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ORIGINAL PAPER

A New Glyptodont (Xenarthra: Cingulata) from the Late Miocene of Argentina: New Clues About the Oldest Extra-Patagonian Radiation in Southern South America

Daniel Barasoain[1] · **Alfredo E. Zurita**[1] · **Darin A. Croft**[2] · **Claudia I. Montalvo**[3] · **Víctor H. Contreras**[4] · **Ángel R. Miño-Boilini**[1] · **Rodrigo L. Tomassini**[5]

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Abstract

Glyptodonts (Xenarthra, Cingulata) are one of the most amazing Cenozoic South American mammals, with some terminal forms reaching ca. two tons. The Paleogene record of glyptodonts is still poorly known, although some of their diversification is observable in Patagonian Argentina. Since the early and middle Miocene (ca. 19–13 Ma), two large clades can be recognized in South America. One probably has a northern origin (Glyptodontinae), while the other one, called the "austral clade", is interpreted to have had an austral origin, with the oldest records represented by the "Propalaehoplophorinae" from the late early Miocene of Patagonian Argentina. In this scenario, the extra-Patagonian radiations are still poorly known, despite their importance for understanding the late Miocene and Pliocene diversity. Here, we carry out a comprehensive revision of late Miocene (Chasicoan Stage/Age) glyptodonts of central Argentina (Buenos Aires and San Juan provinces). Our results show that, contrary to what is traditionally assumed, it was a period of very low diversity, with only one species recognized in this region, *Kelenkura castroi* gen et sp. nov. Our phylogenetic analysis shows that this species represents the sister taxon of the remaining species of the "austral clade", representing the first branch of the extra-Patagonian radiation. Additionally, *K. castroi* is the first taxon showing a "fully modern" morphology of the caudal tube.

Keywords Caudal tube · Diversity · Evolution · Glyptodonts · Neogene · Taxonomy

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✉ Daniel Barasoain
danielbarasoain@gmail.com

Alfredo E. Zurita
aezurita74@yahoo.com.ar

Darin A. Croft
dcroft@case.edu

Claudia I. Montalvo
cmontalvolp@yahoo.com.ar

Víctor H. Contreras
vcontre@unsj-cuim.edu.ar

Rodrigo L. Tomassini
rodrigo.tomassini@yahoo.com.ar

[1] Laboratorio de Evolución de Vertebrados y Ambientes Cenozoicos, Centro de Ecología Aplicada del Litoral (UNNE-CONICET) y Cátedra de Paleontología de Vertebrados, Facultad de Ciencias Exactas, Naturales y Agrimensura, Universidad Nacional del Nordeste, RP5 3400 Corrientes, Argentina

[2] Department of Anatomy, Case Western Reserve University School of Medicine, 10900 Euclid Ave, Cleveland, OH 44106-4930, USA

[3] Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Avenida Uruguay 151, 6300 Santa Rosa, Argentina

[4] Facultad de Ciencias Exactas, Físicas y Naturales, Instituto de Geología Dr. Emiliano P. Aparicio, Departamentos Geología y Biología, Universidad Nacional de San Juan, Avenida Ignacio de La Rosa y Calle Meglioli, Rivadavia 5400 San Juan, Argentina

[5] INGEOSUR, Departamento de Geología, Universidad Nacional del Sur-CONICET, Avenida Alem 1253, 8000 Bahía Blanca, Argentina

Introduction

Xenarthra is an endemic and relictual clade of eutherian mammals from South America (O´Leary et al. 2013; Gaudin and Croft 2015; Foley et al. 2016). Fossil remains of this peculiar clade are known since the early Eocene of Itaboraí basin, Brazil (Oliveira and Bergqvist 1998; Gelfo et al. 2009), although molecular evidence suggests the origin may be much older (ca. 100 Ma; O´Leary et al. 2013; Vizcaíno and Bargo 2014). The evolutionary history of xenarthrans was notably influenced by the "splendid isolation" of South America during most of the Cenozoic (Simpson 1980; Cione et al. 2015). Xenarthra includes two large orders, which are very different both morphologically and ecologically: Pilosa, including Folivora (sloths) and Vermilingua (anteaters), and Cingulata, the so-called "armored" xenarthrans (Delsuc et al. 2004, 2012; Gaudin and Croft 2015).

Fossil cingulates are represented by several lineages that played very diverse ecological roles during their long evolutionary history (Vizcaíno et al. 2012), including Peltephilidae, Dasypodidae, Pampatheriidae, "Palaeopeltidae", Pachyarmatheriidae, and Glyptodontidae (Gaudin and Croft 2015; Gibb et al. 2016; Fernicola et al. 2017). On the contrary, living cingulates are only represented by "armadillos," which are grouped in the families Dasypodidae and Chlamyphoridae (Gibb et al. 2016; Gaudin and Lyon 2017; Feijó et al. 2019; Barasoain et al. 2020).

Glyptodontidae is a clade comprising some of the most amazing and enigmatic armored herbivores that ever existed in America, with an evolutionary history that began in the late Eocene (Zurita et al. 2016) and continued until its extinction in the latest Pleistocene/early Holocene, along with many other megamammals (Cione et al. 2015; Politis et al. 2019). This group includes medium to very large forms, some of them approaching *ca*. two tons (i.e., *Doedicurus*; Vizcaíno et al. 2011; Soibelzon et al. 2012). Records of Pliocene and Pleistocene Glyptodontidae extend into Central and North America, demonstrating that the group successfully participated in the Great American Biotic Interchange (Woodburne 2010; Gillette et al. 2016; Zurita et al. 2018).

Paleogene records of glyptodonts are scarce and mainly limited to isolated osteoderms, providing little evidence of this early period (Gaudin and Croft 2015; Zurita et al. 2016). However, during the early and middle Miocene, glyptodonts became notably more abundant, especially in lower and higher latitudes of South America (Croft et al. 2007; Carlini and Zurita 2010; González-Ruiz 2010; Zurita et al. 2013; Gaudin and Croft 2015). In this context, the most recent phylogenetic proposals suggest the existence of two large clades within Glyptodontidae. One of them, Glyptodontinae, probably originated in northern South America and includes the genera *Glyptodon*, *Glyptotherium*, and *Boreostemma*. The other one, not formally named but called the "austral clade", is interpreted to have had an austral origin, with the oldest records represented by late early Miocene members of the "Propalaehoplophorinae" (sensu Hoffstetter 1958, Paula Couto 1979, and others) of Patagonian Argentina. Representatives of the "austral clade" (except *Propalaehoplophorus* and *Eucinepeltus*) are characterized by a remarkable synapomorphy: the presence of a caudal tube, a structure unique among mammals (see Cuadrelli et al. 2020).

According to the fossil evidence, the "Propalaehoplophorinae" achieved a remarkable diversification in Patagonia during the early and middle Miocene, with records of several genera and species (González-Ruiz 2010; Vizcaíno et al. 2012). During the middle to late Miocene, this group was replaced by the scarcely known "Palaehoplophorini" (Scillato-Yané and Carlini 1998; González-Ruiz et al. 2017). In this scenario, a key point to understand the subsequent evolutionary history of the "austral clade" lies in the study of late Miocene fauna, particularly those assigned to the Chasicoan Stage/Age (Tortonian). However, despite the importance of this interval, there is a lack of taxonomic, anatomical, and phylogenetical revisions. Old general faunal lists indicate a wide diversity of Chasicoan glyptodonts (i.e., "Sclerocalyptinae", Palaehoplophorini, Hoplophorinae), particularly for the type locality of this stage/age (Arroyo Chasicó locality, Buenos Aires Province, Argentina), but without accurate taxonomic identification (see Bondesio et al. 1980; Fidalgo et al. 1987; Oliva 2016). On the contrary, new preliminary contributions (Barasoain et al. 2019, 2021) suggest that glyptodonts from this lapse are represented by a single morphotype for both the dorsal carapace and caudal tube.

We provide here the first comprehensive review of the Glyptodontidae from the Chasicoan Stage/Age (late Miocene). In this context, the aims of this work are to: (1) describe a new genus and species of glyptodont, including a detailed anatomical characterization; (2) include for the first time the representatives from this interval (as well as the "Palaehoplophorini") in a morphological phylogenetic analysis, in order to verify their relationships with respect to ancient and modern faunas; and (3) discuss the origin and evolution of the caudal tube.

Historical Background of Chasicoan Glyptodonts

In recent years, the study of Neogene glyptodonts from Argentina has increased notably (González Ruiz 2010; Zurita et al. 2016, 2017a; Quiñones et al. 2020). However, in this context, little is known about the late Miocene diversity, particularly for the Chasicoan Stage/Age.

Arroyo Chasicó is a classic fossiliferous site of South America, located in the lower reaches of the Chasicó Creek (Buenos Aires Province), with a remarkable abundance and diversity of continental vertebrates (Cabrera and Kraglievich 1931; Bondesio et al. 1980; Croft 2016). It constitutes the type locality of the Arroyo Chasicó Formation (Pascual 1961). The temporal span of this unit at this locality has been estimated from ca. 9.43 to 8.8 Ma, based on an Ar^{40}/Ar^{39} radioisotopic date from volcanic glass (9.23 ± 0.09 Ma) and high-resolution magnetostratigraphic profiles (Zárate et al. 2007). However, this lower limit is based on the age of the C4Ar.2r/C4Ar.2n boundary, which has been revised to 9.647 Ma (Ogg 2020). From a biostratigraphical viewpoint, the faunal assemblage from the Arroyo Chasicó Formation has been used as the basis for the definition of the Chasicoan Stage/Age (Cione and Tonni 2005; Tomassini et al. 2017).

The earliest references to vertebrate remains from this site, including glyptodonts, were those of Santiago Roth in the early 1920s (see Torres 1926). The earliest taxonomic contributions correspond to Cabrera (1928), Cabrera and Kraglievich (1931), Pascual (1961), and Pascual and Bondesio (1968), but none of them focused on glyptodonts. Subsequent studies provided more complete faunal lists and comparisons, in most cases including glyptodonts identified at subfamily or tribe level. It is remarkable that there is no relationship between the diversity mentioned by the different authors; the number of identified taxa varies from one to thirteen, including *Palaehoplophorus* (Pascual 1965) and several representatives of Palaehoplophorini, Plohophorini, and “Sclerocalyptinae” (Fidalgo et al. 1978, 1987; Bondesio et al. 1980) that were interpreted as new genera and species (see Bondesio et al. 1980). Taxonomic assignments in these works were based on isolated osteoderms and small fragments of dorsal carapace and caudal tubes.

In a preliminary contribution, Aramayo and Di Martino (1993) briefly described three complete caudal tubes from Arroyo Chasicó (MMH-CH-83–3-138, MMH-CH-83–3-139, and MMH-CH-87–6-1) and mentioned that the specimen MMH-CH-83–3-139 shows similarities with *Plohophoroides*. We could not find these specimens and, therefore, they were not included in our study.

Zurita and Aramayo (2007) described in detail a very complete specimen (PV-UNS-260; holotype of the new taxon proposed here) and referred it to *Eosclerocalyptus tapinocephalus*. Although the authors assigned this specimen to the Huayquerian Stage/Age (Tortonian-Messinian), it should be noted that recent fieldwork performed in the lower reaches of the Chasicó Creek indicate that faunal assemblages from the different levels of the Arroyo Chasicó Formation correspond to the Chasicoan Stage/Age (Tomassini, personal observation).

In a preliminary analysis of the glyptodont diversity of the Arroyo Chasicó Formation, Oliva (2016, 2017) analysed several dorsal carapace fragments and caudal tubes (MMH-CH 83–03-138, MMH-CH 83–03-139, MMH-CH 83–03-140, MMH-CH 83–03-141, MMH-CH 88–06-57, and MMP-M 984). This author suggested the presence of a new species of *Hoplophractus* and other undetermined Neosclerocalyptini. Some of these materials were included in the present study, while others could not be located.

Other preliminary studies performed by Barasoain et al. (2019, 2021) proposed that Chasicoan glyptodonts are represented by a single morphotype, characterized by dorsal carapace osteoderms with a “rosette” ornamentation pattern and scarce development of additional figures in both osteoderms and caudal tubes. This interpretation contrasts markedly with the high diversity proposed in previous works.

Discoveries of Chasicoan glyptodont remains from other sites of Argentina were also reported in recent years. Montalvo et al. (2019) mentioned the presence of indeterminate glyptodont remains in levels of the Cerro Azul Formation that crop out at the Cerro La Bota site, La Pampa Province. Contreras and Baraldo (2011) indicated the presence of ?*Palaehoplophorus* and ?*Hoplophractus*, but without more details, in levels of the Limolita La Colmena Member of the Loma de Las Tapias Formation (ca. 9–7.8 Ma) that crop out at the Loma de Las Tapias site, San Juan Province. Some of these remains were also included in the present study. A large diversity of glyptodonts has traditionally been recognized since the XIX century for the “Mesopotamian” levels of the Ituzaingó Formation that crop out in Entre Ríos Province. However, all of these taxa are based on very fragmentary specimens lacking diagnostic characters (see Scillato-Yané et al. 2013), and the assemblages recovered possibly include a mixture of Chasicoan and Huayquerian taxa (see Brandoni 2013; Schmidt et al. 2020). Finally, there are some mentions of glyptodonts, represented by scarce and fragmentary remains, for northwestern Argentina, from the lower levels of the Chiquimil Formation (ca. 9.14 to 3.54 Ma; Esteban et al. 2014) in Catamarca Province (Esteban et al. 2019) and the Palo Pintado Formation (ca. 10 to 5 Ma; Galli et al. 2011) in Salta Province (Díaz et al. 1986; Starck and Anzótegui 2001; Zimicz et al. 2018).

Material and Methods

This work includes the analysis of glyptodont remains coming from two sites of central Argentina (Fig. 1), which include deposits that have been referred to the Chasicoan Stage/Age: Arroyo Chasicó (Arroyo Chasicó Formation, Buenos Aires Province; type locality of the Chasicoan Stage/Age) and Loma de Las Tapias (Loma de Las Tapias Formation, San Juan Province). These sites include the most complete specimens known for this interval, such as the holotype

Fig. 1 Map of southern South América. Stars indicate late Miocene formations of Argentina with sediments corresponding to the Chasicoan Age/Stage. 1. Arroyo Chasicó Formation (Buenos Aires Province); 2. Loma de Las Tapias Formation (Juan Province); 3. Cerro Azul Formation (La Pampa Province); 4. Chiquimil Formation (Catamarca Province); 5. Palo Pintado Formation (Salta Province); 6. Ituzaingó Formation (Entre Ríos Province)

and material referred to the new taxon here proposed, as well as other specimens that could not be identified at a specific level (Online Resource 1). Other Chasicoan deposits from different sites of Argentina (i.e., Cerro Azul Formation of La Pampa Province, Chiquimil Formation of Catamarca Province, Palo Pintado Formation of Salta Province, and Ituzaingó Formation—“Mesopotamiense”—of Entre Ríos Province) only include scarce and/or fragmentary remains, mainly represented by isolated osteoderms; however, these records were also considered in this study in order to give a complete scenario of the diversity in southern South America.

The biostratigraphic scheme used, including regional stages/ages, SALMAs (South American Land Mammal Ages), and international stages vary according to the age and locality considered. The general systematic scheme partially follows McKenna and Bell (1997), Fernicola (2008), Gaudin and Lyon (2017), and Cuadrelli et al. (2020). The terminology adopted for descriptions and comparisons follows: Krmpotic et al. (2009) and Porpino et al. (2014) for the dorsal carapace, caudal armor, and osteoderms; Cuadrelli et al. (2019) for appendicular and cranial elements; and González Ruiz et al. (2015) for molariforms. Materials used for comparisons are listed in Online Resource 1. All anatomical measurements were obtained using a 0.02 mm resolution digital caliper. Body mass was estimated following the methodology proposed by Scott (1990), using the equation “log mass = 3.4855 * log F1 – 2.9112”, in which F1 equals femoral length. Although this equation was developed based on modern terrestrial artiodactyls (Scott 1990), it has been used previously to estimate body mass in glyptodonts (see Fariña 1995; Fariña et al. 1998).

Institutional Abbreviations

MMH-CH, Museo Municipal de Ciencias Naturales “Vicente Di Martino”, Colección Arroyo Chasicó, Monte Hermoso (Buenos Aires Province, Argentina); **PVSJ,** Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan (San Juan Province, Argentina); **PV-UNS,** Departamento de Geología, Universidad Nacional del Sur, Paleontología de Vertebrados, Bahía Blanca (Buenos Aires Province, Argentina).

Genus Abbreviations

B, *Boreostemma*; ***C,*** *Cochlops*; ***D,*** *Doedicurus*; ***El,*** *Eleutherocercus*; ***Eo,*** *Eosclerocalyptus*; ***Eu,*** *Eucinepeltus*; ***G,*** *Glyptodon*; ***Gl,*** *Glyptotherium*; ***H,*** *Hoplophorus*; ***K,*** *Kelenkura*; ***N,*** *Neosclerocalyptus*; ***P,*** *Panochthus*; ***Pa,*** *Palaehoplophorus*; ***Pal,*** *Palaehoplophoroides*; ***Par,*** *Parapropalaehoplophorus*; ***Pl,*** *Plohophorus*; ***Pr,*** *Propalaehoplophorus*; ***Pro,*** *Propanochthus*; ***Ps,*** *Pseudohoplophorus*.

Phylogenetic Analysis

We carried out a morphological cladistic analysis in order to determine the phylogenetic relationships of Chasicoan glyptodonts. Character coding was mainly obtained from the two most complete specimens, PV-UNS 260 (holotype of the new taxon proposed here; Arroyo Chasicó Formation, Arroyo Chasicó locality) and PVSJ 366 (Loma de Las Tapias Formation, Loma de las Tapias locality), though other specimens were also considered.

The developed matrix included a total of 28 taxa and 56 characters of the cranium, mandible, and molariforms (#1–16), appendicular skeleton (femur and autopodial elements; #17–19), cephalic shield and dorsal carapace (general morphology and osteoderms; #20–43), and caudal armor (caudal rings and caudal tube; #44–56); 37 of these characters are binary, and the other 19 are multistate (treated as non-additive). Following the criterion of Gaudin (2004), all characters were given equal weight (1.0) and considered unordered. Of the total of characters considered, 42 were selected or modified from Cuadrelli et al. (2020); the other 14 were newly defined in this work (see Online Resource 2). The matrix was built using the software Mesquite 3.04 (Maddison and Maddison 2008). Characters corresponding to structures not preserved were coded as "?", while non-codable characters were coded as "-" (Online Resource 3 and 4).

The armadillo *Euphractus sexcinctus* and the pampatheriid *Pampatherium humboldtii* were used as outgroups to root the phylogenetic trees due to their phylogenetic proximity to Glyptodontidae. The ingroup included the new taxon described in this work plus the following 25 species, which represent the best-known glyptodonts: *Boreostemma venezolensis*, *B. acostae*, *Glyptotherium cylindricum*, *Gl. texanum*, *Glyptodon reticulatus*, *G. munizi*, *G. jatunkhirkhi*, *Propalaehoplophorus australis*, *Eucinepeltus petestatus*, *Cochlops muricatus*, *Palaehoplophorus meridionalis*, *Palaehoplophoroides rothi*, *Eosclerocalyptus proximus*, *Plohophorus figuratus*, *Pseudohoplophorus absolutus*, *Doedicurus clavicaudatus*, *Eleutherocercus solidus*, *El. antiquus*, *Neosclerocalyptus pseudornatus*, *N. ornatus*, *N. paskoensis*, *Hoplophorus euphractus*, *Propanochthus bullifer*, *Panochthus intermedius*, and *P. tuberculatus*.

Character-taxon evaluations were performed through the software TNT, via "implicit enumeration" following the maximum parsimony criterion, as proposed by Goloboff et al. (2008). Clade support values for each node were calculated through a 1000-replicate standard bootstrap via "traditional search" (Felsenstein 1985), jackknife resampling (Farris et al. 1996), and relative and absolute Bremer support (Bremer, 1994). Other obtained values included retention index (RI), consistency index (CI), and tree length (TL), following Goloboff and Farris (2001).

Systematic Palaeontology

Xenarthra Cope 1889
Cingulata Illiger 1811
Glyptodontidae Gray 1869
Kelenkura gen. nov.

Type species: *Kelenkura castroi* sp. nov.

Etymology: The generic name derives from the Mapudungun (Mapuche) word "*këlen*", meaning tail, and "*kura*", meaning rock, in reference to this taxon being the earliest to develop a "fully modern" caudal tube (completely fused and ornamented).

Geographic and stratigraphic occurrence: As for the type species (see below).

Diagnosis: The same as the species by monotypy.

Kelenkura castroi sp. nov.
Figs. 2–5.
Eosclerocalyptus tapinocephalus Zurita and Aramayo, 2007, p. 58, figs. 2–3 (in partim).

Etymology: The specific epithet is dedicated to Mr. D. Castro, who recovered the specimen PVSJ-366, one of the most complete referred materials.

Holotype: PV-UNS-260: a laterally compressed cranium missing the right zygomatic arch with a partially preserved dental series, atlas, partially complete dorsal carapace with many associated isolated osteoderms, complete first caudal ring and several caudal ring fragments, complete caudal tube, complete right femur, fragments of the left femur, distal fragment of left humerus, phalanges, metapodials, and other undetermined limb bone fragments.

Other Referred Materials (Hypodigm): MMH-CH-83–3-136, MMH-CH-88–3-135, MMH-CH-88–6-57, MMH-CH-w/cn, PVSJ-366, and PVSJ-477 (Online Resource 1). Although other materials reflect a single morphotype, they are not included in the hypodigm because the fragmentary nature of the remaining specimens observed prevents a precise taxonomic assignment (see below).

Type Locality and Age: Arroyo Chasicó locality (Epu Leufú site, 38° 31′ 54.20" S, 62° 58′ 54.50" W; 20 km SW of Berraondo train station; see Zurita and Aramayo 2007), Buenos Aires Province, Argentina. Arroyo Chasicó Formation, Chasicoan Stage/Age, (ca. 9.64 to 8.8 Ma, late Miocene).

Geographic and Stratigraphic Occurrence: Arroyo Chasicó locality, Arroyo Chasicó Formation (see above). Loma de Las Tapias locality (San Juan Province), Limolita La Colmena Member of the Loma de Las Tapias Formation (Chasicoan Stage/Age, ca. 9 Ma).

Diagnosis: Medium-size glyptodont, intermediate between *Propalaehoplophorus australis* and *Eosclerocalyptus proximus*, smaller than *Eleutherocercus*, and slightly larger than the glyptodontine *Boreostemma acostae*. Elongated cranium with an unusually narrow occipital area, very different from that of *Eleutherocercus solidus* and *El. antiquus*. Nasals anteriorly projected, without pneumatization. Sagittal crest slightly visible and very poorly developed compared to *Eosclerocalyptus*. Parietal-occipital area much more elevated in relation to the palatal level than in *Eosclerocalyptus tapinocephalus*. Elevated zygomatic arch, similar to that of *Eosclerocalyptus proximus* but much more gracile, particularly towards the posterior half. Infraorbital foramen positioned at the base of the anterior zygomatic process as occur in *Eosclerocalyptus proximus*, but unlike *Eosclerocalyptus tapinocephalus*. Femur with higher curvature than in *Eo. proximus*, but not as much as in *Propalaehoplophorus australis*, and similar to that of *Parapropalaehoplophorus septentrionalis*. Gracile third trochanter, more laterally expanded than in *Eosclerocalyptus*, resembling that of *Pr. australis*. Dorsal carapace with a convexity between that of *Glyptodon* and *Neosclerocalyptus*, similar to that of *Boreostemma acostae*, composed of ca. 35 transverse rows of osteoderms, more than in *Propalaehoplophorus* (ca. 25) and fewer than later-diverging taxa (i.e., *Eo. proximus* and *Neosclerocalyptus*, ca. 45–50). Ornamentation pattern of dorsal carapace osteoderms similar to that of *Eo. proximus* and *Neosclerocalyptus* (i.e., "rosette" ornamentation pattern), but with proportionally larger central figures and less developed peripheral figures. Caudal tube showing an almost "fully modern" anatomy (completely fused and ornamented), very different from the unornamented tubes of the Palaehoplophorini, but resembling the representatives of this group in having visible sutures in the proximal half represented by depressed areas between the caudal rings. Ornamentation pattern of the caudal tube variable according to the region, with the proximal half having elliptical central figures surrounded (but not completely) by poorly developed peripheral figures, and the distal half having similar central figures but few or absent associated peripheral figures.

Descriptions and Comparisons

Cranium

Descriptions are based on the combined observations from two fairly complete crania: the holotype PV-UNS-260 and PVSJ-366 (Fig. 2). Specimen PVSJ-366 is the more complete, although it lacks the molariform series. In the holotype, the dorsal portion is damaged, but the molariform series is partially preserved.

In dorsal view, the cranium is more elongated than in other glyptodonts (i.e., *Eosclerocalyptus*, *Neosclerocalyptus, Glyptodon*), with an anteroposterior length ~ 30% greater than the maximum width. Nasals are not laterally expanded, and there is no pneumatization, unlike *Neosclerocalyptus* and *Panochthus* spp. The rostral area is antero-posteriorly elongated and has a sub-rectangular outline, in contrast to *Eo. tapinocephalus*, *Pr. australis*, and *Eucinepeltus petesatus*, in which it is sub-triangular, but similar to *B. acostae* and *El. solidus*. The sagittal crest starts from the union of the supraoccipital nuchal crests and extends anteriorly to the middle of the frontals, where it bifurcates to join the postorbital process on each side, as in *Eosclerocalyptus*. The sagittal crest is poorly developed and barely noticeable, unlike the well-developed crest of *Eo. proximus* and *Plohophorus figuratus*. Along the parietal surface, there are many vascular foramina. A distinctive feature of *K. castroi* is that the occipital area is proportionally narrower than in the compared species. The cranium is narrowest at the postorbital area. The orbit has a sub-ellipsoid contour, as in *Pl. figuratus* and *Eo. tapinocephalus*, but not *Eo. proximus*, in which it is subcircular. Additionally, this contour is noticeably narrower than in the compared species due to less lateral expansion of the zygomatic arches.

In frontal view, the nasal aperture is heart-shaped, as occurs in *Eosclerocalyptus*, *Plohophorus*, and *Pseudohoplophorus*, but vertically narrower, as in older taxa such as *Pr. australis* and *Eu. petesatus*.

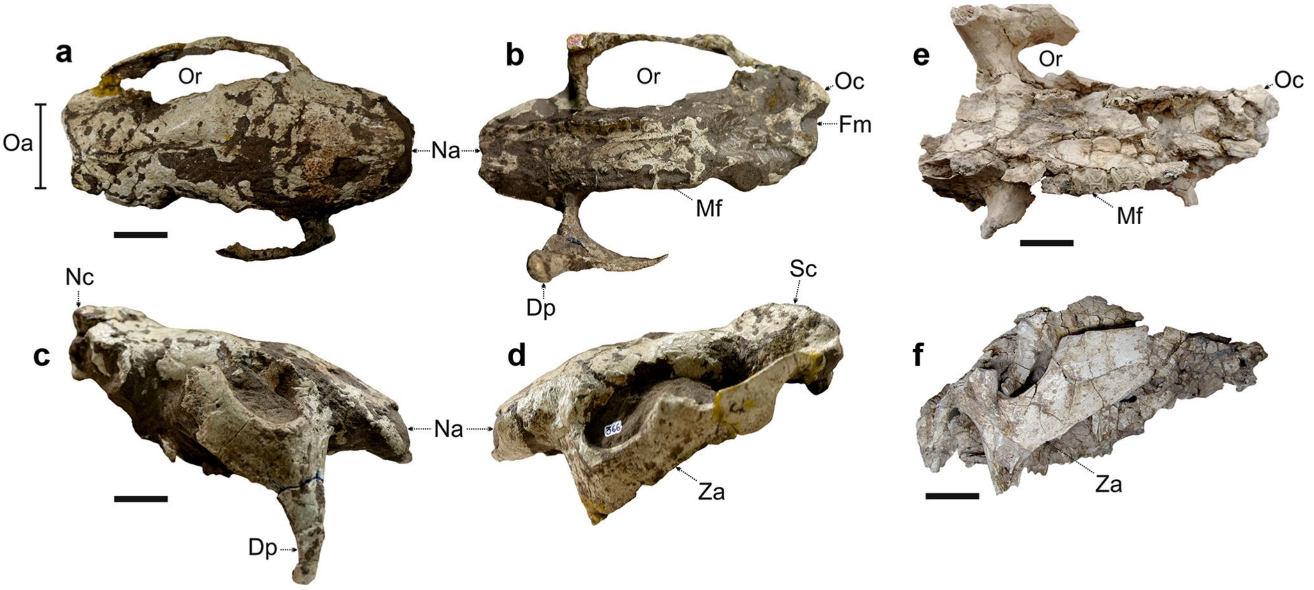

Fig. 2 Crania of *Kelenkura castroi*. Specimen PVSJ-366 in dorsal (**a**), ventral (**b**), right lateral (**c**), and left lateral (**d**) views. Specimen PV-UNS-260 (holotype) in ventral (**e**) and left lateral (**f**) views. Abbreviations: *Dp* descending process, *Fm* foramen magnum, *Mf* molariforms, *Na* nasal aperture, *Oa* occipital area, *Oc* occipital, *Or* orbit, *Sc* sagittal crest, *Za* zygomatic arc. Scale bars equal 5 cm

In lateral view, the parietal-occipital area is much more elevated in relation to the palatal level than the rest of the dorsal surface, as occurs in *Pl. figuratus*, *Pseudohoplophorus absolutus*, and *Eo. proximus*, but not in *Eo. tapinocephalus*. The zygomatic arches are elevated, as in *Eo. proximus*, but much more gracile, especially the posterior process. The descending process of the zygomatic is longer than in *Eosclerocalyptus* spp. It resembles that of *Plohophorus* and *Pseudoplohophorus* but is less compressed antero-posteriorly and terminates with a less-developed posterior curvature. The frontal area is flat, and the nasals are anteriorly projected and tilt slightly downwards, unlike in the compared species, in which the entire area is markedly inclined inferiorly.

The ventral region of the cranium is damaged in both specimens. In PVSJ-366, the dental series are not preserved, but the alveolus of right molariform 8 (Mf8) indicates a fully trilobed molariform. In the holotype, the left Mf7 and the right Mf4, Mf6, and Mf7 are preserved; all of them are trilobed, and they increase in size progressively towards the distal end of the toothrow. The alveolus of the Mf8 denotes a trilobed shape as in PVSJ-366. Molariforms 1–3 are lost from both series, and the contours of the alveoli cannot be distinguished. The infraorbital foramen is positioned at the base of the anterior zygomatic process, as in *Eo. proximus*, while it is more laterally placed in *Eo. tapinocephalus*, *Plohophorus*, and *Pseudoplohophorus*. The condylar width and the foramen magnum are proportionally narrower than in the compared species but show a similar morphology.

Appendicular Skeleton

Humerus The holotype PV-UNS-260 includes a right distal fragment of the humerus. It has a well-developed entepicondylar foramen, as in all non-glyptodontine glyptodonts. The entepicondyle is more laterally projected than in *Neosclerocalyptus*, resembling that of *Eo. proximus*.

Femur The holotype PV-UNS-260 includes a complete right femur (Fig. 3) plus some fragments of the left femur, while PVSJ-366 includes a proximal fragment of the left femur. The general morphology is intermediate between older taxa such as *Propalaehoplophorus australis* and *Parapropalaehoplophorus septentrionalis*, in which it is gracile and has a very curved diaphysis, and more modern taxa like *Eo. proximus* and *Neosclerocalyptus* species, in which it is more massive and robust and has a straighter diaphysis. Using the allometric equation of Scott (1990) and considering a femur length of 295 mm for PV-UNS-260, the body mass of *Kelenkura castroi* is estimated at ~ 160 kg.

The femoral head is proportionally larger than in *Pr. australis*, *Par. septentrionalis* and *Eosclerocalyptus* and more developed in an anteroposterior than in a transverse direction, as in *Neosclerocalyptus*. In proximal view, the articular surface is sub-triangular and very extended anteriorly. On the internal side, the lesser trochanter is located below the femoral head and extends to the middle of the diaphysis as a thin crest, as occurs in *Pr. australis* and *Par. septentrionalis*

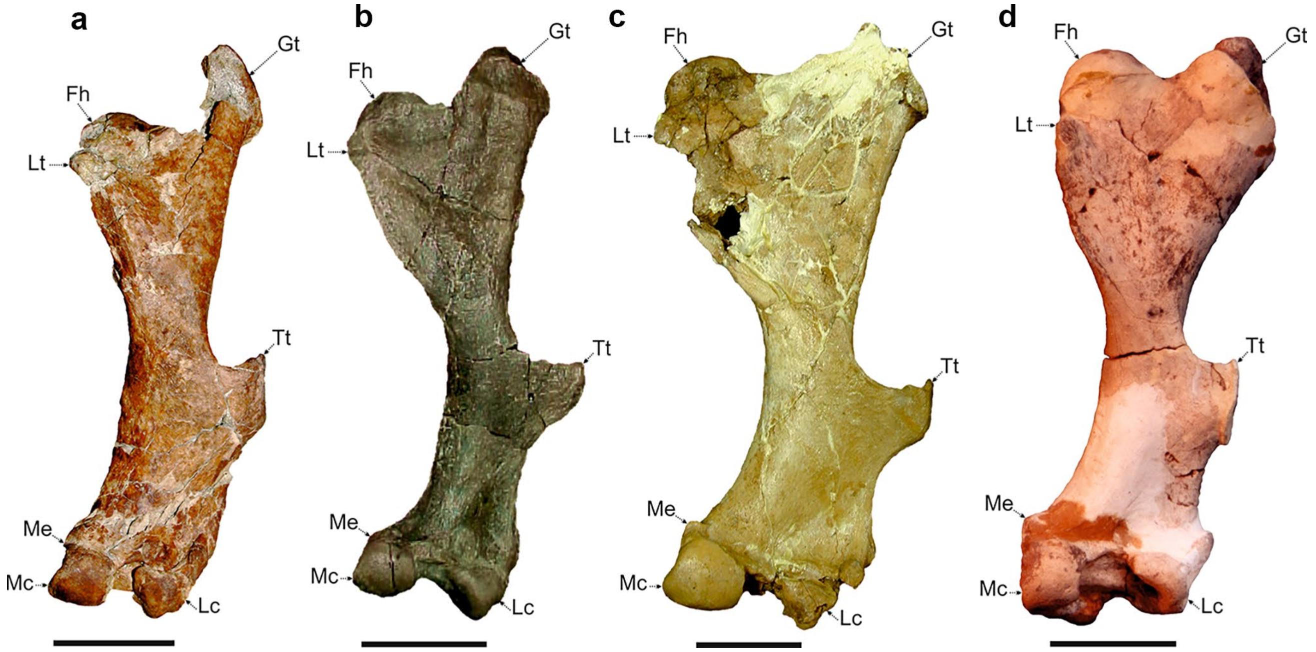

Fig. 3 Glyptodont right femora in posterior view: **a** *Parapropalaehoplophorus septentrionalis*; **b** *Propalaehoplophorus australis*; **c**. *Kelenkura castroi*; **d** *Eosclerocalyptus proximus*. Abbreviations: *Fh* femoral head, *Gt* greater trochanter, *Lc* lateral condyle, *Lt* lesser trochanter, *Mc* medial condyle, *Me* medial epicondyle *Tt* third trochanter. Scale bars equal 5 cm

but not in *Eosclerocalyptus*. The greater trochanter extends above the femoral head, as in *Pr. australis* and *Par. septentrionalis* but contrasting with *Eo. proximus*, in which both are at the same level. In proximal view, the greater trochanter has a very rough dorsal surface with a rhomboidal contour. The femoral head and the greater trochanter are separated by a proximal margin with a concave surface.

In anterior view, a triangular shallow depression occupies the proximal surface of the diaphysis, with its base parallel to the proximal margin. This depression is deeper in *Propalaehoplophorus* but shallower and less extended in *Eosclerocalyptus*. In posterior view, the proximal surface of the diaphysis is flat, except for a small rhomboidal depression just below of the greater trochanter. Towards the middle of the diaphysis, the section becomes sub-circular, reaching its minimum diameter. The third trochanter is located on the outer margin inferior to this point; it is gracile, very laterally expanded, and has triangular shape, as in the genera *Propalaehoplophorus* and *Parapropalaehoplophorus*; in *Eosclerocalyptus, Neosclerocalyptus*, and other more modern taxa, it is robust, little laterally expanded, and develops a sub-rectangular shape.

The distal epiphysis preserves both the internal and external condyles, separated by the femoral trochlea in anterior view, which is composed of two differentiated articular surfaces that converge at the trochlear midpoint and by the intercondylar fossa in posterior view. In anterior view, the supratrochlear fossa is placed above the internal half of the trochlea and develops a triangular shape. The internal condyle has two articular surfaces separated by a convexity; it extends slightly further distally than the external condyle and is slightly larger, as in *Pr. australis*, while in *Eosclerocalyptus*, both condyles are similar in size and positioned at the same level. In posterior view, the popliteus fossa is placed above the external condyle.

Dorsal Carapace

Analysis of the carapace is mainly based on the holotype PV-UNS-260 (Fig. 4), which represents the most complete material. The carapace of the holotype preserves its original contour and proportions and is composed of approximately 35 transverse rows of osteoderms. In comparison, *Propalaehoplophorus* has ca. 24 transversal rows, whereas the number in *Eo. proximus* and *Neosclerocalyptus* is 45–50 (see Zurita et al. 2011). In lateral view, the dorsal profile shows an intermediate morphology between some glyptodontines such as *Glyptodon*, in which it is higher and more convex, and *Neosclerocalyptus*, in which it is lower and subcylindrical. The general morphology is similar to species of *Eosclerocalyptus*, *Plohophorus*, *Boreostemma* and *Pseudohoplophorus* and different from *Panochthus* and *Doedicurus* spp.

Anterior Region In the anterodorsal area, osteoderms have a well-defined pentagonal shape. The ornamentation includes a "rosette" pattern (Barasoain et al. 2019, 2021) that differs from that of the Glyptodontinae (i.e., *Boreostemma*, *Glyptodon*, and *Glyptotherium*) in having a more circular central figure rather than angular (Zurita et al. 2013; Cuadrelli et al. 2019). This pattern is repeated with slight variations along the carapace. In this region, osteoderms are characterized by a large subcircular to circular central figure that is flat or slightly concave and surrounded by a single row of 8–9 peripheral figures. The central figure is larger in these osteoderms than in the rest of the carapace and occupies most of the dorsal surface. Consequently, the peripheral figures are very small, especially the lateral ones. Some osteoderms adjacent to the cephalic notch develop large foramina, as occurs in *Neosclerocalyptus*. Towards the most anterolateral area, the osteoderms are smaller, isodiametric, pentagonal to hexagonal, and with a mostly unornamented surface.

Central Region In the central dorsal area, osteoderms are pentagonal and larger than in the anterior dorsal area. The ornamentation includes a "rosette" pattern, with a central figure that is smaller than that of osteoderms of the anterior dorsal area and surrounded by a single row of 10–11 peripheral figures. More lateral osteoderms are of similar size but hexagonal, with a similar ornamentation pattern and 9–11 peripheral figures. The main difference compared to dorsal osteoderms is that the peripheral figures along the anterior margin are much larger than those of the posterior margin, as occurs in *B. acostae* and *B. venezolensis*, *Eo. proximus*, and some "Propalaehoplophorinae" (i.e., *Propalaehoplophorus* and *Eonaucum*).

Posterior Region In this area, the osteoderms are quite similar to those of the central region. Many osteoderms show 2–5 additional peripheral figures, a feature not observed in other regions; these figures appear mostly isolated and do not form a complete row. Additional figures are also present, in even higher numbers, in other taxa such as *Eo. proximus*, *N. ornatus*, *N. pseudornatus*, and *Hoplophorus euphractus*. Osteoderms adjacent to the caudal notch have an elliptical central figure, with the main axis oriented transversely and a flattened to slightly concave dorsal surface. There are 3–4 peripheral figures in the anterior margin and no figures along the other margins, as in *Eo. proximus* and *Neosclerocalyptus*.

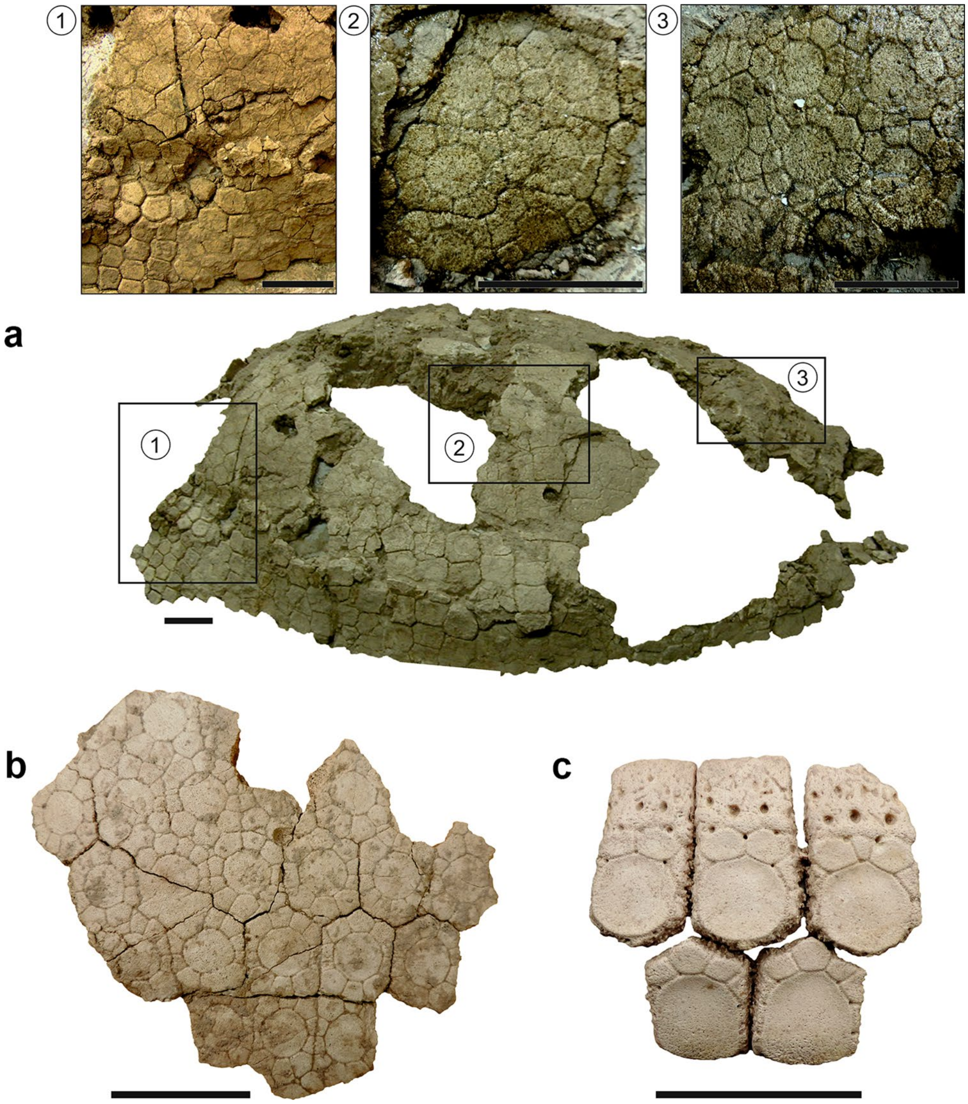

Fig. 4 Carapace and osteoderms of *Kelenkura castroi*: **a** dorsal carapace of PV-UNS-260 (holotype) with detail on the anterior (**1**), central (**2**), and posterior (**3**) regions; **b** articulated osteoderms of the dorsal carapace (MMH-CH-88–6-58); **c** articulated osteoderms of the caudal rings. Scale bars equal 5 cm

Caudal Armor

The holotype PV-UNS-260 includes several articulated ring fragments, isolated osteoderms, and the last caudal ring articulated with the complete caudal tube. Other specimens were also considered in the descriptions and comparisons (Online Resource 1).

Caudal Rings Each ring is composed of two rows of osteoderms with differing morphologies (Fig. 4). Osteoderms of the proximal row are sub-rectangular and divided into an anterior (articular) portion that underlies the more anterior ring and a posterior (ornamented) portion. The articular portion has a rough and unornamented surface that represents approximately 1/3 of the total length. At the anteroposterior midpoint, there is a row of 2–4 large foramina. The ornamentation includes a large circular to subcircular central figure surrounded by 2–3 lateral and anterior rounded peripheral figures. The lateral figures are very small and can be absent, whereas posterior figures are always absent. Osteoderms of the distal row have a pentagonal shape and a completely ornamented dorsal surface. The ornamentation pattern is similar to that of the ornamented portion of osteoderms of the proximal row, though the anterior peripheral figures are pentagonal rather than rounded and slightly larger.

Caudal Tube Five complete caudal tubes (Table 1; Fig. 5) from the Arroyo Chasicó Formation were analysed, (including the holotype) in addition to other small fragments from the Loma de Las Tapias Formation (Fig. 5; Online Resource 1). All tubes are sub-cylindrical and narrow towards the apex, very different from Doedicurinae (i.e., *Eleutherocercus* and *Doedicurus*), in which the tube is distally expanded (see Núñez-Blasco et al. 2021). The tube has a circular section proximally that becomes compressed dorsoventrally towards the apex, as occurs in *Eo. proximus, Neosclerocalyptus* spp.,

Table 1 Caudal tube measurements (in mm) of *Kelenkura castroi*

Specimen	L	AW	MW	PW
PV-UNS-260 (holotype)	343.45	89.15	84.32	42.1
MMH-CH-83-3-136	321.22	75.13	65.57	50.02
MMH-CH-88-3-135	305.32	73.44	65.27	4.75
MMH-CH-88-6-57	384.67	90.21	73.55	42.68
MMH-CH-w/cn	412.12	95.66	85.21	60.11

L total length, *AW* anterior width, *MW* midpoint width, *PW* posterior width at the midpoint of the apical figures, *w/cn* without collection number

and *Pl. figuratus*. The dorsal profile is approximately straight in lateral view, while it is concave in *Eo. proximus* and *Neosclerocalytus* spp. The ornamentation pattern is similar to that of the dorsal carapace and caudal rings; peripheral figures are scarce, poorly developed, and do not form complete rows, allowing central figures to contact one other. In this sense, the ornamentation of *K. castroi* can be considered unique, as it shows a morphological stage intermediate between the Palaehoplophorini (in which no ornamentation pattern can be observed) and later-diverging taxa (i.e., *Eosclerocalyptus*, *Pl. figuratus*, *Neosclerocalyptus*, and *Ps. absolutus*), which always have a complete row of peripheral figures separating central figures.

In dorsal view, central figures are mostly elliptical, with the major axis oriented anteroposteriorly and a slightly convex surface. Three to four small and irregular peripheral figures are located in the lateral margins of central figures. This contrasts with the more numerous peripheral figures present in taxa such as *Pl. figuratus*, *Eo. proximus*, *H. euphractus*, and *Neosclerocalyptus*, in which up to ten peripheral figures can be present. In most cases, peripheral figures are absent from anterior and posterior margins of central figures. In the proximal half of the tube, central figures are arranged into several parallel transverse rings. These rings are completely fused to each other, although the sutures between them are distinguishable and represented by wide depressed areas. In the distal half of the tube, the central figures are subcircular to circular with a flattened to slightly concave surface, and peripheral figures transition from scarce to absent towards the apex. Sutures between central figures are not recognizable.

The ventral ornamentation is quite similar to the dorsal ornamentation. In the proximal half, central figures are elliptical and arranged in rings, but peripheral figures are mostly absent or less developed than in the dorsal surface. Towards the distal half, central figures become larger and subcircular to circular, while peripheral figures are absent. Figures of the apex are the largest and have a rougher and slightly convex surface.

In lateral view, the proximal half has a similar ornamentation to that observed in dorsal view but with a greater development of peripheral figures, which are slightly bigger and number 3–4 in the lateral margins of central figures and 1–2 in the anterior and posterior margins. In the distal half, there are 3–5 large lateral figures, while peripheral figures are absent. The apical figures are inclined towards the medial side and converge at the most distal extreme of the tube. In some cases, these figures cover the entire apical area, while in others they cover only a small lateral portion, as described by Oliva (2016, 2017) for the tubes MMH-CH 83–03-138/139, MMH-CH 88–06-57, and MMP-M 984.

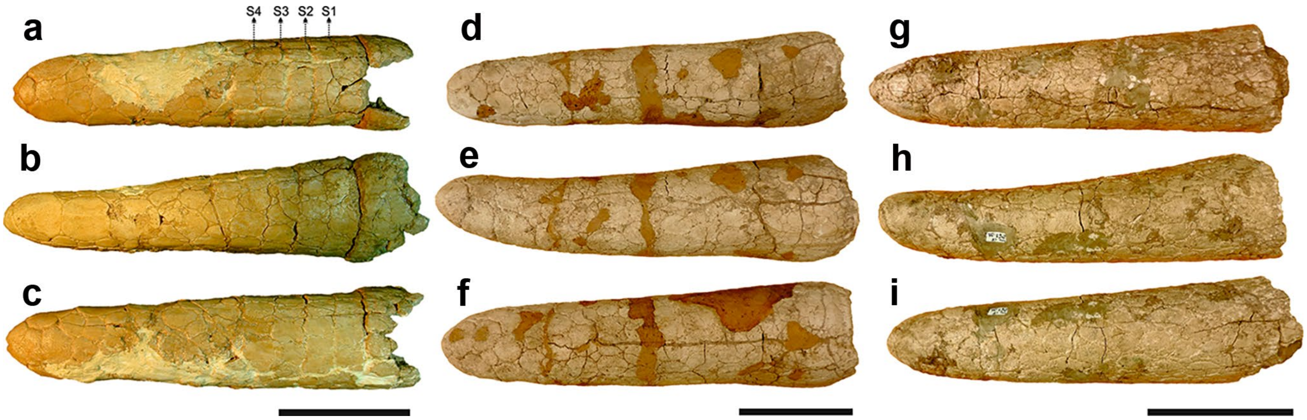

Fig. 5 Caudal tubes of *Kelenkura castroi*. Specimen PV-UNS-260 (holotype) in dorsal **(a)** right lateral **(b)** and ventral **(c)** views. Specimen MMH-CH-88–6-57 in dorsal **(d)** right lateral **(e)** and ventral **(f)** views. Specimen MMH-CH-88–3-135 in dorsal **(g)** right lateral **(h)** and ventral **(i)** views. Abbreviation: *S* sutures between fused rings of the caudal tube. Scale bars equal 10 cm

Fragments of Dorsal Carapace, Caudal Ring, and Caudal Tube Fragments, and Isolated Osteoderms

All of these more limited materials (see Online Resource 1) have a morphology and ornamentation pattern that can be included within the range of variation described above for different carapace portions of the holotype. However, their fragmentary state prevents an unequivocal taxonomic identification (see below). In some cases, this is exacerbated by soil corrosion, which can modify original features of osteoderms with a "rosette" ornamentation pattern (see Zurita et al. 2017b). This may have contributed to the identification of multiple taxa in previous works.

Phylogenetic Affinities of *Kelenkura Castroi*

The analysis resulted in a single MPT (Fig. 6) in which all glyptodonts form a monophyletic group supported by five synapomorphies: 2[0], 4[1], 5[0], 16[0], and 43[1]. Glyptodonts are divided into two clades. One clade corresponds to Glyptodontinae and includes the genera *Boreostemma*, *Glyptotherium*, and *Glyptodon*. It is supported by six synapomorphies: 17[0], 19[0], 25[1], 45[2], 55[0], and 56[1] (see also Cuadrelli et al. 2020). All remaining taxa are included in the "austral clade". It is supported by four synapomorphies: 17[1], 20[0], 55[1], and 56[0]. In general, the topology agrees with that of Zurita et al. (2013, 2017a), Cuadrelli et al. (2020), and Quiñones et al. (2020).

The most basal taxa within the "austral clade" are *Pr. australis* and *Eu. petestatus*, which branch sequentially. Crownward of these taxa, there is a polytomy among *Cochlops muricatus*, the Palaehoplophorini, and the remaining extra-Patagonian diversity. The propalaehoplophorines constitute a paraphyletic group according to this analysis. A clade corresponding to the tribe Palaehoplophorini is also recognized (*Pa. meridionalis* + *Pal. rothi*; see Scillato-Yané and Carlini 1998; González Ruiz et al. 2017), supported by the

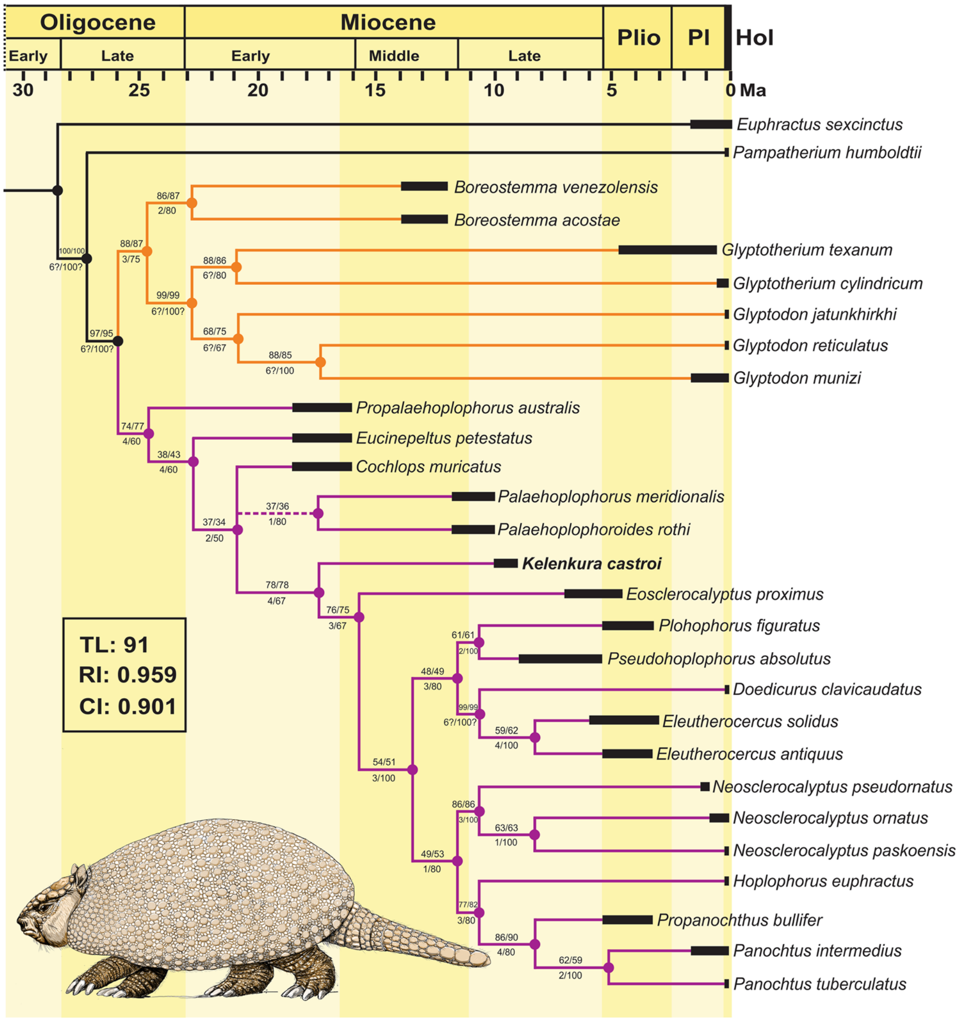

Fig. 6 Most parsimonious tree resulting from the phylogenetic analysis and support values. Numbers above branches indicate values of bootstrap and jackknife support, respectively. Numbers below branches indicate absolute and relative Bremer support, respectively. Black rectangles show the biochron of each species. The discontinuous line indicates a polytomy. Abbreviations: *CI* consistency index, *RI* retention index, *TL* tree length

synapomorphies 49[1] and 53[2]. This is the first analysis to test the monophyly of Palaehoplophorini, corroborating pre-cladistic proposals (see Hoffstetter 1958).

Interestingly, the new taxon *Kelenkura castroi* is positioned as the sister group of the remaining Neogene and Quaternary glyptodonts, in accordance with the age of the specimens studied. It is supported by two autapomorphies, 52[0] and 53[3]. More crownward, *Eo. proximus* (autapomorphy 33[2]) represents the sister group of two clades. The clade that includes the plohophorins (*Pl. figuratus* + *Ps. absolutus*, united by synapomorphies 23[2] and 39[1]) and doedicurines (synapomorphies 23[0], 24[2], 26[2], 31[3], 34[3], 40[0], 47[2], and 48[1]) as sister groups is supported by one synapomorphy (3[2]). Among doedicurines, *D. clavicaudatus* (autapomorphies 41[2] and 42[2]) is the sister taxon of *El. solidus* + *El. antiquus* (with 41[1] and 42[1] representing synapomorphies of each species of *Eleutherocercus*, respectively). The other clade is supported by the synapomorphy 10[1] and includes two subclades. One subclade groups species of *Neosclerocalyptus* (supported by the synapomorphies 14[1] and 38[0]) with *N. pseudornatus* as sister taxon of *N. ornatus* + *N. paskoensis* (united by the synapomorphy 9[2]). The other subclade groups the hoplophorins, supported by the synapomorphies 13[1] and 46[1], with *H. euphractus* as the sister taxon of a clade formed by *Pro. bullifer* and *P. intermedius* + *P. tuberculatus* (united by synapomorphies 1[0] and 11[0]). The same relationship among *Neosclerocalyptus*, *Hoplophorus*, and *Panochthus* was proposed by Porpino et al. (2010).

Discussion

Kelenkura castroi in the Context of the Austral Radiation of Glyptodonts

The oldest records of glyptodonts correspond to the Paleogene (late Eocene; ca. 35 Ma) from Patagonian Argentina (Simpson 1948; Gaudin and Croft 2015). These records are mainly restricted to isolated osteoderms, giving limited evidence about the earliest stages of the evolutionary history of these enigmatic cingulates (Ameghino 1887, 1902; Zurita et al. 2016). Despite this, different osteoderm ornamentation patterns have been used to recognize the subfamilies "Glyptatelinae" (see Hoffstetter 1958; Vizcaíno et al. 2003) and "Propalaehoplophorinae" (Carlini et al. 1997), reflecting an interesting morphological diversification within early glyptodonts (Zurita et al. 2016).

Croft et al. (2007) mentioned that the species *Par. septentrionalis*, from the early Miocene (ca. 19–17 Ma) of Chucal (northern Chile), occupies a more basal position than the "Glyptatelinae" *Glyptatelus* and the "Propalaehoplophorinae" *Propalaehoplophorus*. However, since *Glyptatelus* is only known by osteoderms (in contrast to *Par. septentrionalis* and *Propalaehoplophorus*, which are known from more extensive remains), these results are not definitive.

This lack of fossils during the earliest stages has been interpreted as evidence of a possible rapid evolution from an "armadillo-like" ancestor (see Mitchell et al. 2016). Coincident with this possible early radiation, southern South America experienced a progressive tendency towards more open biomes during the late Eocene–Oligocene (Iglesias et al. 2011), concordant with the interpretation of glyptodonts as grazing herbivores (Vizcaíno et al. 2011). More precisely, the late Oligocene-early Miocene period was characterized by the presence of shrub-herbaceous elements, which began to give a modern appearance to vegetation communities (Barreda and Palazzesi 2007).

The better fossil record of glyptodonts since the early and middle Miocene allows the inclusion of different glyptodonts in cladistic analyses (i.e., Croft et al. 2007; Fernicola 2008; Porpino et al. 2010, 2014; Zamorano et al. 2014). Several studies (Zurita et al. 2013; Cuadrelli et al. 2020; this paper) reveal a basal dichotomy since the early and middle Miocene, separating two clades with very different geographical distributions and evolutionary histories. One of them includes the northern Glyptodontinae, with the oldest records in the middle Miocene of Colombia and Venezuela (Carlini and Zurita 2010). This group shows low diversity but eventually had a wide latitudinal distribution, spanning most of South America and extending into southern North America (Gillette et al. 2016; Zurita et al. 2018; Cuadrelli et al. 2020). The other one, the "austral clade", is larger and more diversified and has its oldest records in the late early Miocene (Santacrucian SALMA, *ca.* 19–17 Ma) of Patagonian Argentina. Fauna and flora related to humid environments and isotopic analyses of herbivore tooth enamel indicate a tropical climate during this period in this region (Zachos et al. 2001, 2008; Catena and Croft 2020; Trayler et al. 2020). The "Propalaehoplophorinae", including several well characterized genera (*Propalaehoplophorus*, *Eucinepeltus*, *Cochlops*, "*Metopotoxus*"), diversified under these conditions (see Scott 1903–1904; González-Ruiz 2010; Vizcaíno et al. 2012).

This glyptodont diversity started to decline during the middle Miocene (Friasian and Mayoan SALMAs, ca. 16–12 Ma), the moment in which a later-diverging group appears in the fossil record of Patagonia, the "Palaehoplophorini" (Scillato-Yané and Carlini 1998; González Ruiz et al. 2016). However, the diversity achieved by the "Palaehoplophorini" seems to be more limited than that of the "Propalaehoplophorinae", since they are only represented by *Pa. meridionalis* and *Pal. rothi* from the late middle Miocene (ca. 12 Ma) of Patagonia (Scillato-Yané and Carlini 1998; González-Ruiz, 2010; González-Ruiz et al. 2016). Though some authors reported the presence of palaehoplophorines in the late Miocene (Chasicoan Stage/Age, ca. 9 Ma) of the Arroyo Chasicó locality (Fidalgo et al. 1978, 1987; Bondesio et al. 1980), our study confirms that there are not records of this tribe; therefore, this limits their biochron to the Mayoan.

Putative "Palaehoplophorini" (i.e., *Pa. antiquus* and *Aspidocalyptus castroi*) are represented by very fragmentary materials lacking any relevant diagnostic characters (Cabrera 1939; Pascual et al. 1965; Dozo et al. 2010; Scillato-Yané et al. 2013). Based on the available evidence, the "Palaehoplophorini" represent the last lineage of Patagonian glyptodonts, with a restricted geographic distribution and "modest" (based on their temporal distribution) evolutionary success. From a phylogenetic viewpoint, our analysis cannot confirm that the "Palaehoplophorini" are the sister-group of the subsequent radiation that began with *K. castroi* (Fig. 4).

In a global perspective, the late Miocene was characterized by important geological and climatic changes that clearly affected terrestrial ecosystems (Zachos 2001; Herbert et al. 2016). This period evidenced a progressive aridification, with the replacement of forested areas by more open biomes with more xerophytic vegetation (Pascual and Ortiz Jaureguizar 1990; Barreda and Palazzesi 2007; Barreda et al. 2007; Hoorn et al. 2010; Domingo et al. 2020). These events mark the beginning of the "Edad de las planicies australes" (Age of the Southern Plains), which is coincident with the Chasicoan Stage/Age (Ortiz-Jaureguizar 1998; Ortiz-Jaureguizar and Cladera 2006). This interval also seems to have been particularly important in the paleobiogeography of austral mammals, including glyptodonts. According to Pascual and Odreman Rivas (1973) and Pascual et al. (1984), cladogenesis in South American mammals subsided in Patagonia during the late Miocene to early Pliocene interval and was displaced northwards.

In this scenario, our analysis reveals that the traditionally proposed high diversity of glyptodonts during the Chasicoan Stage/Age cannot be supported by the current evidence. This period shows a very low diversity, at least considering the fossiliferous localities of central Argentina here studied, only including the new taxon *K. castroi*. On the contrary, younger lineages (Doedicurinae, Neosclerocalyptini, Hoplophorini, Plohophorini) are not registered in Chasicoan deposits in this region. The record of Chasicoan glyptodonts from other regions of Argentina (i.e., northeastern/Ituzaingó Formation and northwestern/Chiquimil and Palo Pintado formations) is very scarce and/or fragmentary (see above), which prevents evaluating the real diversity and comparing with the results obtained here.

Taxonomic, Phylogenetic, and Evolutionary Interpretations of *Kelenkura castroi*

The holotype PV-UNS-260 of *K. castroi* was originally assigned to *Eo. tapinocephalus* by Zurita and Aramayo (2007), a species defined based on cranial elements. Oliva (2016) suggested the presence of a new species of *Hoplophractus* after a preliminary analysis of some materials from the Arroyo Chasicó site. However, following several authors (Perea 2005; Zurita 2007; Zurita and Aramayo 2007), we consider *Hoplophractus* as synonymous with *Eosclerocalyptus*. The present analysis, including new and complete materials, shows significant differences (see above) between *K. castroi* and *Eosclerocalyptus*, supporting the description of the new taxon.

Kelenkura castroi (Fig. 7) has a unique anatomical morphology and, according to our phylogenetic analysis, it is the sister group of the later diversity of the "austral clade". It retains several character states considered to be plesiomorphic among glyptodonts (i.e., osteoderms with a central figure surrounded by a single complete row of peripheral figures, elongated cranium, certain aspects of femur morphology; Fernicola and Porpino 2012; González Ruiz et al. 2016), while others (i.e., totally fused and ornamented caudal tube, greater development of peripheral figures) are derived states shared with later-diverging lineages.

With a dorsal carapace length of ~ 1 m, *K. castroi* represents a medium-sized glyptodont, larger than *Propalaehoplophorus* (~ 0.5 m), similar to *Eosclerocalyptus proximus* (~ 1 m), and smaller than *Eleutherocercus solidus* and *El. antiquus*. The estimated body mass (~ 160 kg) is in concordance with a medium-sized glyptodont. Smaller species have been estimated at ~ 50 kg (Fariña 1995) and ~ 81 kg (Vizcaíno et al. 2012) for *Pr. australis*, ~ 79–86 kg for *C. muricatus*, and ~ 115 kg for *Eu. petesatus* (Vizcaíno et al. 2012), which seems to reflect an increase in body size through time. In turn, Pliocene and Quaternary taxa have much larger body masses, even the smallest ones such as *Neosclerocalyptus* species (~ 295–471 kg; Quiñones et al. 2020).

Cranial remains of *K. castroi* show some plesiomorphic features, such as a generally elongated morphology, anteriorly projected nasals, and a poorly developed sagittal crest. They also present some very unusual characters such as a very narrow occipital area and very gracile posterior zygomatic processes.

The morphology of the femur of *K. castroi* is highly plesiomorphic, being more curved and gracile and with a less robust and much more laterally expanded third trochanter with respect to the later diversity of the "austral clade". This morphology is very similar to that of *Pr. australis* from the late early Miocene of Patagonia (Argentina) but also to that of *Par. septentrionalis* from the late early Miocene of Chucal (Chile), considered a relatively basal representative within Glyptodontidae (Croft et al. 2007). According to Milne and O'Higgins (2012), this modification of the third trochanter structure in later clades is possibly related to significant changes in size and body mass.

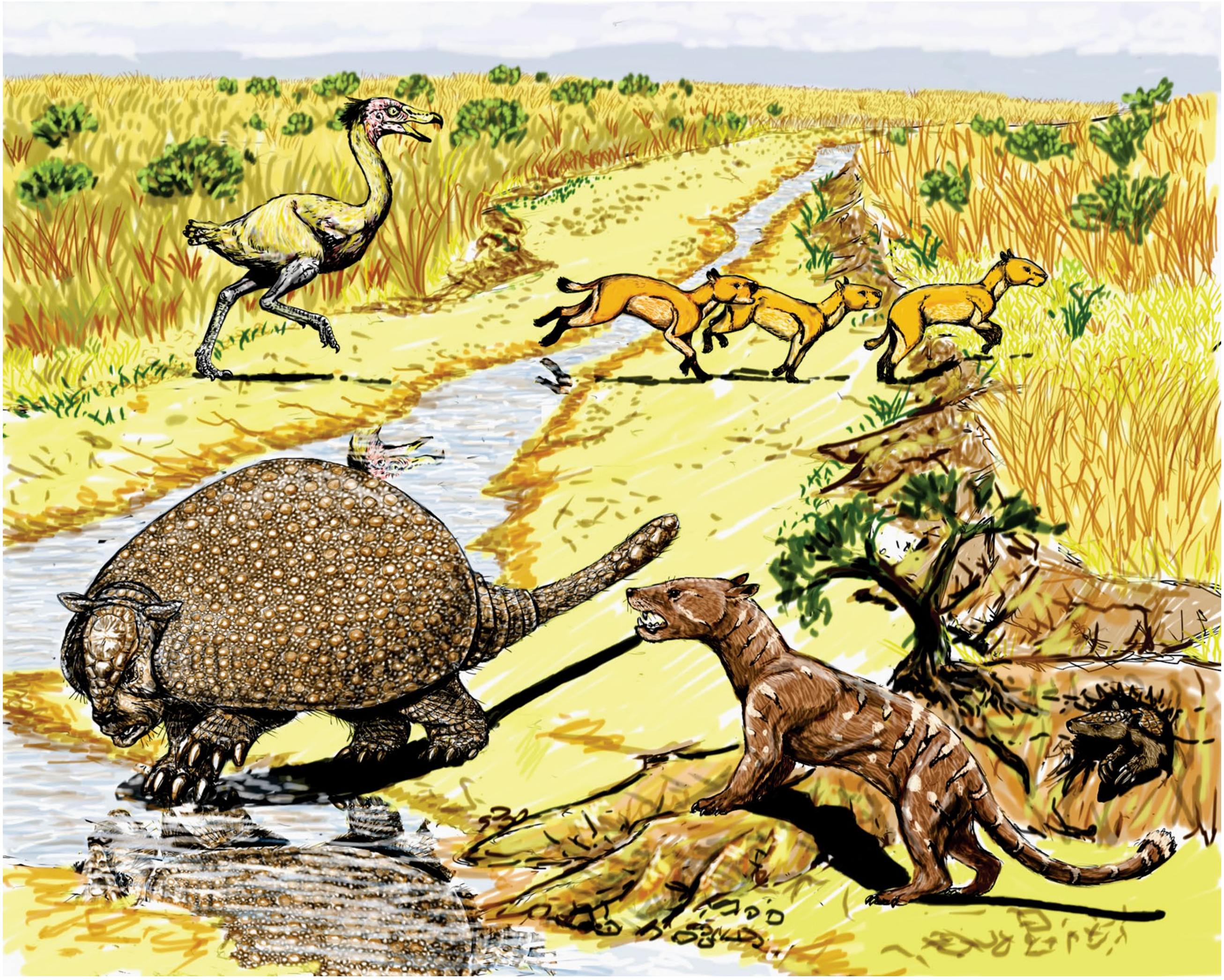

Fig. 7 Reconstruction of the late Miocene environment and fauna of the Arroyo Chasicó site, with the glyptodont *Kelenkura castroi* in the foreground. Artist: Pedro Cuaranta

The dorsal carapace of *K. castroi* shows a more advanced morphological stage than other anatomical regions. The general shape has more similarities with later representatives of the “austral clade” such as *Eosclerocalyptus*, *Plohophorus*, and *Pseudoplohophorus* than earlier taxa (i.e., *Propalaehoplophorus*). The "rosette" ornamentation pattern of osteoderms is considered to be a potential synapomorphy of Glyptodontidae (Porpino et al. 2010; Fernicola and Porpino 2012). In contrast, the increase in the number of peripheral figures and rows of peripheral figures observed in later forms was independently acquired by different lineages (Fernicola 2008), representing two different derived character states.

The caudal tube of *K. castroi* represents the most interesting structure analyzed, since it represents the oldest record of a “fully modern morphology”, completely fused and ornamented. The propalaehoplophorines did not develop a completely fused caudal tube, since in most cases, the caudal armor is composed only of caudal rings (Fernicola and Porpino 2012); only *C. muricatus* shows an incipient development of a caudal tube (Scott 1903–1904, González Ruiz 2010). The palaehoplophorins have a fused caudal tube, but it lacks a true ornamentation pattern, and only sutures among osteoderms are visible (Scillato-Yané and Carlini 1998; González Ruiz et al. 2016). In this respect, further modifications of caudal tube osteoderms, such as a "rosette" ornamentation pattern and large lateral figures, are considered to be derived character states (Scillato-Yané and Carlini 1998; Fernicola and Porpino 2012; Zamorano and Brandoni 2013; Zurita et al. 2013).

The caudal tube of *K. castroi* represents the earliest case of some of these apomorphic character states, including a “rosette” ornamentation pattern that clearly resembles that of the dorsal carapace and large lateral figures that increase in size towards the apex. Peripheral figures are much less developed than in later taxa of the "austral clade" such as *Eosclerocalyptus* and *Neosclerocalyptus*, since they do not completely surround central figures and are absent in the distal half of the caudal tube. Additionally, though the caudal tube is completely fused in *K. castroi*, the sutures between the caudal rings that compose it are still visible along the proximal half of the structure, so that individual fused rings can be differentiated. On the contrary, limits between fused caudal rings are not noticeable in later taxa of the "austral clade".

In summary, the anatomical morphology of *K. castroi*, especially its caudal tube, seems to represent an intermediate evolutionary stage between the early-diverging groups represented in the early and middle Miocene of Patagonian Argentina and the later diversity of the "austral clade", which diverged from the late Miocene onwards. This evidence is in concordance with our phylogenetic analysis, which places *K. castroi* as the sister group to later Neogene and Quaternary diversity, precluding its inclusion in any of the known tribes.

On the Origin and Morphology of the Caudal Tube

As mentioned above, the Paleogene record of glyptodonts is quite scarce. Nevertheless, taking into account the high preservation potential of caudal tubes in the fossil record, the lack of evidence of this structure in representatives of this interval suggests that the caudal armor of the "Propalaehoplophorinae" (except *Cochlops*) and "Glyptatelinae" was completely composed of caudal rings.

Among the earliest well-characterized glyptodonts (i.e., late early Miocene "Propalaehoplophorinae"), *C. muricatus* shows the least derived stage of a caudal tube; the proximal two-thirds of its caudal armor is composed of articulated caudal rings, while the distal third is composed of a partially fused "proto-caudal tube". The caudal tube only developed among representatives of the "austral clade", being absent in the Glyptodontinae, which only have a very small terminal "tubercle" following the caudal rings (see Zurita et al. 2013; Cuadrelli et al. 2019, 2020). According to this point, the presence of a caudal armor composed by caudal rings is the plesiomorphic character state within Glyptodontidae, present in the Glyptodontinae and in the most basal representatives of the "austral clade" (*Pr. australis* and *Eu. petestatus*). The derived state of a caudal tube (at least partially developed) is present in *C. muricatus* and later-diverging members of the "austral clade".

The appearance and further evolution of the caudal tube in the "austral clade" chronologically coincides with the environmental changes that took place during the middle to late Miocene in southern South America, with the replacement of humid and tropical forests by open and arid environments (Age of the Southern Plains; see above). We cannot demonstrate a causal relationship between these patterns, but their coincidental timing is worthy of further investigation.

Anatomical evidence suggests the existence of some kind of niche partitioning among early to middle Miocene "Propalaehoplophorinae", with *Cochlops* more adapted to open paleoenvironments than *Propalaehoplophorus* and *Eucinepeltus* (see Vizcaíno et al. 2011). In this framework, it is interesting to note that the length of the caudal tube of Mayoan middle Miocene "Palaehoplophorini" (Mayoan SALMA) resembles that of more modern taxa but retains some primitive characteristics, such as an absence of ornamentation.

In some later lineages within the "austral clade", such as *Eosclerocalyptus* and Neosclerocalyptini, the morphology of this structure did not undergo significant evolutionary change after the Chasicoan Stage/Age, while in others, such as Pliocene and Quaternary Doedicurinae (*Eleutherocercus* and *Doedicurus*), *Panochthus* spp., and *Hoplophorus euphractus,* the caudal tube was hugely exapted, as suggested by Blanco et al. (2009). These authors argue that a solid caudal structure would generate a larger effective mass, leading to a greater impact force. In this regard, some of the largest and most unusual taxa (i.e., *Panochthus*, *Doedicurus*) developed caudal tubes with terminal spines, which most authors link to fighting behaviors related to intraspecific competition or sexual display (Ferigolo 1992; Fariña 1995; Alexander et al. 1999; Arbour and Zanno 2020). However, the precise mechanisms and ecological pressures that led to the origin of this structure remain unknown, as well as its original function.

Conclusions

The comprehensive review carried out in this study strongly suggests that a single glyptodont taxon is present in the Chasicoan levels (late Miocene, Tortonian Age) of central Argentina. This taxon is represented by a new genus and species, here identified as *Kelenkura castroi*. From phylogenetic and paleobiogeographic viewpoints, *K. castroi* documents the oldest well-characterized extra-Patagonian taxon, being the sister group of the remaining southern South America diversity and supporting the hypothesis that the Chasicoan represents the end of the Patagonian region as an area of cladogenesis. From a morphological viewpoint, this new taxon presents several derived character states compared with earlier glyptodonts (i.e., "Propalaehoplophorinae") but other more primitive character states compared to latest Miocene-Quaternary forms. Additionally, this new taxon documents the earliest occurrence of a "fully modern" morphology of the caudal tube. It is clear that a decrease in diversity of glyptodonts has occurred since the middle

Miocene in southern South America, coincident with the development of more open and arid environments.

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Data Availability All data generated and analyzed during this study are included in this published article and its supplementary files.

Declarations

Conflict of Interests DAC is editor-in-chief of the Journal of Mammalian Evolution but was not involved in the evaluation of this manuscript.

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