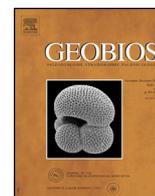




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Original article

A tale of two clades: Comparative study of *Glyptodon* Owen and *Glyptotherium* Osborn (Xenarthra, Cingulata, Glyptodontidae)[☆]



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ABSTRACT

Glyptodon and *Glyptotherium* represent the most conspicuous taxa of late Neogene and Pleistocene glyptodonts in South America and North America, respectively. The earliest records of *Glyptodon* in South America are 1.07 Ma (late early Pleistocene, Calabrian), although the possibility that “*Paraglyptodon uquiensis*” represents a Pliocene specimen of *Glyptodon* cannot be rejected. *Glyptotherium* originated from South American ancestry in northern South America or Central America about 3.9 Ma (early late Pliocene, Zanclean) or earlier. The diversity of South American *Glyptodon* is currently under study, but preliminary evidence would indicate that no more than three species (*G. munizi*, *G. elongatus* and *G. reticulatus*) are valid, plus a possible new Andean species. In turn, according to the updated taxonomy proposed herein, *Glyptotherium* includes two chronospecies. The earliest species, *Gl. texanum*, differs only slightly from the latest species, *Gl. cylindricum*. The relationship of *Glyptodon* and *Glyptotherium* has been problematical since the discovery of the North American lineage, at first identified as various species of *Glyptodon* and later considered a separate genus. *Glyptodon* is recognized as a natural group and recent taxonomic and phylogenetic revisions place all North American glyptodontines into *Glyptotherium*. In this paper, we propose a detailed morphological comparison between the southern South American species of *Glyptodon* and *Glyptotherium* in order to identify diagnostic differences and potential synapomorphies. Both genera can be distinguished mainly by differences in the skull, mandible, dentition, dorsal carapace, and caudal armor, *Glyptodon* being somewhat larger than *Glyptotherium*. Both clades show a highly conservative evolution, which could be interpreted as an anagenesis. The scarce records of glyptodonts in Central America show more morphological affinity with *Glyptotherium* than with *Glyptodon*.

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1. Introduction

Investigations of Xenarthra Glyptodontidae span almost two centuries, beginning with identification of a large number of species and genera, mainly in South America (Ameghino, 1889; McKenna and Bell, 1997) but also in North America as an endemic American clade (O’Leary et al., 2013). Although the monophyly of glyptodonts is well supported (McDonald and Naples, 2007; Fernicola, 2008; Porpino et al., 2010), recent molecular data

suggest that this clade could be a subfamily among Cingulata Dasypodidae rather than a different family (Mitchell et al., 2016).

From a taxonomic viewpoint, most glyptodont taxa were recognized and characterized in strict typological and morphological contexts, mainly using ornamentation patterns of the exposed surface of the osteoderms that constitute the dorsal carapace, but without considering their eventual individual variation (e.g., according to their ontogenetic age or particular position along the dorsal carapace; Soibelzon et al., 2006; Zurita et al., 2011a; González Ruiz et al., 2017). Recent taxonomic and phylogenetic revisions of Glyptodontidae indicate that their diversity is much more limited than previously supposed and that several of the traditionally recognized suprageneric categories (i.e., tribe and subfamily) are not natural groups (Fernicola, 2008; Zamorano and

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Brandoni, 2013; Zurita et al., 2016). In the particular case of Glyptodontinae, whose taxonomic, phylogenetic and biogeographical knowledge has been recently updated (Carlini and Zurita, 2010; Zurita et al., 2011b, 2013; Gillette et al., 2016), available evidences indicate that this is the only glyptodont clade that has its oldest records coming from tropical areas of South America during middle-late Miocene (Carlini et al., 2008; Zurita et al., 2013) and that actively participated in the Great American Biotic Interchange (Woodburne, 2010), reaching Central and North America in the late early Pliocene (ca. 3.9 Ma.; Gillette et al., 2016).

The diversity of late Pliocene and Pleistocene South American Glyptodontinae is currently under revision (Cuadrelli et al., 2016), but preliminary observations suggest that the diversity could be different than previously thought (Zurita et al., 2017). Until now, the evidence showed that in southern South America (ca. 20°S–38°S) two species of *Glyptodon* can be well characterized: *G. munizi* from the early middle Pleistocene, and *G. reticulatus* from the late Pleistocene, plus an Andean new taxon in Bolivia and Peru that is currently under study (Zurita et al., 2017). In addition, the Pliocene “*Paraglyptodon*” *uquiensis* Castellanos, 1953, might also belong to *Glyptodon*, but further studies are needed (Cruz et al., 2016). On the other hand, new evidence indicates that the diversity of glyptodonts in Central and North America is limited to a single, long-lived genus, *Glyptotherium*, spanning at least 3.8 myr. The earliest record of the genus comes from the Pliocene of central México (Gillette et al., 2016). According to recent taxonomic revisions, *Glyptotherium* includes three species: *Gl. texanum*, *Gl. cylindricum* and *Gl. mexicanum* (Ramírez-Cruz and Montellano-Ballesteros, 2014; Gillette et al., 2016). However, here we propose that the diversity is actually limited to only two end-member chronospecies.

Although the natural groups that constitute *Glyptodon* and *Glyptotherium* have been phylogenetically tested (Zurita et al., 2013), their existence as different taxonomic entities has been controversial since the discovery of the North American glyptodonts. At first, they were identified as various species of *Glyptodon* and later considered as species of separate genera (Gillette and Ray, 1981); Rincón et al. (2009) proposed a potential synonymy of *Glyptodon* and *Glyptotherium*, a conclusion that our results do not support. In this paper, we perform a detailed and comprehensive morphological comparison between both genera in order to identify diagnostic differences and potential apomorphies. Additionally, we include remarks about the evolutionary scenario where they differentiated in South and North America and comment on the taxonomic identity of Central America records of glyptodonts.

2. Material and methods

The chronological and biostratigraphic schemes used here correspond to those proposed by Flynn and Swisher (1995); Cione and Tonni (2005) and Croft et al. (2009) for South America, and Woodburne (2010) for North America. The systematics partially follows Hoffstetter (1958); Paula Couto (1979); Gillette and Ray (1981); McKenna and Bell (1997); Fernicola (2008), and Gillette et al. (2016). All measurements are expressed in mm, with an error range of ± 0.5 mm. Measurements smaller than 150 mm were taken with a “vernier” caliper; measurements larger than 150 mm were taken using an anthropometric spreading caliper. The description and terminology for osteoderms mainly follow Krmptotic et al. (2009) and Gillette et al. (2016); for molariforms, González Ruiz et al. (2015).

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; CAL, Colección Paleontológica, Centro de Museos, Universidad de Caldas, Manizales, Caldas, Colombia; IGM, Museo Geológico Nacional, Servicio Geológico

Colombiano (formerly INGEOMINAS); Bogotá D.C., Colombia; MACN, Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MPGJ, Museo de Paleontología, Centro de Geociencias Juriquilla, México; MCA, Museo de Ciencias Naturales “Carlos Ameghino”, Mercedes, Buenos Aires, Argentina; MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Buenos Aires; MSM, Mesa South-west Museum (Arizona Museum of Natural History), Mesa, Arizona, USA; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA.

Anatomical abbreviations: TL, total length; MDZA, maximum diameter between zygomatic arches; ID, interorbital diameter; MDPN, maximum diameter of postorbital narrow; LP, length of palate; LTR, length of tooth rows; APDAR, antero-posterior diameter of the ascending ramus of the mandible; DVDHR, dorso-ventral diameter of the horizontal ramus of the mandible at alveolar level; Mf, mf, upper and lower molariforms, respectively.

Other abbreviations: GABI, Great American Biotic Interchange; n/n, without official catalog number; NALMA, North American Land Mammal Age; SALMA, South American Land Mammal Age.

3. Historical background

3.1. History of Pleistocene Glyptodontinae studies in southern South America

The taxonomic history of *Glyptodon* and some supposed allied Pleistocene genera (e.g., *Neothoracophorus* and *Boreostracon*), is complicated and confusing. Owen (1838) proposed the recognition of *Glyptodon* (but without including any species) on the basis of an isolated molariform that was later reinterpreted as belonging to the genus *Panochthus* (Hoffstetter, 1955). One year later, the same author (Owen, 1839a) recognized *G. clavipes* as the first species of the genus (type-species), characterized on the basis of three different specimens coming from the Pleistocene of Buenos Aires Province (Pampean region of Argentina). Later, Owen (1839b, 1840) erroneously reinforced the morphological characterization of *G. clavipes* mainly on the basis of one specimen placed at the “College of Surgeons” (London), which actually included two specimens belonging to different species. While the dorsal carapace corresponds to *Glyptodon*, the caudal tube belongs to the genus *Neosclerocalyptus* (= *Hoplophorus* = *Sclerocalyptus*) (Ameghino, 1889).

Some years later, Hoffstetter (1955) selected one of the three Owen’s specimens as the lectotype of *G. clavipes* (the specimen from Villanueva, Buenos Aires province), represented only by a complete foot (Mones, 1994). Since then, the morphological characterization of this species has been confusing, mainly because most of the referred materials are not diagnostic, or belong to juvenile individuals (Cuadrelli et al., 2016).

On the other hand, a large number of *Glyptodon* species and supposed allied genera (e.g., *Neothoracophorus* and *Boreostracon*) have been named since the nineteenth century, mainly based on minor morphological details of the external surface of the dorsal carapace osteoderms and/or caudal armor. Burmeister (1870–74), following the erroneous reconstruction of *G. clavipes* carried out by Owen (1839b, 1840), recognized two subgenera based on the presence (*Glyptodon* (*Glyptodon*)) or absence (*Glyptodon* (*Schistopleurum*)) of a caudal tube. Some years later, Ameghino (1889) realized that the caudal tube belonged to a different lineage of glyptodonts (*Neosclerocalyptus*) and split the species of *Glyptodon* into three groups (A, B and C) according to minor osteoderms

details of the dorsal carapace, including the size and morphology of the central and peripheral figures. Lydekker (1894) carried out a revision of the several species of *Glyptodon*, concluding that *G. reticulatus* and *G. clavipes* represent a single species, an interpretation that was strongly rejected by Ameghino (1895) and later by Tonni and Berman (1988). Recently, Zurita et al. (2011a) postulated that most of the traditionally recognized species of *Glyptodon* and allied genera must be interpreted as *nomina dubia* or *species inquirendae*. The diversity of the Glyptodontinae is currently under study by one of us (F.C.), but preliminary evidence indicates that there are as many as three valid species in southern South America: *G. munizi* (early middle Pleistocene), *G. elongatus* and *G. reticulatus* (late Pleistocene) (Zurita et al., 2012). In this context, the situation of *G. elongatus* needs further study. In addition, we cannot reject the possibility that “*Paraglyptodon uquiensis*” belongs to *Glyptodon*.

3.2. History of glyptodont studies in North America

The history of scientific work on glyptodonts in North America has been much less complicated than in South America (for detailed review and listing of all taxonomic assignments, see Gillette and Ray, 1981). Cuatáparo and Ramírez (1875) reported the discovery of glyptodonts in North America as a new species of the South American genus *Glyptodon* (“*G. mexicano*”), based on a nearly complete carapace and associated skeleton from central México. Thereafter, a succession of discoveries expanded the temporal and geographic range of glyptodonts in North America and increased the number of genera from one to five; the new generic names were *Glyptotherium* Osborn, 1903, *Brachyostracon* Brown, 1912, *Boreostracon* Simpson, 1929, and *Xenoglyptodon* Meade, 1953.

Gillette (1974) and Gillette and Ray (1981) concluded that all North American glyptodonts belong to a single genus, including five species: *Glyptotherium texanum*, *Gl. arizonae*, *Gl. floridanum*, *Gl. mexicanum*, and *Gl. cylindricum*. Gillette (1974) proposed a succession of three species in the United States, beginning with *Gl. texanum* in the Blancan and Early Irvingtonian NALMAS, *Gl. arizonae* in the Irvingtonian NALMA and *Gl. floridanum* in the RanchoLabrean NALMA. This anagenetic sequence did not take into account the two Mexican species (*Gl. cylindricum* and *Gl. mexicanum*), for which ages were uncertain. Gillette and Ray (1981) published Gillette’s earlier work with minor changes in illustrations but no taxonomical modification. According to the collections available to Gillette (1974) and Gillette and Ray (1981), *Gl. texanum* seemed to differ from the other four species in its smaller size and apparent lack of pre-iliac and post-iliac break in lateral profile of the carapace. However, that characterization was problematical because the holotype specimen (AMNH 10704; Blanco Beds of western Texas) and a nearly complete individual from Arizona (AMNH 59,599; 111 Ranch fauna) are sub-adults. The authors could not clearly elucidate how the skeletons would differ in adults. Later reports of new glyptodont records in the United States and México variously assigned these specimens to species, but only with tentative confidence, mainly because the distinctions elaborated by Gillette and Ray (1981) were based on what appeared to be unique combinations of characters but with considerable overlap. With the accumulation of new specimens in Arizona and México, Gillette et al. (2016) described adult individuals from the 111 Ranch fauna of Arizona, the same fauna that included the nearly complete skeleton and carapace of a juvenile described in Gillette (1974) and Gillette and Ray (1981). Adults in the 111 Ranch fauna and the much earlier fauna in central México are as large as adults of the other species. Gillette et al. (2016) concluded that the size disparity distinguishing *Gl. texanum* from the other species was incorrect. Instead, all adults in

the available hypodigm of the genus are uniformly large, with little change through the Pleistocene to the extinction of this genus at the end of the Pleistocene.

3.2.1. Synonymy of *Glyptotherium cylindricum*, *Gl. floridanum*, and *Gl. mexicanum*

Gillette (1974) and Gillette and Ray (1981) stated that the only difference in carapacial anatomy between the holotype specimens of *Gl. cylindricum*, *Gl. arizonae* and *Gl. mexicanum* is the outline of the antero-lateral profile. They described the osteoderms of the dorsal carapace of the holotype specimen of *Gl. cylindricum* as markedly conical on the lateral and posterior margins and the central figure of mid-dorsal (hexagonal, symmetrical) osteoderms as large as, or even larger than peripheral figures. This description conforms to the definition of an adult male carapace of *Gl. texanum* (Gillette et al., 2016). The relative size of the central figures is consistent with the emended diagnosis for *Gl. texanum* (= *Gl. arizonae*) of Gillette et al. (2016) and different from the relatively small central figures in *Gl. cylindricum* (= *Gl. floridanum*, see below). The antero-lateral profile is a variable character for the genus, not diagnostic at the species level. Gillette and Ray (1981) concluded that the carapace of the holotype specimen of *G. mexicanum* is nearly identical to that of *Gl. cylindricum*. Carranza-Castañeda and Miller (1987) rediscovered the type specimen (IGM 4006) of *Gl. mexicanum* and provided two additional photographs that support the conclusion that it is indistinguishable from the type specimen of *Gl. cylindricum*. This carapace is clearly an adult and according to Gillette et al. (2016) apparently a male individual.

Recently, Ramírez-Cruz and Montellano-Ballesteros (2014) reported two new records of *Glyptotherium* from the RanchoLabrean NALMA in México and concluded that *Gl. cylindricum* is indistinguishable from *Gl. floridanum* and identified the two new specimens as *Gl. cylindricum*, which has priority. This conclusion differs slightly from the assessment of *Gl. cylindricum* carapace provided by Gillette and Ray (1981), but underscores the broad overlap of carapacial and skeletal characters that no longer distinguish different species. So far, there is no known complete, articulated carapace of *Gl. cylindricum* (= *Gl. floridanum*) in the southern United States for comparison with the Mexican specimens, but there is no reason to believe that an adult carapace would differ from the Mexican specimens.

3.2.2. Synonymy of *Glyptotherium texanum* and *Gl. arizonae*

In their study, Gillette et al. (2016) proposed another synonymy among *Glyptotherium* species with the recognition that *Gl. arizonae* is a junior synonym of *Gl. texanum*, a conclusion reached by analysis of new discoveries and numerous samples from Mexico and Arizona that include growth series and sexual dimorphism. Adults of *Gl. texanum* were previously postulated to be smaller than the much larger later species, but size disparity can no longer be considered a distinctive trait. In México, specimens of *Gl. texanum* from beds that represent the oldest occurrence in North America are now recognized as large as and even larger than individuals from younger sites. Thus, there is no clear change in size over the nearly four-million-year span of their existence in North America.

3.2.3. Identity of *Glyptodontines* from Mexico and Central America

Gillette et al. (2016) reviewed records of glyptodonts from the Irvingtonian NALMA of Central America and concluded they all pertain to *Glyptotherium* and cannot be reliably assigned to species, but as the osteoderm anatomy indicates, a large central figure places them closer to *Gl. texanum* than *Gl. cylindricum*. On the other hand, records of glyptodonts from late Pleistocene (presumably RanchoLabrean NALMA) in México and Central America are mainly isolated osteoderms or fragments of dorsal carapace which cannot

be reliably assigned to a species, but the small central figures of the osteoderms tend to indicate closer affinity with *Gl. cylindricum* than *Gl. texanum*.

4. Results

4.1. Systematic paleontology

Superorder Xenarthra Cope, 1889

Order Cingulata Illiger, 1811

Family Glyptodontidae Gray, 1869

Subfamily Glyptodontinae Gray, 1869

Genus *Glyptodon* Owen, 1839a

1838. *Chlamydotherium* – Bronn, p. 1258.

1856. *Schistopleuron* – Nodot, p. 21, pl. 1–3.

1866. *Schistopleurum* – Burmeister, p. 208, pl. 5–8.

1951. *Pseudothoracophorus* – Castellanos, pp. 69–82.

1976. *Heteroglyptodon* – Roselli, pp. 137–147.

Type Species: *Glyptodon clavipes* Owen, 1839a.

Included species: *Glyptodon reticulatus* Owen, 1845 and *G. munizi* Ameghino, 1881 (valid species). *G. elongatus* Burmeister is known from a dorsal carapace; its validity needs further study. In turn, the lectotype of *G. clavipes* Owen, 1839 (a posterior autopodium) is currently under study, but preliminary evidence suggests that more information is necessary to verify the validity of

this species. Finally, “*Paraglyptodon*” *uquiensis* Castellanos, 1953, could belong to *Glyptodon* (Cruz et al., 2016).

Geographic and biochronological distributions: early middle Pleistocene (ca. 1.07–0.98 Ma) to latest Pleistocene (Soibelzon et al., 2006). Records belonging to *Glyptodon* come from Argentina, Paraguay, Brazil, Uruguay, Bolivia, Peru and Colombia (Zurita et al., 2012; Fig. 1). Until now, there is no reliable evidence of *Glyptodon* in Central America. Alvarado (1986); Gómez (1986) and Lucas et al. (1997) reported the presence of *Glyptodon* in Costa Rica; however, these osteoderms are not well enough preserved to determine their taxonomic identity further than Glyptodontinae.

Measurements: see Table 1.

Diagnosis: Medium to large glyptodont; dorsal carapace longer than *Glyptotherium* (ca. 14%) and much longer than *Boreostemma acostae* (ca. 65%). Skull with subquadrangular rostral area in dorsal view; lower and upper fully trilobed molariforms. Dorsal carapace with the antero-posterior dorsal profile regularly convex, the posterior half higher than the anterior half. Osteoderms with a central figure surrounded by a single row of 5 to 11 peripheral figures. Osteoderms of the lateral margins of the carapace prominent; central and radial sulci of the exposed surface of the osteoderms deeper than *Glyptotherium* and *Boreostemma*. Caudal armor somewhat shorter than *Glyptotherium*, formed by 8 to 9 free caudal rings without an incomplete ring. Each caudal ring (except the most proximal) with conical osteoderms larger than in *Glyptotherium*. Short terminal tube

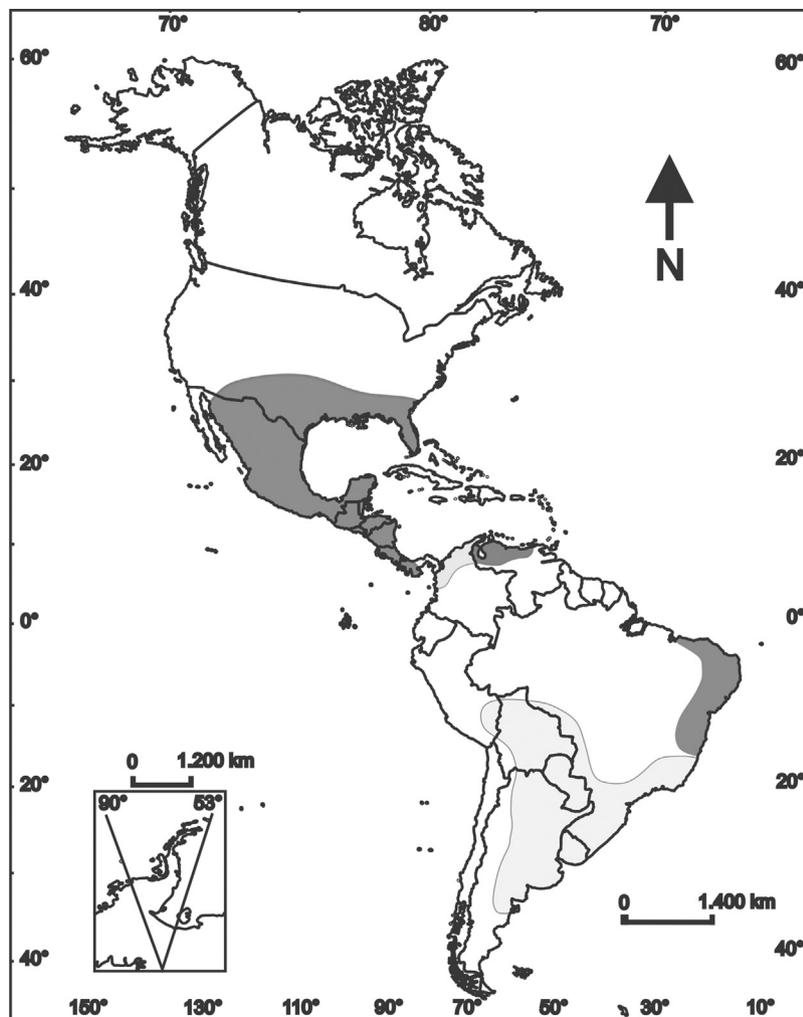


Fig. 1. Geographic distribution of *Glyptodon* Owen (light grey) and *Glyptotherium* Osborn (dark grey) in America.

Table 1
Linear measurements of valid species of *Glyptodon* Owen and *Glyptotherium* Osborn.

| | <i>G. reticulatus</i> (MCA 2015) | <i>G. munizi</i> (MMP 3985) | <i>Gl. texanum</i> (UMMP 34 826) | <i>Gl. cylindricum</i> (AMNH 15,548) |
|----------------------------------|-------------------------------------|--------------------------------|-------------------------------------|---|
| <i>Skull</i> | | | | |
| TL | 293 | 333.17 | 279 | – |
| MDZA | 240 | 278.93 | 253 | – |
| MDPN | 110 | 101.4 | 104 | – |
| LP | 226 | 236.04 | 219 | – |
| LTR | 206.5 | 217.4 | 205 | – |
| <i>Mandible</i> | | | | |
| TL | 317 | 350 | MSM P4818 310 | – |
| LTR | 201.5 | 227 | 211 | – |
| APDAR | | 157.5 | 120.38 | – |
| DVDHR (mfs 1–3) | 64.35 (mf 1) | 70.01 (mf 1) | 41.46 (mf 1) | – |
| | 85.14 (mf 4–5) | 89.5 (mf 4–5) | 78.34 (mf 4–5) | |
| | 81.35 (mf 8) | 88.34 (mf 8) | 78.23 (mf 8) | |
| <i>Dorsal carapace</i> | | | | |
| TLC | 2190 | 2200 | MSM P4464 1400 | 1690 |
| TLSL | 1730 | 1940 | 1250 | 1400 |
| <i>Caudal armor</i> | | | | |
| TL (caudal ring + terminal tube) | MCA 2017 563.6 | 777.8 | AMNH 21080 1010 | – |
| TL terminal tube | 73.23 | 101.9 | 210 | – |
| <i>Humerus</i> | | | | |
| TL | MCA 2017 370 | GFC 10 430 | MSM P4818 380 | – |
| <i>Femur</i> | | | | |
| TL | 426 | 590 | AMNH 21808 455 | – |

formed by two ankylosed caudal rings, different from the longer terminal tube of *Glyptotherium* (with three ankylosed caudal rings). Conical osteoderms of the dorsal carapace and caudal rings are bigger in juvenile specimens than the corresponding elements of *Glyptotherium*.

Remarks: Cruz et al. (2016) reported the presence of *Glyptodon* in Chapadmalalan SALMA (Pliocene) levels of the Atlantic coast of Argentina. However, we do not concur with this determination because the material (MACN 6162, type-specimen of *Paraglyptodon chapadmalensis*) is limited to some isolated osteoderms of the lateral region of the carapace that lack diagnostic characters. On the other hand, the only two regions with reliable records of the early middle Pleistocene species *G. munizi* are Buenos Aires province (Argentina) and Tarija Valley (Bolivia) (Soibelzon et al., 2006; Zurita et al., 2009). The remaining records of *Glyptodon* in South America come from the late Pleistocene.

Genus *Glyptotherium* Osborn, 1903

1875. “*Glyptodon*” – Cuatáparo and Ramírez, p. 362.

1912. *Brachyostrakon* – Brown, p. 169.

1929. *Boreostrakon* – Simpson, p. 581.

1953. *Xenoglyptodon* – Meade, p. 455.

Type species: *Glyptotherium texanum* Osborn, 1903.

Included species: *Glyptotherium cylindricum* (Brown, 1912) (valid species).

Geographical and biochronological distributions: known geographic distribution of *Glyptotherium* includes central México (early Pliocene, Blancan NALMA); México, Arizona, Texas, Oklahoma, Florida (early Pleistocene, Blancan and Irvingtonian NALMA); Central America, México, Texas, Louisiana, Florida, South Carolina (late Pleistocene, RanchoLabrean NALMA). Inferred geographical distribution includes Central America in early Pliocene; there are no records of glyptodonts in the United States referred to middle and late Irvingtonian NALMA, a situation known as the “glyptodont gap”. No glyptodonts have been found in Pacific drainages in the United States or west of the Colorado River. In South America, cf. *Glyptotherium* is recorded in northern Venezuela and eastern Brazil (Fig. 1).

Diagnosis: medium size glyptodont. Dorsal carapace somewhat shorter than *Glyptodon* (ca. 14%), but longer than *Boreostemma acostae* (ca. 51%). Skull with subquadrangular rostral area in dorsal view. Upper and lower anterior molariforms ellipsoidal in cross sections but slightly trilobate; all succeeding teeth with increasing trilobation. Short dorsal carapace, from moderately to highly arched (length to height ratio: 3:2). Adult carapace strongly curved, with convex pre-iliac and concave post-iliac profile (unlike *Glyptodon*). Osteoderms of antero-lateral region quadrilateral and flexible; mid-body osteoderms with central figure surrounded by a single row of 6 to 10 peripheral figures, occasionally overlap to an adjoining osteoderm. Lateral margin composed of osteoderms from anterior strongly conical, to nearly flat at caudal aperture level. Central and radial sulci of the exposed surface of the osteoderms shallower than those of *Glyptodon*. Caudal armor composed of one first incomplete ring, 8 to 9 complete caudal rings (with biseriate or triseriate rows of osteoderms), plus a terminal tube of three conjoined rings; posterior row of osteoderms on each caudal ring strongly conical, but smaller than those of *Glyptodon*. Conical osteoderms of border of the dorsal carapace and caudal rings smaller in juveniles and females.

Remarks: *Glyptotherium texanum* is the Pliocene and early Pleistocene glyptodont in North America and, probably, in Central America, as the earliest species in the *Gl. texanum*-*Gl. cylindricum* chronospecies lineage. *Glyptotherium cylindricum* differs from *Gl. texanum* in the configuration of the external sculpturing of symmetrical, hexagonal osteoderms of the dorsal carapace. In *Gl. texanum* adults the central figures are flat to weakly convex, moderately elevated with respect to the peripheral figures, and large, generally greater than half the transverse diameter of an individual osteoderm (Gillette et al., 2016). The central figures are prominent in articulated osteoderms, so that osteoderms are easily recognized by their rosette patterns. In *Gl. cylindricum* adults, the central figures of symmetrical, hexagonal osteoderms are generally flat, sometimes concave, and the diameter of the central figure is equal to, or less than half the transverse diameter of symmetrical, hexagonal osteoderms which have a distinctive rosette pattern with central figures surrounded by one row of

8–11 peripheral figures. In both species, the proportions change from the midline toward the margins, with gradually increasing diameter of the central figure at the expense of the peripheral ones. In addition, these proportions differ in juveniles, which have markedly larger central figures in relation to the peripheral (Gillette et al., 2016).

Emended diagnosis for the genus is expanded from Gillette et al. (2016), who provided diagnosis for carapacial and caudal armor for Blancan-Irvingtonian NALMA occurrences only (*Gl. texanum* = *Gl. arizonae*). Our contribution includes all North American glyptodonts ranging from Blancan through Rancholabrean NALMAs. Over the course of its existence in North America, *Glyptotherium* was the only genus of glyptodont in its entire geographic extent. The earliest species, *Gl. texanum*, is similar to *Gl. cylindricum*, the latest species (see discussion below), in all aspects of the anatomy other than the external sculpturing of the carapacial osteoderms. This conservative interpretation postulates only minor changes in morphology over the 3.9 myr existence of the genus, which suggests anagenesis (evolution from one species to another) rather than cladogenesis (appearance of an autapomorphy in one lineage, indicating a cladistic event leading to sister taxa). Additional studies are needed, especially on complete, articulated carapaces, caudal armor and skulls to test this hypothesis. Instead, it is possible that all *Glyptotherium* in North America belong to one single species, indicating evolutionary stasis, but the evidence at present indicates that the only two valid species are *Gl. texanum* and *Gl. cylindricum*.

Glyptotherium texanum Osborn, 1903

1926. *Glyptotherium arizonae* – Gidley, p. 96, fig. 4, pl. 40–44.

1930. *Glyptodon petaliferus* (Cope) – Hay and Cook, p. 10 (*nomen nudum*).

1953. *Xenoglyptodon fredericensis* – Meade, p. 455, pl. 1.

1964. *Glyptodon fredericensis* (Meade) – Melton, p. 131, figs. 2–3, pl. 1–3.

Holotype: AMNH 10704 (dorsal carapace, caudal vertebrae, caudal armor, pelvis, and seven chevrons).

Measurements: see Table 1.

Glyptotherium cylindricum (Brown, 1912)

1875. “*Glyptodon mexicano*” – Cuatáparo and Ramírez, p. 362, figs. 1–4 (original description).

1888. *Glyptodon petaliferus* – Cope, p. 346 (*nomen nudum*).

1912. *Brachyostracon cylindricum* – Brown, p. 169, figs. 1–4, pls. 16–18 (original description).

1912. *Brachyostracon mexicanus* (Cuatáparo and Ramírez) – Brown, p. 168, pl. 13–15.

1923. *Glyptodon rivipacis* – Hay, p. 40.

1929. *Boreostracon floridanus* – Simpson, p. 581, fig. 10 (original description).

1981. *Glyptotherium floridanum* (Simpson) – Gillette and Ray, 1981, p. 14.

1981. *Glyptotherium mexicanum* (Cuatáparo and Ramírez, 1875) – Gillette and Ray, p. 16.

Holotype: AMNH 15548 (complete dorsal carapace, 20 isolated teeth, atlas, hyoid fragment, rib fragment, chevron, and caudal ring fragment).

Measurements: see Table 1.

4.2. Comparative descriptions

Skull (Fig. 2(A, B, E, F)). The hypodigm of *Glyptotherium* includes only one complete skull (*Gl. texanum*) (Gillette and Ray, 1981; Gillette et al., 2016), whereas both austral species of *Glyptodon* (*G. munizi* and *G. reticulatus*) include well-preserved skulls

(Soibelzon et al., 2006; Zurita et al., 2009). In frontal view (Fig. 2(E)), in *Glyptotherium* the descending processes of the zygoma are narrow, slender, almost parallel and close to the sagittal plane; in *Glyptodon* (Fig. 2(A)), this structure is broader, robust, divergent rather than parallel and more laterally placed. In turn, the infraorbital foramina are narrow and not visible in anterior view in *Glyptotherium*, but in *Glyptodon* they are broad and clearly visible in anterior view. In lateral view, the dorso-ventral height between the skull roof and the palatal plane in *Glyptodon* decreases anteriorly (Fig. 2(B)), contrary to *Glyptotherium* (Fig. 2(F)); the nasal tip is in a lower plane with respect to the zygomatic arch in *Glyptodon*, but in *Glyptotherium* is higher than the zygomatic arch plane. In *Glyptotherium*, the occlusal lateral profile is slightly curved, whereas it is strongly curved in *Glyptodon*. In *Glyptodon*, the Mf1 is clearly trilobate both lingually and labially, nearly as trilobate as the Mf2; on the contrary, *Glyptotherium* shows a very low trilobation of Mf1, which is elliptical in cross section, the Mf2 is weakly trilobate, and the Mf3 is trilobate. In both genera, the Mf4 to Mf8 are fully trilobate and serially identical.

Mandible (Fig. 2(C, D, G, H)). *Glyptodon* and *Glyptotherium* have little differences in their mandibular morphology and size, being somewhat larger (ca. 10%) in *Glyptodon* (MMP 3985) compared to *Glyptotherium* (MSM P4818). In lateral view, the angle between the occlusal plane and the anterior margin of the ascending ramus is approximately 60° in *Glyptotherium* (Fig. 2(G)) and ca. 65° in *Glyptodon* (Fig. 2(C)); the ventral margin of the horizontal ramus is more concave in *Glyptodon* than in *Glyptotherium*. In occlusal view, the symphysis area is more antero-posteriorly extended in *Glyptotherium* (similar to the antero-posterior length of the two first molariforms; Fig. 2(H)) than in *Glyptodon* (Fig. 2(D)). As with the upper dentition, the mf1 and mf2 are mainly trilobate in *Glyptodon* (Fig. 2(D')), but in *Glyptotherium* the mf1 is ellipsoidal (with lobes only slightly defined), and the mf2 is “submolariform” (Fig. 2(H')). The mf3–mf8 show no significant differences between genera.

Dorsal carapace (Fig. 3). Adult individuals of both genera have a clearly distinctive dorsal carapace. In lateral view, the profile of *Glyptodon* is regularly convex (Fig. 3(A)), with the highest point of the carapace slightly posteriorly displaced from midpoint, but in *Glyptotherium* this point is in the middle of the carapace. In turn, *Glyptotherium* has a dorsal profile markedly arched, with a convex pre-iliac (2/3) and concave post-iliac (1/3) regions, which represents an autapomorphy for the genus (Zurita et al., 2013; Gillette et al., 2016; Fig. 3(C)). In *Glyptodon* the dorso-ventral height of the carapace represents 60% of its total length, whereas in *Glyptotherium* it is ca. 70%. On the other hand, the ventral margin of the dorsal carapace in *Glyptotherium* (Fig. 3(C)) is somewhat rectangular and more concave in *Glyptodon* (Fig. 3(A)). In *Glyptodon*, the antero-lateral region of the dorsal carapace has completely ankylosed osteoderms (and slightly convex in some cases, like in *G. reticulatus* MCNC PV 140), as in the remaining areas of the dorsal carapace (Fig. 3(A')). On the contrary, in *Glyptotherium*, the antero-lateral osteoderms show an imbricated morphology (more evident in *Gl. texanum* than in *Gl. cylindricum*), indicating some degree of carapace flexibility in this region (Fig. 3(C')), unlike other areas of the carapace, which are fully ankylosed in adults. The specimen MPGJ 2042 from Arroyo El Indagazo, Guanajuato (Pliocene of México), dated at 3.9 Ma, shows this flexibility between the most antero-lateral osteoderms of the dorsal carapace, a character that supports its inclusion into *Gl. texanum*.

The angle between the ventral plane of the carapace and the caudal aperture is ca. 100–135° in *Glyptodon*, but only ca. 90° in *Glyptotherium*. The caudal aperture is ventrally oriented in *Glyptodon* (Fig. 3(A, B, E)) and more posteriorly in *Glyptotherium*

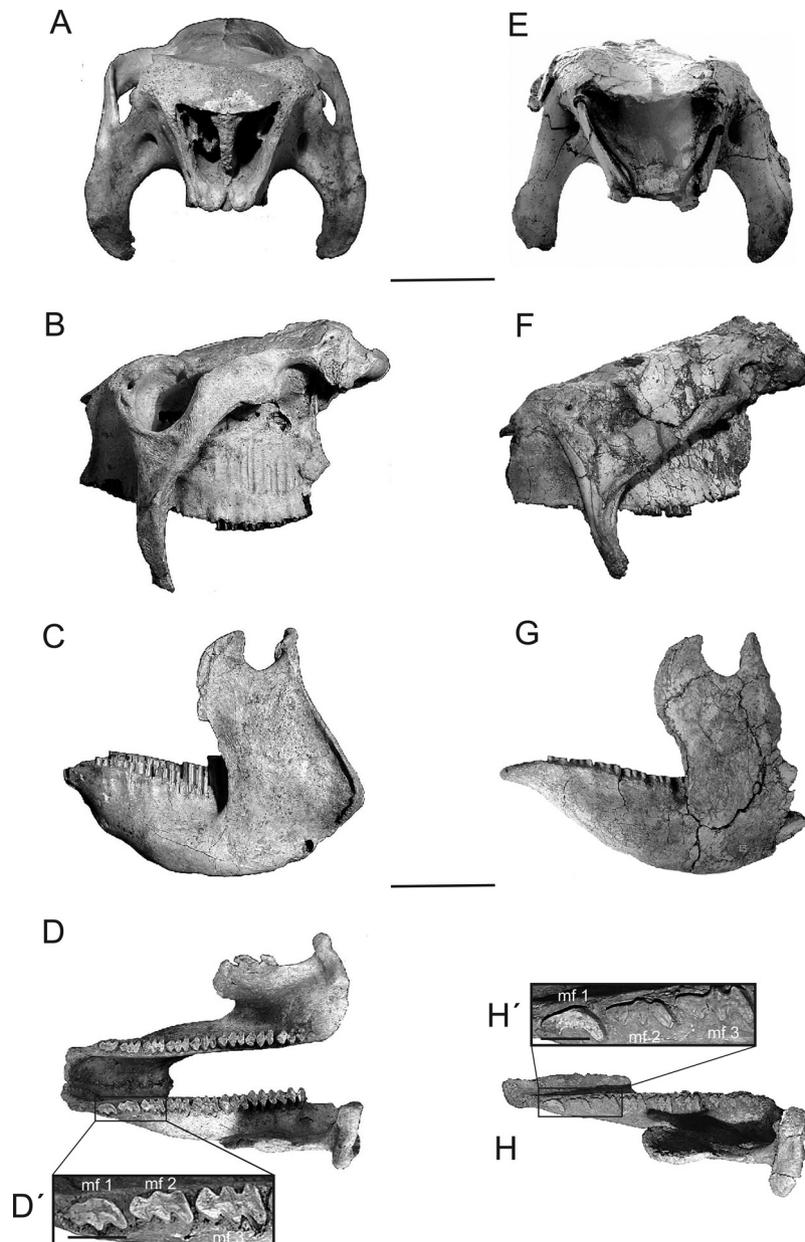


Fig. 2. A–D, D'. *Glyptodon munizi* Ameghino (MMP 3985): skull in frontal (A) and lateral (B) views; mandible in lateral (C) and occlusal (D) views, showing a detail of the mfs 1–3 (D'). E–H, H'. *Glyptotherium texanum* Osborn: skull AMNH FAM 95,737 in frontal (E) and lateral (F) views; mandible MSM 4818 in lateral (G) and occlusal (H) views, showing a detail of the mfs 1–3 (H'). Scale bars: 100 mm (A–H), 20 mm (D', H').

(Fig. 3(C, D, F)). The osteoderms that constitute the caudal aperture are, in general, mainly conical in *Glyptodon* and more rounded in *Glyptotherium*. Gillette et al. (2016) postulated for *Glyptotherium* that adult specimens having strongly conical osteoderms are males and those with less conical osteoderms are females. This anatomical feature differs in the South American *Glyptodon*, in which the morphology of these osteoderms seems to be related to the ontogenetic stage of the specimens (Zurita et al., 2010, 2011b).

Osteoderms (Fig. 4(A–D)). The morphology observed on the exposed surfaces of the osteoderms of the dorsal carapace has been used as a main source of diagnostic characters to separate *Glyptodon* from *Glyptotherium*. Our comparative study shows that some of the most frequently used characters to recognize both genera are questionable, because of considerable overlapping (contra Soibelzon et al., 2006; Oliveira et al., 2010). Among them:

- the number of peripheral figures is similar in both genera (5 to 11);
- some osteoderms of *Glyptotherium* are as thick as those observed in *Glyptodon*, reaching up to 47.17 mm (e.g., MSM P4041);
- the exposed surface of the osteoderms may show the same degree of rugosity in *Glyptodon* and *Glyptotherium*.

However, some characters of the osteoderms, especially concerning the morphology of the radial and peripheral sulci, are consistently diagnostic. Among them:

- usually, the central and radial sulci are deeper and broader in *Glyptodon* (ca. 4–6 mm) than in *Glyptotherium* (ca. 1–2.4 mm; e.g., in *G. texanum* AMNH 59,589, and *G. cylindricum* AMNH 15,548);

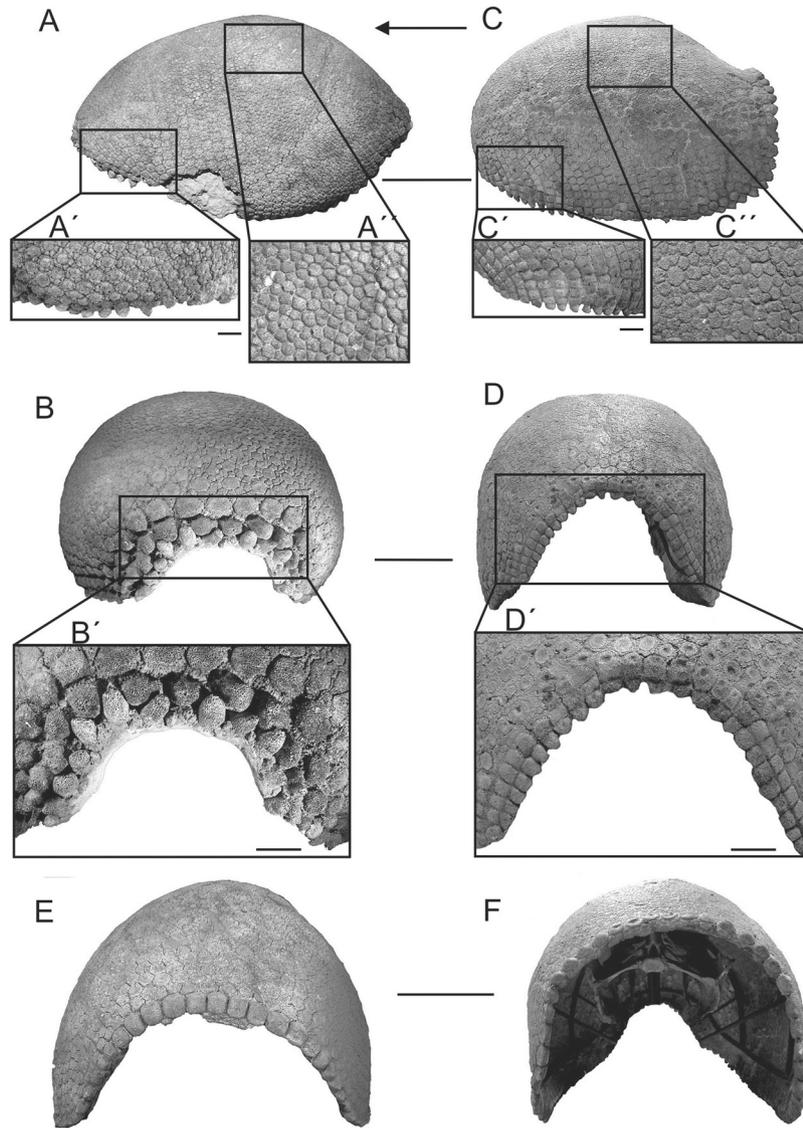


Fig. 3. A, A', A'', B, B', E. *Glyptodon reticulatus* (MCA 2015): dorsal carapace in lateral (A), frontal (B) and posterior (E) views, with detail of the latero-anterior (A') and dorsal (A'') regions, and cephalic notch (B'). C, C', C'', D, D', F. *Glyptotherium cylindricum* (AMNH 15548): dorsal carapace in lateral (C), frontal (D) and posterior (F) views, with detail of the latero-anterior (C') and dorsal (C'') regions and cephalic notch (D'). The arrow indicates anterior in A and C. Scale bars: 300 mm (A-F), 30 mm (A', A'', B', C', C'', D').

- the ornamentation pattern of the dorsal region of the dorsal carapace of *Gl. cylindricum* and *Gl. texanum* always have a “rosette” pattern (i.e., a central figure surrounded by a row of peripheral figures) and occasionally small and intercalated figures with sulci that intersect corresponding sulci on adjacent osteoderms, but do not reach the central figure (Gillette et al., 2016; Fig. 3(C'')).

In *G. reticulatus*, this pattern can vary from a “rosette” pattern in some specimens (e.g., MCA 2017) to a complete reticular pattern (Fig. 3(A'')) where the central and peripheral figures are very convex, having the same size (e.g., MCA 2015), and cannot be easily distinguished between each other.

Caudal armor (Fig. 4(E, F)). As in all Glyptodontinae, the caudal armor is composed of a series of caudal rings ending in a short caudal tube, but the morphology differs between genera. Generally, the morphology of the caudal armor of *Glyptotherium* is more like that of *Boreostemma* (Zurita et al., 2013). The caudal armor is longer in *Glyptotherium* (Fig. 4(F)) than in *Glyptodon* (Fig. 4(E)). In *Glyptotherium*, the caudal armor length represents ca.

50% of the total length of the dorsal carapace, whereas in *Glyptodon*, this value ranges between 30 and 40%. *Glyptodon* has 8–9 complete caudal rings plus one caudal tube, but *Glyptotherium* has 1 incomplete caudal ring, 8–9 complete caudal rings and a caudal tube. In both genera, each caudal ring is composed by two or three transverse rows of ankylosed osteoderms, where the distalmost row of osteoderms shows a more or less developed conical morphology. In *Glyptotherium*, it is possible to observe in some specimens (e.g., AMNH 95,737) a low number of conical osteoderms (generally two). This is different from *Glyptodon*, in which most osteoderms of the distal row (up to 12) present a clear conical morphology. The terminal caudal tube is shorter in *Glyptodon*. In *Glyptotherium*, the terminal tube is composed of 2–3 ankylosed rings (Fig. 4(F')), whereas in *Glyptodon*, it has only two ankylosed rings (Fig. 4(E')). In *Glyptotherium*, this caudal tube represents ca. 20% of the total length of the caudal armor, whereas in *Glyptodon*, this structure represents 13% of the total length. The conical osteoderms are very prominent in *Glyptodon* and less pronounced in *Glyptotherium*. As mentioned above, the morphology of these osteoderms has been interpreted by Gillette et al.

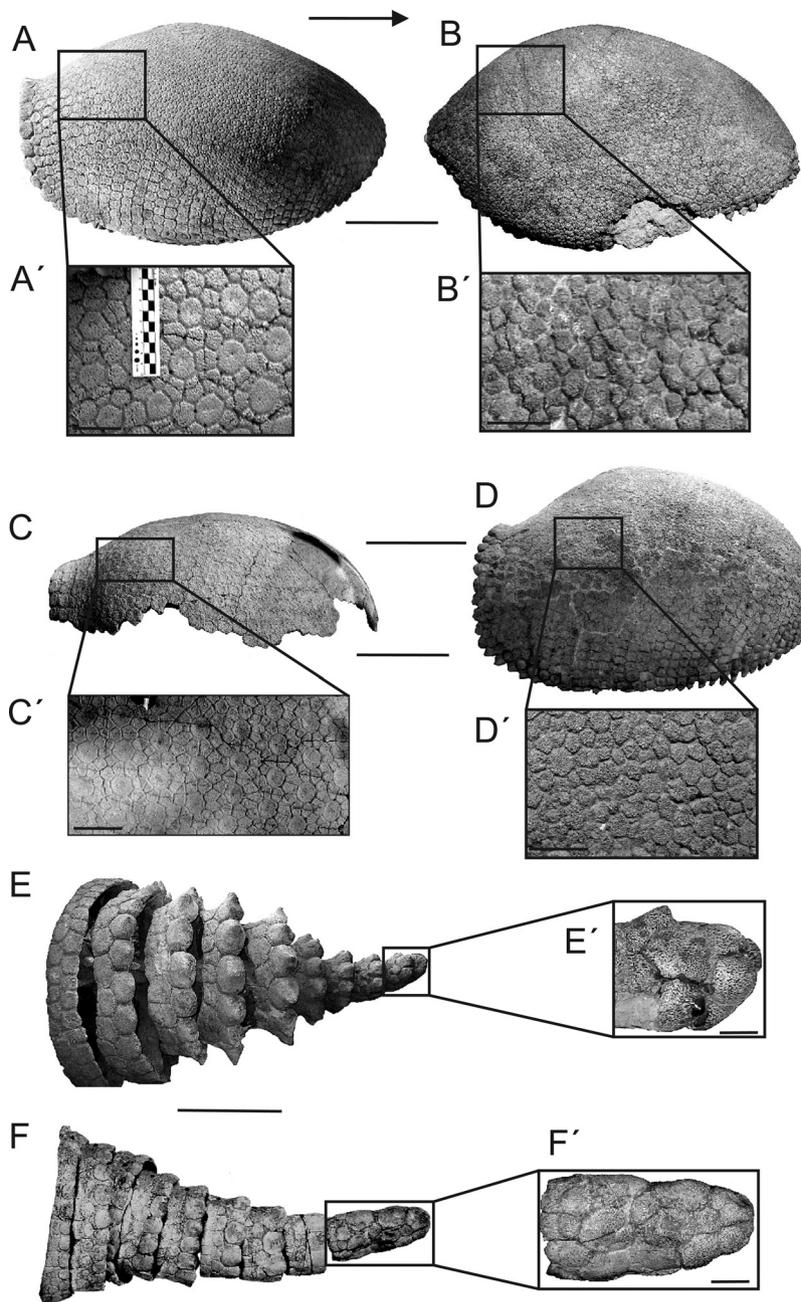


Fig. 4. A, A', B, B'. Dorsal carapace of *Glyptodon munizi* (MMP 3985 (A) and *Glyptodon reticulatus* (MCA 2015) (B) in lateral view, showing a detail of the exposed surface of the osteoderms (A', B'). C, C', D, D'. Dorsal carapace of *Glyptotherium texanum* (MSM P 4465) (C) and *Glyptotherium cylindricum* (AMNH 15548) (D) in lateral view, showing a detail of the exposed surface of the osteoderms (C', D'). E, E', F, F'. Caudal armor of *Glyptodon munizi* (MMP 3985) (E) and *Glyptotherium texanum* (AMNH 21808) (F), showing a detail of the terminal caudal tube (E', F'). Scale bars: 300 mm (A–F), 30 mm (A'–F').

(2016) as indicating sexual dimorphism in *Glyptotherium*; however, in *Glyptodon*, this is clearly related to the ontogenetic stage of the individuals (Zurita et al., 2011a).

5. Discussion

The evolutionary history of *Glyptodon* (Fig. 5(A)) and *Glyptotherium* (Fig. 5(B)) shows some concordances, although some differences can be recognized. According to the available evidence, the earliest record of *Glyptotherium* (ca. 3.9 Ma) seems to be much older than the earliest record of *Glyptodon* (ca. 1.07 Ma). However, our preliminary observations (in agreement with Cruz et al., 2016) show some interesting characters shared between *Glyptodon* and “*Paraglyptodon uquiensis*”, supporting the hypothesis that the skull

MACN PV 5377 (lectotype of “*P. uquiensis*”) could belong to *Glyptodon*. If true, the oldest records of *Glyptodon* would come from the Pliocene of southern South America, indicating a chronological scenario similar to that of *Glyptotherium* in Central and North America.

From a morphological perspective, as shown above, the two genera differ, especially at the level of the skull, dorsal carapace and caudal armor, but the appendicular skeletons are similar. The southern forms of *Glyptodon* (*G. munizi* and *G. reticulatus*) seem to be somewhat larger than *Glyptotherium* (i.e., the dorsal carapace of *G. cylindricum* (AMNH 15,548) is 14% shorter than that of *G. reticulatus* (MCA 2015)). In this context, some remarks can be pointed out in the morphological evolution of *Glyptodon* and *Glyptotherium*, even if both evolved in two completely different

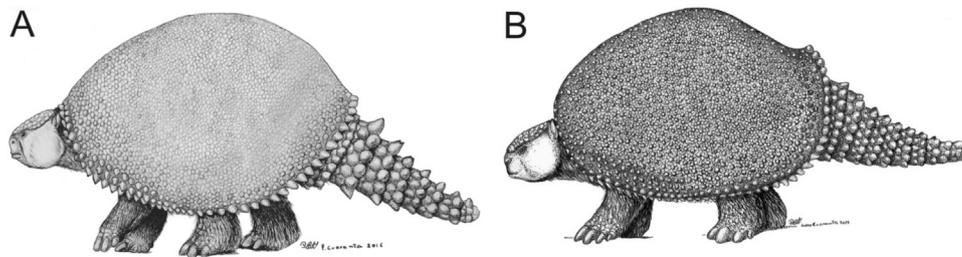


Fig. 5. Reconstruction of *Glyptodon* Owen (A) and *Glyptotherium* Osborn (B).

biogeographical and ecological contexts (McDonald, 2005). In southern South America, *Glyptodon* was sympatric with high diversity of the overall glyptodont fauna (e.g., *Neosclerocalyptus*, *Doedicurus*, *Panochthus* and *Neuryurus*) and a variety of armadillos and pampatheres (Carlini and Scillato-Yané, 1999). In contrast, *Glyptotherium* was the only glyptodont genus in Central and North America, although Cingulata Pampatheriidae (Gois-Lima, 2013) and armadillos were also present and may have been secondary ecological competitors.

In *Glyptodon* and *Glyptotherium*, a similar morphological pattern is especially evident on the exposed ornamentation of the osteoderms of the dorsal carapace throughout their evolution in the Pliocene and Pleistocene. In fact, *G. munizi* and *Gl. texanum* are characterized by having a very well developed central figure which occupies more than 50% of the osteoderm exposed surface. In *G. munizi*, this pattern is especially evident in the lateral, posterior and anterior regions of the dorsal carapace (Fig. 4(A, A')), whereas in *Gl. texanum* it is regularly present along the entire dorsal carapace (Fig. 4(C, C')). In turn, in late Pleistocene species such as *G. reticulatus* (Fig. 4(B, B')) and *Gl. cylindricum* (Fig. 4(D, D')), the central figure becomes smaller compared to the peripheral ones, a feature especially evident at the dorsal region of the carapace.

With respect to overall individual size, *G. munizi* and *G. reticulatus* are somewhat larger when compared to *Gl. texanum* and *Gl. cylindricum*. The dorsal carapace of the specimen AMNH 15,548 (type of *Gl. cylindricum*) is 14% shorter compared to that of *G. reticulatus* (MCNC Pv 140). This is consistent with McDonald's (2005) proposal, according to which the immigrant xenarthrans to North America were smaller than the South American taxa. However, and as remarked by Gillette et al. (2016), there is no evidence of size changes through time from *Gl. texanum* to *Gl. cylindricum*, which are very similar. This situation seems to be different in other xenarthran immigrant clades (McDonald, 2005).

Another convergent evolutionary trait is the slow morphological change shown by both genera, although in South America, the only well-known Pleistocene Glyptodontinae are the southern forms *G. munizi* and *G. reticulatus*. Recent revisions of *Glyptotherium* (Ramírez-Cruz and Montellano-Ballesteros, 2014; Gillette et al., 2016; this study) indicate that this genus has only two end-point species: *Gl. texanum* (early Blancan to early Irvingtonian NALMAs) and *Gl. cylindricum* (late Rancholabrean NALMA). These two chronospecies differ only by minor changes in the osteoderm sculpturing of the carapace. Anagenesis is the best explanation for this highly conservative evolution, displaying limited but similar morphological change in superficial aspects of carapacial anatomy over a timespan of ca. 4 myr without cladogenesis (McDonald and Naples, 2007; Gillette et al., 2016). Perhaps one key point to understand this conservative morphological evolution, at least in *Glyptotherium*, is the fact that, according to Cody et al. (2010), it seems probable that the floristic habitat of South America was present in Central and North America at the beginning of the GABI, prior the arrival of these large armored herbivores. The presence of a similar (and somewhat stable over a long time interval) ecological scenario both in South and North America may have

promoted the slow morphological evolution observed in *Glyptotherium*.

In southern South America, a similar situation can be observed in *G. munizi* (early middle Pleistocene; ca. 1.07–0.78 Ma) and *G. reticulatus* (late Pleistocene), which are remarkably similar taking into account that both species are separated by ca. 1 myr (Soibelzon et al., 2006; Zurita et al., 2009). The main difference is in the dorsal carapace, which is slightly more elongated in *G. munizi* than in *G. reticulatus*. Supporting this interpretation, it is worth noting that the general morphology of the skull of the Pliocene species “*Paraglyptodon uquiensis*” does not show any significant difference compared to the Pleistocene *Glyptodon* species; in the cladistic analysis of Zurita et al. (2013), it appears as the sister species of *Glyptodon* spp. (see also Cruz et al., 2016). This conservative evolutionary history of *Glyptodon* and *Glyptotherium* contrasts with the faster cladogenetic histories of other southern South American clades such as the genus *Neosclerocalyptus*, in which it is possible to recognize four distinct chronospecies within ca. 2.5 myr. This fast morphological evolution could be related to its limited latitudinal distribution in southern South America (Zurita et al., 2011c). Also, related to the conservative nature of the evolution of *Glyptodon* and *Glyptotherium* is the negligible difference in size between the Pliocene and early Pleistocene forms (*Gl. texanum* and *G. munizi*) compared to their ‘terminal’ species (*Gl. cylindricum* and *G. reticulatus*, respectively). For example, the antero-posterior diameter of the dorsal carapace of *G. munizi* (MMP 3985) is 45% larger than that of *G. reticulatus* (MCA 2015). On the other hand, there is no size change in adult individuals of *Gl. texanum* through the late Pliocene and into terminal Pleistocene with *Gl. cylindricum*.

From a paleobiogeographic and systematic viewpoint, the situation of *Glyptodon* seems to be much more complex than that of *Glyptotherium*. In this sense, preliminary evidence suggests that the existence of an “Andean” lineage of *Glyptodon*, represented by a new species that was considerably smaller compared to the Pampean species *G. munizi* and *G. reticulatus*, as observed in the recently described species *Panochthus hipsilis* (Zurita et al., 2017).

Finally, in Central America, several glyptodont records have been reported in the last four decades (mainly including osteoderms, isolated molariforms and fragmentary skulls) in Costa Rica (Valerio et al., 2005; Mora et al., 2005; Valerio and Laurito, 2011), Panamá and Honduras (Webb and Perrigo, 1984; Lucas, 2008) and El Salvador (Cisneros, 2005). Most of the Central American material has been assigned to *Glyptotherium*, in agreement with our observations. Although the general morphology of both genera is similar, the Central America osteoderms show, in their exposed surfaces, shallower sulci compared to *Glyptodon*. One exception seems to be represented by the report of Lucas et al. (1997), who identified four small osteoderms from a site in northwestern Costa Rica as *Glyptodon* sp. Our analysis of those remains precludes any taxonomic identification because the exposed surfaces are quite damaged. We are confident that those osteoderms belong to the Order Cingulata, but generic assignment is not warranted. One of the osteoderms (Lucas et al., 1997: fig. 4A)

has deep sulci on its external surface that are “similar” to that observed in *Glyptodon*; nevertheless, by the size, sculpture and some morphological characters observed in the other osteoderms (e.g., Lucas et al., 1997: fig. 4C), a taxonomic assignment to *Neoglyptatelus* or *Pachyarmatherium* seems better. However, the scarcity of the material limits our observations. The only skull material known from Central America (e.g., AMNH 96366 from Guatemala) is also too fragmentary and should be classified as *Glyptodontinae* indet.

6. Conclusions

As observed, *Glyptodon* and *Glyptotherium* differ mainly at level of the skull, molariforms, mandible, contour of the dorsal carapace, morphology of the exposed surface of the osteoderms and length and morphology of the caudal armor. In overall size, *Glyptodon* is slightly larger than *Glyptotherium*. In turn, and from an evolutionary viewpoint, the overall lack of morphological change in both genera over a long period of time (nearly 4 myr in *Glyptotherium* and at least 1 myr for *Glyptodon*) is remarkable. In this sense, the oldest records of *Glyptotherium* are ca. 3.9 Ma (Pliocene) and 1.07–0.98 Ma (early middle Pleistocene) for *Glyptodon*. However, the record of *Glyptodon* could be older if “*Paraglyptodon uquiensis*” actually belongs to this genus, as we suspect. The occurrence of the genus in the Chapadmalalan Stage (Pliocene) of the Atlantic coast of Argentina is rejected. Finally, the diversity of Central and North American glyptodontines is restricted to *Glyptotherium*, with two successive chronospecies – *Gl. texanum* and *Gl. cylindricum*. In southern South America, the Pleistocene glyptodont diversity is under study, but preliminary evidence indicates that no more than three species could be considered as valid, plus a new species from the Andean region. In addition, in South America, *Glyptotherium cf. cylindricum* is present in northern Venezuela and eastern Brazil.

Bronn, 1838 and Roselli, 1976

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