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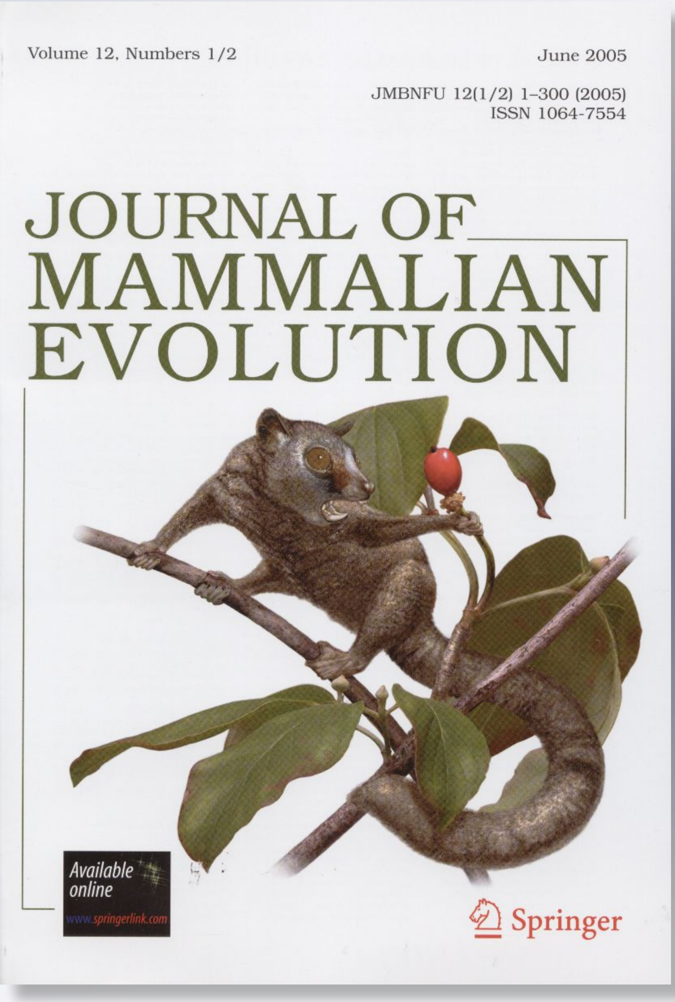

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ORIGINAL PAPER

Exoskeleton and Systematics: A Historical Problem in the Classification of Glyptodonts

J. C. Fernicola · K. O. Porpino

Abstract The glyptodonts (Mammalia: Cingulata) are characterized by an exoskeleton comprising most notably an armored tail and an immobile dorsal carapace formed by a large number of osteoderms. In 1889, Florentino Ameghino published the first phylogenetic scenario for the glyptodonts, based on the sequential application of two transformation series related to the morphology of the tail armor and carapace osteoderms. From the early to mid 1900s, several authors used Ameghino's transformation series subordinated to a model of evolution in which derived glyptodont groups had arisen independently from separate pre-middle Miocene ancestors. This approach, in which the morphological states of Ameghino's series were considered analogous rather than homologous, provided different phylogenetic scenarios and the paraphyletic classification still in use. Two recent cladistic analyses based on cranial and postcranial (including caudal tube) characters support the monophyly of glyptodonts and suggest novel intra-clade relationships. However, neither analysis included the classic osteoderm characters used by earlier authors. Therefore, we propose new osteoderm and carapace characters and evaluate their performance in a new cladistic analysis. We found that: a) some osteoderm characters used by earlier authors to support ancestor-descendent hypotheses are in fact fully homoplastic autapomorphies (e.g., multiplication of the number of rows of peripheral figures); b) characters previously believed to have originated independently in several groups (e.g., presence of caudal tube) are synapomorphies at a wider hierarchical level; c) some ancestor–descendant pre-cladistic hypotheses are incompatible with the topology and synapomorphy distribution obtained; and d) there is no reason to favor exoskeletal characters in glyptodont systematics.

Keywords Glyptodonts · Osteoderms · Caudal tube · Phylogeny · Classification

Introduction

Glyptodonts together with armadillos, pampatheres, and horned peltephilines are grouped as Cingulata, one of the three clades of Xenarthra (Gaudin and McDonald 2008 and references therein). They differ from the remaining cingulates by presenting strongly trilobate dentition, fused vertebral columns, elephantine hind limbs, and an essentially immobile dorsal carapace that covers the top and sides of the trunk (Hoffstetter 1958). This peculiar structure is composed of hundreds of articulated dermal bones, which, together with those present in the shields that cover the head and tail, considerably enhance the fossilization potential of these animals. Although partial or complete exoskeletal

J. C. Fernicola (✉)
CONICET, División Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia,"
Av. Ángel Gallardo 470 1405DJR,
Ciudad Autónoma de Buenos Aires, Argentina
e-mail: jctano@yahoo.com

J. C. Fernicola
e-mail: jctano@macn.gov.ar

J. C. Fernicola
Departamento de Ciencias Básicas,
Universidad Nacional de Luján,
Ruta 5 y Av. Constitución,
6700 Luján, Buenos Aires, Argentina

K. O. Porpino
Departamento de Ciências Biológicas,
Universidade do Estado do Rio Grande do Norte,
Rua Antônio Campos s/n,
Mossoró 59610-090 Rio Grande do Norte, Brazil
e-mail: kleporpino@yahoo.com.br

components have been found in physical association with endoskeletal elements, they have generally been collected independently and disarticulated and in most cases comprise the only preserved parts.

This bias in the fossil record is evident when one takes into consideration the fact that until the first decade of the twentieth century, nearly 30 glyptodont genera were described, but only seven included known skull material: the Plio-Pleistocene genera *Glytodon*, *Panochthus*, *Neosclerocalyptus* (sensu Paula Couto 1957), and *Doedicurus* (see Burmeister 1870–1874; Ameghino 1889) and the Miocene *Propalaehoplophorus*, *Eucinepeltus*, and *Cochlops* (see Ameghino 1889, 1891; Scott 1903–1904). Since then an impressive number of new genera have been added to those previously erected, totaling more than 75, and most of these, with a few exceptions (e. g., Cabrera 1944), have been based solely on exoskeletal elements (see Mones 1986; McKenna and Bell 1997 for a summary; and Croft et al. 2007; Carlini et al. 2008 for recent generic proposals). This bias toward the preservation, collection, and description of exoskeletal elements has led to classifications based mainly on caudal tube and carapace osteoderm characters.

In this context, the proposal of the eminent Argentinean paleontologist Florentino Ameghino is paradigmatic. Thirty years after the publication of the Origin of Species by Charles Darwin (1859), Ameghino published the first systematic synthesis of glyptodonts couched in a transformationist framework (Ameghino 1889). Ameghino's phylogenetic sketch was based on hypothesized transformations in the structure and size of the armored tail and the morphology of carapace osteoderms. These transformations were specified in an a priori fashion. Broadly speaking, this has become the paradigm on which subsequent pre-cladistic phylogenetic hypotheses (Castellanos 1931, 1932, 1959; Hoffstetter 1958) and classification efforts (Castellanos 1931, 1932, 1959; Simpson 1945; Hoffstetter 1958; Paula Couto 1979; McKenna and Bell 1997) have been framed. Intriguingly, these latter classifications have produced diverging taxonomic arrangements, likely reflecting differential weighting and interpretation of exoskeletal characters. Recent cladistic studies based on characters from the endo- and exoskeleton (Fernicola 2008; Porpino et al. 2010) found no support for the monophyly of many of the groups proposed during the late 1800s and early to mid 1900s. However, these cladistic analyses did not include the classic osteoderm characters used by those earlier authors.

The aim of this contribution is to trace and interpret the influence of exoskeletal characters in the suprageneric systematics of glyptodonts from the late 1800s to the middle 1900s, as well as to evaluate the value of these characters and the pre-cladistic phylogenetic hypotheses and classifications based on them using cladistic methodology and assumptions.

Historical Background

The first systematic synthesis of glyptodonts was published by Ameghino (1889) based on exoskeletal morphology. He included in his phylogeny 13 of the 19 genera that he recognized at that time, and grouped these genera into three families: Glyptodontidae (*Glyptodon*, *Neothoracophorus*, and *Cochlops*), Hoplophoridae (*Propalaehoplophorus*, *Protoglyptodon*, *Palaehoplophorus*, *Neosclerocalyptus*, *Plohophorus*, *Nopachthus*, and *Panochthus*), and Doedicuridae (*Neuryurus*, *Plaxhaplous*, and *Doedicurus).*

Ameghino's phylogenetic scheme (Fig. 1) was based on two transformation series polarized a priori: one including the structure and size of the tail and the other the external morphology of the carapace osteoderms. With respect to the armored tail, he recognized the existence of two types, denoted here type A and type B. Type A, present in Glyptodontidae, corresponded to a short, conical tail, thick at the base and blunt at the tip, formed by a series of movable rings extending along its entire length. Ameghino (1889) considered it the most evolved and thus of more recent origin. In spite of certain doubts about the length of the tail of *Cochlops*, Ameghino (1889) included this genus in type A as the oldest and most primitive taxon, from which originated *Glyptodon* and probably *Neothoracophorus*. The remaining genera were included in type B, which was characterized by a long tail composed of movable rings along its entire length, as in *Propalaehoplophorus*, the most primitive and oldest genus within Ameghino's (1889) family Hoplophoridae. According to Ameghino (1889), from this basal form, the caudal tube, present in the remaining Hoplophoridae and Doedicuridae, would have evolved from the fusion of the more caudal rings. This transformation allowed Ameghino to delineate the first branching point of his phylogeny (Fig. 1). The second a priori polarized transformation series allowed Ameghino to resolve the relationships among the genera included in type B group. The main transformation in this series involved the replacement of an ancestral rosette pattern (i.e., a central figure and one single complete row of peripheral figures), as present in *Propalaehoplophorus*, as well as *Cochlops*, *Glyptodon*, and *Neosclerocalyptus*, either by the multiplication of the number of rows of peripheral figures, as observed in *Paleohoplophorus* and *Plohophorus,* which culminated in the hoplophorid lineage, in an external ornamentation formed only by small figures of similar size, as in *Panochthus*; or, in the complete absence of figures in the doedicurid lineages, as in *Doedicurus* (Fig. 1). For Ameghino (1889), the phylogenetic position of *Protoglyptodon* was uncertain (Fig. 1), though this genus was included in Hoplophoridae in his classification. After 1889, Ameghino added several new taxa to Glyptodontidae, Hoplophoridae, and Doedicuridae, and he recognized a new family named Propalaehoplophoridae that included pre-

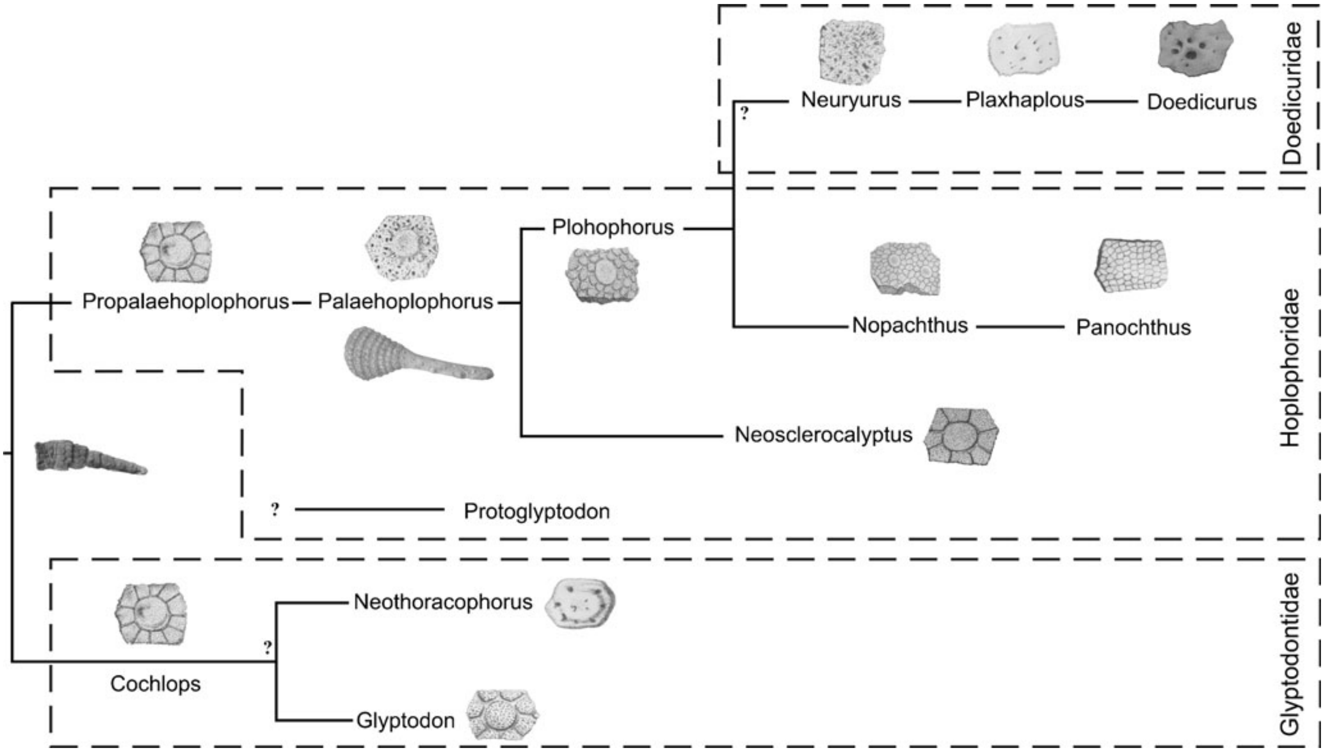

Fig. 1 Phylogenetic scenario of Ameghino (1889) showing the distribution of exoskeletal characters discussed in the text. Modified from Ameghino (1889)

middle Miocene *Asterostemma, Cochlops, Eucinepeltus, Glyptatelus, Lomaphorelus*, *Metopotoxus*, and *Propalaehoplophorus*, but he did not significantly alter the transformation series and the associated phylogenetic scenario described above.

Castellanos (1931, 1932) published a preliminary systematic study of glyptodonts, based on the transformation series proposed by Ameghino (1889), without taking into account Ameghino's order of application (i.e., caudal tube transformation followed by carapace osteoderms character transformations). Castellanos (1931, 1932) recognized five of the seven pre-middle Miocene genera as immediate direct ancestors of his post-middle Miocene groups (Fig. 2). This multiplication of ancestors was reflected in his classification when he divided three of Ameghino's four families (1889) into two subfamilies each. Thus, the Propalaehoplophoridae were subdivided into Propalaehoplophorinae and Glyptatelinae. The former was composed of *Propalaehoplophorus*, considered to be the direct ancestor of three independent lineages, one corresponding to Doedicuridae and the others to Plohophorinae (Fig. 2), and *Cochlops*, which in turn was considered the direct ancestor of Glyptodontidae (Fig. 2). The Glyptatelinae was composed of *Glyptatelus*, *Eucinepeltus*, *Lomaphorelus*, *Metopotoxus*, and *Asterostemma*. Each one of the last three genera originated an independent lineage that together constituted a polyphyletic Hoplophorinae (Fig. 2). Surprisingly, Hoplophorinae together with Plohophorinae were grouped as Hoplophoridae, even though their lineages derived from different ancestral genera (Fig. 2). Finally, Doedicuridae was subdivided into Doedicurinae and Panochthinae.

In 1945, Simpson demoted each suprageneric group of Castellanos to lower ranks. He regrouped all pre-middle Miocene genera in Propalaehoploporinae, which would represent "a horizontal group with primitive allies or ancestors of several or all of the Pliocene-Pleistocene phyla" (Simpson 1945: 194). In the same paragraph he also commented that "Probably these forms do show the beginning of later subdivision, but the connections are now almost purely theoretical *and Ameghino's arrangement still seems most practical*" (Simpson, 1945: 194; italic ours). He accepted Glyptodontinae and the subdivision of Doedicurinae into Panochthini and Doedicurini, excluding the neuryurines from this latter tribe and assigning them to Hoplophorinae. However, he considered the tribal subdivision of Hoplophorinae inconvenient because "…at present it would be surely valid for only a few genera and would leave most *incertae sedis* or classified on grounds more theoretical than subjective [sic objective?]" (Simpson 1945: 194).

The systematic synthesis published by Hoffstetter (1958) attempted to resolve the *incertae sedis* problem of Simpson (1945) via division of groups (Fig. 3). However, Hoffstetter (1958: 572) recognized that the proposition of any phylogenetic relationships and groups would be highly tentative

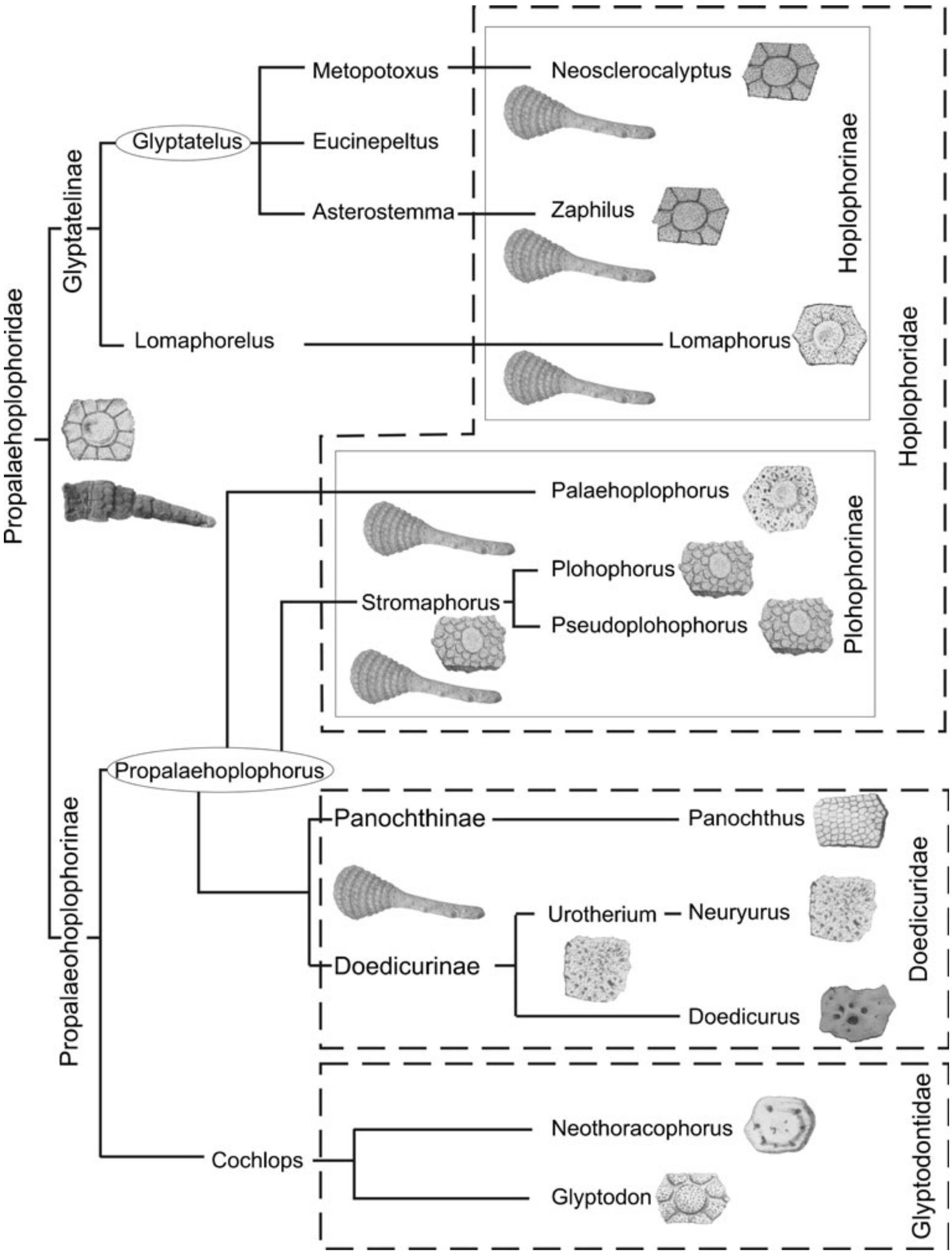

Fig. 2 Phylogenetic scenario of Castellanos (1931, 1932) showing the distribution of exoskeletal characters discussed in the text. Reconstructed from Castellanos (1931, 1932)

because several genera were known by a single osteoderm. Therefore, according to Hoffstetter (1958: 572) “On s’est résolu á accepter, au moins pour les formes anciennes, un sectionnement horizontal, qui n’a évidemment qu’un caractère provisoire. Cést ainsi que les quelques précurseurs du Mustersien et du Déséadien peuvent être désignés par le nom de Glyptatelinae. Les divers types du Colhuéhuapien et du Santacruzien sont habituellement groupés sous le nom de Propalaehoplophorinae.”

The glyptatelines, formed by *Glyptatelus* and *Lomaphorelus*, were diagnosed by Hoffstetter (1958) via the presence of a main figure in the carapace osteoderms that was displaced toward their posterior border and by the possession of trilobate teeth without the axial crest of osteodentine typical of other glyptodontids. However, the association of teeth and osteoderms is dubious (see discussions in Simpson 1948; McKenna et al. 2006; Porpino et al. 2009), and a main figure displaced toward the posterior border in carapace osteoderms is a feature also present in genera other than *Glyptatelus* (see Porpino et al. 2009).

According to Hoffstetter (1958), the Propalaehoplophorinae was formed by *Propalaehoplophorus*, *Asterostemma*, *Cochlops*, *Metopotoxus*, and *Eucinepeltus*. Hoffstetter (1958) characterized this group by the presence of a sculptural rosette pattern on the carapace osteoderms and the absence of a caudal tube, and included the ancestors of the

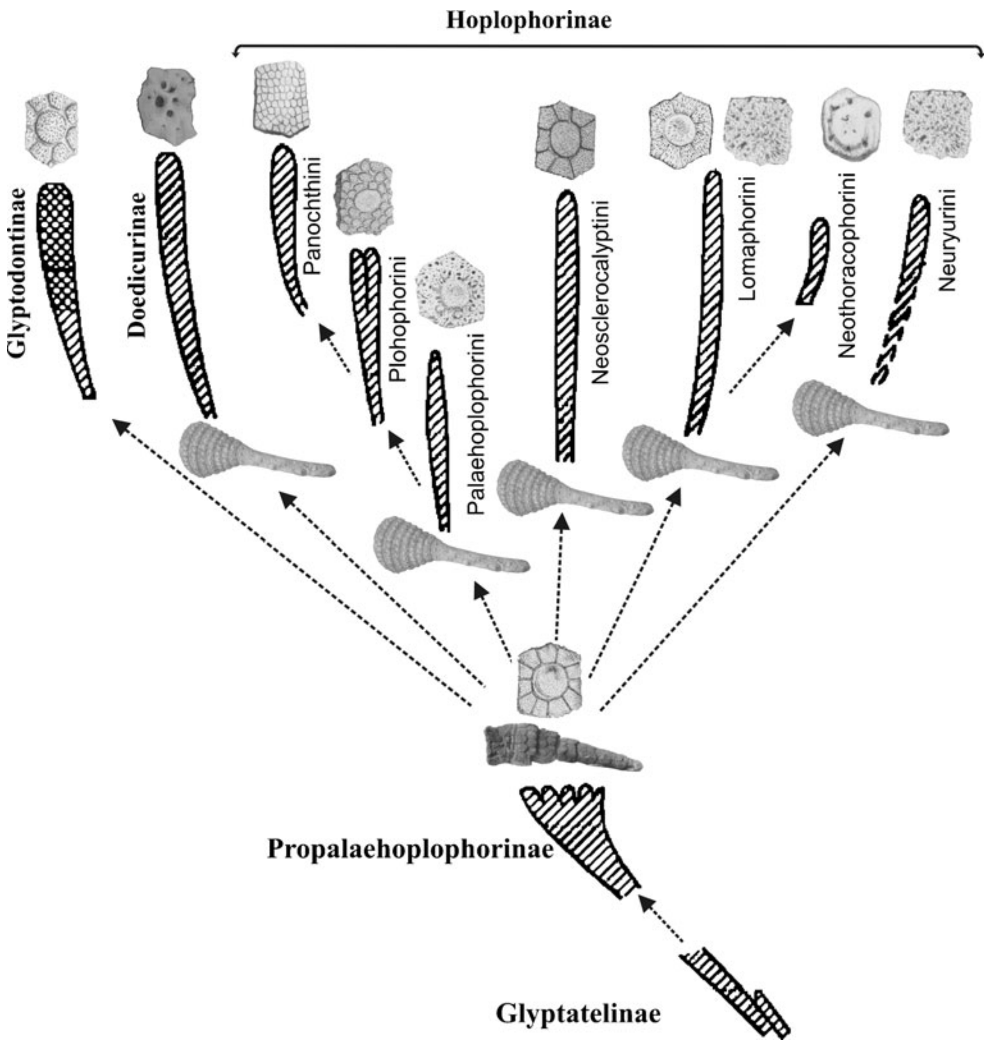

Fig. 3 Phylogenetic scenario of Hoffstetter (1958) showing the distribution of exoskeletal characters discussed in the text. Modified from Hoffstetter (1958)

remaining glyptodontids (Fig. 3). The neothoracophorines were excluded from Glyptodontinae and included as a new tribe within Hoplophorinae. The Glyptodontinae was characterized by the presence of a sculptural rosette pattern on the carapace osteoderms, absence of a caudal tube, lack of the supracondyloid foramen on the humerus, and the presence of secondary ramifications off the axial crest of osteodentine. This last feature, however, was also reported for the molariforms of *Doedicurus* (Doedicurinae) and *Panochthus* (Panochthinae) (Fernicola 2008). The Doedicurinae, comprising only the Doedicurini of Simpson (1945), was characterized as having a distally expanded caudal tube and the completely smooth external surfaces of the carapace osteoderms (i.e., without figures). Finally, Hoffstetter (1958) recognized Hoplophorinae as a large and diverse group characterized by the acquisition of a conical-cylindrical caudal tube in addition to more "specialized" teeth, skull, and limb bones relative to propalaehoplophorines. Hoffstetter (1958) tentatively split Hoplophorinae into seven tribes characterized on the basis of carapace osteoderm and caudal tube morphology: Palaehoplophorini (two rows of peripheral figures and caudal tube without terminal figures), Plohophorini (two rows of peripheral figures and caudal tube with smooth terminal figures), Hoplophorini (rosette sculptural pattern and caudal tube with smooth terminal figures), Panochthini (more than two rows of peripheral figures and caudal tube with conical tubercles), Neuryurini (rugose and punctuate external osteoderm surface and caudal tube with conical tubercles), Lomaphorini (poorly defined peripheral figures and caudal tube with smooth terminal figures), and Neothoracophorini (large main figure associated with a small peripheral area).

Castellanos (1959) published his final systematic proposal (Fig. 4), which replicated the groups Glyptodontinae, Doedicurinae, and Propalaehoplophorinae of Simpson (1945). He considered that *Lomaphorelus* was a direct ancestor of three independent lineages that comprise Hoplophorinae. This last subfamily was divided into three tribes: Plohophorini (including Palaehoplophorini and Plohophorini of Hoffstetter 1958); Trachycalyptini (including Neuryurini and Lomaphorini of Hoffstetter 1958); and, Hoplophorini (only including

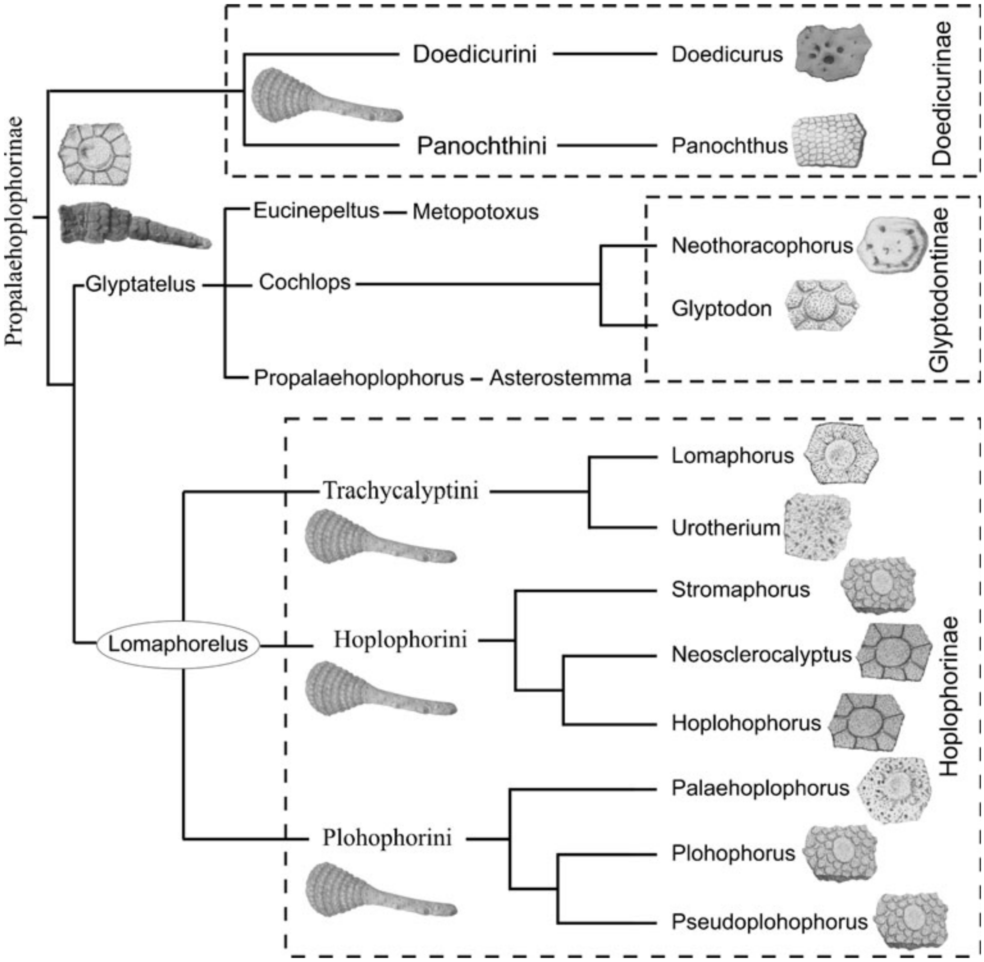

Fig. 4 Phylogenetic scenario of Castellanos (1959) showing the distribution of exoskeletal characters discussed in the text. Modified from Castellanos (1959)

Hoplophorini of Hoffstetter 1958). In this scheme, the exoskeleton features used by Hoffstetter (1958) for defining each tribe were not taken in consideration by Castellanos (1959).

After these works, only four new schemes were formulated. One was generated by Paula Couto (1979), who mixed the Simpson (1945) and Hoffstetter (1958) proposals. He accepted the Propalaehoplophorinae of Simpson (which include doubtfully *Glyptatelus*), and all the subfamilies and the hoplophorine tribes of Hoffstetter (1958). McKenna and Bell (1997) reproduced the classification of Hoffstetter (1958), introducing new genera erected during the second part of the 20th century. Fernicola (2008) carried out a cladistic analysis of craniodental characters for 12 glyptodont genera and found that Hoplophorinae (sensu Hoffstetter 1958) and some of its tribes (Hoplophorini and Plophophorini) were paraphyletic, leading him to propose a new classification for the glyptodonts (see "Discussion" section for details). Finally, Porpino et al. (2010) added several postcranial characters and an additional taxon to Fernicola's dataset. This analysis, as in Fernicola (2008), showed that the Hoplophorinae plus the aforementioned tribes were paraphyletic and that the characters used by Hoffstetter (1958) to support Hoplophorinae (e.g., conical-cylindrical caudal tube in addition to more "specialized" teeth, skull, and limb bones) were not truly diagnostic.

Materials

Acronyms: AMNH, American Museum of Natural History, New York, NY; FC-DPV, Colección de Vertebrados Fósiles, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; MACN A, Colección Ameghino, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MACN Ma, Colección Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires Argentina; MACN Pv, Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MCC, Museu Câmara Cascudo, Natal/RN, Brazil; MEF MLP, Museo de La Plata, La Plata, Argentina; PV UNS, Colección Paleontología de Vertebrados, Universidad Nacional del Sur, Bahía Blanca, Buenos Aires, Argentina.

Abbreviations: CI, consistency index; RI, retention index.

The specimens and references used for character coding in the cladistic analysis (see "Methods") are listed in Appendix I.

Methods

We evaluated the primary exoskeleton characters originally delineated by Ameghino (1889), that served as the basis for defining the relationships among the main groups of glyptodonts in his phylogenetic scenarios and classifications from the late 1880s and early to 1900s. For tail armor, the two states were: an armor formed by rings of osteoderms only or by rings proximally plus a well developed caudal tube distally (Character 146 of Porpino et al. 2010). Concerning the carapace osteoderms, the main states were represented by the sculptural patterns recognized by Ameghino (1889) in his transformation series, including the following: rosette pattern, the presence of two or more rows of peripheral figures, and the complete absence of figures. We proposed two new cladistic multistate characters that subsume this variation in carapace osteoderm morphology among their states (characters 01 and 02; see Appendix II), and two additional exoskeleton characters (characters 03 and 04; see Appendix II), which, though not directly related to the characters delineated by Ameghino (1889), have potential influence on the final outcome of our analysis. Character state assignments were based on the morphology of the osteoderms from the posterodorsal region of the carapace. In primary homology assignments, we considered as figures the areas in the external surface of the osteoderms delimited by sulci. The absence of these kinds of figures was not treated as a primary homology in taxa sharing this condition (*Pampatherium*, *Doedicurus*, and *Urotherium*) because each one of them has a distinctive ornamention pattern that was treated as an additional state of character 2 (see Appendix II). The assignment of state 2 of character 2 to *Panochthus* was based on the morphology observed in *Panochthus intermedius* instead of *Panochthus tuberculatus,* which does not bear central figures except on a few longitudinal rows near the lateral border and one to two transversal rows near the posterior border of the carapace (see Castellanos 1941). While the recognition of this latter pattern would allow the delimitation of an additional state for character 2, it would represent an autapomorphic polymorphism for *Panochthus* and for this reason it was not included.

The new characters were incorporated into a recently published dataset (Porpino et al. 2010), which was based on 18 taxa scored for 151 morphological characters, to create a grand total of 155 characters. The matrix of Porpino et al. (2010) included 84 craniodental characters from Fernicola (2008), of which three were originally proposed by Gaudin and Wible (2006), and 67 postcranial characters, of which 21 were new (including six from the caudal tube) and 46 were taken from Porpino et al. (2009). Character 2 was treated as ordered based on numerical and structural morphoclines following the 'method of intermediates' (Wilkinson 1992). All characters were weighted equally. The expanded new data matrix was analyzed under the criterion of maximum parsimony, using the implicit enumeration algorithm (exhaustive search) of TNT 1.1 software (Goloboff et al. 2008). The same outgroup and ingroup taxa used by Porpino et al. (2010) were employed.

Results

Our analysis resulted in a single most parsimonious tree (Length=330, CI=0.64, RI=0.74), ten steps longer than the tree of Porpino et al. (2010). The topology obtained is identical to that obtained by Porpino et al. (2010) (Fig. 5). The monophyly of Glyptodontia was clearly supported by 37 synapomorphies, of which 36 correspond to those found by Porpino et al. (2010) plus the presence of transverse mobile bands incomplete or absent (Character 4:1). The topology shows a basal dichotomy between propalaehoplophorines and the remaining glyptodonts (Glyptodontoinei sensu Fernicola 2008), which form a well-supported clade diagnosed by seven unambiguous synapomorphies. Of these, six are craniodental and one, the presence of a caudal tube (Character 146 of Porpino et al. 2010), is an exoskeletal character. This phylogenetic hypothesis strongly contradicts the monophyly of Hoplophorinae (sensu Hoffstetter 1958), indicating that it is a paraphyletic assemblage of glyptodonts more derived than the Propalaehoplophoridae (sensu Fernicola 2008). The same paraphyletic result was obtained for the tribes Hoplophorini and Plohophorini (sensu Hoffstetter 1958).

Regarding character 1, the presence of a figure defined by sulci is a plesiomorphy (1:0) while the other states are autapomorphies for *Pampatherium* (1:1), *Doedicurus* (1:2), and *Urotherium* (1:3). With respect to character 2, the presence of a main central figure surrounded by a single row of peripheral figures (2:1) is a potential synapomorphy of Glyptodontia, but the ambiguous optimization (2:0 or 2:1) to the node formed by *Pampatherium* plus Glyptodontia precludes defining its status. On the other hand, a central figure surrounded by at least two rows of peripheral figures (2:2), a primary homology for *Panochthus, Plohophorus*, and *Stromaphorus*, is optimized in the most parsimonious tree as having three independent origins. Finally, a circular or subcircular main figure on the external surface of osteoderm (Character 3:0) is a plesiomorphy of Glyptodontia.

Discussion

In our view, the recurrent alterations in glyptodontid systematics from the late 1800s to the 1900s have two main

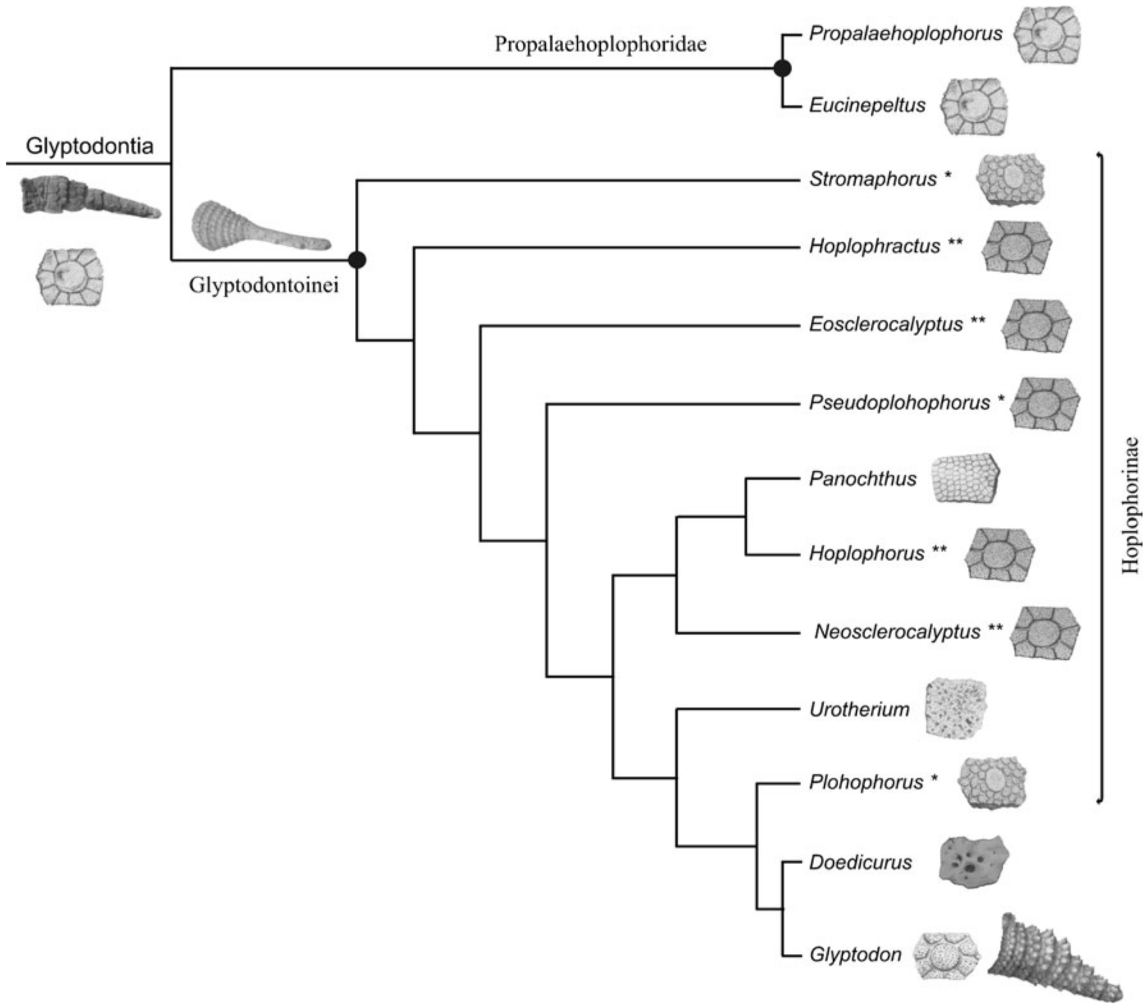

Fig. 5 Cladogram based on the results of the phylogenetic analysis carried out in the present study (Length=330, CI=0.64, RI=0.74) showing the most parsimonious distribution of exoskeletal characters discussed in the text. Genera marked with one and two asterisks were included into Plohophorini and Hoplophorini, respectively, by Hoffstetter (1958). The Hoplophorinae correspond to Hoffstetter (1958)

causes: the sequence by which the transformation series of exoskeletal characters first delineated by Ameghino (1889) were applied to determine phylogenetic relationships and the number of times specific transformations within these series were postulated to occur.

Ameghino (1889) applied his a priori polarized transformation series based on caudal tube morphology to delineate the main branches in his scheme, using a single characteristic, the acquisition of a caudal tube, to diagnose common ancestry of the genera included in type B (see Historical Background) (Fig. 1). Subsequently, he applied his a priori polarized transformation series based on the morphology of osteoderms in order to define subordinated groups within those main branches, obtaining a phylogenetic scenario which implied three main transformations, including a single case of homoplasy: the replacement of the rosette pattern by multiplication of the rows of peripheral figures, followed by a reversion in *Neosclerocalyptus*, and a loss of figures in doedicurines (Fig. 1). It is worth mentioning, however, that by rearranging taxa while maintaining the same polarized transformation series and the specific sequence of application it would be possible to obtain different phylogenetic scenarios with an equal number of implied steps, or even to obtain more parsimonious hypotheses. One could, for instance, reattach the doedicurine branch to any other hierarchical level above *Palaehoplophorus* (Fig. 1) without the need of additional steps. Ameghino (1889) appeared to be at least aware of this possibility as he inserted a question mark at the base of doedicurine branch (Fig. 1). On the other hand, if *Neosclerocalyptus* is interpolated between *Propalaehoplophorus* and *Palaehoplophorus*, a most parsimonious solution is obtained, as no reversion is required and a perfect fit of the postulated transformation series to the phylogenetic scenario is achieved. From a modern point of view, this Ameghinian method encompasses some desirable features, like the assessment of phylogenetic hypotheses by way of transformation series. Nonetheless, it also includes some inherent shortcomings, such as the a priori polarization and selection of the sequence in which the different transformations series should be applied.

The phylogenetic scenarios proposed during the 1900s assumed independent origins for the most derived glyptodont groups (i.e., the post-middle Miocene lineages) from a pre-middle Miocene group represented by the Propalaehoplophoridae/inae (e.g., Hoffstetter 1958; Castellanos 1959). Under this assumption, the transformations series postulated by Ameghino (1889) were not disputed, but were independently applied for each post-middle Miocene lineage. As a result, the characters shared by taxa from distinct lineages were considered analogous rather than homologous, and this led to the development of phylogenies pervaded by exoskeletal homoplasies, in contrast to Ameghino's hypothesis. For instance, the acquisition of a caudal tube, a unique event according to Ameghino (1889) caused by the fusion of the distalmost caudal rings covering the tail (Fig. 1), was independently acquired four (Castellanos 1959), five (Hoffstetter 1958), or six (Castellanos 1931, 1932) times (Figs. 2–4).

Concerning the carapace osteoderm characters, Hoffstetter's (1958) hypotheses (Fig. 3) required four steps, including three cases of homoplasy: one replacement of the rosette pattern by the multiplication of rows of peripheral figures (Plohophorini + Panochthini) and three independent losses of figures (Doedicurinae, Lomophorini, and Neuryurini). The earlier phylogenetic hypotheses of Castellanos (1931, 1932; Fig. 2) had an equal number of steps and of homoplasies relative to Hoffstetter's, including one independent loss of figures (Doedicurinae) and three independent replacements of the rosette pattern via the multiplication of rows of peripheral figures, while his later reconstruction (Fig. 4) implies five steps by including an additional independent loss of figures. A more careful inspection of these hypotheses suggests that the 1900s authors privileged characters from osteoderms at the expense of those from the caudal tube. Symptomatically, Castellanos (1931) disregarded the caudal tube similarities between panocthines and *Hoplophorus* and instead grouped panocthines with doedicurines by assuming, without presenting any palpable evidence, that this latter group presented epidermal scutes with an ornamentation pattern similar to that observed on the external surface of the panocthine carapace osteoderms. In a similar way, Hoffstetter (1958) allied the plohophorines with the panocthines based on a presumed homologous multiplication of rows of peripheral figures on the carapace osteoderms of both taxa (see Fig. 3), while treating as analogous the conical tubercles in the caudal tube of *Panochthus*, *Neuryurus* (Neuryurini), and *Hoplophorus* (Hoplophorini). In short, the main problem with these hypotheses resides not only in their exclusive use of exoskeletal characters (a technique already adopted by Ameghino), but in their commitment to highly homoplastic character transformations scenarios proposed in an ad hoc manner, apparently with the purpose of preserving preconceived ideas regarding taxon evolution. In effect, the adoption of such an approach on matters of phylogenetic inference would allow one to entertain any preconceived phylogenetic hypothesis. Castellanos (1931:9) apparently was aware of this problem when he stated that "El árbol filogenético a que nos referimos fue construido en base a caracteres de evolución de la ornamentación del caparazón, anillos y tubo caudales, porque ellos son los elementos taxonómicos utilizados … … Indudablemente para que esta distribución filogenética sea exacta tendremos que confeccionar otras en base a la morfología del cráneo, a la disposición de la columna vertebral, a los caracteres de los huesos largo de las extremidades, a los arcos escapular y pelviano, etc. Todos estos árboles se combinarán para obtener uno definitivo resultante de la conjunción de la evolución de órganos óseos y dentales de organización y adaptación." This appeal of Castellanos has been met by the cladistic analyses of Fernicola (2008), Porpino et al. (2010), and that presented in this paper (see Methods).

In the most parsimonious topology (MPT) here obtained (Fig. 5), as in Porpino et al. (2010), the presence of caudal tube (Character 146 from Porpino et al. 2010) was optimized as one of the seven synapomorphies supporting the Glyptodontoinei clade (sensu Fernicola 2008; see Fig. 5), the sister group to the Propalaehoplophoridae (sensu Fernicola 2008; see Fig. 5). This result agrees with the original hypothesis of Ameghino (1889) concerning the unique origin of the caudal tube within glyptodonts and is obviously at odds with the hypotheses of Hoffstetter (1958) and Castellanos (1931, 1932, 1959). On the other hand, the absence of this structure in *Glyptodon* corresponds to a reversion in the resulting MPT instead of a symplesiomorphy, which according to the earlier pre-cladistic hypotheses (Ameghino 1889; Castellanos 1931, 1932, 1959; Hoffstetter 1958) would ally *Glyptodon* to the propalaehoplophorines. Concerning the external ornamentation of carapace osteoderms, our analysis shows a homoplastic distribution. Our MPT implies that the number of rows of peripheral figures (Character 2:2) increased from the basal rosette pattern (Character 2:1) independently in *Panochthus*, *Plohophorus*, and *Stromaphorus* (Fig. 5), thereby showing the same level of homoplasy as the hypotheses of Castellanos (1931, 1932, 1959) and much more than in Hoffstetter's (1958), which required only a single origin to account for this feature. However, in our MPT, the clade formed by *Hoplophorus* and *Panochthus* encompasses among its synapomorphies the presence of conical tubercles, which Hoffstetter (1958) considered analogous. It is worth noting that Castellanos (1931, 1932, 1959) recognized two independent losses of figures in the carapace osteoderms and Hoffstetter

(1958) proposed three, while the MPT from the present study implies two, representing the acquisition of two distinct morphological patterns that represent autapomorphies for *Doedicurus* (Character 1:2) and *Urotherium* (Character 1:3). This result follows directly from our observation that the absence of figures in both genera stems from sculpture patterns that are not strictly comparable (see Methods). Yet, the possibility remains that one or both patterns could represent distinct synapomorphies in their own right, but this must be evaluated through the analysis of a more comprehensive matrix, including at least a few other doedicurines and/or lomaphorines. The results of this and Porpino et al.'s (2010) cladistic analysis show that exoskeletal characters carry phylogenetic signal, but their individual contribution to the inference of phylogenetic relationships should be evaluated in conjunction with other skeletal character as there is no a priori reasons to consider them better or worse.

Finally, it is crucial to recognize that the phylogenetic hypotheses under discussion have had varied influences on the classification of glyptodonts. The classification efforts proposed until the 1900s relied on the recognition of both horizontal and vertical paraphyletic groups (sensu Simpson 1945). Horizontal groups were represented by Propalaehoplophoridae/nae and Glyptatelinae (descendants excluded), while the vertical groups encompassed the remaining post-middle Miocene taxa represented by Doedicuridae/nae, Glyptodontidae/nae, and Hoplophoridae/nae (ancestors excluded). Simpson (1945) refused to recognize subdivisions within Hoplophoridae/nae because doing so would leave most taxa as *incertae sedis* (see Historical Background) whereas Hoffstetter (1958) divided this large group into five tribes. In a way, this latter alternative gave the scientific community a helpful framework, though clearly typological, which facilitated intergroup comparison but at the same time constrained evolutionary considerations. The phylogenetic hypothesis obtained in the present paper, as well as those obtained by Fernicola (2008) and Porpino et al. (2010), are incongruent in several aspects with the phylogenetic scenarios proposed during the late 1800s and 1900s and therefore have considerable implications for the classification of glyptodonts, impinging on the recognition of clades and the formalization of suprageneric taxa. Perhaps the most obvious example is represented by the Propalaehoplophoridae/nae. In the cladistic analysis carried out here, it forms a monophyletic group, sister of the remaining glyptodonts. This phylogenetic pattern is not congruent with the pre-cladistic scenarios in which propalaehoplophorines were recognized as the ancestors of more derived lineages (Simpson 1945; Hoffstetter 1958). Nonetheless, for nomenclatural reasons, the name Propalaehoplophoridae (see Fernicola 2008) is retained, notwithstanding the fact that this implies the application of an identical name to taxa recognized under divergent systematic philosophies. A similar problem arises in relation to the Hoplophoridae/nae, as recognized by Simpson (1945) and Hoffstetter (1958), and the tribes Hoplophorini and Plohophorini erected by this latter author to accommodate some genera within Hoplophoridae/nae. In our MPT (Fig. 5), as well as Fernicola (2008) and Porpino et al. (2010), the three taxa defined by Simpson (1945) and Hoffstetter (1958) are paraphyletic (Fig. 5). In this case, however, unlike the case of Propalaehoplophoridae, Hoplophoridae/nae cannot be reasonably redefined and retained because Glyptodontidae has priority (see Simpson 1945: 194 and Fernicola 2008 for an alternative solution adopted here).

Concluding Remarks

1 The Ameghinian method of 1889 was based on the determination of a priori transformation series involving osteoderm and caudal tube characters, which were then applied in a sequential manner to the construction of a phylogenetic scenario. It is possible, however, to formulate alternative hypotheses showing different levels of fit by rearranging taxa while maintaining the same polarized transformation series postulated by Ameghino.

2 The phylogenetic scenarios proposed during the 1900s were based on hypotheses of multiple origins for the most derived groups. Ameghino's transformations series were fitted to this preconceived idea by Hoffstetter (1958) and Castellanos (1931, 1932, 1959) in a way that led to the production of phylogenetic hypothesis supported by character states assumed a priori to be homoplastic.

3 The simultaneous analysis of the available morphological characters through cladistic methodology shows that some osteoderm characters believed to support ancestor-descendent relationships (e.g., presence of at least two rows of peripheral figures) are in fact fully homoplastic autapomorphies, while characters believed to have originated independently in several groups (e.g., presence of caudal tube) are optimized as synapomorphies at a wider hierarchical level. Thus, the exoskeletal characters bear levels of homoplasy similar to those of the endoskeleton and there is no reason to exclude them from the process of phylogenetic inference or to consider them as the sole source of reliable phylogentic signal.

4 The paraphyletic classification of Hoffstetter (1958) was the most widely used by the scientific community. Among the groups evaluated through cladistic analysis, the Hoplophoridae/nae and its tribes Hoplophorini and Plohophorini are deemed paraphyletic, whereas the

Proplaehoplophoridae is recovered as a monophyletic sister group to the remaining glyptodonts. This basal dichotomy is at odds with the multiple origins of post-middle Miocene glyptodonts implied by the 1900s classifications and by those still in use (e.g., McKenna and Bell 1997).

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Appendix I

Table 1 Specimens examined and references consulted for comparative study and cladistic analysis

Taxon	Catalogue number	References
Euphractus	MACN-Ma: 45.30, 50.121, 11.24, 20.3, 20.4, 14317, 34.592, 34.714, 47.204, 299	
Dasypus	MACN-Ma: 49.391, 49.397, 49.350, 49.383, 50.123, 50.124, 39.461	
Eutatus	MACN-A 1122-1132; MACN Pv, 7069	Krmpotic et al. (2009)
Pampatherium	MACN-Pv 11543/4, 11544, 11474, 11522; MLP-81-X-30-1	Scillato-Yané et al. (2005)
Pachyarmatherium	MCC 379-V, 423-V, 996-V, 759-V, 760-V, 761-V, 762-V, 769-V, 783-V, 994-V, 1133-V, 1134-V. UF 64347, 81897, 80371, 67099	Downing and White (1995)
Propalaehoplophorus	AMNH 9197; MPM-PV 3420, MACN-A 4698	Scott (1903–1904)
Eucinepeltus	MEF 1383	Scott (1903–1904)
Eosclerocalyptus	MACN-Pv 4853; MLP 29-10-1024.	Cabrera (1944)
Neosclerocalyptus	MACN-Pv 15345; MLP S/N	Lydekker (1894)
Hoplophorus	MHN 1003; MHN 1004; MHN 1005.	Porpino et al. (2010)
Hoplophractus	MLP-37-III-7-7; PV UNS 260	Cabrera (1944); Zurita and Aramayo (2007)
Panochthus	MLP 16-36;	Castellanos (1941)
Plohophorus	MACN-Pv 16592, 5018, 5296.	Lydekker (1894)
Stromaphorus	MLP-29-X-8-1; MLP 19-36	Cabrera (1944)
Pseudoplohophorus	FC-DPV-475 and -595	Perea (2005)
Urotherium	MACN A-229-A-231	Ameghino (1889); Castellanos (1926)
Glyptodon	MACN-Pv 200, 17566, 10153, 1780	Lydekker (1894)
Doedicurus	MACN-Pv 201, 14751, 13846, 16295	Lydekker (1894); Castellanos (1940)

Appendix II

List of new characters and character states added to the matrix of Porpino et al. (2010) and used in the cladistic analysis. Characters marked with an asterisk (*) are ordered.

01. External surface ornamentation of osteoderms: with figures defined by sulci (0); with a polygonal central area delimited by a dorsal thickening (1); without figures, smooth and perforated by large canals (2); without figures, presenting numerous small foramina associated with poorly developed sulci (3).

02*. Main figure defined by a principal sulcus and peripheral figures: near the posterior edge and peripheral figures absent or poorly developed at the posterior border (0); roughly central, surrounded by a single row of well-developed peripheral figures (1); roughly central, surrounded by at least two single rows of well-developed peripheral figures (2).

03. Outline of main figure defined by sulcus: circular or subcircular (0); roughly oblong (1).

04. Transverse mobile band(s): complete (extending from side to side of the carapace) (0); incomplete (limited to the ventrolateral border of the anterior region) or absent (1).

Appendix III

Table 2 The scoring of the new osteoderm and carapace characters for the 18 taxa used in the cladistic analysis. States marked with N are inapplicable

	01	02	03	04		01	02	03	04
Dasypus	0	0	0	0	*Plohophorus*	0	2	0	1
Eutatus	0	N	1	0	*Urotherium*	3	N	N	1
Euphractus	0	N	1	0	*Panochthus*	0	2	0	1
Pampatherium	1	N	N	0	*Neosclerocalyptus*	0	1	0	1
Pachyarmatherium	0	0	0	0	*Pseudoplohophorus*	0	1	0	1
Propalaehoplophorus	0	1	0	1	*Eosclerocalyptus*	0	1	0	1
Eucinepeltus	0	1	0	1	*Hoplophractus*	0	1	0	1
Glyptodon	0	1	0	1	*Stromaphorus*	0	2	0	1
Doedicurus	2	N	N	1	*Hoplophorus*	0	1	0	1

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