Phylogenetic analysis of the Panochthini (Xenarthra, Glyptodontidae), with remarks on their temporal distribution

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To test the monophyly of Panochthini, a phylogenetic analysis including all the species traditionally referred to the tribe was conducted. The matrix included 16 species of Glyptodontidae and 35 characters, from which 14 correspond to the skull, four to the dentition, two to the cephalic armour, nine to the dorsal carapace and six to the caudal sheath. *Propalaehoplophorus australis* (Propalaehoplophorinae) was used to root the trees. Four most parsimonious trees were obtained (Tree Length = 75, CI = 0.65, RI = 0.70). The strict consensus tree (Tree Length = 77, CI = 0.64, RI = 0.68) has the following topology: *Propalaehoplophorus australis* (*Glyptodon reticulatus* (*Hoplophorus euphractus* (*Panochthus jaguaribensis, P. intermedius* (*P. frenzelianus, P. tuberculatus* (*P. subintemedius, P. greslebini*)))) ((*Pseudoplohophorus absolutus, Plohophorus figuratus*) (*Nopachtus cabrerai, N. coagmentatus, Propanochthus bullifer, Stromaphorus compressidens, Phlyctaenopyga ameghini*))). The results indicate that: 1, Panochthini is not a natural group but polyphyletic; 2, *Panochthus* is monophyletic and, concordant with recent proposals, *Hoplophorus euphractus* is its sister group; and 3, *Nopachtus* and *Propanochthus* are more closely related to species traditionally referred to 'Plohophorini' than to *Panochthus. Nopachtus* and *Propanochthus*, as the 'Plohophorini', are recorded from the latest part of the Neogene, whereas *Panochthus* and *Hoplophorus euphractus* are restricted to the Quaternary.

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XENARTHRA constitutes a group of mammals characteristic of the Neotropical Region, broadly represented in the fossil record of South America by both its abundance and long temporal range (Paula Couto 1979, Scillato-Yané 1982, 1995, Wetzel 1982, Scillato-Yané & Carlini 1995). The group today includes 31 extant species gathered in 14 genera (Wetzel 1985, Redford & Eisenberg 1992, McKenna & Bell 1997, Aguiar & da Fonseca 2008). Its cohesion as a natural group is strongly supported by morphological characters such as xenartria, the shape and relationship of the vertebral metapophysis, the synsacrum, the isqui-sacra union, the sacroischiatic fenestra and features of the dentition (e.g., reduction or absence of enamel, monophiodonty, hypsodonty; see Scillato-Yané 1986, Engelmann 1985, Patterson *et al.* 1989, 1992, Gaudin 1999, McDonald 2003, Vizcaíno 2009). Engelmann (1985) performed a phylogenetic analysis of the Xenarthra and considered them to be a natural group. Subsequent phylogenetic analyses based on molecular data support a common ancestor for, and natural grouping of, the Xenarthra (de Jong, Zweers *et al.* 1985, Sarich 1985, Delsuc *et al.* 2001, 2002, Madsen *et al.* 2001, Murphy *et al.* 2001, Möller-Krull *et al.* 2007, Delsuc & Douzery 2008, Prasad *et al.* 2008). Xenarthra is divided into two main groups: Pilosa and Cingulata.

Cingulata has both skeletal-dental characteristics (see Hoffstetter 1982, Patterson *et al.* 1989, Gaudin 1999, McDonald 2003, Gaudin & Wible 2006, Vizcaíno 2009) and molecular characters (see de Jong *et al.* 1985, Sarich 1985, Delsuc *et al.* 2001, 2002) that distinguish them from the rest of the Xenarthra and support the hypothesis of a common ancestor for this group. The most evident characteristic to differentiate them is the presence of a well-developed carapace formed by osseous dermic plates (osteoderms; Wetzel 1985). Cingulata have the most extensive fossil record of the xenarthrans, represented by two main groups: 1, Dasypodoidea (with extinct and extant representatives); and 2, Glyptodontoidea, with extinct representatives of Glyptodontidae, Palaeopeltidae and Pampatheriidae (see McKenna & Bell 1997).

Glyptodontidae, which have been recorded from the middle Eocene until the early Holocene (Scillato-Yané 1976, Fernicola 2008, Soibelzon *et al.* 2012), includes the largest individuals within Cingulata (Scillato-Yané & Carlini 1998, Fariña 2000), some individuals exceeding 2300 kg in body weight (Soibelzon *et al.* 2012). The most distinctive feature of the glyptodontids is the dorsal carapace, which is composed of osteoderms articulated by rigid sutures along the entire extension of the back, and lacking the intermediate region (or the anterior and intermediate part), which consists of transverse mobile bands, typical of dasypodids and pampatherids (see Ameghino 1889,

Fariña 1985, Ferigolo 1985, Fariña & Vizcaíno 2001, Croft *et al.* 2007, Zurita 2007, Fernicola 2008, Zamorano 2012). The first systematic schemes for the Glypodontidae were not based on strict phylogenetic analyses (see Ameghino 1889, Scott 1903–1904, Castellanos 1931, 1932, 1959, Simpson 1945, Hoffstetter 1958, Paula Couto 1979, McKenna & Bell 1997). However, one of the most accepted classifications divided the family into five subfamilies (i.e., Glyptatelinae, Propalaehoplophorinae, Doedicurinae, Glyptodontinae and Hoplophorinae; Hoffstetter 1958).

The subfamily 'Hoplophorinae' is recorded from the middle Miocene to the early Holocene. Its most notable feature is the early acquisition of the caudal tube (Zurita 2007, Zamorano 2012). However, this subfamily is not considered a natural group (Fariña 1993, Fernicola 2008, Porpino *et al.* 2010). 'Hoplophorinae' incorporates seven tribes (*sensu* Hoffstetter 1958): Palaehoplophorini, Neuryurini, Neothoracophorini, Plohophorini, Hoplophorini, Lomaphorini and Panochthini.

The tribe Panochthini (Pliocene–Pleistocene) includes *Nopachtus* Ameghino, 1888, *Propanochthus* Castellanos, 1925, *Panochthus* Burmeister, 1866, and a doubtful genus from the Pleistocene of Brazil: *Parapanochthus* Moreira, 1971. Some species of *Panochthus* were determined based on characters of the skull, postcranial elements and carapace; whereas other species of this genus and the species of *Nopachtus* and *Propanochthus* were based on characters of the carapace and caudal tube. Several authors related the Panochthini to 'Plohophorini' (see Ameghino 1889, Castellanos 1942, Hoffstetter 1958, Zamorano *et al.* 2011). In turn, the most recent phylogenetic analyses by Porpino *et al.* (2010) and Fernicola & Porpino (2012) show a close relationship between *Panochthus* (Panochthini) and *Hoplophorus* Lund, 1839 (Hoplophorini).

We carried out a phylogenetic analysis including, for the first time, all species traditionally referred to Panochthini in order to test whether the tribe is a natural group.

Institutional abbreviations. AMNH: American Museum of Natural History, New York, USA. DGM: Divisão de Geología e Mineralogía, Rio de Janeiro, Brazil. FC-DPV: Departamento de Paleontología de la Facultad de Ciencias, Universidad de la República, Uruguay. MACN: Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', colección Paleovertebrados (Pv), Ciudad Autónoma de Buenos Aires, Argentina, MCA: Museo Carlos Ameghino, Mercedes, Buenos Aires, Argentina. MHNC: Museo de Historia Natural de Cochabamba 'Alcide d'Orbigny', Bolivia. MHNG: Musée d´Histoire Naturelle, Genève, Switzerland. MNRJ: Museo Nacional, Rio de Janeiro, Brazil. SGB: Serviço Geológico de Rio de Janeiro, Brazil. ZMK: Zoologik Museum, Collection Peter W. Lund, Copenhagen, Denmark.

Materials and methods

The matrix (taxa/characters) included 16 species of Glyptodontidae and 35 morphological characters, of which 14 correspond to the skull, four to the dentition, two to cephalic armour, nine to the dorsal carapace and six to the caudal sheath; 21 are binary characters and 14 are multistate (unordered transformation series; see Appendix A). The species included were *Propalaehoplophorus australis* Ameghino, 1887 (Propalaehoplophorinae), a species morphologically well characterized by Scott (1903–1904) and more recently by González Ruiz (2010), and here used to root the tree; *Glyptodon reticulatus* Owen, 1845 (Glyptodontinae), the species of the subfamily with the most complete specimens; *Plohophorus figuratus* Ameghino, 1887; *Pseudoplohophorus absolutus* Perea, 2005; *Stromaphorus compressidens* (Moreno & Mercerat, 1891); *Phlyctaenopyga ameghini* (Ameghino, 1889) ('Hoplophorinae', 'Plohophorini'); *Hoplophorus euphractus* Lund, 1839 ('Hoplophorinae', Hoplophorini *sensu* Hoffstetter 1958); *Nopachtus coagmentatus* Ameghino, 1888; *N. cabrerai* Zamorano, Scillato-Yané, González Ruiz & Zurita, 2011; *Propanochthus bullifer* (Burmeister, 1874); *Panochthus tuberculatus* (Owen, 1845); *P. frenzelianus* Ameghino, 1889; *P. intermedius* Lydekker, 1895; *P. subintermedius* Castellanos, 1937; *P. greslebini* Castellanos, 1942 and *P. jaguaribensis* Moreira, 1965 ('Hoplophorinae', Panochthini).

The characters used for this analysis were examined in the type specimens and the best available material assigned to each taxon (see Appendix B). Some cranial and postcranial characters used in previous analyses (e.g., Fernicola 2008, Porpino *et al.* 2010) were not taken into account given that the considered specimens did not preserve homologous structures. In addition, the incomplete skull of MLP 84-IX-2-11, assigned to *Panochthus* sp. cf. *P. subintermedius* (see Zamorano 2012, Zamorano & Scillato-Yané 2012), was considered as a part of the morphological characterization of *P. subintermedius*.

All characters were treated as unordered and were assigned the same weight (1.0). Character states not preserved were coded as '?'. The matrix (Appendix C) was developed through the program Mesquite version 2.73 (Maddison & Maddison 2010). The analysis was performed with the program TNT (Tree Analysis using new Technology) 1.1 (Goloboff *et al.* 2008), performing an exact search.

Results of the phylogenetic analysis

Analysis of the morphological data matrix yielded four most parsimonious trees (Fig. 1), with the following characteristics: tree length = 75 steps, consistency index (CI) = 0.65 and retention index (RI) = 0.70. The strict consensus tree (Fig. 2) is represented by tree length = 77 steps, consistency index (CI) = 0.64 and retention index (RI) = 0.68. Furthermore, from the strict consensus tree,
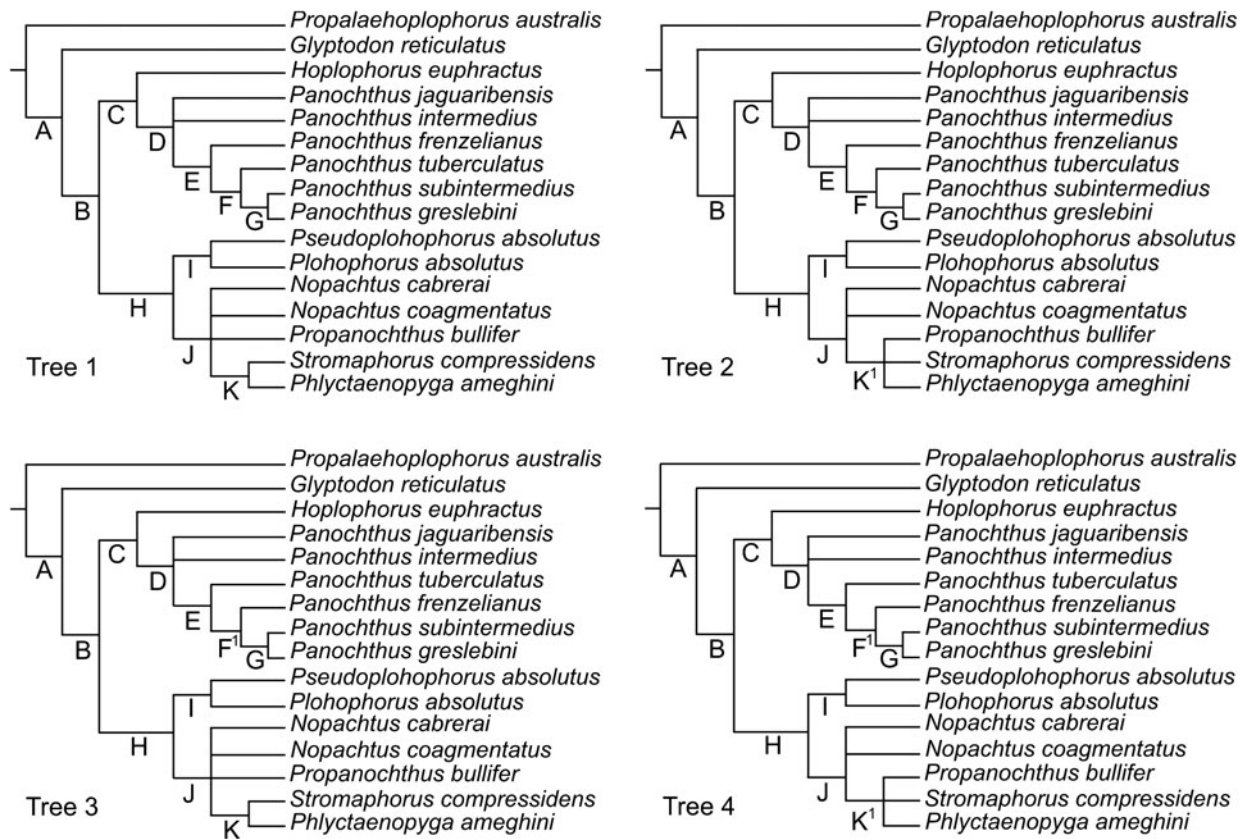
Fig. 1. Result of the phylogenetic analysis showing the four most parsimonious trees. The letters indicate the nodes described in the text.
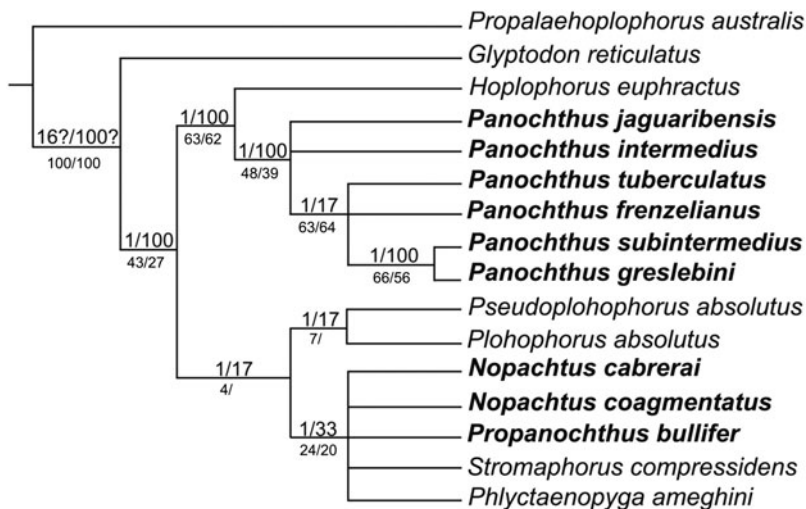

Fig. 2. Strict consensus tree, the numbers indicate the absolute/relative Bremer supports values (above branch) and Jackknife/Bootstrap supports (below branch). Species referred to 'Panochthini' are in bold.

the absolute/relative Bremer support values were obtained (Goloboff & Farris 2001), and Jackknife/Boot-strap supports were indicated. Six characters were not informative.

Description of the nodes. Node A (trees 1–4) includes the taxa considered in the analysis except *Propalaehoplo-phorus australis* (the Glyptodontidae chosen to root the tree). Node B (trees 1–4) includes the species of 'Hoplo-phorinae' considered, and it is supported by five synapo-morphies: character 2:1, character 32:1, character 33:1, character 34:2 and character 35:1. Node C (trees 1–4) is

supported by one synapomorphy, character 29:1. Node D (trees 1–4) includes the species of *Panochthus*, and it is supported by four synapomorphies (Fig. 3): character 4:1 (the nasal area of the skull is antero-ventrally very steep forming an angle between the palatal plane and the plane of rostral area greater than 45°), character 6:1 (length of the skull; the ratio between the length of the skull and the height of the skull less than 1.5), character 12:1 (the ante-ro-ventral orientation of the external nostrils) and charac-ter 33:2 (the central figures in the dorsal region of the caudal sheath are mainly rough). Node E (trees 1–4) is
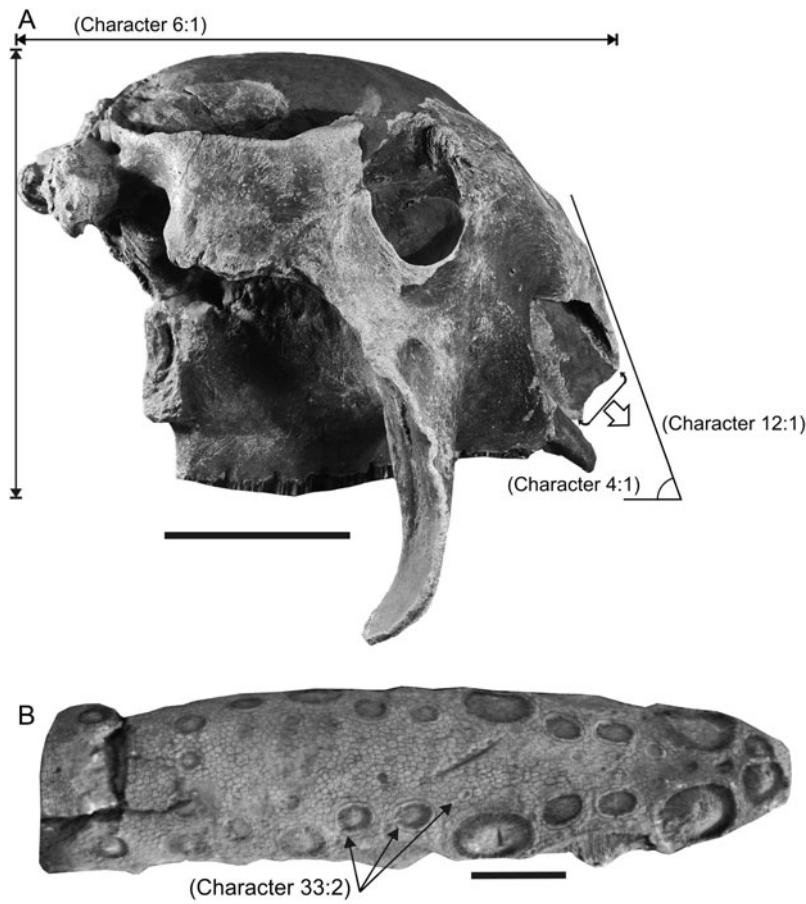
Fig. 3. Panochthus tuberculatus, MLP 16-29. A, skull in right lateral view; B, Caudal tube in dorsal view. The figure shows the four synapomorphies that support the monophyly of *Panochthus*. Scale bar: 100 mm.

supported by six synapomorphies: character 23:1, character 24:2, character 25:2, character 26:2, character 27:2 and character 28:2. Node F (trees 1, 2) is supported by one synapomorphy, character 21:1. Node F^1 (trees 3, 4) is supported by a single synapomorphy, character 1:1. Node G (trees 1–4) is supported by a single synapomorphy, character 34:1. Node H (trees 1–4) includes the 'Plohophorini' considered, *Nopachtus coagmentatus*, *N. cabrerai* and *Propanochthus bullifer*, and is supported by a synapomorphy, character 17:1 (the trilobulation of molariforms starts from M2). Node I (trees 1–4) includes *Plohophorus figuratus* and *Pseudoplohophorus absolutus* ('Hoplophorinae', 'Plohophorini'), and is supported by a synapomorphy, character 21:1. Node J (trees 1–4) includes the panochthines *Nopachtus coagmentatus*, *N. cabrerai* and *Propanochthus bullifer*, and *Stromaphorus compressidens* and *Phlyctaenopyga ameghini* ('Hoplophorinae', 'Plohophorini'). It is supported by two synapomorphies: character 22:0 (the ornamentation of the osteoderms has elevated figures in the dorsal carapace) and character 24:0 (the osteoderm ornamentation of the posterior region of the dorsal carapace has a convex central figure). Node K (trees 1, 3) is supported by a synapomorphy, character 27:0. Node K^1 (trees 2, 4) is supported by a synapomorphy, character 27:0.

In addition, *Glyptodon reticulatus* has three autapomorphies: character 14:0, character 21:1 and character 28:1.

Panochthus jaguaribensis is characterized by an autapomorphy (character 26:1). *Panochthus intermedius* is distinguished by three autapomorphies: character 2:2, character 9:1 and character 10:1. *Panochthus tuberculatus* has four autapomorphies: character 2:2, character 3:1, character 9:1 and character 10:1. *Pseudoplohophorus absolutus* is characterized by a single autapomorphy, character 28:1. *Phlyctaenopyga ameghini* is distinguished by a single autapomorphy, character 27:0. *Stromaphorus compressidens* has six autapomorphies: character 7:0, character 10:1, character 13:0, character 15:1, character 21:1 and character 27:0. Finally, *Propanochthus bullifer* has two autapomorphies: character 26:0 and character 31:2.

Discussion

Ameghino (1889) related the panochthines to the plohophorines, given the similarity between the morphology of the osteoderms present in both taxa. Hoffstetter (1958) recognized that the increment in peripheral figures in the 'Plohophorini' would indicate a close relationship of these with the Panochthini. At the same time, he considered that the Panochthini derived from a taxon related to *Stromaphorus* Castellanos, 1925. Castellanos (1942) also linked *Nopachtus* (Panochthini) with *Stromaphorus* ('Plohophorini'). Later, Zamorano *et al.* (2011) transferred a species

attributed to *Nopachtus* [i.e., *N. trouessarti* (Moreno, 1888)] to *Phlyctaenopyga* [i.e., *P. trouessarti* (Moreno, 1888)], indicating an affinity between these genera and, hence, between the respective tribes.

Phylogenetic analyses of Glyptodontidae are scarce. One of the first attempts by Fariña (1993) refuted the monophyly of 'Hoplophorinae', whereas Hoplophorini remained the sister group to the clade comprising Doedicurinae, Panochthini and Glyptodontinae. Other preliminary analyses, using cranio-mandibular characters, were performed by Fernicola *et al.* (2002) and Fernicola (2005), in which he proposed [*Panochthus* + *Sclerocalyptus* Ameghino, 1891 (=*Neosclerocalyptus* Paula Couto, 1957)] as a natural group.

The latest phylogenetic proposals for Glyptodontidae derive from Fernicola (2008), Porpino *et al.* (2009, 2010) and Fernicola & Porpino (2012). Fernicola (2008) conducted an analysis utilizing cranio-mandibular characters and, agreeing with his result of 2005, indicated a close relationship between *Neosclerocalyptus* and *Panochthus*, a clade with the highest support in the cladogram (Fernicola 2008, fig. 5). Porpino *et al.* (2009) used postcranial characters and, as a result, maintained the close relationship between *Neosclerocalyptus* and *Panochthus*. Porpino *et al.* (2010) and Fernicola & Porpino (2012) suggested the presence of a clade consisting of *Panochthus* and *Hoplophorus* based primarily on characters from the caudal tube. Porpino *et al.* (2010) proposed the restriction of the tribe Hoplophorini to the lineage represented by *Hoplophorus*, recognizing the tribe as the sister group to Panochthini, gathering both tribes within Panochthinae (=*Hoplophorus* + *Panochthus*). They recognized a new subfamily, Neosclerocalyptinae, represented by *Neosclerocalyptus*, thus leaving the latter as the sister group to Panochthinae.

From such previous studies, Panochthini have been linked to 'Plohophorini' (Ameghino 1889, Castellanos 1942, Hoffstetter 1958, Zamorano *et al.* 2011) or to Hoplophorini (Fernicola 2008, Porpino *et al.* 2010, Fernicola & Porpino 2012). The result of the analysis presented herein provides partial support for both proposals. In fact, Panochthini is not monophyletic (hence quotation marks are used for 'Panochthini') because some of its species (i.e., *Nopachtus coagmentatus, N. cabrerai* and *Propanochthus bullifer*) are more closely related to species of 'Plohophorini', whereas *Panochthus* is the sister group to *Hoplophorus euphractus* (Hoplophorini). Furthermore, the results of our analysis sustain the monophyly of *Panochthus*, supported by four synapomorphies (Fig. 3).

The studies that link 'Plohophorini' with 'Panochthini' (Ameghino 1889, Castellanos 1942, Hoffstetter 1958, Zamorano *et al.* 2011) are based on a descriptive methodology, which allowed them to infer such a relationship; whereas the 'Panochthini'–Hoplophorini relationship is based on strict phylogenetic analyses (Fernicola 2008, Porpino *et al.* 2010, Fernicola & Porpino 2012).

Our analysis supports the conclusions of Porpino *et al.* (2010) and Fernicola & Porpino (2012) that *Hoplophorus* (*H. euphractus*, in this contribution) is the sister group to *Panochthus*, and adds a synapomorphy for this clade (the osteoderms of the dorsal carapace have small figures that occupy more than 50% of the surface of the osteoderm) to the five outlined by Porpino *et al.* (2010, p. 920): 'the last seven or all maxillary molariforms trilobed (27); presence of conical tubercle in the lateral and terminal figures of caudal tube (147); length of L1 >90% of the length of terminal figure (149); terminal figures of caudal tube clearly separated dorsally (150); and dorsoventral diameter of L1 subequal to the dorsoventral diameter of the caudal tube at its corresponding position (151)'. At the same time, Porpino *et al.* (2010, p. 911) indicated that: '*Hoplophorus* presents striking, unreported resemblances with *Panochthus* (e.g., more lateromedially elongated cuboid facet of navicular and caudal tube with large lateral figures separated from the terminal ones by a wide space)'.

The relationship between *Nopachtus coagmentatus, N. cabrerai* and *Propanochthus bullifer* with species of 'Plohophorini' (node J) is supported by characters of the ornamentation of the osteoderms from the dorsal carapace. The ornamentation of these osteoderms in *Nopachtus coagmentatus*, *N. cabrerai* and *Propanochthus bullifer* is characterized by a central figure, flat in the anterior region and convex in the posterior one, as in the osteoderms of *Phlyctaenopyga ameghini* and *Stromaphorus compressidens* (see Cabrera 1944).

The central figures of *Pr. bullifer* are surrounded by three to seven rows of small peripheral figures, unlike both *Nopachtus coagmentatus* and *N. cabrerai*, which have one or two rows. *Nopachthus cabrerai* has the central figure of the osteoderms of the posterior region nearly as convex as those of *Phlyctaenopyga ameghini*, a taxon with more blistered figures than the rest of the species in the analysis (see Cabrera 1944, Zamorano *et al.* 2011).

Zurita *et al.* (2011) concluded that *P. intermedius* expresses a more derived condition than *Nopachtus* and *Pr. bullifer*, but retains some primitive features that are not present in the species of the Lujanian Stage/Age (Fig. 4). However, the results presented herein indicate that *Nopachtus* and *Propanochthus* have an evolutionary history distinct from that of *Panochthus*, and that *P. intermedius* retains more primitive characters than the other species of the genus, except for *P. jaguaribensis*.

Given that 'Panochthini' and 'Hoplophorinae' are not natural groups, it is preferable to maintain the genera and species traditionally grouped into 'Panochthini' as members of the family Glyptodontidae without distinction of subfamilies or tribes.

From a chronostratigraphic perspective, the species referred to 'Panochthini' are distributed from the Pliocene to the late Pleistocene. *Nopachtus cabrerai* is recorded in the Monte Hermoso Formation, Buenos Aires Province, Argentina (Zamorano *et al.* 2011), in levels referred to the Montehermosan Stage (early
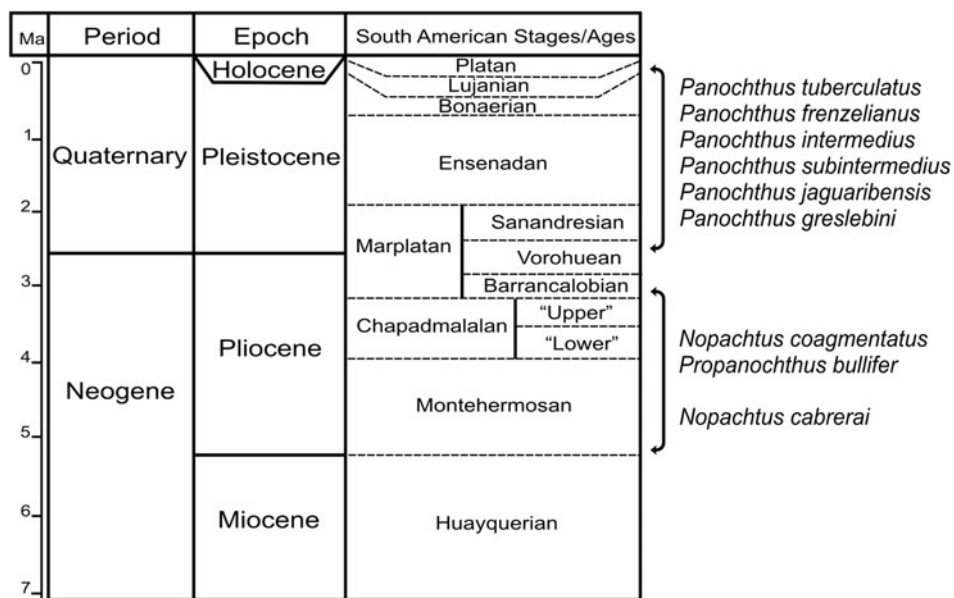
Fig. 4. Chronostratigraphic chart with the chronological distribution of the species referred to 'Panochthini'.

Pliocene, *sensu* Deschamps *et al.* 2012); *Nopachtus coagmentatus* and *Propanochthus bullifer* are recorded in the Brochero Formation, Valle de Traslasierra (Córdoba Province, Argentina), in levels correlated with the Montehermosan–Chapadmalalan Stages (early Pliocene–late Pliocene; Zamorano *et al.* 2011, Cruz, in press); *Panochthus intermedius* and *P. subintermedius* are recorded in the Ensenadan Stage (early–middle Pleistocene) of Buenos Aires Province (Argentina) and, in the case of *P. intermedius*, also in levels dated as early and middle Pleistocene of Cochabamba (Bolivia; Zurita *et al.* 2011); *P. tuberculatus* and *Pa. frenzelianus* have their biochrons limited to the middle Pleistocene–late Pleistocene of Argentina and Uruguay. Finally, *Panochthus jaguaribensis* and *P. greslebini* may only be referred to the Pleistocene *sensu lato* of Brazil (Moreira 1971, Bergqvist 1993, Bergqvist *et al.* 2004). Thus, *Nopachtus* and *Propanochthus* are recorded from the final part of the Neogene (Fig. 4), and are phylogenetically related to *Stromaphorus* and *Phlyctaenopyga*, genera that also have their records during the Neogene (see Marshall & Patterson 1981, Reguero & Candela 2011, Zamorano *et al.* 2011), whereas *Panochthus* is restricted to the Quaternary (Fig. 4) and is more closely related to *Hoplophorus euphractus*, a species distributed during the Quaternary of Brazil (Porpino *et al.* 2010). In this sense, the polyphyletic condition of the group 'Panochthini' (Figs 1 and 2) would reflect the different chronological distribution of the species (Fig. 4).

Conclusions

In summary: 1, 'Panochthini' (*sensu* Simpson 1945, Hoffstetter 1958) is not a natural group, being polyphyletic; 2, *Panochthus* is monophyletic and is the sister group to *Hoplophorus euphractus* (Hoplophorini); 3, *Nopachtus* and *Propanochthus* are phylogenetically

closer to species included in 'Plohophorini' than to *Panochthus*; and 4, *Nopachtus* and *Propanochthus*, as the 'Plohophorini', are restricted to the final part of the Neogene, whereas *Panochthus* and *Hoplophorus euphractus* are restricted to the Quaternary.

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Appendix A Materials used in the phylogenetic analysis

Glyptodon reticulatus MCA 2015.

Hoplophorus euphractus ZMK (holotype).

Nopachtus cabrerai MACN-Pv 2670 (holotype).

Nopachtus coagmentatus MLP 16-122 (holotype).

Panochthus frenzelianus AMNH 11243 (holotype).

Panochthus greslebini DGM 1-M (ex SGB 1784 [see Mones 1986: 239]) (holotype) and MNRJ 2760.

Panochthus intermedius MLP 16-36 (holotype) and MHNC-13491.

Panochthus jaguaribensis MNRJ 2759-V.

Panochthus tuberculatus MLP 16-29 (neotype), MHGN 633/02 (holotype of *Panochthus voghti*) and MLP 16-37b.

Panochthus subintermedius MACN-Pv 5130 (holotype).

Panochthus sp. cf. *P. subintermedius* MLP 84-IX-2-11.

Phlyctaenopyga ameghini MLP 16-101 (holotype), MLP 29-VIII-8-2 and MLP 29-X-10.

Plohophorus figuratus MLP 16-153 (holotype).

Propalaehoplophorus australis MLP 16-15.

Propanochthus bullifer MACN-Pv 1761 (holotype).

Pseudoplohophorus absolutus FC-DPV-475 and 595 (holotype).

Stromaphorus compressidens MLP 16-138 (holotype), MLP 29-X-8-I and MLP 29-X-8-9.

Appendix B List of characters and character states for phylogenetic analysis

Skull

(1) Position of the roof of the skull respects the upper edge of the orbit. Ratio between the height of the skull roof (over the upper edge of the orbit) and the height of the orbit: 0, less than 0.25. 1, between 0.25 and 0.33. 2, greater than 0.33.

(2) Degree of neumatization of the rostral area. The increase of the neumatization is reflected by an increase of the external surface of the fronto-nasal bones. Therefore, this condition can be assessed considering the size of these bones (see Zurita *et al.* 2011). 0, low degree. 1, medium degree. 2, high degree.

(3) Development of postorbital process: 0, incomplete postorbital process. 1, complete postorbital process.

(4) Angle between the palatal plane and the plane of rostral area: 0, less than 45°. 1, greater than 45°.

(5) Outline of the orbital notch in lateral view: 0, dorso-ventrally elongated. 1, subcircular.

(6) Length of the skull. Ratio between the length of the skull and the height of the skull (regardless of the descendant process of the zygomatic arch): 0, greater than 1.5. 1, less than 1.5.

(7) Lachrymal tubercle position: 0, the lachrymal tubercle does not protrude beyond the contour of the orbit. 1, the lachrymal tubercle protrudes the contour of the orbit.

(8) Size of the temporal fossa. Ratio between the antero-posterior length of the temporal fossa and the antero-posterior length of the orbit: 0, more than 2.5 times the antero-posterior length of the orbit. 1, nearly 2 times the antero-posterior length of the orbit

(9) Relation between the dorsoventral diameter of the zygomatic arch below the temporal fossa and the dorsoventral diameter below the orbital fossa: 0, dorsoventral diameter of the zygomatic arch below the temporal fossa similar to the dorsoventral diameter below the orbital fossa. 1, dorsoventral diameter of the zygomatic arch below the temporal fossa almost twice that of the dorsoventral diameter below the orbital fossa.

(10) Orientation of the zygomatic arch (in lateral view): 0, oblique. 1, horizontal.

(11) Cross-section of the occipital condyles: 0, subcircular. 1, subelliptic. 2, nearly square.

(12) Orientation of the external nostrils: 0, anterior. 1, antero-ventral.

(13) Outline of the alveolar edge of the maxillar: 0, sigmoid. 1, nearly straight.

(14) Angle formed by the roof of the palate with the alveolar walls: 0, obtuse. 1, straight.

Upper dentition

(15) Hypsodonty index (expressed as the ratio between the average height of the M6-M8 / the length of the dental series (modified from Zurita, 2007): 0, 0.57–0.63. 1, 0.50–0.56. 2, 0.43–0.49.

(16) Relation between the antero-posterior diameter and the transverse diameter of the M1: 0, almost equal. 1, antero-posterior diameter almost twice that of the transverse diameter.

(17) Initiation of the trilobulation of the molariforms: 0, starts from M3. 1, starts from M2. 2, starts from M1.

(18) Imbrication of the molariforms: 0, molariforms imbricated. 1, molariforms not imbricated.

Cephalic armour

(19) Relative size of the osteoderms that form the cephalic armour: 0, different sizes. 1, almost equal.

(20) Number of peripheral rows that surround the central figure of the central osteoderms: 0, without rows. 1, 1–3 rows. 2, 4–7 rows.

Dorsal carapace

(21) Highest point of the dorsal carapace: 0, at the central region. 1, at the anterior region.

(22) Ornamentation of the osteoderms of the dorsal carapace: 0, osteoderms with elevated figures. 1, osteoderms with flat figures.

(23) Presence of a central figure in the osteoderms of the anterior region: 0, with a central figure. 1, without a central figure.

(24) Ornamentation of the osteoderms of the posterior region: 0, with a convex central figure. 1, with a flat central figure. 2, without a central figure.

(25) Disposition of the small figures of the osteoderms of the anterior region: 0, with a central figure surrounded by 4–7 rows of peripheral small figures. 1, with a central figure surrounded by 1–3 rows of peripheral small figures. 2, without a central figure.

(26) Disposition of the small figures of the osteoderms of the posterior region: 0, with central figure surrounded by 4–7 rows of peripheral small figures. 1, with central figure surrounded by 1–3 rows of peripheral small figures. 2, without a central figure.

(27) Number of small figures in the first row of the osteoderms of the anterior region: 0, more than 12 peripheral small figures. 1, less than 12 peripheral small figures. 2, without a central figure.

(28) Number of small figures in the first row of the osteoderms of the posterior region: 0, more than 10 peripheral small figures. 1, less than 10 peripheral small figures. 2, without a central figure.

(29) Percentage of the surface of the osteoderms of the posterior region formed by small figures: 0, less than 50%. 1, more than 50%.

Caudal sheath

(30) Development of the caudal sheath: 0, sheath with caudal tube less than 100 mm long. 1, sheath with caudal tube greater than 100 mm long. 2, sheath without caudal tube.

(31) Transversal section of the caudal sheath: 0, nearly circular. 1, compressed. 2, depressed.

(32) Central figures in the dorsal region: 0, absent. 1, present.

(33) Form of the central figure in the dorsal region: 0, without central figure. 1, with smooth central figure. 2, with rough central figure.

(34) Form of the distal end: 0, rounded. 1, pointed. 2, blunt.

(35) Ornamentation of caudal sheath and ornamentation of the dorsal portion of the carapace (modified from Zurita 2007): 0, different ornamentation. 1, similar ornamentation.

Appendix C Data matrix used in the phylogenetic analysis

	Characters																																		
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Propalaehoplophorus australis	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0
Glyptodon reticulatus	0	0	0	0	1	0	1	0	0	0	0	0	1	0	2	1	2	1	1	0	1	1	0	1	1	1	1	1	0	2	0	0	0	0	0
Nopachtus coagmentatus	?	?	?	?	?	?	?	0	?	?	0	0	?	?	?	?	?	?	?	?	0	0	0	0	1	1	1	0	0	1	?	1	?	?	1
Nopachtus cabrerai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	1	1	0	0	?	?	?	?	?	?
Propanochthus bullifer	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	0	?	0	0	1	2	?	?	2	?
Panochthus tuberculatus	2	2	1	1	1	1	1	0	1	1	2	1	1	1	2	1	2	1	1	2	1	1	1	2	2	2	2	2	1	1	2	1	2	2	1
Pa. frenzelianus	1	1	0	1	1	1	1	0	1	0	?	1	1	1	2	1	2	1	1	1	0	1	1	2	2	2	2	2	1	1	2	1	2	2	1
Pa. intermedius	2	2	0	1	1	1	1	0	0	1	2	1	1	1	2	1	2	0	0	1	0	0	0	1	1	1	1	0	1	1	2	1	2	2	1
Pa. subintermedius	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	2	1	1	1	2	1	1	2	1	2	1	1
Pa. greslebini	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	2	2	2	2	2	1	1	2	1	2	1	1
Pa. jaguaribensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	?	2	1	1	2	2	2	2	1
Plohophorus figuratus	1	1	0	0	1	0	1	0	0	0	2	0	1	1	2	0	1	1	0	0	1	1	0	1	1	1	1	0	0	1	1	1	1	2	1
Pseudoplohophorus absolutus	1	1	0	0	0	0	1	0	0	0	2	0	1	1	2	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	2	1
Stromaphorus compressidens	1	1	0	0	1	1	0	0	1	0	2	0	0	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	2	1
Phlyctaenopyga ameghini	1	1	0	0	1	0	1	0	0	0	2	0	1	?	2	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	2	1
Hoplophorus euphractus	2	1	0	0	1	0	1	0	?	?	2	0	1	?	2	?	?	?	?	?	0	1	0	1	1	1	1	0	1	1	2	1	1	2	1