

Rev. bras. paleontol. 15(3):273-280, Setembro/Dezembro 2012
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 doi:10.4072/rbp.2012.3.04

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 My) 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 glyptodontine *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 taxonomical 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 *Glyptodon*, 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 Pleistoceno 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 de Glyptodontinae pertencente ao gênero norte-americano *Glyptotherium* (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 desse grupo 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 relato de 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 à terras baixas. Essa distribuição geográfica concorda com a proposição de um corredor oriental durante o Grande Intercâmbio Biótico Americano. Abaixo dessa latitude, o único registro de Glyptodontinae corresponde a *Glyptodon*, 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.

Palavras-chave: taxonomia, América do Sul, Pleistoceno, Glyptodontinae, osteoderms.

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; Porpino *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; Porpino & Bergqvist, 2002; Porpino *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/semiarid/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 Venezuela (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 Paleontología 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.

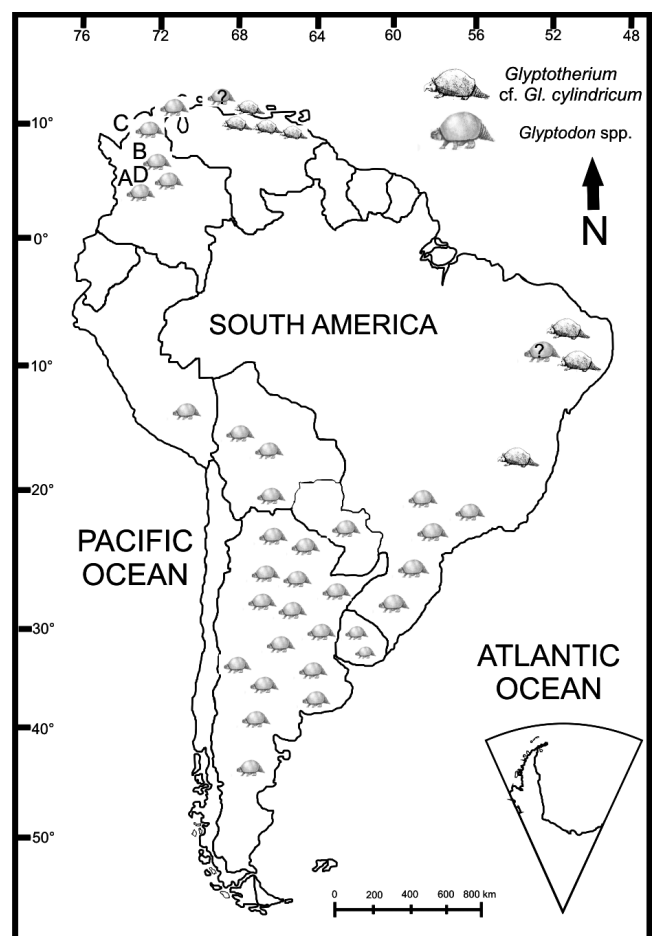


Figure 1. Geographic distribution of *Glyptodon* and *Glyptotherium* cf. *Gl. cylindricum* in South America. In Colombia: **A**, Pubenza, Tocaima, Cundinamarca; **B**, Los Patios, Norte de Santander, **C**, Santa Marta, Magdalena; **D**, Quebrada Las Lajas, Villavieja Village, Huila.

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: two 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 (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 Apolinar (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 America

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 Glyptodontidae 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

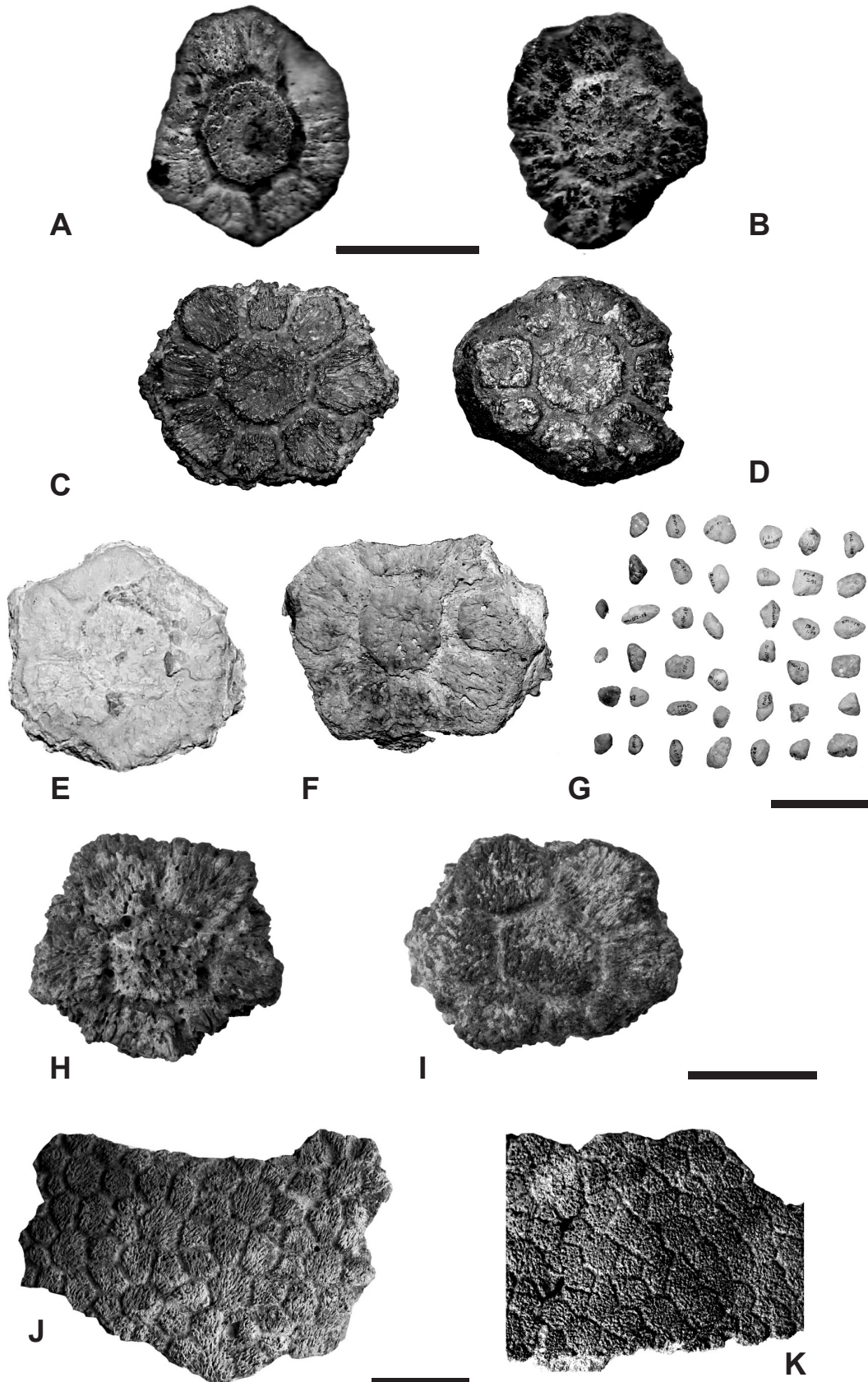


Figure 2. *Glyptodon* sp. Osteoderms of the dorsal carapace in dorsal view. **A-B**, MALV 229, 845, Los Patios Village, Norte de Santander; **C-D**, MHNSL 2348-2349, El Rosario Village, Norte de Santander and unknown locality Santa Marta, Magdalena; **E-G**, ICN (n/n) PubA1 210-223, Pub07 (01) 210-220, 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* (Bombin, 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 Vizcaino *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* is the only Glyptodontinae present in an area parallel to the Cordillera de Los Andes, reaching up to 3300 m. Both *Glyptodon* and *Glyptotherium* are possibly recorded in sympatry 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.

ACNOWLEDGMENTS

The authors thank the staff at the Museo Arqueológico Los Vados, Museo de Historia Natural de La Salle (Bogotá), Instituto de Ciencias Naturales de la Universidad Nacional de Colombia and Museo Geológico Nacional “José Royo y Gómez”, Servicio Geológico Colombiano (formerly Ingeominas) for allowing the study of the materials presented here. A. Mones and an anonymous reviewer are also thanked for their thorough reviews and helpful suggestions. This work was funded by project grants PICTO-UNNE (2007-00164), PICT 1285/2008, and PI Q002-11.

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Received in January, 2012; accepted in August, 2012.