not present the evident bony ridges on the ventral edge that are observed in cf. *Eleutherocercus antiquus* and *Doedicurus*. The descending process of the maxillae is not preserved in its ventral half, but the general morphology is almost identical to that of *P. figuratus*. Ahead of the orbital notch, the dorsal profile of the rostral region shows an angle of ca. 46° with respect to the palatal plane, as in *P. figuratus* (ca. 42°); this angle is 54° in cf. *E. antiquus*.

In dorsal view, "*U. antiquum*" (Fig. 2C) and *P. figuratus* (Fig. 2G) also show the same morphology, which is very different than cf. *Eleutherocercus antiquus* and MMP 4676. The parietal area presents several large foramina on both sides of the sagittal crest, which is clearly developed in *P. figuratus* and was not preserved in "*U. antiquum*". This led several authors to mistakenly interpret it as absent in phylogenetic analyses. In MMP 4676, the parietal region does not show the evident foramina. The orbital notch is posteriorly opened, lacks a postorbital bar, and the left zygomatic arch is identical to that of *Plohophorus*. The rostral area located behind the orbital notch is subtriangular, showing the same morphology as that seen in *P. figuratus*. This morphology completely differs from that of *Doedicurus* and cf. *E. antiquus*, in which the rostral area shows a sub quadrangular contour and a strong postorbital bar is present. Additionally, the zygomatic arch and the orbital notch are evidently more laterally expanded.

In occlusal view (Fig. 2D), it is possible to observe a transversal enlargement of the palate at the level of its proximal and distal borders, and a minimum at level of Mfs 4-5, as in *P. figuratus* (Fig. 2H). In cf. *Eleutherocercus antiquus*, this morphology is also present but is much more evident (Table 1). This particular morphology is not present in MMP 4676, and both molariform series are almost parallel. As in *P. figuratus*, the palate of MACN A-229 has several large foramina at level of the Mfs3 and 4.

The left hemimandible (MACN A-230) described and illustrated by Ameghino (1889: pl. 63, fig. 2) was not found in the collection. However, the general morphology is very similar to that figured by Lydekker (1895, Pl. VIII) and Pascual et al. (1966, Pl. XXXVII), which belongs to *P. figuratus*.

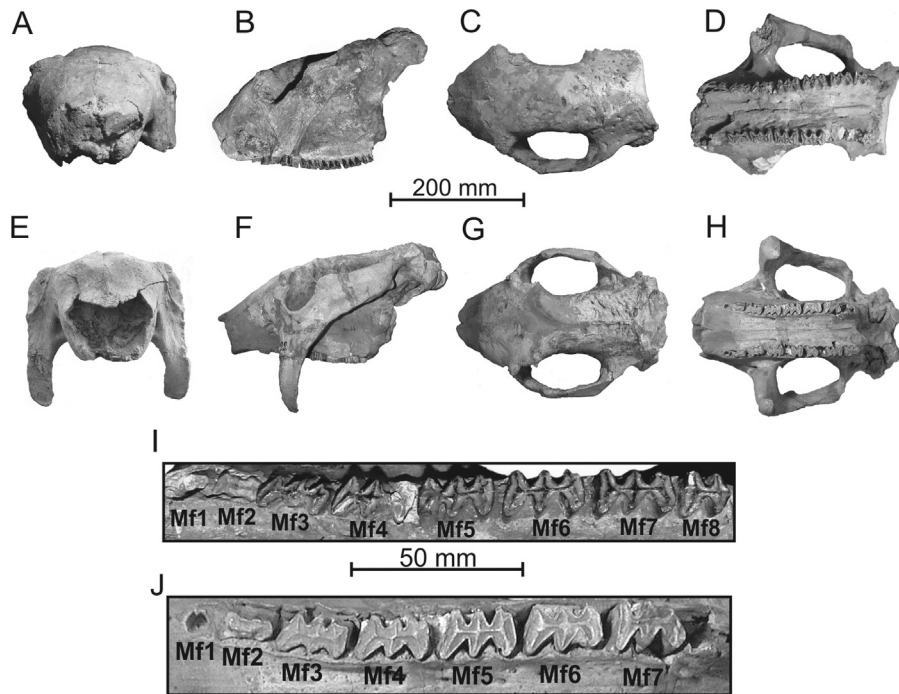


Fig. 2. “*Urotherium antiquum*” (Ameghino) (MACN A-229) (A–D) and *Plohophorus figuratus* Ameghino (MLP 16-153) (E–H). Skulls in frontal (A, E), lateral (B, F), dorsal (C, G), and occlusal (D, H) views. Detail of the upper molariforms of *U. antiquum* (I) and *P. figuratus* (H).

Fig. 2. « *Urotherium antiquum* » (Ameghino) (MACN A-229) (A–D) et *Plohophorus figuratus* Ameghino (MLP 16-153) (E–H). Crâne en vues frontale (A, E), latérale (B, F), dorsale (C, G) et ventrale (D, H). Détail des molariformes supérieures de *U. antiquum* (I) et *P. figuratus* (H).

Table 1

Comparative measurements (in mm) of cf. “*U. antiquum*”, *P. figuratus*, and cf. *E. antiquus*.

Tableau 1

Mesures comparatives (en mm) de cf. « *U. antiquum* », *P. figuratus*, and cf. *E. antiquus*.

	“ <i>U. antiquum</i> ” MACN A-229	<i>P. figuratus</i> MMP 4823	Cf. <i>E. antiquus</i> MMP 4860
TL	220	240	230.74
TDPR	69.63	73.2	108.14
LTS	145.07	154.36	144.44 ^b
TD1	40.13	43.67	58.6
TD5	31.62	35.94	44.4
MTDZA	156 ^a	191	235.18
LP	–	175	157.28
TL/MTDZA	1.41	1.25	0.98
TL/TD1	5.48	5.49	3.93

^a Approximate.

^b Including Mf1–Mf6.

Upper molariforms. The general morphology of the molariforms (Fig. 2I) completely matches those of *P. figuratus* (Fig. 2J), and is different than *Doedicurus*, cf. *Eleutherocercus antiquus* and MMP 4676. The Mf1 is simple, has a subelliptical contour and is almost identical to that of *P. figuratus*. The Mf2 shows an incipient trilobulation, even more evident than that observed in cf. *E. antiquus* but less developed compared to MMP 4676; the Mf3 presents the transversal axis of the first lobe oriented ca. 54.5° with respect of the palatal plane; the first lobe shows a similar bilateral development, unlike cf. *E. antiquus* where the lingual side is much more developed. Both in *P. figuratus* and

MACN A-229, the labial margin of the third lobe shows a “slot”. The Mfs 4–6 are similar in morphology and the third lobe presents in its labial side a “slot”, as in cf. *E. antiquus* and *P. figuratus*. Finally, the Mfs 7 and 8 do not show any differences when compared to *P. figuratus*.

Osteoderms (MACN A-231) (Fig. 3A–E; see also Ameghino, 1889: pl. 62, figs. 6, 6a and 7). According to Ameghino (1889), the osteoderms show two different morphologies, characterizing both the internal and external (=exposed) surfaces. The internal surface (Fig. 3B, C) shows several (5–12) large, uniformly distributed foramina, whereas the articular area between the osteoderms is clearly evident (Fig. 3D, E). In turn, the exposed surface presents rugose aspect and larger number of very small foramina (Fig. 3A). Our observations coincide with the descriptions of Ameghino. However, some interesting observations can be added, suggesting that the osteoderms belong to a juvenile specimen. For this, the material was compared to those of juvenile glyptodonts previously studied by Luna and Krapovickas (2011) and Zurita et al. (2011) in order to find evidences of this ontogenetic stage. The internal surface is slightly concave, consisting of a finely spongy tissue, especially in the central region (Fig. 3C); although this character could be attributed to taphonomic factors, it has been also observed in some juvenile specimens of *Glyptodon* Owen (MCNC-PV-246) (Fig. 3F). This differs from the typical condition observed in adult specimens because the internal surface is smooth, flat or very gently concave, exhibiting macroscopic meshwork of mineralized fiber bundles (Hill, 2006), which are deposited during more advanced ontogenetic stages. Another feature,

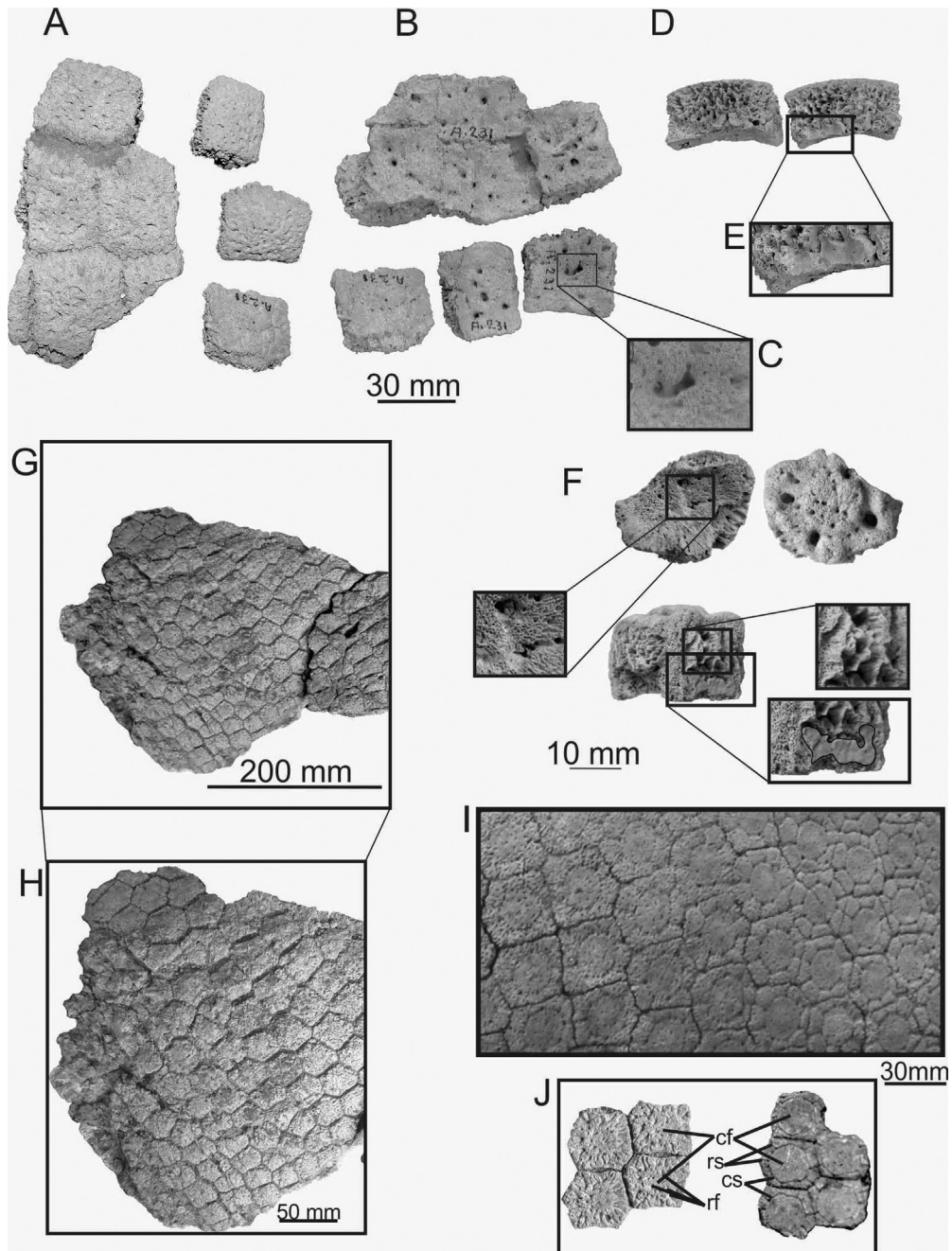


Fig. 3. “*Urotherium antiquum*” (MACN A-231). (A) Exposed surface of associated osteoderms of the dorsal carapace; (B, C), internal surface of associated osteoderms of the dorsal carapace showing some morphological details observed in juvenile specimens; (D, E), articular area showing some morphological details observed in juvenile specimens. *Glyptodon* sp. (MCNC-PV-246); (F) osteoderm belonging to a juvenile specimen. *Plohophorus figuratus* (MMP 4823). (G, H) Antero-lateral region of the dorsal carapace showing the taphonomic alteration, from a real ornamentation pattern to a “*Urotherium*” pattern.

Fig. 3. « *Urotherium antiquum* » (MACN A-231). (A) Surface externe des ostéodermes associés de la carapace dorsale ; (B, C) surface interne des ostéodermes associés de la carapace dorsale, montrant des caractères observés chez les juvéniles ; (D, E), zone articulaire montrant certains détails morphologiques observés chez les juvéniles. *Glyptodon* sp. (MCNC-PV-246) ; (F) ostéoderme d'un spécimen juvénile. *Plohophorus figuratus* (MMP 4823). (G, H) Région antéro-latérale de la carapace dorsale, montrant l'altération taphonomique. *Eosclerocalyptus* (Xen 30) (I, J), détail de la région latérale de la cuirasse dorsale, montrant la l'altération taphonomique et le modèle naturel de l'ornementation d'un « *Urotherium* ».

also observed in juveniles of some genera (e.g. *Glyptodon* and *Neosclerocalyptus* Paula-Couto), is the presence of a particular flat surface in the articular area (under study by one of the authors), which is related to the ossification

mechanism among osteoderms for the development of a rigid dorsal carapace (Fig. 3 E, F). In the adult phase, this structure disappears or is limited to a few relicts through resorption processes. In addition, the development of the

articular area (Fig. 3E) shows a very similar morphology compared to juvenile specimens of *Glyptodon* (Fig. 3F).

Additionally, some years later Ameghino (1895) referred new materials to this species, specifically the specimens illustrated by Lydekker (1895: pl. 9, figs. 1–4) and classified by this author as belonging to *P. figuratus*. The morphology of the exposed surface of this osteoderms is clearly rugose, and is almost identical to that originally described by Ameghino (1889).

4. Discussion and conclusions

The basic taxonomic and phylogenetic arrangements in Xenarthra Cingulata (i.e. Dasypodidae, Peltephilidae, Pampatheriidae, and Glyptodontidae) were primarily defined on the basis of the different patterns on the exposed surface of the osteoderms (Francia et al., 2015; Scillato-Yané et al., 2013). This is indubitably due to the fact that the dorsal carapace of Glyptodontidae may comprise more than 2000 osteoderms (Gillette and Ray, 1981), a situation that imparts an enormous fossilization potential to this clade. In the last years, some contributions have included other anatomical structures, such as skulls, mandibles and appendicular elements, revealing an interesting opportunity to test phylogenetic affinities between the different traditionally recognized groups (Fericola, 2008; Porpino et al., 2010; Zamorano and Brandoni, 2013; Zurita et al., 2013, among others).

One particular ornamentation pattern in the exposed surface of the osteoderms is represented by the presence of a rugose aspect with several small foramina and, in some cases, a poorly defined central figure (“*Neuryurus*” ornamentation pattern). The taxa with this pattern were interpreted by many authors (i.e. Ameghino, 1889; Castellanos, 1932; Hoffstetter, 1958; Paula-Couto, 1979) as belonging to different lineages (i.e. Doedicurinae, Lomaphorini, Neuryurini, Trachycalyptini), reflecting the lack of a good characterization of these taxa. Undoubtedly, the almost exclusive use of osteoderms to recognize and differentiate species, a practice that has been in use since the second half of the nineteenth century, in a strict typological and morphologic taxonomic context, has clearly caused over-diversification within the Cingulata Glyptodontidae (Soibelzon et al., 2006).

This is especially true for some Glyptodontidae associations. In this sense, Zurita et al. (2016) have observed that many of the species recognized from Montehermosan (Early Pliocene) and Chapadmalalan (Late Pliocene) levels that have a “*Neuryurus*” ornamentation pattern (i.e. rugose, without figures and presenting numerous small foramina) are not valid and/or correspond to well-known glyptodonts (*Eosclerocalyptus lineatus* and *P. figuratus*) (Fig. 3G–J). This particular ornamentation pattern is not real, but is the result of a taphonomic alteration of the exposed surface of the osteoderms, related to post-burial corrosion that produced degradation of this surface. In the units under study (Monte Hermoso, Chapadmalal, and El Polvorín formations) we observed that the corrosion affects different taxa of glyptodonts; however, the osteoderms having a “rosette” ornamentation (e.g. *P. figuratus*, *E. lineatus*) pattern show a different “reaction” to that process, and they

are the only ones in which we recognized this type of alteration. On the other hand, some postcranial elements also show some evidence of corrosion; however, we did not carry out any comparisons nor interpretations, mainly due to the fact that the way in which these elements are affected and modified is very different when compared to that observed in the osteoderms.

Considering this, it is possible that the only valid taxon that displays this ornamentation pattern is *Neuryurus* spp., from the Pleistocene of Argentina, which is known only by its dorsal carapace, and caudal and cephalic armors (see Ameghino, 1889; Zurita and Ferrero, 2009; Zurita et al., 2006).

“*U. antiquum*” is traditionally one of the best characterized species of the genus in Montehermosan levels (< 5.28–4.5/5.0 Ma; see Tomassini et al., 2013) in the Pampean region of Argentina. For this reason, it was included in phylogenetic analyses, which inferred a close affinity to the clade composed of *Plohophorus* + (*Glyptodon* + *Doedicurus*) (Fericola, 2008; Fericola and Porpino, 2012).

In this scenario, the comparative study carried out in this work shows that, at the level of the exposed surface of the osteoderms, the characterization of “*U. antiquum*” is based on osteoderms showing some similarity to the Pleistocene genus *Neuryurus* (Zurita et al., 2006). However, in this case, Zurita et al. (2016) demonstrated that this particular ornamentation pattern is due to a taphonomic alteration of the exposed surface of the osteoderms, a process that broadly affects Montehermosan and Chapadmalalan glyptodonts (Fig. 3G–J). As mentioned, this is particularly evident in taxa that have a “rosette” ornamentation pattern, such as *E. lineatus* and *P. figuratus*. Recently, this taphonomic alteration was also observed by one of us (AEZ) in one specimen of *Plohophorus* coming from the Chapadmalal Formation (MMP 4823) (Fig. 3G, H). In addition, some of the characters observed in the osteoderms of “*U. antiquum*” (see Descriptions) suggest that it may correspond to a juvenile specimen, which is congruent with the linear measurements when compared with adult specimens of *P. figuratus* (Table 1). In fact, the large foramina observed in the internal surface of the osteoderms (a character that allowed to some authors to infer a Doedicurinae affinity) are present in juvenile specimens of Glyptodontidae (see Zurita et al., 2011). In agreement with this interpretation, the comparative study indicates that the associated skull (MACN A-229) belongs to *P. figuratus*. This is a widely distributed taxon in Montehermosan and Chapadmalalan levels (Zurita et al., 2016).

Finally, from a taxonomic and nomenclatural view point, the evidence clearly indicates that “*U. antiquum*” should be considered a junior synonym of *P. figuratus*.

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Appendix 1.

Urotherium simplex: MACN Pv 5813 (Type), Castellanos, 1926

Urotherium antiquum: MACN A-229-231. Ameghino (1889, pl. 62, figs. 6 and 7; pl. 63 figs. 1 and 2)

Cf. *Eleutherocercus antiquus*: MMP 4860, 5360, Xen34. Zurita et al. (2014)

Neuryuru: MCNL 6.6. Zurita et al. (2006)

Neuryurus trabeculatus: UAP 1510. Zurita and Ferrero (2009)

Eosclerocalyptus cf. lineatus: Xen 30, Mam-63-4, MMP 4842, 5303, FM 05-266

Plohophorus figuratus: MLP 16-153 (type), MMP 4823; Xen 72

Eleutherocercus antiquus: MLP 16-55 (type). Lydekker (1895, pl. 25)

Doedicurus clavicaudatus: MLP 16-24

Doedicurus sp.: MACN Pv. 2762

Glyptodon sp.: MCNC-PV-246

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