

REPRESENTATIVITY OF QUATERNARY MAMMALS FROM THE SOUTHERN BRAZILIAN CONTINENTAL SHELF

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ABSTRACT – Fossils of terrestrial mammals from the southern Brazilian continental shelf have been known since the late 19th century. The fossils are relatively common and represent several taxonomic groups of the Pleistocene megafauna. Although the systematics of the fossil assemblage is well known, the relative proportions among taxonomic groups and their skeletal elements have not been evaluated yet. Here are presented the results of a survey of the diversity of skeletal elements and taxa among 2,391 specimens belonging to the paleontological collection of the Universidade Federal do Rio Grande (FURG). The survey revealed that the most common taxa are the artiodactyls, ground sloths, glyptodontids and toxodontids, while carnivores, rodents and litopterns are very scarce. The most abundant skeletal elements are osteoderms of cingulates (mostly glyptodontids) and teeth of other groups. Although paleoecological and paleoenvironmental inferences are very hard to obtain because the fossils do not have a stratigraphic setting, encompass a wide time span, of some 700 ky BP, and represent several environments and climates, some patterns of taxonomic abundance are apparently related to ecological factors, while others seem to result from taphonomic processes.

Key words: megafauna, Pleistocene, Southern Brazil, continental shelf.

RESUMO – Fósseis de mamíferos terrestres procedentes da plataforma continental do sul do Brasil são conhecidos desde o século 19. Esses fósseis são relativamente comuns e representam diversos grupos taxonômicos da megafauna do Pleistoceno. Embora a sistemática da assembleia fóssil seja bem conhecida, as proporções relativas entre os diferentes grupos e seus elementos esqueléticos ainda não foram avaliadas. Aqui são apresentados os resultados de um levantamento da diversidade de elementos esqueléticos e táxons entre 2.391 espécimes pertencentes à coleção paleontológica da Universidade Federal do Rio Grande (FURG). O levantamento revelou que os táxons mais comuns são artiodáctilos, preguiças terrícolas, gliptodontídeos e toxodontídeos, enquanto carnívoros, roedores e litopternos são bastante escassos. Os elementos esqueléticos mais abundantes são osteodermos de cingulados com predominância de gliptodontídeos, e dentes de outros grupos. Embora seja difícil fazer inferências paleoecológicas e paleoambientais, devido ao fato de os fósseis não apresentarem contexto estratigráfico, representarem grande intervalo temporal da ordem de 700 ky BP e indicarem diferentes tipos de ambientes e climas, alguns padrões de abundância taxonômica parecem relacionados a fatores ecológicos, enquanto outros parecem ser resultados de processos tafonômicos.

Palavras-chave: megafauna, Pleistoceno, sul do Brasil, plataforma continental.

INTRODUCTION

Fossils of terrestrial mammals have been collected from continental shelves all around the globe, such as the northeastern coast of North America (Whitmore *et al.*, 1967) and the North Sea (Van Kolfschoten & Laban, 1995; Mol *et al.*, 2006). Similar fossils have also been found on the Argentinean continental shelf, in front of the estuary of the La Plata River (Cione *et al.*, 2005) and the coast of Buenos Aires Province (Tonni & Cione, 1999), and on the northeastern Uruguayan coast (Rinderknecht, 2006). In Brazil, fossils of terrestrial mammals preserved on the continental shelf have

been recorded from the coast of Rio Grande do Sul State since the late 19th century, when German naturalist Hermann Von Ihering described in a letter to Argentinean naturalist Florentino Ameghino the presence of some osteoderms of glyptodonts on the beach (Ameghino, 1891). Recently, the presence of such remains in deeper areas of the shelf, collected by fishermen, has also been published (Lopes & Buchmann, 2010). The studies on such fossils have been aimed mostly at their taxonomic identification (*e.g.* Cunha, 1959; Paula Couto & Cunha, 1965; Oliveira, 1992, 1996; Rodrigues & Ferigolo, 2004; Rodrigues *et al.*, 2004; Scherer, 2005; Marcon, 2007; Scherer *et al.*, 2009). Other studies have focused on the distribution of such remains

along the coast (Buchmann, 1994), their taphonomy (Lopes *et al.*, 2008) and ages (Lopes *et al.*, 2010).

The fossils are found disarticulated, exhibiting signs of *post mortem* breakage and abrasion (Lopes *et al.*, 2008). They come from large concentrations of marine and terrestrial skeletal remains on the inner continental shelf, at depths between 0 and 20 m (Figueiredo, 1975; Buchmann, 2002). During autumn and winter, storm waves erode these concentrations and transport the fossils to the beach, where they are collected. Besides terrestrial mammals, the concentrations also contain remains of marine mollusks (Lopes & Buchmann, 2008), corals, echinoderms, crustaceans (Buchmann, 1994; Lopes, 2011), teleost (Richter, 1987) and elasmobranch fishes (Buchmann & Rincón Filho, 1997), pinnipeds (Oliveira & Drehmer, 1997), cetaceans (Cunha, 1982; Ribeiro *et al.*, 1998), seabirds (Lopes *et al.*, 2006) and reptiles (Hsiou & Fortier, 2007; Hsiou, 2009).

The presence of terrestrial fossil mammals in a modern marine environment is attributed to the existence of Pleistocene continental fossiliferous deposits that were reworked by sea-level oscillations. During the Quaternary glacial maxima, the ocean levels reached some 130 m below present-day levels, thus exposing large areas of the continental shelves all around the world that were occupied by terrestrial environments and were covered and reworked by sea level rises at the end of glaciations (Lopes & Buchmann, 2010). Recent ages obtained by Electron Spin Resonance (ESR) on seven fossil teeth from the southern Brazilian continental shelf revealed that the fossils are between 650 ± 100 and 18 ± 3 ky BP, and represent several

temporally distinct fossil assemblages (Lopes *et al.*, 2010). The large age span, the co-occurrence of fossils that indicate arid and open environments such as *Reithrodon* Waterhouse, 1837 and Dolichotinae rodents, and other records (Cunha, 1959; Rodrigues & Ferigolo, 2004) such as *Tapirus* Brunnich, 1772, *Hydrochoerus* Brisson, 1762 and *Myocastor* Kerr, 1792 that indicate permanently humid or forested environments, plus the lack of a precise stratigraphic context, difficult paleocommunity reconstructions based on fossils from the continental shelf.

Although the fossils are somewhat common and several mammalian groups are recognized from these deposits (Table 1), until now there has been no detailed survey regarding the relative proportions among taxa, given that the available taxonomic studies are based on specific groups and isolated specimens. Here is presented a survey of the relative proportions of mammalian taxa and respective skeletal elements found on the southern Brazilian continental shelf. The present survey is aimed at improving the knowledge regarding such taxa and evaluating patterns that may have influenced taxonomic and anatomic representativity. Although representing distinct assemblages with different ages, mixed together by erosive processes related to sea-level oscillations, for the purposes of the present study all fossils are considered as a single assemblage.

GEOLOGICAL SETTING

The Coastal Plain of Rio Grande do Sul State (CPRS) was formed after the split between South America and Africa in the

Table 1. Fossils of terrestrial mammals from the deposits of the southern Brazilian continental shelf (classification according to McKenna & Bell, 1997).

Classe MAMMALIA Linnaeus, 1758	Familia Canidae Fischer de Waldheim, 1817
Ordem PILOSA Flower, 1883	<i>Protocyon</i> Lund, 1842
Familia Megatheriidae Owen, 1843	<i>Dusicyon</i> Hamilton-Smith, 1839
<i>Megatherium</i> Cuvier, 1796	<i>Theriodictis</i> Mercerat, 1891
Familia Mylodontidae Gill, 1872	Ordem RODENTIA Bowdich, 1821
<i>Glossotherium</i> Gervais, 1855	Familia Caviidae Fischer de Waldheim, 1817
<i>Lestodon</i> Gervais, 1855	Dolichotinae indet. Pocock, 1922
<i>Myiodon</i> Owen, 1839	Familia Hydrochoeriidae Brisson, 1762
<i>Catonyx</i> Ameghino, 1891	<i>Hydrochoerus</i> Brisson, 1762
Ordem CINGULATA Illiger, 1881	Familia Muridae (= Cricetidae) Illiger, 1811
Familia Dasypodidae Bonaparte, 1838	<i>Reithrodon</i> Waterhouse, 1837
<i>Propaopus</i> Ameghino, 1881	Familia Echimyidae Gray, 1825
Familia Pamphathiidae Paula Couto, 1954	<i>Myocastor</i> Kerr, 1792
<i>Holmesina</i> Simpson, 1930	Heteromysopinae indet. Anthony, 1917
<i>Pamphathium</i> Ameghino, 1875	Ordem URANOTHERIA McKenna & Bell, 1997
Familia Glyptodontidae Burmeister, 1879	Familia Gomphotheriidae Hay, 1922
<i>Doedicurus</i> Burmeister, 1874	<i>Stegomastodon</i> Pohlig, 1912
<i>Glyptodon</i> Owen, 1845	Ordem PERISSODACTYLA Owen, 1848
<i>Panochthus</i> Burmeister, 1872	Familia Equidae Gray, 1821
<i>Neuryurus</i> Ameghino, 1889	<i>Equus</i> Linnaeus, 1758
<i>Pachyarmatherium</i> Downing & White, 1995	<i>Hippidion</i> Owen, 1869
Ordem LITOPTERNA Ameghino, 1889	Familia Tapiridae Gray, 1821
Family Macraucheniidae Gervais, 1855	<i>Tapirus</i> Brunnich, 1772
<i>Macrauchenia</i> Owen, 1838	Ordem ARTIODACTYLA Owen, 1848
Familia Protheroheriidae Ameghino, 1887	Familia Camelidae Gray, 1821
<i>Neolicaphrium</i> Frenguelli, 1921	<i>Lama</i> Cuvier, 1800
Ordem NOTOUNGULATA Roth, 1903	<i>Hemiauchenia</i> Gervais & Ameghino, 1880
Familia Toxodontidae Owen, 1845	Familia Cervidae Goldfuss, 1820
<i>Toxodon</i> Owen, 1838	<i>Antifer</i> Ameghino, 1889
Ordem CARNIVORA Bowdich, 1821	<i>Morenelaphus</i> Carette, 1922
Familia Felidae Gray, 1821	Family Tayassuidae Palmer, 1897
<i>Smilodon</i> Lund, 1842	Tayassuidae indet.

Late Cretaceous, by accumulation of sediments eroded from the older, higher geomorphologic units (Figure 1). Between the Neogene and Quaternary the morphology of the CPRS was affected by glacioeustatic oscillations, which led to the formation of two major depositional systems: the Alluvial Fans System and the Pleistocene-Holocene Complex Multiple Barrier (Villwock & Tomazelli, 1995).

The latter unit is subdivided into four large barrier-lagoon depositional systems and associated features. Each barrier-lagoon was formed by a marine transgression, correlated to late Pleistocene-Holocene interglacial episodes (Tomazelli *et al.*, 2000). The constituent sediments are essentially siliciclastic,

well-sorted and mature sands, with small amounts of organic matter, biogenic carbonate, diagenetic clays and concentrations of heavy minerals (Villwock & Tomazelli, 1995).

The continental shelf, which constitutes the submerged portion of the CPRS, has a low slope (average ratio of 1:1.000) and the shelf break is located at depths between 80 and 120 meters. The middle-central portion of the shelf is wide, morphologically reworked and presents paleofluvial channels and sand banks (Corrêa *et al.*, 1996). During the Holocene transgression of 6-7 ky BP, variations in the rates of sea-level rise promoted the reworking and concentration of clastic terrigenous sediments and formed abrasion terraces on the shelf (Kowsmann & Costa, 1974; Martins *et al.*, 1996). The deposits of the shelf containing terrestrial remains were formed during sea-level regressions, when large portions of the then exposed shelf were occupied by terrestrial ecosystems (Lopes *et al.*, 2010; Lopes & Buchmann, 2010).

MATERIAL AND METHODS

Systematic collecting of fossils along the beaches of Rio Grande do Sul State has been performed in the last 15 years by researchers from the Universidade Federal do Rio Grande (FURG). The collection sites are concentrated in the southern portion of the coast, between the estuary of Patos Lagoon and Chuí Creek. During these activities, 1 km-long sections of the coast, between the surf zone and frontal dunes, are surveyed for fossils and geological samples. The remains are found disarticulated and exhibit signs of abrasion by transport; most fossils are incomplete, and compact-shaped elements such as osteoderms, astragali and phalanges are generally the best preserved (Lopes *et al.*, 2008). The occurrence of fossils along the coast is not uniform (Buchmann, 1994). The largest concentration of mammalian remains is found in a ~40 km-long sector where large and thick *konzentrat-lagerstätte* of fossil marine shells, called “concheiros” (Figure 2) are formed on the beach by redeposition of bioclasts transported from the continental shelf by storm waves (Figueiredo Jr., 1975).

The studied specimens, a total of 2,391 fossils, are deposited in the paleontological collection of FURG. Each specimen was identified to the lowest taxonomic category where possible, and classified as cranial elements (skulls, mandibles, antlers), isolated teeth, axial elements (vertebrae and ribs), appendicular elements (scapulae and long bones), podials (carpals, metacarpals, tarsals, metatarsals and phalanges) and accessory elements (osteoderms, caudal tubes).

Abbreviations. CPRS, coastal plain of Rio Grande do Sul State; FURG, Universidade Federal do Rio Grande; LGP, Laboratório de Geologia e Paleontologia; LGP-E, Toxodontidae; LGP-F, Litopterna; LGP-G, Gomphotheriidae; LGP-I, Artiodactyla; LGP-K, Perissodactyla; LGP-N, Dasypodidae; LGP-P, Glyptodontidae; LGP-PC, continental shelf; LGP-Q, Mylodontidae.

RESULTS

The most abundant skeletal elements are osteoderms of cingulates, followed by teeth (Figure 3). The most common cranial elements are incomplete cervid antlers and fragments of the occipital portion of skulls; the most complete skull is almost unrecognizable, but seems to be of a ground sloth

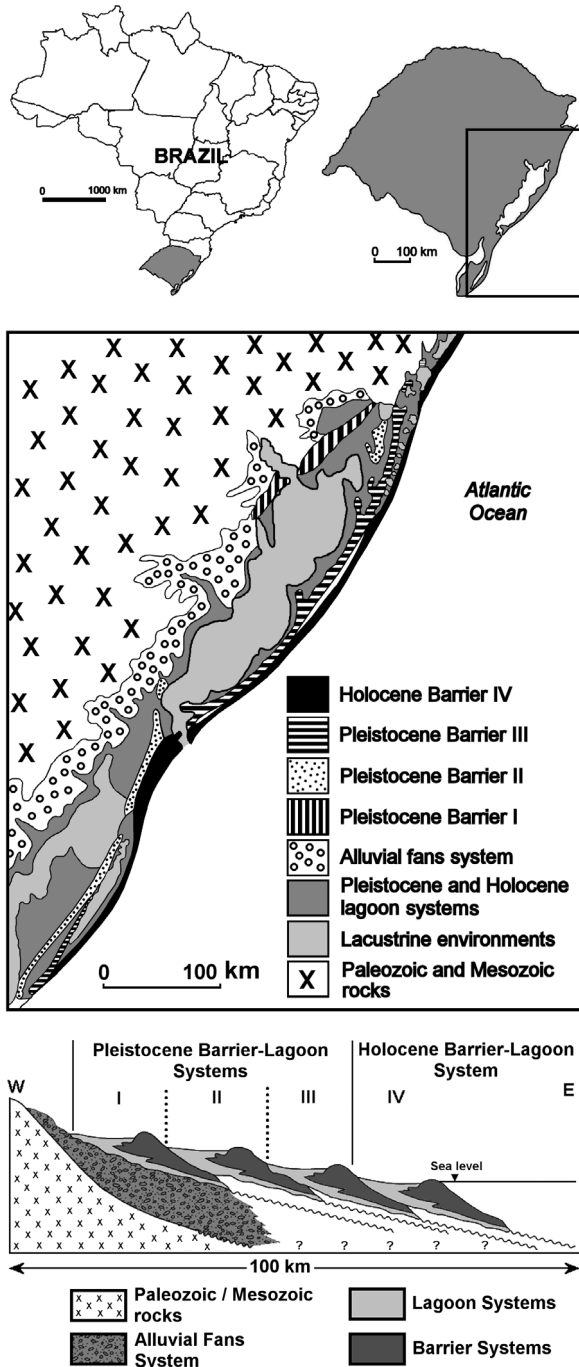


Figure 1. Location of Rio Grande do Sul State and simplified structure of the coastal plain (modified from Tomazelli *et al.*, 2000).



Figure 2. Osteoderm of *Glyptodon* associated with marine fossil remains in the “concheiros”, CPRS, southernmost Brazil. Not in scale 1/1.

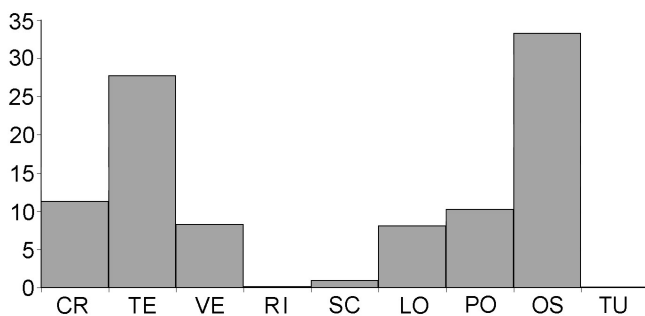


Figure 3. Relative percentages among the identified skeletal remains. **Abbreviations:** CR, cranial elements; TE, teeth; VE, vertebrae; RI, ribs; SC, scapulae; LO, long bones; PO, podials; OS, osteoderms; TU, caudal tubes.

because of the internal pneumatization (Figure 4A). The most common podial elements are astragali (Figures 4B, C), followed by phalanges and carpals/tarsals (Figure 4D). Long bones are represented essentially by incomplete specimens (Figures 4E-G). Vertebrae include complete specimens, but most are incomplete or fragments represented by centra without neural arches and isolated neural spines, difficult to assign to any specific taxon. Scapulae and ribs are all incomplete specimens.

Of the total analyzed specimens, 214 could not be taxonomically identified due to reworking by marine dynamics,

which destroys most of the diagnostic characters by abrasion and/or fragmentation (Lopes *et al.*, 2008). These include 121 vertebrae, 33 podials, 26 long bones, 22 scapulae, 9 skulls and 3 ribs. The remaining 2,177 elements could be assigned to several taxonomic groups (Figure 5), but not all known taxa from the continental shelf are represented, among them the rodents and canids. The most common taxa are artiodactyls, represented mostly by antler fragments, podials and teeth. Among the antlers, 145 could be identified, being 28 of *Antifer* Ameghino, 1,889 and 117 of *Morenelaphus* Carette, 1922; the remaining 167 could not be assigned to any specific genus due to abrasion and fragmentation. Podials and teeth of this group are very common and well preserved; however, a detailed revision is needed in order to distinguish between cervids and camelids. The medium-sized taxa (those with body mass between 10 and 100 kg, according to estimates by Fariña *et al.*, 1998), represented by cervids, are the most common, followed by large-sized ones (body masses between 100 and more than 1000 kg), such as glyptodontids, ground sloths, toxodontids, litopterns, proboscideans and carnivores. Although Fariña *et al.* (1998) and Cione *et al.* (2003) did not provide estimates of body mass for pampatheriids and proterotheriids, these can be considered medium-sized taxa.

Cingulate xenarthrans are very common, with glyptodontids as the most conspicuous group, followed by pampatheriids and

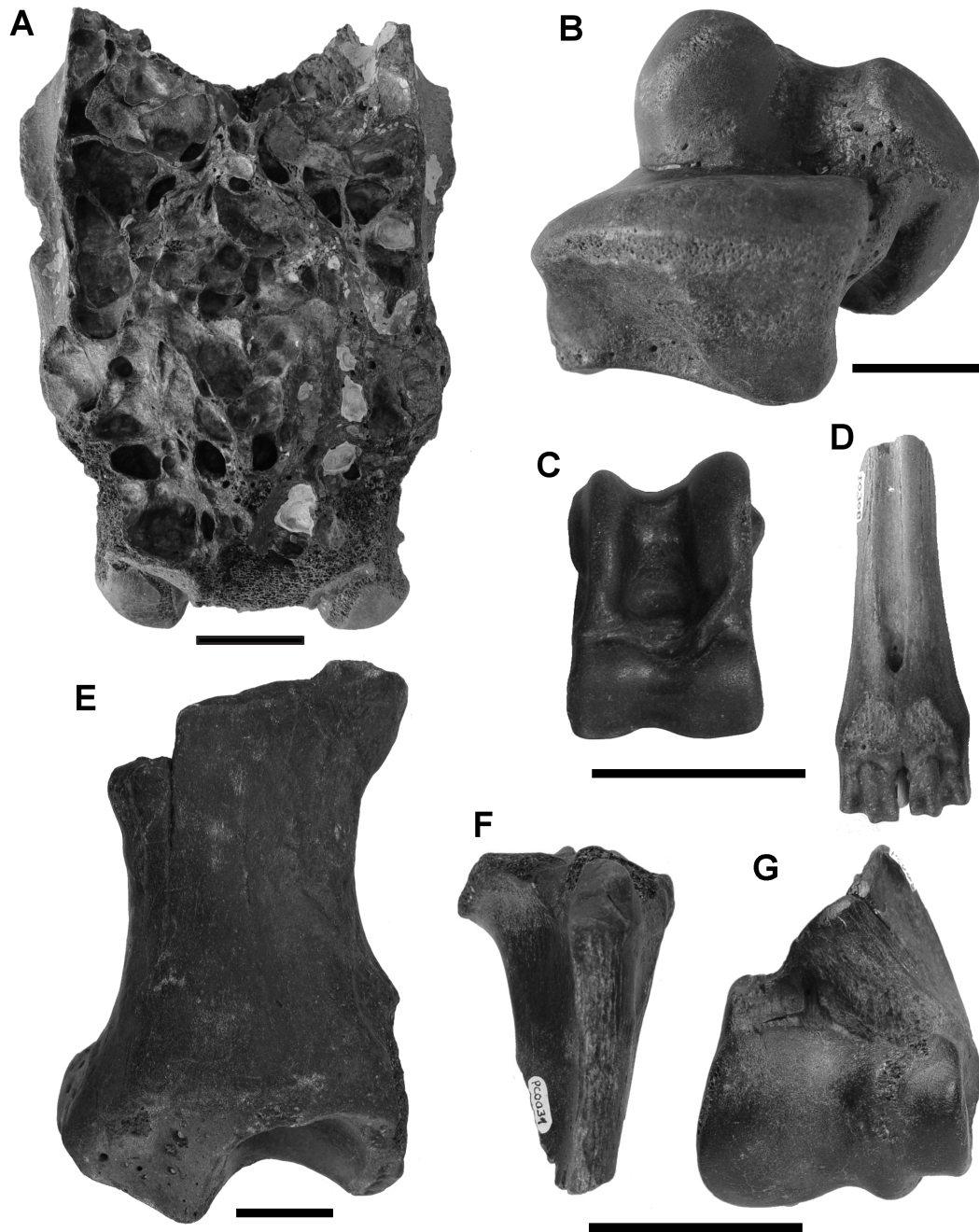


Figure 4. Fossils of terrestrial mammals. **A**, LGP-PC0045, unidentified skull, probably a ground sloth (in dorsal view); **B**, LGP-Q0013, right astragalus of *Lestodon* sp.; **C**, LGP-I0017, astragalus of an artiodactyl; **D**, LGP-I0308, metatarsal of an artiodactyl; **E**, LGP-Q0016, tibia of *Lestodon* sp.; **F**, LGP-PC0031, unidentified proximal end of a tibia; **G**, LGP-PC0205, unidentified distal end of a humerus. Scale bars = 50 mm.

dasypodids (Figure 6). Glyptodontids are easily diagnosed by the external morphology of the carapace osteoderms. The identified genera include *Glyptodon* Owen, 1845 (501 specimens), *Panochthus* Burmeister, 1872 (44), *Doedicurus* Burmeister, 1874 (23) and *Neuryurus* Ameghino, 1889 (8). Identification of the latter, which have osteoderms with irregular surface and without distinct textures (Zurita *et al.*, 2006) is sometimes dubious, because abrasion can obliterate the fine-scale textures on osteoderms of *Panochthus* making them look like *Neuryurus*. Some specimens of *Glyptodon* and *Panochthus* are represented by two or more fused osteoderms. Besides osteoderms, the only identified glyptodontid remains are two teeth fragments and

incomplete caudal tubes attributed to *Panochthus*. Pamphateriids are represented by 116 osteoderms of *Pamphaterium* Ameghino, 1875 and 53 of *Holmesina* Simpson, 1930. The most numerous are the elongated, subrectangular osteoderms of the mobile belt, although elements from the cephalic shield and pelvic and pectoral bucklers are common. The genus *Pachyarmatherium* Downing & White, 1995 is represented by only three osteoderms. This taxon was only recently described from fossiliferous deposits of the continental shelf (Bostelmann *et al.*, 2008; Ribeiro, 2008) and also from Pleistocene deposits in northeastern Brazil (Porpino *et al.*, 2009). Dasypodid fossils are very scarce, consisting of only seven osteoderms attributed to *Propraopus*

Ameghino, 1881, plus three others that could not be identified.

Remains of pilose xenarthrans include members of the Mylodontidae (131 specimens) and Megatheriidae (44). Mylodontid sloths are represented by *Glossotherium* Gervais, 1855 (22 specimens), *Lestodon* Gervais, 1855 (14), *Myodon* Owen, 1839 (11) and *Catonyx* Ameghino, 1891 (5), as well as 83 unidentified specimens. The most conspicuous fossils of this group are isolated teeth, which are difficult to identify because of the similar morphology of the first molariform teeth. In *Catonyx*, the teeth have a subtriangular transverse profile distinct from those of the mylodontines. Other features that allowed distinguishing between some genera are the morphology of the distal portion of the tibia and the astragalus (Kraglievich, 1934). The megatheriid sloths were identified by teeth (38 specimens) and one ungual phalange. Although *Megatherium* Cuvier, 1796 is the only megatheriid cited for the deposits of the CPRS, the genus *Eremotherium* Spillmann, 1948, previously recorded from other areas of Rio Grande do Sul (Toledo, 1986; Oliveira *et al.*,

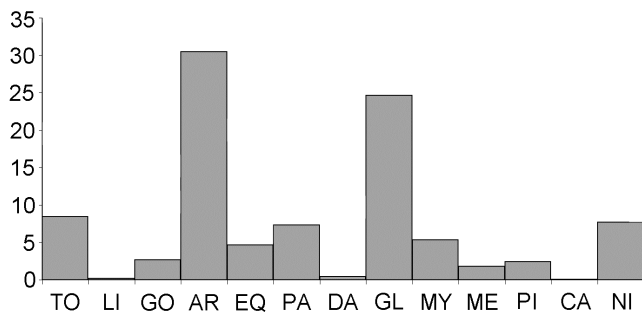


Figure 5. Relative percentages of the taxonomic groups. **Abbreviations:** TO, Toxodontidae; LI, Litopterna; GO, Gomphotheriidae; AR, Artiodactyla; EQ, Equidae; PA, Pampatheriidae; DA, Dasypodidae; GL, Glyptodontidae; MY, Mylodontidae; ME, Megatheriidae; PI, Pilosa indet.; CA, Carnivora; NI, unidentified.

2002), was recently identified in the CPRS from deposits of Chui Creek (Pereira *et al.*, 2010), so it is possible that this genus may also be present among the remains from the continental shelf.

Among the Toxodontidae, the only genus recognized for Rio Grande do Sul is *Toxodon* Owen, 1838, although a Toxodontidae indet. was recognized the continental shelf by a distal portion of a femur (Paula Couto, 1944; Cunha, 1959) and Oliveira (1992) mentioned the presence of the genus *Trigodon* Ameghino, 1887 on the basis a fragmentary tooth from the continental shelf. *Toxodon* was identified in the present analysis by 189 teeth, 15 long bones, 3 skull fragments and 1 astragalus (Figure 7A). Litopterns are rare in the fossil deposits of Rio Grande do Sul (Scherer *et al.*, 2009). The macraucheniid litopterns are represented by two fragmentary teeth and a cervical vertebra of *Macrauchenia* Owen, 1838 (Figure 7B), while protherotheriids are represented by a single astragalus, attributed to *Neolicaphrium* Frenguelli, 1921 (Figure 7C).

The Gomphotheriids found in the CPRS are represented by the genus *Stegomastodon* Pohlig, 1912 according to Marcon (2007). Fossils of this taxon are mostly teeth (62 specimens), but two fragments of dentaries and one tibia were also identified. The teeth include both molar and incisors, mostly fragmented (Figures 7D, E). The most common equid remains are teeth (Figure 7F), although two metatarsals were also identified in the collection. A detailed revision of this material is needed, because the abrasion and fragmentary condition of most of the teeth make it difficult to assign them to a specific genus. However, the identified specimens belong to *Equus* Linnaeus, 1758 and *Hippidion* Owen, 1869, previously identified among the material from the continental shelf (Cunha, 1959) and from Chui Creek (Pereira *et al.*, 2010). The only carnivore specimen in the collection is a left astragalus of *Smilodon* Lund, 1842 (Lopes & Buchmann, 2010).

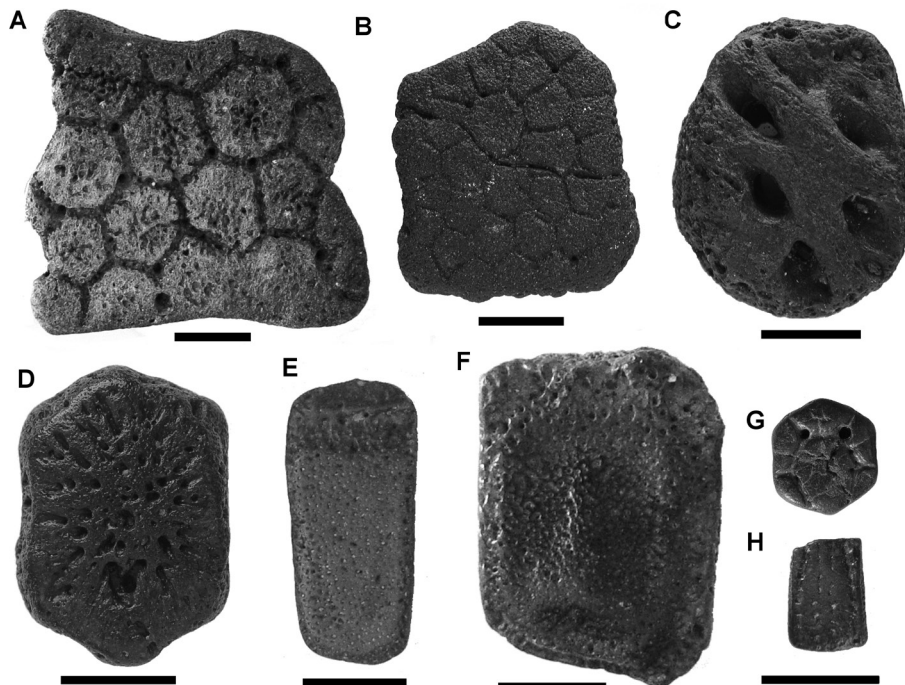


Figure 6. Osteoderms of cingulates. A, LGP-P0256, *Glyptodon*; B, LGP-P0099, *Panochthus*; C, LGP-P0098, *Doedicurus*; D, LGP-P0255, *Neuryurus*; E, LGP-N0207, *Pampatherium*; F, LGP-N0019, *Holmesina*; G, LGP-P0211, *Pachyarmatherium*; H, cf. LGP-N0060, *Propraopus*. Scale bars = 20 mm.

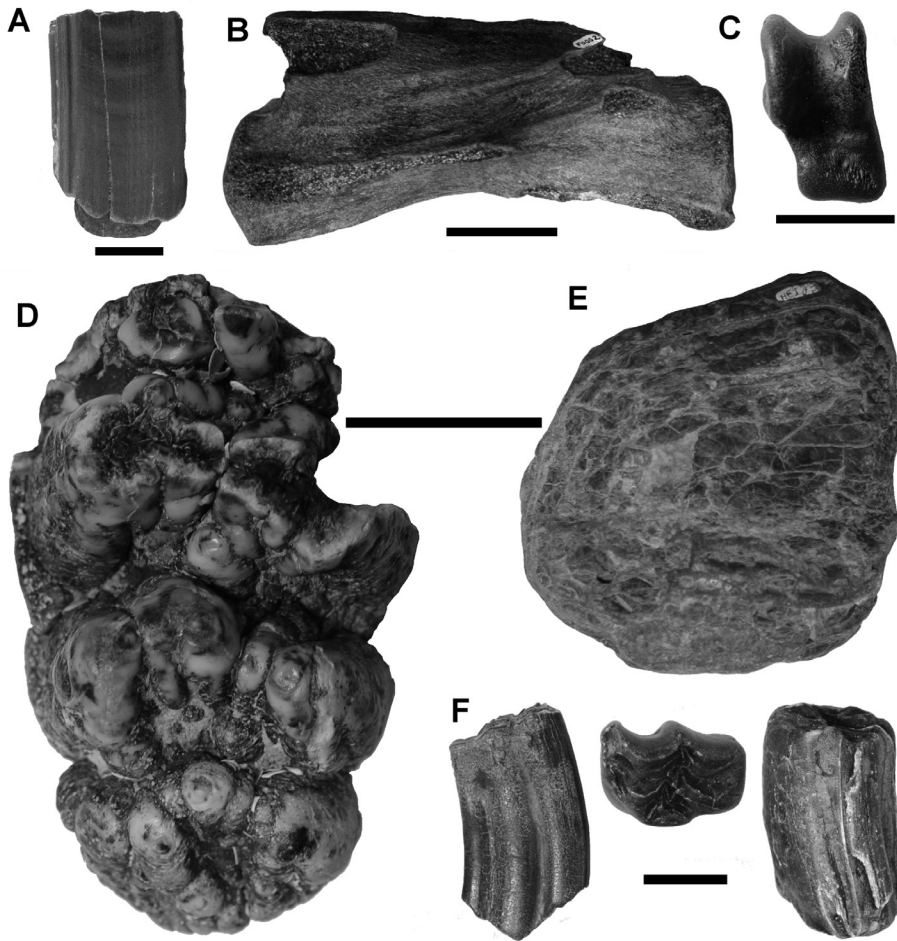


Figure 7. A, LGP-E0126, lower incisor of *Toxodon*; B, LGP-F0001, cervical vertebra of *Macrauchenia*; C, LGP-F0004, astragalus of *Neolicaphrium*; D, LGP-G0044, molar of *Stegomastodon*; E, LGP-G0051, fragment of an incisor of *Stegomastodon*; F, LGP-K0009, 0016 and 0017, equid teeth. Scale bars: A, C, F = 20 mm; B, D, E = 50 mm.

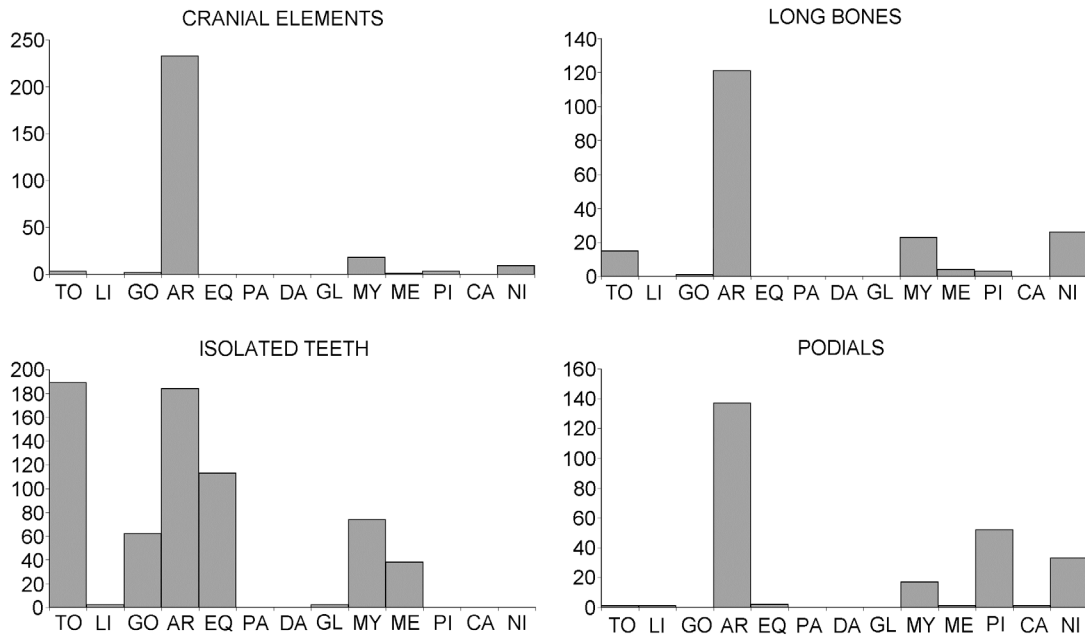


Figure 8. Relative proportions (in absolute numbers) of the different skeletal elements relative to the taxonomic groups. **Abbreviations:** TO, Toxodontidae; LI, Litopterna; GO, Gomphotheriidae; AR, Artiodactyla; EQ, Equidae; PA, Pampatheriidae; DA, Dasypodidae; GL, Glyptodontidae; MY, Mylodotidae; ME, Megatheriidae; PI, Pilosa indet.; CA, Carnivora; NI, unidentified.

DISCUSSION

The analysis of the fossil specimens revealed important variations in the relative proportions among the different mammalian taxonomic groups and respective skeletal elements (Figure 8). Considering that the fossil assemblage from the continental shelf contains remains that encompass a time span of some 700 ky BP (Lopes *et al.*, 2010), reworked and mixed together by the late Pleistocene-early Holocene sea-level oscillations, such variations cannot be attributed only to intrinsic aspects of the paleocommunities. The abundance of glyptodontids among the specimens is a combination of the large number of osteoderms (up to 2000) in the carapace of an individual, plus the small size and compact shape of the osteoderms, which cause them to be easily transported by waves and currents. Among the glyptodontid specimens, however, the predominance of *Glyptodon* over other genera probably reflects the original diversity pattern among these taxa. Given the similar shape and dimensions of the carapace osteoderms found in these taxa, which results in similar preservation and transport potentials, one should expect to find similar proportions among these genera; however, the marked differences suggest a greater relative abundance of *Glyptodon* over the other genera in the paleoecosystems of the CPRS. A similar pattern is found among glyptodontid remains from Chuí Creek, which seem to represent a shorter time interval.

Pilose xenarthrans also present differences in relative abundance, with megatheriids less abundant than mylodontids. Among the latter, the mylodontines, represented by *Glossotherium*, *Lestodon* and *Myodon* are more abundant than scelidotheriines, represented solely by *Catonyx* according to Lopes & Pereira (2010). Gaudin (2004) stated that the low representativity of scelidotheriines in Pleistocene fossil assemblages is a product of the low taxonomic diversity of this group.

The record of carnivores is also very scarce, possibly reflecting the low specific richness of this group in South America (Prevosti & Vizcaíno, 2006). Ecological factors may also be responsible for the low representativity of large-bodied taxa such as *Tapirus* and *Macrauchenia*. The abundance of large mammals that presumably inhabited open grassland environments such as ground sloths, mastodonts and glyptodonts (Oliveira, 1999) indicates that the Pleistocene environments of the CPRS were mostly open environments, which would not be suitable for the forest-dwelling *Tapirus*. Although its remains can be found from Bolivia to Chile (Scherer *et al.*, 2009), it is not clear why *Macrauchenia* is so scarce in the coastal area of Rio Grande do Sul. Given that this taxon had low-crowned teeth, it is possible that it could feed only on trees and shrubs with soft leaves, instead of the abrasive grasses found in grassland environments. A detailed review on the teeth and postcranial specimens of artiodactyls from the CPRS is necessary in order to evaluate the relative proportion between camelids and cervids.

Other factors to be considered regarding the representativity of the fossils involve taphonomy, mostly the selection by transport and mechanical destruction of the fossils by waves. The fossils are preserved in biodetrital accumulations on the continental shelf until their removal and transportation to the beach by storm waves (Buchmann, 2002; Lopes & Buchmann, 2010). This process seems to be the main one responsible for the low proportion of large cranial and postcranial remains of large-bodied taxa such as sloths, toxodontids and gomphotheriids. While smaller, more compact remains of small-bodied taxa are

easily transported by waves under normal conditions, the larger elements can be transported only by high energy waves, which occur only during extreme storms (Calliari *et al.*, 1998; Lopes *et al.*, 2006). Thus, these large remains rarely come to the beach, but once deposited there, would be removed only by a similar storm, so their residence time on the beach is longer than that of a small fossil continuously moved by normal wave regimes.

Given that the selective transportation results in relatively few large skeletal elements of large-bodied taxa being deposited on the beach, one could expect to find a relatively larger proportion of fossils of smaller-bodied taxa. However, the continuous transportation and reworking in the surf zone by wave action even under normal meteorological conditions results in a higher degree of abrasion, fragmentation and finally destruction of these remains. Even more massive skeletal remains are mostly fragmented and abraded; smaller and more compact-shaped elements are complete but most exhibit a high degree of abrasion due to their higher transportation potential (Lopes *et al.*, 2008). This process explains the abundance of podials of artiodactyls. The abundance of osteoderms of glyptodonts and pampatheriids is a combination of the large proportion of these elements from a single individual and the higher transportability of these elements. The osteoderms of smaller cingulates, such as dasypodids, are more prone to mechanical destruction and abrasion in comparison to osteoderms of glyptodonts and pampatheriids, thus are less abundant.

The higher mechanical resistance of teeth, even those of the xenarthrans that do not bear enamel, contributes to the large proportion of such remains. The abrasion and destruction of most of the fossils is not just a product of present day marine dynamics, but can also be attributed to past sea-level transgressions. Dillenburg (1994) demonstrated that a marine transgression could erode the upper 10 m of the continental shelf, which would also affect the fossil remains preserved in this area. Past fluvial dynamics could also promote mechanical alteration on these fossils; studies have shown that during sea-level low stands several fluvial channels existed on the exposed portions of the shelf (Weschenfelder *et al.*, 2008; Silva, 2009), thus these rivers could also have transported and destroyed the fossil remains.

The fossil assemblage of the continental shelf represents a time interval that encompasses at least the last 700 ky BP, which was marked by glacioeustatic oscillations. These oscillations reworked and mixed together remains of distinct ages, creating a large parautochthonous assemblage that represents a large time-averaging interval (Lopes *et al.*, 2010). This mixing is responsible for the co-occurrence of non-analogous taxa (*sensu* Lundelius, 1989), such as organisms that inhabit open, semiarid environments (Dolichotinae, *Reithrodon*), together with others that indicate forested (*Tapirus*) and permanently humid (*Myocastor*, *Hydrochoerus*) environments. Alternatively, this mixing could be related to the existence in the Pleistocene of environmental conditions not found in modern ecosystems. A similar pattern is observed in fossil assemblages from continental deposits of the Sopas Formation of Uruguay (Ubilla, 2004) and Chuí Creek, although in the latter the mixing could be in fact the result of time-averaging and erosive processes (Lopes, *in press*).

CONCLUSIONS

Although the fossil assemblage from the southern Brazilian continental shelf does not represent a single paleocommunity or paleoecosystem, and encompasses remains of different ages,

the analysis of the skeletal remains revealed that the taxonomic representativity of this assemblage seems to be influenced by a combination of ecological and taphonomic factors. The relative abundance among glyptodontid taxa from this assemblage probably reflects the original taxonomic abundance within this group, with *Glyptodon* being more diverse and abundant than other glyptodontids. The low ecological diversity explains the scarcity of fossils of carnivores and scelidotheriine sloths. The relative absence of other taxa such as *Macrauchenia* and *Tapirus* seems to be related to ecological factors, given that remains of these large-bodied taxa would not be as much affected by taphonomic factors as the small-bodied taxa. This question could be resolved with detailed paleoecological studies and comparison with other geographically and temporally close fossil assemblages.

Taphonomic factors affect the relative proportions of taxa by selective transportation and destruction of the smaller and/or compact-shaped remains. Once removed from the deposits on the shelf, these remains are continuously moved and transported by waves that promote their abrasion and destruction; this process would be a major reason for the relative absence of small organisms such as rodents and protheriids. Larger elements, on the other hand, are removed and transported to the beach only on rare occasions when extreme storm waves affect the deposits.

The high proportion of osteoderms of glyptodontids and pampatheriids results from a combination of the large number of these elements on a single individual, plus their higher transportation potential due to their small size and compact shape. The lower proportion of the smaller osteoderms of dasypodids, however, is likely to be a result of mechanical fragmentation and abrasion.

The results presented here are partially hampered by the abrasion and fragmentation of most of the specimens, and also by the lack of a detailed revision of certain groups (e.g. Mylodontidae, Equidae). A careful taxonomic analysis shall improve the taxonomic resolution of the material and improve the estimates of diversity of those groups.

Although it cannot be considered as representing a paleocommunity or paleoenvironment, given the large time-averaging of the remains, further research on continental fossil localities of more restricted age should provide additional information regarding the Pleistocene mammalian communities and a means for paleoecological comparisons with the assemblage from the continental shelf. This study also reinforces the importance of evaluating the taphonomic processes that affect fossil assemblages when using fossil remains for reconstructing paleoenvironments and paleocommunities.

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