

PALEONTOLOGICAL NOTE

## Paleogene Glyptodontidae Propalaeophophorinae (Mammalia, Xenarthra) in extra-Patagonian areas

Alfredo E. Zurita<sup>1</sup>, Laureano R. González-Ruiz<sup>2</sup>, Angel R. Miño-Boilini<sup>1</sup>, Rafael Herbst<sup>3</sup>,  
Gustavo J. Scillato-Yané<sup>4</sup>, Pedro Cuaranta<sup>1</sup>

<sup>1</sup> Centro de Ecología Aplicada del Litoral (CECOAL-CONICET) y Universidad Nacional del Nordeste, Ruta 5, km. 2,5, 3400, CC 128 Corrientes, Argentina.

azurita@cecoal.com.ar; angelmioboilini@yahoo.com.ar; cuaranta2004@yahoo.com.ar

<sup>2</sup> Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Universidad Nacional de la Patagonia "San Juan Bosco" sede Esquel (UNPSJB), Centro de Investigaciones Esquel de Montaña y Estepa Patagónica (CIEMEP-CONICET), Roca 780, 9200, Esquel, Chubut, Argentina.

gonzalezlaureano@yahoo.com.ar

<sup>3</sup> Instituto Superior de Correlación Geológica (INSUGEO-CONICET), Las Piedras 201 7ºB, 4000 San Miguel de Tucumán, Argentina. rafa.herbst36@gmail.com

<sup>4</sup> División Paleontología de Vertebrados, Museo de La Plata, Universidad Nacional de La Plata (CONICET), Paseo del Bosque, s/n 1900 La Plata, Buenos Aires, Argentina.

scillato@fcnym.unlp.edu.ar

---

**ABSTRACT.** Paleogene records of Cingulata Glyptodontidae are scarce. The only well described comes from the Paleogene of Argentine Patagonia. Two subfamilies have been reported for that period: Glyptatelineae and Propalaeophophorinae. Until this contribution, the latter taxon was geographically restricted to the locality of El Pajarito (Late Oligocene, Deseadan SALMA), Chubut province, Argentina. Here we present and describe the northernmost record of a Paleogene Propalaeophophorinae. The material is represented by three associated osteoderms of the dorsal carapace from the Fray Bentos Formation (Late Oligocene, Deseadan SALMA) in the locality of Cueva del Tigre, Chajarí, Entre Ríos province, Argentina. Morphologically, these remains are almost identical to those reported from the late Oligocene of the Patagonian region, showing that during the Paleogene the Propalaeophophorinae had a larger latitudinal distribution than previously known.

*Keywords:* Glyptodonts, Osteoderms, Mesopotamian Region, Fray Bentos Formation, Oligocene.

**RESUMEN. Registros paleógenos de Glyptodontidae Propalaeophophorinae (Xenarthra, Cingulata) en áreas extrapatagónicas.** Los registros paleógenos de Cingulata Glyptodontidae son muy escasos y los mejores conocidos provienen de la actual región patagónica de Argentina. Dos subfamilias han sido descritas: Glyptatelineae y Propalaeophophorinae. Los registros paleógenos de Propalaeophophorinae provienen de la localidad El Pajarito (Oligoceno Tardío, SALMA Deseadense), provincia de Chubut, Argentina. Aquí damos a conocer el registro más septentrional de un Propalaeophophorinae, proveniente de la Formación Fray Bentos (Oligoceno Tardío, SALMA Deseadense) de la localidad Cueva del Tigre, Chajarí, provincia de Entre Ríos, Argentina. Desde una perspectiva morfológica, estos restos son casi idénticos con aquellos reportados para El Pajarito. Esto demuestra que durante el Paleógeno la distribución latitudinal de los Propalaeophophorinae fue mucho mayor a la previamente conocida.

*Palabras clave:* Gliptodontes, Osteodermos, Región Mesopotámica, Formación Fray Bentos, Oligoceno.

## 1. Introduction

The Glyptodontidae (Mammalia, Cingulata) comprise an American endemic clade without extant representatives. During a large period of the Cenozoic, these armored herbivores constituted one of the most conspicuous lineages, reaching enormous sizes during some intervals, especially in the Oligocene and Pleistocene (Scillato-Yané, 1977, 1986; Scillato-Yané and Carlini, 1998; Vizcaíno *et al.*, 2011). The oldest records assignable to Glyptodontidae come from the Late Eocene (Mustersian South American Land Mammal Age or SALMA) in the Patagonian region of Argentina and were assigned to the subfamily Glyptatelinae (late Eocene-late Pleistocene). These remains, represented by isolated osteoderms of the dorsal carapace, were described by Ameghino (1902) as *Glyptatelus fractus* Ameghino (Simpson, 1948; Scillato-Yané, 1977; McKenna *et al.*, 2006). In the Glyptatelinae, the osteoderms of the dorsal carapace are characterized by a central figure displaced posteriorly and surrounded by a row of peripheral figures that are absent on the posterior margin and, in some cases, on the lateral margins as well (Hoffstetter, 1958; Scillato-Yané, 1977).

During the late Oligocene (Deseadan SALMA) a diversification among the Glyptodontidae is observed, and large-sized species such as *Chypeotherium magnum* Scillato-Yané, 1977 were present among the Glyptatelinae (Scillato-Yané, 1977). The presence of the subfamily Propalaeophorinae (Late Oligocene-Middle Miocene) adds to these older records (see Scillato-Yané, 1977; González-Ruiz *et al.*, 2011). From a morphological point of view, the osteoderms of the Propalaeophorinae are characterized by a “rosette” ornamentation pattern, *i.e.*, a central figure surrounded by a row of smaller peripheral figures, including some accessory ones (Ameghino, 1889; Scott, 1903-1904).

Most of the few Paleogene records of both subfamilies come from the Argentine Patagonian region. Outside this area, the record is still scarce, and the majority of the materials have not been figured or described. Scillato-Yané (1986, 1988) mentioned the presence of Glyptatelinae nov. sp. and Glyptodontidae *incertae sedis* for the Late Oligocene (Deseadan SALMA) from Quebrada Fiera, Mendoza province (Argentina). Outside Argentina, Glyptatelinae cf. *Glyptatelus* sp. was mentioned in the locality of Salla-Luribay (Bolivia) in Late Oligocene sediments

(Deseadan SALMA) (Hoffstetter, 1968; Marshall and Sempere, 1991). Finally, Glyptodontidae *incertae sedis* was recorded from Fray Bentos Formation (Late Oligocene, Deseadan SALMA), outcropping in Uruguay (Ubilla, 2004; Bostelmann *et al.*, 2010, 2011). In this context, the finding of Paleogene Glyptodontidae becomes important, especially outside Patagonia, because it represents a larger latitudinal distribution for this group during the Oligocene than previously supposed, supporting the presence of other Oligocene cingulates in Fray Bentos Formation (Perea *et al.*, 2014).

Here we describe new remains of Glyptodontidae assignable to Propalaeophorinae from the locality of Cueva del Tigre, Entre Ríos province (Argentina) (Fig. 1) from the Fray Bentos Formation (Fig. 2). This is the first extra-Patagonian Paleogene record of these glyptodonts with an adequate description.

## 2. Geology

The Fray Bentos Formation was formally defined by Harrington (1956) in Uruguay, where this unit comprises more than 90 m in the Santa Lucía basin, but in outcrops only up to 15-18 m, especially along the Uruguay river, from Colonia up north to the Brazilian border (Ubilla, 2004). These are the “Santalucience” and “Palmirensis” units, respectively, described by Kraglievich (1932). This unit is mainly composed of fine and medium sandstones, silts, sometimes calcareous, and conglomerates; the dominant colors are reddish-gray and reddish-brown. According to most authors, they are continental, mainly fluvial and only in part eolian (Goso and Bossi, 1966; Ubilla, 2004). Climatically, they were deposited under warm and dry conditions (Ferrando and Dasa, 1974). This unit has also been recognized in Argentina, more precisely in Corrientes and Entre Ríos provinces (Herbst, 1980; Herbst and Santa Cruz, 1999), based on the very close similarity of its lithology and stratigraphic position: directly over the Serra Geral basalts and the Plio-Pleistocene sands and conglomerates of the Salto (or Ituzaingó) Formation (Fig. 2). In Argentina, the unit is composed of “very fine sandstones to silts, with clayish to calcareous-clayish cements” (Herbst, 1980: 309). In the provinces of Corrientes and Entre Ríos, Herbst (1980) recognized two sections: a lower one known as “calcareous sediments of *Curuzú Cuatiá*” and an upper one composed of reddish lime-sandstones.

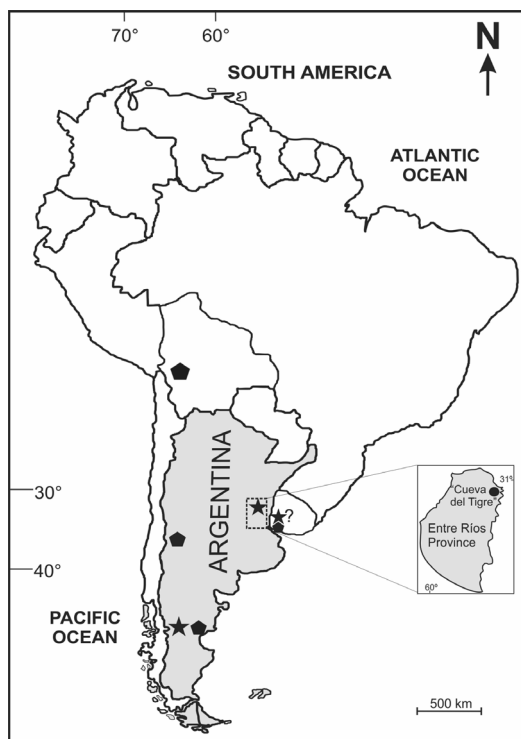


FIG. 1. Map showing fossiliferous localities with Paleogene records of Glyptodontidae. ☆ Propalaeohoplophorinae ◻ Glyptatelinae.

The materials herein described come from the latter, corresponding to this upper section (Fig. 2).

Traditionally, the Fray Bentos Formation has been assigned to a Deseadan SALMA *sensu lato* (Álvarez, 1978; Ubilla *et al.*, 1994; Bond *et al.*, 1998), with a time span of 29-24,5 Ma (Bond *et al.*, 1998 and references therein). More recently, the age of the unit has been restricted to the Late Oligocene (Ubilla, 2004; Perea *et al.*, 2014).

### 3. Materials and methods

The materials studied are housed in the paleontological collection of the Universidad Nacional del Nordeste, Facultad de Ciencias Exactas y Naturales y Agrimensura, Corrientes, Argentina (CTES-PZ). The materials for comparison correspond to specimens of Glyptatelinae, Propalaeohoplophorinae, "Hoplophorinae" Palaeohoplophorini, Hoplophorini, and Neosclerocalyptini; Glyptodontinae and Glyptodontidae *incertae sedis* hosted in the following institutions: American Museum of Natural History, New York, USA (AMNH); División Paleontología

de Vertebrados, Facultad de Ciencias Naturales y Museo-Universidad Nacional de La Plata, La Plata, Argentina (MLP); Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN); Museo Paleontológico "Egidio Feruglio", Trelew, Argentina (MPEF); Museo Municipal de Ciencias Naturales de Mar del Plata, "Lorenzo Scaglia", Buenos Aires, Argentina (MMP); Museo Nacional de Historia Natural, Santiago, Chile (SGO); Yale Peabody Museum, New Haven, USA (YPM). These include *Glyptatelus tatusinus* Ameghino, 1897 (MACNA 12361 ex 52-356, type), *Glyptatelus malaspinensis* Ameghino, 1902 (MACN A 12362 ex 52-357, type), *Glyptatelus fractus* Ameghino, 1902 (MACN A 12565 ex 52-569, type), *Clypeotherium magnum* (MLP 61-IV-11-76, type), *Propalaeohoplophorus australis* Ameghino, 1887 (MLP 16-15), *P. minus* Ameghino, 1891 (AMNH 9197), *Cochlops muricatus* Ameghino, 1889 (MACN A 2121, YPM-VPPU 16000), *Eucinepeltus petesatus* Ameghino, 1891 (MPEF Pv 1383), *Palaeohoplophorus meridionalis* Ameghino, 1904 (MACN A-11137,

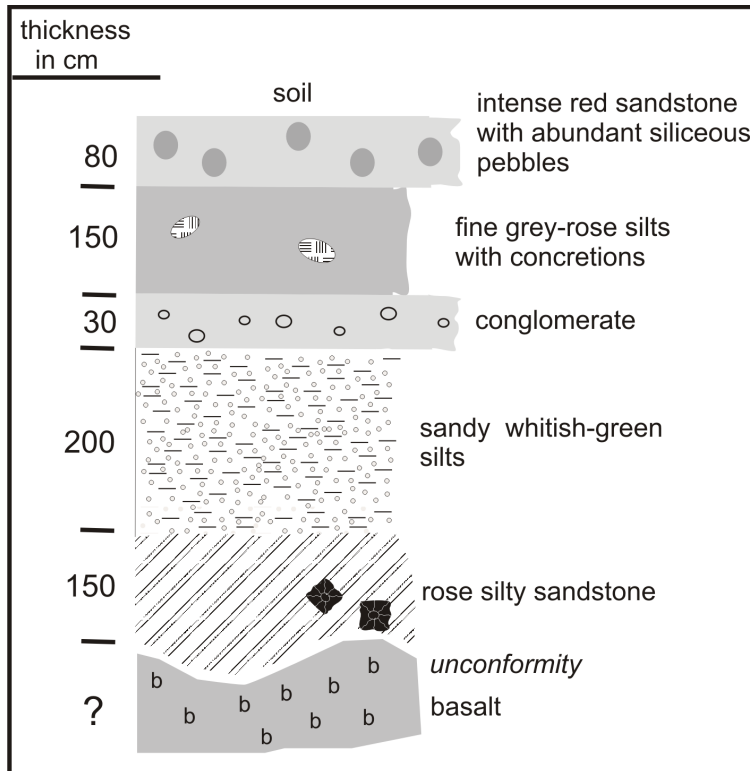


FIG. 2. Stratigraphic profile showing the location of the osteoderms.

syntype), *Parapropalaeophorus septentrionalis* Croft *et al.*, 2007 (SGO PV 4165, type; provisionally housed in Case Western Reserve University School of Medicine, Cleveland, USA), *Neosclerocalyptus ornatus* Owen 1845 (MLP 16-28) and *Glyptodon munizi* Ameghino, 1881 (MMP 3985). It was not possible to find the osteoderms referred by Scillato-Yané (1977) to a Propalaeophorinae gen et sp. indet. (MLP 61-IV-11-208 to 238, MLP 61-IV-11-255 to 266) in the MLP, so comparisons were made with illustrations and descriptions made by Scillato-Yané (1977, plate II, figs. 1-10).

#### 4. Systematic Paleontology

Xenarthra Cope, 1889  
 Cingulata Illiger, 1811  
 Glyptodontidae Gray, 1869  
 Propalaeophorinae Ameghino, 1887

Propalaeophorinae indet.

Fig. 3

**Material:** CTES-PZ 3512: three associated osteoderms of the dorsal carapace (Fig. 3).

**Locality and horizon:** Cueva del Tigre, Chajarí, Entre Ríos province, Argentina (30°46'33"S-57°58'28"W) (Fig. 1); Fray Bentos Formation (Deseadan SALMA; late Oligocene) (Fig. 2).

**Description and comparisons:** The three osteoderms show a finely dotted exposed surface and an evident "rosette" ornamentation pattern (Figs. 3 and 4). This pattern consists of a polygonal central figure delimited by a central groove, from which radial grooves that define peripheral figures (anterior, lateral and posterior) emerge and surround the central one. An evident foramen is present in most of the intersections between the radial grooves and the groove that defines the central figure (Ameghino, 1889). The grooves delimiting the peripheral figures are shallow and parabolic in sagittal section ("V"-shaped; see Carlini *et al.*, 2008). The osteoderms present 11 (A), 10 (B) and 11 (C) peripheral figures surrounding the central figure, while two osteoderms have 2 (A), 1 (B) and 4 (C) latero-anterior accessory

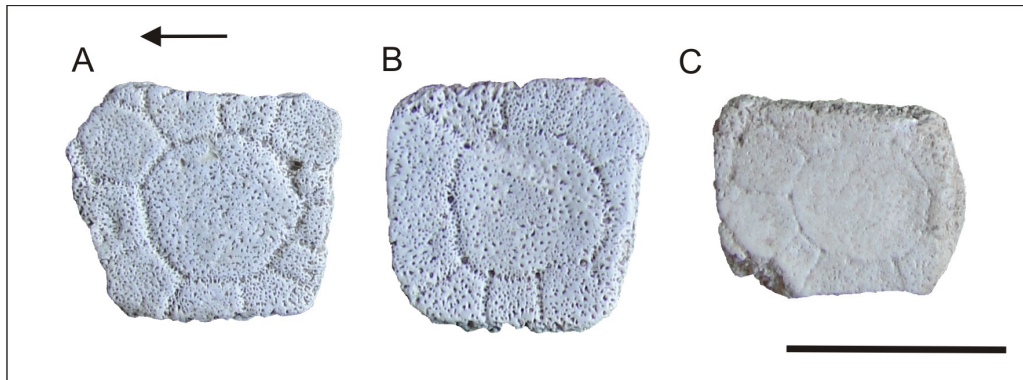


FIG. 3. CTES-PZ 3512. Three associated osteoderms from the lateral region of the dorsal carapace (A,B,C). Scale bar: 30 mm.

peripheral figures (Figs. 3 and 4). The presence of these small accessory figures allows assigning these osteoderms to the lateral region of the dorsal carapace, because it is the region in the carapace of the Propalaeohoplophorinae where they are usually developed. (Scott, 1903-1904; González, 2010). One of the osteoderms (Fig. 3C) probably corresponds to a more lateral region of the carapace, since it has a great development of the anterior peripheral figures, while the posterior ones are much less visible, as observed in the Neogene species of Propalaeohoplophorinae (e.g., *Propalaeohoplophorus minus*).

The contact area and articulation between adjacent osteoderms is relatively flat, although rather rough. The ventral surface of each osteoderm is slightly concave in its central area, where 3-6 larger foramina can be seen. The osteoderms measure: (A) 35.24 mm (antero-posterior diameter) x 26.56 mm (dorso-ventral diameter) x 9.71 mm (transverse diameter); (B) 32.65 mm x 32.42 mm x 9.85 mm; (C) 37.44 mm x 31.42 mm x 9.27 mm. (Fig. 2).

The morphology of the exposed surface of the osteoderms described here is clearly different from that of Paleogene Glyptatelineae (*Glyptatelus fractus*, *Glyptatelus tatusinus* and *Clypeotherium magnum*), in which the central figure reaches the posterior edge, the peripheral figures are limited to the anterior and lateral edges (the lateral ones generally reduced or absent), there are no accessories latero-anterior peripheral figures, and the figures are convex and rounded (except in *Clypeotherium* where they are flat), and the grooves that delimit the figures are deep (Ameghino, 1897; Hoffstetter, 1958; Scillato-Yané, 1977. In addition to this, we observed only two or

three large anterior figures in most of the osteoderms, whereas in Glyptodontidae Propalaeohoplophorinae there are generally four. In this scenario, it is remarkable that most of the Glyptatelineae characters are absent in *Glyptatelus malaspinensis*, suggesting that the type material (osteoderms) corresponds in fact to a Propalaeohoplophorinae, but further studies are necessary. Compared to *Parapropalaeohoplophorus* (Glyptodontidae *incertae sedis*) the osteoderms of Propalaeohoplophorinae indet. From the Fray Bentos Formation are different because they have conspicuous foramina in the intersection of the grooves that delimit the figures and the presence of the typical “rosette” pattern, both characters absent in *Parapropalaeohoplophorus*.

## 5. Discussion

At the level of the osteoderms of the dorsal carapace, the “rosette” ornamentation pattern (i.e., a central figure surrounded by a complete row of peripheral figures) appears for the first time in Propalaeohoplophorinae glyptodonts (Ameghino, 1889; Scott, 1903-1904) during the Late Oligocene (see Scillato-Yané, 1977). This pattern probably originated from a previous one (with a smaller number of lateral peripheral figures and absence of posterior peripheral figures) present in the Glyptatelineae and in a Glyptodontidae *incertae sedis* (*Parapropalaeohoplophorus*) of the Early and Middle Miocene of northern Chile and Perú (Hoffstetter, 1958; Carlini et al., 1997; Croft et al., 2007; Tejada et al., 2011). Although the Glyptatelineae pattern is apparently observed in *Parapropalaeohoplophorus*,

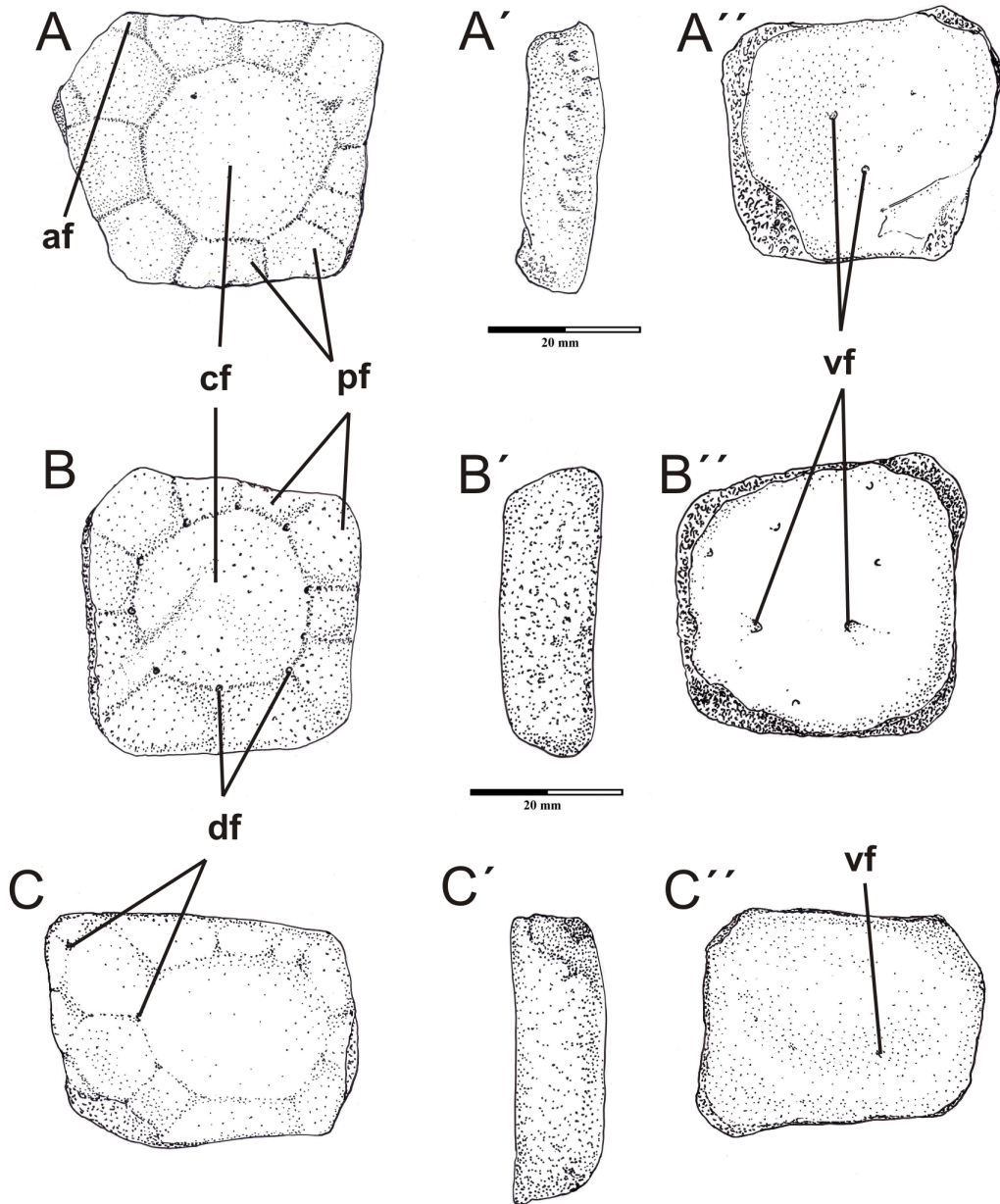


FIG. 4. Anatomical nomenclature used in this contribution. **cf**: central figure; **pf**: peripheral figures; **af**: accessories figures; **df**: dorsal foramina; **vf**: ventral foramina. A-C: dorsal views; A'-C': lateral views; A''-C'': ventral views. Scale bar: 20 mm.

in some osteoderms from the lateral region of the carapace of the Propalaeohoplophorinae, and in fixed osteoderms of Cingulata Dasypodidae, there are differences between all of them, such as the position of the central (=principal) figure in dorsal osteoderms (along the posterior edge, near posterior edge, or roughly central, among others; see Croft *et al.*, 2007).

The “rosette” pattern is present practically unchanged in all genera of Propalaeohoplophorinae (see Scott, 1903-1904; Scillato-Yané, 1977, 1986; González, 2010). In the genus *Cochlops* Ameghino, 1889, at the level of the pelvic region, osteoderms present a clear “cone-like” elevation, in both central and peripheral figures, showing some analogy

with that observed in the peripheral osteoderms of Glyptodontinae (Ameghino, 1889; Zurita et al., 2013). In the same region, *Propalaeohoplophorus* shows some convexity in the central figures of the osteoderms although such elevation is not as marked as in *Cochlops*. However, in any case, the “rosette” pattern is not modified.

The comparison between the Oligocene osteoderms described and figured by Scillato-Yané (1977) and those studied here shows that there are no significant differences in morphology or size. In fact, the osteoderms A and B figured here are almost identical to those figured by Scillato-Yané (1977, plate II) as 1 and 3, whereas the osteoderm C is very similar to that figured and numbered as 7.

This “rosette” pattern is also present in several lineages of subsequent glyptodonts, such as some “Hoplophorinae” Palaehoplophorini (González, 2010; González et al., 2011) and Neosclerocalyptini (Zurita, 2007), and in the subfamily Glyptodontinae (Ameghino, 1889; Zurita et al., 2013). However, these groups show very marked differences compared to the Propalaeohoplophorinae. In the Palaehoplophorini (Middle Miocene-Late Miocene; Scillato-Yané and Carlini, 1998; González, 2010; Scillato-Yané et al., 2013) it is possible to observe several different morphologies. In *Palaehoplophorus meridionalis* Ameghino, some osteoderms have a rough exposed surface with grooves delimiting the central figure and the peripheral ones, which are wider and deeper (González, 2010). Other species have two or three rows of small peripheral figures and a depressed central figure (e.g., *Palaehoplophorus antiquus* Ameghino, 1883) (Scillato-Yané et al., 2013), whereas others may show a series of clearly circular small peripheral figures (e.g., *Aspidocalyptus castroi* Cabrera, 1939).

The Neosclerocalyptini (e.g., *Neosclerocalyptus*) also show a “rosette” ornamentation pattern, which, in some sectors of the carapace, presents a remarkable similarity with the Propalaeohoplophorinae (see Zurita, 2007). However, and in contrast to that observed in this subfamily, the lateral osteoderms show an equivalent development of the peripheral figures in the anterior and posterior edges. In fact, in the Propalaeohoplophorinae, the more antero-lateral region of the carapace presents a very different morphology from that of *Eosclerocalyptus* C. Ameghino, 1919 and *Neosclerocalyptus* Paula Couto, 1957. In Neosclerocalyptini, the osteoderms of this region have a pentagonal or hexagonal outline while in the

Propalaeohoplophorinae the osteoderms have a clear rectangular morphology.

Finally, another group is represented by the subfamily Glyptodontinae (middle-late Miocene-early Holocene) (e.g., *Boreostemma* Carlini et al., 2008 and *Glyptodon* Owen, 1839). However, in this clade, there are trends that allow differentiating them from the Propalaeohoplophorinae. This group shows a progressive increase in the roughness of the exposed surface, an increase in the denticulation of the area of contact between adjacent osteoderms, an increase in the thickness of the osteoderms, and grooves that delimit the figures in “U” shape, together with the absence of additional small peripheral figures and fewer small peripheral figures (Carlini et al., 2008; Zurita et al., 2013).

## 6. Conclusions

The comparative study shows that the morphology of the exposed surface of the osteoderms studied in this contribution is almost identical to the other Paleogene record assigned to Propalaeohoplophorinae coming from the Patagonian region of Argentina. From a paleobiogeographical perspective, as mentioned above, the Paleogene records of Propalaeohoplophorinae are scarce. Until this contribution, these were limited with certainty to one record from the Argentine Patagonia (Scillato-Yané, 1977). Although Bostelmann et al. (2010) mentioned the probable presence of Propalaeohoplophorinae indet. In Nueva Palmira (Uruguay), he reinterpreted the specimens as belonging to Glyptodontidae *incertae sedis* (Bostelmann et al., 2011). However, only the Patagonian Propalaeohoplophorinae records have been figured (Scillato-Yané, 1977, plate II).

In summary, this is the northernmost record of a Paleogene Propalaeohoplophorinae, thus significantly expanding its latitudinal distribution, which now ranges from 43°51' S to 30°46' S. This indicates that during the Paleogene, the Propalaeohoplophorinae had a larger latitudinal distribution than previously supposed.

## Acknowledgments

The authors wish to thank D. Croft for the pictures of *Parapropalaeohoplophorus*. Dr. E. Bostelmann read the manuscript and made lots of useful comments. This contribution was partially funded by project grants PI Q 001/13 (SGCyT-UNNE) and PIP 0150 (CONICET).

## References

- Álvarez, B.B. 1978. Noticias sobre una fauna de la Formación Fray Bentos (Oligoceno inferior), provincia de Corrientes, Argentina. *FACENA* 2: 253-258.
- Ameghino, F. 1881. La antigüedad del hombre en el Plata 2: 1-557. Paris-Buenos Aires.
- Ameghino, F. 1883. Sobre una colección de mamíferos fósiles del piso mesopotámico de la formación patagónica recogidos por el Profesor Pedro Scalabrini. *Boletín de la Academia Nacional de Ciencias en Córdoba* 5: 1-34. Buenos Aires.
- Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1: 1-26. Buenos Aires.
- Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias en Córdoba* 6: 1-1027.
- Ameghino, F. 1891. Mamíferos y aves fósiles argentinas. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1 (4): 240-259.
- Ameghino, F. 1897. Mammifères crétacés de l'Argentine. *Boletín del Instituto Geográfico Argentino* 18 (4-6): 406-521.
- Ameghino, F. 1902. Notices préliminaires sur les Mammifères nouveaux des terrains crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias en Córdoba* 17: 5-70.
- Ameghino, F. 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina* 58: 56-291.
- Ameghino, C. 1919. Sobre mamíferos fósiles del Piso Araucanense de Catamarca y Tucumán. *In Reunión Nacional de la Sociedad Argentina de Ciencias Naturales*, No. 1, Actas: 151-152. Láminas III y VII.
- Bond, M.; López, G.; Reguero, M.A.; Scillato-Yané, G.J.; Vucetich, M.G. 1998. Los Mamíferos de la Formación Fray Bentos (Edad Mamífero Deseadense, Oligoceno Superior?) de las Provincias de Corrientes y Entre Ríos, Argentina. *Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, Publicación Especial* 5: 41-50.
- Bostelmann, E.; Rinderknecht, A.; Ciancio, M.R.; Toriño, P.; Perea, D. 2010. Oligocene Glyptodontidae (Mammalia, Cingulata) from the Fray Bentos Formation of Uruguay. *In Congreso Uruguayo de Zoología*, No. 1, y Jornadas de Zoología del Uruguay, No. 10, "Prof. Federico Achaval": 74. Montevideo.
- Bostelmann, E.; Ciancio, M.R.; Rinderknecht, A.; Perea, D. 2011. The Cingulata (Mammalia, Xenarthra) of the Fray Bentos Formation (Late Oligocene) of Uruguay. *Ameghiniana* 48 (4): R145-R146.
- Cabrera, A. 1939. Sobre vertebrados fósiles del Plioceno de Adolfo Alsina. *Revista del Museo de La Plata (Nueva Serie)* 2 (6): 3-35. La Plata.
- Carlini, A.A.; Vizcaíno, S.F.; Scillato-Yané, G.J. 1997. Armored Xenarthrans: a unique taxonomic and ecologic assemblage. *In Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia* (Richard, R.H.M.; Kay, R.; Cifelli, R.; Flynn, J.J.; editors). Smithsonian Institution Press: 213-226. Washington and London.
- Carlini, A.A.; Zurita, A.E.; Scillato-Yané, G.J.; Sánchez, R.; Aguilera, O. 2008. New Glyptodont from the Codore Formation (Pliocene), Falcón State, Venezuela, its relationship with the *Asterostemma* problem, and the paleobiogeography of the Glyptodontinae. *Paläontologische Zeitschrift* 82 (2): 139-152.
- Cope, E. 1889. The Edentata of North America. *The American Naturalist* 23: 657-664.
- Croft, D.A.; Flynn, J.J.; Wyss, A.R. 2007. A new basal Glyptodontoid and other Xenarthra of the early Miocene Chucal Fauna, Northern Chile. *Journal of Vertebrate Paleontology* 27 (4): 781-797.
- Ferrando, L.; Dasa, M. 1974. Mineralogía de la fracción arcillosa de la Formación Fray Bentos. *In Congreso Brasileiro de Geología*, No. 28, Actas 2: 3-13. Porto Alegre.
- González, L.R. 2010. Los Cingulata (Mammalia, Xenarthra) del Mioceno temprano y medio de Patagonia (edades Santacrucense y "Friasense"). Revisión sistemática y consideraciones bioestratigráficas. Ph.D. Thesis (Unpublished), Universidad Nacional de La Plata: 471 p.
- González, L.R.; Zurita, A.E.; Scillato-Yané, G.J.; Zamorano, M.; Tejedor, M.F. 2011. Un nuevo Glyptodontidae (Mammalia, Xenarthra, Cingulata) del Mioceno de Patagonia (Argentina) y comentarios acerca de la sistemática de los gliptodontes del SALMA "Friasense". *Revista Mexicana de Ciencias Geológicas* 28 (3): 566-579.
- Goso, H.; Bossi, J. 1966. Cenozoico. *In Geología del Uruguay* (Goso, H; editor). Departamento de Publicaciones, Universidad de la República: 469 p. Montevideo.
- Gray, J.E. 1869. Catalogue of carnivorous, pachydermatous and edentate Mammalia in the British Museum. *British Museum (Natural History)*: 398 p. London.



- Harrington, H. 1956. Uruguay. *In Handbook of South American geology. An explanation of the geologic map of South America* (Jenks, W.; editor). *Memories of the Geological Society of America* 65: 115-128.
- Herbst, R. 1980. Consideraciones estratigráficas y litológicas sobre la Formación Fray Bentos (Oligoceno inferior-medio) de Argentina y Uruguay. *Revista de la Asociación Geológica Argentina* 34 (3): 308-317.
- Herbst, R.; Santa Cruz, J.N. 1999. Mapa litoestratigráfico de la provincia de Corrientes. *D'Orbignyana* 2: 1-69.
- Hoffstetter, R. 1958. Xenarthra. *In Traité de Paléontologie* (Piveteau, P.; editor). *Masson et Cie* 2 (6): 535-636. Paris.
- Hoffstetter, R. 1968. Un gisement de mammifères déséadiens (Oligocène inférieur) en Bolivie. *Compte Rendu de l'Académie des Sciences* 267:1095-1097.
- Illiger, C. 1811. *Prodromus Systematicus Mammalium et Avium Additis Terminis Zoographicis Utriusque Cassis. Sumptibus C. Salfeld*: 301 p. Berlín.
- Kraglievich, L. 1932. Nuevos apuntes para la geología y paleontología de la República Oriental del Uruguay. *Anales del Museo de Historia Natural de Montevideo* 2: 257-321.
- Marshall, L.G.; Sempere, T. 1991. The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review. *In Fósiles y Facies de Bolivia* (Suárez-Soruco, R.; editor). *Revista Técnica de YPF* 12 (1): 631-652.
- McKenna, M.C.; Wyss, A.R.; Flynn, J.J. 2006. Paleogene Pseudogliptodont Xenarthrans from Central Chile and Argentine Patagonia. *American Museum Novitates* 3536: 1-18.
- Owen, R. 1839. Description of a tooth and part of the skeleton of the *Glyptodon*, a large quadruped of the edentate order, to which belongs the tessellated bony armour figured by Mr. CLIFT in his memoir on the remains of the *Megatherium*, brought to England by Sir Woodbine PARISH, F.G.S. *Proceedings of the Geological Society of London* 3: 108-113
- Owen, R. 1845. Descriptive and illustrated catalogue of the fossil organic remains of Mammalia and Aves contained in the Museum of the Royal College of Surgeons of London: 391 p.
- Paula-Couto, C. 1957. Sobre um gliptodonte do Brasil. *Boletim Divisão de Geologia e Mineralogia* 165:1-37. Rio de Janeiro.
- Perea, D.; Toriño, P.; Ciancio, M. 2014. La presencia del xenartro *Palaelopeltis inornatus* Ameghino, 1894, en la Formación Fray Bentos (Oligoceno tardío), Uruguay. *Ameghiniana* 51 (3): 254-258.
- Scillato-Yané, G.J. 1977. Sur quelques Glyptodontidae nouveaux (Mammalia, Edentata) du Déséadien (Oligocène inférieur) de Patagonie (Argentine). *Bulletin du Muséum National D'Histoire Naturelle* 64: 249-262.
- Scillato-Yané, G.J. 1986. Los Xenarthra fósiles de Argentina (Mammalia, Edentata). *In Congreso Argentino de Paleontología y Bioestratigrafía*, No. 4, Actas 2: 151-155. Mendoza.
- Scillato-Yané, G.J. 1988. Algunos Cingulata (Mammalia, Edentata) del Oligoceno de Quebrada Fiera (Mendoza, Argentina). *In Jornadas Argentinas de Paleontología de Vertebrados*, No. 5, Resúmenes: p. 26. La Plata, Buenos Aires.
- Scillato-Yané, G.J.; Carlini, A.A. 1998. Un gigantesco Gliptodonte en los alrededores de la Ciudad de La Plata. *Museo* 2 (11): 45-48.
- Scillato-Yané, G.J.; Góis, F.; Zurita, A.E.; Carlini, A.E.; González-Ruiz, L.R.; Krmpotic, C.M.; Oliva, C.; Zamorano, M. 2013. Los Cingulata (Mammalia, Xenarthra) del "Conglomerado Osífero" (Mioceno tardío) de la Formación Itzaingó de Entre Ríos, Argentina. *In El Neógeno de la Mesopotamia argentina* (Brandoni, D.; Noriega, J.I.; editors). *Asociación Paleontológica Argentina, Publicación Especial* 14: 118-134.
- Scott, W.B. 1903-1904. Mammalia of the Santa Cruz Beds. I Edentata. *Reports of the Princeton University Expedition to Patagonia (1896-1899)* 5:1-226. Princeton.
- Simpson, G.G. 1948. The beginning of the Age of Mammals in South America. *Bulletin of the American Museum of Natural History* 91: 1-232.
- Tejada, J.; Antoine, P.-O.; Baby, P.; Pujos, F.; Salas-Gismondi, R. 2011. Basal or not basal cingulates in the middle Miocene of Peruvian Amazonia. *Ameghiniana* 48, Suplemento Resúmenes 4: R128-R129.
- Ubilla, M.; Perea, D.; Bond, M. 1994. The Deseadan Land-Mammal-Age in Uruguay and the report of *Scarrittia robusta* n.sp. (Leontiniidae, Notoungulata) in the Fray Bentos Formation (Oligocene-?Lower Miocene). *Geobios* 27: 95-102.
- Ubilla, M. 2004. La Formación Fray Bentos (Oligoceno Tardío) y los Mamíferos más antiguos de Uruguay. *In Cuencas Sedimentarias de Uruguay* (Veroslavsky, M.; Ubilla, M.; Martínez, M.; editores), *DIRAC, Facultad de Ciencias*: 83-104. Montevideo.
- Vizcaíno, S.F.; Cassini, G.H.; Fernicola, J.C.; Bargo, M.S. 2011. Evaluating habitats and feeding habits through ecomorphological features in glyptodonts (Mammalia, Xenarthra). *Ameghiniana* 48 (3): 305-319.

Zurita, A.E. 2007. Sistemática y evolución de los Hoplophorini (Xenarthra, Glyptodontidae, Hoplophorinae. Mioceno tardío-Holoceno temprano). Importancia bioestratigráfica, paleobiogeográfica y paleoambiental. Ph.D. Thesis (Unpublished), Universidad Nacional de La Plata: 363 p.

Zurita, A.E.; González-Ruiz, L.; Gómez-Cruz, A.; Arenas-Mosquera, J.E. 2013. The most complete known Neogene Glyptodontidae (Mammalia, Xenarthra, Cingulata) from northern South America: taxonomic, paleobiogeographic and phylogenetic implications. *Journal of Vertebrate Paleontology* 33: 696-708.

---

Manuscript received: November 19, 2014; revised/accepted: September 22, 2015; available online: September 23, 2015.