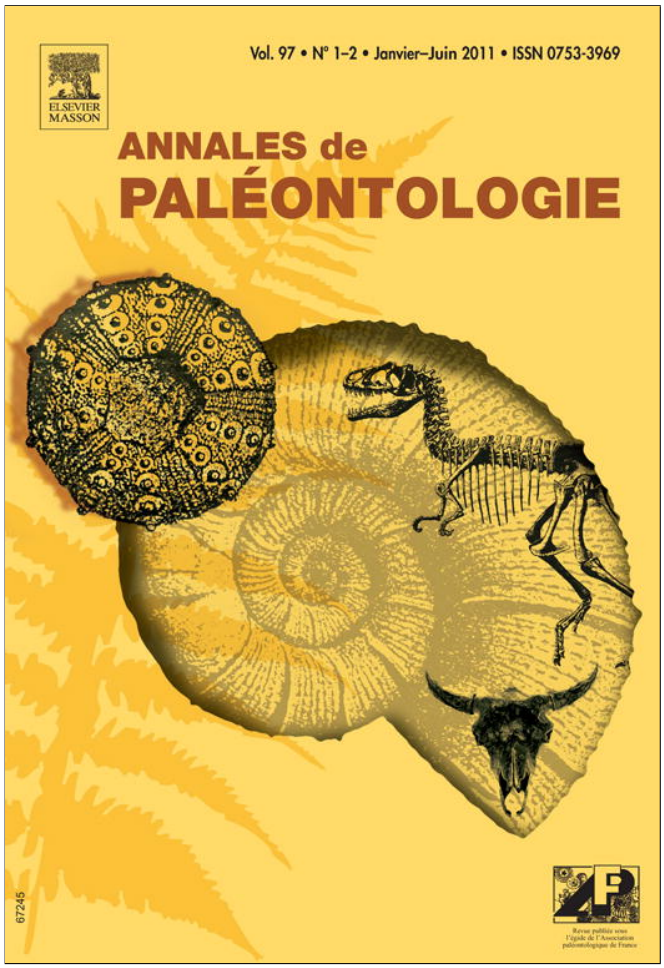

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Original article

On the taxonomic status of some Glyptodontidae (Mammalia, Xenarthra, Cingulata) from the Pleistocene of South America

Sur le statut taxonomique de quelques Glyptodontidae (Mammalia, Xenarthra, Cingulata) du Pléistocène d'Amérique du Sud

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Abstract

The anatomical and taxonomic knowledge of some groups of Glyptodontidae (Mammalia, Cingulata) is still very poor. In addition, a strict typological/morphological taxonomic criterion was used in recognizing many taxa, especially during the second half of the 19th century and the first of the 20th century. This particular situation resulted in a clear overestimation diversity, mainly with respect to the South American glyptodonts. In this scenario, this paper analyzes the taxonomic status of some Glyptodontinae through a precise comparative study with well characterized taxa. The main results show that the genera *Pseudothora-*

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cophorus Castellanos (*P. depressus*) and *Chlamydotherium* Lund, one species of the genus "*Boreostracon*" Simpson (*B. corondanus*), and one species of the genus *Glyptodon* Owen (*G. falkneri),* actually represents juvenile specimens referable to *Glyptodon* Owen; the genus *Neothoracophorus* Ameghino (*N. elevatus*) could be related either to *Glyptodon* Owen or *Glyptotherium* Osborn. Another species, *Heteroglyptodon genuarioi*, presents an almost identical morphology compared with the recognized species of *Glyptodon* (e.g. *G. munizi* and *G. reticulatus*). In this sense, the diagnostic characters described for *Glyptodon perforatus* Ameghino, a taxon with biostratigraphic relevance since it is characteristic of the Lujanian Age/Stage (late Pleistocene-early Holocene), are also present in other species of *Glyptodon*, especially *G. reticulatus* and *G. clavipes*, very frequent taxa in southern South America.

Keywords: Glyptodontidae; Juvenile specimens; Osteoderms; Taxonomy; Ontogeny; South America

Résumé

La connaissance anatomique et taxonomique sur certains groupes de Glyptodontidae (Mammalia, Cingulata) est encore très limitée. En effet, un critère strictement typologique/morphologique a été employé pour reconnaître beaucoup de taxons, spécialement pendant la seconde moitié du XIX^e^ siècle et la première moitié du XX^e^. Cette situation particulière a donné comme résultat une très nette surestimation de la diversité, surtout en ce qui concerne les glyptodontes sud-américains. Dans ce scénario, cet article analyse le status taxonomique de quelques Glyptodontinae au travers d'une étude comparative précise avec des taxons bien caractérisés. Les résultats principaux montrent que les genres *Pseudothoracophorus* Castellanos (*P. depressus*) et *Chlamydotherium* Lund, une espèce du genre « *Boreostracon* » Simpson (*B. corondanus*), ainsi qu'une espèce du genre *Glyptodon* Owen (*G. falkneri*) représentent en fait des spécimens juvéniles qui se réfèrent à *Glyptodon* Owen ; le genre *Neothoracophorus* Ameghino (*N. elevatus*) pourrait correspondre à *Glyptodon* Owen ou *Glyptotherium* Osborn. Une autre espèce, *Heteroglyptodon genuarioi*, présente une morphologie presque identique comparée aux espèces reconnues de *Glyptodon* (par exemple *G. munizi* et *G. reticulatus*). De même, les caractères diagnostiques décrits pour *Glyptodon perforatus* Ameghino, espèce à intérêt biostratigraphique parce qu'elle est caractéristique de l'étage Lujanien, (Pléistocène tardif-début Holocène), sont aussi présents chez d'autres espèces de *Glyptodon*, particulièrement *G. reticulatus* et *G. clavipes*, espèces très fréquentes au sud de l'Amérique du Sud.

Mots clés : Glyptodontidae ; Spécimens juvéniles ; Ostéodermes ; Taxonomie ; Ontogénie ; Amérique du Sud

1. Introduction

Among the Cenozoic paleofauna of South America, Cingulata Glyptodontidae (late Eocene-earliest Holocene; Fernícola, 2008; Paula Couto, 1979) have been one of the most conspicuous taxa, with a diversification reaching more than 65 genera and 220 species (McKenna and Bell, 1997). Although glyptodonts reached evident diversification, especially in South America, it is clear that their current taxonomic status is overestimated. This situation is due in part to the fact that most of the taxa were recognized and described in a strict typological/morphological context during the 19th century and the first half of the 20th century (see Tinaut and Ruano, 2000).

In glyptodonts taxonomy, one of the most useful characters is represented by the particular ornamentation of the exposed surface of the osteoderms (see, among others, Ameghino, 1889; Duarte, 1997; Hoffstetter, 1958; Paula Couto, 1979). However, the ontogenetic variation of the morphology of the osteoderms, the variability within populations, and the possible taphonomic

processes that could have affected this structure have not been correctly evaluated yet and, in some cases, underestimated (Zurita et al., 2009a). This situation certainly overestimates the taxonomy of late Cenozoic glyptodonts and originates a complex nomenclature problem.

In this context, some of the most frequent glyptodonts during the Pleistocene (ca. 2.588–0.0117 Ma) were Glyptodontidae Glyptodontinae, with a noticeable latitudinal distribution, from 22° S to 4° N (Zurita et al., 2009a). Another group, the Neothoracophorini, include a series of species traditionally linked either to Glyptodontines (Ameghino, 1889; Castellanos, 1951; Nodot, 1857) or to "Hoplophorinae" (Hoffstetter, 1958; Pascual et al., 1966; Paula Couto, 1979). Currently, the Neothoracophorini are interpreted as a group with an uncertain phylogenetic relationship with other Glyptodontidae (Fernícola, 2008; McKenna and Bell, 1997).

From a taxonomic point of view, a large number of genera (ca. 11) and species (ca. 30) have been recognized in both Glyptodontinae and Neothoracophorini, most of them in a strict typological context (Ameghino, 1889; Castellanos, 1947a, b, 1951, 1958; Nodot, 1857; Roselli, 1976).

In the present work, the taxonomic status of some species of glyptodonts (some with biostratigraphic importance) is discussed, with emphasis on the genera *Glyptodon* Owen, "*Boreostracon*" Simpson, *Pseudothoracophorus* Castellanos, *Neothoracophorus* Ameghino, *Chlamydotherium* Bronn and *Heteroglyptodon* Roselli.

2. Material and Methods

The chrono and biostratigraphic scheme adopted in this work follows Cione and Tonni (2005) and Soibelzon et al. (2008). The systematics partially follows Hoffstetter (1958), Paula Couto (1979), McKenna and Bell (1997) and Fernícola (2008).

AMNH: American Museum of Natural History, New York, USA; **Ctes-PZ:** Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; **EPM**: Museu Emígdio Pereira Martino, Santa Vitória do Palmar, RS, Brazil; **GCF:** Grupo Conservacionista de Fósiles, Museo Paleontológico "Fray Manuel de Torres", San Pedro, Buenos Aires, Argentina; **MACN:** Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MCN:** Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MLP:** División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; **MCA:** Museo de Ciencias Naturales "Carlos Ameghino", Mercedes, Buenos Aires, Argentina; **MFCA:** Museo Universitario "Florentino y Carlos Ameghino", Universidad Nacional de Rosario (ex Instituto de Fisiografía y Geología "Alfredo Castellanos"), Rosario, Santa Fe, Argentina; **MNPA-V:** Museo Nacional Paleontológico-Arqueológico, Vertebrados, Tarija, Bolivia; **MMNP:** Museo Municipal de Nueva Palmira "Francisco Lucas Roselli", Nueva Palmira, Colonia, Uruguay; **MHD-P**: Museo Histórico Departamental de Artigas. Paleontología. Uruguay; **MCN-PV**: Museu de Ciencias Naturais da Fundaçao Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MNPA:** Museo Nacional de Paleontología y Antropología, Tarija, Bolivia; **PVE-F:** Colección Paleontología de Villa Escolar, Formosa, Argentina; **MPAB:** Museo Paleontológico "Alejandro Berro". Mercedes, Soriano, Uruguay; **MNRJ**: Museu Nacional, Rio de Janeiro, Brazil; **MNHNP:** Muséum National dïHistoire Naturelle, Paris, France; **MCNC**: Museo provincial de Ciencias Naturales de Córdoba, Argentina; **LIL-PZ:** Paleontología Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto "Miguel Lillo", Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; **PMHU:** Palaeontologisches Museum, Humboldt Universität, Berlin, Germany. **MCPU-PV:** Museu de Ciências Naturais da Pontifícia Universidade Católica do Rio Grande do Sul, Brazil; **MMC:** Museo Municipal de Colonia "Dr. Bautista

Rebuffo", Colonia, Uruguay; **EPM:** Museu Emígdio Pereira Martino, Santa Vitória do Palmar, Rio Grande do Sul, Brazil.

3. Paleobiogeographic remarks on South American Glyptodontidae Glyptodontinae

From a traditional perspective, the diversity of South American glyptodontines in the Pleistocene was restricted to the genus *Glyptodon* Owen, in which it is possible to recognize at least four well-characterized species (*G. munizi, G. reticulatus, G. elongatus* and *G. clavipes*) (Ameghino, 1889; Soibelzon et al., 2006; Zurita et al., 2009a). However, the recognition of the North American genus *Glyptotherium* (*G.* cf. *cylindricum*) in the late Pleistocene of South America has been well established (Carlini et al., 2008; Oliveira et al., 2009, 2010). From a paleobiogeographic point of view, the distribution of *Glyptodon* seems to be restricted to the southern part of South America, especially in the current territories of Argentina, Bolivia, Peru, Uruguay, Paraguay and southern Brazil (ca. N 13° – 40° S; Zurita et al., 2009a). The records of *Glyptotherium* are restricted to the localities of Conceição das Creoulas and Fazenda Nova (Pernambuco), Lajedo da Escada (Rio Grande do Norte), and Lagoa Santa (Minas Gerais) (Brazil) (Oliveira et al., 2009, 2010). In Venezuela, the records correspond to the northern area (Muaco, Taima-Taima, Quebrada Ocando, Cucuruchú) (Carlini et al., 2008) (Fig. 1).

4. Anatomical aspects

The morphological analysis of many juvenile specimens of Glyptodontidae Glyptodontinae (Appendix B) reveals that the main characters observed in the osteoderms include: **1)** earlier juvenile stage: **a**) central and peripheral figures absent, **b**) exposed surface clearly punctuate, **c**) smooth lateral surfaces (Fig. 2A); **2)** later juvenile stage: **a)** a central and peripheral convex figures, **b)** occasionally, the peripheral figures may be replaced by radial groves and, in those cases, the central figure is higher than the peripheral area, **c)** the sulci are usually well developed, **d)** there are three to six large foramina, **e)** the osteoderms are poorly sutured; **f)** the ventral surface is always concave, with some (one to four) large foramina located in its central area (Fig. 2B, C).

5. Systematic paleontology

Magnorder Xenarthra Cope, 1889
Order Cingulata Illiger, 1811
Suborder Glyptodontia Gray, 1869 (*nom. transl.* Ameghino, 1889)
Family Glyptodontidae Gray, 1869
Subfamily Glyptodontinae Gray, 1869 (*nom. transl.* Trouessart, 1898)
Tribe Neothoracophorini Castellanos, 1951
Referred taxa:
Neothoracophorus Ameghino, 1889
Thoracophorus Gervais & Ameghino, 1880 (*non* Hope, 1840)

Type species: *Glyptodon elevatus* Nodot, 1857
Neothoracophorus elevatus (Nodot, 1857) Ameghino, 1889
Fig. 3A
Glyptodon elevatus Nodot, 1857

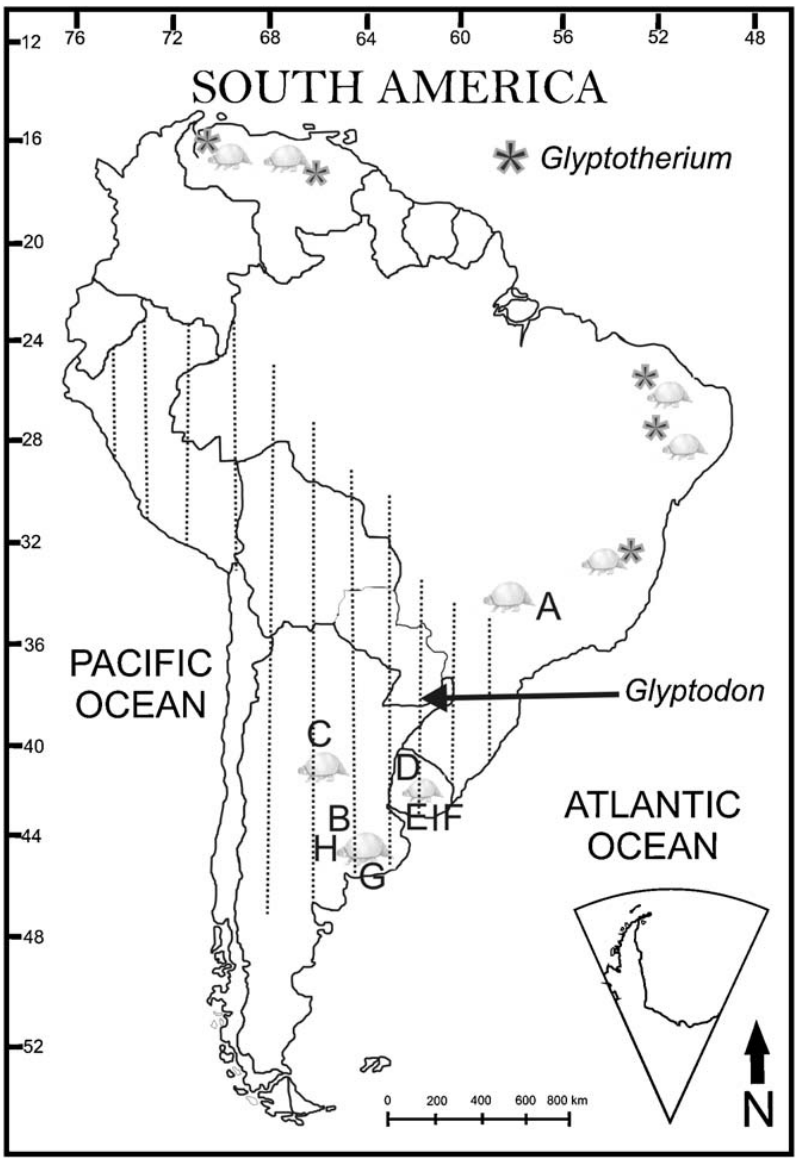


Fig. 1. Geographic distribution of *Glyptodon* Owen (III) and *Glyptotherium* Osborn (✱) in South America. **A)** *Neothoracophorus elevatus* (Nodot) **(MNHNP BRD-20)**; **B)** *Pseudothoracophorus depressus* (Ameghino) **(MLP-)**; **C)** *"Boreostracon" corondanus* Castellanos **(MFCA 760)**; **D)** *Chlamydotherium sellowi* (Lund) **(PMHU?-)**; **E)** *Chlamydotherium subelevatum* (Nodot) **(MNHNP PAM-216)**; **F)** *Chlamydotherium oliveirai* (Castellanos) **(MNRJ 549M)**; **G)** *Glyptodon perforatus* Ameghino **(MACN-)**; **H)** *Glyptodon falkneri* Ameghino **(MACN 1225)**; **I)** *Heteroglyptodon genuarioi* Roselli (**MMNP 563**).

Carte montrant la distribution géographique de Glyptodon Owen (III) et Glyptotherium Osborn (✱) en Amérique du Sud. **A)** *Neothoracophorus elevatus (Nodot)* **(MNHNP BRD-20)***;* **B)** *Pseudothoracophorus depressus (Ameghino)* **(MLP-)***;* **C)** « *Boreostracon* » *corondanus Castellanos* **(MFCA 760)***;* **D)** *Chlamydotherium sellowi (Lund)* **(PMHU?-)***;* **E)** *Chlamydotherium subelevatum (Nodot) (***MNHNP PAM-216)***;** **F)** *Chlamydotherium oliveirai (Castellanos)* **(MNRJ 549M);** **G)** *Glyptodon perforatus Ameghino* **(MACN-)***;* **H)** *Glyptodon falkneri Ameghino* **(MACN 1225)***;* **I)** *Heteroglyptodon genuarioi Roselli (***MMNP 563)**.

Thoracophorus elevatus (Nodot, 1857) Gervais and Ameghino, 1880

Holotype: **MNHNP BRD-20**, a large fragment of dorsal carapace composed of approximately 26 transverse rows of osteoderms (Fig. 3A).

Stratigraphic and geographical origin: Rio das Velhas, Minas Gerais, Brazil. Pleistocene (Fig. 1A).

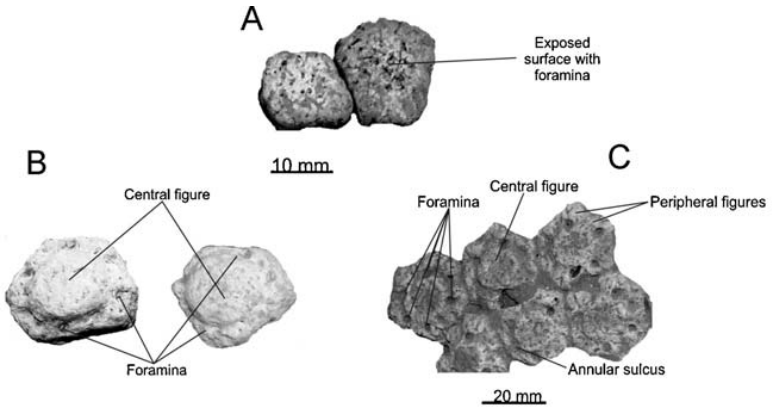


Fig. 2. Morphology of the exposed surface of the osteoderms in earlier **(A)** and later **(B-C)** juveniles stages of Pleistocene Glyptodontinae.
Morphologie de la surface externe des ostéodermes à des stades juvéniles précoces **(A)** *et tardifs* **(B-C)** *d'exemplaires juvéniles de Gyptodontidae pléistocènes.*

Taxonomic comments: *N. elevatus* was originally recognized and included by Nodot (1857) in the genus *Glyptodon* (*G. elevatus*). Later, this taxon was transferred by Gervais and Ameghino (1880) to a new genus, *Thoracophorus* Gervais and Ameghino (*T. elevatus*). One year later, Ameghino (1881) included two new species in this genus: *T. depressus* Ameghino and *T. minutus* Ameghino. Since this generic name was preoccupied (*Thoracophorus* Hope, 1840), Ameghino (1889) erected the genus *Neothoracophorus*, in which he finally included three species: *N. elevatus* (Nodot), *N. depressus* (Ameghino), and *N. minutus* (Ameghino). Some years later, Ameghino (1895) synonymized *N. depressus* with *N. minutus*. The last taxonomic revision of this genus was carried out by Castellanos (1951), who accepted as valid only one species: *N. elevatus,* transferring *N. depressus* to another new genus (*Pseudothoracophorus*, see below). In this sense, the possibility that the holotype of this taxon and most of the associated material could belong to a juvenile specimen of *Glyptodon* was suggested by Zurita et al. (2009a), Oliveira et al. (2009), Krapovickas and Luna (2010) and Luna and Krapovickas (2011). However, since the presence of the genus *Glyptotherium* in that area (Minas Gerais, Brazil) has been recently well established by Oliveira et al. (2010), it seems probable that the holotype of *N. elevatus* could also be related to this North American genus.

Morphology and comparisons: As mentioned, the holotype of *N. elevatus* consists of a large fragment of dorsal carapace poorly preserved (Fig. 3A). Most of the osteoderms are pentagonal or hexagonal in outline, and 15-18 mm thick. This material was fully described by Nodot (1857: 95–97), Ameghino (1889: 790–791) and Castellanos (1951: 66–67). Although the exposed surface of the osteoderms presents a high degree of erosion, it is clearly punctuate, having a central convexity that occupies more than 50% of the surface. The central elevation becomes larger in the lateral osteoderms. In some osteoderms, some foramina are present around this central elevation, as mentioned by Nodot (1857: 96) and Castellanos (1951: 66). The articular surface among osteoderms is completely smooth, a character that was remarked by Ameghino (1889) and Castellanos (1951) in the characterization of the genus. A precise comparison between the holotype (MNHNP BRD-20) and most of the material related to this species reveals that this set of characters is almost identical to that observed in many juvenile specimens of *Glyptodon* and *Glyptotherium* (e.g. PVE-F 85, MCA 2013, AMHN 23547) (Fig. 3A'). In these juvenile specimens, the exposed surfaces of the osteoderms may be almost completely smooth or slightly punctuate (Fig. 2A), while in somewhat older glyptodontines there is a more defined

central and peripheral figure (Fig. 2B, C) (e.g. PVE-F 85). In some older Glyptodontinae specimens (e.g. *Glyptodon* cf. *G. reticulatus,* MCA 2017; *Glyptodon* sp., GCF 10; PVE-F 2, 19; *Glyptotherium floridanum,* AMNH 23547), the central and peripheral figures are better developed. In addition, the ventral surface of the osteoderms in this juvenile glyptodont is slightly concave, another character mentioned by Ameghino (1889) and Castellanos (1951). It is remarkable that Zurita et al. (2009a, b) proposed that all the material from Tarija previously assigned to *Neothoracophorus* corresponds to juvenile specimens of *Glyptodon*. Certainly, these specimens offer characters present in juvenile stages of *Glyptodon*.

Tribe Glyptodontini Gray, 1869 (*nom. transl.* Castellanos, 1951)
Glyptodon Owen, 1839
Referred taxa:
Pseudothoracophorus Castellanos, 1951

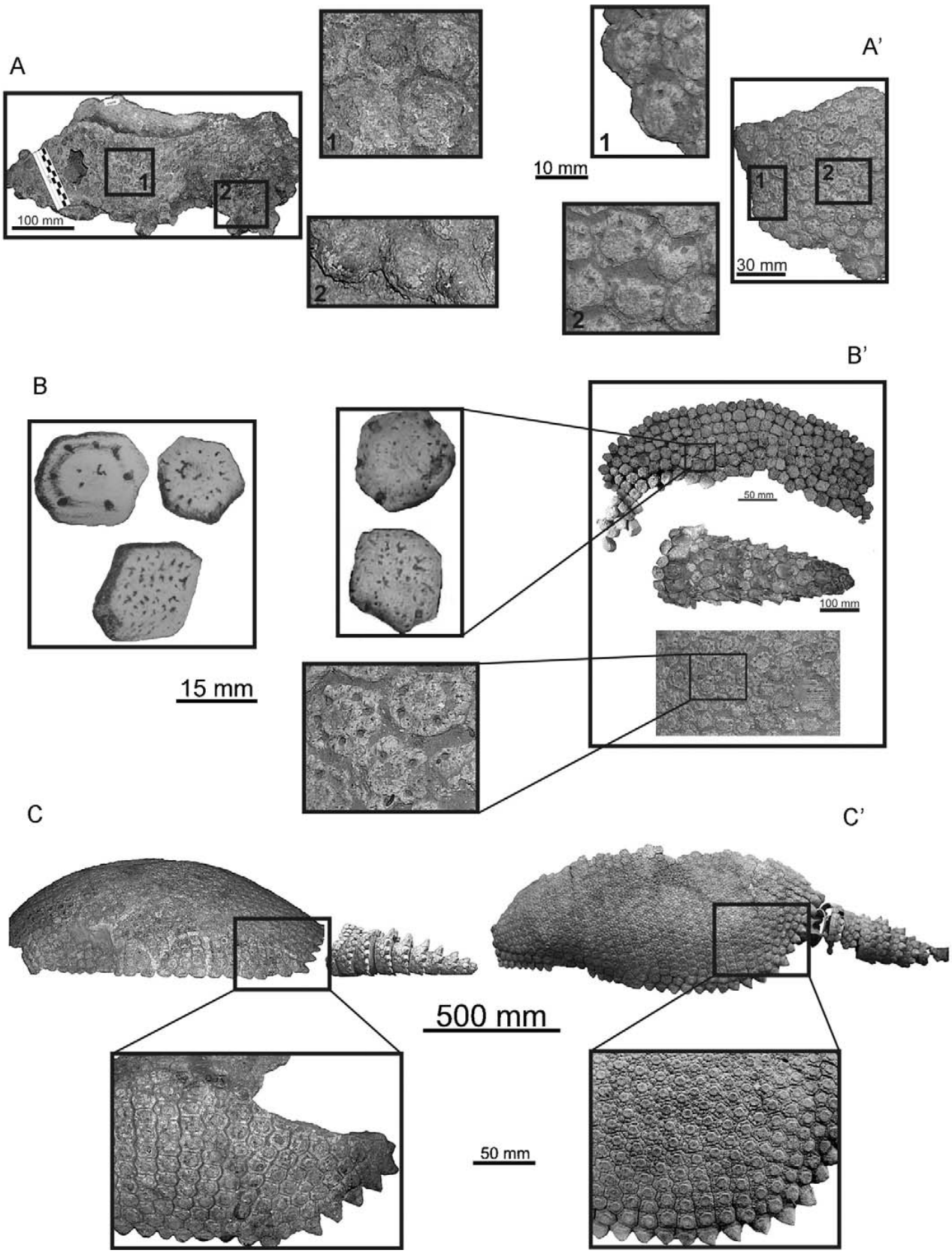
Type species: *Thoracophorus depressus* Ameghino, 1881
Pseudothoracophorus depressus (Ameghino, 1881) Castellanos, 1951
Fig. 3B
Thoracophorus depressus Ameghino, 1881
Neothoracophorus depressus (Ameghino, 1881) Ameghino, 1889
= *Thoracophorus minutus* Ameghino, 1881 *sensu* Ameghino (1895)
= *Neothoracophorus minutus* Ameghino, 1881 (Ameghino, 1889) *sensu* Ameghino (1895)

Holotype: **MLP** (-) (see Mones, 1986), some isolated osteoderms. The type material was also carefully searched by one of the authors (GJSY) in the collections of the MLP without success.

Stratigraphic and geographical origin: near the city of Mercedes, Buenos Aires province, Argentina. Late Pleistocene (Fig. 1B).

Taxonomic comments: As mentioned, *T. depressus* and *T. minutus* were originally recognized by Ameghino (1881) but later transferred to the genus *Neothoracophorus* (Ameghino, 1889). The type material of these two species consists of some isolated osteoderms of the dorsal carapace found in the surroundings of Luján and Mercedes, Buenos Aires province (late Pleistocene) (Ameghino, 1889; Castellanos, 1951). Ameghino (1889: 792) assigned new material to *N. depressus* (collected by his brother Carlos), particularly a fragment of dentary that preserves some molariforms. Some years later, the same author (Ameghino, 1895), as previously proposed by Lydekker (1894), accepted the synonymy of these species. In the last systematic revision of this group of glyptodonts, Castellanos (1951) erected a new genus, *Pseudothoracophorus*, in which he included the species *P. depressus*. In that contribution, Castellanos (1951: 73) assigned new materials to this species, especially some osteoderms that originally belonged to the collections of Museo Paleontológico "Alejandro Berro" Mercedes, Soriano, Uruguay (MPAB 1540), but now belonging to the collections of the Museo Universitario Florentino y Carlos Ameghino (Rosario, Argentina) (MFCA 1280). Finally, it is noteworthy that in this work, Castellanos (1951: 77–79, figs. 3–5) referred this last specimen as the "type" of the new genus, being this a mistake of the author.

Morphology and comparisons: A comparison of the osteoderms cited by these authors reveals a clear morphological affinity with those belonging to juvenile specimens. In fact, while the osteoderms figured by Ameghino (1889) seem to belong to a very juvenile *Glyptodon* (e.g. PVE-F 85), those illustrated by Castellanos (1951) are almost identical to those belonging to immature specimens assigned to *Glyptodon* (e.g. MCA 2017; GCF 10; MNPA-V005423), which present



a more defined central elevation, clearly punctuate, with an area surrounded by 4-7 foramina (Fig. 3B').

In addition, the described morphology of the dentary and the preserved molariforms clearly coincide with the description of an unborn specimen of *Glyptodon* (Zurita et al., 2009b).

"*Boreostracon*" Simpson, 1929 (partim)

Type species: *Boreostracon floridanus* Simpson, 1929

Taxonomic comments: Simpson (1929) established the genus *Boreostracon* in North America to name a new taxon of Glyptodontinae, *B. floridanus*. The holotype (AMNH 23547) is represented by a rear portion of dorsal carapace, including the posterior border. In their systematic revision of North American glyptodonts, Gillette and Ray (1981:14) included this species in the genus *Glyptotherium* Osborn (*G. floridanum*). Interestingly, most of the osteoderms that belong to the holotype seem to correspond to a juvenile specimen. In fact, a comparison with a juvenile *Glyptodon* from South America reveals strong similarities. The punctuate exposed surface comprises a central figure which is elevated with respect to the rest of the surface; the peripheral figures are poorly developed and, in some cases, they are replaced by radial grooves. Finally, there are three to seven evident foramina surrounding the central figure. This particular morphology of the osteoderms described by Simpson (1929) allowed Castellanos (1947a) to postulate, for the first time, the presence of the genus *Boreostracon* in South America. In that paper, Castellanos (1947a) recognized the species *B. oliveirai* while in the same year he transferred *Glyptodon subelevatus* Nodot, 1857 to *B. subelevatus* (Castellanos, 1947b). Some years later, Paula Couto (1948, 1954) reconsidered the holotypes and included both *B. subelevatum* and *B. oliveirai*, as well as *B. sellowi,* in the genus *Chlamydotherium* Bronn (1838). Apparently, those papers were ignored by Castellanos (1958), when he described a new species of "*Boreostracon"*, *B. corondanus.* In summary, he listed all the known species of *Boreostracon* of South America: 1. *B. subelevatus*; 2. *B oliveirai*; 3. *B. sellowi*; 4. *B. corondanus*. A precise comparison of the holotype of these taxa with immature specimens of *Glyptodon* reveals, as in the previous cases, strong similarities. In this sense, this study partially agrees with the proposal of Rinderknecht (2000), who interpreted the South American species of "*Boreostracon*" as *nomina dubia*.

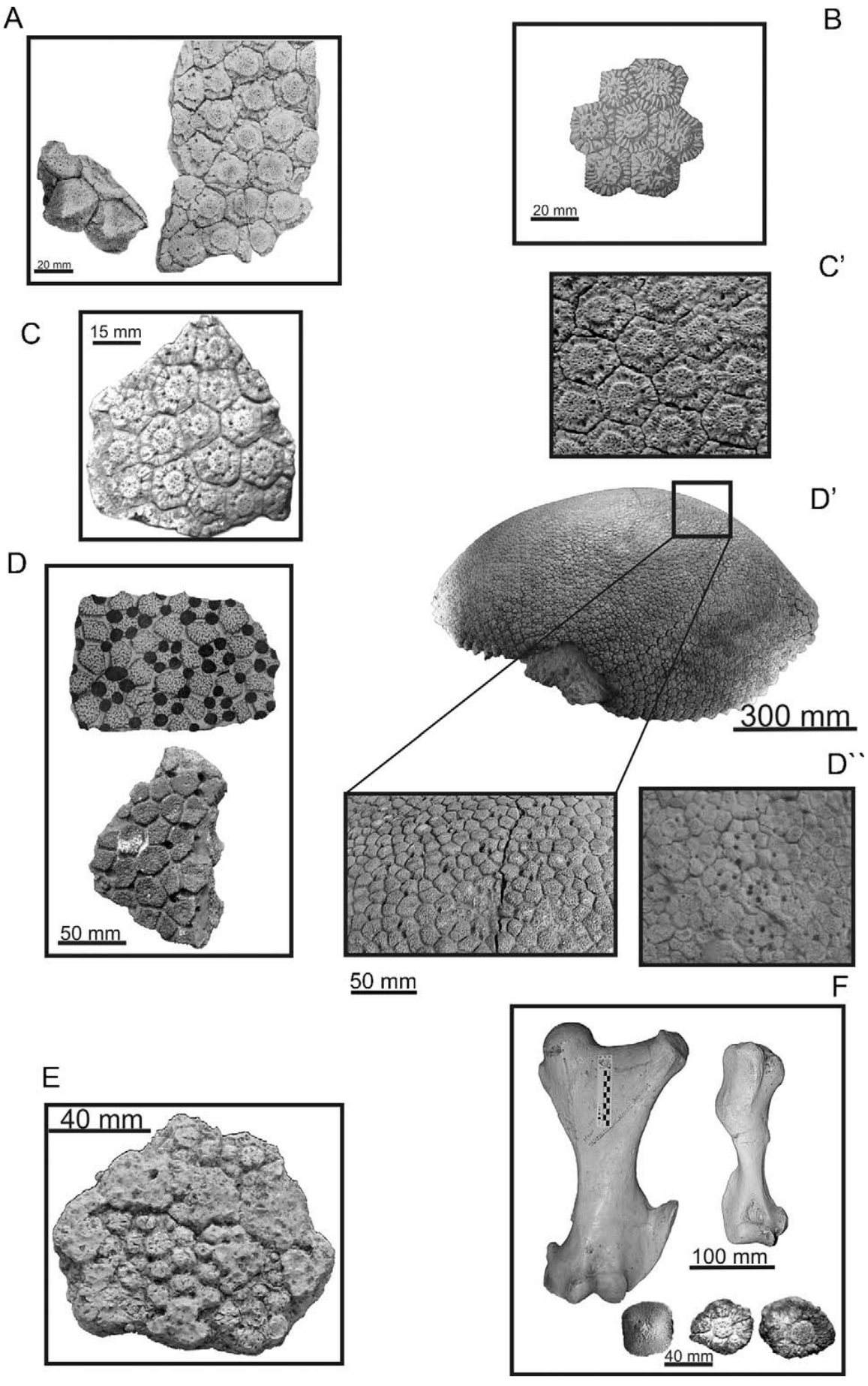
"*Boreostracon*" corondanus Castellanos, 1958

Fig. 3C

Holotype: **MFCA 760**, three large portions of the dorsal carapace (belonging to the anterior part, left and right laterals, and some small groups of osteoderms of the central region of the carapace), left scapula, caudal armor, atlas and fragments of the pelvis (Fig. 3C).

Fig. 3. **Glyptodontinae Neothoracophorini: A)** *Neothoracophorus elevatus* (Nodot) (**MNHNP BRD-20**, holotype), fragment of the dorsal carapace; **A")** *Glypodon* sp. (**PVE-F 85**). ***Glyptodon***: **B)** *Pseudothoracophorus depressus* (Ameghino, 1889, pl. LIV, figs. 7,8,10), three osteoderms of the dorsal carapace; **B")** *Glyptodon* sp. **(PVE-F 85)**; **C)** *Boreostracon corondanus* Castellanos (**MFCA 760**, holotype**)**, dorsal carapace and caudal armor; **C")** *Glyptodon* cf. G. *reticulatus* **(MCA 2013)**.

Glyptodontinae Neothoracophorini: A) *Neothoracophorus elevatus (Nodot) (***MNHNP BRD-20***, holotype), fragment de la carapace dorsale;* **A")** *Glypodon sp. (***PVE-F 85***).* ***Glyptodon****:* **B)** *Pseudothoracophorus depressus (Ameghino, 1889, pl. LIV, figs. 7,8,10), trois ostéodermes de la carapace dorsale;* **B")** *Glyptodon sp.* **(PVE-F 85)***;* **C)** *Boreostracon corondanus Castellanos (***MFCA 760***, holotype***)***, carapace dorsale et armure caudale;* **C")** *Glyptodon cf. G. reticulatus* **(MCA 2013)**.



Stratigraphic and geographic origin: Coronda River, between Punta Piedras and Puerto Aragón localities, Santa Fe province, Argentina. Middle Pleistocene (Fig. 1C).

Morphology and comparisons: The dorsal carapace of the holotype is 1250 mm long, and its dorsal profile is clearly convex. This species was fully described by Castellanos (1958). All the osteoderms that form the dorsal carapace show the typical morphology of juvenile specimens of *Glyptodon*. The exposed surface of each osteoderm has a central figure evidently elevated; surrounding this central figure there is a single row of poorly defined peripheral figures; sometimes, the peripheral figures are not present and they are replaced by series of radial grooves; one conspicuous character is the existence of some foramina (ca. 3–8) surrounding the central figure. The caudal armor comprises a series of 10 rings with a very short tube at the distal tip. Each ring is formed by a double or a triple row of osteoderms. The osteoderms in the last row are conical. Suggestively, a well-defined sharp tip that gives a "spine"-like appearance is very common in young *Glyptodon* specimens (MCA 2013; PVE-F 85), while this structure generally presents blunter apices when the animal becomes older (e.g. Ctes-PZ 7334). In this context, it is important to remark that this set of morphological and morphometric characters are almost identical to those seen in an exceptional juvenile specimen of *Glyptodon* cf. *G. reticulatus* (MCA 2013) (Fig. 3C').

Chlamydotherium Bronn, 1838

Type species: *Hoplophorus selloi* Lund, 1839

Chlamydotherium sellowi (Lund, 1839) Paula Couto, 1954

Fig. 4A

Hoplophorus selloi Lund, 1839

Glyptodon selloi (Lund, 1839) Gervais and Ameghino, 1880

Glyptodon euphractus (Lund, 1839) Ameghino, 1889 (*partim*)

= *Hoplophorus clausseni* Claussen, 1841 (an objective junior synonym, see Paula couto, 1954; Mones and Francis, 1973)

= *Boreostracon sellowii* Paula Couto, 1948 (an objective junior synonym, see Paula couto, 1954)

Type: **PMHU?** (-) (see Mones and Francis, 1973): some dorsal and marginal fragments of the carapace, and part of the anterior limb originally figured by Weiss (1830) and D'Alton (1835). It is remarkable that Paula Couto (1948) implicitly considered these remains as pertaining to

Fig. 4. ***Glyptodon*** **A)** *Chlamydotherium sellowi* (Lund) (**PMHU?-**, lectotype, from Weiss, 1830, pl. I, fig. 1), fragment of the dorsal carapace; **B)** *C. subelevatum* (Nodot) (**MNHNP PAM-216**, holotype, from Nodot, 1857, pl. XI, fig. 1), two fragments of the lateral and central? regions of the dorsal carapace; **C)** *C. oliveirai* (Castellanos) (**MNRJ 549-M**, holotype); **C')** *Glyptodon* cf. *G. reticulatus* (**MCA 2013**); **D)** *Glyptodon perforatus* Ameghino (from Ameghino, 1889, pl. LIV, fig. 5; MACN 6954), two fragments of the dorsal carapace; **D')** *Glyptodon reticulatus* Owen (**MCA 2015**) and **D")** *G. clavipes* Owen (**MNAP-V 6146**); **E)** *Glyptodon falkneri* Ameghino (**MACN 1225**, holotype), associated osteoderms of the dorsal carapace; **F)** *Heteroglyptodon genuarioi* Roselli (**MMNP 563**, holotype), right humerus, left femur and isolated osteoderms.

Glyptodon **A)** *Chlamydotherium sellowi (Lund)* (**PMHU?-**, *lectotype, de Weiss, 1830, pl. I, fig. 1), fragment de la carapace dorsal;* **B)** *C. subelevatum (Nodot)* (**MNHNP PAM-216**, *holotype, Nodot, 1857 pl. XI, fig. 1*), *deux fragments des régions latérale et centrale? de la carapace dorsale;* **C)** *C. oliveirai (Castellanos, 1947)* (**MNRJ 549-M**, *holotype)* **C')** *Glyptodon cf. G. reticulatus* (**MCA 2013**)*;* **D)** *Glyptodon perforatus Ameghino* (**Ameghino, 1889, pl. LIV, fig. 5; MACN 6954**), *deux fragments de la carapace dorsale;* **D')** *Glyptodon reticulatus Owen* (**MCA 2015**) *et* **D")** *G. clavipes Owen* (**MNAP-V 6146**). **E)** *Glyptodon falkneri Ameghino* (**MACN 1225**, *holotype*), *ostéodermes associés de la carapace dorsale.* **F)** *Heteroglyptodon genuarioi Roselli (***MMNP 563**, *holotype*), *humérus droit, fémur gauche et ostéodermes.*

different specimens, although, according the available data, this can not be confirmed neither refuted. **Lectotype**: PMHU? (-): one carapace fragment figured by Weiss (1830: pl. I, fig. 1), designed as "type" by Paula Couto (1948). **Paralectotypes**: PMHU? (-): the rest of the carapace fragments figured by Weiss (1830: pl. I, figs. 2–3; pl. II, figs. 4–7). Part of a left hand, an ungueal phalanx, left radius and left ulna figured by D'Alton (1835), although these last remains were considered as a Glyptodontinae indet. by Paula Couto (1948, 1954).

Stratigraphic and geographical origin: Arapey Grande River, Uruguay Pleistocene? (Fig. 1D).

Taxonomic comments: *Chlamydotherium* is a name conditionally proposed by Bronn (1838) to refer some fossil remains collected in nineteen century by the naturalist Friedrich Sellow in Uruguay, particularly some carapace fragments undoubtedly belonging to a glyptodont (it is noteworthy that, as it was appointed by Mones (1986), the genus was originally created as a *genus coelebs*). These remains were originally described and figured by Weiss (1830) as *"Megatherium"*, and later by D'Alton (1835) as a cingulate. Although additional data about the collect of these remains are unknown, Weiss (1830) suggested the possibility that at least one of the carapace fragments could correspond to a different specimen, according with the morphology of the external surface (Pl. II, fig. 7 of that work). On the basis of the descriptions given by Weiss and D'Alton, Lund (1839) created the species *Hoplophorus selloi* (it is noteworthy that he did not know the name *Chlamydotherium* previously proposed by Bronn). Later, Gervais and Ameghino (1880) considered that this species must be included in the genus *Glyptodon*, showing some similarities with *G. clavipes*. Some years later, Ameghino (1889) considered this species as a junior synonym of *"Glyptodon" euphractus* (Lund). Finally, using the same remains, Paula Couto (1948) described the species *Boreostracon sellowii*, thus ignoring the original name proposed by Lund. More recently, Paula Couto (1954) considered *Chlamydotherium* as a valid name, and determined *C. sellowi* (Lund) as its type species. This author also included in the genus *C. oliveirai* (Castellanos) and *C. subelevatum* (Nodot) from South America, and *C. floridanum* (Simpson) from North America (see below). It is remarkable that previously Castellanos (1947a) had described a new species assigned to the North American genus *Boreostracon* (*B. oliveirai*), based on remains that Paula Couto (1954) considered belonging to the original Sellowĭs collection from Uruguay. Moreover, Paula Couto suggested the possibility that the specimen used by Castellanos to describe *B. oliveirai*, could be the same first figured by Weiss (1830) and used by Lund (1839) to create (by indication) the species *H. selloi*. In this sense, both species could be objective synonyms, as proposed by this author. According to Mones and Francis (1973), the holotype of *H. selloi* was searched in the collections of the Paläeontologisches Museum of the Humboldt Universität (Berlin) and in the Statens Naturhistoriske Museum of Copenhagen without successful, being actually considered as lost. A comparison between the fragments that compound the holotype of *C. oliveirai* (Fig. 4C) and the remains figured by Weiss (1830) (Fig. 4A), offers many similarities; however it is not conclusive. In these conditions, we are unable to affirm if both species are based in the same specimen. Therefore, it seems convenient to continue recognizing them. Although, and according to the circumstances, the case of *C. sellowi* can be considered as a *nomen dubium*.

Morphology and comparisons: The osteoderms figured by Weiss (1830: pl. I) and Paula Couto (1948: pl. I) (Fig. 4A) show a clear similarity with those belonging to juvenile specimen of *Glyptodon* (e.g. MCA 2013) (Fig. 4C'). The central figure is evidently elevated and convex, and surrounded by a single row of poorly defined peripheral figures; sometimes, the peripheral figures are not present and they are replaced by series of radial grooves. This set of characters clearly shows that this material belongs to a juvenile specimen of *Glyptodon*.

Chlamydotherium subelevatum (Nodot, 1857) Paula Couto, 1954
Fig. 4B
Glyptodon subelevatus Nodot, 1857
Boreostracon subelevatus (Nodot, 1857) Castellanos, 1947b
Holotype: **MNHNP PAM-216,** fragments of the dorsal carapace.
Stratigraphic and geographical origin: surroundings of Montevideo, Uruguay. Pleistocene (Fig. 1E).
Taxonomic comments: This species was recognized by Nodot (1857) as *Glyptodon subelevatus*, based on a set of osteoderms from the Pleistocene of Uruguay and later transferred to the genus *Boreostracon* by Castellanos (1947b). Some years later, Paula Couto (1954) included this taxon in the genus *Chlamydotherium* (*C. subelevatum*), and considered it as a possible synonym of *C. sellowi*.
Morphology and comparisons: This species was initially correctly interpreted by Nodot (1857: 94–95) as belonging to a juvenile specimen of *Glyptodon* (*G. subelevatus*); "...le peu de solidité des sutures annonce que l'individu n'était point arrivé à l'âge adulte" (Nodot, 1857: 95). The other diagnostic characters given by Nodot (1857), Ameghino (1889) and Castellanos (1947b) evidently coincide with the morphology observed in juvenile specimens of *Glyptodon* (Fig. 4C').

Chlamydotherium oliveirai (Castellanos, 1947a) Paula Couto, 1954
Fig. 4C
Boreostracon oliveirai Castellanos, 1947a
Holotype: **MNRJ 549-M**, some portions of the dorsal carapace.
Stratigraphic and geographical origin: Pleistocene? Uruguay? (Fig. 1F)
Taxonomic comments: As demonstrated by Oliveira et al. (2010), this species must be referred to as a young specimen of *Glyptodon*. As noted by Paula Couto (1954), the type material of *C. oliverai* is very similar to the Sellowĭs specimen described by Weiss (1830) and D'Alton (1835) and is impregnated with a carbonate crust on the external surface. This impregnation pattern is very characteristic in fossils recovered from Pleistocene fluvial deposits of the Uruguay River (Ubilla et al., 2004). Moreover, two fragments of rocks housed in MNRJ and identified with the same number of the osteoderms described as *C. oliveirai* are remains of carbonate concretions. We have revised some osteoderm characters of *C. oliveirai* and found that some features of MNRJ 549-M are due to juvenile conditions. These include the poorly co-ossified sutures between osteoderms, especially when viewed from the internal surface, the poorly defined peripheral figures and the protruding central figure (Oliveira et al., 2010). Thus, it is very likely that the type specimen of *C. oliveirai* represents a juvenile glyptodontine specimen.

Glyptodon Owen, 1839
Type species: *Glyptodon clavipes* Owen, 1839

Glyptodon perforatus Ameghino, 1889
Fig. 4D
Holotype: MACN (-) (Mones, 1986).

Stratigraphic and geographic origin: According to Ameghino (1889), the materials come from Buenos Aires province, Argentina. Late Pleistocene (Fig. 1G).

Taxonomic comments: *G. perforatus* was originally recognized by Ameghino (1882, 1883) but was not drawn or described (*nomen nudum*). The first formal description of the species was provided by Ameghino some years later, including two drawings of the material constituted by some associated osteoderms (Ameghino, 1889: 787, pl. LIV, fig. 5; pl. XCI, fig. 1). This material was attempted to be located in the collections of the MACN without success. In this context, despite its poor morphological identity and lack of diagnostic characters, *G. perforatus* was interpreted by many authors (Carlini and Scillato-Yané, 1999; Cione and Tonni, 1995, 1999, 2005; Scillato-Yané et al., 1995) as a characteristic taxon of the Lujanian Age/Stage (late Pleistocene-earliest Holocene) of the Pampean region, with biostratigraphic importance.

Morphology and comparisons: The main diagnostic characters listed by Ameghino (1889) are the reticular morphology of the exposed surface of the osteoderms. In each osteoderm, both the central and peripheral figures are very angular and convex, and have almost the same size. It is therefore very difficult to differentiate the central figure from the peripheral ones, and the central and radial sulci are deeper than those of *G. munizi.* Surrounding the central figure, and in the intersection between the central and radial sulci, there are 3-5 well-developed foramina. According to Ameghino (1889), the osteoderms are up to 40-45 mm thick. In this context, a revision of the late Pleistocene Glyptodontinae (Zurita et al., 2009a) reveals that this set of characters is also present in some specimens of *Glyptodon reticulatus* (e.g. PVL 4733; MCA 2015, 2017) and *G. clavipes* (e.g. MNAP-V 6146*)* (Fig. 4D', D"). In fact, the description of *G. perforatus* coincides with the morphology of the osteoderms belonging to the posterior-dorsal region of the carapace of *G. reticulatus* and *G. clavipes*: a) the osteoderms reach their maximum thickness; b) surrounding the central figure there are three to six large foramina; c) the central and peripheral figures show a clear reticular pattern (Duarte, 1997). This interpretation corroborates the proposal of Fernández (1922), who related these large foramina to glandular structures without taxonomic relevance.

Glyptodon falkneri Ameghino, 1889
Fig. 4E
Glyptostracon falkneri (Ameghino, 1889) Castellanos, 1953

Holotype: MACN 1225, some fragments of the dorsal carapace (Fig. 4E).

Stratigraphic and geographic origin: Luján, Buenos Aires province. Middle-late Pleistocene (Fig. 1H).

Taxonomic comments: This species was recognized by Ameghino (1889; pls L (4), LIII (7)) on the basis of some fragments of the dorsal carapace coming from a single specimen. Many years later, Castellanos (1953) used this species to create a new genus, *Glyptostracon*. Nevertheless, this genus was considered by McKenna and Bell (1997) as a junior synonym of *Glyptodon*.

Morphology and comparisons: A comparison of the type material with those belonging to juvenile specimens of *Glyptodon* reveals strong similarities. The central and peripheral figures are clearly convex, with evident foramina. The ventral surface is concave, showing one or two evident foramina in its central area. The noticeable morphological similarity between this taxon and *Neothoracophorus* was recognized by Ameghino (1889) himself, interpreting this new species as a transitional form towards the genus *Glyptodon*.

Heteroglyptodon Roselli, 1976

Type species: *Heteroglyptodon genuarioi* Roselli, 1976.

Heteroglyptodon genuarioi Roselli, 1976.

Fig. 4F

Holotype: **MMNP 563**, right humerus; both femurs and patellae; rigth astragalus; right calcaneous; distal part of a tibia; some tarsal elements (cuneiform, sesamoid); phalanges; three complete caudal vertebrae and several fragments of other ones; some isolated osteoderms from dorsal carapace (dorsal and lateral regions) and from caudal rings.

Stratigraphic and geographical origin: Right margin of Del Chileno Creek, about 200 m from Paso Gómez, 30 Km east from Nueva Palmira, Colonia Department, Uruguay. Libertad Formation, Pleistocene (Fig. 1I).

Taxonomic comments: The genus and the species were created by Roselli (1976) on the basis of a single individual, and since then the validity of the taxon has never been reviewed. In addition, no other specimens have been referred to it.

Morphology and comparisons: The morphology of the preserved osteoderms (four of the caudal aperture and some of the dorsal carapace) does not present any significant differences with those of *Glyptodon* (Ameghino, 1889; Burmeister, 1870–1874; Soibelzon et al., 2006). The femurs are also very similar in shape and size with those of *Glyptodon*. In the description, Roselli (1976) did not recognize any character that differentiates this taxon from *Glyptodon*. The only exception is represented by the supposed presence of a small articular bridge in the distal part of the femur, which connects the facies patellaris with the outer condyle. The astragalus, calcaneous, humerus, the caudal vertebrae and osteoderms do not offer distinctive characters.

6. Discussion

One of the main problems in glyptodonts taxonomy is related to the fact that several species were recognized on the basis of isolated osteoderms, in a strict morphological/typological context. Therefore, the possible variations of the exposed surface of the osteoderms related to the different regions of the dorsal carapace, the different ontogenetic stages and the effects of taphonomic processes are factors poorly evaluated in relation with the identification of many taxa of glyptodonts.

In the case of *Glyptodon* and *Glyptotherium* (the best known taxa of the subfamily Glyptodontinae), although they present some important differences in the endoskeleton (mainly the skull), both genera are similar at the exoskeleton level, even with isolated osteoderms that are difficult to distinguish them. Moreover, in recent times the presence of the genus *Glyptotherium* has been proposed in areas of South America in which traditionally was recognized only the presence of *Glyptodon*, as in the case of North-Eastern Brazil (Oliveira et al., 2009, 2010.). Nevertheless, taking account its similarities, it is remarkable that the presence of *Glyptodon* in these areas can not be discarded by the simple fact concerning to the presence of *Glyptotherium*. This situation outlines a new and more complex paleobiogeographic scenario, with a possible superimposed geographic distribution at least in that part of South America. Finally, taking account that the morphology of the osteoderms in both genera is quite similar at the adult stage, it is highly probable that in its juvenile specimens those being virtually equal. As will be seen below, this can affect the generic assignation of juvenile specimens coming from this region.

Concerning the Neothoracophorini, and according to Hoffstetter (1958) and Paula Couto (1948) the tribe must be included in the subfamily "Hoplophorinae", but they did not provide any convincing evidence. Currently, the latest taxonomic schemes (Fernícola, 2008; McKenna and Bell, 1997) included the Neothoracophorini (*Neothoracophorus* Ameghino and *Pseudothoracophorus*

Castellanos) in the Glyptodontidae, but without a clear connection with other glyptodonts, especially the Glyptodontinae. In this context, this study provides new and clear evidence to interpret that species included in the genera *Neothoracophorus* (*N. elevatus*) and *Pseudothoracophorus* (*P. depressus*) are based on juvenile specimens related to Glyptodontinae.

In the case of *N. elevatus*, the holotype undoubtedly corresponds to a juvenile specimen, but due to the fact that it comes from an area where both, *Glyptotherium* and *Glyptodon* could be present, it is difficult to assign it to a particular genus. In this sense, the status of *Neothoracophorus* (*N. elevatus*) in relation with the genera *Glyptodon* and *Glyptotherium* will remain as a complex taxonomic problem. Nevertheless, although the holotype could corresponds either to *Glyptodon* or *Glyptotherium*, we consider that most of the associated materials traditionally assigned to this genus (coming from southern South America) is referable to *Glyptodon* sp.

In the case of *P. depressus*, it is clear that the holotype and referred materials belong to *Glyptodon*. Finally, it is noteworthy that in this work we include these genera and species in the Glyptodontinae, thus reconsidering the original proposal of Castellanos (1951).

In turn, the comparative morphology between the holotype of "*Boreostracon" corondanus* and *Glyptodon* cf. *G. reticulatus* (MCA 2013) shows that this species was erected on the basis of a juvenile specimen of *Glyptodon*. In addition, the morphology of the exposed surface of the osteoderms the species of *Chlamydotherium* and one species of *Glyptodon* (*G. falkneri*) clearly demonstrates that they correspond to immature specimens of *Glyptodon*.

On the other hand, *Heteroglyptodon* (*H. genuarioi*) did not show any significant differences with *Glyptodon*, while the main characters described for *Glyptodon perforatus* (Ameghino, 1889) are also present in other species of *Glyptodon*, especially in *G. reticulatus* and *G. clavipes*. In this sense, the area of the dorsal carapace in which these large foramina appear (posterior-dorsal) suggests that it could be related to glandular structures, as observed in some Dasypodidae (Krmpotic et al., 2010) or Glyptodontidae (Chimento et al., 2010; Fernández, 1922).

7. Conclusions

The available evidence suggests that:

- the compared morphology of the exposed surface of the osteoderms between the Neothoracophorini, "*Boreostracon" corondanus*, *Chlamydotherium*, *Glyptodon falkneri,* and immature specimens of *Glyptodon* and *Glyptotherium* reveals a set of shared characters:
  - the central figure is always convex and elevated with respect to the rest of the exposed surface,
  - the central figure is usually surrounded by 3-6 large foramina,
  - the peripheral figures are replaced by a rough surface with radial grooves,
  - in very young Glyptodontinae, the exposed surface is smooth and slightly punctuate. According to this, the genera included in tribe Neothoracophorini (*Pseudothoracophorus* and *Neothoracophorus*), the genus *Chlamydotherium,* part of the genus *"Boreostracon"* (*B. corondanus*), and *Glyptodon falkneri* must be interpreted as based on juvenile specimens referable to the genus *Glyptodon* Owen, or even related to *Glyptotherium* Osborn (the latter in the case of the holotype of *N. elevatus*);
- the main diagnostic characters proposed for *Heteroglyptodon genuarioi* are common to other species of *Glyptodon*;
- in this context, the materials referred to as *Glyptodon perforatus*, a species with biostratigraphic importance since it has been interpreted by many authors as an exclusive taxon of the

Lujanian Age/Stage (late Pleistocene-early Holocene; ca. 130-10 ka), seem to correspond to *G. reticulatus* and/or *G. clavipes*.

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Appendix A. Taxonomic/nomenclatural synthesis

Taking into account the arguments exposed in this work, most of the genera reviewed here (except for *Neothoracophorus* Ameghino), can be referred to the genus *Glyptodon* Owen. On the other hand, *Chlamydotherium* Bronn, *Pseudothoracophorus* Castellanos and *Heteroglyptodon* Roselli are considered junior synonyms of *Glyptodon* Owen. Nevertheless, *Chlamydotherium* offers a particular case that must be treated carefully, because this genus was erected in 1838, while the genus *Glyptodon* Owen (as it is known today) was erected in 1839. This way, following the nomenclatural rules, *Chlamydotherium* would be a senior synonym of *Glyptodon*, thus invalidating a name widely used in the last 170 years. For this reason, we propose in this case that the principle of priority of the International Code of Zoological Nomenclature (see ICZN, 1999) must not be applied. Consequently, this case must be presented to the International Commission on Zoological Nomenclature, remaining under request until then.

At the species level, all taxa studied here (except *N. elevatus*) may be referred to the genus *Glyptodon* Owen. However, since they are based on juvenile and/or incomplete specimens, it is difficult to assign them to other well-established species of the genus (i.e. *G. clavipes, G. reticulatus, G. munizi, G. elongatus*). We therefore consider that most of the referred species must be treated as inquiry species (*species inquirendae*), with the hope that in the future new findings (mainly of juvenile specimens) can contribute to elucidating their status, and improving our understanding of the ontogeny of glyptodontines.

Subfamily Glyptodontinae Gray, 1869 (*nom. transl.* Trouessart, 1898)

Tribe Neothoracophorini Castellanos, 1951

Genus *Neothoracophorus* Ameghino, 1889
Neothoracophorus elevatus Nodot, 1857 (Ameghino, 1889) ***species inquirenda***

Tribe Glyptodontini Gray, 1869 (*nom. transl.* Castellanos, 1951)

Genus *Glyptodon* Owen, 1839
= *Chlamydotherium* Bronn, 1838 **New synonymy** (under request)

= *Pseudothoracophorus* Castellanos, 1951 **New synonymy**
= *Heteroglyptodon* Roselli, 1976 **New synonymy**
Glyptodon depressus (Ameghino, 1881) **nov. comb. species inquirenda**
Glyptodon corondanus (Castellanos, 1958) **nov. comb. *species inquirenda***
Glyptodon sellowi (Lund, 1839) **nov. comb. *nomen dubium***
Glyptodon subelevatus Nodot, 1857 ***species inquirenda***
Glyptodon oliveirai (Castellanos, 1947a) **nov. comb. *species inquirenda***
Glyptodon perforatus Ameghino, 1889 ***species inquirenda***
Glyptodon falkneri Ameghino, 1889 ***species inquirenda***
Glyptodon genuarioi (Roselli, 1976) **nov. comb. *species inquirenda***

Appendix B. List of materials analyzed in this paper. A) juvenile specimens; B) adult specimens; C) Cingulata Glyptodontidae indet.

B.1. ***A)***

PVE-F 2, 7, 11, 19, 46, 53, 59, 64, 81, 85, *Glyptodon* sp.
GCF 10, *Glyptodon* sp.
MNPA-V005423, *Glyptodon* sp.
MFCA 1134, 1183, *Glyptodon* sp. (referred by Castellanos, 1951 as *Pseudothoracophorus depressus*).
MMNP 563, *Glyptodon* sp. (holotype of *H. roselli*).
MFCA 760, *Glyptodon* sp. (holotype of *B. corondanus*).
MFCA 1434, *Glyptodon* sp.
MNHNP PAM-216, *Glyptodon* sp. (holotype of *C. subelevatum*).
MNRJ 549-M, *Glyptodon* sp. (holotype of *C. oliveirai*).
MACN 1225, *Glyptodon* sp. (holotype of *G. falkneri*).
MACN 759, 6954, 11530, *Glyptodon* sp. (referred as *G. perforatus*).
MNHNP BRD-20 *Neothoracophorus elevatus* (holotype).
AMHN 23547 *Glyptotherium floridanum*
MHD-P-266, *Glyptodon* sp. (see Ubilla, 1996).
EPM 0436, *Glyptodon* sp. (referred as *Chlamydotherium sellowi*? by Oliveira, 1996).
MCN-PV 1439, 1456, *Glyptodon* sp. (referred as *Chlamydotherium sellowi*? by Oliveira, 1992).
MCNC-PV-246, *Glyptodon* sp.

B.2. ***B)***

Ctes-PZ 7334, *G. reticulatus*
MCA 2013, *Glyptodon cf. G. reticulatus*
PVL 4733, *G. reticulatus*
MCA 2015, 2017, *G. reticulatus*
MDVS-PV 0014, *G. reticulatus*
MACN 200, *G. reticulatus*
MNAP-V 6146, *G. clavipes*
MMP 3985, *G. munizi*

B.3. ***C)***

MNAP-V R-F 5-22 Glyptodontidae indet. (referred by Coltorti et al. (2006) as *Neothoracophorus*).

MCPU-PV, 136, 224. Glyptodontidae indet. (referred by Kerber and Oliveira (2008) as *Nethoracophorus* aff. *N. elevatus*).

MCN-PV 1468, 1469, Glyptodontidae indet. (referred by Oliveira (1992) as *Neothoracophorus* aff. *N. elevatus*).

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