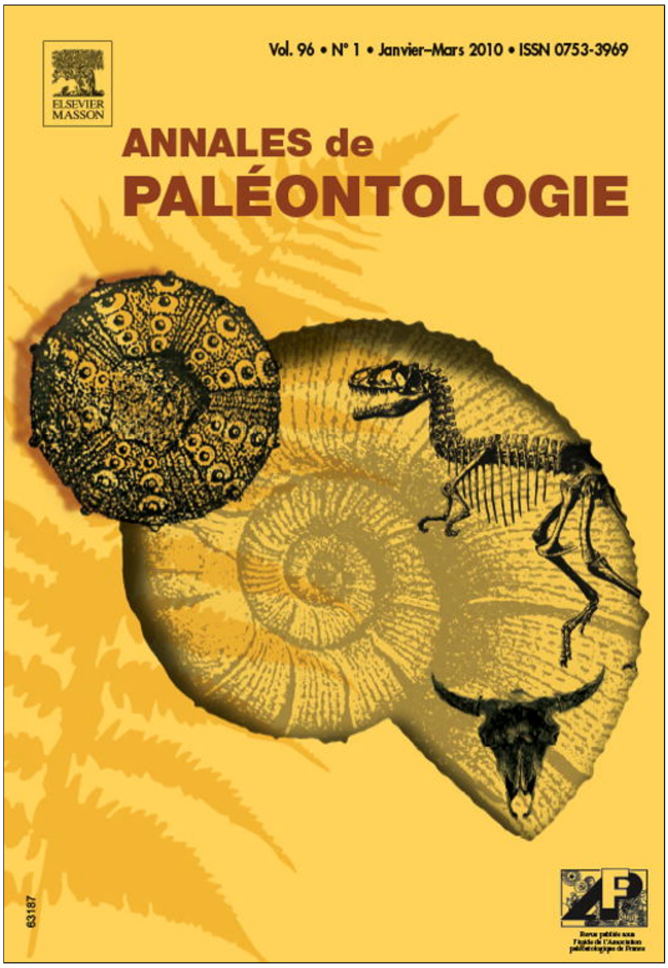
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Original article

# Accessory protection structures in *Glyptodon* Owen (Xenarthra, Cingulata, Glyptodontidae)

## *Structures accessoires de protection en Glyptodon Owen (Xenarthra, Cingulata, Glyptodontidae)*

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## Abstract

The Glyptodontidae (Mammalia, Xenarthra) are one of the most common paleofaunistic elements in the South American megafauna. In this context, of the six genera most frequently recorded in the South American Pleistocene (*Glyptodon*, *Neosclerocalyptus*, *Hoplophorus*, *Neuryurus*, *Panochthus* and *Doedicurus*), at least four (*Hoplophorus*, *Neuryurus*, *Panochthus* and *Doedicurus*) present structures in their caudal armor that could have had defensive/offensive functions, in addition to a solid dorsal carapace and cephalic shield. In this article, we provide the first record and description of a series of highly modified osteoderms, located at the anterolateral region and over the cephalic notch of the dorsal carapace. These "spine"-like osteoderms were found in two of the largest Pleistocene glyptodonts: *Glyptodon munizi* (early-middle Pleistocene) and, *G. reticulatus* (late Pleistocene-early Holocene). We propose that they are structures for protection of the neck and abdomen, the most vulnerable body regions of these large armored animals, since they are not

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covered by the cephalic shield, carapace or caudal armor. Noteworthy, structures like those described herein are not known in glyptodonts recorded before the Great American Biotic Interchange (GABI), so it could be a reaction to the arrival of *Smilodon* and *Arctotherium* (Carnivora, Mammalia) the largest terrestrial carnivores that ever lived in South America.

*Keywords:* Argentina; South America; *Glyptodon*; Pleistocene; Palaeoecology

## Résumé

Les Glyptodontidae (Mammalia, Xenarthra) sont l'un des éléments paléofaunistiques les plus communs de la mégafaune en Amérique du Sud. Dans ce contexte, des six genres le plus souvent enregistrés dans le Pléistocène (*Glyptodon*, *Neosclerocalyptus*, *Hoplophorus*, *Neuryurus*, *Panochthus* et *Doedicurus*), au moins quatre (*Hoplophorus*, *Neuryurus*, *Panochthus* et *Doedicurus*) présentent dans leur armure caudale des structures qui auraient pu avoir des fonctions défensives/offensives, en plus d'une carapace dorsale solide et un bouclier céphalique. Dans cet article, nous proposons le premier enregistrement et la description d'une série d'ostéodermes très modifiés, situés dans la région antérolatérale et au-dessus de l'encoche céphalique de la carapace dorsale. Ces structures se rencontrent chez deux espèces du genre *Glyptodon*, l'une des plus grandes formes de Glyptodontidae du Pléistocène, *G. munizi* (Pléistocène inférieur et moyen), et *G. reticulatus* (Pléistocène supérieur - Holocène inférieur). D'un point de vue morphologique, ces ostéodermes montrent une forme caractéristique en « épine ». Les ostéodermes décrits ici sont interprétés comme des structures de protection et de défense du cou et du ventre, régions les plus vulnérables de ces grands animaux à armure, car elles ne sont pas recouvertes par le bouclier céphalique, la carapace ou l'armure caudale. Enfin, il est intéressant de noter que ces types de structure ne sont pas enregistrés dans la paléofaune de Glyptodontidae qui vivaient avant le *Great American Biotic Interchange* (GABI), un processus migratoire qui marque l'arrivée de certains des plus grands prédateurs (Carnivora), ayant jamais vécu en Amérique du Sud (par exemple *Smilodon*, *Arctotherium*).

*Mots clés :* Amérique du Sud ; Pléistocène ; *Glyptodon* ; Paléoécologie

## 1. Introduction

Glyptodonts (Glyptodontidae, Xenarthra) were frequent elements among the South American Cenozoic megaherbivores. Their wide fossil record ranges from the late Eocene to the earliest Holocene (Paula Couto, 1979).

During the Pleistocene (*ca*. 2.6-0.011 Ma, see ICS, 2008) some glyptodonts reached body masses of, at least, 250 kg (e.g., *Neosclerocalyptus*), while others were well above 1000 kg (e.g., *Panochthus intermedius*; *Glyptodon elongatus*, *Doedicurus clavicaudatus*; see Fariña, 1995; Fariña and Vizcaíno, 1999).

Of the six genera that occur most frequently in the fossil record of South America (*Glyptodon*, *Neosclerocalyptus*, *Hoplophorus*, *Neuryurus*, *Panochthus* and *Doedicurus*; see Paula Couto, 1979), at least four (*Hoplophorus*, *Neuryurus*, *Panochthus* and *Doedicurus*) present structures in their caudal armor that could have had defensive/offensive functions (Fariña and Vizcaíno, 1999; Fariña, 2000). These structures located on the lateral sides of the caudal tube, representing remarkable cases of convergence, and consist of a series of depressions (two to five) with rough surface, which probably represents the area of insertion of conical spines (Hoffstetter, 1958). In some cases, (e.g., *Doedicurus*), the distal tip of the caudal tube is flattened forming a mace-like structure (see Lydekker, 1894: pl. XXVII).

In other forms, such as *Glyptodon* (Glyptodontinae), the caudal armor comprises a series of rings with a very short tube at the distal tip. Each ring is formed by a double or triple row of osteoderms, of which the ones in the last row are conical (Ameghino, 1889; Soibelzon et al., 2006). This kind of conical osteoderms are also present at the margins of the dorsal carapace, and it quite probably represents a synapomorphy of the Glyptodontinae (Carlini and Scillato-Yané, 1999; Carlini et al., 2008).

In some *Glyptodon* specimens (e.g., MBM-PV 000778), a double or triple row of modified osteoderms may be observed at the anterolateral margin of the dorsal carapace; however, and unlike the specimens described here, these structures are part of the dorsal carapace (i.e., they are joined by synostoses) and their apices are conical-rounded.

In support of the postulated defensive/offensive function, it is worth noting that fractured dorsal armors have been found in some specimens (e.g., *Doedicurus clavicaudatus* MLP 16-94; *Glyptodon reticulatus* MACN 200), and these have been interpreted as the result of intraspecific combats (Alexander et al., 1999).

The occurrence of osteoderms on the ventral region of the Glyptodontidae was originally mentioned by Burmeister (1864). Later (Burmeister, 1870–1874), provided illustrations of these structures, particularly for the genera *Panochthus* and *Glyptodon*, suggesting that these glyptodonts could also have possessed osteoderms at the level *"...de la orilla anterior sobre las espaldas, de los pies o de las mejillas"* (Burmeister, 1870–1874: 110). The presence of a continuous ventral plastron (as conceived by Burmeister) in the Glyptodontidae was seriously challenged by Ameghino (1889) and later by Castellanos (1940, 1941); however, Ameghino (1889) did recognize the presence of a series of "ossicles" within the dermis, but with no defined articulation among them.

Recently, Tauber and Di Ronco (2000) and Soibelzon et al. (2006) have positively confirmed the presence of osteoderms on the ventral and facial regions of *Glyptodon reticulatus* and *G. munizi* respectively, while Rinderknecht (2002) has reported similar elements in the hind limbs of *Glyptodon*. Unlike the ones described here, elements described by these authors have no defined shape, are small to medium-sized, and were probably completely embedded within the dermis (see Fig. 1C, D in Soibelzon et al., 2006).

In this context, the goals of our study are:

- to describe, for first time, those highly modified osteoderms, located on the anterolateral region and cephalic notch of the dorsal carapace in *Glyptodon munizi* and *G. reticulatus*;
- to advance paleobiological and paleoecological hypotheses regarding the appearance and function of these structures.

The chrono and biostratigraphic scheme adopted in this work follows Cione and Tonni (2005) and Soibelzon et al. (2008). The fossils presented here are from the Ensenadan (*Mesotherium cristatum* Biozone) and Bonaerian (*Megatherium americanum* Biozone) + Lujanian (*Equus (A.) neogaeus* Biozone.

**Abbreviations: MLP**, Museo de La Plata, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires; **MMP**, Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia", Buenos Aires. **MBM-PV**, Museo Provincial de Ciencias Naturales "Bartolomé Mitre", Córdoba; **MCA**, Museo de Ciencias Naturales "Carlos Ameghino" (Mercedes, Buenos Aires).

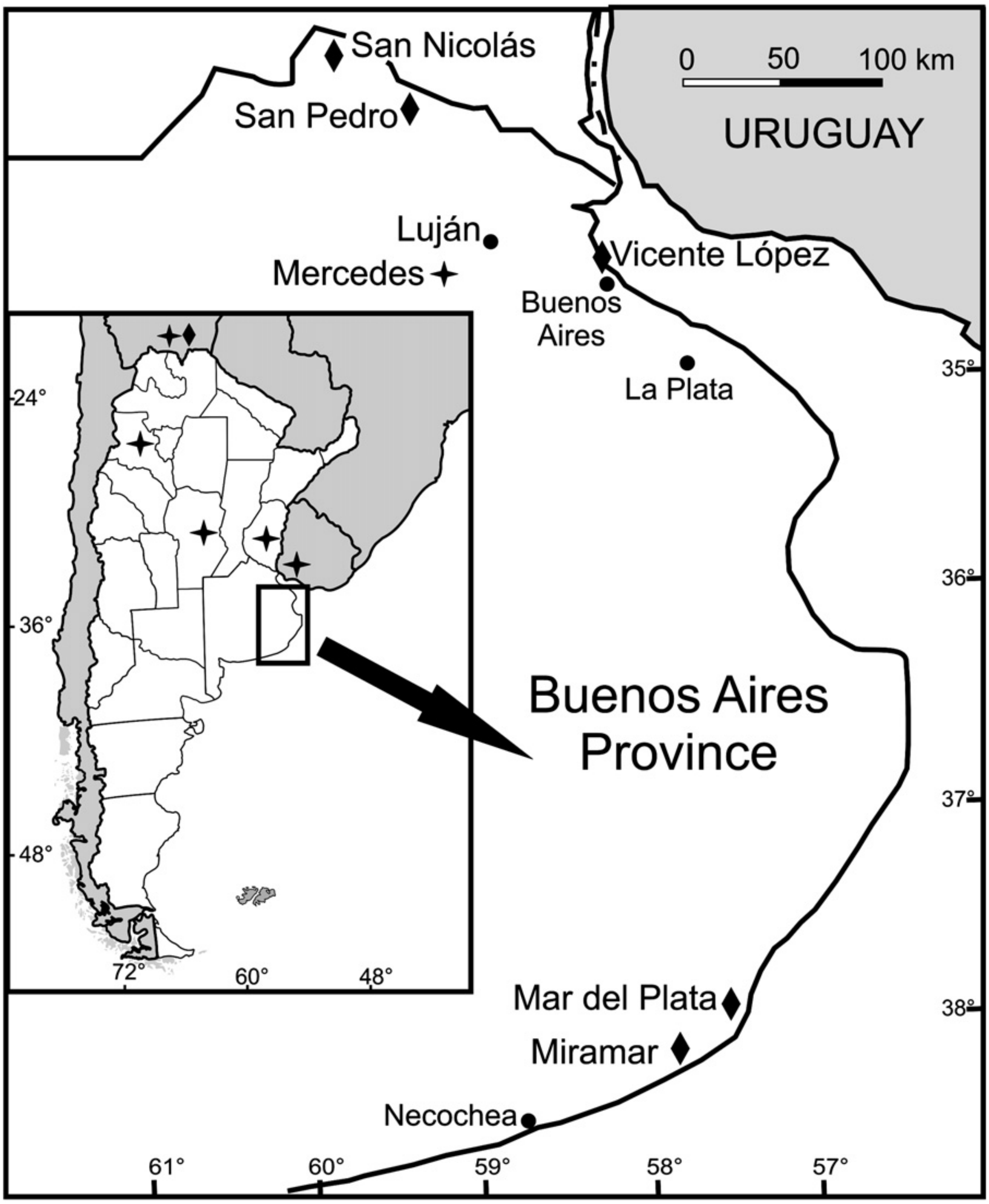

Fig. 1. Location map showing the localities mentioned in the text. Black stars show the provenance of *Glyptodon reticulatus*; black diamonds show the provenance of *Glyptodon munizi*; black circles represent cities of Buenos Aires Province as a location references.

*Carte montrant l'emplacement des localités mentionnées dans le texte. Les étoiles noires montrent la provenance de Glyptodon reticulatus ; les diamants noirs indiquent la provenance de Glyptodon munizi ; les cercles noirs représentent les villes de la province de Buenos Aires comme des lieux de références.*

## 2. Systematic paleontology

Order CINGULATA Illiger, 1811.
Family GLYPTODONTIDAE Gray, 1869.
Genus ***Glyptodon*** Owen, 1838.
Glyptodon munizi Ameghino, 1881.

**Holotype:** MLP s/n (missing, Mones, 1986). Large portion of dorsal carapace from Arroyo del Medio, San Nicolás, Buenos Aires. Ensenadan (Ameghino, 1881).

**Stratigraphic and geographical distribution:** Ensenadan (lower to middle Pleistocene, see Soibelzon et al., 2008) of Argentina: Buenos Aires province (San Nicolás, San Pedro, Vicente López, Mar del Plata and Miramar; Soibelzon et al., 2006); Pleistocene of Bolivia: Tarija (Zurita et al., 2009) (Fig. 1).

**Referred material MLP 07-V-3-2:** (Fig. 2), large portion of a dorsal carapace and cephalic shield from the marine cliff at "Baliza Chica" (in front of Miramar Golf Club; 38° 15′ 22.9″ S and 57° 47′ 52.2″ W), Miramar, General Alvarado County, Buenos Aires (Fig. 1). Ensenadan.

**Stratigraphic remarks:** At this locality, the base of the cliff is conformed by edaphized reddish loessic levels corresponding to Chapadmalal Fm. (Chapadmalalan, *Neocavia depressidens* Biozone, middle Pliocene) and the top by a relict sandy loess level corresponding to Lobería Fm. (Lujanian-Platan, *Equus [A.] neogaeus-Lagostomus maximus* biozone, late Pleistocene-Holocene). The middle levels comprise facies of alluvial events represented by sandy silts with different degree of aquatic reworking. Among these, the level from where **MLP 07-V-3-2** was exhumed comprises greenish-gray sandy clays probably originated in a restricted lentic water body. Middle and upper levels were referred to the "Ensenadan" by Ameghino (1908); later Kraglievich (1952) assigned them to his Vorohué Formation. This criterion has been maintained until present days. However, and in contrast with this traditional interpretation, the record of *G. munizi*, an exclusive Ensenadan taxon (see Cione and Tonni, 2005; Soibelzon et al., 2008) in the middle levels of this sector of the cliffs favoring the Ameghino's (1908) original idea about the age of these levels (see Soibelzon et al., 2009a,b). Additionally, a new record of *Mesotherium cristatum* (another exclusive Ensenadan taxon) comes from the same levels (Bogan, pers. com. to MMC). Outstandingly these records provide one of the few undisputable Ensenadan assignation to a cliff' level between Mar del Plata and Miramar.

## 3. Description

**Dorsal carapace** (Fig. 2): according to Soibelzon et al. (2006), *G. munizi* was a very large Glyptodontinae, larger than the Lujanian Glyptodontinae taxa. Its dorsal carapace is elongated, oblong-oval in shape, with thick and relatively small osteoderms that show central figures always larger than the peripheral ones. A central concavity occupies most of the osteoderm surface; it is especially evident in the carapace's periphery. The caudal armor is formed by nine rings, as in the other species of the genus.

Osteoderms are pentagonal with rough and punctuated dorsal surface that presents a well-defined subcircular central figure and a row of angular peripheral figures, following the characteristic *Glyptodon* morphology (Ameghino, 1889). The sulci that delimitate the central figure are deep and wide with parallel sides; this is a synapomorphy of the Glyptodontinae (Carlini et al., 2008). Distally, the central figure of each osteoderm becomes more noticeable with respect to the peripheral figures, which tend to be poorly developed or absent, condition common to all the Glyptodontidae that presents this "rosette" ornamentation pattern.

**Osteoderms:** On the ventral side of the dorsal carapace could be observed three rows of highly modified osteoderms running anteroposteriorly and conforming an almost flat plane obliquely oriented respect to the body sagittal plane (see Fig. 2[A, B]). Thus, the row of osteoderms in contact with the osteoderms of the carapace's peripherial row are conical with blunt apices; caudally, the osteoderms are taller, with a well-defined sharp tip that produce a "spine"-like appearance. The base of these osteoderms is quadrangular to subcircular (approximately 4.9 mm

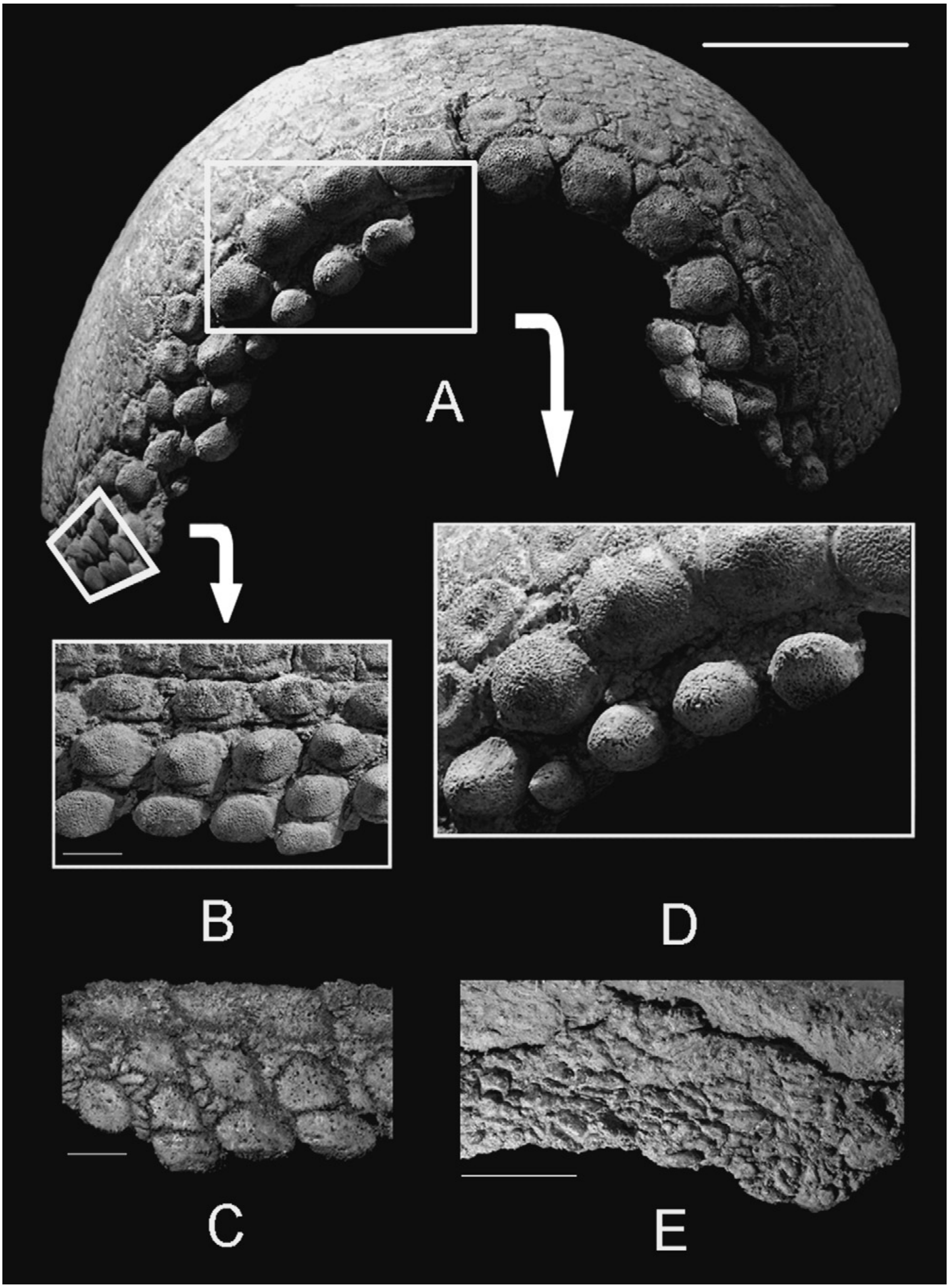

Fig. 2. *Glyptodon munizi* **MLP 07-V-3-2**. **A**. Dorsal carapace in anterior view. Scale bar = 25 cm. **B, C**. Lateral osteoderms. Scale bar = 5 cm. **C.** Inner view. **D, E**. Osteoderms of the cephalic notch. Scale bar = 5 cm. **D.** Inner view.
*Glyptodon munizi MLP 07-V-3-2.* **A.** *Carapace dorsale en vue antérieure. Échelle = 25 cm.* **B, C.** *Ostéodermes latérales. Échelle = 5 cm.* **C.** *En vue interne.* **D, E.** *Ostéodermes de l'encoche céphalique. Échelle = 5 cm.* **D.** *En vue interne.*

by 4.1 mm) and is loosely sutured to adjacent osteoderms. The rows run toward the cephalic notch; in MLP 07-V-3-2 at least one of them is preserved. The space delimited by the vertices of the osteoderms is occupied by small amorphous osteoderms that are only visible on the inner surface of the carapace (Fig. 2[C]). These osteoderms are approximately 2.7 mm by 1 mm and somewhat similar to the facial osteoderms described for *G. munizi* by Soibelzon et al. (2006).

At the cephalic notch, there is one row of osteoderms with pointed apices, loosely articulated to the osteoderms of the carapace. Similar like the lateral osteoderms, the space between each osteoderm is occupied by smaller and oval osteoderms (see Fig. 2[D, E]).

Glyptodon reticulatus Owen, 1845.

**Holotype:** MACN 200, complete dorsal carapace. Lujanian (late Pleistocene-early Holocene). Argentina: Catamarca, Buenos Aires, Entre Ríos and Córdoba provinces (Ameghino, 1889; Duarte, 1997; Tauber and Di Ronco, 2000; Noriega et al., 2004); Uruguay (Ameghino, 1889). Pleistocene of Tarija (Bolivia) (see Takai et al., 1982; Zurita et al., 2009) (Fig. 1).

**Referred material MCA 2015 and 2017:** (Fig. 3), two dorsal carapaces with conical osteoderms at the level of the cephalic notch, loosely joined to the rest of the carapaces. From a quarry located 4 km from Mercedes city (34° 38′ 34.03″ S and 59° 18′ 4.38″ W), Buenos Aires, Argentina. Luján Fm., Lujanian (late Pleistocene-early Holocene).

**Description:** According to Duarte (1997) in *G. reticulatus*, the cephalic opening is larger than the caudal one and both are semicircular. The osteoderms are quadrangular to hexagonal. The central figure is pentagonal to octagonal and flat or slightly convex. It is surrounded by seven quadrangular, pentagonal or hexagonal peripheral figures separated by deep and wide sulci. Four or five perforations (ranging from small to large size) appear at the intersection of the radial sulci (developed between peripheral figures) and the central sulcus (that runs around the central figure). It is especially evident at the central-medial sector of the carapace. The dorsal carapace shows the clearly convex dorsal outline characteristic of this species (see Ameghino, 1889).

Specimens MCA 2015 and 2017 present on the dorsal carapace, especially at the cephalic notch, peculiar structures like to those described on MLP 07-V-3-2 (Fig. 3). At this notch, there is a double accessory row of extremely modified osteoderms with pointed apices, as in MLP 07-V-3-2, loosely articulated to carapace osteoderms. Each row is formed by approximately 14 osteoderms, whereas the cranial row is composed by smaller osteoderms, and each of them are located between two osteoderms of the caudal row (see Fig. 3).

## 4. Paleoecological context

Before Pleistocene (i.e., late Miocene of Catamarca province and Pliocene of the Pampean region), there are no records of Glyptodontinae specimens with osteoderms like those described here. In addition, Glyptodonts recorded before GABI (e.g., *Paraglyptodon uquiensis* from late Pliocene of Jujuy province, Argentina) are smaller than those recorded after this event (e.g., *Glyptodon munizi*; see Soibelzon et al., 2006). Noteworthy, the first records of osteoderms (apart from those conforming the dorsal carapaces, cephalic shield and caudal armors; see Tauber and Di Ronco, 2000; Rinderknecht, 2002; Soibelzon et al., 2006), as well as those described here, are coincident to the arrival of the large predators from North America. Notably, these highly modified osteoderms have not been observed in North American glyptodonts (see Gillette and Ray, 1981).

Gillette and Ray (1981) have reported for *Glyptotherium texanum* the finding of a specimen with evidences of having been attacked by a large-sized predator; in South America, Prevosti and Palmqvist (2001) have postulated that the canid *Theriodictis platensis* could have preyed upon some Pleistocene Glyptodontidae (e.g., *Neosclerocalyptus*).

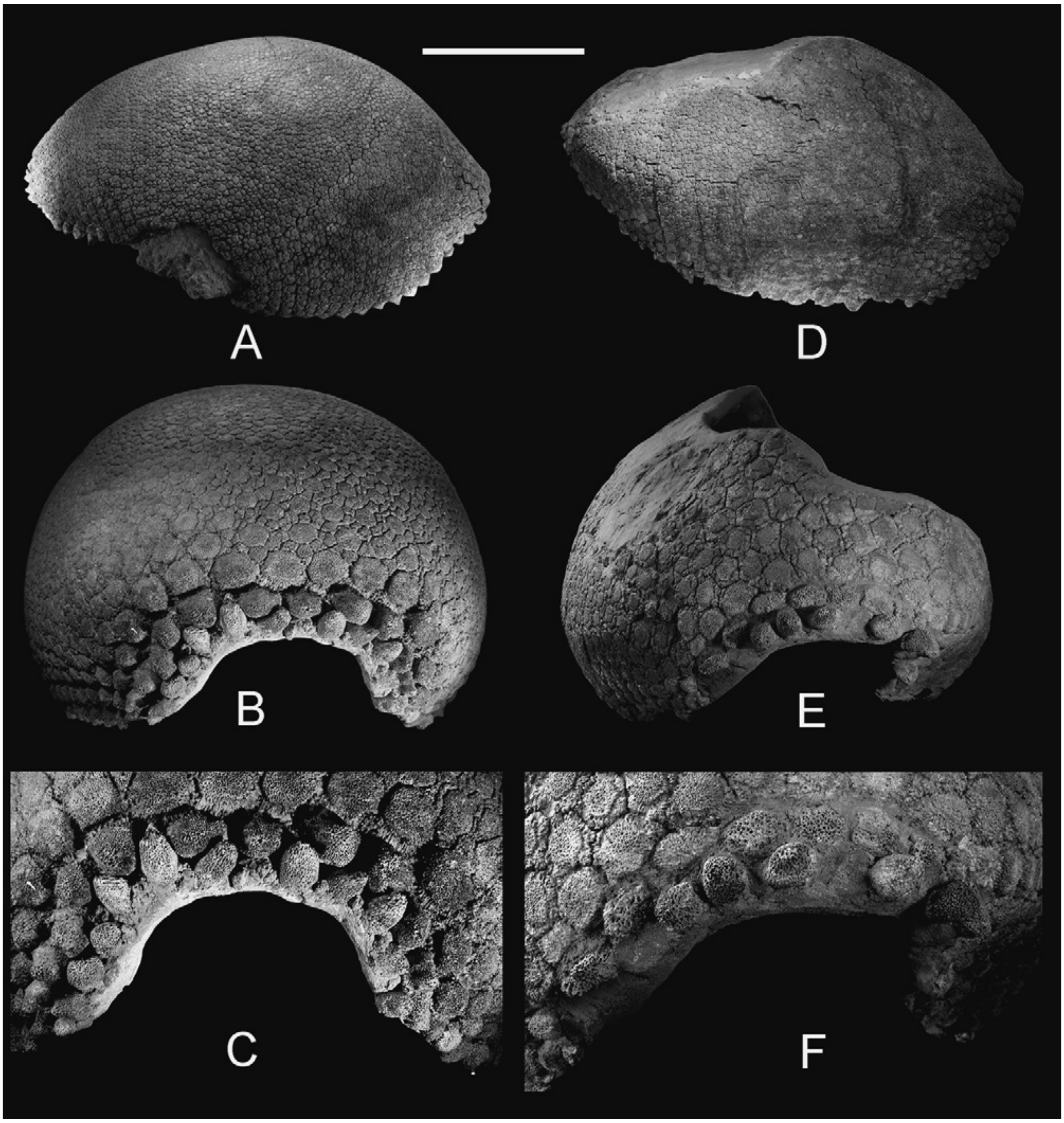

Fig. 3. *Glyptodon reticulatus*. **A–C. MCA 2015**. **D–F. MCA 2017**. **A, D**. Dorsal carapace in lateral view. **B, E**. Dorsal carapace in anterior view. **C, F**. Osteoderms of the cephalic notch. Scale bar = 50 cm.
*Glyptodon reticulatus.* **A–C** *: MCA 2015 ; D–F: MCA 2017.* **A, D** *: carapace dorsale en vue latérale ;* **B, E** *: carapace dorsale en vue antérieure ;* **C, F** *: ostéodermes de l'encoche céphalique. Échelle = 50 cm.*

In this context, Soibelzon et al. (2009b) suggested that the arrival in South American of large carnivores (e.g., *Arctotherium angustidens*, (Gervais and Ameghino) Ursidae and *Smilodon populator*, (Lund) Felidae) during Ensenadan, could have triggered some adaptative responses among native mammalian fauna, since large carnivores were absent of South America during most of the Cenozoic. Only the medium-sized carnivore *Thylacosmilus* Riggs (marsupial saber tooth cat), together with small carnivorous marsupials (*Thylophorops* and *Hyperdidelphis*), omnivorous procyonids (*Cyonasua* Ameghino and *Chapadmalania* Ameghino) and phororhacoid birds were present before GABI. After the Plio-Pleistocene boundary (subsequent to GABI), the top predator guild in the South America Ensenadan ecosystems included seven species: *Theriodictis platensis* Mercerat, *Protocyon scagliorum* Kraglievich, *P. troglodytes* (Lund) and *Canis* (?)

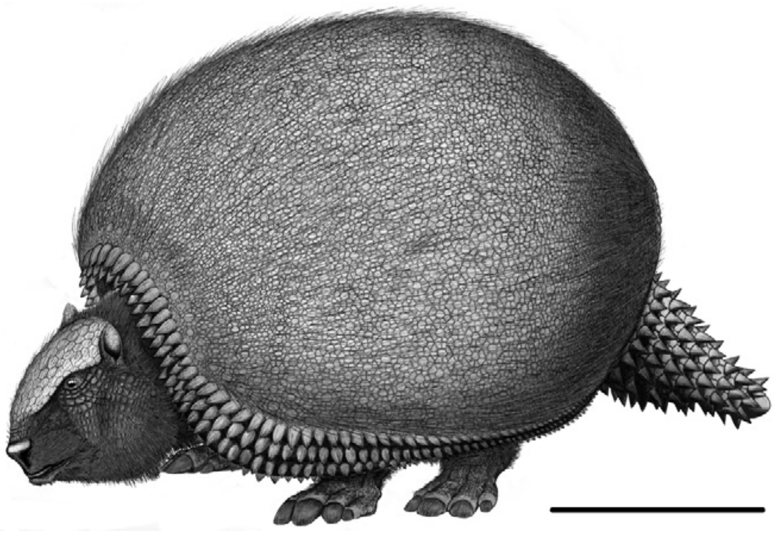

Fig. 4. Reconstruction of *Glyptodon*. Scale bar = 100 cm.
*Reconstruction de Glyptodon. Échelle = 100 cm.*

*gezi* Kraglievich (Canidae: Prevosti, 2007), *Smilodon populator*, *Panthera onca* (Linnaeus) and *Puma Jardine* (Felidae: Soibelzon and Prevosti, 2007), and *Arctotherium angustidens* (Ursidae, Soibelzon, 2004; Soibelzon et al., 2005) (see Webb, 2006).

The fast diversification of carnivore guild possibly led to the evolution of different strategies (e.g., behavioral, physiological, anatomical) in the potential prey (Soibelzon et al., 2009b).

## 5. Discussion and conclusions

The presence of isolated osteoderms and included in the dermis, lacking defined articulation, were confirmed in *Glyptodon* (see Tauber and Di Ronco, 2000; Rinderknecht, 2002; Soibelzon et al., 2006). These findings partially supports the Burmeister (1874) and Ameghino (1889) hypothesis. Since these osteoderms are not firmly attached to the rest of the shield, it is not surprising the high amount of specimens without them.

The structures described here could represent selected features favored by the presence of the newly arrived carnivores in order to protect vulnerable areas of these armored xenarthrans: the neck and abdomen. We suggest that these modified osteoderms could have had a horny sheath that almost certainly made their apices even more pointed and increased their efficiency (Fig. 4). Thus, the description of Pleistocene Glyptodontinae is updated with the addition of new structures.

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