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Pleistocene mammals from the southern Brazilian continental shelf

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ABSTRACT

Fossils of terrestrial mammals preserved in submarine environment have been recorded in several places around the world. In Brazil such fossils are rather abundant in the southernmost portion of the coast, associated to fossiliferous concentrations at depths up to 10 m. Here is presented a review of such occurrences and the first record of fossils in deeper areas of the continental shelf. The fossils encompass several groups of both extinct and extant mammals, and exhibit several distinct taphonomic features, related to the marine environment. Those from the inner continental shelf are removed and transported from the submarine deposits to the coast during storm events, thus forming large *konzentrat-lagerstätte* on the beach, called "Concheiros". The only fossils from deeper zones of the shelf known so far are a portion of a skull, a left humerus and of a femur of *Toxodon* sp. and a lower right molar of a *Stegomastodon waringi*, all collected by fishermen at depths around 20 m. The presence of fossils at great depths and distances from the present coastline, without signs of abrasion and far from areas of fluvial discharges does indicate that these remains have not been transported from the continent to the shelf, but have been preserved directly on the area that today correspond to the continental shelf. These remains indicate the existence of large fossiliferous deposits that have developed during periods of sea-level lowstand (glacial maxima) and have been submerged and reworked by the sea-level rise at the end of the last glaciation.

1. Introduction

Fossils of terrestrial mammals have been recorded on continental shelves of the Sea of Japan, the northeastern coast of North America (Whitmore et al., 1967; Hoyle et al., 2004), the North Sea (Van Kolfschoten and Laban, 1995; Mol et al., 2006), in the Argentinean continental shelf (Tonni and Cione, 1999; Cione et al., 2005) and the northeastern coast of Uruguay (Rinderknecht, 2006). The presence of such remains in submarine environment is attributed to fossiliferous deposits that were formed on areas of the continental shelf that have been under subaerial exposure due to sea-level oscillations during the Quaternary (glacio-eustasy). This exposition is correlated to glacial maxima, when sea-level dropped 120 m below the present level all around the globe (Villwock, 1984; Corrêa et al., 1996; Bridgland, 2002). In the Brazilian continental shelf, such fossils have been recovered so far only from its southernmost portion, in the coast of the Rio Grande do Sul State, mostly on the beach but also from deeper locations, such as the Parcel do Carpinteiro, a submarine rocky structure located at 32°16′S × 051°47′W at a depth of 25 m (Buchmann, 1994; Buchmann et al., 2001). Here is presented a review of the presence of fossils of terrestrial mammals in nearshore environments, and some specimens collected from deeper areas far from the coast are described for the first time in the Brazilian coast.

2. Geological setting

The Coastal Plain of the of Rio Grande do Sul State (RSCP, Fig. 1) is a 620 km-long geomorphological unit located between the latitudes 29°18′31″S and 33°43′17″S, and constitutes the area of the coastal province of Rio Grande do Sul that remains above sea-level. It corresponds to the upper portion of the Pelotas Basin, the southernmost Brazilian marginal sedimentary basin. This basin has a maximum thickness of 10 km and was formed by the accumulation of sediments eroded from Paleozoic and Mesozoic rocks of the continental geological units after the split between South America and Africa in the Late Cretaceous (Closs, 1970). After the opening of

Abbreviations: LGP, Laboratório de Geologia e Paleontologia; E, Notoungulata: Toxodontidae; G, Proboscidea: Gomphotheriidae.

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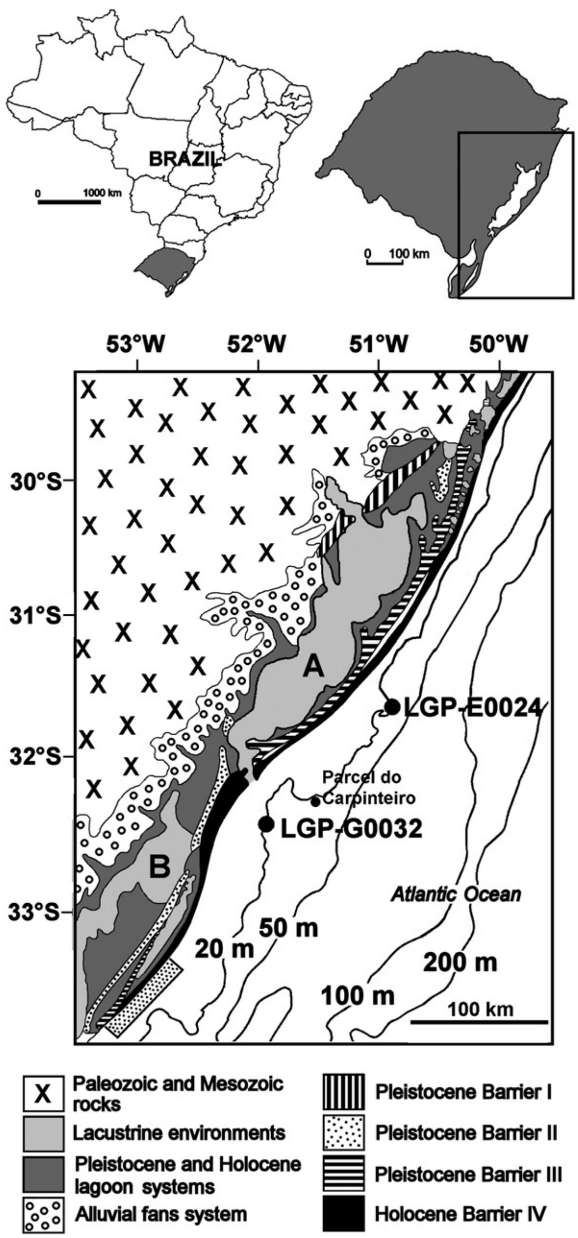

Fig. 1. Map of the State of Rio Grande do Sul showing the structure of the coastal plain (modified from Tomazelli et al., 2000), plus bathymetric lines and places where the specimens LGP-E0024 and G0032 were collected. The area of the "Concheiros" is indicated by the stippled rectangle on the south. A – Patos Lagoon; B – Mirim Lake.

the Atlantic Ocean, the Brazilian continental margin was subject to deposition of sediments eroded from continental areas and transported to the coastal areas by fluvial systems. In the Pelotas basin, Albian sediments mark the transition from continental to marine transgressive enviroments (Bueno et al., 2007). Between the Tertiary and Quaternary the morphology of the RSCP was influenced by eustatic oscillations correlated to the glacial–interglacial cycles, represented by facies changes and microfossil assemblages recovered from drilling holes (Closs, 1970; Carreño et al., 1999). As a result of these oscillations, two major depositional systems were formed parallel to the coastline: the Tertiary Alluvial Fans System and the Quaternary Complex Multiple Barrier system (Villwock, 1984; Villwock et al., 1986).

The Complex Multiple Barrier System is subdivided into four major barrier-lagoon depositional systems and associated features. Each system was formed in response to a major sea-level transgression during interglacial episodes. The exact ages of such deposits is still undetermined, but are correlated to the interglacial maxima at 400 ky (Barrier-Lagoon System I), 325 ky, (Barrier-Lagoon System II), 123 ky (Barrier-Lagoon System III) and 6 ky (Barrier-Lagoon System IV) (Villwock and Tomazelli, 1995; Tomazelli et al., 2000). The sediments that constitute these systems are essentially terrigenous sicliciclastic, well-selected and mature, with small fractions of organic matter, biogenic carbonate and diagenetic clays, with some expressive concentrations of heavy minerals (Villwock and Tomazelli, 1995). In the southen portion of the coast, large concentrations of Pleistocene marine bioclasts, composed mostly by rounded shell fragments, are found (Buchmann et al., 2009; see below). Figueiredo (1975) obtained 14C ages between 16 ka and more than 30 ka for fossil marine shells collected from the continental shelf. These bioclasts can be classified as palimpsests, i.e., relict sediments (deposited during and/or right after the last glacial maximum) that are being reworked by dynamic processes of today (Pilkey and Frankenberg, 1964; Swift et al., 1971). Some 70% of the sediments from continental shelves around the world can be classified as relicts (Emery, 1968).

The continental shelf, which constitutes the submarine portion of the coastal province, has a low topographic gradient (a 1:1.000 average ratio) and the shelf break is located at depths between 80 and 170 m. The shelf is broad and was subject to extensive reworking and contains submerged paleo-fluvial channels and sand banks (Corrêa et al., 1996). During the Holocene sea transgression, around 6–7 ky, variations in the rates of sea-level rise resulted in the reworking and concentration of terrigenous clastic sediments of the shelf, and erosive terraces were formed in response to episodes of sea-level stabilization (Kowsmann and Costa, 1974; Martins et al., 1996). Sediments that constitute the upper portion of the shelf are clastic terrigenous, originated in the older geomorphologic units, and were deposited by several fluvial systems during the sea-level lowstands, including the La Plata river (Tomazelli, 1978; Martins, 1983).

The fossils described here come from two distinct areas of the shelf: the inner shelf (from the surf zone up to depths of 10 m, roughly the zone affected by wave action), and the outer shelf (at depths of 20 m and more, where the action of waves does not reach the ocean bottom). Although the presence of fossils from the nearshore has been recorded all along the coast of Rio Grande do Sul, such remains are more conspicuous in the southernmost portion (Buchmann, 1994). Fossils from the outer continental shelf are described here for the first time for the Brazilian coast.

3. Fossils from the inner continental shelf

The presence of fossils of terrestrial mammals on the coast of Rio Grande do SulState, in southernmost Brazil, has been known since the late XIX century, when German naturalist Herman von Ihering described in a letter to the Argentinean paleontologist Florentino Ameghino some remains of glyptodonts that he had collected on the beach (Von Ihering, 1891). Throughout the XX century, the fossils have been subject of several studies, focusing mostly on its systematics (e.g. Cunha, 1959 47 p.; Paula Couto and Cunha, 1965; Oliveira, 1992, 1996; Rodrigues et al., 2004; Scherer, 2005; Marcon, 2007). Other studies have described the distribution of these remains along the shoreline (Buchmann, 1994) and its taphonomy (Lopes et al., 2008).

These fossils are found associated to large concentrations of fossil shellfish and other marine organisms found on the inner continental shelf (Figueiredo (1975)). During autumn and winter, storm waves erode these deposits, removing the fossils and throwing it onto the beach. The fossil shellfish accumulated throughout the years along the beach constitutes a large *konzentrat-lagarstätte* called “Concheiros” along the southernmost portion of the coast. Such *lagerstätte* did not exist on the beach until the early 1970s (Luiz Rota, pers. comm.); Figueiredo (1975) described it as patches of fossil shellfish measuring few kilometers in length, some 5 m in width and 3 cm in thickness. Today the “Concheiros” are large fossil concentrations extending continuously for some 40 km, measuring up to 2 m in thickness, and have been expanding northwards and southwards throughout the years (Buchmann, 2002). The origin and evolution of such concentrations is probably related to the marine erosive processes that have been affecting this portion of the coast in the last decades (Dillenburg et al., 2004) and remove the recent sedimentary cover, exposing the underlying Pleistocene sediments. The shellfish fossils encompass both taxa that live in the surf zone and others that live in deeper areas (Lopes and Buchmann, 2008), thus these concentrations do not represent a community, but instead are a result of sedimentological processes.

The fossils are found disarticulated and scattered along the beach. Although remains of several marine organisms such as teleost and elasmobranch fishes (Richter, 1987; Buchmann and Rincón Filho, 1997), shellfish (Figueiredo (1975); Lopes and Buchmann, 2008), echinoderms, crustaceans (Buchmann, 1994; Lopes, 2009), pinnipeds (Oliveira and Drehmer, 1997), cetaceans (Cunha, 1982; Ribeiro et al., 1998) and seabirds (Lopes et al., 2006) are found in these concentrations, the most remarkable are the fossils of terrestrial mammals (Fig. 2). Several taxa are represented among these remains, most of them extinct (Table 1). Some Pleistocene taxa are recorded in Rio Grande do Sul State only by fossils collected in the “Concheiros” (Rodrigues et al., 2004; Rodrigues and Ferigolo, 2004; Bostelmann, 2008; Ribeiro et al., 2008; Scherer et al., 2009), and an alligatorid fossil has also been recorded (Hsiou and Fortier, 2007). Because these fossils are found removed from its deposits they do not have a precise stratigraphic context, and this has led to several misconceptions regarding the geological origin of these remains. In the first systematic geological mapping of the coast of Rio Grande do Sul (Delaney, 1965), the remains were associated to Tertiary deposits of the “Graxaim Formation” (now recognized as the Alluvial Fans Systems) that presumably extended in subsurface from the continent to the continental shelf. Later, this assumption was challenged because no vertebrate fossil was ever recovered from the “Graxaim Formation” (Paula Couto and Cunha, 1965). Soliani (1973) described the stratigraphy of the Chuí Creek, a fossiliferous continental deposit in the southern portion of the RSCP containing the same fossils found along the beach, thus he concluded that both deposits had the same age and were part of the “Santa Vitória Formation”, a scheme that has

Fig. 2. A detail of the “Concheiros”, with a fossil of terrestrial mammal (distal portion of the caudal tube of the glyptodont *Panochthus*) (the scale measures 50 mm).

Table 1
Terrestrial mammals found in fossiliferous deposits of the southern Brazilian continental shelf (following the classification of McKenna and Bell, 1997).

Phyllum CHORDATA Bateson, 1885
Class MAMMALIA Linnaeus, 1758
Superorder XENARTHRA Cope, 1889
Order PILOSA Flower, 1883
Family MEGATHERIIDAE Owen, 1843
Megatherium Cuvier, 1796
Family MYLODONTIDAE Gill, 1872
Glossotherium Gervais, 1855
Lestodon Gervais, 1855
Mylodon Owen, 1839
Catonyx Ameghino, 1891
Order CINGULATA Illiger, 1881
Family DASYPODIDAE Bonaparte, 1838
Propraopus Ameghino, 1881
Family PAMPATHERIIDAE Paula Couto, 1954
Holmesina Simpson, 1930
Pampatherium Ameghino, 1875
Family GLYPTODONTIDAE Burmeister, 1879
Doedicurus Burmeister, 1874
Glyptodon Owen, 1845
Panochthus Burmeister, 1872
Neuryurus Ameghino, 1889
Pachyarmatherium Downing & White, 1995
Order LITOPTERNA Ameghino, 1889
Family MACRAUCHENIIDAE Gervais, 1855
Macrauchenia Owen, 1838
Family Proterotheriidae Ameghino, 1887
Neolicaphrium Frenguelli, 1921
Order NOTOUNGULATA Roth, 1903
Family TOXODONTIDAE Owen, 1845
Toxodon Owen, 1838
Order CARNIVORA Bowdich, 1821
Family FELIDAE Gray, 1821
Smilodon Lund, 1842
Family CANIDAE Fischer de Waldheim, 1817
Protocyon Lund, 1842
Dusicyon Hamilton-Smith, 1839
Theriodictis Mercerat, 1891
Order RODENTIA Bowdich, 1821
Family CAVIIDAE Fischer de Waldheim, 1817
cf. *Cavia* Pallas, 1766
Dolichotinae (indet.) Pocock, 1922
Family HYDROCHOERIIDAE Brisson, 1762
Hydrochoerus Brisson, 1762
Family OCTODONTIDAE Waterhouse, 1839
cf. *Ctenomys* Blainville, 1826
Family MURIDAE (=CRICETIDAE) Illiger, 1811
Reithrodon Waterhouse, 1837
Family ECHIMIYDAE Gray, 1825
Myocastor Kerr, 1792
Heteromysopinae (indet.) Anthony, 1917
Order URANOTHERIA McKenna & Bell, 1997
Family GOMPHOTHERIIDAE Hay, 1922
Stegomastodon Pohlig, 1912
Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Equus Linnaeus, 1758
Hippidion Owen, 1869
Family TAPIRIDAE Gray, 1821
Tapirus Brunnich, 1772
Order ARTIODACTYLA Owen, 1848
Family CAMELIDAE Gray, 1821
Lama Cuvier, 1800
Hemiauchenia Gervais & Ameghino, 1880
Family CERVIDAE Goldfuss, 1820
Antifer Ameghino, 1889
Morenelaphus Carette, 1922
Family TAYASSUIDAE Palmer, 1897
Tayassuidae indet.

been adopted throughout the years (Oliveira, 1992, 1996; Lopes et al., 2005). However, datings by electron spin resonance (ESR) in enamel samples extracted from teeth, obtained ages between 650 ± 100 ka and 18 ± 3 ka for the fossils from the nearshore and between 34 ± 7 ka and 42 ± 3 ka for those from the Chuí Creek (Lopes et al., 2010), thus indicating that both deposits are distinct units, formed at different epochs.

The vertebrate fossils exhibit remarkable taphonomic features, related to its preservation in marine environment. All specimens are heavily mineralized and exhibit dark colors, ranging from reddish to black, probable due to the influence of elements such as iron and manganese. Most of the fossils are broken and abraded due to erosion and transportation by waves (Lopes et al., 2008). Although unidentifiable, broken and very abraded bone fragments are the most common (Fig. 3), sometimes larger and even complete specimens are found. Some fossils are either embedded in coquina blocks (Fig. 4) or have cavities filled with sand or mud that was lithified by precipitation of calcium carbonate, features related to the Taphofacies II of Lopes et al. (2008) (Table 2). The precipitation of carbonate cement under a warmer climate regime during the Pleistocene was responsible by the formation of lithified paleo-beachlines that are found in the near continental shelf and are the source of the blocks of coquinas found thrown onto the beach by storms (Asp, 1999; Buchmann et al., 2001; Buchmann, 2002).

These fossils are subject to two major environmental processes: exposure in the water–sediment interface due to removal of Holocene sediments by long-term erosion of the shelf, related to shoreface retreatment, and removal and transportation to the beach by waves. Two types of waves affect the fossil remains: storm waves, which remove and transport large amounts of fossils and redeposit it onto the beach, and "normal" waves, which continuously rework smaller remains in the surf zone. These physical processes are the main cause of biostratinomic alteration on these remains, although some features are probably related to preservation on continental environment, prior to its exposure to marine environment (Lopes et al., 2008).

In a biostratigraphic sense, Paula Couto and Cunha (1965) correlated these mammalian fossils to the "Pampeano Superior" (Bonaerean) of Argentina. Later, Bombin (1975) correlated these remains to the Lujanian Land-Mammal Age of the Pampean Region of Argentina based on the presence of fossils of *Equus* (*Amerhippus*)

Fig. 3. Unidentified fossil fragments (scale bar 20 mm).

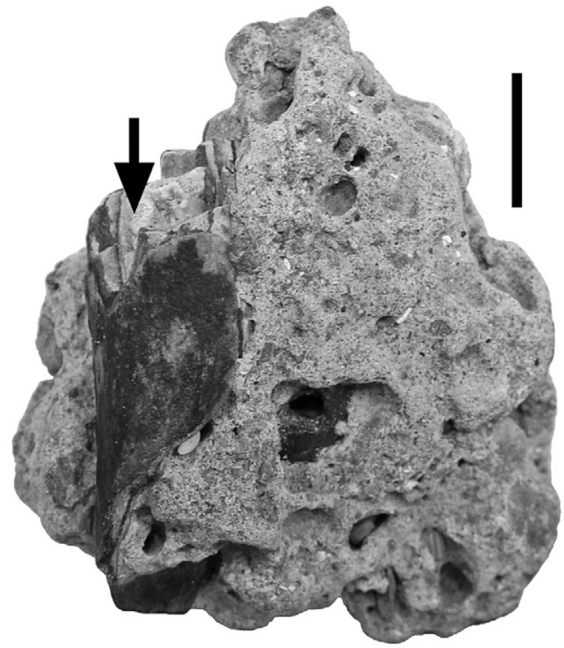

Fig. 4. A molariform of a mylodontid ground sloth (indicated by arrow) embedded in a coquina (scale bar 20 mm).

neogaeus, and this has been accepted throughout the years. More recently, Cione and Tonni (1995) have replaced the South American "Land-Mammal Age" concept for the chronostratigraphic Stage/Age scheme, placing the Lujanian Stage/Age between 130 and 8,5 ka AP. However, the ESR ages indicate that the fossils from the continental shelf are not only of Lujanian bus also of Ensenadan and Bonaerean Stage/Ages (Lopes et al., 2010). Although these fossils do not have a precise stratigraphic context, the ages are correlated to marine isotope stages (MIS) 16, 12, 8, 6, 4 and 2, indicating that the organisms occupied the area during the glacial maxima. According to Rabassa et al. (2005), during these maxima the Pampean fauna would have extended its distribution area farther to the north, following the northward migration of the climatic belt. The northern distribution of certain mammalian taxa, such as *Megatherium americanum* and *Doedicurus clavicaudatus* is restricted to southern Brazil, probably reflecting the maximum reach of the climatic belt during glaciations. During interglacials, on the other hand, elements of the Brazilian fauna such as *Tapirus* and *Holochilus* reached the Pampean area of Argentina, reflecting the southward migration of the climatic belts.

A survey among 1819 fossils from the paleontological collection of Universidade Federal do Rio Grande (FURG), all collected along the 226 km-long shoreline between Rio Grande and Chuí during the last 15 years, has shown that the most common remains are teeth (Fig. 5), followed by osteoderms and cranial elements (Table 3). The osteoderms belong to cingulates, mostly glyptodontids. The glyptodontid osteoderms occur mostly isolated, but partial carapaces, formed by several osteoderms fused together, can also be found (Fig. 6). Osteoderms of pampatheriids and dasypodids are also common, found only as isolated elements. The osteoderms are found mostly complete, but sometimes it is difficult to see morphological details because of abrasion.

The cranial remains are represented mostly by cervid antlers, but some jaw and skull fragments of other taxa are also found. The most conspicuous autopodial elements are astragali of artiodactyls and mylodontid sloths; phalanges of ground sloths are also common (Fig. 7). These smaller elements are found mostly complete, although

Table 2
Taphofacies recognized among the fossils from the continental shelf (Lopes et al., 2008).

Taphofacies	Features	Depositional context
I	Very fragmented and abraded fossils, without colonization or carbonate cement	Remains that were covered by sediments, now exposed by erosive processes and continuously under influence of waves.
II	Fossils fragmented and very abraded; associated to coquinas	Remains that were reworked and redeposited on beach environments in the past, when climatic conditions allowed the formation of coquinas. Currently associated to rocky structures representing paleo-beachlines that are being eroded.
III	Fossils with better preservation, mostly incomplete, but with few or no signs of abrasion. Colonization by epi- and endoskeletozoans	Remains currently exposed on the sediment–water interface, below the zone influenced by waves. Probably reworked in the past during a sea-level transgression

some are much abraded. Most of the limb bones belong to large-bodied taxa such as toxodontids and sloths, but bones of smaller organisms, although less common, can also be found. Limb bones exhibit the largest range of taphonomic variation, from specimens nearly unrecognizable due to abrasion and/or fragmentation to complete or nearly complete specimens. The transport of larger limb fossils to the beach requires extremely strong waves, thus these are not very common, but once thrown onto the beach such bones would not be reworked or transported again until the next extreme storm surge. On the other hand, limbs of smaller specimens are more easily transported and removed, thus are more likely to be destroyed by mechanical action of the waves in the surf zone. Vertebral elements occur mostly as broken neural arches or centra. Complete or near complete vertebrae are mostly smaller ones that belong to artiodactyls. Other elements, found as fragments, include scapulae, ribs and caudal tubes of glyptodontids (Fig. 8).

Very few of the fossils that are transported to the beach exhibit signs of boring or fouling by marine organisms, such as barnacles, pelecypods, corals or bryozoans. The remains that do not exhibit bioerosion are either being constantly subject to moving by waves and currents, or are covered with sediments until being exhumed and transported to the beach (Lopes et al., 2008). The recorded taxa are mostly large-bodied herbivores such as toxodonts, mastodonts, glyptodonts, horses and cervids. A remarkable fact is that in comparison to other Pleistocene fossil localities in Brazil the record of cervids is much more abundant. Other organisms such as macrauchenids, proterotheriids and rodents, although scarce, can also be found (Rodrigues and Ferigolo, 2004; Scherer et al., 2009). The latter

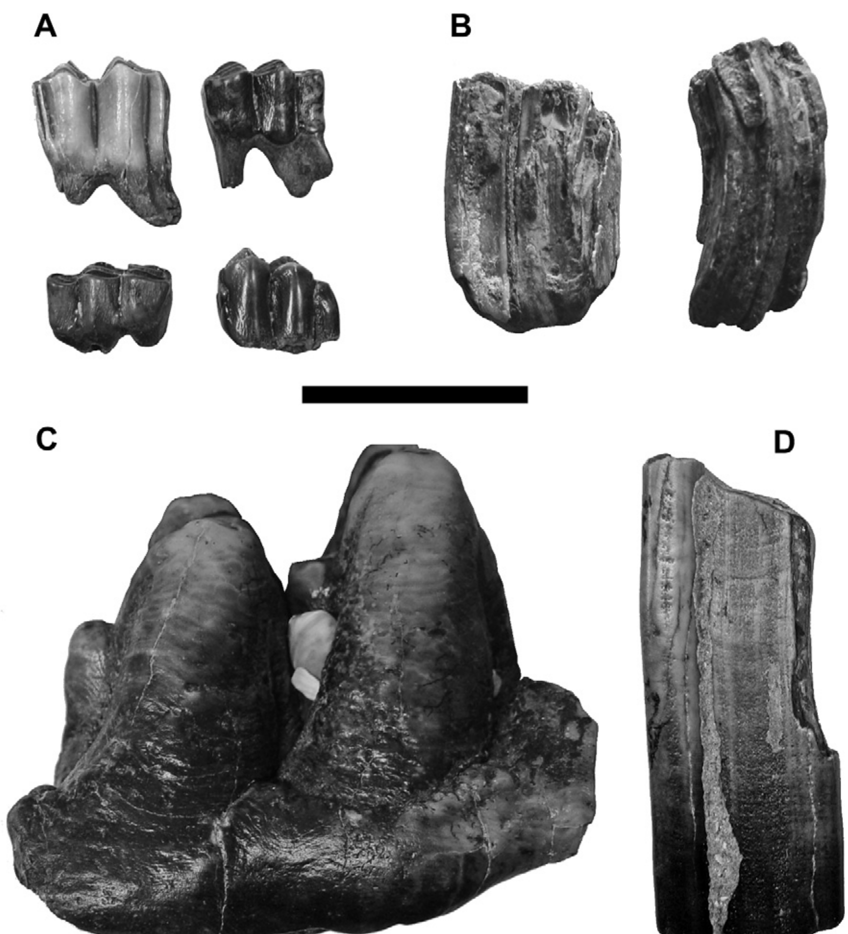

Fig. 5. Isolated teeth collected in the "Concheiros". A: artiodactyls; B: equids; C: *Stegomastodon*; D: *Toxodon* (scale bar 50 mm).

Table 3
Relative proportions of fossil specimens from the neashore in the paleontological collection of FURG.

Skeletal parts	N
Teeth (isolated)	659
Osteoderms	466
Skull elements (including jaws)	255
Autopodial elements (carpal, metacarpals, tarsals, metatarsals, phalanges)	180
Limb bones (humeri, ulnae, radii, femora, tibiae)	135
Vertebrae	102
Scapulae	19
Ribs	3
TOTAL	**1819**

are represented mostly by isolated teeth, and the absence of other skeletal elements is probably due to mechanical destruction by waves.

4. Fossils from the outer continental shelf

The presence of fossils of large vertebrates found on the continental shelf of Rio Grande do Sul at depths up to 46 m have been cited on the literature (Villwock, 1984; Buchmann, 1994), but because no detailed description of such fossils was ever published, it is not possible to evaluate whether these were from marine or terrestrial taxa. Here is presented the first detailed description of fossils unambiguously identified as extinct terrestrial mammals found in the outer continental shelf.

The fossils are part of the paleontological collection of the Universidade Federal do Rio Grande (FURG), and consist of a partial skull (catalog number LGP-E0020), a left humerus (LGP-E0021) and a distal fragment of a right femur (LGP-E0024), all belonging to *Toxodon* sp. Owen, 1838. The other fossil is a lower right m3 (LGP-G0032) of a *Stegomastodon waringi* Holland, 1920. These specimens (Fig. 9) were brought to FURG in the early 1990s by fishermen who caught it in bottom trawlers between the central and southern sectors of the coast. However, because the fishing technique requires the fishing net to be dragged for long distances, and the fossils have been collected before the adoption of GPS, only two have the exact location described. One of these (LGP-E0024) was collected at depths around 20 m, some 100 km to the north of the city of Rio Grande and some 20 km offshore. The other (LGP-G0032) was collected some 16 km to the south of the city, some 36 km offshore, in an area known by the fishermen as “graveyard” due to the presence of several bones (mostly cetaceans) on the bottom, that are brought to the surface by the fishing nets.

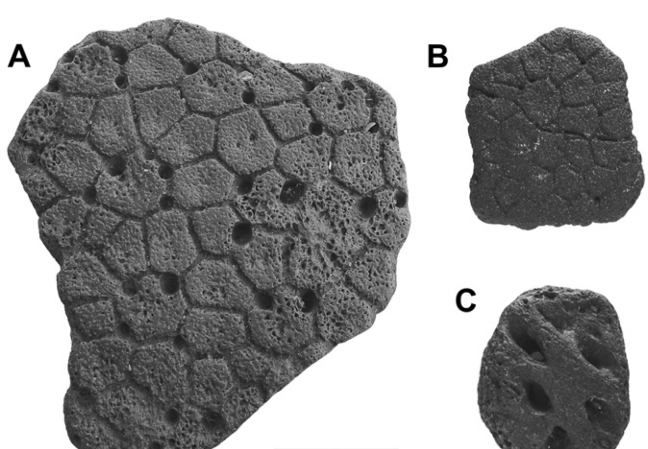

Fig. 6. Osteoderms of cingulates: fused osteoderms of *Glyptodon* (A); isolated osteoderms of *Panochthus* (B) and *Doedicurus* (C) (scale bar 50 mm).

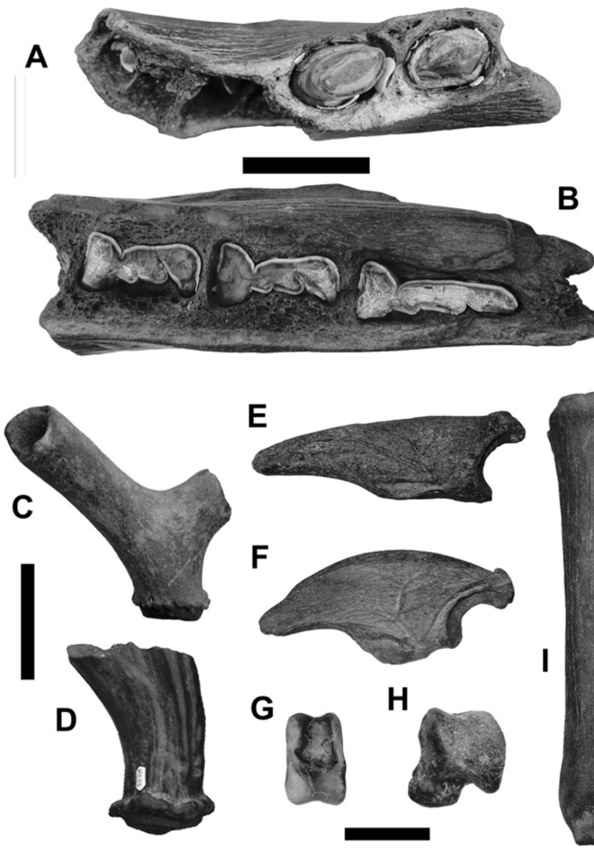

Fig. 7. A) fragment of a mylodontid sloth dentary; B) fragment of a *Toxodon* dentary; C) antler of *Morenelaphus*; D) antler of *Antifer*; E) mylodontid sloth ungueal phalange; F) megatheriid sloth ungueal phalange; G) artiodactyl astragalus; H) astragalus of *Smilodon*; I) equid metatarsal (scale bars 50 mm).

The specimen LGP-E0020 (Fig. 9a) is an occipital portion of the skull of a *Toxodon* sp. The dorsal margin of the skull is partially broken, but the sagittal crest and the caudal portion of the zygomatic arches are preserved. The specimen LGP-E0021 (Fig. 9b) is a left humerus of *Toxodon*, originally mentioned by Buchmann (2002). This fossil is fractured on its proximal end. The internal cavity of the bone is hollow and has some fine sediment within. The shaft was damaged right above the distal articular surface during the recovery from the bottom of the sea, and part of the bone above the entepicondyle was lost.

The specimen LGP-E0024 (Fig. 9c) is the lower portion of a right femur of a *Toxodon* sp. This fossil exhibits little colonization by organisms. The medial side of the patellar surface is the only portion with significant colonization; few other organisms are found isolated along the specimen. The medullar cavity is hollow, and contains vestiges of mud. Longitudinal crackings are visible long the axis of the bone, and both articular condyles are covered by reticulate crackings. These features may be result of the exposition to weathering for some time before the final burial (Lopes et al., 2008). The molar of *Stegomastodon* (Fig. 10d) was originally described by Marcon (2007). This fossil consists of the crown of a right lower m3, without the roots. The protolophid and metalophid exhibit wearing due to mastication, while the 3rd, 4th and 5th lophids are partially fractured, but exhibit no signs of wear. This specimen does also exhibit little colonization by episkeletozoans, encrusted on the labial side of the caudal end.

The skull and humerus are almost entirely colonized by encrusting (episkeletozoans, sensu Taylor and Wilson, 2002) marine organisms such as ostreids (*Ostrea* cf. *equestris*), barnacles (*Toracica*

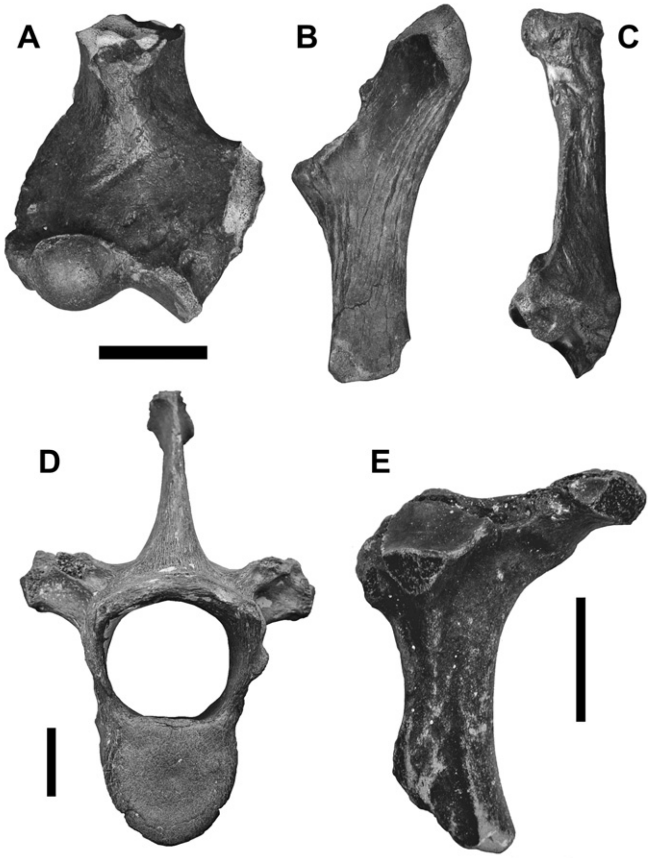

Fig. 8. A) distal portion of the humerus of a mylodontid sloth; B) ulna, and C) radius of *Toxodon*; D) unidentified vertebra; E) proximal end of a rib (scale bars 50 mm).

balanus), galleries of polychaets (*Spirolis* sp.), corals (*Astrangia rathbuni*) and an unidentified coelenterate. The humerus does also exhibit colonization by a boring (endoskeletozoan) pelecypod (*Litophaga* sp.) (Fig. 10). The colonizing organisms are recent, as indicated by the presence of soft tissues associated. Some valves of *Ostrea* do also exhibit small (about 1 mm in diameter) circular borings identical to those present on fossil shellfish from the coastal plain (Lopes and Buchmann, 2008) and attributed to the ichnogenus *Entobia* sp.

The age of these remains is uncertain, but probably encompasses the time interval between 650 and 18 ka at least, by extrapolating the ages of the fossils dated by Lopes et al. (2010).

5. Discussion

The main difference between the fossils collected along the shoreline and those from the outer continental shelf is the presence of colonizing organisms on the latter. This feature allows a correlation of these remains to the Taphofacies III of Lopes et al. (2008), characterized by relatively well-preserved remains exhibiting endo- and episkeletozoans, indicating that these fossils remain total or partially exposed for long periods on the water–sediment interface, at depths below the influence of the waves (Table 2). Other preservation features include the absence of abrasion and the longitudinal fractures along the axis of the specimen LGP-E0024. The pattern of plain fractures does indicate that the remains were subject to some post-fossilization reworking. This could only have occurred in the past, probably by sea-level oscillations, because the fossils are currently preserved at depths below the influence area of the waves, thus are not moved. The m3 of *Stegomastodon* and the humerus of *Toxodon* were fractured during its retrieval from the bottom of the sea, and had to be restored in laboratory. The recent fractures exhibit different color in comparison to the rest of the bone.

Cunha (1959, 47 p.) described several dental and postcranial isolated remains attributed to *Toxodon platensis*, plus a distal end of a right femur classified as Toxodontidae indet., all collected along the beach. However, the wide time span obtained by Lopes et al. (2010) for the fossils from the continental shelf, encompassing from Ensenadan to Lujanian, imply that other species of *Toxodon* may be represented among the specimens from the continental shelf. The specimens MOT0035 and MOT0027, with ages of 650 100 ka and 480 30 ka, respectively, were classified as *T. platensis*, but now should be considered *Toxodon* sp. and the same should be applied to all toxodontid remains from the continental shelf. According to Bond (1999), *T. ensenadensis* is a valid Ensenadan taxa, while *T. platensis*, *T. burmeisteri*, *T. darwinii*, *T. paradoxus*, *T. bilobidens*, *T. gracilis* and *T. gezi* are valid Lujanian taxa found in Argentina, although only *T. platensis* and *T. burmeisteri* survived into the upper Lujanian. Because the systematics of these taxa is based mostly on dental features and body size, a revision of the southern Brazilian toxodontid remains is necessary in order to clarify the taxonomic status of the toxodontid remains from the continental shelf.

From the Holocene onwards, the formation of the Barrier-Lagoon System IV blocked all significant fluvial discharges that would reach the coastline of Rio Grande do Sul, thus the fossils could not have been transported to the shelf during post-Pleistocene times. Besides, after the formation of the MirimLake and Patos Lagoon, between 325 and 120 ka AP, most of the fluvial discharge became retained in these bodies and could not reach the sea anymore. Nevertheless, several seismic studies have demonstrated that during sea-level lowstands related to glacial maxima, the then exposed continental shelf was cut by the Guaíba, Camaquã, Piratini, Jaguarão, Tacuari and Cebollati rivers (Corrêa, 1990; Abreu and Calliari, 2005; Weschenfelder et al., 2008; Silva, 2009). These rivers have transported and distributed clastic terrigenous sediments that today cover the continental shelf (Tomazelli, 1978; Martins, 1983). The available seismic studies, however, focus on the central and northern portions of the continental shelf; the only seismic survey on the southern portion of the shelf was aimed at mapping Mesozoic and Tertiary paleo-fluvial channels deep in the sedimentary sequences, thus have not the necessary resolution to reveal details on the Pleistocene paleodrainages (Silva, 2009).

According to Corrêa (1990) the Jaguarão, Tacuari and Cebollati rivers converged to form a single channel that passed trough a gap in the Pleistocene barriers II and III. This gap is found in the area of a negative gravimetric anomaly (Taim Anomaly) related to a series of E-W-oriented fault and dyke systems of the underlying Precambrian bedrock (Rosa, 2009) (Fig. 11). Vertebrate remains could have been transported to the continental shelf by these paleo-fluvial systems but the largest fossiliferous area of the coast, the “Concheiros”, is far from the area that could have been influenced by these systems. Besides, the absence of abrasion on the fossils from the outer shelf suggests that transportation of these remains, if happened, was minimal. On the other hand, the specimen LGP-E0024 was collected in an area of the shelf that was cut by the paleo-channel of the Camaquã river during sea-level lowstands (Toldo et al., 1991; Weschenfelder et al., 2008).

It seems probable that the fossiliferous deposits on the shelf do represent continental environments that were covered by the sea advance at the end of the major Late Pleistocene glaciations. Several features found along the continental shelf do indicate the presence of continental environments in the past, such as paleo-beachlines (Asp, 1999; Buchmann et al., 2001), concentrations of heavy minerals (Corrêa and Ade, 1987) and terrigenous sediments (Kowsmann and Costa, 1974), as well as channels that represent paleo-fluvial

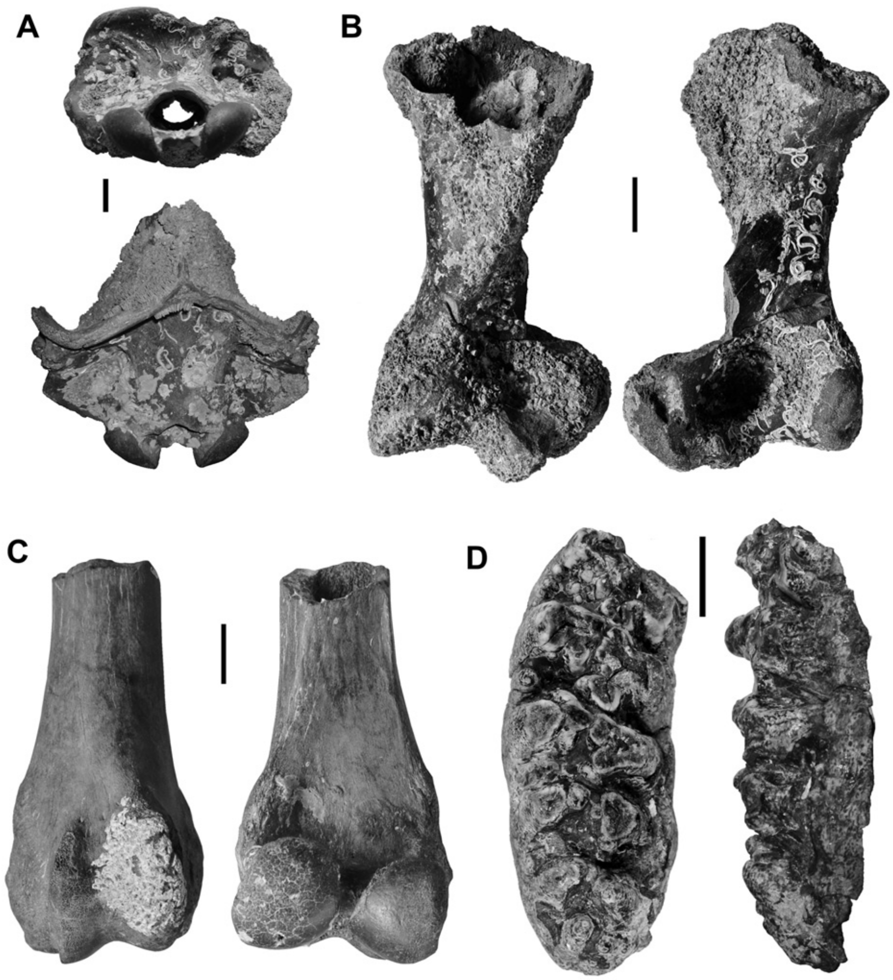

Fig. 9. Fossils of terrestrial mammals from the outer continental shelf: A) LGP-E0020 in caudal and dorsal views; B) LGP-E0021 in anterior and posterior views; LGP-E0024 in anterior and posterior views; D) LGP-G0032 in occlusal and labial views (scale bars 50 mm).

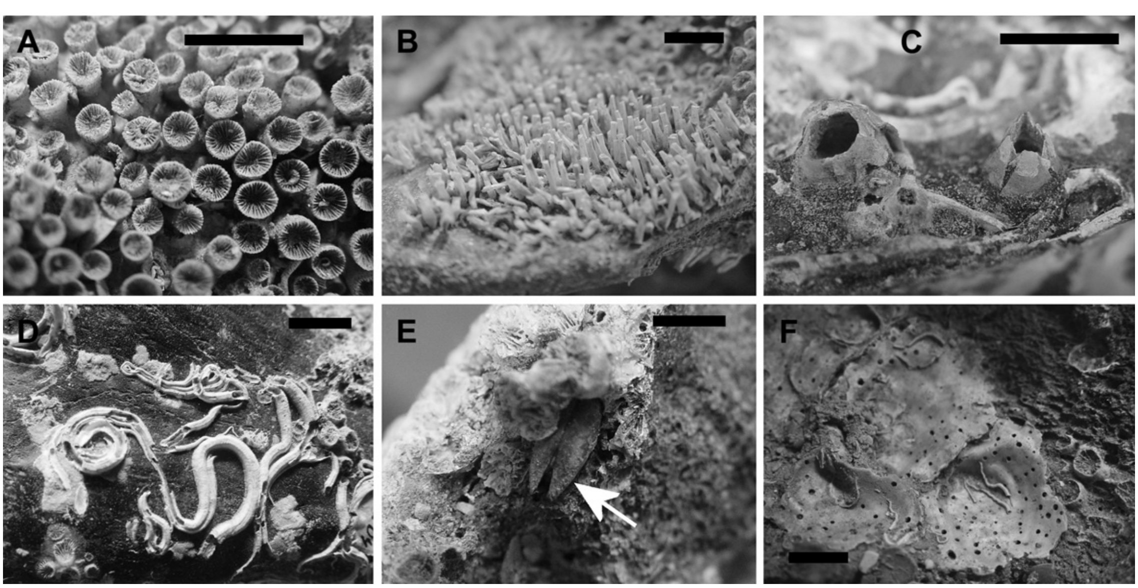

Fig. 10. Marine organisms found associated to the fossils from the outer continental shelf: A) coral *Astrangia rathbuni*; B) unidentified coelenterates; C) barnacles *Toracica balanus*; D) galleries of *Spirolis* sp. polychaets; E) a boring pelecypod *Litophaga* sp. (indicated by arrow); F) ostreids *Ostrea* cf. *equestris*, showing bioerosion (ichnogenus *Entobia* sp.) caused by clionid sponges (scale bars 10 mm).

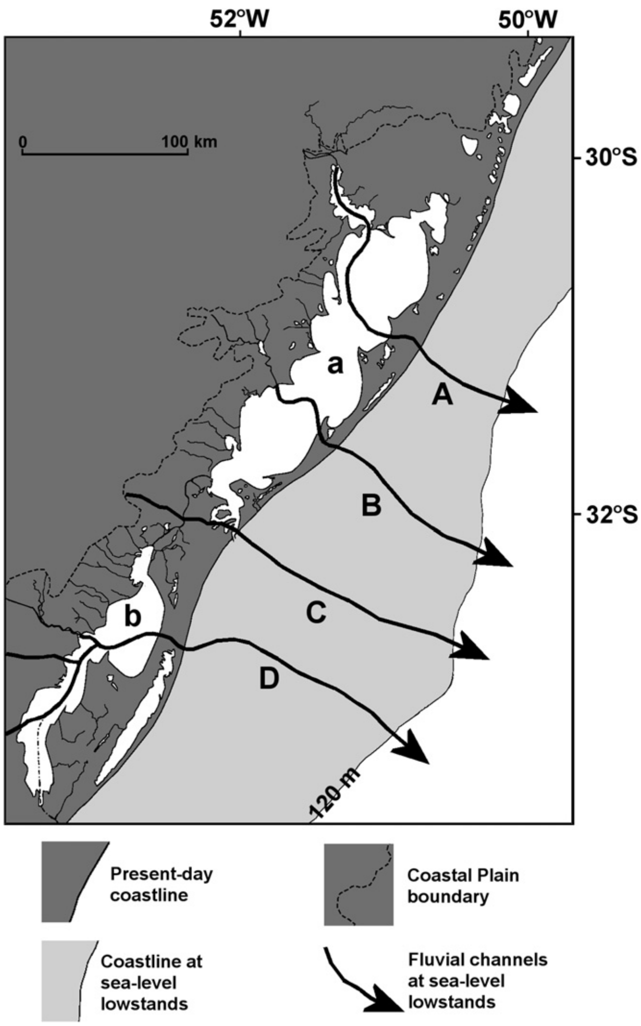

Fig. 11. Paleo-drainages recorded on the RS continental shelf during pre-Holocene sea-level lowstands, associated to the Patos Lagoon (a) and Mirim Lake (b): A - Guaíba River, B - Camaquã River, C – PiratiniRiver, D – Jaguarão, Tacuari and Cebollati rivers. Modified from Weschenfelder (2005) and Silva (2009).

drainages (Abreu and Calliari, 2005; Weschenfelder, 2005; Weschenfelder et al., 2008). Due to the low slope, any sea-level oscillation would have affected large portions of the shelf; during the glacial maxima, when the sea-level reached some 120 m below the present (Corrêa et al., 1996; Martins et al., 1996), the coastline would have been located some 100 km to the east. As a result, during sea-level lowstands the emergent area of the coastal province was twice that of the present. During sea-level transgressions these continental deposits would have been eroded, reworking and redepositing the fossils in submarine environments. The association of terrestrial fossils with lithified beach sediments (coquinas) is also an indicator that older continental fossiliferous deposits have been reworked by eustatic oscillations in the past. By modeling the influence of a sea-level transgression over the northern coast of Rio Grande do Sul, Dillenburg (1994) concluded that such an event would erode at least 10 m of the sediment cover of the shelf. This erosion would rework older fossils and redeposit them together with younger remains.

The presence of large herbivores in areas far from the present coastline does not only indicate that large areas of the continental shelf have been exposed during sea-level lowstands, but also that these areas have been occupied by terrestrial environments suitable for these organisms. Paleofloristic reconstructions have demonstrated that the lowlands of southern and southeastern Brazil, to latitudes of at least 20° S, have been covered by grasslands during the glacial maxima (Behling, 2002). Because of the sea-level lowstands related to the glacial maxima, such environments would have expanded not only latitudinally, but also farther to the east, thus the organisms would have also extended its distribution. The Brazilian continental shelf is wider between 22° and 33° S, thus this is potentially a large fossiliferous area.

The concentration of marine and terrestrial fossils at the "Concheiros" seems to be the result of the exhumation of the large fossiliferous concentrations located on the inner continental shelf that today are being reworked by erosion and shoreline retreatment that have been affecting some 80% of the coast of Rio Grande do Sul for the last 5 ka (Esteves et al., 2002; Dillenburg et al., 2004). This process is more visible during autumn and winter, when storm surges caused by polar fronts affect the coast (Calliari et al., 1998a). During these events large areas of the beach can be covered by shell fragments in a matter of hours. In the "Concheiros" the beach presents a steeper slope and coarser sediment, which affect the coastal dynamics in the area (Calliari and Klein, 1993). The erosive processes that affect this area, related to sediment starvation (Dillenburg et al., 2004) and wave dynamics (Calliari et al., 1998b) are probably the responsible for the exhumation of the Pleistocene deposits of the inner shelf, while the storm surges are responsible for transporting the fossils from these deposits to the beach.

6. Conclusions

The fossil remains of terrestrial mammals found along the coast of Rio Grande do Sul State were originally preserved in continental environments on areas of the continental shelf that have been exposed in the Pleistocene because of the sea-level regressions during the glacial maxima. Although some large fluvial systems did cut the exposed continental shelf during sea-level lowstands, there is no conclusive correlation between the presence of paleo-fluvial channels and terrestrial vertebrate fossils, save possibly for the specimen LGP-E0024 collected in the area near the paleo-channel of the Camaquã river. Detailed seismic and geological surveys in the southern portion of the coast should reveal if the largest concentration of mammalian fossils at the "Concheiros" is related to paleo-fluvial discharges.

The presence along the beach of fossils from the inner shelf is probably a combination of two processes: a) the long-term erosion that have been affecting the coast for the last 5 ka, removing the Holocene sediment cover and exposing the underlying fossiliferous Pleistocene sediments; b) removal and transportation by storm waves. This characterizes these fossils as palimpsest sediments (Pleistocene sediments that are being reworked by revcent processes). The fossils collected on the continental shelf off the coast of Rio Grande do Sul are currently below the depth influenced by waves, thus its partial or total exposure on the water–sediment interface is a result of past erosive processes, probably related to sea-level advances at the end of glaciations. Although these remains could have been transported from the continent to the shelf by paleo-fluvial systems during sea-level lowstands, preservation of these remains indicates that such transport, if it happened, was minimal, thus the fossils were preserved on the then exposed shelf. Its presence in areas much farther from the coast than those collected on the beach does indicate that the fossiliferous area of the shelf is much larger than previously known. Moreover, it does indicate that the terrestrial environments suitable for these organisms (open grasslands) occupied large (if not all) areas of the shelf that remained above the sea-level during glacial maxima. The wide geographic distribution of fossils of terrestrial mammals along the South American coast suggests that all the continental shelf has a great potential for paleontological surveys, mostly on the southern and southeastern Brazilian coast, where the shelf is wider.

The fossiliferous deposits of the continental shelf were formed during episodes of sea-level lowstand related to glacial cycles. The intervening sea-level transgressions eroded the deposits and reworked the fossils, resulting in a mixture of remains of different ages. Despite its broad age range, the fossils of terrestrial mammals do not constitute “true” time-averaged assemblages, because the accumulation of these remains was not a continuous process. Although there is a taxonomic correlation of the fossils from the submarine deposits with those from the Chuí Creek, both fossiliferous concentrations have distinct origins, and the former encompass a much wider time span.

The presence of fossils of terrestrial mammals on marine environment opens new perspectives for studies on the paleogeography, paleoclimates and paleoenvironments of the eastern South American continental shelf during glacial episodes, not only in southern and southeastern Brazil, but also in Uruguay and Argentina as well. The submarine nature of these fossiliferous concentrations demands a multidisciplinary approach, congregating paleontologists, marine geologists geophysicists and oceanographers, using different study techniques such as shallow high-resolution seismic profiling, side scan profiling, piston corers, bottom trawling and scuba diving in order to understand the Quaternary evolution of the continental shelf.

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