The most complete known Neogene Glyptodontidae (Mammalia, Xenarthra, Cingulata) from northern South America: taxonomic, paleobiogeographic, and phylogenetic implications

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THE MOST COMPLETE KNOWN NEOGENE GLYPTODONTIDAE (MAMMALIA, XENARTHRA, CINGULATA) FROM NORTHERN SOUTH AMERICA: TAXONOMIC, PALEOBIOGEOGRAPHIC, AND PHYLOGENETIC IMPLICATIONS

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ABSTRACT—The knowledge of northern South American Glyptodontidae (Mammalia, Xenarthra, Cingulata) is very scarce compared with that of southern South American taxa, which have been systematically studied since the 19th century. Recently, the northern taxa (originally assigned to the Glyptodontidae Propalaehoplophorinae *Asterostemma* and *Propalaehoplophorus*) have been reinterpreted as basal Glyptodontinae, belonging to the new genus *Boreostemma*. In this contribution, we present and describe the most complete Neogene Glyptodontidae from northern South America (middle Miocene of the Honda Group, La Venta, Colombia), and its main taxonomic, paleobiogeographic, and phylogenetic implications. This new material expands the morphological characterization of *B. acostae* and corroborates differences compared with Glyptodontidae from Miocene southern South America. A cladistic analysis corroborates the monophyly of the Glyptodontinae, that *B. acostae* and *B. venezolensis* being the sister group of the remaining taxa of Glyptodontinae. The traditionally recognized genera (e.g., *Glyptodon* and *Glyptotherium*) constitute natural groups. Whereas the Miocene seems to represent a diversification period for Glyptodontidae in southern South America, the recorded taxa in northern South America are restricted with certainty only to the Glyptodontinae *Boreostemma*.

INTRODUCTION

Until some years ago, most of the knowledge of late Paleogene and Neogene Cingulata Glyptodontidae came from southern South America (ca. 48°–20°S), especially from the Pampean and Patagonian regions of Argentina (Ameghino, 1889, 1902; Lydekker, 1894; González, 2010a, 2010b; González Ruiz et al., 2011) and Chile (Croft et al., 2007), where this clade had been systematically studied since the 19th century (see, among others, Ameghino, 1887a, 1889; Lydekker, 1894; Scott, 1903–1904; Scillato-Yané, 1986).

This situation contrasted with the knowledge of northern South America Glyptodontidae (ca. 11°N–5°S), which, until recently, was restricted to the contributions of Royo y Gómez (1945), Simpson (1947), De Porta (1962, 1969), Villarroel (1983), Carlini et al. (1997), and Villarroel and Clavijo (2005). These glyptodonts, which came mostly from the middle Miocene of Colombia and Venezuela, were traditionally linked to the southern South American Glyptodontidae Propalaehoplophorinae, as belonging to the genera *Asterostemma* Ameghino, 1889 (*A. venezolensis* Simpson, 1947, *A.? gigantea* Carlini, Vizcaíno, and Scillato-Yané, 1997, and *A. acostae* Villarroel, 1983), and *Propalaehoplophorus* Ameghino, 1887a (De Porta, 1962). However, the morphological differences between both groups of Glyptodontidae raised some questions about the real relationship between them (Villarroel, 1983:30; Carlini et al., 1997:223).

In this scenario, a new analysis of the northern South American Glyptodontidae (see Carlini et al., 2008a; Carlini and Zurita, 2010; Zurita et al., 2011a), originally classified as *Asterostemma* spp. and *Propalaehoplophorus*, has shown that these glyptodonts do not belong to the southern South American Propalaehoplophorinae, because they are currently interpreted as basal Glyptodontinae, belonging to the new genus *Boreostemma* Carlini et al., 2008a. This hypothesis is congruent with most of the middle Miocene Xenarthra from northern South America (especially those from the Honda Group, La Venta, Colombia), which show noticeable taxonomic differences from the Miocene forms from southern South America (Carlini et al., 1997; Villarroel, 1998, 2000).

The two species of *Boreostemma* from the middle Miocene of Honda Group, La Venta, Colombia, are *B. gigantea* (coming from La Victoria Formation) and *B. acostae* (from La Victoria and Villavieja formations). Both species were previously known only by their type materials and isolated fragments.

In addition to '*Asterostemma*,' Carlini et al. (1997) and Villarroel and Clavijo (2005) recognized the presence of two species of middle Miocene Glyptodontidae Glyptatelinae in Colombia: *Neoglyptatelus originalis* and *N. sincelejanus*. The Glyptatelinae are known from the late Paleogene (late Eocene–late Oligocene) in Patagonia and Bolivia (Scillato-Yané, 1977; Carlini et al., 2005), and then in the early Neogene (middle to late Miocene) of Colombia, Uruguay, and Brazil (Vizcaíno et al., 2003; Cozzuol, 2006) but not in the Patagonian Neogene.

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The goals of this contribution are (1) to present and describe the most complete known Neogene Glyptodontidae in northern South America; (2) to expand the morphological characterization of *B. acostae*; (3) to establish a detailed comparison with Glyptodontidae from the Miocene of southern South America in order to differentiate them; and (4) to provide new evidence linking this new material to the subfamily Glyptodontinae.

MATERIALS AND METHODS

The chronological and biostratigraphic schemes used in this work correspond to those proposed by Flynn and Swisher (1995), Cione and Tonni (2005), and Croft et al. (2009). The systematics partially follows Hoffstetter (1958), Paula Couto (1979), McKenna and Bell (1997), and Fernicola (2008).

All the values included in tables are expressed in millimeters (mm), with an error range of 0.5 mm. Measurements smaller than 150 mm were taken with 'vernier' calipers; measurements greater than this value were taken using an anthropometric spreading caliper. The description and terminology for osteoderms follow mainly Zurita (2007) and Krmpotic et al. (2009). Details on the cladistic analysis used are given in the Phylogenetic Analysis section. Linear measurements are provided in Table 1. Appendix 1 shows the specimens of Glyptodontidae used in the cladistic analysis. Appendix 2 shows the characters and character states of the matrix.

Most of the comparison with Miocene glyptodonts is performed with Santacrucian Propalaehoplophorinae, because 'Friasian' and Chasicoan glyptodonts are still poorly characterized, mainly on the basis of isolated osteoderms and fragments of the caudal armor. Nevertheless, a few interesting considerations can be drawn when comparing some 'Friasian' Palaehoplophorini with northern taxa.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, U.S.A.; **AMU-CURS**, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; **CAL**, Colección Paleontológica, Centro de Museos, Universidad de Caldas, Manizales, Caldas, Colombia; **Ctes-PZ**, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; **FC-DPV**, Departamento de Paleontología de la Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; **ICN-P**, Instituto de Ciencias Naturales, Universidad Nacional del Colombia, Bogotá D.C., Colombia (Vertebrate paleontological collections currently in Departamento de Geociencias, Facultad de Ciencias, Universidad Nacional de Colombia, Sede Bogotá, Colombia); **IGM**, Museo Geológico Nacional, Servicio Geológico Colombiano (formerly INGEOMINAS), Bogotá D.C., Colombia; **LIEB-PV**, Laboratorio de Investigaciones en Evolución y Biodiversidad, Universidad Nacional de La Patagonia 'San Juan Bosco,' Sede Esquel, Argentina; **MACN**, Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MCA**, Museo de Ciencias Naturales 'Carlos Ameghino,' Mercedes, Buenos Aires, Argentina; **MCL-PUC/MG**, Museu de Ciências Biológicas da Pontifícia Universidade Catolica de Minas Gerais, Belo Horizonte, Brazil; **MCN**, Museo de Ciencias de Caracas, Caracas, Venezuela; **MHD-P**, Museo Histórico Departamental de Artigas, Artigas, Uruguay; **MLP**, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; **MMP**, Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia,' Buenos Aires, Argentina; **MPEF**, Museo Paleontológico 'Egidio Feruglio,' Colección Paleontología de Vertebrados (**PV**), Trelew, Argentina; **SGO PV**, Vertebrate Paleontology collections, Museo Nacional de Historia Natural, Santiago, Chile; **YMP**, Yale Peabody Museum of Natural History, Princeton University Collection (**PU**), Yale University, New Haven, Connecticut, U.S.A.;

UCMP, University of California, Museum of Paleontology, Berkeley, California, U.S.A.; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Other Abbreviations—M, m, upper and lower molariforms, respectively; **n/n**, without official catalog number.

CRONOSTRATIGRAPHY AND GLYPTODONTIDAE PALEOFAUNAL CONTEXT IN SOUTHERN SOUTH AMERICA

The 'Friasian' age includes four successive middle Miocene mammal faunas: the Friasian s.s. (ca. 16.5 Ma), Colloncuran (ca. 15.7 Ma), Laventan (ca. 11.8–13.5 Ma), and Mayoan (ca. 11.8 Ma), placed between the early Miocene Santacrucian (ca. 17.5–16 Ma) and the late Miocene Chasicoan (ca. 9.2 Ma) ages (Kraglievich, 1930; Flynn and Swisher, 1995; Madden et al., 1997; Schultz et al., 2004). From a chronostratigraphic point of view, there is an evident hiatus between the Colloncuran and Mayoan faunas in Patagonia (Madden et al., 1997; González Ruiz et al., 2011), which is partially represented by the Laventan fauna in Colombia.

According to González (2010a, 2010b), the Glyptodontidae species recognized for the Santacrucian age in Patagonia are the Propalaehoplophorinae *Propalaehoplophorus australis* Ameghino, 1887a, *P. minus* Ameghino, 1891, *Cochlops muricatus* Ameghino, 1889*, C.? debilis* Ameghino, 1891, *Metopotoxus? Anceps* Scott, 1903–1904, and *Eucinepeltus petesatus* Ameghino, 1891. In the 'Friasian' age, the species recognized include *Eonaucum colloncuranum* Scillato-Yané and Carlini, 1998 (Glyptodontidae incertae sedis), *Propalaehoplophorus informis* Roth, 1899 (Propalaehoplophorinae), *Palaehoplophoroides rothi* Scillato-Yané and Carlini, 1998 (Palaehoplophorini), *Palaehoplophorus meridionalis* Ameghino, 1904 (Palaehoplophorini), and *Paraeucinepeltus raposeirasi* González-Ruiz, Scillato-Yané, Zamorano, Zurita, and Tegedor, 2011 (Glyptodontidae incertae sedis). In addition, Rusconi (1946) described *Asterostemma barrealense* from late early Miocene of San Juan Province (Argentina) (López et al., 2011) and Croft et al. (2007) recognized *Parapropalaehoplophorus septentrionalis* (Glyptodontidae incertae sedis) in the late early Miocene of Chile. In turn, there are no species recognized for the Chasicoan, except some mentions corresponding to Glyptodontidae 'Hoplophorinae' indet, Palaehoplophorini, gen. et sp. indet., Plohophorini, gen. et sp. indet., and Hoplophorini (= Sclerocalyptini), gen. et sp. indet. (Bondesio et al., 1980).

To summarize, the Glyptodontidae from northern South America (Glyptodontinae) are absent in the southern South America (Patagonian) Miocene. It is remarkable that there is only one modern record of Glyptodontinae (*Glyptodon clavipes*) (Ameghino 1900–1902; Parodi, 1930) in the Quaternary of Patagonia, but this represents an immigration of northern forms.

SYSTEMATIC PALEONTOLOGY

Magnaorder XENARTHRA Cope, 1889
Order CINGULATA Illiger, 1811
Suborder GLYPTODONTIA Ameghino, 1889
Superfamily GLYPTODONTOIDEA Gray, 1869
Family GLYPTODONTIDAE Gray, 1869
Subfamily GLYPTODONTINAE Gray, 1869
Genus *BOREOSTEMMA* Carlini, Zurita, Scillato-Yané,
Sánchez, and Aguilera, 2008
BOREOSTEMMA ACOSTAE (Villarroel, 1983)
(Figs. 1, 2)

Asterostemma? acostae Villarroel, 1983:30, figs. 2–4.

Holotype—ICN-P-225–1, a fragment of dorsal carapace belonging to the left lateral region (Fig. 2A).
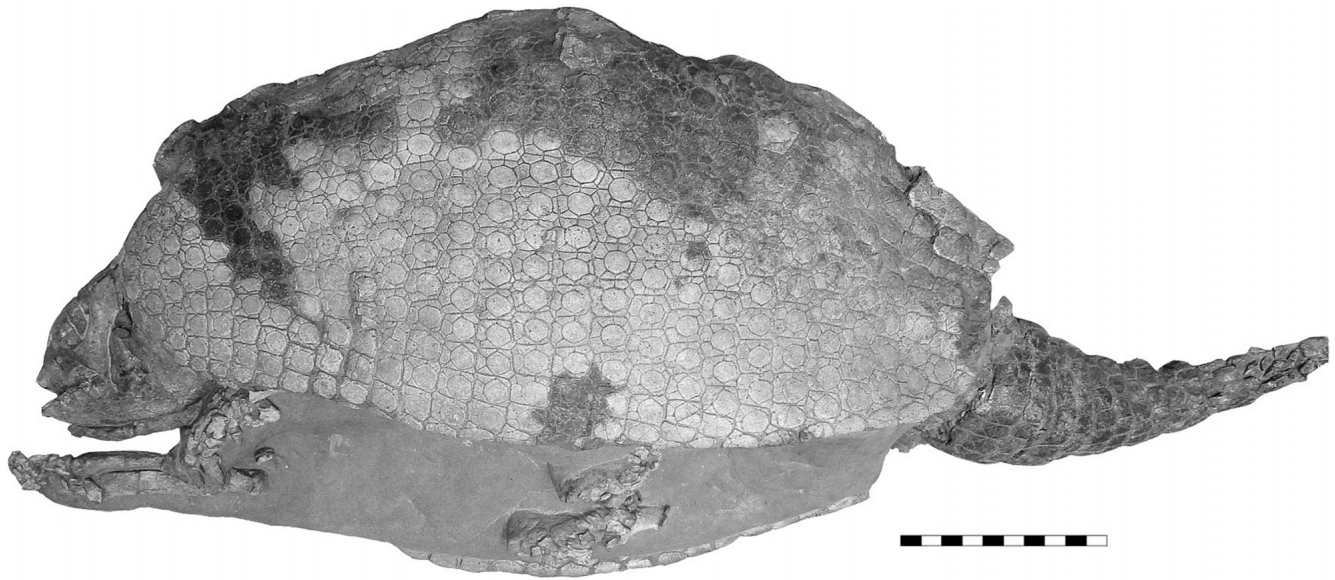
FIGURE 1.   Complete specimen of *Boreostemma acostae* CAL-896. Scale bar equals 10 cm.
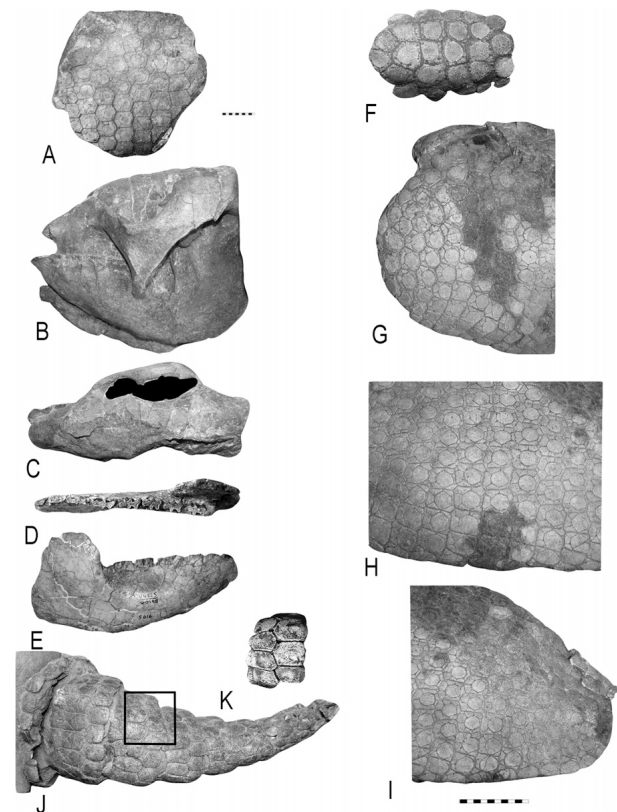

FIGURE 2. **A**, fragment of dorsal carapace belonging to the left lateral region ICN-P-225-1 (holotype); **B**, skull and mandible CAL-896 in left lateral view and **C**, dorsal view; **D**, right hemimandible UCMN 40198 in oclusal view and **E**, lateral view; **F**, cephalic armor in dorsal view; **G**, cephalic region of the dorsal carapace CAL-896; **H**, middle region; **I**, caudal region; **J**, complete caudal armor; **K**, detail of the caudal ring. Scale bars equal 10 cm.

Geographic and Stratigraphic Provenance—La Venta, Huila, Colombia. Monkey Beds Unit, Baraya Member, Villavieja Formation (Figs. 3, 4).

Referred Material—CAL-896 (almost complete specimen, consisting of skull, mandible, cephalic armor, dorsal carapace, and caudal armor; see Description); ICN-P-225-2, IGM p2114/1, 2, IGM p2116/1-8, IGM p2143/1-3, IGM p2107/1-10, IGM 2242, IGM p809901, IGM p182739, IGM p182781, IGM p182786, IGM p182924, IGM p182963, IGM p183018, IGM p183023, IGM p183031, IGM p183042, IGM p183090, IGM

TABLE 1.   Linear measurements (in mm) of *Boreostemma acostae*.

Element	*Boreostemma acostae* (CAL-896)
Skull	
Total length	195.05
Maximum transverse diameter between zygomatic arches	56.40
Anteroposterior diameter of zygomatic arch	51.54
Dorsoventral diameter of zygomatic arch	37.22
Height of narial aperture	27.32
Transverse diameter of narial aperture	35.63
Transverse diameter of postorbital region	44.07
Mandible	
Total length	173.19
Anteroposterior diameter of ascending ramus at alveolar level	63.57
Dorsoventral diameter of ascending ramus	101
Length of the symphysis	64.15
Height of the horizontal ramus at level of m1	32.50
Height of the horizontal ramus at level of m4	50.44
Height of the horizontal ramus at level of m6	55.51
Cephalic armor	
Maximum transverse diameter	109.99
Anteroposterior diameter	79.85
Carapace	
Total length	770
Anteroposterior length along dorsal curvature	922
Caudal armor	
Total length	443

FIGURE 3. Stratigraphic profile of the Honda Group (La Victoria and Villavieja formations) showing the provenance of the holotype ICN-P-225-1 of *Boreostemma acostae* and referred materials. (Modified from Guerrero, 1987.)

p183155, IGM p183228, IGM p183238, IGM p183241, IGM p183273, IGM p183801, IGM p183813, IGM p184256, IGM p183910, IGM p183982, IGM p184088, IGM p184197, IGM p182887, IGM p183382, IGM p184094, IGM p182677 (numerous osteoderms of the dorsal carapace and caudal armor); IGM p183625, IGM p183764, IGM p183654, IGM p183315,

IGM p183935 (six osteoderms and other indeterminate remains); IGM p183265 (left hemimandible, three osteoderms and a fragment of femur); IGM p183782 (one molariform, fragments of mandible, and other indeterminate remains); IGM p183307 (three osteoderms of the caudal rings and three molariforms); IGM p183908 (fragment of femur and

FIGURE 4.   Location map showing the locality where CAL-896 was found. Geological base simplified from Guerrero (1997).
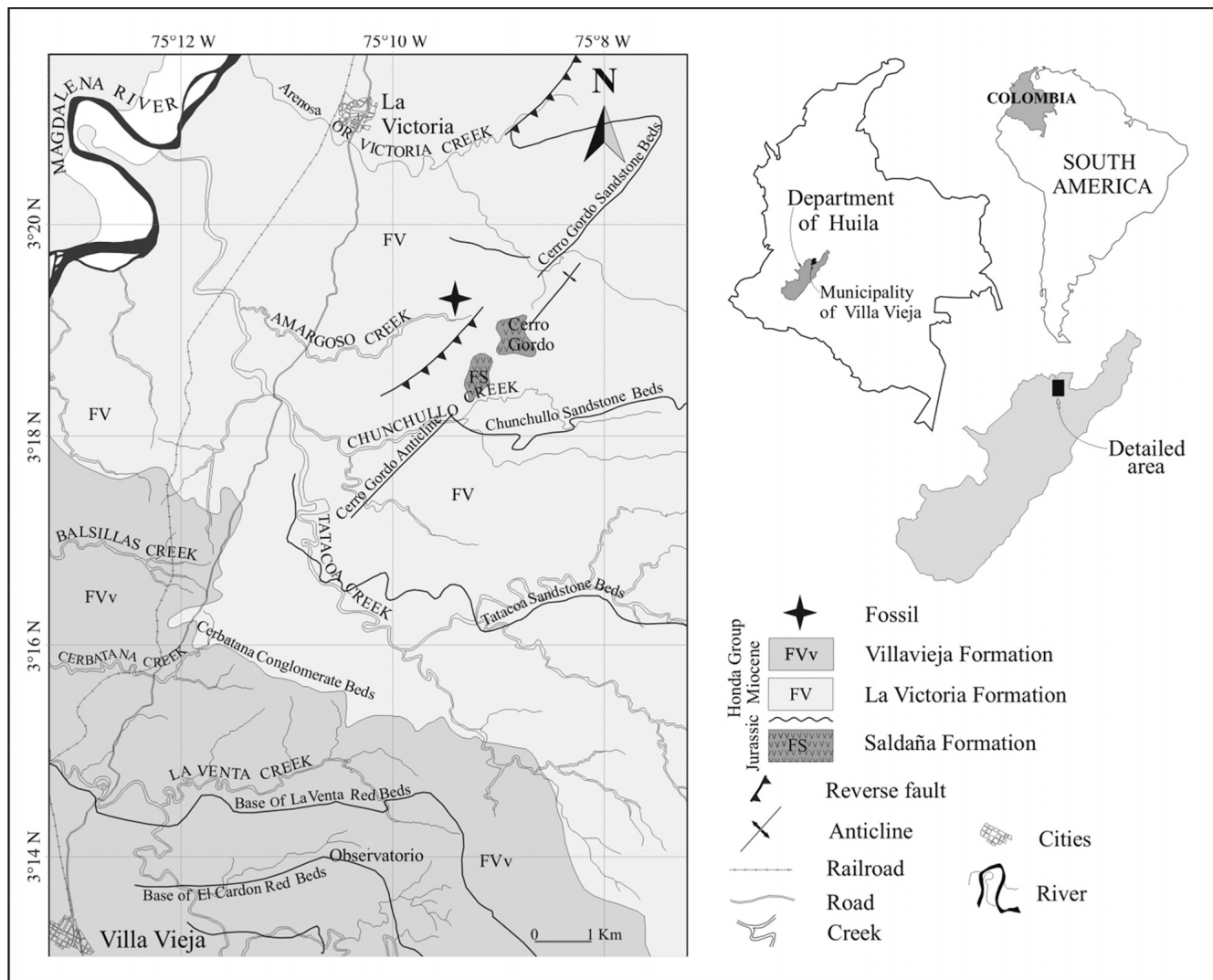
partial mandible); IGM p253101 (five associated osteoderms and partial mandible); UCMP 38039 (skull and mandible).

Stratigraphic Provenance of the Referred Material—La Victoria Formation and the lower section of the Villavieja Formation, Baraya Member (see Flynn et al., 1997; Guerrero, 1997) (Fig. 3). Figure 4 shows the geographic and stratigraphic provenance of the best-preserved specimen (CAL-896).

Diagnosis—From Villarroel (1983:32). Osteoderms of the dorsal carapace slightly larger than those of *Asterostemma venezolensis* Simpson. Exposed surface of the central figures of the dorsal and dorsolateral osteoderms flat or convex, whereas the osteoderms located in the margins have a flat central figure: the diameter of each peripheral figure, considered in isolation, represents on average between 40% and 50% of the diameter of the adjacent central figure; the mandibular posterior teeth are narrow and trilobate; furthermore, each one of them is different from the other two.

Emended Diagnosis—Glyptodontidae larger than the southern South American Propalaehoplophorinae, more similar in size to *Boreostemma venezolensis*; dorsal carapace composed of 29 transversal rows of osteoderms; sulci that delimit the central and peripheral figures more marked (wider and deeper) and more angular than those of Propalaehoplophorinae and 'Hoplophori-

nae' Hoplophorini; osteoderms of the lateral region of the dorsal carapace with the central figure displaced toward its posterior border; each osteoderm bears a maximum of 12 peripheral figures; the rostral area of the skull very anteroposteriorly extended, showing a morphology similar to that observed in Cingulata Pampatheriidae; ventral half of the descending process of the maxillae evidently less dorsoventrally elongated than that of Propalaehoplophorinae, with its main axis in an angle of about 90° with respect to the palatal plane; M1–m1 lobate; caudal armor composed of eight caudal rings, ending in a very short caudal tube.

DESCRIPTION

Skull

The skull is almost complete and slightly laterally compressed (Fig. 2B, C). Its general morphology is very different from that of Propalaehoplophorinae species, in which the skull is known (*Propalaehoplophorus australis*, *P. minus*, *Cochlops muricatus*, *C.? debilis*, *Eucinepeltus petesatus*, and *Metopotoxus? anceps*). The dorsal profile is clearly convex, with the rostral area located at a lower level with respect to the posterior half of the skull. This morphology is similar to that observed in *C.? debilis* and

M.? anceps. In lateral view (Fig. 2B), the zygomatic arch and the upper half of the descending process of the maxillae are clearly much more robust than those of Propalaehoplophorinae species but similar in its almost straight ventral margin.

Compared with Propalaehoplophorinae species, the ventral half of the descending process of the maxillae shows a unique morphology. It is evidently less dorsoventrally elongated, with its main axis located in an angle of about 90° with respect of the palatal plane (Fig. 2B). This is different from that known in all Glyptodontidae, in which the ventral half of the descending process of the maxillae is curved posteriorly. The orbital notch is dorsoventrally elongated (Fig. 2B), similar to that of *E. petesatus*, and different from that of *P. australis* and *C. debilis*, in which the ventral margin of the orbital notch constitutes a 'V,' whereas in *B. acostae* and *E. petesatus* this ventral margin is evidently rounded. As in all Propalaehoplophorinae, the orbit is posteriorly opened. The rostral area located ahead of the orbitals is more elongated than that observed in all Propalaehoplophorinae (Fig. 2B, C).

In dorsal view (Fig. 2C), the sagittal crest diverges posteriorly at the level of half of the zygomatic arches, like in *P. australis*, *P. minus*, *E. petesatus*, and *M.? anceps*. In the other species of Propalaehoplophorinae (*C. muricatus* and *C.? debilis*), the morphology of the sagittal crest is not well known because that area is not well preserved or is covered by the cephalic shield. In this view, the orbital notch is evidently much more anteroposteriorly elongated than that known in all Propalaehoplophorinae. Unlike that observed in all Propalaehoplophorinae, the rostral area located in front of the orbitals is more elongated, showing a morphology similar to that observed in Cingulata Pampatheriidae (e.g., *Pampatherium* Ameghino, 1875). In fact, in *B. acostae*, this rostral area shows a very primitive morphology, different from that observed in the remaining Glyptodontidae.

In frontal view, the nares have the same morphology as those of Propalaehoplophorinae, with a typical 'cordiform' shape.

It is not possible to observe this skull in ventral and occipital view in the specimen CAL-896, because the sediment that fills it does not allow the separation of the skull from the mandible. However, the specimen UCMP 38039 shows a lobation starting at M1/m1 level. This is clearly different from that observed in the Propalaehoplophorinae and *P. septentrionalis*, in which the labial lobation begins at m3–m4.

Mandible

In lateral view (Fig. 2D, E), the ascending ramus of the mandible is much less robust than that of *P. australis*, because this structure is not so anteroposteriorly elongated; in addition, the symphysis area in *P. australis* is more steeply inclined than in *B. acostae*. The mandible differs notably from that of *Parapropalaehoploprus septentrionalis* because in this taxon the ascending ramus is in an angle of 90° with respect to the horizontal ramus. Compared with *E. petesatus*, *C. muricatus*, and *P. minus*, the ventral margin of the mandible in *B. acostae* is more convex, similar to that of the Pleistocene genus *Glyptodon* Owen, 1839.

Only the three first molarifoms (m1–m3) are visible in CAL-896. They differ from those of the southern South American Propalaehoplophorinae and *P. septentrionalis*, in which the well-defined labial trilobation of the molariforms occurs from m3 or m4 to m8. In contrast, in *B. acostae*, the lobes are less rounded and the m2 is fully trilobate labially. The m1 differs from those of all Propalaheoplophorinae because it is anteroposteriorly elongated and its lingual and labial margins show a small, marked lobation, whereas in Propalaehoplophorinae this molariform is elliptical or subcircular; the m2 shows a well-differentiated trilobation, especially in its lingual side, whereas in Propalaehoplophorinae this molariform is simple or bilobated, without evidence of lobation; m3 shows an evident trilobation in both margins, and is morphologically different from that of Propalaehoplophorinae because the anterior and posterior borders of the first and third

lobes, respectively, are pointed, whereas in Propalaehoplophorinae those margins are rather rounded.

Cephalic Armor

The cephalic armor is complete, and composed of 26 articulated osteoderms with rough surface (Fig. 2F). The most evident difference is that in *B. acostae* all the osteoderms are similar in size. By contrast, in all Propalaehoplophorinae the central osteoderms are much larger than those located at the margins of the cephalic armor.

The morphology of the exposed surface of each osteoderm is very different from that of Propalaehoplophorinae, and thus more similar to that of the Pleistocene genus *Glyptodon* and *B. pliocena*. Each osteoderm has a large, elevated central figure that occupies more than 90% of the exposed surface of the osteoderm. Surrounding this central figure, there are some poorly developed peripheral figures, with three to nine large foramina. In *P. australis* and probably in *C.? debilis* (see Scott, 1903–1904), the exposed surface of the osteoderms is smoother, with greater peripheral figures, resembling a 'rosette' pattern ornamentation, similar to that observed in the dorsal carapace; in contrast, the cephalic armor of *E. petesatus* is composed of a smaller number of osteoderms (11–15), with a convex surface that shows a very rough evident central depression; in addition, there is no evidence of peripheral figures (Scott, 1903–1904). Finally, the known osteoderms of *Paraeucinepeltus raposeirasi* are much larger and, like *Eucinepeltus*, very convex, without any evidence of ornamentation; however, the complete cephalic armor is still unknown (González-Ruiz et al., 2011).

Dorsal Carapace

The dorsal carapace is broken in its midline, with the left side in a very good state of preservation, and is composed of 29 transverse rows of osteoderms (Fig. 1). In contrast, in the most complete Propalaehoplophorinae, *P. minus*, the number of transverse rows of osteoderms may vary between 27 transverse bands in the lateral margins to 19–20 in the median dorsal line (Scott, 1903–1904)

The dorsal profile is convex, and similar to that of *B. venezolensis* and the Pleistocene Glyptodontinae *Glyptodon munizi* Ameghino, 1881 (see Soibelzon et al., 2006). In addition, the exposed surface of the osteoderms is clearly much rougher and the sulci that delimit the central and peripheral figures are more marked and more angular than those of Propalaehoplophorinae and 'Hoplophorinae' Hoplophorini, similar in this way to *Glyptodon* Owen, 1839 (Fig. 2G–I).

The osteoderms that constitute the caudal notch have a central figure that is posteriorly displaced, surrounded by only three to four proximal peripheral figures without peripheral accessory figures, a morphology very similar to that seen in the other taxa of Glyptodontidae Glyptodontinae (see Gillette and Ray, 1981; Zurita et al., 2011a, 2011c); this is clearly different from that observed in *P. australis*, *P. minus*, *C. muricatus*, and *Neosclerocalyptus* Paula Couto, 1954, in which those osteoderms show a large number of peripheral figures (up to nine), also located in the lateral margins of the osteoderms; in addition, it is possible to observe some peripheral accessory figures in the limit between two osteoderms. In *B. acostae*, the morphology of the second row of osteoderms is very similar to the osteoderms of the caudal notch (Fig. 2I), whereas in the southern South American Propalaehoplophorinae, those osteoderms (except those located near the lateral margin) are completely surrounded by a series of peripheral figures, which acquire a typical 'rosette' pattern of ornamentation almost identical to the rest of the dorsal carapace.

Anteriorly, the osteoderms of the central-dorsal region of the carapace are six-sided and become larger (in fact the largest ones), surrounded by 9–10 peripheral figures (exceptionally 11)

(Fig. 1), whereas in *P. australis* and *C. muricatus* the number of peripheral figures can be up to 13–14.

Towards the margins of the dorsal carapace, the osteoderms of *B. acostae* show a very primitive pattern, almost unique among Glyptodontidae, very similar to that of *Boreostemma venezolensis* and Glyptatelinae; in fact, the morphology observed resembles that of *Parapropalaehoplophorus septentrionalis*. In *B. acostae* and *B. venezolensis*, the exposed surface of the osteoderms is rougher and the sulci that divide the central and peripheral figures are more marked than in *Parapropalaehoplophorus septentrionalis*; in addition, the osteoderms of *B. acostae* have a more developed peripheral figures and reduced posterior figures (Fig. 2H, I) (absent in *Parapropalaehoplophorus*; see Croft et al., 2007). The number of peripheral figures in the lateral margins ranges between seven and four, similar to that observed in *B. venezolensis*, whereas in Propalaehoplophorinae it is possible to observe up to 10 peripheral figures.

In *B. acostae*, towards the dorsal region of the dorsal carapace, the central figures of the osteoderms are surrounded by a complete series of peripheral figures. In this region, the main difference with *B. gigantea* is that in this taxon the sulci of the osteoderms are less marked.

The most anterolateral region of the dorsal carapace bears the smallest osteoderms, with a clear Glyptatelinae ornamentation pattern; each osteoderm is five-sided, whereas the central figure is surrounded by three to four peripheral figures (Fig. 2G); this morphology differs in Propalaehoplophorinae, in which the osteoderms of this region are mostly four-sided with an increased number of peripheral figures (four–six).

Caudal Armor

The caudal armor is complete, and composed of eight articulated caudal rings and a very short caudal tube (Fig. 2J), showing a primitive morphology among Glyptodontidae, resembling that of *Glyptotherium* Osborn, 1903, and *Glyptodon*. The morphology of this caudal armor differs from that known in the Miocene southern South American Glyptodontidae. Each caudal ring is composed of two rows of osteoderms with different morphology. The osteoderms of the proximal row are four- to five-sided, clearly anteroposteriorly elongated; its proximal articular half shows the typical morphology of that of Glyptodontidae, whereas the distal half is somewhat convex. In turn, the osteoderms of the distal row are five-sided and have a more isodiametric shape, and some of them have a small, 'spine-like' structure on its posterior border (Fig. 2K). This particular structure is also present (although much more developed) in late Neogene and Quaternary Glyptodontidae Glyptodontinae. None of the osteoderms of both rows present any kind of ornamentation in their exposed surface, except the first row of the most proximal caudal ring, in which it is possible to observe in its posterior section a five-sided central figure. In contrast, in *Palaehoplophoroides rothi* and *Palaehoplophorus meridionalis* ('Hoplophorinae' Palaehoplophorini), and in *C. muricatus* (Propalaehoplophorinae), the caudal armor is characterized by the presence of a series of caudal rings followed by a rigid caudal tube (although is much less developed in *C. muricatus*); in turn, in *E. petesatus* and *P. raposeirasi*, each osteoderm that constitutes the caudal rings shows a series of proximal peripheral figures surrounding a central figure, resembling a Glyptatelinae pattern (see Scillato-Yané, 1977).

PHYLOGENETIC ANALYSIS

To evaluate the monophyly of Glyptodontinae within Glyptodontidae, and the phylogenetic relationship of *Boreostemma acostae* with respect to the other recognized taxa of the subfamily, we performed a cladistic analysis. The matrix includes 18 taxa and 26 morphological characters (Appendix 1). The characters include six from the skull and dentition, one from the

cephalic armor, 13 from the dorsal carapace, five from the caudal armor, and one from the appendicular skeleton (Appendix 2). All the characters were scored via direct observation of the specimens and treated as unordered and equally weighted characters. The phylogenetic trees were rooted with the subfamily Pampatheriidae (*Pampatherium humboldtii* (Lund, 1839)), currently interpreted as the closest sister taxa to the Glyptodontidae. The taxa of the outgroup represent three of the five subfamilies recognized by Hoffstetter (1958): (1) Propalaehoplophorinae (*P. australis, Cochlops muricatus* and *Eucinepeltus petesatus*); (2) Doedicurinae (*Doedicurus clavicaudatus* Owen, 1847); and (3) 'Hoplophorinae' Hoplophorini (*Neosclerocalyptus paskoensis* Zurita, 2002, and *Hoplophorus euphractus* Lund, 1839), Plohophorini (*Pseudoplohophorus absolutus* Perea, 2005), and Panochthini (*Panochthus tuberculatus* (Owen, 1845)); within Hoplophorinae, the tribes Palaehoplophorini, Lomaphorini, and Neuryurini were excluded from the analysis because of the scarce knowledge of these taxa, most of which are restricted to isolated osteoderms of the dorsal carapace and/or fragments of the caudal armor (see Hoffstetter, 1958; Paula Couto, 1979; Zurita and Ferrero, 2009). The ingroup includes the subfamily Glyptodontinae (*Boreostemma venezolensis*, *B. acostae*, *Glyptotherium texanum* Osborn, 1903, *G. arizonae* Gidley, 1926, *Paraglyptodon uquiensis* Castellanos, 1953b, *Glyptodon munizi*, and *G. reticulatus* Owen, 1845). The species *Glyptodontidium tuberifer* Cabrera, 1944, *Boreostemma gigantean*, and *B. pliocena* Carlini et al., 2008a, were excluded from the analysis because these taxa are characterized mainly on the basis of their osteoderms; additionally, it is important to remark that several taxa traditionally linked to Glyptodontinae (*Neothoracophorus* Ameghino, 1889, *Pseudothoracophorus* Castellanos, 1951, *Boreostracon* Simpson, 1929, *Chlamydotherium* Lund, 1839, and *Heteroglyptodon* Roselli, 1976) actually represent juvenile specimens of the Pleistocene genera *Glyptodon* and *Glyptotherium* (see Oliveira et al., 2010; Zurita et al., 2011c). Finally, Glyptatelinae and the Glyptodontidae incertae sedis *Parapropalaeoplophorus septentrionalis* (see Croft et al., 2007) were also excluded because of their poor characterization.

The character-taxon matrix (Appendix 3) was analyzed via 'implicit enumeration' using 'TNT,' under the criterion of maximum parsimony (Goloboff et al., 2008). The analysis resulted in one most parsimonious tree (tree length [TL]: 34; consistency index [CI]: 0.941; retention index [RI]: 0.973). Clade support was accessed via relative Bremer support (from 578 trees; see Bremer, 1994; Goloboff and Farris, 2001), in addition to a bootstrap analysis using the option 'implicit enumeration' with 1000 replicates.

In the topology obtained (Fig. 5), a basal polytomy can be observed among *P. australis*, a large clade composed of taxa that have their records limited to southern South America (except the Pleistocene genus *Panochthus*, which is also recorded in northwestern areas), and another that includes the Glyptodontinae. The southern South American clade is supported by two synapomorphies (6:2; 22:1). *Eucinepeltus* appears as the sister taxon of the remaining taxa; this clade is supported by one synapomorphy (21:1). This is congruent with the original proposal of Ameghino (1889), Porpino et al. (2010), and Fernicola and Porpino (2012), because the evolution of the caudal tube is in this contribution interpreted as unique evolutionary event; the Santacrucian species *Cochlops muricatus* is positioned as the sister group of the clade composed of *P. absolutus* + *D. clavicaudatus* + *N. paskoensis* + *H. euphractus* + *P. tuberculatus* (20:1; 23:1). The relationship among *P. absolutus*, *D. clavicaudatus*, and the Panochthini and Hoplophorini cannot be solved. In turn, the clade composed by *N. paskoensis*, *H. euphractus*, and *P. tuberculatus* is supported by three synapomorphies (0:1; 6:1; 25:1). In agreement with Fernicola (2008) and Porpino et al. (2010), *N. paskoensis* is located as the sister group of the clade formed by *P. tuberculatus* and *H. euphractus* (12:2; 23:2; 24:1).
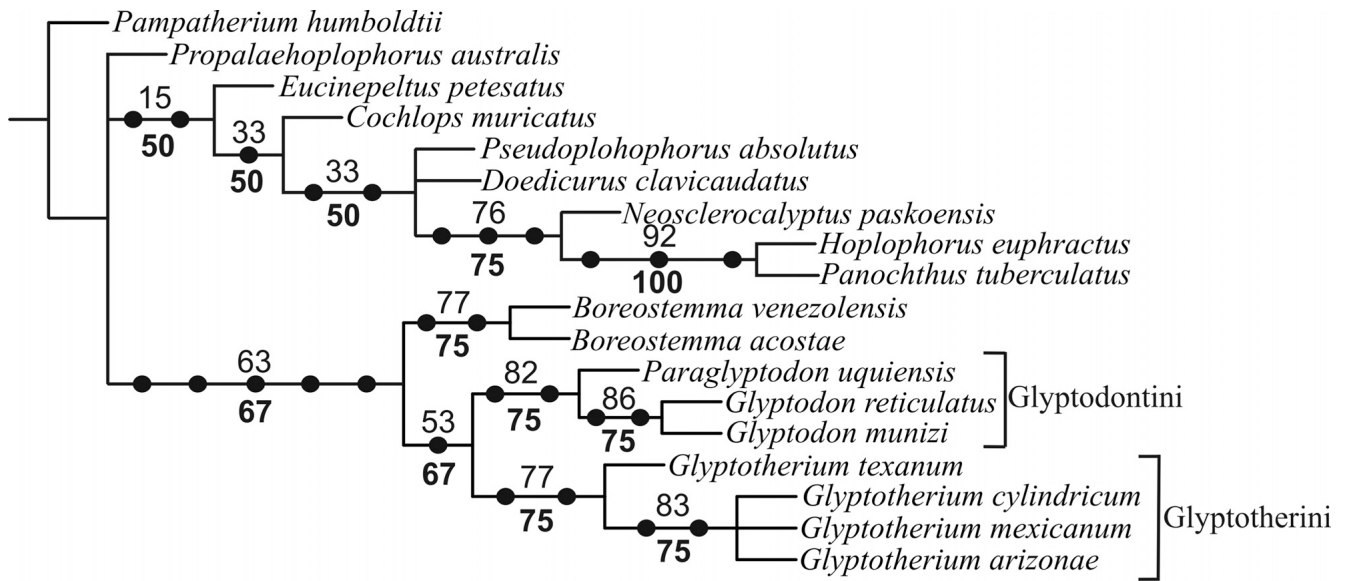
FIGURE 5. Phylogeny of Glyptodontinae based on TNT analysis of 26 osteological characters in 18 taxa (TL: 34; CI: 0.941; RI: 0.973). The numbers above each node represent bootstrap values; numbers in bold show relative Bremer support.

The other main clade is composed of the subfamily Glyptodontinae (sensu Carlini et al., 2008b; Zurita et al., 2011a), which is supported by five synapomorphies (9:1; 10:0; 11:0; 12:1; 22:2). All the genera traditionally recognized emerge as natural groups. The clade composed of *Boreostemma acostae* + *B. venezolensis* is supported by two synapomorphies (8:1; 13:1) and is positioned as the sister group of the remaining Glyptodontinae (*P. uquiensis* + *Glyptodon munizi* + *G. reticulatus* + *Glyptotherium texanum* + *G. cylindricum* + *G. mexicanum* + *G. arizonae*). Interestingly, in this clade it is possible to observe two natural groups, one composed of the South American forms (*P. uquiensis* + *Glyptodon* spp.) (5:1; 16:1) (Glyptodontini sensu Castellanos, 1951), and the other composed of the North American taxa (*Glyptotherium* spp.; Glyptotherini sensu Castellanos, 1953a) (14:1; 19:1). Within the South American clade, the Pliocene species *P. uquiensis* is located as the sister group of the Pleistocene genus *Glyptodon*, *G. munizi* and *G. reticulatus* (3:1; 4:1). In turn, within the North American clade, the Pliocene species *Glyptotherium texanum* is located as the sister group of the Pleistocene species of *Glyptotherium* (17:1; 18:1). However, the relationship among these species cannot be solved. This may be the result of a complex taxonomic situation in which it is possible that some species are synonymous (Carranza-Castañeda and Gillete, 2011).

DISCUSSION

Southern versus Northern South American Neogene Glyptodontidae

Among Glyptodontidae, the most primitive osteoderm ornamentation pattern in the dorsal carapace seems to be that present in the Glyptatelinae *Glyptatelus* (late Eocene), *Clypeotherium* Scillato-Yané, 1977 (late Oligocene), and *Neoglyptatelus* Carlini, Vizeaíno, and Scillato-Yané, 1997 (middle Miocene–Pleistocene), and in the Glyptodontidae incertae sedis *Parapropalaehoplophorus* (early Miocene) (Ameghino, 1902; Scillato-Yané, 1977; Carlini et al., 1997; Villarroel and Clavijo, 2005; Croft et al., 2007). As mentioned previously, this pattern is constituted by a main figure that is displaced towards its posterior border, so the few peripheral figures are present only in the lat-

eral and distal margins of each osteoderm; in addition, there are no accessory peripheral figures (Scillato-Yané, 1977). This morphology is very similar to that present in most Cingulata Dasypodidae (e.g., *Dasypus* Linnaeus, 1758).

In this context, the 'rosette' pattern ornamentation (which is a central figure surrounded by a complete series of peripheral figures) appears in the Glyptodontidae Propalaehoplophorinae in the Patagonian region of Argentina from, at least, late Oligocene (Scillato-Yané, 1977). Compared with the 'Glyptatelinae' pattern, this morphology is clearly more derived, because there are many peripheral figures, with the presence of some lateroanterior accessories, whereas the main figure is located in the central area of the exposed surface of the osteoderm.

As pointed out by Fernicola (2008) and González-Ruiz et al. (2011), taking into account that most of the lineages were already differentiated in the late Miocene, the early to middle Miocene (23.03–11.608 Ma) (International Commission on Stratigraphy, 2010) periods constitute a key interval in the diversification of Glyptodontidae. However, the paleontological evidence suggests that, whereas in southern South America the middle Miocene could have represented a diversification period for Glyptodontidae, in northern South America the situation was very different, because the only Glyptodontidae recorded during the middle Miocene–late Pleistocene interval are Glyptodontinae (and probably Glyptatelinae, but see Porpino et al., 2009).

In agreement with this hypothesis, Cozzuol (2006) reported some Glyptodontidae taxa of the Acre region (Brazil) (Huayquerian age; ca. 9 Ma). These include *Plohophorus* Ameghino, 1887b, *Paraglyptodon*, *Neoglyptatelus*, and *Asterostemma*. Although it is reasonable to find *Paraglyptodon*, *Asterostemma* (= *Boreostemma*), and *Neoglyptatelus*, it is possible that the identification of *Plohophorus* is incorrect, because the first record of the genus corresponds to the Montehermosan Age (ca. 6.8–3.9 Ma) of the Pampean region of Argentina (see Scillato-Yané et al., 1995). In fact, this particular paleobiogeographic scenario could have persisted until the late Pleistocene, because the most frequently (and almost the only glyptodont) recorded are the Glyptodontinae *Glyptodon* and *Glyptotherium* (see Carlini et al., 2008b; Zurita et al., 2009). The only other Pleistocene taxa recorded is the genus *Panochthus*, but it is restricted to the

Atlantic regions of South America (Porpino et al., 2004; Zurita et al., 2009).

In contrast with this situation, in the same gap (Huayquerian age), the diversity of Glyptodontidae in southern areas comprises almost all the known main lineages: 'Hoplophorinae' (Hoplophorini, Palaehoplophorini, Panochthini, Plohophorini, Neuryurini) and Doedicurinae (Cabrera, 1944; Paula Couto, 1979; Carlini and Scillato-Yané, 1999).

In this paleobiogeographical context, the remains of Neogene Glyptodontidae from middle latitude in South America are almost unknown (see Marshall and Sempere, 1991; Scillato-Yané and Carlini, 1999; Antoine et al., 2007; Tejada et al., 2011), including a possible Propalaehoplophorinae, *Propalaehoplophorus andinus* Frailey, 1988. A taxonomic revision of these remains is needed.

In this scenario, *B. acostae* shows a unique combination of derived and primitive characters. The morphology of the osteoderms of the lateral region of the dorsal carapace is very primitive, similar to that of *Glyptatelus*, *Clypeotherium*, and *Parapropalaehoplophorus*, but with some differences. Compared with *Parapropalaehoplophorus*, the osteoderms of *B. acostae* show deeper and wider sulci, with the lateral peripheral figures a little better developed, whereas the main figure is more angular, as observed in all Glyptodontinae. In turn, *Glyptatelus* and *Clypeotherium* have some conspicuous foramina that are not present in *B. acostae*. At the level of the skull, the high level of lobulation of the molariforms in *B. acostae* is remarkable, whereas the overall form of the skull seems to be very primitive, similar to that of the Pampatheriidae *Pampatherium*, the sister group of the Glyptodontidae clade (Porpino et al., 2010). Another remarkable character is the lobulation of the first molariform tooth, unique among Neogene Glyptodontidae; in fact, in the most derived Pleistocene forms, only *Panochthus* and the Glyptodontinae *Glyptodon* and *Glyptotherium* share this character (see Burmeister, 1870–1874; Gillette and Ray, 1981; Soibelzon et al., 2006). On the other hand, the caudal armor preserves a very primitive morphology, typical of Glyptodontinae; this contrasts with the southern taxa, in which the presence of a well-developed caudal tube is already observed in the middle Miocene Palaehoplophorini (ca. 12.2–11.8 Ma).

The presence of primitive characters in *Boreostemma* among Glyptodontidae could be correlated with its geographical origin, because it is proven in Xenarthra that taxa of intertropical origin tend to retain a large number of primitive characters (e.g., *Eremotherium* Spillman, 1948; *Holmesina* Simpson, 1930; Scelidotheriinae Ameghino, 1904; Carlini et al., 1997; Carlini and Zurita, 2010; Miño-Boilini, 2012; Gois et al., 2012).

CONCLUSIONS

The description and comparison of this new material assigned to *B. acostae* with southern forms (especially Propalaeohoplophorinae and 'Hoplophorinae' Palaehoplophorini and Hoplophorini) corroborate the noticeable morphological differences between both groups.

Boreostemma acostae shows a combination of primitive and derived characters. The cladistic analysis supports the monophyly of Glyptodontinae within Glyptodontidae, whereas *Boreostemma* is located as the sister group of the remaining taxa of Glyptodontinae. In turn, the genera *Glyptodon* and *Glyptotherium* appear as monophyletic groups.

The evidence indicates that most of the main lineages of Glyptodontidae have their oldest records in southern areas of South America, except Glyptodontinae, whose oldest records came from northern South America. Interestingly, it is probable that Glyptodontinae were the only Glyptodontidae participating in the Great American Biotic Interchange (GABI), because *Pachyarmatherium* is currently interpreted by some authors as a non-Glyptodontidae.

This particular paleobiogeographic pattern seems to persist until the late Pleistocene because the Glyptodontidae most frequently recorded in northern areas are Glyptodontinae. In addition to Glyptodontinae, the only other taxon recorded is the Panochthini *Panochthus*, but restricted to the Atlantic coast of South America.

LITERATURE CITED

Ameghino, F. 1875. Notas sobre algunos fósiles nuevos de la Formación Pampeana. Obras Completas y Correspondencia Científica 2:11–17.
Ameghino, F. 1881. La antigüedad del hombre en el Plata 2:1–557. G. Mason-Igon Hermanos, París-Buenos Aires.
Ameghino, F. 1887a. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo La Plata. Boletín del Museo La Plata 1:1–26.
Ameghino, F. 1887b. Apuntes preliminares sobre algunos mamíferos estinguidos del yacimiento de "Monte Hermoso" existentes en el "Museo de La Plata." Boletín del Museo de La Plata 1:1–20, láms. 1–2.
Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas de la Academia Nacional de Ciencias de Córdoba 6:1–1027.
Ameghino, F. 1891. Nuevos restos de mamíferos fósiles descubiertos por Cárlos AMEGHINO en el eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correcciones. Revista Argentina de Historia Natural 1:289–328.
Ameghino, F. 1900–1902. L'âge des formations sédimentaires de Patagonie. Anales de la Sociedad Científica Argentina 50:109–130, 145–165, 207–229 (1900); 51:20–39, 65–91 (1901); 52:189–197, 244–250 (1901); 54:161–180, 220–240, 283–342 (1902).
Ameghino, F. 1902. Notices préliminaires sur des mammifères nouveaux des terrains crétacés de Patagonie. Boletín de la Academia Nacional del Ciencias de Córdoba 17:71–138.
Ameghino, F. 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. Anales de la Sociedad Científica Argentina 58:35–41.
Antoine, P. O., R. Salas-Gismondi, P. Baby, M. Benammi, S. Brusset, D. de Franceschi, N. Espurt, C. Goillot, F. Pujos, J. Tejada, and M. Urbina. 2007. The Middle Miocene (Laventan) Fitzcarrald fauna, Amazonian Peru; pp. 19–24 in E. Díaz-Martínez and I. Rábano (eds.), 4th European Meeting on the Palaeontology and Stratigraphy of Latin America. Cuadernos del Museo Geominero, nº 8. Instituto Geológico y Minero de España, Madrid.
Bondesio, P., J. H. Laza, G. J. Scillato Yané, E. P. Tonni, and M. G. Vucetich. 1980. Estado actual del conocimiento de los Vertebrados de La Formación Arroyo Chasicó (Plioceno temprano) de La Provincia de Buenos Aires. Actas, II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología, Buenos Aires, 1978, Tomo III:101–127.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10:295–304.

Burmeister, G. 1870–1874. Monografía de los Glyptodontes en el Museo Público de Buenos Aires. Anales del Museo Público de Buenos Aires 2:1–412.

Cabrera, A. 1944. Los Gliptodontoideos del Araucaniano de Catamarca. Revista del Museo de La Plata (Nueva Serie) 3(15):5–76.

Carlini, A. A., and G. J. Scillato-Yané. 1999. Evolution of Quaternary Xenarthrans (Mammalia) of Argentina; pp. 149–175 in J. Rabassa and M. Salemme (eds.), Quaternary of South America and Antarctic Peninsula, Volume 12, Quaternary of South America and Antarctic Peninsula. A. A. Balkema, Rotterdam.

Carlini, A. A., and A. E. Zurita. 2010. An introduction to cingulate evolution and their evolutionary history during the Great American Biotic Interchange: biogeographical clues from Venezuela; pp. 233–255 in M. Sánchez-Villagra, O. Aguilera, and A. A. Carlini (eds.), Urumaco and Venezuelan Paleontology. Indiana University Press, Bloomington, Indiana.

Carlini, A. A., M. Ciancio, and G. J. Scillato-Yané. 2005. Los Xenarthra de Gran Barranca: más de 20 Ma de historia. XVI Congreso Geológico Argentino. Actas:419–424. La Plata.

Carlini, A. A., S. F. Vizcaíno, and G. J. Scillato-Yané. 1997. Armored xenarthrans: a unique taxonomic and ecologic assemblage; pp. 213–232 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics, Volume 13, The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington D.C. and London.

Carlini, A. A., A. E. Zurita, and O. Aguilera. 2008b. North American Glyptodontines (Xenarthra, Mammalia) in the upper Pleistocene of northern South America. Palaeontologische Zeitschrift 82:139–152.

Carlini, A. A., A. E. Zurita, G. J. Scillato-Yané, R. Sánchez, and O. A. Aguilera. 2008a. New Glyptodont species from Codore Formation (Pliocene), Estado Falcón (Venezuela), its relationship with the 'Asterostemma' problem, and the paleobiogeography of the Glyptodontinae. Palaeontologische Zeitschrift 82:125–138.

Carranza-Castañeda, O., and D. D. Gillette. 2011. Origin of North American glyptodonts: Glyptotherium texanum from Mexico and the United States (Pliocene Epoch). IV Congreso Latinoamericano de Paleontología de Vertebrados, San Juan, Argentina. Resúmenes:122.

Castellanos, A. 1951. Acotaciones al género Neothoracophorus Ameghino. Revista de la Asociación Geológica Argentina 6:63–82.

Castellanos, A. 1953a. Anotações e retificações ao genero "Glyptodon" Owen e a familia "Glyptodontinae." Anais da Academia Brasileira de Ciencias 4:391–410.

Castellanos, A. 1953b. Descripción de restos de Paraglyptodon uquiensis n. sp. de Uquía (Senador Pérez), Jujuy. Memorias del Museo de Entre Ríos 32 (Paleontología):1–32.

Cione, A. L., and E. P. Tonni. 2005. Bioestratigrafía basada en mamíferos del Cenozoico Superior de la provincia de Buenos Aires, Argentina. 16th Congreso Geológico Argentino. La Plata, Buenos Aires. Relatorio:183–200.

Cope, E. D. 1889. The Edentata of North America. American Naturalist 23:657–664.

Cozzuol, M. A. 2006. The Acre vertebrate fauna: age, diversity, and geography. Journal of South American Earth Sciences 21:85–203.

Croft, D. A., J. J. Flynn, and A. R. Wyss. 2007. A new basal Glyptodontoid and other Xenarthra of the early Miocene Chucal Fauna, northern Chile. Journal of Vertebrate Paleontology 27:781–797.

Croft, D. A., F. Anaya, D. Auerbach, C. Garzione, and B. J. MacFadden. 2009. New Data on Miocene Neotropical Provinciality from Cerdas, Bolivia. Journal of Mammal Evolution 16:175–198.

De Porta, J. 1962. Edentata Xenarthra del Mioceno de La Venta (Colombia), 1: Dasypodoidea y Glyptodontoidea. Boletín de Geología, Universidad Nacional del Santander, Bucaramanga 22–23:5–32.

De Porta, J. 1969. Les vertébrés fossiles de Colombie et les problèmes posés par l'isolement du continent Sud-Américain. Paleovertebrata 2:77–94.

Fernicola, J. C. 2008. Nuevos aportes para la Sistemática de los Glyptodontia Ameghino 1889 (Mammalia, Xenarthra, Cingulata). Ameghiniana 45:553–575.

Fernicola, J. C., and K. O. Porpino. 2012. Exoskeleton and systematic: a historical problem in the classification of glyptodonts. Journal of Mammalian Evolution 19:171–183.

Flynn, J. J., and C. C. Swisher. 1995. Cenozoic South American Land Mammal Ages: correlation to global geochronologies. Geochronology Time Scales and Global Stratigraphic Correlations, SEMP (Society for Sedimentary Geology) Special Publication 54:317–333.

Flynn, J. J., J. Guerrero, and C. C. Swisher. 1997. Geochronology of the Honda Group; pp. 44–59 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C. and London.

Frailey, C. D. 1988. The Miocene vertebrates of Quebrada Honda, Bolivia. Part II. Edentata. Occasional Papers of the Museum of Natural History, The University of Kansas 123:1–13.

Gidley, J. W. 1926. Fossil Proboscidea and Edentata of the San Pedro Valley, Arizona. United States Geological Survey Professional Paper 140B:83–95, 13 plates, 4 figures.

Gillette, D. D., and C. E. Ray. 1981. Glyptodonts of North America. Smithsonian Contributions to Paleobiology 40:1–251.

Gois, F., G. J. Scillato-Yané, A. A. Carlini, and M. Ubilla. 2012. Una nueva especie de Holmesina Simpson (Xenarthra, Cingulata, Pampatheriidae) del Pleistoceno de Rondônia, sudoeste de la Amazonia, Brasil. Revista Brasileira de Paleontologia 15:211–227.

Goloboff, P. A., and J. S. Farris. 2001. Methods for quick consensus estimation. Cladistics 17:26–34.

Goloboff, P., J. Farris, and K. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

González, L. R. 2010a. Los Cingulata (Mammalia, Xenarthra) del Mioceno temprano y medio de Patagonia (edades Santacrucense y "Friasense"). Revisión sistemática y consideraciones bioestratigráficas. Ph.D. dissertation, Universidad Nacional de La Plata, La Plata, Buenos Aires, 471 pp.

González, L. R. 2010b. Los Cingulata (Mammalia, Xenarthra) del Mioceno temprano y medio de Patagonia (edades Santacrucense y "Friasense"). Revisión sistemática y consideraciones bioestratigráficas. Mastozoología Neotropical 17:402–403.

González-Ruiz, L. R., G. J. Scillato-Yané, M. Zamorano, A. E. Zurita, and M. F. Tejedor. 2011. Un nuevo Glyptodontidae (Mammalia, Xenarthra, Cingulata) del Mioceno de Patagonia (Argentina) y comentarios acerca de los gliptodontes del SALMA "Friasense." Revista Mexicana de Ciencias Geológicas 28:566–579.

Gray, J. E. 1869. Catalogue of Carnivorous, Pachydermatous and Edentate Mammalia in the British Museum. British Museum (Natural History), London, VII + 398 pp.

Guerrero, J. 1997. Stratigraphy, sedimentary environments, and the Miocene uplift of the Colombian Andes; pp. 15–43 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C. and London.

Hoffstetter, R. 1958. Xenarthra; pp. 535–636 in P. Piveteau (ed.), Traité de Paléontologie, Vol. 2, No. 6, Mammifères, Evolution. Masson, Paris.

Illiger, C. 1811. Prodromus Systematis Mammalium et Avium Additis Terminis Zoographicis Utriudque Classis. C. Salfeld, Berlin, xviii + 301 pp.

International Commission on Stratigraphy (ICS), International Union of Geological Sciences (IUGS). 2010. International Stratigraphic Chart. http://www.stratigraphy.org

Kraglievich, L. 1930. La Formación Friaseana del río Frias, río Fénix, Laguna Blanca, etc., y su fauna de mamíferos. Physis 10(35):127–161.

Krmpotic, C., M. Ciancio, C. Barbeito, R. C. Mario, and A. A. Carlini. 2009. Osteoderm morphology in recent and fossil euphractine xenarthrans. Acta Zoologica 90:339–351.

Linneaus, C. 1758. Systema Naturae. 10th edition. Laurentii Salvii, Stockholm, Volume 1: II + 824 pp.

López, G., M. G. Vucetich, M. M. Carlini, M. Bond, M. E. Pérez, M. R. Ciancio, D. J. Pérez, M. Arnal, and I. Olivares. 2011. New Miocene mammal assemblages from Neogene Manantiales basin, Cordillera Frontal, San Juan, Argentina; pp. 211–226 in J. A. Salfity and R. A. Marquillas (eds.), Cenozoic Geology of the Central Andes of Argentina. SCS Publisher, Salta.

Lund, P. W. 1839. Coup-d'oeil sur les espèces éteintes de mammifères du Brésil; extrait de quelques mémoires présentés à l'Académie royale des Sciences de Copenhague. Annales des Sciences Naturelles, Tome 11 (Zoologie 2):214–234.

Lydekker, R. 1894. Contribution to knowledge of the fossil vertebrates of Argentina. Part 2. The extinct Edentates of Argentina. Anales del Museo de La Plata (Paleontología) 3:1–118.

Madden, R. H., J. Guerrero, R. F. Kay, J. J. Flynn, C. C. Swisher III, and A. H. Walton. 1997. The Laventan stage and age; pp. 499–519 in M. R. H. Kay, F. R., Cifelli, and J. J. Flyn (eds.), Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta. Smithsonian Institution Press, Washington, D.C. and London.

McKenna, M. C., and S. K. Bell 1997. Classification of Mammals: Above the Species Level. Columbia University Press, New York, 631 pp.

Marshall, L. G., T. Sempere, 1991. The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review; pp. 631–652 in R. Suárez-Soruco (ed.), Fósiles y Facies de Bolivia, 1: Vertebrados, vol. 12. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos.

Miño-Boilini, A. R. 2012. Sistemática y evolución de los Scelidotheriinae (Xenarthra, Mylodontidae) cuaternarios de Argentina. Importancia bioestratigráfica, paleobiogeográfica y paleoambiental. Ph.D. dissertation, Universidad Nacional de La Plata, La Plata, Buenos Aires, 301 pp.

Oliveira, E. V., K. Porpino, and A. F. Barreto. 2010. On the presence of *Glyptotherium* in the Late Pleistocene of Northeastern Brazil, and the status of "*Glyptodon*" and "*Chlamydotherium*." Paleobiogeographic implications. Neues Jahrbuch für Geologie und Paläontologie 258/3:353–363.

Osborn, F. H. 1903. *Glyptotherium texanum*, a new Glyptodont from the lower Pleistocene of Texas. Bulletin of the American Museum of Natural History 19:491–494, pl. 1.

Owen, R. 1839. Description of a tooth and part of the skeleton of the *Glyptodon*, a large quadruped of the edentate order, to which belongs the tessellated bony armour figured by Mr. CLIFT in his memoir on the remains of the *Megatherium*, brought to England by Sir Woodbine PARISH, F.G.S. Proceedings of the Geological Society of London 3:108–113.

Owen, R. 1845. Descriptive and Illustrated Catalogue of the Fossil Organic Remains of Mammalia and Aves Contained in the Museum of the Royal College of Surgeons of London. R. and J. E. Taylor, London, 391 pp.

Owen, R. 1847. Notices of some fossil Mammalia of South America; pp. 65–67 in Report of the 16th Meeting of the British Association for the Advance of Science, Southampton, 1846. British Association for the Advance of Science, London.

Parodi, L. J. 1930. Sobre nuevos restos de mamíferos de la fauna pampeana en Patagonia. Physis 10:21–34.

Paula Couto, C. 1954. Sobre um gliptodonte do Uruguai e um tatu fóssil do Brasil. Divisão de Geologia e Mineralogia, Notas preliminares e Estudos 80:1–10.

Paula Couto, C. 1979. Tratado de Paleomastozoologia. Academia Brasileira de Ciências, Rio de Janeiro, 590 pp.

Perea, D. 2005. *Pseudoplohophorus absolutus* n. sp. (Xenarthra, Glyptodontidae), variabilidad en Sclerocalyptinae y redefinición de una biozona del Mioceno superior de Uruguay. Ameghiniana 42:175–190.

Porpino, K. O., F. C. M. Dos Santos, and L. P. Bergqvist. 2004. Registros de Mamíferos fósseis no Lajedo de Soledade, Apodi, Rio Grande do Norte, Brasil. Revista Brasileira de Paleontologia 7:349–358.

Porpino, K. O., J. C. Fernicola, and L. P. Bergqvist. 2009. A new cingulate (Mammalia, Xenarthra) *Pachyarmatherium brasiliense* sp. nov., from the late Pleistocene of Northeastern Brazil. Journal of Vertebrate Paleontology 29:881–893.

Porpino, K. O., J. C. Fernicola, and L. P. Bergqvist. 2010. Revisiting the intertropical Brazilian species *Hoplophorus euphractus* (Cingulata, Glyptodontoidea) and the phylogenetic affinities of *Hoplophorus*. Journal of Vertebrate Paleontology 30:911–927.

Roselli, F. L. 1976. Contribución al Estudio de la Geo-Paleontología. Departamentos de Colonia y Soriano, República Oriental del Uruguay, Montevideo, 175 pp., 30 figures.

Roth, S. 1899. Apuntes sobre la geología y paleontología de los Territorios del Río Negro y Neuquén. Revista del Museo de La Plata 9:141–197.

Royo y Gómez, J. 1945. Los Vertebrados del Terciario continental Colombiano. Revista de La Academia Colombiana de Ciencias Exactas, Físicas y Naturales 6:496–511.

Rusconi, C. 1946. Presencia de mamíferos terciarios en San Juan. Publicaciones del Instituto de Fisiografía y Geología 6:1–11.

Schultz, P. H., M. Zárate, B. Hames, C. Koeberl, T. Bunch, D. Storzer, P. Renne, and J. Wittke. 2004. The Quaternary impact record from the Pampas, Argentina. Earth and Planetary Science Letters 219:221–238.

Scillato-Yané, G. J. 1977. Sur quelques Glyptodontidae nouveaux (Mammalia, Edentata) du Déséadien (Oligocéne inférieur) de Patagonie (Argentine). Bulletin du Muséum National d'Histoire Naturelle 487:249–260.

Scillato-Yané, G. J. 1986. Los Xenarthra fósiles de Argentina (Mammalia, Edentata). IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, Argentina. Actas 2:151–155.

Scillato-Yané, G. J., and A. A. Carlini. 1998. Nuevos Xenarthra del Friasense (Mioceno Medio) de Argentina. Stvdia Geologica Salmantisencia 34:43–67.

Scillato-Yané, G. J., and A. A. Carlini. 1999. Nuevos Xenarthra del Mioceno de Quebrada Honda, Bolivia; p. 39 in Congreso Internacional, Evolución Neotropical del Cenozoico, Programa y Resúmenes, La Paz, Bolivia.

Scillato-Yané, G. J., A. A. Carlini, S. F. Vizcaíno, and E. Ortiz Jaureguizar. 1995. Los Xenarthros; pp. 183–209 in M. T. Alberdi, G. Leone, and E. P. Tonni (eds.), Evolución Biológica y Climática de la Región Pampeana Durante los Últimos Cinco Millones de Años. Un Ensayo de Correlación con el Mediterráneo occidental. Volume 12. Museo de Ciencias Naturales, Consejo de Investigaciones, Monografías CSIC, Madrid.

Scott, W. B. 1903–1904. Mammalia of the Santa Cruz Beds. I. Edentata. Reports of the Princeton University Expedition to Patagonia (1896–1899) 5:1–364.

Simpson, G. G. 1929. Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida. Bulletin of the American Museum of Natural History 56:561–599, 22 figures.

Simpson, G. G. 1930. *Holmesina septentrionalis*, extinct giant armadillo of Florida. American Museum Novitates 422:1–10.

Simpson G. G. 1947. A Miocene glyptodont from Venezuela. American Museum Novitates 1368:1–10.

Soibelzon, E., A. E. Zurita, and, A. A. Carlini. 2006. *Glyptodon munizi* Ameghino (Mammalia, Cingulata, Glyptodontidae): redescripción y anatomía. Ameghiniana 43:377–384.

Spillmann, F. 1948. Beiträge zur Kenntnis eines neuen gravigraden Riesensteppentieres (*Eremotherium carolinenese* gen. et. spec. nov.), seines Lebensraumes und seiner Lebensweise. Palaeobiologica 8:231–279.

Tejada, J., P.-A. Antoine, P. Baby, F. Pujos, and R. Salas-Gismondi. 2011. Basal or not so basal Cingulates in the Middle Miocene of Peruvian Amazonia IV Congreso Latinoamericano de Paleontología de Vertebrados, San Juan, Argentina. Resúmenes:400.

Villarroel, C. 1983. Descripción de *Asterostemma*? *acostae*, nueva especie de propalaehoplophorino (Glyptodontidae, Mammalia) del Mioceno de La Venta, Colombia. Geología Norandina 7:29–34.

Villarroel, C. 1998. Los Nothrotheriinae (Megatheriidae, Gravigrada) del Mioceno de La Venta (Colombia). Descripción de *Huilabradys magdaleniensis*, Nuevo Género y Especie. Revista Academia Colombiana de Ciencias Exactas, Físicas y Naturales 22:497–506.

Villarroel, C. 2000. Un nuevo Mylodontinae (Xenarthra, Tardigrada) en la Fauna de La Venta, Mioceno de Colombia: estado actual de la Familia Orophodontidae. Revista Academia Colombiana de Ciencias Exactas, Físicas y Naturales 24:117–127.

Villarroel, C., and J. Clavijo. 2005. Los mamíferos fósiles y las edades de las sedimentitas continentales del Neógeno de la costa caribe colombiana. Revista de la Academia Colombiana de Ciencias XIX:345–356.

Vizcaíno, S. F., A. Rinderknecht, and A. Czerwonogora. 2003. An enigmatic Cingulata (Mammalia: Xenarthra) from the late Miocene of Uruguay. Journal of Vertebrate Paleontology 23:981–983.

Zurita, A. E. 2002. Nuevo Gliptodonte (Mammalia, Glyptodontoidea) del Cuaternario de la Provincia del Chaco (Argentina). Ameghiniana 39:175–182.

Zurita, A. E., 2007. Sistemática y evolución de los Hoplophorini (Xenarthra, Glyptodontidae, Hoplophorinae. Mioceno tardío-Holoceno temprano). Importancia bioestratigráfica, paleobiogeográfica y paleoambiental. Ph.D. dissertation, Universidad Nacional de La Plata, La Plata, Buenos Aires, 367 pp.

Zurita, A. E., and B. Ferrero. 2009. Una nueva especie de *Neuryurus* Ameghino (Mammalia, Glyptodontidae) en el Pleistoceno tardío de la Mesopotamia de Argentina. El registro más completo del género fuera de la región Pampeana. Geobios 42:663–673.

Zurita, A. E., A. A. Carlini, D. D. Gillette, and R. Sánchez. 2011a. Late Pliocene Glyptodontinae (Xenarthra, Cingulata, Glyptodontidae) of South and North America: morphology and

paleobiogeographical implications in the GABI. Journal of South American Earth Sciences 31:178–185.

Zurita, A. E., A. R. Miño-Boilini, E. Soibelzon, A. A. Carlini, and F. Paredes-Ríos. 2009. The diversity of Glyptodontidae (Xenarthra, Cingulata) in the Tarija Valley (Bolivia): systematic, biostratigraphic and paleobiogeographic aspects of a particular assemblage. Neues Jahrbuch für Geologie und Palaontologie 251–252:225–237.

Zurita, A. E., A. Scarano, A. A. Carlini, G. J. Scillato-Yané, and E. Soibelzon. 2011b. *Neosclerocalyptus* spp. (Cingulata: Glyptodontidae: Hoplophorini): cranial morphology and palaeoenvironments along the changing Quaternary. Journal of Natural History 45:893–914.

Zurita, A. E., E. Oliveira, P. Toriño, S. Rodriguez-Bualó, G. J. Scillato-Yané, C. Luna, and J. Krapovickas. 2011c. On the taxonomic status of some Glyptodontidae (Mammalia, Xenarthra, Cingulata) from the Pleistocene of South America. Annales de Paleontologie 97:63–83.

APPENDIX 1. Specimens examined and references consulted for comparative study and cladistic analysis.

Boreostemma acostae: ICNUNC P-225-1 (Type); UCMP 38039; CAL-896; Villarroel (1983).

Boreostemma gigantea: IGM 250928 (Type); Carlini et al. (1997).

Boreostemma pliocena: AMU-CURS 158 (Type); Carlini et al. (2008b).

Boreostemma venezolensis: FM 39574 (Type); Simpson (1947).

Clypeotherium magnum: MLP 61-IV-11-76; Scillato-Yané (1977).

Cochlops? debilis: MACN A 4752 (Type); YMP PU 15592.

Cochlops muricatus: MACN A 1036-1039, MACN 2121, MACN 2113; YMP PU 15331.

Eucinepeltus petesatus: MACN A 4758, and 4760 (Type); MPFE Pv-1383.

Glyptodon munizi: MMP 3985; Soibelzon et al. (2006).

Glyptodon reticulatus: MCA 2015 and 2017; Zurita et al. (2010).

Glyptodontidium tuberifer: MLP 29-X-8-3 (Type); Cabrera (1944).

Glyptotherium arizonae: USNM 10536 (Type); AMNH 21808; Gillette and Ray (1981).

Glyptotherium cylindricum: AMNH 15548 (Type); MCN n/n; Gillette and Ray (1981).

Glyptotherium texanum: AMNH 1074 (Type); Gillette and Ray (1981).

Metopotoxus? anceps: YMP PU 15612 (Type).

Neoglyptatelus sincelejanus: IGM p174925 (JC 529454 A1-4); Villarroel and Clavijo (2005).

Neosclerocalyptus paskoensis: Ctes-PZ 5879 (Type); Zurita et al. (2011a,b).

Pampatherium humboldtii: MCL-PUC/MG 900; MHD-P 28.

Panochthus tuberculatus: MLP 16-29.

Paraeucinepeltus raposeirasi: LIEB-PV-6000 (Type).

Paraglyptodon uquiensis: MACN 5377, 5530, 5355 (Type); Castellanos (1953b).

Parapropalaehoplophorus septentrionalis: SGO PV 4165 (Type); Croft et al. (2007).

Propalaehoplophorus australis: MLP 16-15, MLP 16-16; YMP PU 15212.

Propalaehoplophorus minus: MACN A 4757 (Type); AMNH 9197.

Pseudoplohophorus absolutus: FC-DPV 475 and 595; Perea (2005).

APPENDIX 2. List of characters and character states used in the cladistic analysis. All characters are treated as unordered.

(0) Pneumatization of the rostral area of the skull: absent (0); present (1).

(1) M1/m1 fully lingually and labially trilobated: absent (0); present (1).

(2) Morphology of the dorsal area located ahead the orbitals: non-quadrangular (0); quadrangular (1).

(3) Angle between the palatal plane and the ventral half of the descending process of the maxillae: approximately 90° (0); more than 90° (1).

(4) Morphology of the infraorbital foramen: circular or oval (0); oval with a lower channel (1).

(5) Morphology of the orbital notch in lateral view: dorsoventrally elongated (0); circular (1).

(6) Morphology of the cephalic armor: cephalic armor composed of small osteoderms with rough surface (0); cephalic armor composed of large osteoderms with a rosette ornamentation (1); cephalic armor composed by large osteoderm without peripheral figures (2).

(7) Cephalic notch with osteoderm 'spine-like': absent (0); present (1).

(8) Central figure of the osteoderms of the caudal notch: without a trapezoidal central figure (0); with a trapezoidal central figure (1).

(9) Ornamentation pattern of the lateral region of the dorsal carapace: rosette pattern with circular central figure (0); rosette pattern with angular central figure (1).

(10) Maximum number of peripheral figures: up to 12 (0); up to 14 (1); more than 14 (2).

(11) Number of rows of peripheral figures: one row without accessory (= additional) peripheral figures (0); one row with accessory peripheral figures (1); absent (2).

(12) Morphology of the caudal notch: osteoderms with lateral and one row of proximal peripheral figures (0); osteoderms with one row of proximal peripheral figures (1); osteoderms with two or more rows of proximal peripheral figures (2).

(13) Lateroventral region of the dorsal carapace: central figure located in the central or posterior area of the osteoderms with more than six peripheral figures (0); central angular figure located in the posterior area of the osteoderms with four to five peripheral figures (1).

(14) Dorsal profile of the caudal notch: ventrally inclined (0); dorsally inclined (1).

(15) Morphology of the osteoderms that constitute the border of the carapace: 'spine-like' osteoderms absent or limited to the caudal notch (0); 'spine-like' osteoderms present around the dorsal carapace (1).

(16) Development of the central sulci of the osteoderms of the dorsal area of the carapace: little or moderately developed (width less than 4 mm) (0); maximum development (ca. 4–6 mm) (1).

(17) Dorsal carapace divided into preiliac and postiliac regions, occupying two-thirds and one-third of the curvature, respectively: absent (0); present (1).

(18) Morphology of the border of the carapace between the caudal notch and the most posterior region: limit between both structures forming an angle (0); limit between both structures rounded (1).

(19) Exposed surface of the central figure of the osteoderms of the posterior region of the carapace: smooth or concave (0); with a central concavity (1).

(20) Caudal tube representing more than the 50% of the total length of the caudal armor: absent (0); present (1).

(21) Morphology of the caudal armor: composed of caudal rings representing more than 90% of the total length (0); composed by caudal rings + caudal tube (this representing

more than the 30% of the total length of the caudal armor) (1).

(22) Morphology of the exposed surface of the osteoderms of the caudal rings: exposed surface of the osteoderms smooth and without ornamentation (0); exposed surface of the osteoderms smooth with peripheral figures (1); exposed surface of the distal rows of osteoderms with 'spine-like' structure (2).

(23) Lateral area of the caudal tube: without ornamentation (0); lateral figures (1); lateral and 'spine-like' figures (2); only 'spine-like' figures (3).

(24) Presence of conical tubercle in the lateral and terminal figures of caudal tube (modified from Porpino et al., 2010): absent (0); present (1).

(25) Supratrochlear fossa of the femur deep and triangular: absent (0); present (1).

APPENDIX 3.   Character-taxon matrix used in phylogenetic analysis.

	0 4	9	1 4	1 9	2 4
Pampatherium humboldtii	00000	0000-	----0	0-00-	000--0
Propalaehoplophorus australis	00000	01000	11000	00000	000000
Eucinepeltus petesatus	00000	02000	11000	00000	001?0?
Cochlops muricatus	00000	0?000	11000	00000	01100?
Doedicurus clavicaudatus	00000	0200-	----0	0-00-	110300
Neosclerocalyptus paskoensis	10000	01000	11000	00000	111101
Panochthus tuberculatus	10000	01000	21200	00000	111211
Hoplophorus euphractus	100?0	0?000	11200	00000	111211
Pseudoplohophorus absolutus	00000	02000	11000	?00?0	11?10?
Glyptotherium texanum	00000	0?001	00101	10001	002000
Glyptotherium arizonae	00000	0?001	00101	10111	002000
Glyptotherium mexicanum	?????	????1	00101	1011?	?02?0?
Glyptotherium cylindricum	00???	???01	00101	10111	?02?00
Boreostemma acostae	00000	00011	00110	00000	00200?
Boreostemma venezolensis	?00??	??011	00110	000?0	??2?0?
Paraglyptodon uquiensis	0??00	1???1	00?00	?1???	??2?0?
Glyptodon munizi	01111	10101	00100	11000	002000
Glyptodon reticulatus	01111	10101	00100	11000	002000