Journal of South American Earth Sciences 100 (2020) 102566

Contents lists available at ScienceDirect

Journal of South American Earth Sciences

journal homepage: www.elsevier.com/locate/jsames

# Late Pleistocene-Holocene fossils from Mirim Lake, Southern Brazil, and their paleoenvironmental significance: I - Vertebrates

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## ARTICLE INFO

*Keywords:*
Quaternary
Pleistocene
Mirim lake
Paleoenvironment
Vertebrate paleontology
Geomorphology

## ABSTRACT

Mirim Lake is located in the southern Brazilian/northeastern Urugayan coastal plain. Fossils of mollusks have been discovered on its shores since the XIX century, and in recent years, several new remains of invertebrates and vertebrates have been found in the Brazilian area of the lake that provide insights on the geological evolution and environmental changes that affected this lake during the late Quaternary. In this first of two papers describing these new findings we focus on vertebrates, consisting of aquatic and terrestrial taxa. The former include the first associated fossil remains of one adult and one juvenile balaenid whale known in Brazil, probably a female and calf of the southern right whale (baleia-franca) *Eubalaena australis*, besides bull sharks (*Carcharhinus leucas*) also recorded for the first time in southern Brazil, rays (Dasyatidae and Myliobatidae) and teleost fishes. The fossils of terrestrial vertebrates include several extinct mammals, found on the margins and retrieved from the lake bottom by fishermen at depths of up to 4 m. One molar tooth of *Toxodon* discovered *in situ* in one irrigation channel yielded an electron spin resonance (ESR) age of 68 ± 13 ka, in agreement with an age of 32.8 ± 5.1 ka obtained in quartz grains extracted from a caliche nodule collected above that fossil and dated by optically-stimulated luminescence (OSL). Other quartz grains in the same nodule that yielded ages of 16.9 ± 2.5 ka indicate partial dissolution of the caliche by increased rainfall at the beginning of the last glacial-interglacial transition (Termination I) . The lake was invaded by marine waters and organisms during the Holocene sea-level highstand of +3 m around 5–6 ka b2k through paleo-connections with the Atlantic Ocean, becoming a paleo-lagoon. At that time coastal waters were warmer than today, as indicated by the presence of the tropical shark *C. leucas*. The ESR and OSL ages indicate chronocorrelation with the Pleistocene fossil-bearing Santa Vitória Formation that outcrops to the east. The fossil and sedimentary records indicate that the geological evolution and environmental conditions of the lake were controlled by climate and sea-level oscillations related to glacial-interglacial cycles.

## 1. Introduction

The coastal plain of the state of Rio Grande do Sul (CPRS), in southern Brazil (Fig. 1A), is dominated by two large coastal lacustrine bodies, the Patos Lagoon, stretching along the northern and central CPRS, and the Mirim Lake in the south (Fig. 1B). Both are connected through the São Gonçalo channel, and Mirim Lake is also connected to Mangueira Lake through the wetlands of Taim, thus forming the largest coastal wetlands complex of South America. Mirim Lake is located in the southern CPRS between 31°30′S and 34°30′S, covering an area of some 3750 km$^2$, with a maximum length of 185 km, maximum width of some 20 km, and depths up to 8 m. Its eastern shore and northwestern

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https://doi.org/10.1016/j.jsames.2020.102566
Received 17 October 2019; Received in revised form 10 January 2020; Accepted 11 March 2020

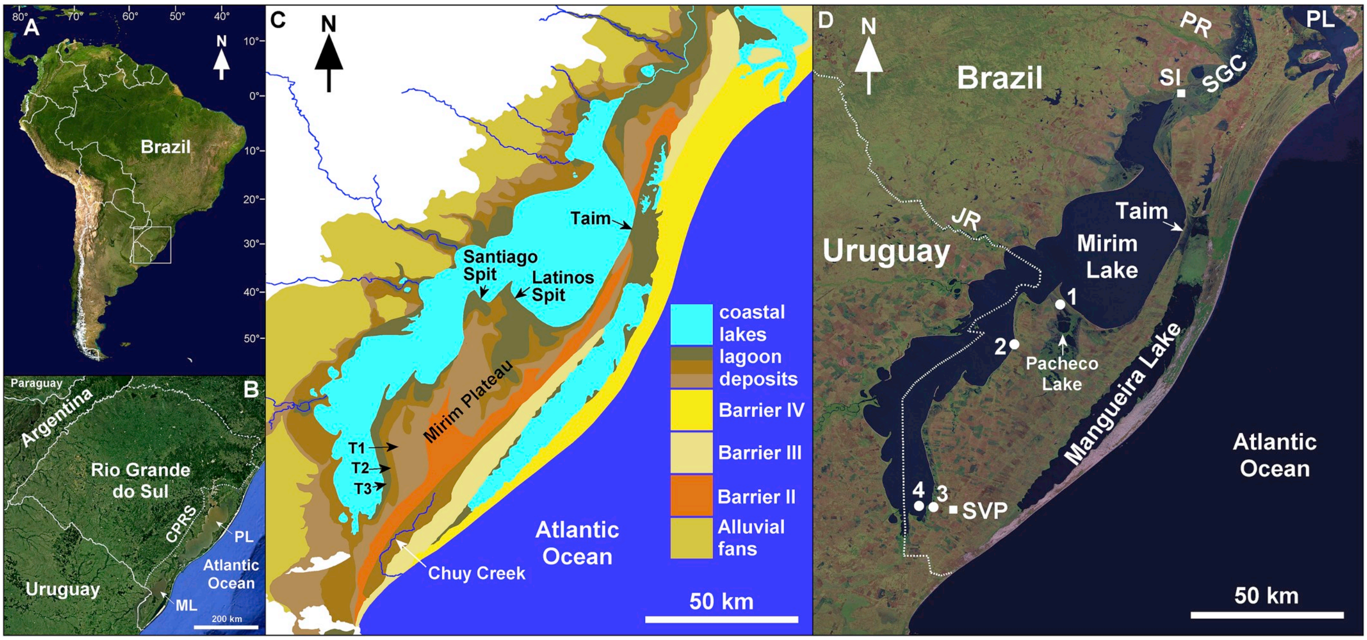

**Fig. 1.** A) Blue Marble image (https://visibleearth.nasa.gov/) of South America, the white square indicates the location of Rio Grande do Sul. B) Google Earth image (earth.google.com/web) of Rio Grande do Sul with the area of the CPRS outlined (ML: Mirim Lake, PL: Patos Lagoon). C) Configuration of the depositional systems of the southern CPRS (after Villwock and Tomazelli, 1995), with features mentioned in the text indicated (T1, T2 and T3: lagoon terraces). D) LANDSAT image of the southern CPRS, with the fossiliferous sites mentioned in the text indicated by numbers (PL: Patos Lagoon, PR: Piratini River, SGC: São Gonçalo Channel, SI: Santa Izabel, SVP: Santa Vitória do Palmar). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

shores are located in Brazilian territory and its southwestern shore is within Uruguayan territory (Fig. 1A, B).

The lake receives constant water input from rivers that discharge on its western shore, such as the Piratini (in Brazil), the Jaguarão at the Brazil-Uruguay border, and the Tacuari, Cebollati, Sarandi and San Miguel in Uruguay, besides smaller and ephemeral streams. On its eastern shore, the only water input comes from Mangueira Lake through Taim and from small rainwater-fed streams that flow from the Barrier II and terraces on the lake shore. Until the 1970s, the lake also received input of marine waters from the Patos Lagoon to the north through the 75 km-long São Gonçalo channel during periods of severe droughts, when the water level of Patos Lagoon was lowered, thus allowing for marine waters to invade the lagoon (von Ihering, 1885). In 1977 a dam was constructed in the São Gonçalo channel in order to block the influx of saltwater to Mirim Lake during droughts (Burns et al., 2009), thus ensuring a constant supply of freshwater to the local people.

The first records of fossils in Mirim Lake date back to the late XIX century, (von Ihering, 1885). In recent years, several fossils of vertebrates have been found by local people from the town of Santa Vitória do Palmar, in the southern CPRS (Pereira and Lopes, 2012). These new records led to systematic surveys along the Brazilian side of the lake in order to identify fossiliferous sites and collect specimens. Here is presented a report on the results obtained by these surveys so far, with descriptions of the collected fossils, stratigraphy, and datings, together with analyses and interpretation of the environmental changes and geological evolution of the lake within a chronostratigraphic framework. This contribution is divided in two parts, being the first one focused on the vertebrates, followed by a second one describing the invertebrates. The fossils discovered so are relevant because they provide invaluable information on how the past climate and sea-level oscillations promoted changes in the ecosystems and geography of the lake, thus improving the understanding about the geological processes and past climate changes that affected the development of the CPRS during the late Quaternary.

**Abbreviations**: MCTFM and EPM: Paleontological collections of Museu Coronel Tancredo Fernandes de Mello, Santa Vitória do Palmar county, Brazil; PV: Vertebrate Palaeontology.

## 2. Geological setting

The coastal area stretching from the states of Santa Catarina and Rio Grande do Sul, in southern Brazil, to the northeastern coast of Uruguay, encompasses the onshore portion of the Pelotas Basin (Barboza et al., 2008), bounded to the west by rocks of Precambrian to Mesozoic age. Along the CPRS two sets of depositional systems are recognized: the Alluvial Fans System, of Miocene-Pliocene age (Closs, 1970), and the Quaternary Barrier-Lagoon Systems (Fig. 1C). The latter include units of Pleistocene (Systems I, II and III) and Holocene (System IV) ages, each one representing a 4th order depositional sequence developed in response to a marine transgression correlated to an interglacial epoch (Villwock and Tomazelli, 1995; Rosa et al., 2017). Those systems are characterized by long sandy barriers developed parallel to the coastline, with lakes, lagoons and wetlands developed in the backbarrier lowlands. The sediments that compose these systems are essentially siliciclastic very fine to medium sands, with subordinate heavy minerals and feldspars; the subaerially-exposed weathered sediments exhibit clays, iron-manganese oxides and caliche of pedogenic origin (Villwock and Tomazelli, 1995).

Mirim Lake is part of the Lagoon System II, developed landward of the coastal Barrier II and bounded to the west by the Alluvial Fans System (Fig. 1C). The subaerial portion of that barrier consists of ancient eolian deposits formed by quartz sand, modified by weathering and pedogenesis (Villwock and Tomazelli, 1995), and reaches up to 25 m in altitude. It was formed by a marine highstand correlated to the marine isotope stage (MIS) 7, that reached maximum amplitude of some 10 m above the present mean sea-level around 220 ka ago, based on shallow marine deposits preserved in subsurface (Lopes et al., 2014a; Rosa et al., 2017). From then on, all fluvial discharge coming from the continental areas to the west became trapped in the backbarrier, thus cutting the sediment supply to the coastline and forming Mirim Lake.

The lagoon deposits of System II form most of the lake margin in Brazilian territory (Fig. 1C). At the northern end of the lake a plateau developed on its eastern margin protrudes to the west toward the opposite margin. The two margins converge at the mouth of São Gonçalo channel, which connects the lake with the Patos Lagoon to the north. Prior to the construction of the aforementioned dam, the water flow along this channel was bi-directional: when Mirim Lake was flooded its waters flowed through the channel towards Patos Lagoon, whereas during periods of drought the marine waters invaded the latter and flowed in the opposite direction (von Ihering, 1885).

To the south of the aforementioned plateau the lake widens eastward, forming a large embayment that reaches close to the Barrier II. In the northeastern area of this embayment the Pleistocene Barriers II and III are interrupted at Taim, a ~12 km-long lowland area occupied by wetland environments. This lowland area is interpreted as an incised valley developed on top of E-W oriented fractures on the crystalline basement, and acted as a paleo-inlet that connected Mirim Lake to the Atlantic Ocean through fluvial systems during glacial sea-level lowstands and allowed marine waters to invade the lake during interglacial sea-level highstands (Buchmann et al., 1998; Barboza et al., 2007; Rosa et al., 2007).

The southeastern margin of the lake is characterized by a wide projection, hence named Mirim Plateau, that protrudes westward from the Barrier II (Fig. 1B). This plateau exhibits one inner lacustrine terrace (T1) closer to the Barrier II that reaches altitudes of 7–10 m, one intermediate terrace (T2) reaching up to 5–6 m, and a marginal terrace (T3) closer to the present lake shore that reaches 2–3 m. These terraces are interpreted as formed by past lake levels higher than the present one (Gomes et al., 1987), probably controlled by interglacial sea-level highstands correlated to the formation of Barrier-Lagoon Systems II (T1), III (T2) and IV (T3).

Along the terrace T3 on the northern margin of the plateau a sandy feature named Latinos Spit was developed. This spit extends to the northwest and then curves to northeast, and is bounded to southwest by the Santiago Spit (Fig. 1B). Other two smaller spits, also N-NE-oriented, are found along the lake shore farther to the south. The development of sandy spits on the margins of lakes, estuaries or embayments is controlled by the prevailing direction of incidence of waves (Zenkovich, 1967), therefore the N-NE-oriented spits along the Mirim Plateau indicate predominance of waves generated by the strong S-SW winds that affect the region (Villwock and Tomazelli, 1995). The presence on the inner and intermediate terraces of NE-oriented curved spits far from the present day lake shore ('paleo-spits'), reinforces the interpretation of higher lake levels in the past.

The surface of the plateau is covered by deflation basins, several of these occupied by wetlands, eolian deposits, and is dissected by dry channels and small streams that today are active only during rainy seasons. The ancient streams that flowed from the barrier toward the lake deposited sediments as small alluvial fans in the lower adjacent terraces (Gomes et al., 1987).

## 3. Methods

Most of the discoveries of fossils in the Brazilian area of Mirim Lake in the last 10 years have resulted from a public awareness campaign developed by the museum Coronel Tancredo Fernandes de Mello, in the town of Santa Vitória do Palmar, through activities with school students, newspaper articles and radio interviews. As a result of this campaign, several local people donated fossils they have accidently found or informed the researchers about the presence of fossil-bearing sites. Following the directions provided, several fossiliferous sites were mapped and additional fossils were discovered along the southeastern lake shore, in irrigation channels excavated perpendicular to the shore.

### 3.1. The fossil sites in Mirim Lake

The oldest published records of fossils from the lake were provided by Herrmann von Ihering (1885), who mentioned the presence of concentrations of the molluscan shells on the western bank of the São Gonçalo channel, near the locality of Santa Izabel (SI in Fig. 1D), at depths of 20–40 cm below the surface. Although mentioning the presence of fish remains in those deposits this material was not described in detail. That author also reported the presence of marine shells on the bed of a small lake located some 6 km upstream in the banks of the Jaguarão River (Fig. 1B), exposed during droughts. Molluscan fossils were also found in Latinos Spit (Abreu et al., 1985), Taim (Buchmann et al., 1998), and several localities on the southwestern lake shore in Uruguay (Martínez, 1989).

The fossils described here were found in four sites located on the southeastern part of the lake:

*Site 1* - The northernmost site encompasses the area of Latinos Spit (Fig. 1C and D). Here, the fossiliferous deposits consist of shell concentrations (Fig. 2A) developed within a series of regressive sand ridges parallel to the lake shore (Abreu et al., 1985). The collecting efforts provided the first vertebrate fossil from those concentrations, besides several additional molluscan species, which will described in a next paper.

*Site 2* - A severe drought in the 1980s lowered the lake level, thus exposing the skeleton of a whale close to the shore in the embayment to the south of the Santiago Spit (Fig. 1D). Some bones were brought to the museum by local people, and although the surveys made in this area failed to find other parts of the skeleton, several remains of other vertebrates were found among sediments removed during the excavation of an irrigation channel along the terraces T3 and T2 in that site (Fig. 2B).

*Site 3* - This site encompasses the shore around the port of Santa Vitória do Palmar, where small fragmented fossils can be found scattered along the shore and also along irrigation channels excavated perpendicular to the shore. In one large channel excavated to the north of the port (Fig. 2C), fossils were also found by local people among sediments removed from the channel and piled along its margins. A survey along the channel during a drought revealed the presence of several fossils *in situ*, embedded in the sediment exposed at the base of the channel (Fig. 2D) some 1.7 km landward of the lake shore.

*Site 4* - This site encompasses areas within the lake around the port of Santa Vitória do Palmar (Fig. 1D). Here, fossils have been collected directly from the bottom of the lake through nets laid by local fishermen, at depths of up to 4 m and distances of up to 1 km from the modern lake shore.

### 3.2. Stratigraphy

The fossils from the irrigation channel in the Site 3 (Fig. 2D) are the only vertebrate remains found *in situ* in the surroundings of Mirim Lake so far. The stratigraphic setting of the remains was described, and sediment samples were collected for laboratory studies. Grain size and petrographic analyses were performed at Universidade Federal do Pampa (UNIPAMPA), using a Microtrac S3500 Laser Diffraction Particle Size Analyzer and petrographic microscope equipped with digital imaging equipment.

The irrigation channel was excavated along the terrace T3 that rises up to about 2.5 m above the lake, and extends for some 1.7 km from the shore up to the 3-4 m-high terrace T2. This terrace is bounded landward by the >7 m-high terrace T1, developed on a paleo-spit projected to the north that forms an embayment around T2 (Fig. 3G). The channel is usually filled by lake water, but a drought exposed the ~1.5 m-thick sediment succession along its banks and revealed the presence of the fossils *in situ* close to the boundary between T2 and T3.

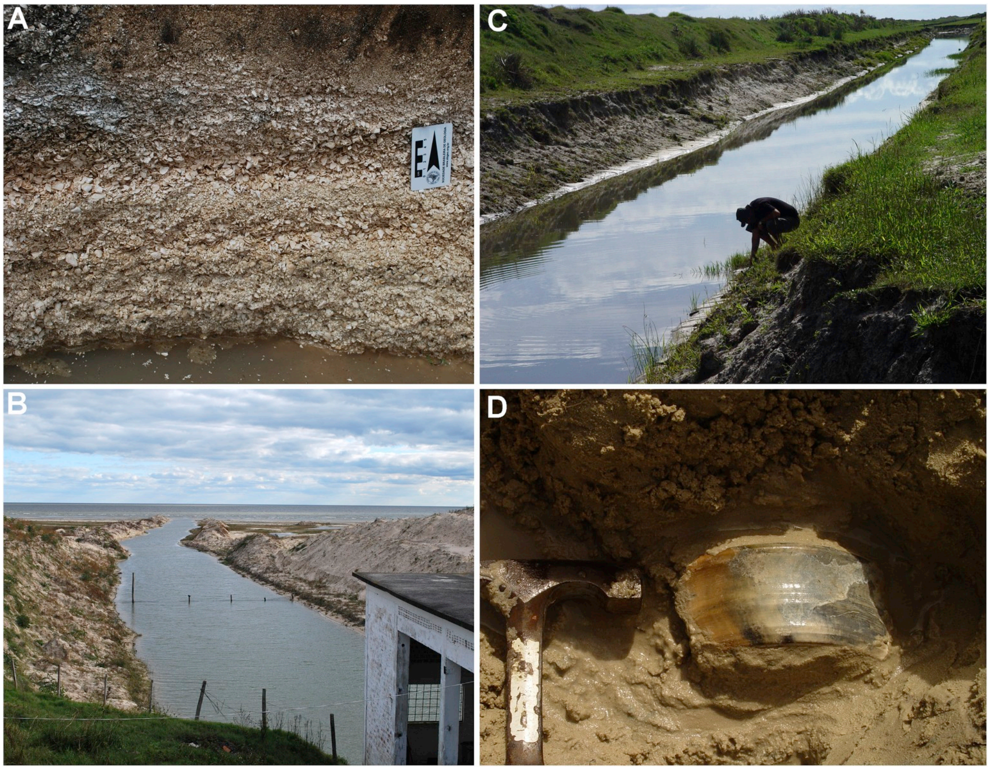

**Fig. 2.** A) Shell concentration in the Latinos Spit (Site 1). B) view of the irrigation channel (Site 2) with Mirim Lake in the background. C) Irrigation channel (Site 3) close to the port of Santa Vitória do Palmar. D) Molariform of *Toxodon* (specimen MCTFM-PV0680d, also shown in Fig. 6D) found *in situ* at the base of the bank of the channel shown in C.

The sediment exposed along the channel banks consist essentially of quartz sand with variable amounts of silt and clay (Fig. 3A). The lithologic variations allowed recognizing a vertical succession of four facies, without apparent erosive surfaces at the contacts:

*Facies A* - Located at the base of the portion of the banks exposed above the low water level (lwl), consists of the fossil-bearing massive, fine to medium sand with small amounts of silt and clay, exhibiting the olive gray color (5Y 5/2 in the Munsell scale) common of waterlogged sediments found the CPRS. Besides the fossils found *in situ*, the ones found among the sediments removed during the excavation of the channel and piled along its margins presumably also came from this layer.

*Facies B1* - Composed of light ochre (2.5 Y/3) fine sand with a relative high proportion of clay and fine silt. This facies exhibits a ~10-20 cm-thick petrocalcic horizon (Fig. 3B) formed of irregular caliche nodules and also precipitated around plant roots, forming rhizocretions (Klappa, 1980). At some points along the banks the caliche forms vertical melikaria-like structures (Fig. 3C). A petrographic analysis (Lopes et al., 2016) showed that the caliche consists of Alpha-type, inorganically-precipitated carbonate (Wright, 1990) exhibiting an equigranular micrite matrix precipitated around quartz and feldspar grains, with some larger bladed crystals developed inside voids and fissures (Fig. 3D).

*Facies B2* - This facies is characterized by an increase in the proportion of sand relative to the Facies B1. It is massive, light ochre (2.5 Y/3) and exhibits small, irregular concentrations of iron and manganese oxides are present, indicating poor drainage and oscillations of the water table (Vepraskas, 2015).

*Facies C* - This is a massive light ochre (2.5 Y/3) muddy sand. At its base, some 400 m from the fossiliferous site toward the lake on L3, there is a tabular laminated deposit of consolidated but friable white powdery material, measuring about 10 cm in thickness and some 2–3 m across (Fig. 3D). Tests for carbonate using 10% HCl showed very weak reaction, and its macroscopic features suggested it could be a diatomite (Harwood, 1999). An analysis under electron scanning microscope with X-ray diffraction at the Centro de Microscopia Eletrônica of Universidade Federal do Rio Grande (CEME-Sul FURG), however, showed no evidence of diatom frustules and that it is formed of very fine grains of amorphous silica measuring $<200$ µm with frosted and pitted surfaces (Fig. 3F), containing some phytoclasts. Siliceous-rich deposits formed of well-preserved diatom frustules (diatomites) have been found in different areas of the southern CPRS, including the bottom of Mirim Lake (Lopes et al., 2016c).

The modern soil at the top of the succession is an organic-rich muddy sand, classified as a Hydromorphic Quartzenic Neosoil (Streck et al., 2008).

### 3.3. Dating

The specimens found *in situ* in the Facies A consist of parts of the skull and postcrania of a notoungulate *Toxodon platensis* Owen, 1838, including teeth. Being the only fossils known so far from the Lagoon System II found in a defined stratigraphic setting, these provided an opportunity for interpreting their depositional history and chronostratigraphy. One of the teeth (specimen MCTFM-PV0680d) was selected for dating using the electron spin resonance (ESR) method, which has been used to determine the ages of fossil teeth and molluscan shells found in the CPRS (Lopes et al., 2010, 2014b). A ~2g sample of enamel and dentine was mechanically extracted from the base of the tooth using a hand drill. The sample was submitted to a thermal treatment (Kinoshita et al., 2008), through freezing in liquid nitrogen and heating at room temperature. After a few repetitions, the enamel detached from the dentin. The enamel was subjected to a 1N HCl acid treatment, in an ultrasonic bath for 3 min to extract an outer layer for cleaning and eliminate the influence of α-particles. Initial thickness was 1500 µm and after bath, 1200 µm. Then the enamel was crushed manually until to form a powder with particles of diameter 200–400 mesh (38–76 µm). This material was divided into 10 aliquots of approximately 30 mg for irradiation with additive doses, for the construction of the dose-

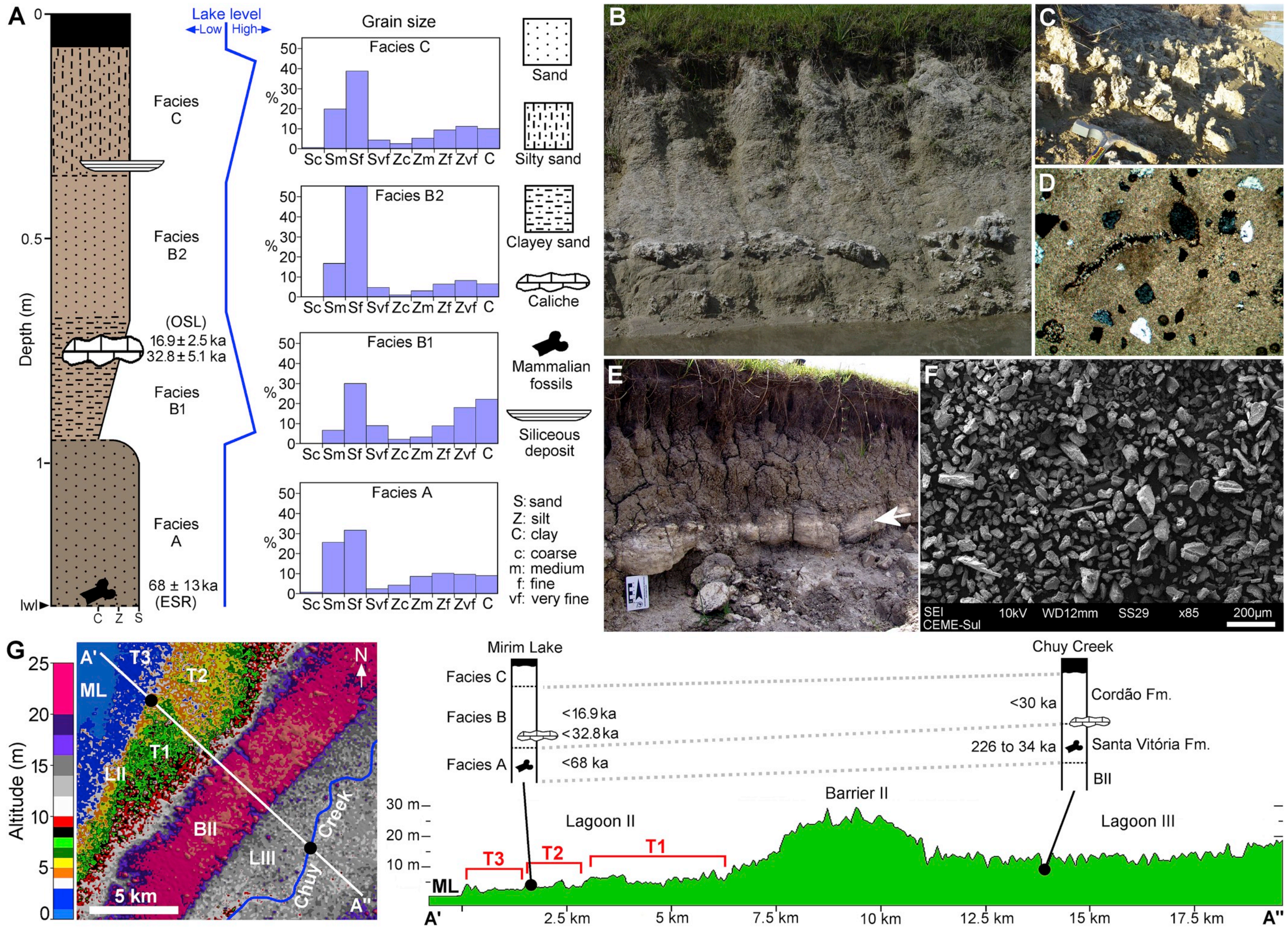

**Fig. 3.** A) Vertical facies succession and grain size variation along the irrigation channel in Site 3; relative variations in lake water are explained in the Discussion (lwl = lake water level). B) View of the irrigation channel, showing the petrocalcic horizon exposed above the water. C) melikaria-like caliche formations. D) petrographic image of one caliche nodule showng the micrite matrix (5 × magnification). E) tabular-shaped, laminated siliceous deposit indicated by the arrow (scale bar = 50 mm). F) SEM image of the amorphous silica grains from the deposit. G) digital elevation map and topographic profile generated with the Shuttle Radar Topographic Mission (SRTM) data showing the location and chronostratigraphic correlation of the Site 3 with the fossiliferous deposits of Chuy Creek (ML = Mirim Lake, LII = Lagoon II, BII = Barrier II, LIII = Lagoon III).

response curve (DRC). The aliquots (except one) were irradiated with gamma radiation at dose rate of 634 Gy/h dose rate, using a 5 mm acrylic layer for electronic equilibrium production, up to a dose of 8 kGy. This value was estimated by comparing the spectrum of original samples with one of irradiated enamel with of known dose value, since the DRC curve should contemplate values of 10 times the Equivalent Dose ($D_e$).

The spectrum of all aliquots, original and irradiated, was recorded on the JEOL FA-200 X-Band ESR spectrometer. The peak-to-peak intensity of the dosimetric signal in $g_\perp$ ($g = 2.0018$) was associated with the additive dose for the construction of the dose-response curve. The equivalent dose ($D_e$) was determined through the fitting with single saturating exponential function (Ikeya, 1993):

$$I = I_0 * (1 - e\wedge - (D + D_e)/D_0)$$

where $I$ represents the ESR signal amplitude, $D$ is the added dose and $I_0$ and $D_0$ are the values of Intensity and Dose at saturation, respectively.

The enamel, dentine and sediment associated with the tooth were analyzed through Neutron Activation Analysis (NAA) to determine the concentrations of Uranium, Thorium and Potassium (Table 1). The obtained $D_e$ was converted into age through the DATA software (Grün, 2009). The cosmic dose rate of 208 μGy/year was calculated taking into account latitude (33.497 S), longitude (53.417 W), altitude (∼2.5 m) and the depth (1.5 m) at which the fossils were obtained (Prescott and Hutton, 1994). The fossils were located at the phreatic level, and the water content in the sediment was considered as 100%.

**Table 1**

Concentrations of Uranium, Thorium and Potassium in the analyzed materials.

| | U (ppm) | Th (ppm) | K (%) |
|---|---|---|---|
| Sediment | 0.79 ± 0.01 | 4.70 ± 0.20 | 1085 ± 10 |
| Enamel | 40.0 ± 1.0 | 1.11 ± 0.06 | <750 |
| Dentine | 84.0 ± 2.0 | 0.85 ± 0.02 | <750 |

In order to cross-check the age of the fossil and attempt to establish the timing of carbonate precipitation, the nodule shown in Fig. 3D was selected for dating using optically stimulated luminescence (OSL). The rationale was that the dating of quartz grains would indicate the time when the grains were exposed to sunlight for the last time before being buried and covered by carbonate, therefore allowing to estimate the maximum age of the caliche. The sample was chemically cleaning with hydrogen peroxide during 24 h to remove organic material, then washed with distilled water and immersed in 10% hydrogen fluoride (HF) for 45 min to remove carbonates and the surface of the quartz grains, thus eliminating the ionization from the α-particles, followed by washing with distilled water. It was then immersed in 10% hydrochloric acid (HCl) for 2 h, to eliminate possible fluorides which are formed with the HF bath and washed with distilled water. Finally, the sample was immersed in sodium polytungstate (SPT), to eliminate feldspar (2.62 $gcm^{-3}$) and heavy minerals (2.75 $gcm^{-3}$) in order to obtain pure quartz grains.

The OSL measurements were performed in the Laboratory for Sustainable Energy Technical University of Denmark, with an automated TL/OSL reader, model Risø TL/OSL-DA-20, and were made with blue light excitation (470 nm) and detected in UV region using U-340 optical filter. The samples were irradiated with a $^{90}Sr/^{90}Y$ beta source with dose rate of 0.081 Gy/s. The natural radioactive contents (U, Th and K-40) were determined by γ-spectroscopy, γ-rays spectra of the samples were measured with hyper-pure germanium (HPGe) detector with ultra-low background shield of Canberra Inc. and compared with the soils patterns spectra JR-1, JB-3, JG1a and JG-3; the contributions of the cosmic radiations were calculated theoretically using the equations of Prescott and Hutton (1994). Finally, the annual dose rates are evaluated with the U, Th and K-40 concentrations and the conversion table cited by Adamiec and Aitken (1998).

The equivalent doses ($D_e$) are determined by the Single Aliquot Regeneration protocol (Wintle and Murray, 2006), using 48 aliquots (~3 mg of 180–210 μm fraction) of the sample. The $D_e$ results which passed the recycling ($\pm$10%) and recuperations ($<$5%) tests were used to final $D_e$ value. The final $D_e$ value was calculated with the 'Radial Plot' (Galbraith and Roberts, 2012) and using the 'NumOSL Program', the best results were obtained with Finite mixture age model, FMM (Peng et al., 2013).

When appropriate, the ages are reported as b2k (before year 2000 AD), following the Greenland Ice Core Chronology 2005 (GICC, Andersen et al., 2006).

## 4. Results

### 4.1. Age and stratigraphic position of the fossils

The ESR results of the molar of *Toxodon* found in the Facies A indicate an age of 68 ± 13 ka (Table 2) according the early uptake (EU) age model and 127 ± 24 ka according to the linear uptake (LU) model. The EU age model assumes that the Uranium uptake occurred shortly after the final burial of the material, thus providing the minimum possible age of the specimen (Blackwell et al., 1992), whereas the LU model assumes that the uptake occurred continuously at a constant rate since the final burial, thus giving a median age. Considering that this fossil was reworked from older deposits (see Dicussion), it seems unlikely that the uptake was continuous, therefore the age determined by the EU model is regarded here as the most reliable result.

The quartz grains enclosed by the caliche nodule collected from the carbonate horizon provided one OSL age of 29.1 ± 4 ka according to the Central Model, and two age groups using the Finite Mixture Model (FMM): 48% of the sediments were dated as of 32.8 ± 5.1 ka, and 52% were dated as of 16.9 ± 2.5 ka (Table 3). These two age groups in the same nodule are somewhat unexpected, but suggest that the caliche was formed after 32.8 ka b2k, and around 16.9 ka b2k part of the quartz grains were exposed to sunlight, probably because of partial dissolution of the carbonate.

Both ESR and OSL results allowed establishing chronocorrelation of the fossil-bearing Facies A with the fossiliferous Santa Vitória Formation (SVF), exposed along the banks of Chuy Creek some 13 km to the west of Mirim Lake (Fig. 3G). That formation contains fossils of mammals dated as of 226 to 34 ka b2k, in agreement with luminescence ages (Lopes et al., 2010, 2014a,b; 2019), and it is overlain by the caliche-bearing Cordão Formation, formed of loess deposited between about 30 and 10 ka b2k according to OSL ages (Lopes et al., 2016b).

**Table 2**
External dose ($D_e$) and age measured in the fossil of *Toxodon* according to the Early Uptake (EU) and Linear Uptake (LU) models.

| Age model | $D_e$ (Gy) | Age (ka) |
|---|---|---|
| EU | 579 ± 25 | 68 ± 13 |
| LU | 580 ± 25 | 127 ± 24 |

### 4.2. The vertebrate fossil assemblages

The first known records of vertebrate fossils from the Mirim Lake are the teeth of 'selachians' and *Pogonias cromis* (Linné, 1766), mentioned by von Ihering (1885, 1907) but without detailed descriptions.

The vertebrate remains recently found on the Brazilian side of the lake consist of both marine and terrestrial taxa, the latter including Pleistocene extinct megafauna (body mass between 44 kg and ≥ 1000 kg). These specimens are deposited at the paleontological collection of the Museu Coronel Tancredo Fernandes de Mello, in the town of Santa Vitória do Palmar.

#### 4.2.1. Marine vertebrates

CHORDATA Haeckel, 1874
CHONDRICHTHYES Huxley, 1880
MYLIOBATIFORMES Compagno, 1973
MYLIOBATIDAE Bonaparte, 1838
cf. *Myliobatis* Cuvier, 1817.

*Material*: Fragment of a mouthplate (MCTFM-PV1109, Fig. 4A).
*Provenance*: Site 2.
*Description*: Diagnosed as a myliobatid based on the pavement-like teeth crown, with roots formed of labiodentally elongated ridges (ten ridges are preserved in this specimen), separated by sulci (Cuvier, 1817; Agassiz, 1843). Although incomplete, the elongated shape of the plate indicates that it is from the central series, which in myliobatids can include up to seven plates (Woodward, 1888; Bigelow and Schroeder, 1953). The surface of the crown is rough, and does not exhibit the pitted aspect that indicates abrasion (Woodward, 1888; Richter, 1987). Tentatively assigned to *Myliobatis* based on the presence of four species of that genus that inhabit the coastal waters of Rio Grande do Sul today: *M. fremvillei*, *M. goodei*, plus two other species that are distinguished by DNA and tooth morphology, namely "narrow" and "broad" teeth morphotypes (Vooren, 1997; Vooren et al., 2005). Fossil myliobatid mouthplates are common in fossil concentrations found in the continental shelf and shoreline of the CPRS (Richter, 1987).

DASYATIDAE Jordan, 1888
*Dasyatis* sp. Rafinesque, 1810
aff. *D. centroura* (Mitchill, 1815).

*Material*: Dermal buckler (MCTFM-PV1107; Fig. 4B).
*Provenance*: Site 2.
*Description*: The specimen is a brown-colored, oval-shaped, dorsoventrally biconvex buckler. It possesses a small blunt elongated ridge along the midline, and reaches 25.94 mm in length, 19.6 mm in width and 8.2 mm in thickness. The large size and oval shape, without radial furrows, indicates that it is from the scapular or metapterygial series of the dorsum (Bigelow and Schroeder, 1953; Deynat, 1998) and could belong to *D. centroura* or a similar species (P. Deynat, pers. comm., 2016). This species, together with *D. say* (Le Sueur, 1817) is found in the coast of southern Brazil only during summer months (Vooren, 1997). *D. say*, however, does not exhibit dorsal bucklers or spines, only a ridge of small tubercles along the dorsal midline and scapula (Le Sueur, 1817; Bigelow and Schroeder, 1953). *D. centroura* is found along the Atlantic coast of the Americas from Argentina (41°S) up to the United States (42°N), where it enters estuaries during the summer (Bigelow and

**Table 3**
Annual and external doses measured in the caliche sample and ages obtained with the Central and Finite Mixture models (*calculated with U = 5.30 ± 1.24 ppm; Th = 11.91 ± 1.95 ppm, and K content below detection limit. O.D. = 30).

| Sample | Annual Dose (Gy/a) | Model | $D_e$ (Gy) | Age (ka) |
|---|---|---|---|---|
| Mirim Lake (caliche) | (2.0 ± 0.2)* | Central | 60.8 ± 5.2 | 29.1 ± 4 |
| | | Finite Mixture | 35.0 ± 1.3 (52%) | 16.9 ± 2.5 |
| | | | 75.1 ± 3.7 (48%) | 32.8 ± 5.1 |

Schroeder, 1953; Menezes et al., 2003; Cousseau et al., 2007; Menni et al., 2007). According to Last et al. (2016), the genus *Dasyatis* is polyphyletic, and *D. centroura* should be re-named *Bathytoshia centroura*.

CARCHARHINIFORMES Compagno, 1977
CARCHARHINIDAE Jordan and Evermann, 1896
*Carcharhinus leucas* Müller and Henle, 1841

*Material*: Upper (MCTFM-PV1026) and lower (MCTFM-PV1027) tooth (Fig. 4C and D).

*Provenance*: Site 2.

*Description*: These fossils are the first record of this species in southern Brazil. Both specimens are complete, with well-preserved serrations along the edges, and are diagnosed as *C. leucas* by the arched roots, which tend to be almost straight in other carcharhinids (Compagno, 1984). The upper tooth is triangular-shaped, its proximal edge is straight, with fine serrations formed by minute denticles. The distal edge forms an angle of ~15°; the serrations along this edge are coarser than those on the anterior one, with larger denticles located at

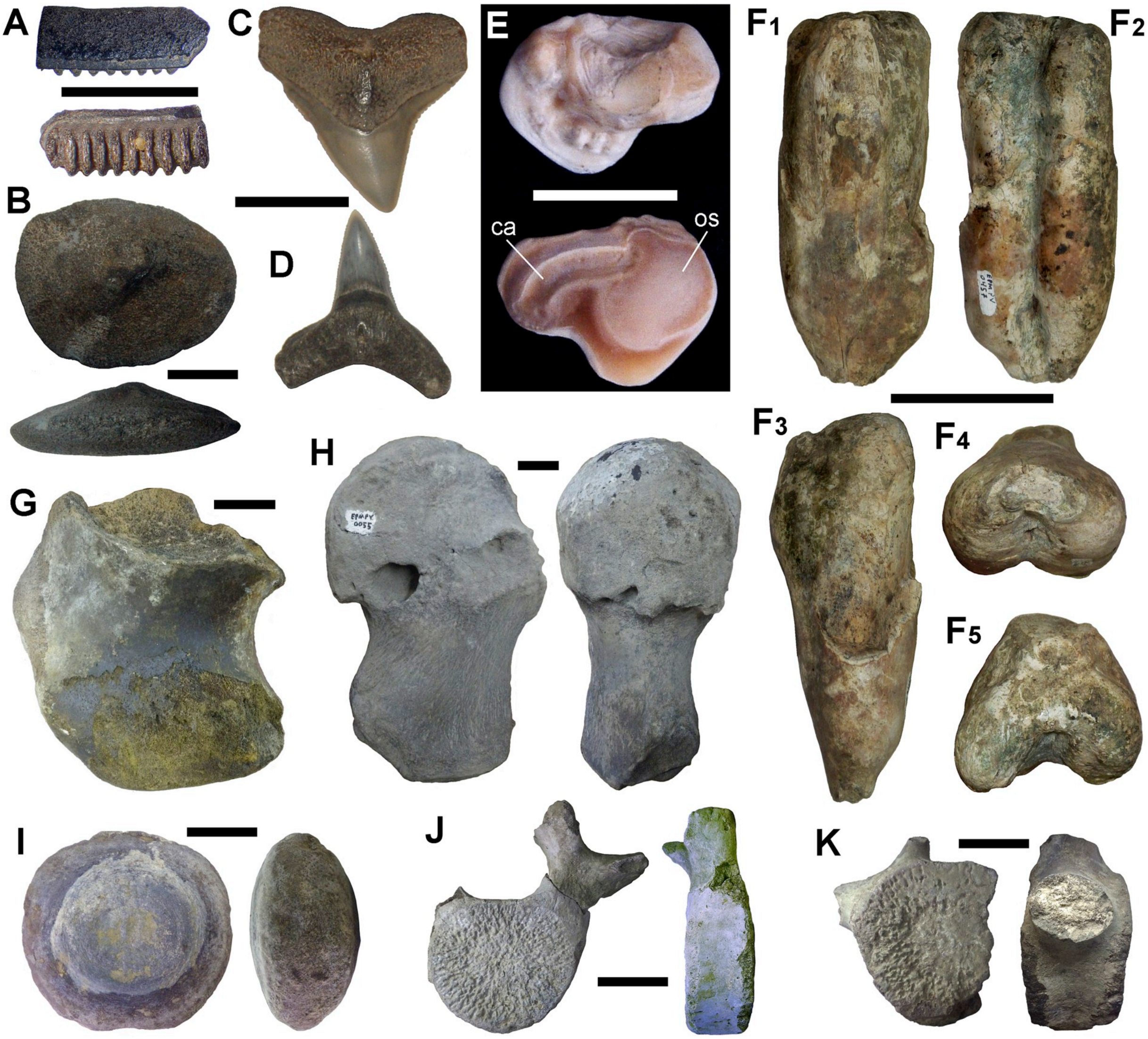

**Fig. 4.** A) Tooth plate of myliobatid ray (MCTFM-PV1109) in occlusal (above) and root (below) views. B) Dermal buckler of dasyatid ray (MCTFM-PV1107) in dorsal (above) and lateral (below) views. C) Upper (MCTFM-PV1026) and D) lower (MCTFM-PV1027) tooth of *Carcharhinus leucas*. E) Sagitta otolith of *Micropogonias furnieri* (MCTFM-PV1179) in external (above) and internal (below) views (ca = cauda, os = ostium). Pterygiophore of cf. *Pogonias cromis* (EPM-PV0457) in anterior (F1), posterior (F2), lateral (F3), basal (F4) and apical (F5) views. G) Unidentified whale bone (EPM-PV0054). H) Right humerus of an adult mysticete whale (EPM-PV0055) in lateral (left) and caudal (right) views. I) Vertebra of the terminal caudal series of a whale (MCTFM-PV1206) in cranial or caudal (left) and lateral views. Dorsal vertebrae MCTFM-1207 (J) and MCTFM-PV1208 (K) of a juvenile mysticete whale. Scale bars = and 10 mm (A–E), 50 mm (F), 100 mm (G–K); the three whale vertebrae are shown in the same scale.

the angled part of the crown. The lower tooth has an erect crown with triangular outline, taller than wide, with serrations along both edges. The denticles located closer to the root and tip of the crown are smaller than those of the middle part of the crown; the root is broad and arched. The adult females of this species breed inside lagoons, where the juveniles dwell until leaving to the sea upon reaching maturity (Sadowski, 1971; Snelson et al., 1984). This taxon is not found living in the coast of Rio Grande do Sul today (Vooren, 1997; Vooren et al., 2005).

ACTINOPTERYGII Klein, 1885
ACANTHURIFORMES Jordan, 1923
SCIAENIDAE Owen, 1846
*Micropogonias furnieri* (Desmarest, 1823).

*Material*: Left otolith (*sagitta*), specimen MCTFM-PV1179 (Fig. 4E).

*Provenance*: Site 1.

*Remarks*: This specimen was found among the shell concentrations at the Latinos Spit. The morphological features that allow identifying this specimen as belonging to *M. furnieri* include: piriform outline with convex anterior and posterior margins, convex irregular dorsal margin, sinuous ventral margin, the expanded portion of the ostium does not reach the margin of the otolith, the ostio-caudal insertion is dorsally positioned, the cauda has a disc-like distal end and is bent toward the ventral margin (Chao, 1978; Corrêa and Vianna, 1993). The otolith measures 14.29 mm in length and 11.06 mm in height; the size and polygonal shape indicates that it belonged to a subadult individual of total body length >120 mm (Volpedo and Echeverría, 1999; Waessle et al., 2003). By applying the linear relationship between the standard body length (SL) and otolith length (OL):

$$SL = 15.102 * OL^{1.090} \; (r^2 = 0.983)$$

obtained by Waessle et al. (2003) from juvenile *M. furnieri* from the La Plata River, it was estimated that the individual measured about 270 mm in length at the time of death.

*M. furnieri* is a marine, estuarine-dependant species (Vazzoler, 1962; FAO, 1988) common in the coastal waters of Rio Grande do Sul today. The adults breed into the estuary of Patos Lagoon, where the juveniles remain until leaving to the ocean when reach the sexual maturity size of about 30 cm in length (Haimovici, 1997; Fischer et al., 2011; Costa et al., 2014).

*Pogonias* cf. *cromis* (Linné, 1766).

*Material*: Pterygiophore, specimen EPM-PV0457 (Fig. 4F).

*Provenance*: Site 1.

*Remarks*: This specimen was found by a fisherman in the Pacheco Lake, located some 4 km inland at Latinos Spit (Fig. 1). It is subcylindrical in shape, with a pointed proximal (basal) end and a blunt apical end. Its anterior side exhibits a rounded longitudinal keel and on its posterior side there is a deep longitudinal groove bounded laterally by two rounded keels, resulting in a subtriangular transverse outline. Pterygiophores are bone elements positioned between the spinous processes of the vertebrae and the insertion of the radii of dorsal (called interneurals) and anal (interhemals) fins; also known as interspinal bones, they serve as attachments for the radii and erector and depressor muscles (Cuvier, 1837; Todd, 1836; Rojo, 2018). This specimen is apparently a dorsal-fin pterygiophore based on its elongate shape, remarkable by its large dimensions (115.7 mm in length and maximum width of 48.7 mm). Its robust aspect is the result of hyperostosis, a condition relatively common in pterygiophores (Gervais, 1875; van Beneden, 1891; Konnerth, 1966), and produced by overgrowth of bones by stimulated periostic osteogenesis. Originally thought to be pathologic, it is now recognized as of ontogenic origin (Meunier et al., 2008; Witten and Hall, 2015).

Hyperostotic bones, also known as ‘tilly bones', were first described in the XVII century (Worm, 1655), and occur in at least 22 families of tropical and subtropical teleost fishes, including 6 species of sciaenids (Smith-Vaniz et al., 1995). Barcellos (1962) reported hyperostosis in recent *M. furnieri* from southern Brazil, and Pilleri (1973) described one recent *P. cromis* with thickened dorsal and ventral spines in Uruguay. In the CPRS, specimens of fossil hyperostotic pterygiophores attributed to *P. cromis* were described from storm-generated shelly concentrations on the shore (Souza Cunha and Nunan, 1980; Richter, 1987). Although another similar species, *P. courbina* (La Cepède, 1803) also occurs in southwestern Atlantic, its hyperostotic pterygiophores are less robust than in *P. cromis* (Azpelicueta et al., 2019). Because of its large size the specimen EPM-PV0457 is tentatively assigned to an old individual of *P. cromis*, a species whose adults can reach up to 140 cm in total length, 40 kg in weight and live up to 40 years (Haimovici, 1997; Fischer et al., 2011). As *M. furnieri*, this species is estuarine-dependant; the adults are live and breed in coastal waters but the juveniles inhabit the estuary of Patos Lagoon until reaching sexual maturity.

CETACEA Brisson, 1762
MYSTICETI Cope, 1890
BALAENIDAE Gray, 1821
cf. *Eubalaena australis* (Desmoulins, 1822).

*Material*: unidentified bone (EPM-PV0054; Fig. 4G), humerus (EPM-PV0055, Fig. 4H) and caudal vertebra (MCTFM-PV1206) of an adult individual, and two dorsal vertebrae (MCTFM-PV1207 and MCTFM-PV1208) of a juvenile.

*Provenance*: Site 2.

*Description*: According to local people, the skeleton of a whale was exposed on the lake bottom not far from the shore, which had receded due to a severe drought in the 1980s. The skeleton was complete and had no teeth, and the humerus and unidentified bone were collected and donated by a farmer. The humerus is short and robust, with the head positioned caudally relative to the shaft of the bone, which is mediolaterally compressed, indicating that it is from a balaenid mysticete (van Beneden and Gervais, 1880; Howell, 1930). The absence of sutures indicates that it was an adult individual at the time of death.

More recently, other people found three vertebrae thrown on the lake shore by waves. The caudal vertebra (PV1206) is disk-shaped, with strongly convex articular facets and without processes or spines, thus it is from the terminal portion of the caudal series (van Beneden and Gervais, 1880). The two other vertebrae are smaller than PV1206 and identified as belonging to a mysticete by the absence of articular facets for ribs on the body, and as a juvenile individual by the rugose articular surfaces indicating the epyphyses were not fused (van Beneden and Gervais, 1880). The vertebra PV1207 is more compressed anteroposteriorly and its transverse process arises from the neural arch, thus it is from the anterior portion of the dorsal series, whereas in PV1208 the transverse process is located in the upper part of the body, therefore is from the distal portion of the series. The morphology of the humerus and vertebrae are compatible with the southern right whale (baleia-franca in Portuguese), *Eubalaena australis* (Desmoulins, 1822) (van Beneden and Gervais, 1880), which is relatively common in the coastal waters off southern Brazil during winter and spring and reportedly breeds in bays of the state of Santa Catarina (Castello and Pinedo, 1979; Pinedo, 1997). The association of an adult and a juvenile indicates a mother and its calf that entered Mirim Lake for shelter when it was a large lagoon connected to the ocean (see Discussion) and became stranded close to the shore. The fossils of cetaceans found in the CPRS described so far consist of remains transported from the continental shelf to the beach by storms (Souza Cunha and Nunan, 1980; Souza Cunha et al., 1992; Ribeiro et al., 1998; Bergqvist et al., 1999; Aires et al., 2010).

### 4.2.2. Terrestrial vertebrates

These fossils were collected in the sites 2, 3 and 4. All specimens

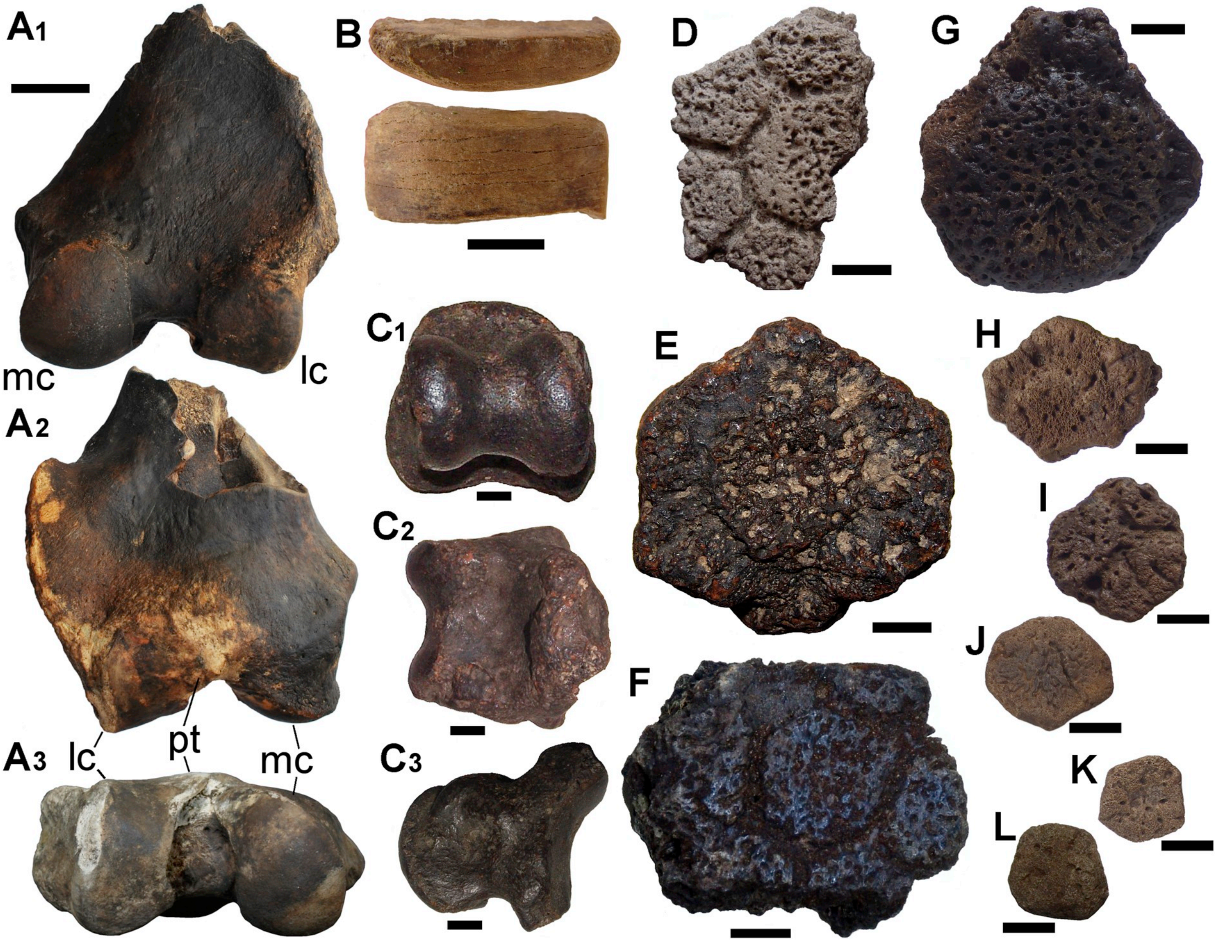

**Fig. 5.** A) right femur of megatheriid sloth (cf. *Eremotherium laurillardi*; MCTFM-PV0981) in anterior (A1), posterior (A2) and distal (A3) views (lc = lateral condyle, mc = medial condyle, pt = patellar trochlea). B) fragmented molar of a megatherid (MCTFM-PV1180) in occlusal (top) and mesial/distal (bottom) views. C) middle phalanx (MCTFM-PV1182) of a mylodontid? sloth in anterior (C1), dorsal (C2) and lateral (C3) views. Osteoderms of *Glyptodon* cf. *reticulatus*: D) MCTFM-PV0761, E) MCTFM-PV1181, F) MCTFM-PV1183 and G) MCTFM-PV1008. Osteoderms of unidentified glyptodontids: H) MCTFM-PV1178, I) MCTFM-PV1006. Osteoderms of unidentified cingulates: J) MCTFM-PV1011, K) MCTFM-PV1009 and L) MCTFM-PV1007. Scale bars = 100 mm (A) and 10 mm (B–L).

were found disarticulated and most are incomplete. Those retrieved from the lake bottom range in color from reddish brown to black, which indicates precipitation of elements such as iron and manganese dissolved in the water and bacterial activity (Lopes and Ferigolo, 2015), whereas other specimens are light brown.

MAMMALIA Linné, 1758
XENARTHRA Cope, 1889
PILOSA Flower, 1883
MEGATHERIIDAE Gray, 1821
cf. *Eremotherium laurillari* Lund, 1842

*Material:* Distal portion of a right femur (MCTFM-PV0981, Fig. 5A).
*Provenance*: Site 4.
*Description*: This specimen was retrieved from the bottom of the lake by a fisherman at about 1 km far from the southeastern shore, at an estimated depth of 4 m. The epiphysis fused to the diaphysis indicate an adult individual. Although the diaphysis is broken just above the epicondyles, the remaining portion shows that it was anterioposteriorly compressed, twisted relative to the plane formed by the lateral and medial condyles, and mediolaterally constricted, features that indicate it is from a giant sloth. The shape of the diaphysis differs from that of *Glossotherium robustum* Owen, 1842 (Pl. XVII-XVIII) and *Lestodon armatus* Gervais (1855) (Gervais, 1873; Pl. 26). The patellar trochlea is slightly concave mediolaterally, distolaterally contiguous with the lateral condyle, and extends proximomedially beyond the midplane of the intertochlear space, almost reaching the medial condyle (Fig. 3A2 and A3), resulting in a narrow space between the medial and lateral condyles. These features indicate affinity with *E. laurillardi*, because in *Megatherium americanum* Cuvier, 1796 the trochlea does not reach as far as the vertical midplane of that space (De Iuliis, 1996; Pl. 98). This assignment, however, is inconclusive due to the absence of additional diagnostic features. Other taxonomically relevant features present in the specimen such as the degree of torsion of the shaft and the shape of the epicondyle are variable and exhibit considerable overlapping between the two taxa (De Iuliis, 1996). Fossils of *M. americanum* and *E. laurillardi* have been found in the southern CPRS (Pereira et al., 2012; Lopes and Pereira, 2019), and this specimen could be the second record of the latter in this area.

Megatheriidae indet.

*Material*: Fragment of a molariform (MCTFM-PV1180, Fig. 5B).
*Provenance*: Site 3.
*Description*: This specimen was found stranded on the lake shore, close to the mouth of the irrigation channel. Although only a fragment, the chiseled shape of the occlusal surface indicates that it is from a megatheriid sloth.

Family MYLODONTIDAE? Gill, 1872

*Material*: phalanx, MCTFM-PV1182 (Fig. 5C).

*Provenance*: Site 3.

*Description*: The specimen is complete and consists of the middle phalanx of a digit II or III, with which the distal (ungueal) phalanx articulated distally. Its proximal articulation is elongated in the dorsopalmar direction, concave, with two dorsoventrally elongated shallow depressions separated by a medial ridge. In front of the lower articular tuberosity there is a deep concavity that allowed the dorsoventral flexion of the ungueal phalanx. The distal articular area consists of two dorsoventrally semicircular articular facets divided by a median sulcus; the larger facet is the outer one (Stock, 1925), thus indicate that this bone is from a left hand. The morphology is compatible with that of a mylodontid sloth, possibly *Glossotherium robustum* Owen, 1842 or *Lestodon armatus* Gervais, 1855, both common in the fossiliferous deposits of the CPRS.

CINGULATA Illiger, 1811
GLYPTODONTIDAE Gray, 1869
*Glyptodon* Owen, 1839
*Glyptodon* cf. *reticulatus* Owen, 1845

*Material:* carapace osteoderms MCTFM-PV0761 (Fig. 5D), MCTFM-PV1183 (Fig. 5E), MCTFM-PV1181 (Fig. 5F), MCTFM-PV1008 (Fig. 5G), MCTFM-PV1178 (Fig. 5H) and MCTFM-PV1006 (Fig. 5I).

*Provenance*: Site 3 (PV0761, PV1183 and PV1181); Site 2 (PV1008, PV1006 and PV 1178).

*Description*: Assigned to *Glyptodon* based on the presence of a larger central figure surrounded by smaller peripheral figures, all separated by relatively wide sulci. The osteoderms are mostly fragmented and exhibit color varying from light brown to black. Although both *G. reticulatus* and *G. clavipes* Owen, 1839 have been described from the deposits in the CPRS, these two species are probably synonymous (Lydekker, 1894), and apparently the only valid Late Pleistocene glyptodontid species are *G. reticulatus* and *G. elongatus* Burmeister, 1864 (Zurita et al., 2018). The specimens presented here exhibit pitted, rough surfaces, whereas in *G. elongatus* the surface is smoother (Burmeister, 1870), therefore the material is tentatively assigned to *G. reticulatus*. The morphology of the specimens D, E and F indicates that they are from the dorsal region of the carapace, whereas the specimen G is from the lateral region (Burmeister, 1870). Although only fragments, the specimens H and I appear to be also from the dorsal region.

Glyptodon sp.

*Material*: osteoderms MCTFM-PV 1011 (Fig. 5J), MCTFM-PV1009 (Fig. 5K) and MCTFM-PV1007 (Fig. 5L).

*Provenance*: Site 2.

*Description*: The polygonal outline and the absence of ornamentation apart from small round perforations (specimens PV1107 and 1009) or sinuous grooves (PV1011), suggest that these osteoderms were from the tail, apparently from one of the proximal caudal rings, of a *Glyptodon* (Burmeister, 1870). The three specimens are small and exhibit a spongy texture, thus suggesting that they were from a juvenile. Although found disarticulated, they were collected from the same channel, therefore could have belonged to the same individual.

NOTOUNGULATA Roth, 1903
TOXODONTIDAE Owen, 1845
*Toxodon* Owen, 1838.
*Toxodon platensis* Owen, 1837

*Material*: right zygomatic arch and part of the frontal (MCTFM-PV0680a and b, Fig. 6A), part of a left zygomatic process of the temporal bone (MCTFM-PV0680C, Fig. 6B), upper right molars (MCTFM-PV0757 and 0680d, Fig. 6C and D, respectively), an ulna (Fig. 6E) and a metapodial (MCTFM-PV0682, Fig. 6F).

*Provenance*: Site 3.

*Description*: These are the only mammalian fossils found *in situ* so far on the shores of Mirim Lake, buried some 1.5 m below the surface in a muddy sand layer exposed along the irrigation channel (Fig. 2C), except for the tooth PV0757 and the metapodial, found among sediments piled along the margin of the channel. The tooth PV0680d was the one dated by ESR. The morphology of the specimens are consistent with *T. platensis* (Owen, 1838; Gervais, 1855; Burmeister, 1864; Ameghino, 1889), a taxon rather common in the fossil deposits of the CPRS. The presence of different skull and postcranial elements found associated suggests that these represent reworked parts of the same individual. Some teeth fragments of *Toxodon* were also recovered from the channel in the Site 2.

PROBOSCIDAE Illiger, 1811
GOMPHOTERIIDAE Hay, 1922
*Notiomastodon* Cabrera, 1930
*Notiomastodon platensis* Ameghino, 1888

*Materials*: molariform (EPM-PV0435) from Site 3 (Fig. 7A); right dentary (MCTFM-PV0715, Fig. 7B) from Site 4.

*Description*: This specimen was found by a schoolboy among sediments piled along the margin of the same irrigation channel where the aforementioned fossils of *Toxodon* were collected later. It is almost complete, lacking the tips of the roots. Identified as a mastodont by the crown formed by five pairs of conical-shaped cusps (lophids), separated by a medial sulcus (Cuvier, 1806). The presence of a rudimentar 6th lophid indicates that it is a lower third molar (Osborn, 1936). The 2nd, 3rd and 4th lophids exhibit central conulids distally. This specimen is identified as a right molar based on the pretrites positioned on the labial side (Gadens Marcon, 2007). The degree of wearing of the cusps progressively decreases distally along the postrite. The wearing indicates that this tooth had completely erupted at the time of death, thus suggesting that the animal was at least five years old, by comparison with the pattern of eruption in modern African elephants (Johnson and Buss, 1965). This tooth is larger than the specimens found in other parts of Brazil (maximum length = 215 mm and maximum width = 920 mm), except in Rio Grande do Sul, and comparable to those of Argentina (Gadens Marcon, 2007). The specimen PV0715 was identified as the dentary of a proboscidean based on its large size (it measures 660 milimeters in length) and by the general morphology similar to that of gomphotheriid mandibles (Cuvier, 1806; Osborn, 1936), with a mesiodistal curvature and the lateral side inflated dorsoventrally. The fossil was retrieved from the bottom of the lake by a fisherman, and is poorly preserved, consisting of the horizontal ramus and the base of the coronoid process, lacking the symphyseal and articular areas and the teeth. The lateral side is dorsoventrally inflated and better preserved than the mesial one, and exhibits two mentonian foramina at the anterior end. Although this specimen is mostly dark brown, some fragmented areas are light-colored, thus indicating that it was broken after fossilization (Lopes and Ferigolo, 2015). Although the gomphotheriid materials from Rio Grande do Sul were identified as belonging to *Stegomastodon waringi* (Holland, 1922) (Gadens Marcon, 2007), the specimens described here are assigned to *Notiomastodon platensis* following the revision by Mothé et al. (2012).

PERISSODACTYLA Owen, 1848
EQUIDAE Gray, 1821
*Equus* Linné, 1758
*Equus* (*Amerhippus*) *neogeus* Lund, 1840

*Material*: lower molar tooth (MCTFM-PV1023, Fig. 7C).

*Provenance*: Site 2.

*Description*: Longitudinally bilobated tooth, identified as belonging to *Equus* based on the laterally compressed lateral lobes (rounded in *Hippidion*), by the presence on its lateral side of an ectoflexid projected

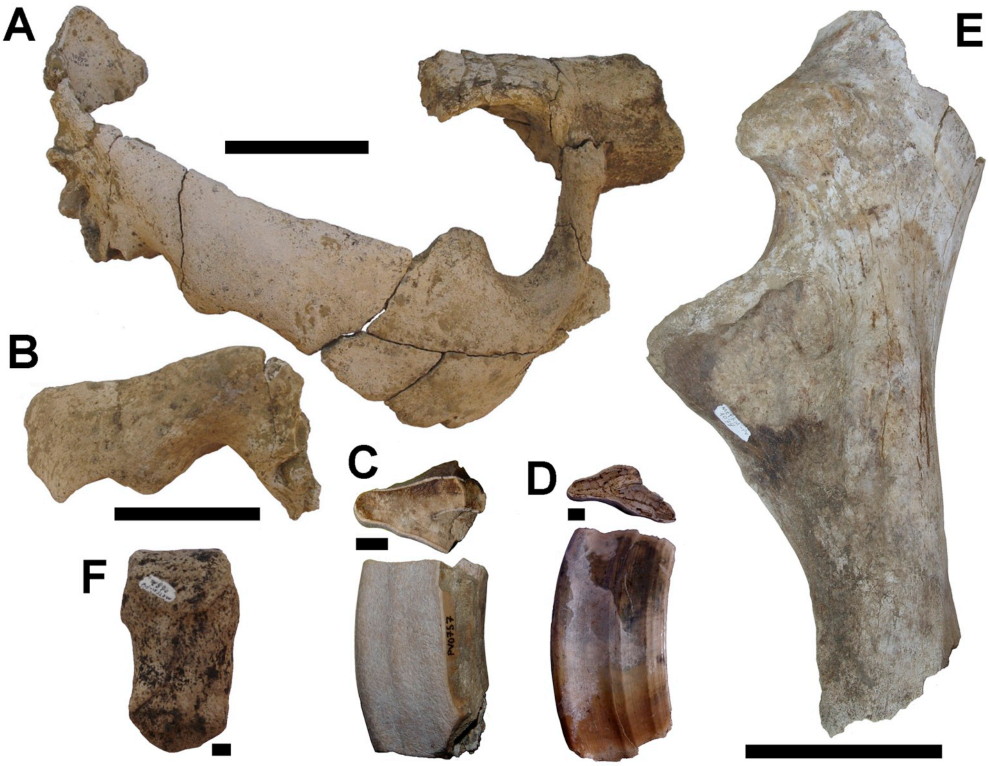

**Fig. 6.** Fossils of *Toxodon platensis* found *in situ* at Site 3: A) right zygomatic arch (MCTFM-PV0680a,b), B) fragment of the left zygomatic process, C) upper molar (MCTFM-PV-0757), D) upper molar (MCTFM-PV0680d), E) ulna (MCTFM-PV1079), F) metapodial (MCTFM-PV0682). Scale bars = 100 mm (A,B,E) and 10 mm (C,D,F).

inwards, almost reaching the linguaflexid, and by the presence of two enamel wrinkles projected inward from the lingual side and is expanded mesiodistally forming the preflexid and postflexid (Ameghino, 1889). The first equid fossils from the CPRS were collected along the shore and identified as *Equus* sp. (Souza Cunha, 1959). Later, both *Equus* cf. (*A*) *neogeus* and *Hippidion* sp. were described from fluvial deposits of Chuy Creek (Pereira et al., 2012). In a review of the equid fossils from Brazil, Alberdi et al. (2003) identified H. *principale* (Lund, 1846), *H. devillei* (Gervais, 1855) and *E.* (*A.*) *neogeus*. Following their conclusions the specimen found in the Mirim Lake is assigned to the latter species.

ARTIODACTYLA Owen, 1848
CERVIDAE Gray, 1821
*Morenelaphus* Carette, 1922
Morenelaphus sp.

*Material*: incomplete antlers: MCTFM-PV1003 (Fig. 7D) MCTFM-PV1066 (Fig. 7E) and MCTFM-PV1102 (Fig. 7F). Fragments of antlers: MCTFM-PV1184 (Fig. 7G), MCTFM-PV 1185 (Fig. 7H) and MCTFM-PV1186 (Fig. 7I).

*Provenance*: Site 3 (PV1184, 1185 and 1186) and Site 4 (PV1003, 1066 and 1102).

*Description*: The specimen PV1003 is the lower portion of an antler, from the rosette up to the just below the 3rd ramification. According to the fisherman who retrieved it from the lake bottom, part of it broke and fell from the fishing net and could not be recovered. The first ramification is present, but the second was broken prior to the collecting, as indicated by the mud-filled internal cavity. The surface of these specimens is smooth, with shallow longitudinal grooves and small isolated tubercles. The other two incomplete materials do not have the basal rosette, therefore are probably from the distal portion of the antler, above the 2nd ramification. Two of the fragments (PV1184 and 1185) are from the base of the antlers as indicated by the rosettes, whereas the other (PV1186) is part of one of the ramifications. The overall morphologies are consistent with the genus *Morenelaphus*, which has been found in the shoreline deposits and Chuy Creek (Scherer et al., 2007; Pereira et al., 2012). The species could be either *M. lujanensis* or *M. brachyceros* (Alcaraz, 2010).

Cervidae indet.

*Material*: tip of antler (MCTFM-PV0758, Fig. 7J) and right astragalus (MCTFM-PV1016, Fig. 7K).

Provenance: Site 2 (PV1016) and Site 3 (PV0758).

*Description*: The fragment PV0758 is identified as the tip of a cervid antler by its conical, pointed shape, but its morphology does not allow identifying to which species it belonged. This specimen was collected in sediments removed during excavation of the channel where the aforementioned remains of *Toxodon* were found. The astragalus bears the characteristic double pulley structure of the artiodactyls, with a proximal trochlea for the tibia formed by two semicircular crests (the lateral one is taller) separated by a deep sulcus, and a distal, smaller trochlea with articular surfaces for the scaphoid and cuboid bones (Ameghino, 1889). The specimen presented here is complete, but exhibits some signs of abrasion, mostly on the distal portion. It is identified as belonging to a cervid based on the less developed lateral condyle compared to that of camelids (Scherer, 2005).

RODENTIA Bowdich, 1821

*Material*: incisor (MCTFM-PV1106, Fig. 7L).

*Provenance*: Site 2.

*Description*: The specimen is dark-colored, with chiseled occlusal surface and open root end. It does not bear diagnostic features, but the size seems compatible with that of *Myocastor coypus* (Molina, 1782), a taxon that has already been found in other sites of the CPRS (Rodrigues and Ferigolo, 2004; Pereira et al., 2012).

## 5. Discussion

The vertebrate assemblage described here includes terrestrial and marine taxa found in other fossiliferous deposits of the CPRS (Oliveira,

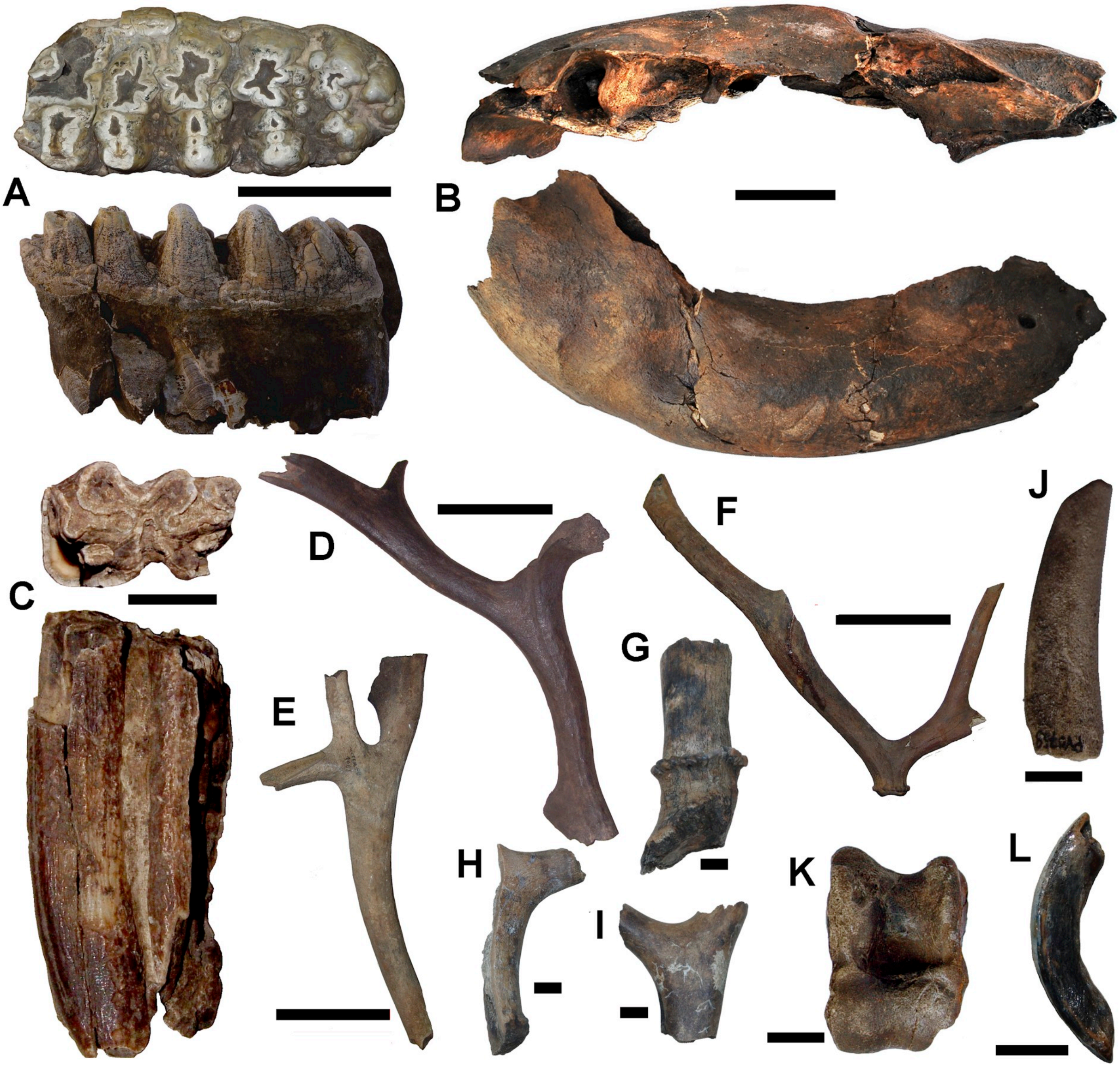

**Fig. 7.** Fossils of *Notiomastodon platensis*: A) 3rd lower molar (EPM-PV0435), B) right dentary (MCTFM-PV0715). C) lower molar of *Equus* (MCTFM-PV1017). Antlers of cervids (cf. *Morenelaphus* sp): D) MCTFM-PV1003, E) MCTFM-PV1066, F) MCTFM-PV1102, G) MCTFM-PV1184, H) MCTFM-PV1185, I) MCTFM-PV1186 J) tip of antler (MCTFM-PV0758). K) astragalus of cervid (MCTFM-PV1016). L) incisor of rodent (MCTFM-PV1106. Scale bars = 100 mm (A,B,D-F) and 10 mm (C, G-L).

1992; Lopes and Buchmann, 2010; Aires and Lopes, 2012; Pereira et al., 2012), but their relevance resides on being the first remains found in Mirim Lake, besides including some taxa previously unrecorded in this area. The presence of remains of both terrestrial and marine in a lake that today is essentially freshwater points to marked evironmental changes that can be related to its geological history. Of special importance are the fossils found *in situ*, because the stratigraphic setting and associated age of these remains allow establishing a chronocorrelation with other fossiliferous units and assess the geological evolution of the lake margin within a chronostratigraphic setting.

### 5.1. Taphonomy of the fossil remains

The fossils found *in situ* at the Facies A were all excavated at the same point along the channel and belong to *Toxodon*, which suggests that these are skeleton parts of the same individual. The fragmentary state of the fossils, the absence of other bones of the same animal, plus the possible association with disarticulated/fragmented remains of other taxa (removed from the channel during its excavation) such as mastodonts and glyptodonts, indicate that these fossils were subject to *post mortem* reworking, probably by streams flowing from the higher terrace T1. This is also seems to be the case of the disarticulated/fragmented fossils found along the lake shore close to Site 3 and on the terrace T3 to the north (Site 2).

In terms of preservation these fossils are similar to those from Chuy Creek, deposited and reworked in fluvial systems (Lopes and Ferigolo, 2015). The ulna of *Toxodon* (Fig. 6E) exhibits some longitudinal crackings indicative of weathering (Behrensmeyer, 1978). The absence of these features in the other remains indicate that these were not subaerially exposed for long periods after death, whereas the ulna, being a larger bone, remained exposed for some time prior to burial. The plain fractures show that they were subject to breakage after fossilization, because fresh bones when broken tend to produce irregular fractures (Holz and Simões, 2002).

The state of preservation of most of the fossils collected from the bottom of the lake is similar. The margin along the broken end of the femur of cf. *Eremotherium* exhibits rounded, abraded edges (see Fig. 5A2). The fracturing pattern is irregular, suggesting the bone was broken while still fresh (Holz and Simões, 2002) possibly as the result of trampling or scavenging, and the abrasion would have been caused by sediment-laden flowing water. The size, weight and flattened shape of this specimen seems to preclude active transportation by water, but it could have remained in place with the broken portion oriented against water flowing from the opposite direction. Long bones tend to remain stable if their long axes become aligned parallel to the water current, thus resulting in one end more abraded than the opposite one (Behrensmeyer, 1991). In that femur and in the dentary of *Notiomastodon* (Fig. 7B) some broken areas exhibit light color relative to the dark reddish brown on most of the surface of these fossils, indicating post-fossilization abrasion and breakage. These remains were found hundreds of meters from the present position of the lake shore, at depths of about 2–4 m. It is unlikely that lake hydrodynamics would be able to transport, break or produce abrasion in such large bones. Although carcasses in advanced state of decay could have floated into the lake until sinking (Holz and Simões, 2002), this process could not account for the fragmentary/abraded state of the fossils. The most likely explanation for their presence far from the present shore would be burial and fossilization at or close to the paleo-shoreline at a time when the area of the lake was reduced, probably a during a glacial period when climate was dry and the lower sea-level exposed most of the continental shelf and lowered the regional base level. The Holocene Barrier -Lagoon System IV had not been formed yet and the lake was connected to the ocean through fluvial systems flowing along an incised valley at Taim (Barboza et al., 2007). The presence of those fossils at depths of up to 4 meters provide an estimate of the area covered by the lake at that time (Fig. 8A). During a following period of increased rainfall and fluvial input the fossils would have been exhumed and abraded by streams flowing toward the lake. The antlers of cervids retrieved from the bottom, on the other hand, were probably carried by streams that discharged into the lake, which would have caused their fracturing.

Despite the surveys performed in Site 2, the adult whale skeleton exposed in the 1980s was not located, suggesting that it remains covered by water. The only bone presumably from that skeleton found so far on the shore is the caudal vertebra (Fig. 4I), which was found in the same area of the two juvenile vertebrae (Fig. 4J and K). This association and the morphology of the bones consistent with the species *Eubalaena australis* indicates a mother and calf of entered Mirim Lake at the time it was connected to the Atlantic Ocean (see below) and died at the same site. Several strandings of this species along the seashore of the CPRS between 1977 and 1995 may be explained by sea-level rise of up to +2 m during storm surges, which caused the whales to seek shelter in shallower areas close to the shore and became stranded as the water level lowered after the surge (Greig et al., 2001). Considering the westward-facing shoreline at Site 2 (Fig. 1C) adjacent to the large flat area of the lake to the SW which provides a long wind fetch, it is possible that surges produced by the strong S-SW winds that predominate during winter (Villwock and Tomazelli, 1995) led the whales to seek shelter close to the lake shore and became stranded. In fact, the dense shell concentrations found at Latinos Spit (Fig. 2A) indicate storm processes within the lake, as will be discussed in other paper.

Given the size of the vertebrae it seems unlikely that they were transported for long distances and mixed together by physical processes; instead, they were probably removed from the skeletons located close to the shore at this site. After death the skeletons would have been disarticulated and the vertebrae transported to the shore by wind-generated waves, which are a major mechanism of circulation in coastal lagoons (Bird, 1994), especially in the CPRS where the amplitude of the astronomical tides is negligible (<30 cm) (Villwock and Tomazelli, 1995). Vertebrae are apparently moved by waves with relative ease compared to other bones, as indicated by the common occurrence today of recent whale vertebrae removed from carcasses found scattered along the seashore in the southern CPRS (Fig. 8B). Wind-generated waves and currents are the mechanisms responsible for transporting fossils, including fossilized whale vertebrae (Souza Cunha and Nunan, 1980; Aires et al., 2010), from fossiliferous concentrations (lag deposits) on the inner continental shelf to the beach today (Lopes and Buchmann, 2010).

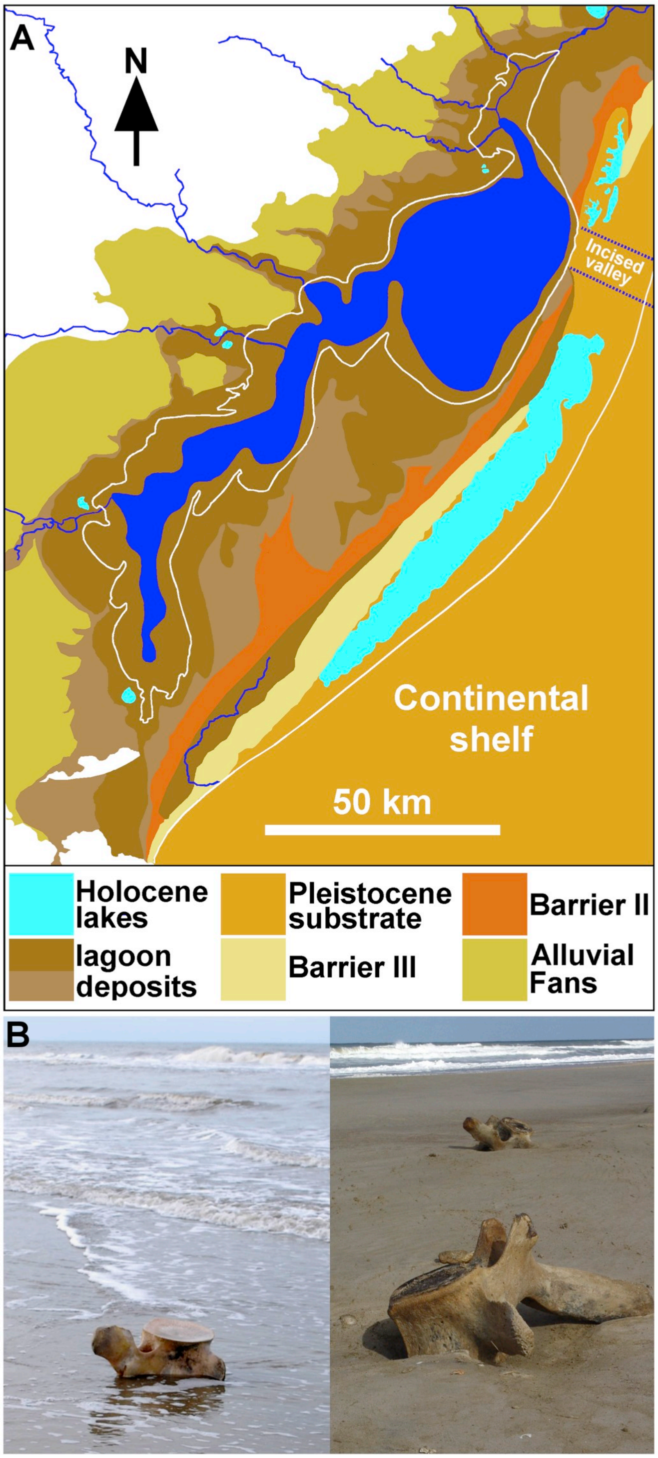

**Fig. 8.** A) Paleogeographic map of the southern CPRS showing the hypothetical area occupied by Mirim Lake in glacial times when it was some 4 meters lower than today (based on bathymetric lines from Vieira, 1995) and sea-level was >100 meters lower; the white outline shows the area of the lake today and the modern coastline. B) Recent vertebrae of whales stranded on the seashore in the southern CPRS.

### *5.2. Implications for the geological and environmental evolution of Mirim Lake*

The ESR age of the tooth of *Toxodon* (68 ± 13 ka) and the overlying caliche (32.8 ± 5.1/16.9 ± 2.5 ka) from the channel put these deposits in chronostratigraphic correlation with the fossil-bearing Santa Vitória

Formation, exposed along the banks of Chuy Creek (Fig. 3G; Lopes et al., 2010, 2014a,b). The different depositional environments indicated by the facies succession observed on the banks of the creek can be linked to climate changes (Lopes et al., 2016, b), therefore, it is likely that such changes also affected the lake and its surroundings. By comparing the ages, fossils and facies successions along the creek and the irrigation channel, it is possible to define a sequence of events and conditions that controlled the evolution of the lake margin within a chronostratigraphic framework.

### 5.2.1. MIS 3-MIS 2 (~68–16.9 ka b2k)

The absence of perennial rivers reaching the lake from the east indicates that the sediments accumulated on its eastern shore were eroded from the Barrier II and deposited by ephemeral streams flowing during phases of increased precipitation and by eolian processes during dry phases, as indicated by the inactive channels, alluvial fans and deflation basins developed along the terraces (Gomes et al., 1987). The minimum ESR age obtained in the tooth of *Toxodon* and the OSL age of the overlying caliche-bearing sediments show that the fossils found on the channel were transported and buried between ~68 ka and >32.8 ka b2k by alluvium (Facies A) eroded from the nearby higher terrace T1. This mechanism explains the presence of cone-shaped alluvial deposits found along the terraces of the Mirim Plateau (Gomes et al., 1987).

The reworking and burial of fossils at that time was probably driven by increased precipitation controlled by relatively warmer and wetter climate. The timing of deposition of the Facies A corresponds to the interstadial MIS 3, that lasted from 57 to 29 ka b2k (Lisiecki and Raymo, 2005). Precipitation in the southern CPRS was increased during MIS 3 as indicated by one fossil of a stork excavated from an ephemeral fluvial deposit of the Santa Vitória Formation dated by OSL as of ~37.9 ka b2k as (Lopes et al., 2019). Periods of higher precipitation during MIS 3 are also indicated by other geological records in southern Brazil and attributed to higher influence of the South American Summer Monsoon (SASM) correlated with warming pulses in Antarctica (Cruz et al., 2006; Lopes et al., 2019). Increased rainfall at that time formed semi-permanent streams flowing from the Barrier II to the east (Santa Vitória Formation) and to the west toward Mirim Lake. Progradation of the lake shore through deposition of sediments eroded by streams during lake lowstands was probably the main mechanism responsible for building the Mirim Plateau since the Barrier II was formed in the middle Pleistocene.

The relatively high percentage of very fine silt and clay in the Facies B1 indicates deposition under low hydrodynamics related to higher lake water that remained up to ~0.5 m above the present level until at least 32.8 ka b2k (Fig. 3A). That highstand would have been the result of one of the pulses of higher rainfall that characterized MIS 3, as mentioned above, which would have driven an increase of fluvial discharges reaching the lake. In fact, long periods of high precipitation today, such as recorded during El Niño events, can rise the lake level by > 1 m (see Fig. 9A and B). Besides increased rainfall and fluvial discharges, a higher water level around that time could also have been influenced by the relatively high sea-level (−5 to −23 m relative to the present m.s.l.) recorded in southern Brazil between ~47.7 and ~36.2 ka b2k (Dillenburg et al., 2019). Because of the connection through the paleo-incised valley at Taim, a higher sea-level would have raised the regional base level, thus contributing for rising the lake water.

After this highstand, the region was subject to a dry phase when desiccation cracks were developed in the subaerially-exposed clayey sediment, followed by deposition of silt and precipitation of caliche as nodules and also around plant roots and infilling the desiccation cracks, thus indicate a lake lowstand (Fig. 3A). The timing of silt and caliche deposition, after 32.8 ka b2k, probably was driven by cold and dry climate during the last glacial epoch (stadial MIS 2, 29–11.7 ka b2k), a period of increased eolian-driven processes and reduced plant cover that resulted in widespread loess deflation and transportation by suspension from the Pampean Sand Sea of Argentina up to Uruguay and southern Brazil (Clapperton, 1993; Iriondo, 1999; Prado and Alberdi, 1999; Zárate, 2003; Munyikwa, 2005).

Pedogenic caliche is formed in the vadose zone of subaerially-exposed sediments under climate with mean annual precipitation ≤750 mm (Kholodov, 2007), and is a common feature in loess deposits (Iriondo, 1997; Zárate, 2003). It is also found on the loessic Cordão Formation exposed along Chuy Creek (Lopes et al., 2016b), whose OSL ages of <30 ka indicate deposition during MIS 2, therefore chronocorrelated with the Facies B1 exposed on the lake margin (Fig. 7G). Caliche deposits have not been found so far in the Pleistocene Barriers II and III, but its presence in the Cordão Formation and in silt deposits found along the Mirim Plateau interpreted as of eolian origin (Gomes et al., 1987; Lopes et al., 2016) indicates loess as the probable source material for the precipitated carbonate (Lopes et al., 2016b).

The OSL age group of 16.9 ± 2.5 ka in the dated nodule indicates that these quartz grains were exposed to sunlight at that time, indicating erosion and partial exposure of the caliche. This erosion would have been caused by rain-fed ephemeral streams related to increased precipitation, driven by deglaciation (Termination I) that started around 20 ka b2k and marks the beginning of the transition from glacial (MIS 2) to interglacial (MIS 1) climate (Hulton et al., 2002; Seltzer et al., 2002; Denton et al., 2010). Increased precipitation after 18 ka b2k is recorded in speleothems from tropical and subtropical Brazil and associated with strengthening of the South American Summer Monsoon (SASM) driven by the Heinrich stadial (HS) 1 in the northern Hemisphere (Cruz et al., 2006; Novello et al., 2017).

The increased precipitation after 18 ka b2k would have formed streams flowing from the Barrier II and higher terraces to the lake, starting another phase of alluvial deposition (Facies B2) on top of the Facies B1. Besides streams, small lakes or ponds would have been formed on the lake shore, as indicated by the tabular siliceous deposit (Fig. 3D), which suggests low hydrodynamic conditions that allowed for the settling of the fine siliceous particles; its laminated aspect points to seasonal variations in particle input. The origin of this deposit is probably the dissolution of diatom frustules or other siliceous material (such as phytoliths) by fluctuating pH followed by re-precipitation as amorphous silica, conditions similar to those that lead to the formation of chert in Australian lakes (Peterson and von der Borch, 1965).

### 5.2.2. MIS 2-MIS 1 (~16.9–5 ka b2k)

The late Pleistocene-middle Holocene post-glacial marine transgression (PMT) that started around 18 ka b2k in response to the melting of ice caps and glaciers, together with increased precipitation, would have led to another lake highstand (Fig. 3A). Sea-level curves obtained from several sites along the Brazilian coast show that a mean sea level (m.s.l) equal to the present one was reached at ~7 ka b2k, and continued to rise until reaching up to +5 m between 6 and 5 ka b2k (Martin et al., 2003; Angulo et al., 2006). In the CPRS the PMT formed the Barrier IV, and the estimates based on geologic and fossil records indicate that it reached amplitude of about 2–3 m above the present m.s.l. (Barboza and Tomazelli, 2003; Caron, 2007; Lima et al., 2013; Dillenburg et al., 2017).

Core samples obtained in Taim show that during the PMT the incised valley across this area was an inlet that connected the Atlantic Ocean and Mirim Lake (Buchmann et al., 1998), still apparent today during periods of flooding (Fig. 9A and B). This connection implies that the sea-level controlled the level of Mirim Lake during the highstand. The maximum amplitude of +3 m reached during the sea-level highstand and the ~12 km-long connection with the ocean through Taim would have resulted in the invasion of the lake by seawater, drowning large portions of the lake margins including the terrace T3 and most of the São Gonçalo channel (Fig. 9C), thus transforming Mirim Lake in an open, Type III paleo-lagoon in the classification of Lankford (1977). The area of Latinos Spit and Pacheco Lake would have been an embayment open to the northern end of Mirim Plateau. It was during this highstand

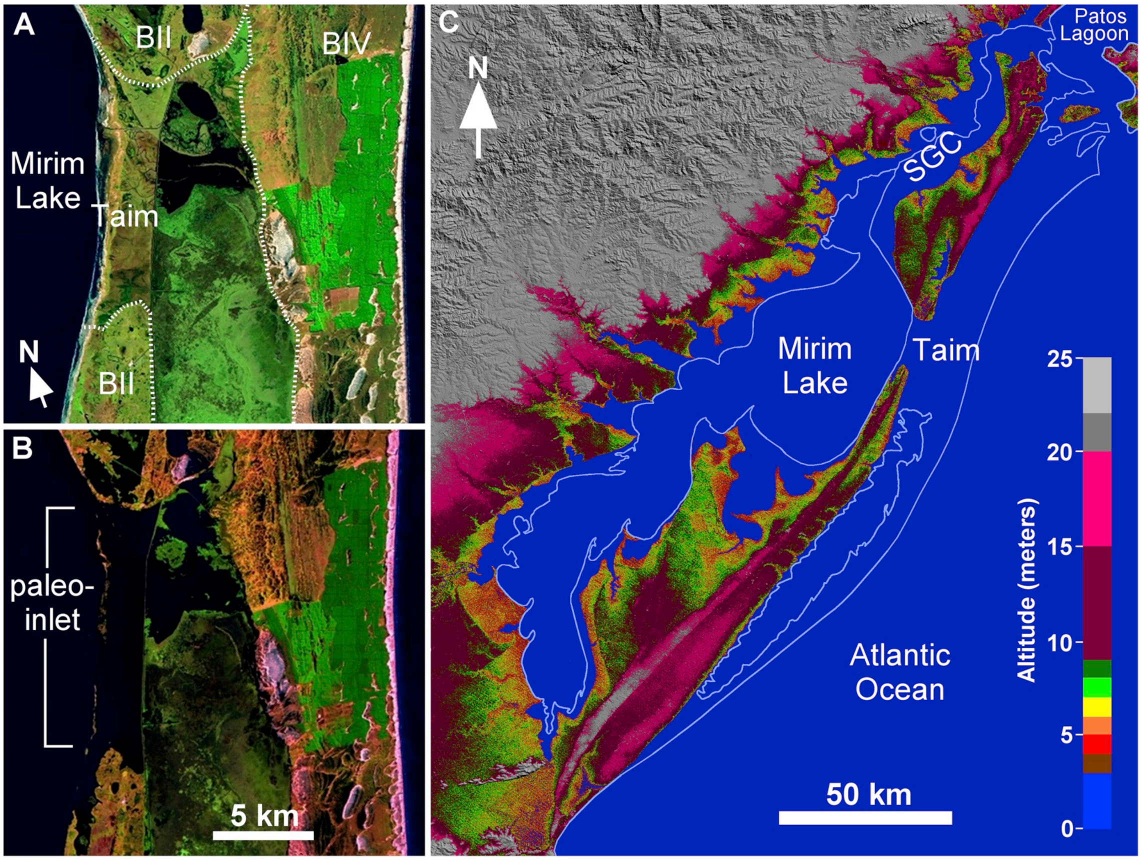

**Fig. 9.** LANDSAT image of Taim under 'normal' conditions (A), compared with an image taken during an El Niño event in the year 2000 (B); the flooded area shows the extension of the paleo-inlet that connected the Atlantic Ocean and Mirim Lake across the Barriers II and III before the Holocene barrier (BIV) was established. C) Digital elevation map made with SRTM data showing the configuration of the southern CPRS during the Holocene highstand, considering a maximum amplitude of 3 m a.s.l. The light blue outline corresponds to the modern coastal configuration and shows that most of the lowest terrace (T3) around Mirim Lake was drowned (the Barrier IV had not yet attained its present-day configuration and was omitted here for clarity). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that sediments eroded from the higher ground and deposited as the uppermost Facies C exposed along the Site 3 were cut into a terrace (T3). Considering that the height of T3 is similar to the amplitude of the Holocene highstand, it can be hypothesized that the 5-6 m-high terrace T2 was formed during the Pleistocene highstand of ~125 ka b2k, that reached 7 ± 1 m above the present sea-level and originated the Barrier III (Tomazelli and Dillenburg, 2007). In a similar way, the terrace T1 would have been produced by the middle Pleistocene highstand that reached about +10 m around 220 ka b2k and formed the Barrier II (Lopes et al., 2014a). Terraces at similar altitudes are also found on the southwestern lake shore in Uruguay (Montaña and Bossi, 1995).

The fossils of marine vertebrates were collected at or close to the bottom surface, therefore it is likely that they occupied the Mirim paleo-lagoon during the Holocene highstand. Adults of *Pogonias cromis* such as the one represented by the pterygiophore EPM-PV0457 inhabit fully marine waters, although the juveniles occupy estuarine environment (Silverman, 1979; Haimovici, 1997). The specimens of *Carcharhinus leucas*, dasyatid and myliobatid rays found some 65 km to the SW of Taim (Site 2) indicate the extension of marine conditions inside the Mirim paleo-sea. *C. leucas* inhabits marine, estuarine waters, and even in rivers, due to its high tolerance to variable salinities (Sadowski, 1971; Thorson, 1972; Thomerson et al., 1977; Compagno, 1984; Snelson et al., 1984). The occurrence of *C. leucas* in Rio Grande do Sul has paleoclimatic significance, because this species is characteristic of warm, tropical waters; its center of abundance is located in the West Indies and Caribbean (Baughman and Springer, 1950), and along the Brazilian coast it is found from the equatorial region up to Cananeia (state of São Paulo), at about 25°S (Sadowski, 1971). It is rare in the waters off southern Brazil, found mostly close to the shore (Amorim et al., 1998), and despite the intense fisheries along the coast of Rio Grande do Sul, there are no confirmed records of this species in this area (Vooren, 1997; Vooren et al., 2005), or in the Uruguayan coast (Menni et al., 2007). The southernmost record of *C. leucas* is on coastal waters off the Buenos Aires Province, Argentina, based on two specimens collected in the 1970s (Chiaramonte, 1998). Based on the tropical habit of that species, such occurrences represent seasonal migrations during summer months. The presence of *C. leucas* in Mirim Lake indicates warmer coastal waters in the region during the Holocene highstand, in agreement with the fossils of molluscan species with extralimital distribution described by Martínez (1989) from deposits in the Uruguayan lake shore.

The presence of associated remains of a juvenile and an adult balaenid whales of the species *E. australis* inside the Mirim paleo-lagoon is consistent with the behavior of nursing females of that species, i.e., strong bond with the calf and the habit of occupying low-hydrodynamic coastal environments such as bays and open lagoons for shelter (Thomas and Taber, 1984; Elwen and Best, 2004; Failla et al., 2008; Santos et al., 2010). Living whales were observed inside Patos Lagoon only in areas under direct influence of marine waters, up to about 10 km from its mouth, but fossilized remains were discovered more than 300 km to the north (von Ihering, 1885). The presence of remains of a mother and calf in association reported here is, as far as we know, the first record of such behavior recorded in fossil remains from Brazil, and reinforces the fully marine conditions Mirim Lake was subject during past sea-level highstands.

The otolith of *Micropogonias furnieri* was found among the shell concentrations at Latinos Spit, which are dominated by the brackish-tolerant mollusks *Erodona mactroides* Bosc, 1802 and *Heleobia* (= *Littoridina*) *australis* (d'Orbigny, 1840). This association, plus the fact that the otolith belongs to a sub-adult with estimated length of 270 mm, indicates that at the time it was living the Mirim paleo-lagoon had changed from fully marine to estuarine conditions, related to the sea-level retreatment after the highstand. This environmental change is also indicated by molluscan remains found in the lake, which will be described in the second part of this contribution.

## 6. Conclusions

The remains presented here are the first vertebrate fossils described from the Brazilian area of Mirim Lake. The presence of both marine and terrestrial organisms indicates that the evolution of the lake was controlled by the interplay between lowstands (periods when the lake was smaller in volume and area) and highstands (periods of increased water level), which would have been controlled by climate changes and sea-level oscillations.

The well-defined chronostratigraphic setting of the fossils found *in situ*, as determined by absolute ESR and OSL datings contribute for the understanding of the geological evolution of the lake shore in light of the late Pleistocene climate changes. The reworked fossils and facies succession observed along the channel indicate that the deposits on the lake shore were formed by sediments eroded from higher areas and deposited as prograding sequences by ephemeral streams during lowstands, whereas the lake highstands controlled by sea-level oscillations reworked these deposits as terraces.

Deposition during lowstands would have been driven by climatic variations (phases of increased-decreased precipitation), and the fossils found far from the present shore indicate transport and deposition by ephemeral streams at times when the area covered by the lake was reduced, as the result of sea-level lowstands and dry climate.

The altitude of the terrace T3 close to the fossils of *Toxodon* found *in situ* indicates that it was cut by the Holocene sea-level highstand that reached a maximum altitude of +3 m between 6 and 5.1 ka b2k. At that time Mirim Lake was invaded by the Atlantic Ocean through Taim and São Gonçalo channel, becoming a large paleo-lagoon with conditions suitable for its occupation by marine organisms, including sharks, rays, teleost fishes and whales. The coastal waters were warmer than today, as indicated by the presence of fossils of the shark *Carcharhinus leucas*, common in tropical areas.

## Declaration of competing interest

The authors declare no conflict interest.

## Acknowledgments

The authors would like to express their gratitude for the people who found and donated the fossils described here to the museum Coronel Tancredo Fernandes de Mello: Edmilson Pereira (antler PV1003), Eranio dos Santos Rodrigues (antler PV1006), Gilson Borges Moreno (antler 1102), Jaime Renato Silveira do Amaral (molar PV0435) Jandira Corrêa Borges (vertebrae PV1206, 1207 and 1208), Maicon Machado Souza (osteoderm PV1181 and phalanx 1182), Neurimar Borba Muniz (pterygiophore PV0457) and Oldemar Borges Moreno (femur PV0981). Thanks also to Dr. Pascal P. Deynat (ODONTOBASE Project) for the information and discussion on dermal structures of rays, and Dr. Gerardo De Iuliis (University of Toronto) for comments on the anatomy of the megatheriid femur. This research was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) through the Postdoctoral Research Grant no. 150153/2014–7 to the first author.

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