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A new species of *Neosclerocalyptus* Paula Couto (Mammalia: Xenarthra: Cingulata): the oldest record of the genus and morphological and phylogenetic aspects

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Abstract

Among South American Quaternary Glyptodontidae (Mammalia, Cingulata), *Neosclerocalyptus* Paula Couto represents one of the best known genera. Prior to this contribution, four species were recognized. *N. pseudornatus* (Ameghino) and *N. ornatus* (Owen) (Ensenadan Age/Stage, early-middle Pleistocene); *N. gouldi* Zurita (Bonaerian Age/Stage, middle Pleistocene-late Pleistocene), and *N. paskoensis* (Zurita) (Lujanian Age/Stage, late Pleistocene-early Holocene). One of the most notable characters of the species of the genus is a modified area located in the distal part of the nasals, recently interpreted as a neomorphic structure derived from the ossification of the nasal cartilages. In this contribution, a new species of *Neosclerocalyptus* (*N. castellanosi* **sp. nov.**), which in turn represents the oldest record of the genus, is presented and described. In addition, a cladistic analysis is carried out to test the monophyly of *Neosclerocalyptus* and the phylogenetic position of this new species. The material comes from Vorohuean (late Pliocene) levels in the surroundings of Mar del Plata, Buenos Aires Province, Argentina. Among other morphological characters, this new species has ossified nasal cartilages restricted to the latero-dorsal area of the nasals, whereas in the remaining species these structures are more expanded and both sides contact in the midline of the skull. In turn, the phylogenetic analysis confirmed the monophyly of *Neosclerocalyptus*, whereas *N. castellanosi* **sp. nov.** appears closely related to *N. pseudornatus*, being *N. ornatus* the sister taxa of this clade. On the other hand, *N. gouldi* + *N. paskoensis* constitute the other clade. The clade constituted by *Hoplophorus euphractus* Lund + *Panochthus intermedius* Lydekker constitutes the sister taxa of *Neosclerocalyptus.*

Key words: Glyptodontidae, Southern South America, taxonomy, late Pliocene, phylogeny

Introduction

One of the most conspicuous clades of endemic Cenozoic South American mammals is represented by the Glyptodontidae Gray (Xenarthra, Cingulata) (late Eocene-early Holocene; Hoffstetter 1958; Paula Couto 1979). However, during most of the twentieth century, knowledge of these large armored herbivores remained very scarce because most of the contributions dated back to the nineteenth century and the first half of the twentieth century (see, among others, Burmeister 1874; Ameghino 1889; Lydekker 1895; Castellanos 1940, 1941, 1942; Cabrera 1944).

In recent times, taxonomic, anatomic and phylogenetic knowledge of this clade has been improved (Zurita *et al.* 2007; Fernicola 2008; Porpino *et al.* 2009, 2010; González Ruiz 2010; Fernicola & Porpino 2012; Zamorano

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2012a,b; Zamorano & Brandoni in press), although most taxa still need revision with modern taxonomic criteria (Soibelzon *et al.* 2006; González-Ruiz *et al.* 2011). As observed by Hoffstetter (1958) many species and even genera and tribes of Glyptodontidae are recognized on the basis of isolated osteoderms of the dorsal and/or caudal armor (e.g "Hoplophorinae" Palaeohoplophorini, Lomaphorini, Neuryurini) (Hoffstetterm 1958; Paula Couto 1979; Zurita *et al.* 2011a).

In this scenario, *Neosclerocalyptus* Paula Couto (=*Sclerocalyptus* Ameghino) represents one of the best characterized Pleistocene genera of Glyptodontidae together with *Panochthus* Burmeister (Zamorano 2012a; Zamorano & Brandoni 2013) *Doedicurus* Burmeister and *Glyptodon* Owen (Burmeister 1874; Ameghino 1889; Zurita *et al.* 2009). *Neosclerocalyptus* has a latitudinal distribution limited to the southern part of South America, from Santa Cruz de la Sierra, Bolivia (17°47´ S, 63°11´ W), to Lobería (38°10 S, 58°46W) and Bahía Blanca (38°43´ S, 62°16´ W), Buenos Aires province, Argentina. It represents one of the smallest Pleistocene genera, with adults reaching *ca*. 250 kg (Vizcaíno *et al*. 2011), and its records are mostly related to arid/semiarid and cool environments of the Pleistocene (Zurita 2007; Zurita *et al.* 2009, 2011b).

Four species have been recognized previously: *N. pseudornatus* (early-middle Pleistocene; ca. 1.07–0.98 Ma), *N. ornatus* (early-middle Pleistocene (ca. 0.78 Ma), *N. gouldi* (middle Pleistocene; ca. 0.4 Ma), and *N. paskoensis* (late Pleistocene-early Holocene; ca. 120 ka–0.11 ka) (Zurita 2002, 2007; Zurita *et al.* 2008, 2009).

One of the most striking characters of the species of the genus is the progressive development and differentiation of the anterior part of the nasal region of the skull, which acquires an evident globular aspect in the Bonaerian and Lujanian species. Recently, Fernicola *et al.* (2012) have interpreted this structure as a neomorphic ossification, derived from an ossification of the nasal cartilage. This feature has not been observed previously in any other glyptodont and could thus represent a potential autapomorphy of the genus.

In this contribution, we present and describe a new species belonging to *Neosclerocalyptus*, which in turn represents the oldest record of the genus. We also perform a cladistic analysis to test the monophyly of *Neosclerocalyptus* and the phylogenetic position of this new species.

Material and methods

The chronological and biostratigraphic schemes used in this work correspond to those proposed by Cione and Tonni (2005). 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, whereas measurements greater than 150 mm were taken with an anthropometric spreading caliper. The description and terminology partially follow Zurita (2007) and Fernicola *et al.* (2012). 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 and comparative study. Appendix 2 shows the characters and character states of the matrix (Table 3).

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; **Ctes-PZ**, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; **MUFyCA**, Museo Universitario Florentino y Carlos Ameghino, Rosario, Santa Fé, Argentina; Museo Universitario "Florentino y Carlos Ameghino", Universidad Nacional de Rosario, Rosario, Argentina; **MACN**, Colección Nacional de Paleontología de vertebrados del, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MCA**, Museo de Ciencias Naturales "Carlos Ameghino", Mercedes, Buenos Aires, Argentina; **MCN**, Museo de Ciencias de Caracas, Venezuela; **MLP**, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; **MHNC,** Museo de Historia Natural de Cochabamba "Alcide d'Orbigny", Bolivia; **MPH**, Museo Municipal "Punta Hermengo", Miramar, Buenos Aires, Argentina; **YMP**, Yale Peabody Museum of Natural History, Princeton University collection (**PU**), Yale University, New Haven, USA; **USNM**, National Museum of Natural History, Smithsonian Institution. **Anatomical abbreviations—TL,** total length; **MDZA,** maximum diameter between zygomatic arches; **ID,** interobitary diameter; **MDPN,** maximum diameter of postorbital narrow; **MTDRA**, maximum transverse diameter of rostral area at level of ossified nasal cartilages; **LP**, length of palate; **LTR,** length of tooth rows. **Other abbreviations—M, m**, upper and lower molariforms respectively; **n/n**, without official catalog number.

TABLE 1. Linear measurements (in mm) of *Neosclerocalyptus* spp.

	N. pseudornatus (MUFyCA 107)	*N. ornatus* (MLP 16–28)	*N. gouldi* (MCA 2010)	*N. paskoensis* (MACN-Pv 18107)	*N. castellanosi* nov. sp. (MPH 0114)
TL	304	320	310	289	255.31
MDZA	215	230	205	233	207.8*
ID	127	121	170	153	160
MDPN	103	96	……..	110	96.57
MTDRA	152	180	190	197	162.16
LP	205	216	195	210	……
LTR	171	179	175	183	97* (M1-M5)

Phylogenetic analysis: To evaluate the monophyly of *Neosclerocalyptus* within Glyptodontidae, and the phylogenetic relationship of this new species with respect to the other recognized species of the genus, we performed a cladistic analysis. The matrix included 13 taxa and 23 morphological characters (Table 3). The characters included 13 from the skull and dentition, 1 from the cephalic armor, 4 from the dorsal carapace, and 5 from the caudal (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 using the Miocene Glyptodontidae Propalaehoplophorinae *Propalaehoplohorus australis* Ameghino (see González Ruiz 2010). The taxa of the out-group represent four of the five subfamilies recognized by Hoffstetter (1958): 1- Propalaehoplophorinae (*Cochlops muricatus* Ameghino); 2- Doedicurinae (*Doedicurus clavicaudatus* Owen); 3- "Hoplophorinae" *Hoplophorus euphractus* Lund; "Plohophorini" (*Plohophorus figuratus* Ameghino) and "Panochthini" (*Panochthus intermedius* Lydekker); and 4- Glyptodontinae (*Glyptodon* and *Glyptotherium* Osborn). Within "Hoplophorinae", the tribes Palaehoplophorini, Lomaphorini and Neuryurini were excluded from the analysis because of the scarce knowledge on these taxa, most of which is restricted to isolated osteoderms of the dorsal carapace and/or fragments of the caudal armor (Hoffstetter 1958; Paula Couto 1979; Zurita & Ferrero 2009). The in-group included the four recognized species of *Neosclerocalyptus: N. pseudornatus*, *N. ornatus*, *N. gouldi*, and *N. paskoensis*, plus the new species described in this paper. The character-taxon matrix (Table 3) was analyzed via "Implicit enumeration" using "TNT", under the criterion of maximum parsimony (Goloboff *et al*. 2008). Clade support was accessed via Relative Bremer support (from 461 trees; see Bremer 1994; Goloboff & Farris 2001), in addition to bootstrap analysis using the option "Implicit enumeration", with 1000 replicates.

TABLE 2. Character-taxon matrix used in phylogenetic analysis.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
P. australis	0	0	-	0	-	0	0	0	-	2	0	0	0	0	0	0	1	0	0	0	0	0	0
N. pseudornatus	1	2	0	?	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1
N. ornatus	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	1
N. gouldi	1	1	1	2	1	0	1	1	1	0	0	0	0	1	?	?	?	?	?	?	?	?	?
N. paskoensis	1	1	1	2	1	0	1	1	1	0	0	0	0	1	0	1	0	0	1	1	0	0	1
G. reticulatus	0	0	-	0	-	0	0	0	-	2	0	0	1	0	1	0	0	1	0	0	0	1	0
D. clavicaudatus	0	0	-	0	-	0	0	0	-	2	0	0	0	0	0	0	2	1	1	3	0	0	1
P. figuratus	0	0	-	0	-	0	0	0	-	2	0	0	0	0	0	0	1	1	1	1	0	0	1
P. intermedius	0	0	-	0	-	0	0	0	-	1	1	1	0	0	0	0	1	0	1	2	1	0	1
H. euphractus	0	0	-	0	-	0	0	0	-	1	1	1	0	0	0	0	0	0	1	2	1	0	1
Glyptotherium	0	0	-	0	-	0	0	0	-	2	0	0	1	0	1	0	0	1	0	0	0	1	0
N. castellanosi	1	2	0	0	0	1	0	0	0	0	0	0	0	?	?	?	0	?	?	?	0	?	?
C. muricatus	0	0	-	0	-	0	0	0	-	2	0	0	0	0	0	0	0	1	1	0	0	0	0

Results

Systematic Paleontology

Superorder XENARTHRA Cope, 1889

Order CINGULATA Illiger, 1811

Superfamily GLYPTODONTOIDEA Gray, 1869

Family GLYPTODONTIDAE Gray, 1869

Genus *Neosclerocalyptus* Paula Couto, 1957

***Neosclerocalyptus castellanosi* nov. sp.**
Fig 1 A–E

Holotype. MPH 0114, partial skull and fragment of the dorsal carapace corresponding to the most antero-lateral region.

Etymology. Named in honor of Alfredo Castellanos (1893–1975), doctor and self-taught paleontologist, for his extensive and laborious dedication to the scientific study of glyptodonts.

Type locality. "Las Antenas Militares" (38°14'23.75" S, 57°45'42.40" W), South of Mar del Plata city, General Pueyrredón, Buenos Aires province, Argentina (Fig 2).

Stratigraphic origin. Vorohué Formation, Marplatan Age/Stage, Vorohuean Subage/Substage (late Pliocene). *Ctenomys chapadmalalensis* Biozone (Cione and Tonni 1995, 2005; Cione *et al*. 2007) (Fig 3).

Stratigraphic comments. The material described here represents the first record of a *Neosclerocalyptus* species from the Vorohué Formation (Vorohuean Subage, late Pliocene). Remains of *Auliscomys* cf *A. osvaldoreigi* (MMP 5356) were collected from the infilling of an ancient vertebrate burrow situated at the same stratigraphic level where *N. castellanosi* was recovered. *A. osvaldoreigi* is a species restricted to the *Ctenomys chapadmalalensis* Biozone (Quintana 2002). Thus *N. castellanosi* **sp. nov.** cannot be more modern than Sanandresian Subage, according to the time averaged character of this bioconstruction. In this context, Kraglievich (1952) provided a litostratigraphic chart identifying those levels as Vorohuesian subage.

Diagnosis. Species of the genus showing the lowest degree of development of the ossified nasal cartilages, which are restricted to the antero-dorsal area of the nasals (Fig 1 C). Unlike that observed in *N. pseudornatus*, *N. ornatus*, *N. gouldi*, and *N. paskoensis*, the left and right sides of the ossified cartilages do not contact in the midline of the skull, occupying less than 40% of the dorso-ventral diameter of the skull in frontal view (Fig 1 B). Between these structures there is a "V" depression. The narial aperture (Fig 1 A–B) has a larger dorso-ventral and transverse diameter, related to the lower degree of development of the ossified nasal cartilage, and is more similar to that in *Glyptodon* than to that observed in the remaining species of *Neosclerocalyptus*. The ventral margin of the orbital notch is at the same plane as the lower part of the ossified nasal cartilage (Fig. 1 A), whereas in the other species the orbital notch is always located in a higher plane. The lachrymal tubercle is similar to but more developed than that of *N. pseudornatus*, and much more developed than that of *N. ornatus*, *N. gouldi* and *N. paskoensis*.

Description. The material corresponds to an adult specimen, and the cranial sutures are no visible. The general morphology of the skull resembles that of *N. pseudornatus*, but shows an evident lower degree of development of the ossified nasal cartilages.

In lateral view (Fig 1 A), these structures have the same globular morphology as in *N. pseudornatus*, thus clearly differing from that seen in *N. ornatus*, *N. gouldi* and *N. paskoensis,* in which they are much larger, completely covering the distal part of the nasals. The orbital notch has the typical subelliptical contour, dorso-ventrally extended, but unlike that observed in the remaining species, its ventral margin is located at the same plane of the lower margin of the ossified nasal cartilage. In *N. pseudornatus*, *N. ornatus*, *N. goudi* and *N. paskoensis,* the ventral margin of the orbital notch is always placed at an upper plane. In turn, the distance between the anterior margin of the orbital notch and the ossified nasal cartilages is similar to that in *N. pseudornatus*. In *N. paskoensis* and *N. gouldi*, as a consequence of the larger development of the ossified nasal cartilages, both structures are in

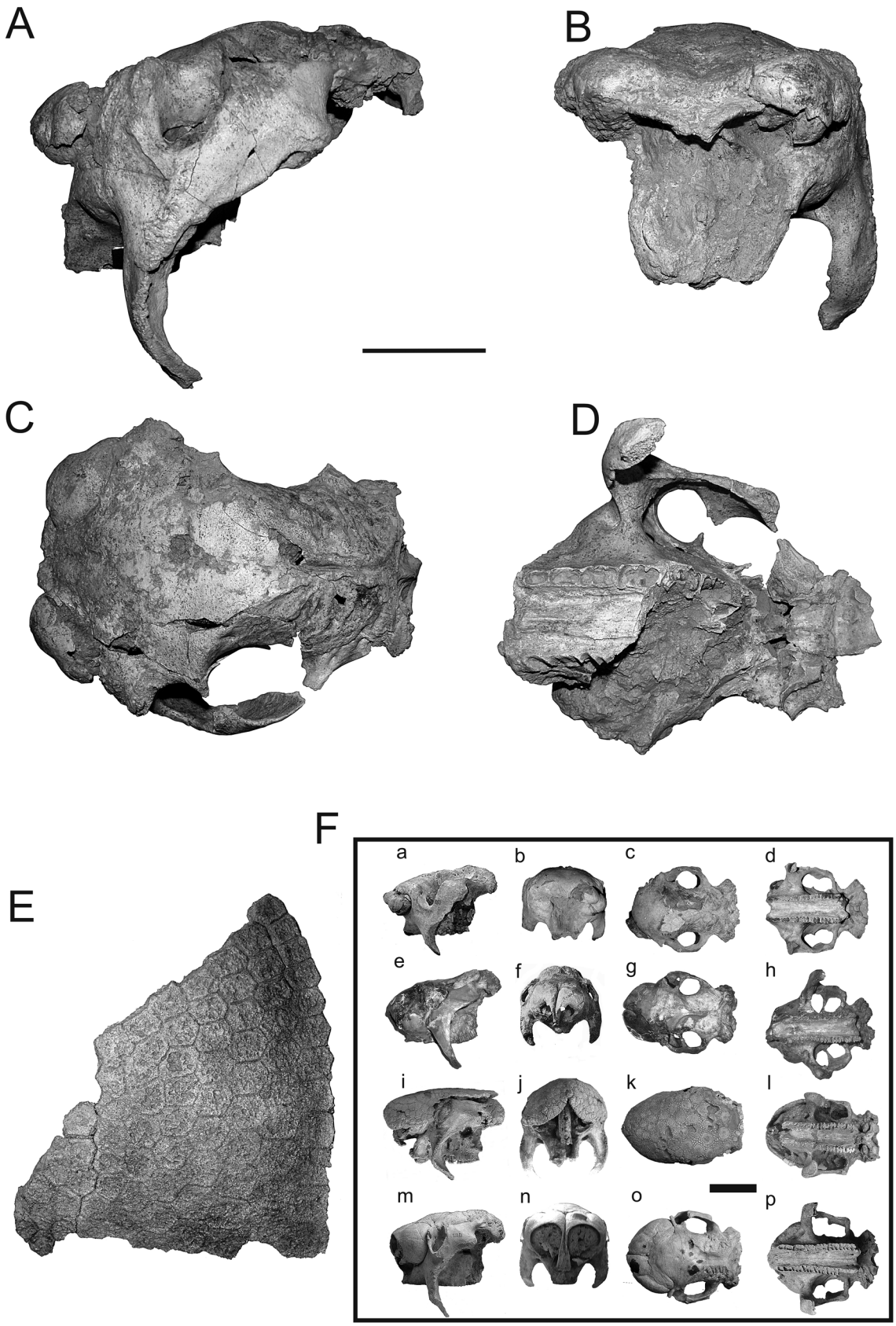

FIGURE 1. *Neosclerocalyptus castellanosi* **sp. nov.** (MPH 0114). Skull in **A**, lateral, **B**, frontal, **C**, dorsal and **D**, ventral views. **E**, associated osteoderms belonging to the most antero-lateral region of the dorsal carapace. **F** (**a**–**d**) *Neosclerocalyptus pseudornatus* (MACN-Pv 8579); (**e**–**h**) *Neosclerocalyptus ornatus* (MLP 16–28); (**i**–**l**) *Neosclerocalyptus gouldi* (MCA 2010); (**m**–**p**) *Neosclerocalyptus paskoensis* (MACN-Pv 18107). Scale bar: 100 mm.

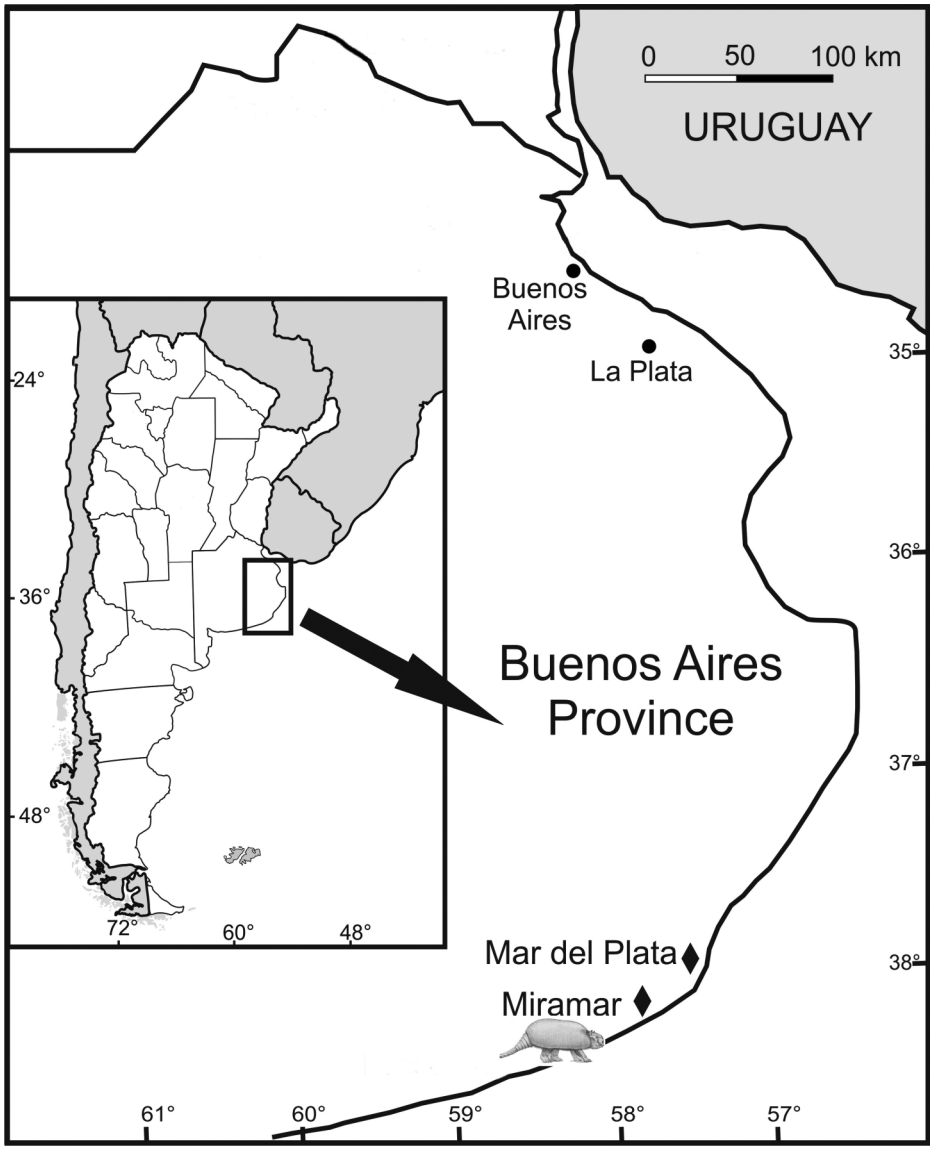

FIGURE 2. Map showing the locality where the type specimen (MPH 0114) of *Neosclerocalyptus castellanosi* **sp. nov.** was recovered**.**

contact. The lachrymal tubercle is morphologically similar to that observed in *N. pseudornatus*, but more developed and thus, much more evident in this new species than in the other species. The zygomatic arch is more developed than in *N. ornatus*, *N. gouldi* and *N. paskoensis*, and is morphologically similar to that of *N. pseudornatus* (i.e, a quadrangular outline). As observed in all species of the genus, the postero-ventral margin of the zygomatic arch has a tubercle morphologically very similar to that of *N. paskoensis*. The descending process of the zygoma shows a strong dorso-ventrally extended crest.

In frontal view (Fig 1 B), the ossified nasal cartilage is quite similar to that of *N. pseudornatus*, but with some evident differences. The left and right sides do not contact in its midline, as in the other species of the genus. In *N. paskoensis*, *N. gouldi*, and *N. ornatus*, both ossified cartilages are separated by the *sulcus supraseptalis* and the *septum nasi* (Fernicola *et al.* 2012); in contrast, in this new species, both ossified nasal cartilages are limited to the latero-dorsal region of the nasals. In the midline of the nasals, there is a depressed area, suggesting that another structure could have been present. Compared with *N. ornatus*, *N. gouldi* and *N. paskoensis*, the differences are even more marked, because in these species the more evident development of the ossified nasal cartilage completely covers the distal area of the skull and, according to Fernicola *et al.* (2012), the narial aperture is in fact constituted by the *apertura piriformis*. Conversely, both in this new species and in *N. pseudornatus*, the lateral and ventral edges of the narial aperture are formed by the nasal, maxillaries and pre-maxillaries, being the ossified nasal

cartilage limited to the latero-dorsal part of the narial aperture. Whereas in *N. pseudornatus* this cartilage occupies more than 50% of the total dorso-ventral diameter of the narial aperture in frontal view, in this new species, it represents less than 40%. As a consequence, the narial aperture is completely different, more similar to that of *Glyptodon* than to that of the other species of *Neosclerocalyptus*. In *N. gouldi* and *N. paskoensis*, the internal cavity is filled with a spongy tissue (*maxilla-atrio turbinate*), not observed in this new species.

In dorsal view (Fig. 1 C), the most differentiated area is that corresponding to the nasals, being the region constituted by the frontals, parietals and occipital similar to that of the other species of *Neosclerocalyptus*. Distally to the nasals, the ossified cartilages show a condition comparable to that observed in *Neosclerocalyptus pseudornatus*, but with some remarkable differences, especially with respect to a lower degree of development. As mentioned, the sides do not contact, but instead they are separated in the midline and restricted to a latero-dorsal location. In *N. pseudornatus*, both cartilages are in contact, whereas in *N. ornatus*, *N. gouldi* and *N. paskoensis* the left and right ossified nasal cartilages project distally and ventrally, related to the fact that the development is clearly more evident. Proximally, these structures are separated from the nasals by a marked groove, as in *N. pseudornatus* and *N. ornatus*, being in *N. gouldi* and *N. paskoensis* much less visible. One remarkable difference is that concerning the distal outline of the skull in dorsal view, which is sub-circular in all species except in this new species, in which it acquires a more quadrangular morphology, similar to that in *Glyptodon* or *Plohophorus* Ameghino. The parietal and occipital areas of the skull do not show significant differences from those of *N. ornatus* and *N. pseudornatus*.

In occlusal view (Fig 1 D), the most noticeable difference is that the ossified nasal cartilages are not visible; in contrast, this structure is clearly observable in all the other species, being more evident in *N. ornatus*, *N. gouldi* and *N. paskoensis*. Only the distal half of the palate is preserved, except for the pre-maxillae. This preserved part does not show significant differences with the other species. Although only the M5 is preserved, it is possible to infer the morphology of the M1–M4, which are very similar to those of the other species of the genus.

The dorsal carapace preserved corresponds to the most antero-lateral area and is constituted by 76 associated osteoderms (Fig 1 E). The general morphology of the osteoderms is similar to that known for the other species (Zurita 2007). The exposed surface of the osteoderms is highly eroded, thus precluding the observation of the real pattern of ornamentation.

Phylogenetic analysis. The cladistic analysis resulted in one most parsimonious trees (TL: 30; CI: 0.967; RI: 0.978). The topology of the tree obtained is similar to that previously obtained (Zurita *et al.* 2013) (Fig 4). It is possible to recognize two large basal natural groups: one constituted by the subfamily Glyptodontinae (*Glyptodon* + *Glyptotherium*) (12:1; 14:1; 21:1) and another one supported by a single synapomorphy (18:1). In this latter clade (19:1; 22:1) a basal polytomy is observed among the taxa *D. clavicaudatus*, *P. figuratus* and the clade constituted by *Panochthus* + *Hoplophorus*, and *Neosclerocalyptus* spp, which is supported by one synapomorphy (17:0). In turn, the clade constituted by *P. intermedius* + *H. euphractus* (10:1; 11:1; 19:2; 20:1) appear as sister taxa of *Neosclerocalyptus* spp. This phylogenetic hypothesis is in agreement with that proposed by Fernicola (2008), Porpino *et al*. (2009, 2010), Zamorano (2012a,b), Zamorano & Brandoni (2013), and Zurita *et al.* (2013). In turn, the genus *Neosclerocalyptus* appears as an evident natural group, a condition supported by four synapomorphies: distal area of the skull with ossified nasal cartilages (0:1); morphology of the distal area of the nasals modified into a single globular structure (1:1); cephalic armor presenting an evident rectangular contour (13:1); and dorsal carapace low and elongated, sub-cylindrical, and with dorsal outline almost straight (15:1). Within *Neosclerocalyptus*, two main clades can be recognized. One of them is composed of the Bonaerian and Lujanian species (*N. gouldi* + *N. paskoensis*). The synapomorphies supporting this condition are: distal margin of the rostrum constituted by the ossified nasal cartilages, which are straight (3:2); the presence of an evident *septum nasi* separating both ossified nasal cartilages (6:1); the presence of a spongy tissue in the distal area of the nasals (7:1). The other clade is formed by the Ensenadan and Vorohuean species (*N. ornatus* + *N. pseudornatus* + *N. castellanosi* **sp. nov.** (5:1; presence of a "V" groove separating the modified nasal area from the rest of the skull). There, *N. ornatus* is positioned as the sister taxon of *N. pseudornatus* + *N. castellanosi* sp. nov; both species are characterized by the following synapomorphies: morphology of the distal area of the nasals modified into a globular structure with two protuberances (1:2); antero-posterior development of the ossified nasal cartilages representing less than the 10% of the total length of the skull (2:0); ventral edge of the orbital notch coinciding with the lower half of the ossified nasal cartilages (4:0); distance between the anterior edge of the orbital notch and the posterior border of the ossified nasal cartilages larger than the antero-posterior diameter of the orbital notch (8:0).

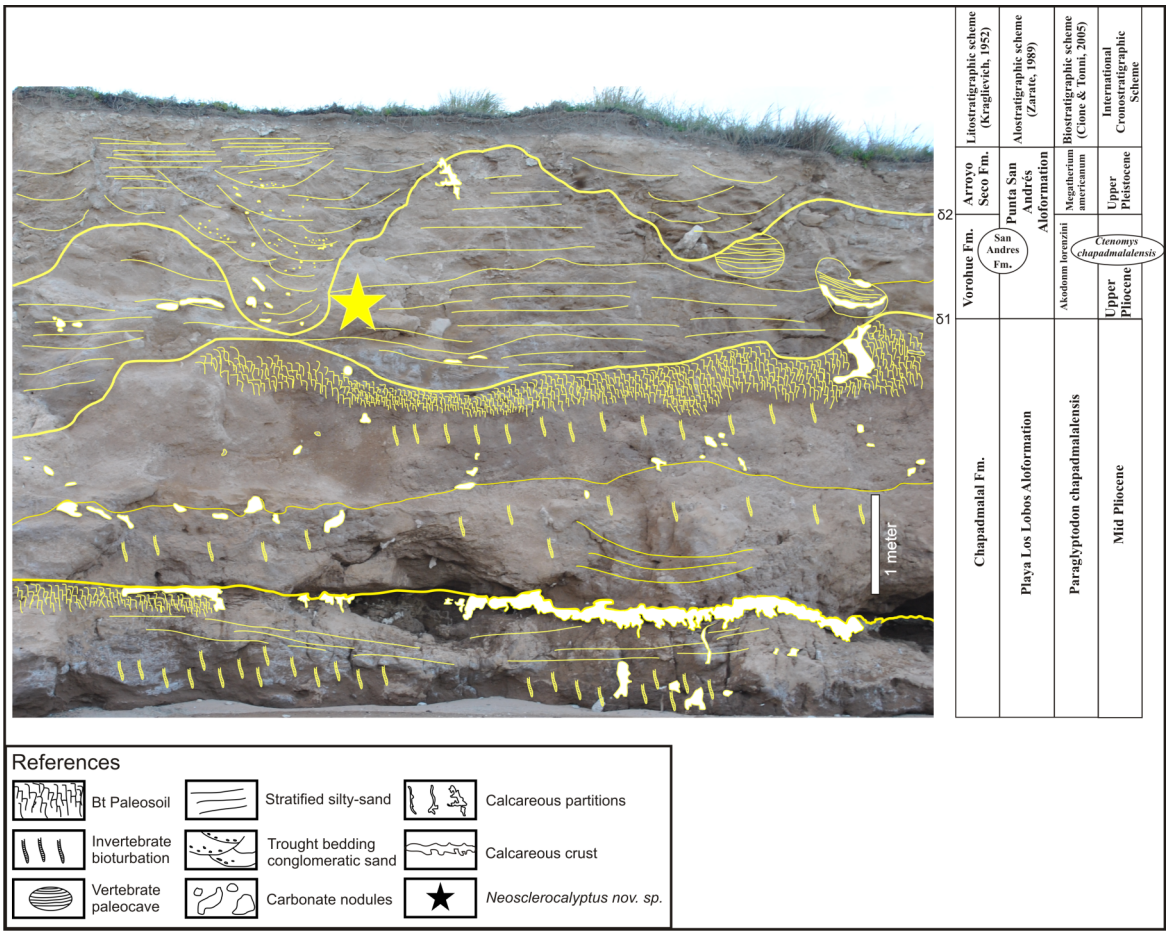

FIGURE 3. Lithostratigraphic profile showing the fossiliferous level.

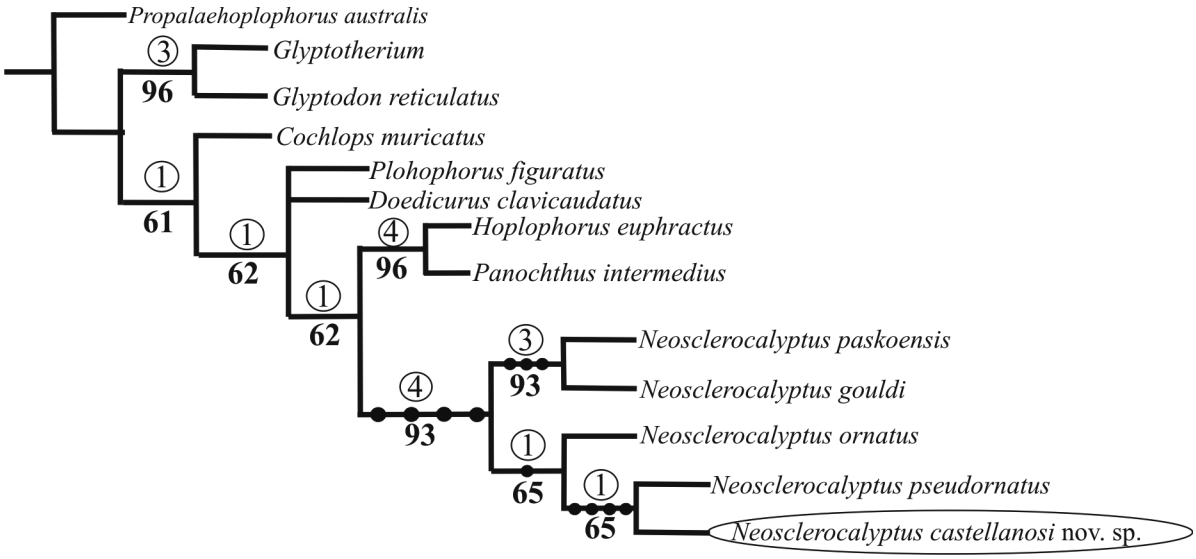

FIGURE 4. Phylogeny of Glyptodontidae based on TNT analysis of 22 osteological characters in 13 taxa (TL: 30; CI: 0.967; RI: 0.978). The numbers above each node represent bootstrap values; numbers in bold show Relative Bremer support.

Discussion

As mentioned, four species of the genus *Neosclerocalyptus* have been recognized: *N. pseudornatus*, *N. ornatus*, *N. gouldi* and *N. paskoensis*, reaching from the Ensenadan Age/Stage of "las Toscas del Río de La Plata" (early-

middle Pleistocene) to the Lujanian Age/Stage (late Pleistocene-early Holocene) (Soibelzon *et al.* 2010). Among other morphological characters, these species show a development of the most anterior area of the skull (Zurita 2007; Zurita *et al.* 2011b), currently interpreted as a neomorphic ossification of the nasal cartilages (Fernicola *et al*. 2012). This may vary "*from a single globular structure (N. ornatus, N. gouldi and N. paskoensis) to a globular structure showing two protuberances separated by grooves"* (*N. pseudornatus*) (Fernicola *et al*. 2012: 15). Unfortunately, none of the known specimens of *N. pseudornatus* preserve the most anterior part of the ossified nasal cartilages, thus their complete real morphology cannot be inferred.

In this morphological scenario, the modified anterior region of the skull of *Neosclerocalyptus castellanosi* shows the lowest degree of development, because the ossified nasal cartilages are restricted to the latero-dorsal area of the nasals. From an overall point of view, they are somewhat similar to that observed in the Ensenadan species *N. pseudornatus*, but with some remarkable differences (see "Description"). Among these, the left and right ossified nasal cartilages do not contact in the midline, whereas their lateral and ventral development is less evident. The area located between both ossified cartilages shows a "V" depression, suggesting that another structure could have been present.

From a phylogenetic perspective, the cladistic analysis confirms the monophyly of the genus *Neosclerocalyptus*, in which two main clades may be recognized. The new species appears closely related to the Ensenadan species *N. pseudornatus*, being *N. ornatus* the sister taxa. On the other hand, the relationship between *Neosclerocalyptus*, *Panochthus* and *Hoplophorus* shows no differences from that proposed by Porpino *et al*. (2010), Zamorano (2012a,b), and Zamorano & Brandoni (2013).

Conclusions

This new species constitutes the oldest record of the genus, whose previous oldest record came from the Ensenadan of "las Toscas del Río de La Plata". In turn, the phylogenetic analysis corroborates the monophyly of the genus *Neosclerocalyptus*. The clade *Panochthus* + *Hoplophorus* appears as the sister taxa of *Neosclerocalyptus*, although the relationship with the other taxa of the out-group (*D. clavicaudatus* and *P. figuratus*) cannot be solved. Two main clades can be recognized in *Neosclerocalyptus*: one constituted by the Bonaerian and Lujanian species (*N. gouldi* + *N. paskoensis*); in the other clade, the late Ensenadan species (*N. ornatus*) appears as the sister taxa of *Neosclerocalyptus pseudornatus* + *Neosclerocalyptus castellanosi*. Finally, both *N. pseudornatus* and *N. castellanosi* exhibit a similar morphology of the ossified nasal cartilages, being less developed in this new species.

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

Propalaehoplophorus australis: MLP 16-15, MLP 16-16; YMP PU 15212.
Cochlops muricatus: MACN-Pv A 1036-1039, MACN 2121, MACN 2113; YMP PU 15331.
Plohophorus figuratus: MLP 16-153 (Type)
Glyptodon reticulatus: MCA 2015 and 2017.
Glyptotherium texanum: AMNH 1074 (Type).
Glyptotherium arizonae: USNM 10536 (Type); AMNH 21808.
Glyptotherium cylindricum: AMNH 15548 (Type); MCN n/n.
Panochthus intermedius: MLP 16-36 (Type); MHNC-13491.
Doedicurus clavicaudatus: MLP 16-25.
Neosclerocalyptus paskoensis: Ctes-PZ 5879 (Type); MACN-Pv 18107.
Neosclerocalyptus pseudornatus: MUFyCA 107; MACN-Pv 5879.
Neosclerocalyptus ornatus: MLP 16-28; MUFyCA 656.
Neosclerocalyptus gouldi: MCA 2010 (Type).
Neosclerocalyptus castellanosi **sp. nov.** MPH 0114.

APPENDIX 2. List of characters and character states used in the cladistic analysis.

All characters were scored via direct observation of the specimens.

0 Distal area of the skull with ossified nasal cartilages: (0) absent; (1) present.
1 Morphology of the distal area of the nasals: (0) normal morphology; (1) modified into a single globular structure; (2) modified into a globular structure with two protuberances.
2 Antero-posterior development of the ossified nasal cartilages in dorsal view on sagittal plane: (0) representing less than the 10% of the total length of the skull; (1) representing more than the 10 % of the total length of the skull.

3 Distal margins of the rostrum: (0) formed by the nasals and premaxillae; (1) formed by the ossified nasal cartilages, which are curved inward; (2) formed by the ossified nasal cartilages, which are straight.
4 Ventral edge of the orbital notch: (0) coinciding with the lower half of the ossified nasal cartilages; (1) coinciding with the 50% of the dorso-ventral diameter of the ossified nasal cartilages.
5 Presence of a "V" groove separating the modified nasal area from the rest of the skull: (0) absent; (1) present.
6 Presence of an evident *septum nasi* separating both ossified nasal cartilages: (0) absent; (1) present.
7 Presence of a spongy tissue in the distal area of the nasals: (0) absent; (1) present.
8 Distance between the anterior edge of the orbital notch and the posterior border of the ossified nasal cartilages in lateral view: (0) larger than the antero-posterior diameter of the orbital notch; (1) smaller than the antero-posterior diameter of the orbital notch.
9 Contour of the distal area of the skull in dorsal view: (0) semicircular; (1) triangular; (2) subrectangular or quadrangular.
10 Naso-frontal and occipital areas of the skull ventrally inclined: (0) absent; (1) present.
11 Presence of a notch in the margins of the narial aperture in lateral view: (0) absent; (1) present.
12 Morphology of M1/m1: (0) lobes absent or limited to a single margin; (1) labial and lingual margins with lobes.
13 Cephalic armor: (0) subtriangular contour; (1) subrectangular contour.
14 Morphology of the osteoderms that constitute the border of the carapace: (0) "spine like" osteoderms absent or limited to the caudal notch; (1) "spine like" osteoderms present around the dorsal carapace.
15 Presence of a dorsal carapace low and elongated, sub cylindrical, dorsal outline almost straight: (0) absent; (1) present.
16 Pattern of ornamentation of the lateral area of the dorsal carapace: (0) rosette pattern with a single row of peripheral figures; (1) rosette pattern with two or more rows of peripheral figures; (2) perforated.
17 Pattern ornamentation of the dorsal carapace and the caudal tube: (0) similar ornamentation pattern; (1) different ornamentation pattern.
18 Morphology of the caudal armor: (0) composed by caudal rings representing more than 90% of the total length; (1) composed by caudal rings plus caudal tube representing more than the 40% of the total length of the caudal armor.
19 Lateral area of the caudal tube: (0) without ornamentation; (1) lateral figures; (2) lateral and "spine like" figures; (3) only "spine like" figures.
20 Presence of conical tubercle in the lateral and terminal figures of caudal tube (modified from Porpino *et al*., 2010): (0) absent; (1) present.
21 Exposed surface of the distal row of osteoderms of the caudal armor modified into "spine like" structure: (0) absent; (1) present.
22 Length of the caudal tube vs length of the caudal rings: (0) caudal tube shorter than the caudal rings; (1) caudal tube longer than the caudal rings.