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Late Pliocene Glyptodontinae (Xenarthra, Cingulata, Glyptodontidae) of South and North America: Morphology and paleobiogeographical implications in the GABI

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ABSTRACT

Knowledge of the main aspects of the Great American Biotic Interchange (GABI) concerning the glyptodontine Glyptodontidae (Xenarthra) is very scarce. A bidirectional dispersal process was recently proposed for this clade, with the presence of the North American genus *Glyptotherium* Osborn recognized in latest Pleistocene sediments of northern South America (Venezuela and Brazil). However, the earliest stages of this paleobiogeographical process remain poorly understood, mainly because of the limited fossil record on this clade in late Pliocene sediments. The goals of this contribution are: a) to present and describe the first record of a glyptodontine glyptodontid from the late Pliocene of northern South America, tentatively assigned to a new species of *Boreostemma* Carlini et al. (*Boreostemma*? sp. nov); and b) to analyze its paleobiogeographical implications with respect to the GABI. This new material was recovered from the San Gregorio Formation (late Pliocene, prior the GABI) in northern Venezuela, where it is represented by several osteoderms of the dorsal carapace. A comparison among the three known late Pliocene glyptodontine glyptodontids of a) southern South America (*Paraglyptodon*), b) northern South America (*Boreostemma*), and c) southern North America ("*Glyptotherium*"), reveals a series of shared characters between (b) and (c), not present in (a). The most important of these shared characters in (b) and (c) are: all the osteoderms present a great development of the central figure, which is always larger than the peripherals; the sulcus that delimits the central and peripheral figures is narrower and shallower; and all the osteoderms present are relatively thin. This evidence suggests that the lineage of Glyptodontine which participated in the GABI and subsequently diversified in North America originated in northern South America. Moreover, the evident morphological differences between these glyptodontines with respect to the southern South American forms show a significant separation of both lineages since at least latest Miocene-early Pliocene.

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1. Introduction

The glyptodontine Glyptodontidae (middle Miocene-early Holocene; ca. 12–0.0011 MybP) constituted one of the most conspicuous xenarthran taxa that were involved in the Great American Biotic Interchange (GABI) (Carlini et al., 2008a; Webb, 1985, 2006; Woodburne et al., 2006), reaching in North America as far as 36°37′N latitude (Czaplewski, 2004). Another group of Glyptodontidae, the Glyptatelinae, also participated in the GABI, but their success was poor compared with the glyptodontines (Downing and White, 1995; Carlini and Zurita, 2010). Paleobiogeographically, the Glyptodontinae are the most widespread among the Glyptodontidae, its range extending from southern Argentina to Oklahoma, approximately 22°S to 36°N (Gillette and Ray, 1981; Zurita et al., 2009).

From a morphological and phylogenetic perspective, the main synapomorphy of the glyptodontines is represented, among others,

by the distinctive "rosette" ornamentation pattern in the osteoderms of the dorsal carapace and caudal armor (Ameghino, 1889; Gillette and Ray, 1981; Soibelzon et al., 2006). In addition, the ventral border of the carapace presents a row of highly modified conical osteoderms, which could have had defensive functions (see Zurita et al., 2010).

In South America the earliest record of glyptodontines comes from the Middle Miocene-Pliocene interval (ca. 12−6 MybP) of northern areas (Venezuela and Colombia; ca. 11°−2°N), and were recently included in the new genus *Boreostemma* Carlini et al. (2008b). This genus could represent the first stage in the cladogenesis and radiation of the glyptodontine clade (Carlini et al., 2008b). Afterward, during late Miocene and Pliocene (Huayquerian - Marplatan SALMA) the glyptodontines reached southern areas (23°−38°S). The taxa are represented by *Glyptodontidium tuberifer* (Huayquerian SALMA of northwestern Argentina), *Paraglyptodon chapalmalensis* and cf. *P. chapalmalensis* (upper Chapadmalalian SALMA of central eastern Argentina) (Cabrera, 1944; Oliva et al., 2010), and *P. uquiensis* (Marplatan SALMA of northern Argentina) (Castellanos, 1953). Through the Pleistocene (ca. 2.6−0.0011 MybP), the genus *Glyptodon* Owen is among the most frequent of all glyptodonts in South America (Zurita et al., 2009).

In North America, the oldest record belongs to specimens identified as *Glyptotherium* from the Pliocene of central México (ca. 3.9 MybP; Carranza-Castañeda and Miller, 2004; but see comments in Carlini et al., 2008b); curiously, the subsequent records are from the middle-late Blancan NALMA (Late Pliocene) of southern USA (*Glyptotherium texanum*; ca. 2.6 MybP; Gillette and Ray, 1981), more than one million years younger. Later, during the Irvingtonian and Rancholabrean NALMAs (early Pleistocene - late Pleistocene) the genus considerably expanded its geographical range southward, from 36°N to the current nations of Panama, Honduras, El Salvador and Costa Rica (13−14°N) (Webb and Perrigo, 1984; Jackson and Fernandez, 2005; Cisneros, 2005; Mora et al., 2005). Carlini et al. (2008c) reported the first records of *Glyptotherium* (*Glyptotherium* cf. *G. cylindricum*) in the latest Pleistocene (ca. 12 ka) of northern South America. This occurrence indicates a bidirectional faunal expansion during later stages of the GABI and the repeated re-immigration of South American clades from North America (Scillato-Yané et al., 2005; Carlini et al., 2008a; Carlini and Zurita, 2010). Nevertheless, knowledge of the earliest stages of this process in this clade is still poorly developed (Carlini and Zurita, 2010). This is mainly due to the fact that, until now, the only two late Pliocene glyptodontines (chronologically close to the GABI) were restricted to southern South America and southern North America.

In this context, Carlini et al. (2008c) reported the first records of Glyptodontinae from the late Pliocene of northern South America (Estado Falcón, Venezuela; 11°12′N, 75°15′W), consisting of numerous osteoderms of the dorsal carapace obtained from the San Gregorio Formation (Fig. 1). In addition, new and significant material referred to cf. *Glyptotherium texanum* has been recovered from the 111 Ranch locality (late Pliocene of Arizona, USA). The newly collected specimens from 111 Ranch include partial skeletons of young, juvenile, and adult individuals and permit preliminary analysis of ontogenetic changes with growth.

In this scenario, the main goals of this contribution are: 1- to present and describe the first record of a new glyptodontine glyptodontid from the late Pliocene of northern South America (*Boreostemma*? sp. nov); 2- to make a precise comparison of osteoderms anatomy among the three best known late Pliocene glyptodontines; 3- to analyze the attendant paleobiogeographic and phylogenetic implications in the context of the GABI.

2. Morphology, taxonomy, chronology and paleobiogeography of the late Pliocene Glyptodontinae

2.1. Southern South America

The Pliocene Glyptodontinae of southern areas of South America are included in the genus *Paraglyptodon* (Chapadmalalan-Marplatan
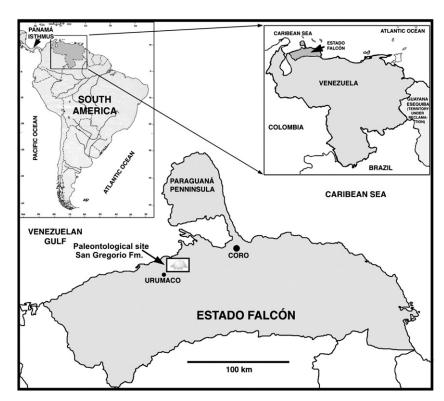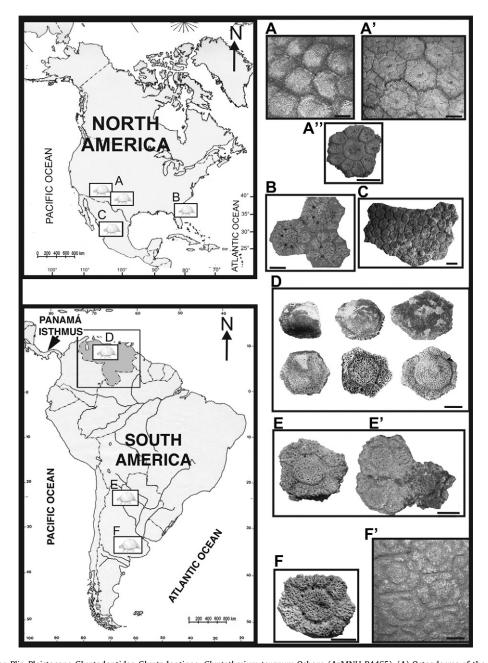

Fig. 1. Map showing the locality where the type specimen of *Boreostemma*? sp. nov. was recovered.

SALMA; ca. 3.8–1.8 MybP) (see Oliva et al., 2010). The only late Pliocene species is *Paraglyptodon uquiensis*, recovered from the Uquía Formation (Esquina Blanca de Uquía, Jujuy province; 23°18′S, 65°21′W) (Castellanos, 1953) (Fig. 2 (E– E′)). Several lines of evidence strongly suggest that most of the remains of *P. uquiensis* are derived from the lower and middle levels of this geological unit (see Reguero et al., 2007). Therefore, the biochron of the species could be restricted to ca. 3.6–2 MybP. From a paleobiogeographical perspective, the paleofaunal association suggests a paleoecological scenario different from that inferred for the pampean region of Argentina (Reguero et al., 2007).

During the Pleistocene, the first reliable record of a glyptodontine corresponds to the Ensenadan species *Glyptodon munizi*.

Until now, this taxon has been recorded in "las toscas del Río de La Plata" and Mar del Plata localities (Buenos Aires province, Argentina) (ca. 1.07–0.98 MybP) (Soibelzon et al., 2006, 2008), and in the Ensenadan of Tarija Valley, Bolivia (Zurita et al., 2009) (Fig. 2 (F–F′)).

Paraglyptodon uquiensis was fully described and characterized by Castellanos (1953), who remarked on the similarity to the genus *Glyptodon* and its smaller size. The most useful elements comprise a partial skull and some osteoderms of the dorsal carapace and caudal armor belonging to the holotype (MACN 5330, 5332, 5344, 5355, 5377, 5396). A reanalysis of this material, including a comparison with the recognized species of the genus *Glyptodon* [*G. munizi* (MMP 3985), *G. reticulatus* (MCA 1086), *G. elongatus* and

Fig. 2. Location map of the Plio-Pleistocene Glyptodontidae Glyptodontinae. *Glyptotherium texanum* Osborn (AzMNH P4465). (A) Osteoderms of the anterolateral region of the dorsal carapace; (A″) Osteoderms of the lateral-dorsal region; (A′) Osteoderm of the dorsal region. *Glyptotherium floridanum* Simpson (AMNH 23556). (B) Osteoderms of the lateral region. *Glyptotherium* cf. *cylindricum* (CIAAP n/n) (C) Osteoderms of the central region. *Boreostemma?* sp. nov. (AMU-CURS n/n) (D) Osteoderms of the dorsal and lateral regions. *Paraglyptodon uquiensis* Castellanos (MACN 5330) (E) Osteoderm of the lateral-dorsal region; (E′) Osteoderms of the lateral region. *Glyptodon munizi* (MMP 3985). (F) Osteoderm of the dorsal region; (F) Osteoderms of the lateral region. Scale bar: 20 mm.

Glyptotherium [*G. texanum* (AMNH 1074, F: AM 59583), *G. arizonae* (UMMP 34826, AMNH 21808), *G. cylindricum* (AMNH 15548) and *G. floridanum* (AMNH 23547)] shows a clearer affinity with *Glyptodon* than *Glyptotherium*.

Despite its fragmentary state, the skull of *P. uquiensis* (MACN 5377) is similar to that of *Glyptodon*. As in this genus, the nasals and premaxillae are noticeably shortened. In frontal view, the nasal aperture has a subtrapezoidal shape, as in *Glyptodon*; the descending processes of the maxillae are clearly laterally expanded, having an evident transverse diameter, as in *Glyptodon* and different from *Glyptotherium* (see Castellanos, 1953; Gillette and Ray, 1981; Soibelzon et al., 2006); the infraorbital foramina have the same morphology and position as in *Glyptodon*; in dorsal view the rostral area located anterior to the plane of the descending processes of the maxillae presents a flat surface, with a morphology very similar to that observed in *Glyptodon* and different from *Glyptotherium* (see Gillette and Ray, 1981; Carlini et al., 2008a). In occlusal view, the palate only preserves the M3 and M4 molariforms, almost identical to those of *Glyptodon*. The ventral borders of the descending processes of the maxillae are more laterally expanded than in *Glyptotherium*, showing the same condition as *Glyptodon*.

Four osteoderms of the lateral-dorsal region (MACN 5330), one osteoderm of the anterior region (MACN 5344) (Fig. 2(E′)) and one of the central-dorsal (MACN 5330) (Fig. 2(E)) region of the dorsal carapace are among the best preserved elements. Also, one osteoderm of the caudal notch (MACN 5355) and two of the caudal armor (MACN 5332) are preserved. A comparative study with the corresponding osteoderms of *Glyptodon* suggests a marked similarity. In both taxa, the osteoderms of the lateral-dorsal region have a central figure that occupies approximately 50% of the exposed surface, which is clearly punctate, as in *Glyptodon*. In both taxa, the sulci that divide the central and peripheral figures are wider and deeper than those of *Glyptotherium*, morphologically very similar to those of *Glyptodon* (Fig. 2(F–F′)) (see Ameghino, 1889; Gillette and Ray, 1981; Soibelzon et al., 2006). The osteoderm of the central-dorsal region has the same morphology observed in *Glyptodon* (see Fig. 2 (E–F)).

2.2. Southern North America

The latest systematic revision by Gillette and Ray (1981) placed all the Glyptodontinae from Central and North America in the genus *Glyptotherium*, with five species: *G. texanum* (2.7–2.2 MybP) (Fig. 2 (A–A″)), *G. arizonae* (2.2–1.0 MybP), and *G. cylindricum* (Fig. 2C)), *G. mexicanum* and *G. floridanum* (Fig. 2(B)) from the Rancholabrean NALMA (late Pleistocene).

As mentioned, the chronology of the arrival of the first glyptodonts into North America was recently updated by Carranza-Castañeda and Miller (2004) and Flynn et al. (2005), who reported the presence of the Glyptodontinae in north-central Mexico in Pliocene sediments (ca. 3.6–3.9 MybP); unfortunately the remains, consisting of isolated osteoderms, were not illustrated. Subsequently, definitive glyptodontine remains occur next at the 111 Ranch locality (Arizona), and in the Blanco beds of western Texas (Gillette and Ray, 1981). Traditionally, this sedimentary sequence was dated at approximately 2.6 MybP (late Blancan NALMA) (Morgan and White, 2005).

Taxonomically, those earlier glyptodonts are included in the basal species *Glyptotherium texanum*, the sister taxon of the remaining species of the genus *Glyptotherium* (Gillette and Ray, 1981). *Glyptotherium texanum* is the best represented species, known from complete dorsal carapace, caudal armor, caudal vertebrae, pelvis, and chevrons (AMNH 10704 holotype) and additional material, mainly osteoderms, listed by Gillette and Ray

(1981) from western Texas; and carapace (F: AM 59581, 59599), skull (F: AM 59583), nearly complete mandible, skeleton, and carapace, (F: AM 95737), and additional isolated elements (Gillette and Ray, 1981). New and significant material referred to *Glyptotherium texanum* was recently collected from the 111 Ranch locality by field crews led by Richard White. This new material, currently under study, consists of a partial carapace, isolated osteoderms, mandible with dentition, caudal vertebrae and armor, forelimb, pelvis, and sacrum (AzMNH P4818) (Fig. 2(A–A″)); a partial carapace of a young individual (AzMNH P3875), a nearly complete dorsal carapace, isolated osteroderms (AzMNH P4465); and a variety of isolated osteoderms and noncarapacial elements. In addition to *G. texanum*, the following discussion includes the hypodigm of *G. arizonae* (Gillette and Ray, 1981).

The morphology of the exposed surface and thickness of the osteoderms of the Plio-Pleistocene southern South America glyptodontines (*Paraglyptodon uquiensis* and *Glyptodon* spp.) and the North American *Glyptotherium* are very different. In *Glyptotherium*, the sulci that divide the central and peripheral figures are always narrower and shallower than in *P. uquiensis* and *Glyptodon*. In *Glyptotherium texanum* and *G. arizonae* the central figure is always larger than the peripherals, even at the level of the most dorsal ones of the carapace (Fig. 2(A″)) (see Gillette and Ray, 1981: 169; Zurita et al., 2008); this condition represents a primitive morphology for the Glyptodontinae (see Carlini et al., 2008b). On the contrary, in *P. uquiensis*, *Glyptodon munizi* and *G. reticulatus*, the central figures are almost the same size as the peripherals in the central-dorsal region of the carapace, but larger in the lateral areas of the dorsal carapace. In addition, the thickness of individual osteoderms (measured from the interior surface of osteoderm to its external surface) of *G. texanum* and *G. arizonae* never reaches the conspicuous thickness observed in *Glyptodon*. In *Glyptodon reticulatus*, the osteoderms of the lateral region of the dorsal carapace reach ca. 21 mm in thickness while in *Glyptotherium* cf. *G. cylindricum* and *G. floridanum* these reach a thickness of ca. 13–17 mm.

Dimensions taken directly from non-marginal osteoderms in the 111 Ranch fauna (*Glyptotherium texanum*) (Fig. 2(A–A″)) provide a thickness ratio (side-to-side diameter/thickness) of 2.7–2.8 for adults, and 2.0–2.1 for the young individual. This range indicates allometric growth, with greater ontogenetic increase in width than thickness of individual osteoderms.

On the other hand, the skull morphology is very different among *P. uquiensis*, *Glyptodon* and *Glyptotherium* (see Castellanos, 1953; Gillette and Ray, 1981; Carlini et al., 2008a; Zurita et al., 2008).

2.3. Northern South America

The phylogeny of the Glyptodontidae Glyptodontinae has been newly reinterpreted by Carlini et al. (2008b), who demonstrated that the Miocene-Pliocene glyptodonts (ca. 12–6 MybP) traditionally included in the subfamily Propalaehoplophorinae (*Asterostemma* spp.) are now seen as basal Glyptodontinae (*Boreostemma* spp.). Their arrival in southern areas coincides with the maximum geographic spread of the "Edad de las Planicies Australes" ("Age of the southern plains") (see Pascual and Bondesio, 1985). More precisely, the evidence suggests that the earliest southern glyptodontine records are from the latest Miocene or Pliocene (ca. 7 MybP), when these plains would have reached their maximum extension, spreading from northern Patagonia to Venezuela (Marshall et al., 1983; Ortiz Jaureguizar and Cladera, 2006).

The glyptodontines from the late Pliocene of northern South America were previously unknown. Until now, the youngest record corresponded to *Boreostemma pliocena*, from El Jebe Member of the Codore Formation (Carlini et al., 2008a). According to Linares (2004), on the basis of the mammalian fauna, an age

corresponding to the Monthermosan SALMA was assigned (late Miocene-early Pliocene) for the El Jebe Member of the Codore Formation, suggesting a probable age of 6 MybP for the contact between the Urumaco and Codore formations. In this context, Paula Couto (1983) had reported the presence of cf. *Paraglyptodon* in late Pliocene (?) sediments from northwestern Brazil, but the bad state of preservation of the osteoderms only allow us to classifythem as belonging to Glyptodontidae Glyptodontinae indet.

Recently, Carlini et al. (2008c) presented the first records of a late Pliocene (in sediments younger than those of Codore Fm.) glyptodontine from northern South America. The remains, represented by several osteoderms of the dorsal carapace (AMU-CURS n/n), are from the San Gregorio Formation (Urumaco area, Falcon State, Venezuela) (Figs. 1–2). This unit overlaps the Codore Formation and it is considered late Pliocene in age (see González de Juana et al., 1981; Rey, 1990), in that it lacks evidence of Holarctic taxa. The fauna suggests that this unit is chronologically earlier than the main phase of the GABI, in which glyptodonts are involved (see Woodburne et al., 2006). This new material includes: a) six osteoderms of the most anterior-ventral region; b) five osteoderms of the anterior-lateral region; c) one highly modified "conical" osteoderm that constitutes the ventral margin; d) two osteoderms of the dorsal region (Fig. 3).

The morphology of the osteoderms suggests tentatively that this carapace must be included in a new species of the genus *Boreostemma* (*Boreostemma*? sp. nov). As in *Boreostemma pliocena*, the exposed surface is extremely punctate, but even more prominent in this new taxon, and the central figure is always larger than the peripherals. The radial and annular sulci are less developed (shallower) compared with *Paraglyptodon uquiensis* and *Glyptodon*, but somewhat wider (ca. 3 mm) than in *B. pliocena* (ca. 2 mm). Compared with *B. pliocena*, the osteoderms are approximately 13% larger (see description below), having almost the same thickness (ca.16–11 mm) than in *B. pliocena* (see Carlini et al., 2008b). Future discoveries of more complete remains, together with a comprehensive phylogenetic and taxonomic analysis of the southern and northern forms of glyptodontines, will allow future analysis to refute or accept this taxonomic hypothesis.

On the other hand, a comparative study with the late Pliocene glyptodonts from southern South America (*Paraglyptodon uquiensis*) and southern North America, *Glyptotherium texanun* (AMNH 10704, holotype from western Texas) and *G. texanum* from the 111 Ranch fauna from southern Arizona, reveals a series of shared characters between the late Pliocene Glyptodontinae from southern USA and this new glyptodontine from the late Pliocene of Venezuela; these characters are not present in either *P. uquiensis* or *Glyptodon* (Pleistocene).

The osteoderms of the Venezuelan San Gregorio fauna are categorized into five groups according their location in the dorsal carapace:

Fig. 3. *Boreostemma*? sp. nov. (AMU-CURS n/n). (A) Osteoderms of the most anterior-ventral region of the dorsal carapace (six in external view, one in lateral view). (B) Osteoderms of the antero-lateral region of the carapace. (C) Osteoderms from the latero-dorsal region of the carapace (two in external view, one in lateral view). (D) One highly modified conical osteoderm corresponding to the lateral margin of the carapace. Scale bar: 20 mm.

a) Six osteoderms of the most anterior-ventral region of the carapace. The larger ones are 44 mm by 38 mm in diameter, and 15 mm thick, while the smaller are 39 mm by 33 and 14 mm, respectively. One is hexagonal, the others are pentagonal. The dorsal surfaces are extremely punctuate, and having a large convex central figure, occupying more than the 90% of the exposed surface; only the anterior peripheral figures are developed. This general morphology is almost identical to that observed in *Glyptotherium texanum* (Fig. 3(A)).

b) Six osteoderms correspond to the anterior-lateral region of the carapace. The larger one measures 58 mm by 51 in diameter and 13 mm thick, while the smaller ones are 49 mm by 44 mm and 12 mm thick. All are hexagonal and the exposed surfaces are clearly rugose and punctate. The central figure is well developed and much larger than the peripheral figures, as in *G. texanum*. The central figure is convex, a character that is variable in *G. texanum* in which the central figure is slightly raised above the level of the peripheral figures and convex to weakly concave. As in *G. texanum* the sulci are clearly much less developed than in *P. uquiensis* and *Glyptodon* (Fig. 3(B)).

c) One highly modified conical osteoderm corresponds to the ventro-lateral margin of the carapace, and represents a synapomorphy for the subfamily Glyptodontinae (see Ameghino, 1889; Duarte, 1997; Zurita et al., 2010). It measures 63 mm by 61 mm in diameter and 19 mm thick (Fig. 3(D)).

d) Osteoderms from the dorsal region of the carapace (Fig. 3C). The largest one measures 54 mm by 48 mm in diameter and 10 mm thick, while the smallest has 49 mm by 40 mm and 11 mm thick. These dimensions are different from those of *P. uquiensis*, in which the homologue region presents smaller but thicker osteoderms (ca. 37 mm by 31 mm in diameter and 16 mm thick). In *P. uquiensis*, the central-dorsal osteoderm reaches 21 mm thick, while in *Glyptodon* are even thicker. As in *G. texanum*, the sulcus presents the same morphology; in turn, this is very different from *P. uquiensis*, in which the morphology is much more similar to that observed in *Glyptodon*.

In sum, the shared characters between the northern South American and the southern North American taxa may be listed as follows: a) all the osteoderms present a great development of the central figure, which is much larger than the peripheral ones, representing a primitive condition seen in *Boreostemma*; in *P. uquiensis* and the basal species of *Glyptodon* (*G. munizi*) the central figures become larger toward the posterior, anterior and lateral regions of the dorsal carapace, while in the central area this central figure seems to be as large as the peripheral ones; b) the annular and radial sulci that delimit the central and peripheral figures are much narrower and shallower than in *P. uquiensis* and *Glyptodon munizi*; this particular morphology is preserved in derived species of *Glyptotheriun* (*G. arizonae*, *G. cylindricum*, *G. mexicanum* and *G. floridanum*) (see, among others, Osborn, 1903; Simpson, 1929; Gillette and Ray, 1981); on the contrary, in derived species of *Glyptodon* (e.g., *Glyptodon reticulatus*) the annular and radial sulcus become deeper and more pronounced (Duarte, 1997; Zurita et al., 2010); c) in *P. uquiensis* the preserved osteoderms seem to be smaller, but thicker than those of *G. texanum*. In fact, the relationship between the maximum diameter and the thickness of the osteoderms of the lateral-dorsal and dorsal regions of the carapace is approximately 4.4–5.4 in *Boreostemma*? sp. nov., while this ratio reaches 3.9–2.9 in *B. pliocena*, and 2.3–2.5 in *P. uquiensis*, very close to that observed in *Glyptodon* (ca.2.3–2.1). In *Glyptotherium texanum* this ratio is approximately 3.2–3.4 for adult individuals, closer to the Pliocene species of *Boreostemma* than that observed in *Paraglyptodon* and *Glyptodon*.

Currently, a more comprehensive systematic analysis, including the complete diversity of glyptodontine cingulatans is in process. This will clarify the taxonomic status of these earlier glyptodonts.

3. Discussion

3.1. The glyptodonts and the GABI

As pointed out by McDonald (2005), the xenarthrans were perhaps the most successful South American elements not only participating in the GABI, but having a radiation in North America; some groups, such the tardigradan *Megalonyx* reached as far north as Alaska and Northwest Territories of Canada (McDonald et al., 2000). Despite considerable work concerning the GABI and the Xenarthra, especially Tardigrada (see, among others, Carranza-Castañeda and Miller, 2004; Morgan, 2005; White and Morgan, 2005; Webb, 2006; Woodburne, 2010), the understanding regarding this paleobiogeographical process concerning the Cingulata (especially glyptodonts) is much more limited (Carlini and Zurita, 2010). Until recently, knowledge of the North and Central American Plio-Pleistocene glyptodonts was summarized in Gillette and Ray (1981), in which the evolution of the Glyptodontinae was seen mostly as an anagenetic process (McDonald and Naples, 2007). This evolutionary process has been ascribed to other clades of Xenarthrans, such us the Tardigrada Mylodontidae (Flynn et al., 2005).

Taxonomically, all the North and Central American members of the Glyptodontinae were included in the genus *Glyptotherium* (ca. 2.7 MybP–0.0011 MybP), with *G. texanum* (ca. 2.7–2.2 MybP) the basal species. New lines of evidence stimulated by the recovery of new material from the 111 Ranch fauna suggest that additional taxonomic revision of North American glyptodonts is warranted, tentatively indicating that the earlier taxa (*G. texanum* and *G. arizonae*) are more closely related to each other than to later taxa, and these two groups might be reasonably distinguished as separate genera (Gillette et al., in prep.). Apparently, the northern limit of *Glyptotherium* was reached by *G. arizonae* (36°37′N); later, the glyptodonts disappeared in the USA between the end of the early Irvingtonian (ca. 1 MybP) and the beginning of the Rancholabrean NALMA (late Pleistocene) (Morgan, 2005). However, they are recorded in this interval in southern areas such as the current territory of El Salvador, Central America (Cisneros, 2005), suggesting a possible retraction of the glyptodont fauna to southern areas during glacial times (Morgan, 2005; Mead et al., 2006).

Gillette and Ray (1981) considered the basal *G. texanum* as much smaller (ca. 230 kg) than *G. arizonae* (ca. 800 kg); but the newly recovered specimens from the 111 Ranch fauna indicate that adult *G. texanum* were as large as adult *G. arizonae*. Interestingly, the Ensenadan (early-middle Pleistocene) South American *Glyptodon munizi* had a much larger body size than its predecessor, *P. uquiensis*. It is possible to postulate that the biochron of *G. munizi* coincided with the arrival of some of the largest predators ever to inhabit South America and that the increase in size of *G. munizi* represents a reaction to the arrival of *Smilodon* and *Arctotherium* (Carnivora, Mammalia) (Zurita et al., 2010). These and related predators were present in North America with the arrival of the first wave of South American immigrants involved in the GABI and might have stimulated a similar increase in body size in *Glyptotherium*.

A few years ago, Carranza-Castañeda and Miller (2004) and Flynn et al. (2005) recorded the presence of the Glyptodontinae in north-central Mexico at ca. 3.9 MybP (middle Blancan NALMA), suggesting an earlier arrival into North America than previously thought. In addition, Carlini et al. (2008a) have made a reinterpretation of the GABI, at least for some xenarthran cingulates (Pampatheriidae and *Glyptotherium*). These taxa seem to have re-entered South America during the late Pleistocene, suggesting

a bidirectional migration process during the GABI. The population expansions manifested by these cingulates could be associated with the existence of lowland "corridors" that would have connected the Florida peninsula with Mexico, and/or Central America and the northern extreme of South America (Morgan and Hulbert, 1995; Webb, 2006). These lowland "corridors" would have developed during the LGM (Last Glacial Maximum) when the sea level dropped up to 120–140 m below present sea level (Rabassa et al., 2005). The late dispersal of *Glyptotherium* into South America could have followed an "Atlantic route", reaching as far as 8°S, as indicated by Oliveira et al. (2009, 2010) who reported the presence of *Glyptotherium* in northeastern Brazil in late Pleistocene sediments.

Despite this and recent additions to knowledge concerning the GABI and glyptodontid cingulates, the available information about its earliest stages in South America remains poorly documented. This lack of data is due, in part, to the lack of fossil evidence in late Pliocene sediments that are chronologically close to the GABI. As mentioned, the phylogeny and some paleobiogeographical aspects of South American Glyptodontinae have been partially reinterpreted with the recognition that the most basal taxa correspond to *Boreostemma* spp., from the middle Miocene and Pliocene of northern South America. Subsequently, the northern glyptodontines reached southern areas of South America during latest Miocene-early Pliocene (see Carline et al., 2008a,b,c; Oliva et al., 2010).

In this paleobiogeographical context, the new specimens of Glyptodontinae (*Boreostemma*? sp. nov) from the late Pliocene of northern South America (Venezuela) prior the GABI allows us to greatly improve the knowledge about the earliest stages of this process. Until now, there have been so far neither hypotheses nor speculation about which group of South American Glyptodontinae could have participated in the GABI.

Comparative morphology suggests a close relationship between northern South American and southern North American taxa. This body of evidence suggests that the lineage of Glyptodontinae which participated in the GABI and diversified in North and Central America was closely linked with this newly recovered southern South American, late Pliocene glyptodont. Moreover, the evident morphological differences between these glyptodontines with respect to the southern South American forms shows a significant separation of both lineages since at least latest Miocene-earliest Pliocene. In fact, this separation may have occurred after the arrival in southern latitudes at some point in the latest Miocene (*Glyptodontidium tuberifer*) or early Pliocene (*Paraglyptodon chapalmalensis* and *Paraglyptodon* cf. *P. chapalmalensis*) (see Ameghino, 1908; Cabrera, 1944; Oliva et al., 2010). It is notable that while *Glyptodontidium tuberifer* (ca. 7 MybP), had well developed conical osteoderms of the caudal notch, these structures are not yet evident in *G. texanum* (ca. 2.7 MybP), but are prominent in *G. arizonae* (ca. 2.-1 MybP). In addition, differences in skull anatomy between *P. uquiensis* and *Glyptotherium texanum* support this hypothesis. Therefore, while the skull morphology of *P. uquiensis* "predicts" that of *Glyptodon* (see Soibelzon et al., 2006), *G. texanum* is morphologically closer to the more derived species of the genus (see Gillette and Ray, 1981).

4. Conclusions

1- The morphology of this new late Pliocene glyptodontine suggests its preliminary inclusion in a new species of the genus *Boreostemma* (*Boreostema*? sp. nov). Future discovery of more complete remains, together with a comprehensive analysis of the complete diversity of the Glyptodontinae will permit confirmation or refutation this taxonomic assignment.

2- Despite this, the comparison among the three best known late Pliocene Glyptodontinae shows a clear morphological affinity between the northern South America taxon (*Boreostemma*? sp. nov.) and the southern North America taxon (*Glyptotherium texanum*).

3- In turn, the southern South American form (*Paraglyptodon uquiensis*) is clearly different from these two taxa from northern South America and southern North America, respectively. Its morphology (especially that of the dorsal carapace and skull) is very similar to that observed in the Pleistocene (ca.1.7–0.0011 MybP) genus *Glyptodon*.

4- This evidence suggests that the origin of the lineage of Glyptodontinae that participated in the GABI and subsequently diversified in North America is located in northern South America.

5- Morphological differences between these glyptodontines with respect to the southern South American forms show a separation of both lineages since at least late Miocene-early Pliocene.

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