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First Neogene skulls of Doedicurinae (Xenarthra, Glyptodontidae): morphology and phylogenetic implications

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Among Glyptodontidae, Doedicurinae (late Miocene–early Holocene) includes the glyptodonts with the largest size and latest records. Doedicurinae is mainly characterised by a smooth surface of the osteoderms with large foramina, and a particular morphology of the caudal tube. All taxa except one (*Doedicurus clavicaudatus*) have been recognised and characterised on the basis of remains of caudal tubes and/or dorsal carapaces. This situation produced an evident overestimation of the real diversity of this group, and a taxonomic revision is needed. In fact, no Neogene skulls were known. We present and describe the first two Neogene skulls belonging to Doedicurinae (cf. *Eleutherocercus antiquus*). The materials come from the El Polvorín and Chapadmalal Formations, in the surroundings of Olavarría and Mar del Plata localities, respectively (Buenos Aires province, Argentina). A cladistic analysis was carried out in order to situate these materials among Glyptodontidae and inferring new synapomorphies at skull level in Doedicurinae. Cf. *Eleutherocercus antiquus* clusters with the Pleistocene species *Doedicurus clavicaudatus* showing three unambiguous synapomorphies, which in turn represents the first skull synapomorphies for Doedicurinae. Finally, the presence of cf. *Eleutherocercus antiquus* in the El Polvorín and Chapadmalal Formations suggests that the stratigraphic distribution of this species could include the Montehermosan–Chapadmalalan interval.

Keywords: Xenarthra; Pliocene; *Eleutherocercus*; Argentina; morphology; phylogeny

1. Introduction

Xenarthra constitutes one of the main clades of Placentalia and the molecular and palaeontological evidence strongly suggests that this group would have differentiated in South America (Delsuc and Douzery 2008). The family Glyptodontidae (late Eocene–early Holocene), which represents one of the most conspicuous taxa of Xenarthra in South America, reached Central and North America during the Great American Biotic Interchange (Woodburne 2010).

Morphologically, the most distinctive feature of glyptodonts is the presence of an immobile dorsal carapace composed of osteoderms and trilobate molariforms. In some intervals of the Cenozoic (e.g. Oligocene and Pleistocene), these large armoured herbivores attained giant forms, with species having almost two tons (Vizcaíno et al. 2011) or even more (Soibelzon et al. 2012), especially in late Pleistocene taxa.

More than 67 genera have been recognised (see McKenna and Bell 1997). However, most of the studies have been conducted in a strict typological/morphological taxonomic context, without a precise morphological characterisation. Consequently, many taxa need an urgent revision with modern taxonomic criteria. In recent times, the morphological and phylogenetic knowledge of some lineages of Glyptodontidae has been largely improved (Croft et al. 2007; Zurita 2007; González 2010; Porpino et al. 2010; Zamorano 2012; Zamorano and Brandoni 2013; Zurita, González-Ruiz, et al. 2013). In addition, there is evidence that some of the traditionally recognised taxa (see Hoffstetter 1958; Paula-Couto 1979) do not constitute natural groups (see, among others, Fernicola 2008; Porpino et al. 2010; Fernicola and Porpino 2012).

This particular problematic is due in part to the fact that most of the well-known taxa come from the Pleistocene (ca. 2.6–0.0011 Ma), whereas the knowledge of Palaeogene and Neogene glyptodonts is much more limited (see Scott 1903; González-Ruiz et al. 2011). Tribes (e.g. Neothoracophorini and Palaehoplophorinae) and even subfamilies have been characterised on the basis of scarce remains of the dorsal carapace and/or caudal armor (Zurita et al. 2011). In fact, the only well-characterised Tertiary taxa correspond to the subfamily Propalaehoplo-

phorinae, a diversified clade from the Miocene of the Patagonian region (see Scott 1903; González 2010).

In this scenario, one of the most particular groups of glyptodonts is represented by the Doedicurinae (late Miocene–early Holocene), perhaps the assemblage with the southernmost distribution in South America, almost exclusively in the current territories of Argentina and Uruguay (Ubilla et al. 2004; Zurita et al. 2009). Several Neogene (e.g. *Eleutherocercus* Koken, 1888; *Palaeodaedicurus* Castellanos, 1927; *Prodaedicurus* Castellanos, 1927; *Xiphuroides* Castellanos, 1927; *Castellanosia* Kraglievich, 1932; *Comaphorus* Ameghino, 1886) and Pleistocene taxa (e.g. *Plaxhaplous* Ameghino, 1884; *Daedicuroides* and *Doedicurus* Burmeister, 1874) have been recognised (see Ameghino 1889; Castellanos 1940). Prior to this contribution, all taxa except the Pleistocene genus *Doedicurus* (which includes complete specimens) are based on remains of the dorsal carapace and/or caudal tube.

One of the most distinctive characters of Doedicurinae includes the exposed surface of the osteoderms, which is completely smooth with large foramina, and the particular morphology of the caudal tube (i.e. a distally expanded caudal tube; see Castellanos 1940; Oliva and Aramayo 2006). From a phylogenetic viewpoint, Doedicurinae has been interpreted as the sister group of the Glyptodontinae (Croft et al. 2007; Fernicola 2008; Porpino et al. 2010), although other cladistic analyses do not support this interpretation (see Oliva and Aramayo 2006; Zurita, González-Ruiz, et al. 2013).

In this contribution, we present and describe the first Neogene skulls belonging to Doedicurinae, cf. *Eleutherocercus antiquus*, which come from Upper Chapalmalalan levels (late Pliocene) of the localities of Mar del Plata (Chapadmalal Formation) and Olavarría (El Polvorín Formation), Buenos Aires province, Argentina (Figure 1). We also carried out a cladistic analysis to test the phylogenetic location of this species, and to obtain, for the first time, synapomorphies at skull level.

2. Materials and methods

The chronological and biostratigraphic schemes used in this contribution follow Cione and Tonni (2005), Cione et al. (2007) and Tomassini et al. (2013). Stratigraphic schemes follow Kraglievich (1952), Zárate (1989) and Zárate and Fasano (1989) for Chapadmalal Formation and De los Reyes et al. (2013) for El Polvorín Formation. The systematics partially follows Hoffstetter (1958), Paula-Couto (1979), McKenna and Bell (1997) and Fernicola (2008). All the values included in the tables are expressed in millimetres, with an error range of 0.5 mm. The description and terminology for osteoderms and molariforms follow mainly Zurita (2007), Krmpotic et al. (2009)
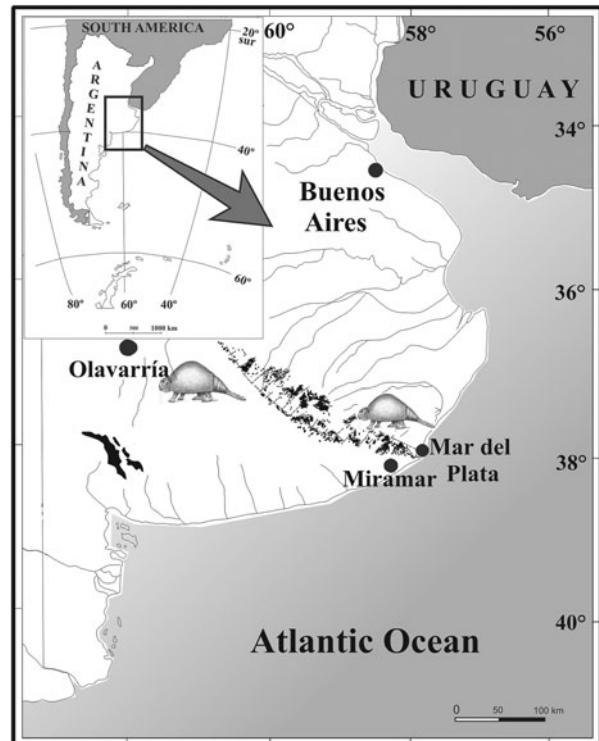
Figure 1.   Map showing the fossiliferous localities.

and Gonzalez-Ruiz et al. (in press). Details on the cladistic analysis used are given in Section 2.1. Linear measurements are provided in Table 1. Appendix 1 shows the list of character and character states. Appendix 2 includes the character–taxon matrix used in the cladistic analysis.

The examined material that provided the main basis for comparative study and phylogenetic analysis is as follows: *Cochlops muricatus* Ameghino, 1889 (MACN A 1036–1039, MACN 2121, MACN 2113; YMP VPPU 15331); *Glyptodon reticulatus* Owen, 1845 (MCA 2015 and 2017); *Glyptotherium arizonae* Gidley, 1926 [USNM 10536 (type), AMNH 21808, Gillette and Ray 1981]; *Glyptother-*

Table 1.   Linear measurements (in mm) of cf. *Eleutherocercus antiquus*.

	MMP 4860	Xen 34
Skull		
Total length	230.74	–
Maximum transverse diameter between zygomatic arches	235.18	280
Height of narial aperture	71.70	58.43
Transverse diameter of narial aperture	98.82	102.5
Transverse diameter of postorbital region	108.14	–
Length of the tooth series	144.44 (M1–M6)	178.50
Length of the palate	157.28	–
Transverse diameter at the level of M1	115.20	102.64

ium cylindricum (Brown, 1912) [AMNH 15548 (type), MCN n/n]; *Glyptotherium texanum* Osborn, 1903 [AMNH 1074 (type), Gillette and Ray 1981]; *Neosclerocalyptus paskoensis* (Zurita, 2002) (Ctes-PZ 5879 type, MACN-Pv 18107); *Neosclerocalyptus pseudornatus* (Ameghino, 1889) (MUFyCA 107, MACN-Pv 5879); *Neosclerocalyptus ornatus* (MLP 16-28, MUFyCA 656); *Neosclerocalyptus gouldi* Zurita, Carlini and Scillato-Yáné, 2008 (MCA 2010, type); *Neosclerocalyptus castellanosi* Zurita, Taglioretti, Zamorano, Scillato-Yané, Luna, Boh and Magnussen Saffer, 2013 (MPH 0114, type); *Panochthus tuberculatus* (Owen, 1845) (MLP 16-29); *Propalaehoplophorus australis* Ameghino, 1887a (MLP 16-15, MLP 16-16, YMP VPPU 15212); *Doedicurus clavicaudatus* (Owen, 1847) (MLP 16-24, MMP 4782); *Doedicurus* sp. (MACN Pv. 2762); *Eleutherocercus antiquus* (Ameghino, 1887) (MLP 16-55, type); *Palaeodaedicurus chapadmalensis* (MACN 6289, type).

2.1 Phylogenetic analysis

To test the location of cf. *Eleutherocercus antiquus* within Glyptodontidae and identify new potential synapomorphies for Doedicurinae, we performed the cladistic analysis presented next. The matrix included 15 taxa and 30 morphological characters (Appendix 2). Most characters were based on two previous analyses (see Zurita, González-Ruiz, et al. 2013; Zurita, Taglioretti, et al. 2013), and four new characters (14, 15, 16, 20) were added. The characters included 17 from the skull and dentition, 1 from the cephalic armour, 7 from the dorsal carapace and 5 from the caudal armour (Appendix 1). Twenty-five are binary characters and five multistate. All characters were treated as unordered, with the same weight (1.0). Character states that were not preserved were coded as '?'. The matrix was developed through the Nexus Data Editor (0.5.0) software. The character–taxon matrix (Appendix 2) was analysed via 'Implicit enumeration' using 'TNT', under the criterion of maximum parsimony (Goloboff et al. 2008). Clade support was accessed via Relative Bhremer support (from 375 trees; see Bhremer 1994; Goloboff and Farris 2001), in addition to bootstrap analysis we use the option 'Implicit enumeration', with 1000 replicates. All the characters were scored via direct observation of the specimens. The well-characterised Miocene Glyptodontidae Propalaehoplophorinae *Propalaehoplophorus australis* (see González 2010) was used to root the tree. The taxa analysed are as follows: (1) Propalaehoplophorinae (*Cochlops muricatus*); (2) Doedicurinae (*Doedicurus clavicaudatus*, *Doedicurus* sp., cf. *Eleutherocercus antiquus* and *E. antiquus*); (3) 'Hoplophorinae' *Hoplophorus euphractus* Lund, 1839; 'Plohophorini' (*Plohophorus figuratus* Ameghino, 1887b) and Panochthini (*Panochthus intermedius* Lydekker, 1895); (4) Glyptodontinae (*Glyp-*

todon and *Glyptotherium*). Within 'Hoplophorinae', the tribes Palaehoplophorini 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 armour (Hoffstetter 1958; Paula-Couto 1979; Zurita and Ferrero 2009). In the case of the 'Hoplophorinae' Lomaphorini, the available evidence suggests that this is not a real group because the related specimens correspond to well-known taxa belonging to other clades (see Oliva et al. 2013). In addition, in that concerning the Doedicurinae, the genera *Xiphuroides*, *Castellanosia* and *Comaphorus* were not taken into account due to their bad morphological characterisation and the lack of homologous structures (see Oliva 2008).

2.2 Institutional abbreviations

AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; AMNH, American Museum of Natural History, New York, USA; CAL, Colección Paleontológica, Centro de Museos, Universidad de Caldas, Manizales, Caldas, Colombia; Ctes-PZ, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; LIEB-PV, Laboratorio de Investigaciones en Evolución y Biodiversidad, Universidad Nacional de La Patagonia 'San Juan Bosco', Sede Esquel, Argentina; MACN, Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCA, Museo de Ciencias Naturales 'Carlos Ameghino', Mercedes, Buenos Aires, Argentina; MMP, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia', Mar del Plata, Buenos Aires, Argentina; MCN, Museo de Ciencias de Caracas, Venezuela; MHD-P, Museo Histórico Departamental de Artigas, Uruguay; MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia', Buenos Aires; MPEF, Museo Paleontológico 'Egidio Feruglio', colección Paleontología de Vertebrados (PV), Trelew, Argentina; Xen, Collection 'Cementos Avellaneda', Olavarría, Buenos Aires, Argentina; YMP, Yale Peabody Museum of Natural History, Princeton University collection (VPPU), Yale University, New Haven, USA; USNM, National Museum of Natural History, Smithsonian Institution, USA.

2.3 Other abbreviations

Mf, upper molariform teeth; n/n, without official catalogue number.

3.   Systematic palaeontology

Xenarthra Cope, 1889

Cingulata Illiger, 1811

Glyptodontia Ameghino, 1889

Glyptodontoidea Gray, 1869

Glyptodontidae Gray, 1869

Doedicurinae Trouessart, 1897

Eleutherocercus antiquus (Ameghino, 1887b)

Holotype: MLP 16-55, dorsal carapace and caudal tube.

Geographic and stratigraphic provenance: Farola Monte Hermoso, Buenos Aires province. Monte Hermoso

Formation (early Pliocene; ca. 5.28–4.5 Ma; see Tomassini et al. 2013).

Cf. *Eleutherocercus antiquus* (Ameghino, 1887b)

(Figures 2 and 3)

Referred material: MMP 4860, skull partially preserved; MMP 5360: several associated osteoderms of the dorsal carapace; Xen 34, skull partially preserved; Xen 81-1 (1–5), numerous associated osteoderms of the dorsal carapace, and a fragment of right hemimandible preserving m6 and m7.

Geographic and stratigraphic provenance of the referred materials: Xen 34 and Xen 81-1 (1–5) were
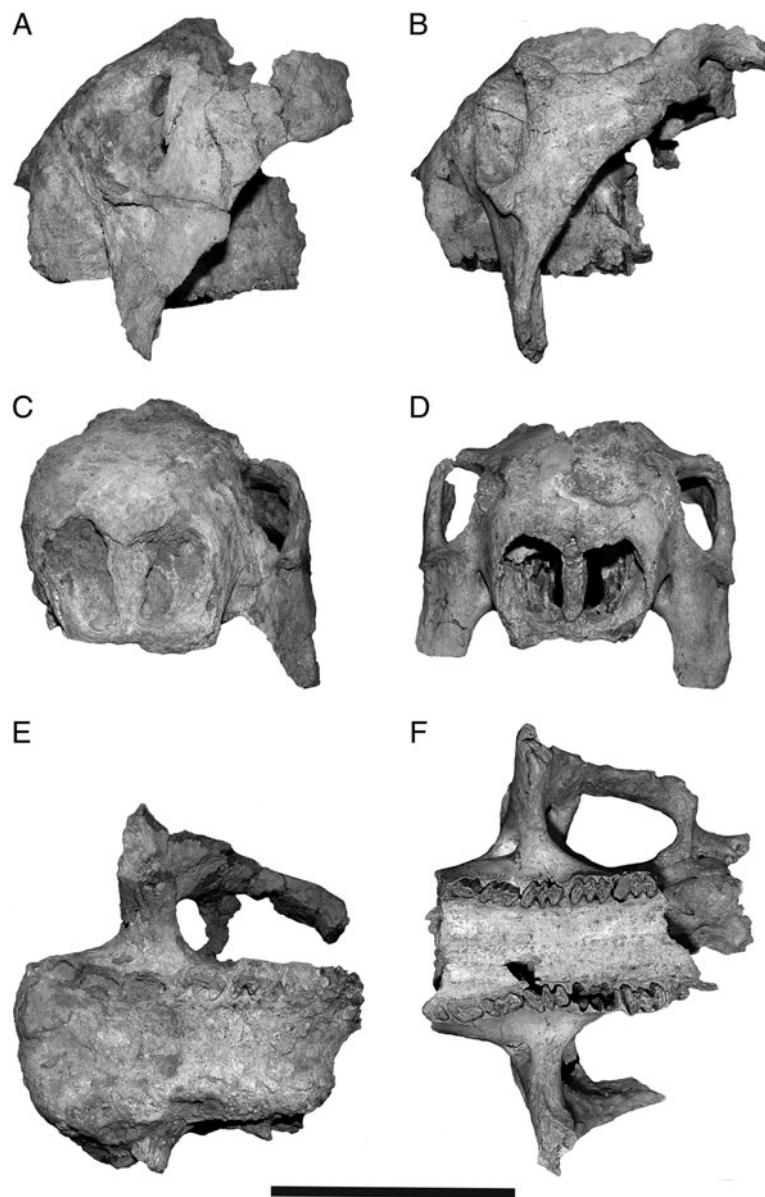

Figure 2.   Skulls of cf. *Eleutherocercus antiquus* in lateral (A, B), frontal (C, D) and occlusal views (E, F) (A, C, E: Xen 34; B, D, F: MMP 4860). Scale bar: 100 mm.
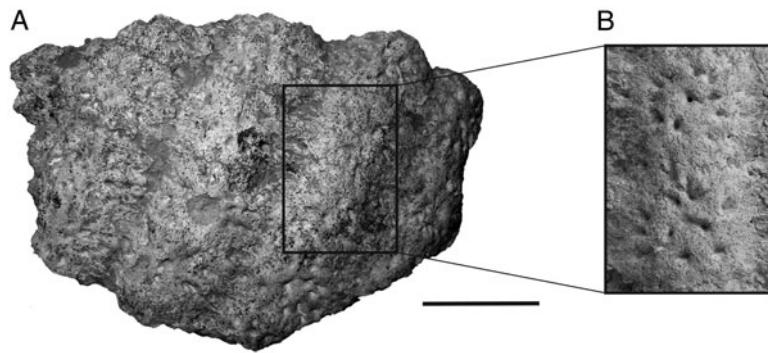
Figure 3. Xen 81.1. (A) Fragment of dorsal carapace corresponding to the posterior region; (B) detail of the exposed surface. Scale bar: 50 mm.

collected nearby Olavarria city, in the quarry 'Calera Avellaneda', El Polvorín Formation (Chapadmalalan, upper Pliocene) (36°59′17.21″ S, 60°14′8.02″ W) (see Poiré et al. 2005; De los Reyes et al. 2013). MMP 4860 and MMP 5360 come from El Marquesado, Mar del Plata, Buenos Aires province, Chapadmalal Formation (see Kraglievich, 1952), Playa Los Lobos Aloformation, Upper Alomember (see Zárate 1989; Zárate and Fasano 1989), Chapadmalalan and Upper Pliocene (see Cione and Tonni 2005; Cione et al. 2007) (38°14′02″ S−57°44′43.9″ W) (Figure 1).

3.1   Description and comparisons

3.1.1   Skull and dentition

Both skulls have a similar condition of preservation, with their left side more complete than the right one. The occipital, parietal and part of the frontal area are missing in the two skulls (Figure 2).

In lateral view (Figure 2(A),(B)), the zygomatic arch shows an evident development (much more than that seen in *Doedicurus clavicaudatus* and *Doedicurus* sp.), with a notable dorso-ventral diameter. The dorsal margin describes a concavity, much more marked than that observed in *Doedicurus clavicaudatus*, and similar to *Doedicurus* sp. The orbital notch is clearly subelliptical, with its major axis dorso-ventrally oriented. This is different from that observed in *Doedicurus clavicaudatus* and *Doedicurus* sp., in which the orbital notch is subcircular. The posterior margin is remarkably vertical, delimiting an angle of ca. 90° with respect to the palatal plane; in most Glyptodontidae the formed angle is always larger than ca. 90°. Like in *Doedicurus*, the ventral margin of the orbital notch shows a prominent bony crest, but in cf. *Eleutherocercus antiquus* it is more developed. The rostral area behind the zygomatic arch is ventrally inclined, being relatively similar to that of *Doedicurus* sp. and *Panochthus*, and different from that of *Glyptodon* and *Doedicurus clavicaudatus*.

In the frontal view (Figure 2(C),(D)), the nares are morphologically different from those of *Doedicurus clavicaudatus*, and more similar to those of *Doedicurus* sp. *Plohophorus figuratus* and *Eosclerocalyptus tapinocephalus* (Cabrera, 1939). Like in *Doedicurus* sp. and *Plohophorus figuratus*, in cf. *Eleutherocercus antiquus* the transverse diameter is larger than the dorso-ventral one, with convex lateral margins. This contrasts with that observed in *Doedicurus clavicaudatus*, in which the nares have a larger dorso-ventral diameter than the transverse one, and the lateral margins are almost straight, acquiring a subrectangular contour. Like in *Doedicurus clavicaudatus* and *Doedicurus* sp., along the dorso-ventral axis of the nares, it is possible to observe a well-developed *septum nasi*. The ventral margin of the orbital notch presents a strong bony crest, comparable to that of *Doedicurus clavicaudatus*, but more developed. The descending process of the maxillae is similar in morphology to that of *Doedicurus*, but with a more evident transverse diameter.

In the dorsal view, the general morphology of the skull resembles that of *Doedicurus clavicaudatus* and *Doedicurus* sp., but including some noteworthy differences. Unlike that observed in *Doedicurus clavicaudatus*, the rostral region located in front of the orbital notch is much less antero-posteriorly extended, delimiting a subrectangular contour. In contrast, in *Doedicurus clavicaudatus* and *Doedicurus* sp., this region is more extended, acquiring a subtriangular contour, similar to that seen in *Panochthus tuberculatus* and *Plohophorus figuratus*. Like in *Doedicurus*, the orbital notch is posteriorly closed by a strong postorbital bar.

In the occlusal view (Figure 2(E),(F)), the most notable characters include an evident enlargement of the transverse diameter of the palate at the level of Mf1, like in *Doedicurus clavicaudatus* and *Doedicurus* sp. This particular condition has not been observed in any other Glyptodontidae and may thus represent a potential synapomorphy for Doedicurinae. In the skull (Xen 34), the tooth series is not well preserved, but MMP 4860

preserves the Mf1–Mf4 and the Mf6 of the right side, and the Mf2–Mf6 of the left side. The Mf1 is subelliptical, without lobation, showing a similar morphology than in *Doedicurus*. One striking character in both taxa is the relationship of dimension between the first two molariforms. The antero-posterior diameter of the Mf1 represents <50% of the same diameter of Mf2. The Mf2 is bilobed and has its major axis parallel to the longitudinal axis of the tooth series, whereas in *Doedicurus* this molariform shows a high degree of lobation, with three lobes. The Mf3 is morphologically similar to that of *Doedicurus*, but in cf. *Eleutherocercus antiquus* the anterior margin of the first lobe is more rounded. The Mf4–Mf6 are very similar to those of *Doedicurus clavicaudatus* and *Doedicurus* sp., in which it is possible to observe a concavity in the labial half of the posterior margin of the third lobe. In cf. *Eleutherocercus antiquus*, this structure presents but less developed. Another character shared with *Doedicurus* is the presence of two large foramina with an anterior channel in the palate, located at the level of the limit between the Mf3 and the Mf4. In this area, the palate shows its minimum transverse diameter.

3.1.2   Hemimandible

It corresponds to a little fragment of right hemimandible, preserving the m6 and the m7. The molariforms are clearly trilobed and morphologically very similar to those of *Doedicurus clavicaudatus* and *Doedicurus* sp.

3.1.3   Osteoderms

The exposed surface of the osteoderms is completely smooth with large foramina, a character only observable in Doedicurinae (Figure 3B). Like in *Eleutherocercus antiquus* and the holotype of *P? chapadmalensis*, the central area of the osteoderms is slightly convex, and the largest foramina are located surrounding this area, although not so evident than that observed in *Doedicurus clavicaudatus*. This is different to than seen in *Plaxhaplous*, in which the foramina are distributed on the entire exposed surface of the osteoderms. Unlike *Doedicurus clavicaudatus*, most of the foramina do not cross the entire thickness of the osteoderms. Like that observed in *Eleutherocercus antiquus*, the larger foramina are in the numbers of 4–9. A large fragment composed of 16 associated osteoderms, corresponding to the posterior area of the dorsal carapace (Figure 3(A)), shows a very similar morphology compared with the holotype of *Eleutherocercus antiquus*. In both materials, the central areas of the osteoderms are clearly elevated with respect to the lateral areas, delimiting a depressed region with a dorso-ventral direction.

3.2   *Phylogenetic affinities of cf.* Eleutherocercus antiquus

The cladistic analysis yielded one most parsimonious tree (L: 37; RI 0.981; CI 0.973) (Figure 4), with a topology showing two large clades (for more details, see Zurita, González-Ruiz, et al. 2013; Zurita, Taglioretti, et al. 2013). One (A) included the Glyptodontidae Glyptodontinae, a diverse clade probably originated in tropical environments of South America (see Zurita, González-Ruiz, et al. 2013), as well as other lineages of Cingulata, particularly the Dasypodidae Dasypodini (Carlini et al. 2013).
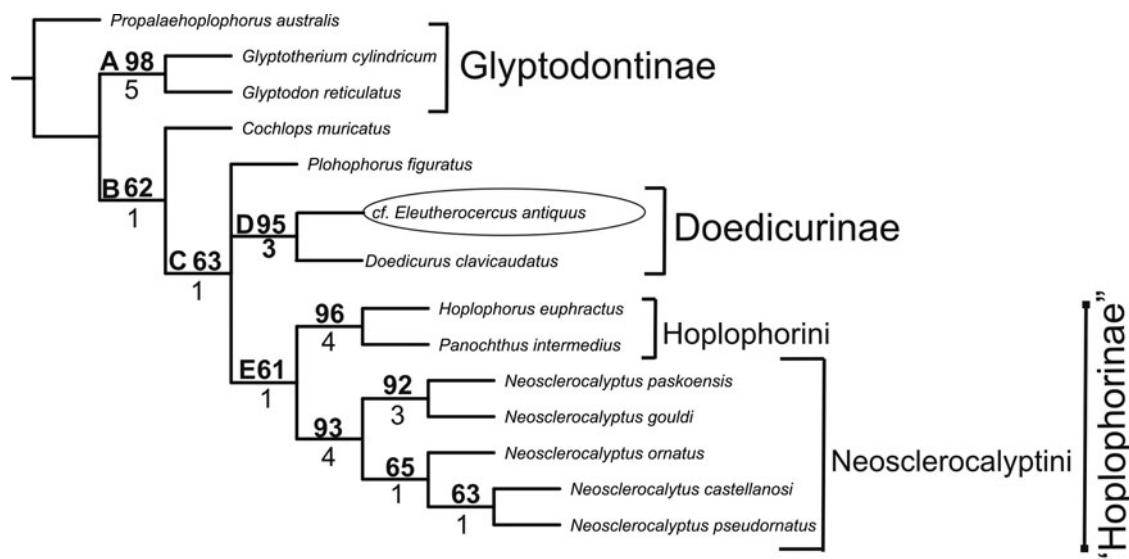

Figure 4.   MPT resulting from the cladistic analysis of Glyptodontidae (Tree length (TL): 37; Retention Index (RI): 0.981; Consistency Index (CI): 0.973). Capital letters indicate nodes discussed in the text. The numbers above each node represent bootstrap values; numbers in bold show relative Bhremer support.

The other node (B) is formed by the remaining Glyptodontidae, whose oldest records correspond to *Cochlops muricatus* (Santa Cruz Formation, Santacrucian Age). The main synapomorphy of this clade corresponds to a well-developed caudal tube (25:1), as originally postulated by Ameghino (1889). Within this clade, there is a basal polytomy among *Plohophorus figuratus*, Doedicurinae (D) and the remaining Glyptodontidae (E). As mentioned, the node D clusters the Doedicurinae (*Doedicurus clavicaudatus* + cf. *Eleutherocercus antiquus* + *E. antiquus*). This is represented by a polytomy, only supported by a single unambiguous synapomorphy (20:2) and a low value of Boostrap (41) and Bhremer support (1). This problem is mainly due to the missing data of the material type of *Eleutherocercus antiquus* (MLP 16-55), known only by a partial dorsal carapace and caudal tube. When this species is removed from the analysis, Doedicurinae (*Doedicurus clavicaudatus* + cf. *Eleutherocercus antiquus*) becomes a well-supported clade, with four unambiguous synapomorphies: 14:1 (transversal length of Mf1 equal to the distance between Mf1 and Mf4), 15:1 (length of Mf1 smaller than 50% of the antero-posterior diameter of Mf2), 16:1 (palate with proximal and distal margins expanded) and 20: 2 (exposed surface of the osteoderms of the dorsal carapace smooth with large foramina), and a higher value of Boostrap (95) and Bhremer support (3) (Figure 4).

As observed, the subfamily Doedicurinae forms part of a large clade whose oldest records correspond to southern areas of South America.

4. Discussion and conclusions

As mentioned, approximately 9 genera and 20 species have been traditionally included within Doedicurinae (late Miocene–early Holocene; see Castellanos 1940; Soibelzon et al. 2012). However, most of the species have been recognised only on the basis of caudal tubes (~60%), followed by species characterised by isolated osteoderms or partial carapaces (~19%) and partial carapaces + partial caudal tubes (~9%). Only two species include complete or almost complete specimens (~9%). Undoubtedly, the real diversity of this group is overestimated and a taxonomic revision with modern taxonomic criteria is needed.

The last taxonomic revision of Doedicurinae corresponds to Castellanos (1940). In the Monte Hermoso Formation (early Pliocene), this author recognised the presence of three taxa (*Eleutherocercus antiquus*, *Palaeodaedicurus antiquus* and *Palaeodaedicurus antiquus dubius*) of which only *Eleuterocercus antiquus* is well characterised on the basis of a dorsal carapace and caudal tube (see Ameghino 1887b; Lydekker 1895) and restricted to the Montehermosan Stage (early Pliocene). It cannot

rule out the possibility that these species represent in fact the same taxon.

In this scenario in the Chapadmalal Formation (late Pliocene), the only species corresponds to '*Doedicurus*' *chapadmalensis*, recognised by Ameghino (1908) on the basis of four osteoderms of the dorsal carapace. Some years later, Castellanos (1927, 1940) tentatively included this species in the genus *Palaeodaedicurus* (*Palaeodaedicurus? chapadmalensis*), although none of the known species of this genus included osteoderms. The stratigraphic range of this species is limited to Chapadmalal Formation.

A taxonomic revision of Tertiary Doedicurinae is beyond the scope of this work and will be treated in a future contribution, but a preliminary comparison among the material studied in this contribution and the type materials of *Eleutherocercus antiquus* (MLP 16-55) and *Palaeodaedicurus? chapadmalensis* (MACN Pv 6289) suggest a similar morphology at the level of the exposed surface of the osteoderms of the dorsal carapace. This similitude is especially evident when comparing with *Eleutherocercus antiquus* because the osteoderms of *P? chapadmalensis* are not well preserved. In fact, the hypothesis that both species (*Eleutherocercus antiquus* and *Palaeodoedicurus*? *chapadmalensis*) are synonyms cannot be discarded, but a more integral revision is needed. If this is the case, *P? chapadmalensis* must be considered as a junior synonym of *Eleutherocercus antiquus*. The fact that the materials studied in this contribution (late Pliocene) and the holotype of *Eleutherocercus antiquus* (early Pliocene) show a different chronostratigraphic record precludes a precise taxonomic assignation.

Prior to this contribution, no Neogene skulls belonging to Doedicurinae were known, being limited to the Pleistocene *Doedicurus clavicaudatus* and *Doedicurus* sp. The comparative and cladistic study carried out in the present contribution allowed recognising, for the first time, some potential synapomorphies at skull level in this group. In the cladistic analysis, cf. *Eleutherocercus antiquus* conforms a cluster with *Doedicurus clavicaudatus*, a condition supported by three unambiguous synapomorphies. One (14:1) corresponds to a particular morphology of the Mf1 when compared with the rest of molariforms (Mf2–Mf8), whereas the other is represented by a notable transversal enlargement of the distal part of the palate at the level of Mf1 (15:1), and the last (16:1) is related to a particular morphology of the palate.

From a chrono-stratigraphic perspective, the presence of cf. *Eleutherocercus antiquus* in the Chapadmalalan Formation (stratotype for the Upper Chapadmalalan Age; Cione and Tonni 2005; Cione et al. 2007) suggests that the biochron of *Eleutherocercus antiquus* could include the Montehermosan (ca. 5–4.5 Ma; Tomassini et al. 2013)–Chapadmalalan interval (ca. 4.5–3.2 Ma; Zárate, 2005), as observed in other taxa (see Rasia and Candela 2013;

Taglioretti et al., 2014). In turn, the presence of cf. *Eleutherocercus antiquus* in the El Polvorín Formation provides evidence that partially demonstrate its relationship with the Chapadmalal Formation (Kraglievich 1952) and the Chapadmalalan Age.

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Appendix 1. List of character and character states used in the cladistic analysis

Characters 1–13 and 21–29 are reproduced or modified from Zurita, González-Ruiz, et al. (2013) and Zurita, Taglioretti, et al. (2013).

(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 the dorsal view on sagittal plane: (0) representing < 10% of the total length of the skull; (1) representing > 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 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 the 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 the 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 the lateral view: (0) absent; (1) present.

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

(13) Morphology of Mf1/mf1: (0) lobes absent or limited to a single margin; (1) labial and lingual margins with lobes (= fully lingually and labially trilobated).

(14) Transverse diameter of the palate at the level of Mf1: (0) equal to the antero-posterior diameter occupied by the Mf1–Mf3; (1) equal to the antero-posterior diameter occupied by the Mf1–Mf4.

(15) Antero-posterior diameter of Mf1: (0) $>50\%$ of the antero-posterior diameter of Mf2; (1) $<50\%$ of the antero-posterior diameter of Mf2.

(16) Morphology of the palate: (0) with a transverse expansion absent or limited to one margin; (1) with a transverse expansion in its distal and proximal margins.

(17) Cephalic armour: (0) subtriangular contour; (1) subrectangular contour.

(18) 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.

(19) Presence of a dorsal carapace low and elongated, subcylindrical, dorsal outline almost straight: (0) absent; (1) present.

(20) Pattern of ornamentation 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) smooth with large foramina.

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

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

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

(24) Pattern ornamentation of the dorsal carapace and the caudal tube: (0) similar ornamentation pattern; (1) different ornamentation pattern.

(25) Morphology of the caudal armour: (0) composed of caudal rings representing $>90\%$ of the total length; (1) composed of caudal rings plus caudal tube representing $<40\%$ of the total length of the caudal armour.

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

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

(28) Exposed surface of the distal row of osteoderms of the caudal armour modified into 'spine-like' structure: (0) absent; (1) present.

(29) Length of the caudal tube versus length of the caudal rings: (0) caudal tube shorter than the caudal rings; (1) caudal tube longer than the caudal rings.

Appendix 2. Character–taxon matrix used in the cladistic analysis

Taxon	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
Propalaehoplophorus australis	0	0	–	0	–	0	0	0	–	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Neosclerocalyptus pseudornatus	1	2	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1
Neosclerocalyptus ornatus	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1
Neosclerocalyptus gouldi	1	1	1	2	1	0	1	1	1	0	0	0	0	0	0	0	0	1	?	?	0	0	?	0	?	?	?	?	?
Neosclerocalyptus paskoensis	1	1	1	2	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1
Glyptodon reticulatus	0	0	–	0	–	0	0	0	–	2	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0
Doedicurus clavicaudatus	0	0	–	0	–	0	0	0	–	2	0	0	0	0	1	1	1	0	0	2	–	0	0	1	1	3	0	0	1
Plohophorus figuratus	0	0	–	0	–	0	0	0	–	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	1
Panochthus intermedius	0	0	–	0	–	0	0	0	–	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	2	1	0	1
Hoplophorus euphractus	0	0	–	0	–	0	0	0	–	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	1
Glyptotherium cylindricum	0	0	–	0	–	0	0	0	–	2	0	0	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0
Neosclerocalyptus gouldi	1	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	?	?	?	?	?	0	?	?
Cochlops muricatus	0	0	–	0	–	0	0	0	–	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Cf. *Eleutherocercus antiquus*	0	0	–	0	–	0	0	0	–	2	?	0	0	0	1	1	1	?	?	2	–	?	?	?	?	?	?	?	?
Eleutherocercus antiquus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	–	?	?	1	1	3	0	0	1

Note: ?, missing data.