THE PLEISTOCENE GLYPTODONTIDAE GRAY, 1869 (XENARTHRA: CINGULATA) OF COLOMBIA AND SOME CONSIDERATIONS ABOUT THE SOUTH AMERICAN GLYPTODONTINAE

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ABSTRACT – Until recently, one well-characterized Pleistocene genus of the subfamily Glyptodontinae (Glyptodon ca. 1.08-0.0011 Ma) was recognized in South America. In recent times, some authors have demonstrated, through the re-analysis of material originally classified as Glyptodon Owen and Hoplophorus Lund, the presence of a second species belonging to the North American glyptodont Glyptotherium Osborn (ca. 58-12 ky BP), currently known from in Venezuela and Brazil. This situation implies the need for a new study, with modern taxonomic criteria, of those materials belonging to the Glyptodontinae, particularly in those territories where the knowledge of these taxa is scarce. Presented here is a new analysis of the Pleistocene Glyptodontidae from Colombia, including some taxonomic and paleobiogeographic remarks. The results show that the only reported Glyptodontidae specimens in Colombia belong to Glyptodon sp. In turn, the evidence suggests that only one single species of Glyptotherium is present in South America, currently assigned to Glyptotherium cf. Gl. cylindricum. However, a more accurate analysis is necessary to confirm or refute this taxonomic identification. To date, Glyptotherium present has been found only in an area parallel to the Caribbean Sea and the Atlantic Ocean (northern Venezuela and eastern Brazil), up to 20°S, and is always linked to lowlands. This geographic distribution agrees with the proposition of an eastern corridor during the Great American Biotic Interchange. Below this latitude, the only recorded glyptodontine corresponds to Glypton, which is also recorded in a strip parallel to the Cordillera de Los Andes reaching Colombia and Venezuela. Taking into account this distribution, the presence of this genus in Central America cannot be discarded.

Key words: taxonomy, South America, Pleistocene, Glyptodontinae, osteoderms.

RESUMO – Até pouco tempo, um único gênero endêmico do Plioceno pertencente à subfamília Glyptodontinae (Glyptodon ca. 1.08-0.0011 Ma) era reconhecido para a América do Sul. Recentemente, alguns autores têm demonstrado, através de novas análises do material originalmente classificado como Glyptodon Owen e Hoplophorus Lund, a presença de uma segunda espécie pertencente ao gênero norte-americano Glyptotherium Osborn (ca. 58-12 ka AP), atualmente presente na Venezuela e Brasil. Essa situação implica na necessidade de uma nova análise do material referente à Glyptodontinae, com um critério taxonômico mais moderno, especialmente em localidades onde o conhecimento do gênero é escasso. Na presente contribuição, é apresentada uma nova análise taxonômica dos Glyptodontidae encontrados na Colômbia, incluindo algumas observações taxonômicas e paleobiogeográficas. Os resultados demonstram que o único gênero do Glyptodontidae para a Colômbia pertence à Glyptodon sp. Porém, a evidência sugere que somente uma única espécie de Glyptotherium Osborn está presente na América do Sul, atualmente atribuída a Glyptotherium cf. Gl. cylindricum. Uma análise mais precisa é necessária para confirmar sua identificação taxonômica. Até agora, Glyptotherium está presente em uma faixa paralela ao Mar Caribenho e Oceano Atlântico (Norte da Venezuela e região oriental do Brasil), até 20°S, e sempre vinculado a terras baixas. Essa distribuição geográfica concorda com a proposta de um corredor oriental durante o Grande Intercâmbio Biotico Americano. Abaixo dessa latitude, o único registro de Glyptodontinae corresponde a Glypton, o qual também é registrado em uma faixa paralela a Cordilheira dos Andes, alcançando Colômbia e Venezuela. Levando em consideração essa distribuição, a presença desse gênero na América Central não deveria ser descartada.


INTRODUCTION

Knowledge of the geographic distribution of the Pleistocene family Glyptodontidae Gray, 1869 (Cingulata) in South America has recently been discussed and improved (see Carlini et al., 2008; Zurita et al., 2009; 2011a; Oliveira et al., 2009, 2010). To date, the evidence suggests that the main lineages of the Glyptodontidae show a particular paleogeographic pattern, because most of their records are restricted to southern areas of South America (Zurita et al., 2009). In fact, the largest diversity of Pleistocene Glyptodontidae is present in the current territory of the
Pampean region (Argentina) and adjacent areas, such as the Mesopotamian region and central-northern areas of Argentina, the western sector of Uruguay and southern Brazil; latitudinally, this area is located between 39°S and 20°S. This is especially evident in some taxa, such as the Doedicurinae (Doedicurus Burmeister, 1874 and Plaxhaplous Ameghino, 1884), “Hoplophorinae” Hoplophorini (Neosclerocalyptus Paula Couto, 1957), and Neuryurini (Neuryurus Ameghino, 1889) (see Carlini & Scillato-Yané, 1999; Rinderknecht, 1999; Pomi, 2008; Zurita et al., 2011c; Soibelzon, 2008; Soibelzon et al., 2010; Ubilla et al., 2004; Ribeiro & Scherer, 2009).

From a paleogeographic point of view, only three taxa are certainly recorded above 20°S (see Zurita et al., 2009). One particular intertropical Glyptodontidae, Hoplophorus Lund, 1839 seems to be restricted to about 20°S in the current territories of Brazil and Bolivia (see Hoffstetter, 1963; Paula-Couto, 1957; Pompino et al., 2010); Paula Couto (1983) reported Hoplophorus from the Acre region, Brazil, but the material (only one isolated osteoderm) has never been figured. Other taxa, the genus Panochthus Burmeister, 1866, had a wider geographic distribution, reaching probably from 49°S (Tauber & Palacios, 2007) to 5°S (Moreira, 1965; Pompino & Bergqvist, 2002; Pompino et al., 2004; Zamorano et al., 2012). The evidence suggests that Panochthus is a taxon with wide ecological tolerance, since its records come from arid/semi-arid/cold (Carlini & Scillato-Yané, 1999) and wetter and warmer environments (Carlini et al., 2008).

Besides this, the most recorded taxa in South America are the Glyptodontidae Glyptodontinae, since their latitudinal distribution ranges from southern Buenos Aires Province (Argentina) to Colombia and Bolivia (Carlini et al., 2008; Rincón et al., 2008) (Figure 1). Until recently, one well characterized genus, Glyptodon Owen, 1839, was recorded in South America. This situation changed after Carlini et al. (2008) and Oliveira et al. (2010) reinterpreted some latest Pleistocene specimens from Venezuela and Brazil, originally classified as Glyptodon and Hoplophorus, as belonging to the North American glyptodontine Glyptotherium Osborn, 1903 (see Gillette & Ray, 1981). As suggested by Carlini et al. (2008) and Carlini & Zurita (2010), this can be interpreted as the result of a bidirectional migratory pattern during the GABI.

This situation implies the need for a new revision of those materials belonging to Pleistocene Glyptodontinae in South America in order to clarify their taxonomy, especially in those territories where this group is poorly known. In particular, in South America, Colombia is one of the least known places regarding the presence of Pleistocene Glyptodontidae. The improvement in knowledge on the paleogeographic distribution of both taxa, Glyptodon and Glyptotherium, will allow us to hypothesize some considerations about the likely dispersal route of Glyptotherium in South America after its entry.

Therefore, this contribution aims to provide a taxonomic revision of the Glyptodontinae present in the Pleistocene of Colombia, and present some paleobiogeographic and taxonomic considerations about the genera Glyptodon and Glyptotherium.

**Institutional abbreviations.** AMNH, American Museum of Natural History, New York, USA; ICN, Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Bogotá, Colombia; IGM, Museo Geológico Nacional “José Royo y Gómez”, INGEOMINAS, Bogotá, Colombia; MCA, Museo de Ciencias Naturales “Carlos Ameghino”, Mercedes, Buenos Aires, Argentina; MCN, Museo de Ciencias, Caracas, Venezuela; MHNLS, Museo de Historia Natural de La Salle, Bogotá, Colombia; MALV, Museo Arqueológico Los Vados, Municipio de Los Patios, Departamento de Norte de Santander, Colombia; PVE-F, Colección Paleontológica de Villa Escolar, Formosa, Argentina; UNEFM- CIAAP, Universidad Nacional Experimental Francisco Miranda, Coro, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Venezuela.

**Other abbreviations.** n/n, without official catalog number; GABI, Great American Biotic Interchange.

![Figure 1. Geographic distribution of Glyptodon and Glyptotherium cf. Gl. cylindricum in South America. In Colombia: A, Pubenza, Tocaima, Cundinamarca; B, Los Patios, Norte de Santander, C, Santa Marta, Magdalena; D, Quebrada Las Lajas, Villavieja Village, Huila.](image-url)
SYSTEMATIC PALEONTOLOGY

Superorder XENARTHRA Cope, 1889
Order CINGULATA Illiger, 1811
Suborder GLYPTODONTIA Ameghino, 1885
Family GLYPTODONTIDAE Gray, 1869
Subfamily GLYPTODONTINAE Gray, 1869

Glyptodon Owen, 1839

Type species. Glyptodon clavipes Owen, 1839.

Glyptodon sp. (Figure 2 A-I)

Referred material and geographic and stratigraphic provenance. MALV-229, 845: two osteoderms of the dorsal carapace, Los Patios, Norte de Santander (a. 7°51’N, 72°29’W), Colombia; Pleistocene. MHNLS 2348, 2349: nine osteoderms of the dorsal carapace and one of the most lateral area, near the ventral margin (this material was referred by Bombin (1982) as Glyptodon clavipes Owen), El Rosario, Norte de Santander (7°51’N, 72°29’W) and Sierra Nevada de Santa Marta (Magdalena), Colombia; Pleistocene. ICN-PubA1 210-223, ICN-Pub07(01) 210-220, ICN-PubD 210-220, ICN-Pub 84 153, ICN-Pub 84 163: some osteoderms of the dorsal carapace, and many small and irregular osteoderms, Pubenza, Tocaima, Cundinamarca (a. 4°24’ N, 74°44’W), Colombia, latest Pleistocene. ICN-PubA1 210-223, ICN-Pub07(01) 210-220, ICN-PubD 210-220, ICN-Pub 84 153, ICN-Pub 84 163: some osteoderms of the dorsal carapace, and many small and irregular osteoderms, Pubenza, Tocaima, Cundinamarca (a. 4°24’ N, 74°44’W), Colombia, latest Pleistocene (see Correal-Urrego et al., 2005). IGM p174998 (a,b,c), IGM p174999 (a,b,c), IGM p175000 (a,b,c): nine osteoderms of the dorsal carapace from sandstone levels into conglomerate of Mesa Formation, Quebrada Las Lajas, NW Villavieja Village, Huila (3°14’N, 75°12’W), Colombia; Pleistocene. ICN-PubA1 210-223, ICN-Pub07(01) 210-220, ICN-PubD 210-220, ICN-Pub 84 153, ICN-Pub 84 163: some osteoderms of the dorsal carapace, and many small and irregular osteoderms, Pubenza, Tocaima, Cundinamarca (a. 4°24’ N, 74°44’W), Colombia, latest Pleistocene (see Correal-Urrego et al., 2005). IGM p174998 (a,b,c), IGM p174999 (a,b,c), IGM p175000 (a,b,c): nine osteoderms of the dorsal carapace from sandstone levels into conglomerate of Mesa Formation, Quebrada Las Lajas, NW Villavieja Village, Huila (3°14’N, 75°12’W), Colombia; Pleistocene (see Butler, 1942; Fields, 1959; Takay et al., 1992) (Figure 1).

Description and comparisons. As mentioned above, the reports of Glyptodontidae are very scarce in Colombia, and the only species reported is Glyptodon clavipes Owen, 1839. In fact, the published contributions are restricted only to those of Apolinari (1926), Bombin (1982) and Correal-Urrego et al. (2005), plus two new osteoderms from Los Patios (Norte de Santander) and nine from Quebrada Las Lajas, Villavieja town (Huila).

A new analysis of the available materials shows that the morphology of the exposed surface of the osteoderms is typical of Glyptodon and different from the known South American Glyptotherium specimens. The annular and radial sulci are somewhat wider than those observed in Glyptotherium, with almost vertical sides and a wide, almost flat bottom, forming an angle of 90°; in Glyptotherium, the sulci show a more concave morphology. In addition, in many osteoderms of Glyptotherium (see Oliveira et al., 2010; p. 357, fig. 3A-B; MCN n/n; UNFEM-CIAAP n/n) it is possible to observe numerous foramina; the ducts that correspond to the foramina are arranged obliquely to the osteoderm surface. To date, this particular morphology has been observed only in the South American Glyptotherium and in the North American species Gl. floridanum (Simpson, 1929) (AMNH 23547); in contrast, in Glyptodon the surface is clearly rugose, but without this kind of foramina.

The evidence clearly shows that the osteoderms classified as G. clavipes by Bombin (1982) must be assigned only to Glyptodon sp. (Figures 2C-D). In addition, Bombin (1982: 1) did not mention any character to support this assignation. Interestingly, the osteoderms figured by Correal-Urrego et al. (2005) (Figures 2E-F) appear to be associated with an archaeological site dated to ca. 16 ky BP. Together with these osteoderms, there are many small and irregular osteoderms that show a morphology very similar to that of those figured by Tauber & Di Ronco (2000) and Soibelzon et al. (2006) belonging to the lateral areas of the skull and pubic region (Figure 2 G). The two osteoderms from Los Patios (Norte de Santander) did not show any significant differences from those of Glyptodon (Figures 2A-B). Finally, the nine osteoderms from Quebrada Las Lajas show the typical morphology observed in Glyptodon. The annular and radial sulci have almost vertical sides and a wide, almost flat bottom, forming an angle of 90°, and are somewhat wider than in Glyptotherium, which shows a more concave sulci morphology (Figures 2H-I).

To summarize, to date, all the records of the Glyptodontinae belong to Glyptodon, which represents the only Glyptodontinae recorded in the Pleistocene of the current territory of Colombia.

DISCUSSION

Glyptotherium and Glyptodon in South America

Several species of Glyptodon (ca. 13) have been recognized, most of them without a truly diagnostic morphological characterization (Ameghino, 1889; Mones, 1986; Soibelzon et al., 2006). However, some preliminary revisions have suggested there could be no more than five valid species: G. munizi Ameghino, 1881 (Ensenadan Age/Stage; early Pleistocene-middle Pleistocene; see Soibelzon et al., 2006; Zurita et al., 2009), G. elongatus Burmeister, 1866, G. reticulatus Owen, 1845 (Bonaerian-Lujanian Ages; middle Pleistocene–early Holocene; see Ameghino, 1889; Duarte, 1997), G. clavipes Owen, 1839, and a probable morphotype with a complex nomenclatural situation (see Zurita et al., 2009, 2011b). Interestingly, this latter species is probably restricted to Andean areas, having a smaller size than the Pampean species (e.g. G. elongatus, G. munizi). This particular situation could be due to the fact that such mountain habitats support smaller species (see Rodriguez et al., 2008). This is also concordant with a similar condition observed in Peruvian Megatheriinae sloth (see Pujos, 2008).

The evidence shows that at least one of the most cited species of Glyptodon is not valid because the main characters of G. perforatus Ameghino, 1889 are not diagnostic (e.g. PVE-F 85, MCA 2013) (see Zurita et al., 2011b).

The situation for Glyptotherium is somewhat different, with in having undergone a recent taxonomic revision (see
Figure 2. Glyptodon sp. Osteoderms of the dorsal carapace in dorsal view. A-B, MALV 229, 845, Los Patios Village, Norte de Santander; C-D, MHNLS 2348-2349, El Rosario Village, Norte de Santander and unknown locality Santa Marta, Magdalena; E-G, ICN (n/n) PubA1 210-223, Pub07 (01) 210-220, PubD 210-220, Pub 84 153, Pub 84 163, Pubenza, Tocaima Village, Cundinamarca; G, osteoderms of the facial region; H-I, IGM p174998, 174999, Quebrada Las Lajas, Villavieja Village, Huila. Glyptotherium cf. Gl. cylindricum. Osteoderms of the dorsal carapace in dorsal view; J-K, MCN (n/n), Falcon State, Venezuela. Scale bars = 30 mm.
Gillette & Ray, 1981). According to Gillette & Ray (1981), five species can be recognized; however, it is possible that some of them could be synonymous [e.g. Gl. texanum Osborn, 1903 and Gl. arizonae (Gidley, 1926) (Carranza-Castañeda & Gillette, 2011)]. The late Pleistocene species are Gl. cylindricum (Brown, 1912) Gl. mexicanum (Cuatáparo & Ramirez, 1875) and Gl. floridanum. As observed previously (Zurita et al., 2008) both, Glyptodon and Glyptotherium, are well differentiated by many characters, especially at the level of the dorsal carapace and skull.

At least for the South American specimens of Glyptotherium, it is possible to differentiate them from Glyptodon on the basis of the osteoderms of the dorsal carapace (see Carlini et al., 2008; Oliveira et al., 2009; 2010). Among the most prominent characters, the osteoderms of Glyptotherium show a less evident development of the annular and radial sulci and, in some cases, it is possible to observe very developed small foramina on all of the dorsal surface (e.g. MCC 2202, 268-V). As mentioned by Dantas et al. (in press), other usually mentioned characters, such as the number of peripheral figures, are common to both genera. In this context, a comparison with the material figured by Oliveira et al. (2010) did not show any significant differences from the Venezuelan material, suggesting that one single species is present in South America.

Outside southern South America, northern records of Glyptodon are usually attributed to G. clavipes (Bombín, 1982; Bocquentin-Villanueva, 1982; Paula-Couto, 1983; Pujos & Salas, 2004; Dantas et al., 2005; Dantas, 2009; Rincón & White, 2007; Rincón et al., 2008), whereas southern records are sometimes reported as G. reticulatus (Kerber et al., 2010). In this sense, it is important to mention that most of these assignments were carried out on the basis of fragments of the dorsal carapace and/or isolated osteoderms, which did not allow an accurate taxonomic identification to be obtained. This is mainly due to the noticeable morphological variations that the osteoderms have depending on their location on the dorsal carapace, which for most species have not been quantified enough (but see Duarte, 1997).

In this context, the new analysis of the known materials from Colombia shows that they belong to Glyptodon sp. The absence of Glyptotherium in this territory and in southern areas could be related to the presence of mountain barriers (see de Porta, 2003; Mora et al., 2008). In fact, the distribution of the records of Glyptotherium allows us to suggest that, after its entry into South America during the GABI, Glyptotherium could have followed a migratory route parallel to the Caribbean Sea (see Carlini et al., 2008) and the Atlantic Ocean towards southern areas, reaching up to 20°S (Oliveira et al., 2010) (Figure 1).

In this scenario, Oliveira et al. (2010) proposed a paleobiogeographic distribution pattern for Glyptotherium and Glyptodon, in which Glyptotherium occupied northeastern and southeastern areas of Brazil whereas Glyptodon occupied the current territories of Argentina, Bolivia, Uruguay, Paraguay and the southernmost areas of Brazil (Figure 1). Recently, Rincón & White (2007), Rincón et al. (2008) and Dantas et al. (in press) have reported the occurrence of Glyptodon in Venezuela and in the intertropical region of Brazil. The taxonomic identification carried out by Dantas et al. (in press) seems to be very doubtful, mainly because of the poor preservation of the osteoderms. In addition, the main character mentioned (a concavity in each central figure of the osteoderms) is also present in some other glyptodontines such as Glyptotherium arizonae (AMNH 21808). In contrast, the taxonomic identification carried out by Rincón & White (2007) and Rincón et al. (2008) seems to be more accurate, because the material shows a clear affinity with Glyptodon. Despite this, if this is correct, Glyptotherium and Glyptodon could have shared the same geographic distribution in central-north and eastern areas of South America (Venezuela and Brazil, respectively), approximately from 11°N to 10°S (Figure 1). In this context, it is important to remark that this sympatry does not imply necessarily that both genera coexisted.

However, some noteworthy considerations can be made. Interestingly, Glyptodon is the only glyptodontine present in the southernmost region of South America, up to 20°S. Above 20°S, in the western part of South America, parallel to the Cordillera de Los Andes, Glyptodon is the only observed glyptodontine (and the most frequently recorded Glyptodontidae), its recorded presence reaching over 3300 m (Pujos & Salas, 2004), up to Colombia and Venezuela. In turn, Glyptotherium is recorded only in an area parallel to the Caribbean Sea and the Atlantic Ocean, and always associated with lowlands (Figure 1). The geographic distribution of Glyptotherium agrees with the eastern corridor proposed by Webb (1978, 1985; see also McDonald, 2005), which was used by many clades of mammals as a dispersal route. In contrast to Glyptodon, the evidence shows that Glyptotherium is recorded in the lowlands.

To date, Glyptodon is recorded only in South America, but taking into account the records published by Rincón et al. (2008), the presence of Glyptodon in Central America cannot be discarded. Therefore, a modern taxonomic revision of Central America Glyptodontinae is required.

Like Glyptodon, Glyptotherium seems to have been present in arid/semiarid areas (e.g. Taima Taima, Venezuela; see Ochsenius, 1978, 1980) and in the intertropical region of South America (e.g. Minas Gerais, Brazil). A recent analysis based on stable isotopes performed by Pérez-Crespo et al. (2012) has shown that the late Pleistocene Mexican species of Glyptotherium were able to consume both C4 and C3 plants, suggesting that this taxon was a grazer adapted to open environments, like Glyptodon (Pérez et al., 2000; see also Vizcaíno et al., 2011).

CONCLUSIONS

In the current territory of Colombia, the evidence shows that, to date, the remains of Glyptodontidae must be referred to Glyptodon sp. In South America, only one Glyptotherium species can be recognized. This species shares some characters with the North American species Gl. cylindricum. However,
a more accurate analysis is necessary to either confirm or refute this hypothesis. To date, *Glyptotherium* has only been recorded in South America in a strip parallel to the Caribbean Sea and to the Atlantic Ocean, up to 20°S. This geographic distribution agrees with the eastern corridor proposed by Webb (1985) during the GABI. The records of *Glyptotherium* from Venezuela (ca. 14-12 ky BP) and eastern Brazil (ca. 58-68 ky BP) are associated with lowlands. In turn, *Glyptodon* and *Glyptotherium* are possibly recorded in sympathy from 11° N to 10°S. This does not necessarily imply that the two genera coexisted. Both genera can be recognized on the basis of isolated osteoderms of the dorsal carapace of adult specimens; in contrast, the osteoderms of juvenile individuals show the same morphology. Taking the northern records of *Glyptodon* in South America into account, the presence of this genus in Central America cannot be discarded.

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