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Article

CONTRIBUTION TO THE KNOWLEDGE OF FOSSIL FISHES (CHONDRICHTHYES AND ACTINOPTERYGII) FROM QUATERNARY DEPOSITS OF THE PELOTAS BASIN, SOUTHERN BRAZIL

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ABSTRACT – Fossils of fishes represented by disarticulated, strongly mineralized and abraded skeletal elements, are relatively common in surface deposits of the Pelotas Basin along the coastal plain of the State of Rio Grande do Sul (CPRS), in southern Brazil, especially on storm wave-generated *Konzentratt-Lagerstätten* known as *concheiros* formed on the beach. Here, new specimens of chondrichthyan and actinopterygian fishes are presented from Quaternary (Middle Pleistocene to Holocene) coastal depositional environments that increase the diversity and distribution of fossil fishes in the Pelotas Basin. The fossils found along the beaches consist of dermal bucklers of rays (Dasyatidae), new specimens of Sciaenidae that include otoliths of *Micropogonias furnieri* and disarticulated but associated skeletal elements of *Pogonias cromis*, unidentified scales, opercles and one hyperostotic vertebra, and the first record of porcupine fishes (Diodontidae) in the Pelotas Basin, represented by jaw elements. Other fossils include the first Pleistocene fishes from marine and fluvial deposits exposed along Chuy Creek, represented by one hyperostotic pterygiophore of *P. cromis* and disarticulated but associated bones of catfishes (Siluriformes), including one partial skeleton associated with a fossil (probably mammalian) rib fragment reworked by fluvial erosion. Other fossils include one broken vertebral centrum from subsurface Pleistocene marine or lagoon deposits located to the east of the creek, and a vertebra of cf. *P. cromis* from Mirim Lagoon. Differences in representativity of chondrichthyans and actinopterygians seem related to taphonomic destruction of less resistant and/or skeletal elements of smaller species in wave-dominated marine settings, whereas freshwater/lagoon environments favor better preservation of fish remains.

Keywords: fish fauna, Dasyatidae, Pimelodidae, Sciaenidae, Diodontidae, *concheiros*.

INTRODUCTION

The Pelotas Basin (Figure 1A–B) is the southernmost marginal sedimentary basin of the trailing-edge (passive) Brazilian Continental Margin (BCM), bounded to the north by the Florianópolis High and to the south by the Polonio High in Uruguay (Barboza *et al*., 2021a). It is formed of sediments eroded from Precambrian to Mesozoic rocks of the Sul-Rio-Grandense Shield, the intracratonic Paraná Basin, and the Andes mountains (Villwock & Tomazelli, 1995; Carassai *et al*., 2019; Chemale Junior *et al*., 2021). The sediments infilling the basin accumulated from the Early Cretaceous onwards, after the split between South America and Africa, representing marine, transitional, and terrestrial environments (Closs, 1970; Bueno *et al*., 2007).

Most of the uppermost Pelotas Basin is occupied by the coastal plain of the State of Rio Grande do Sul (CPRS), which is the result of cyclic (~100 ka) Quaternary eustatic oscillations driven by glacial-interglacial cycles (Rosa *et al*., 2017). The southern sector of the ~620 km-long CPRS is known for the presence of Middle-late Pleistocene fossils of marine and terrestrial organisms. Most Quaternary fossils from the CPRS are found in transgressive lag deposits formed on the continental shelf by reworking and mixing of fossils by sea-level oscillations (Figueiredo Junior, 1975; Kowsmann *et al*., 1977; Villwock, 1984; Lopes & Buchmann, 2008, 2010; Ritter *et al*., 2017). These deposits contain mostly fossilized marine molluscan shells and other invertebrates, but also include marine and terrestrial vertebrates, all of which are reworked and transported to the beach by storm waves, thus forming large *Konzentratt-Lagerstätten* locally known as *concheiros* (Lopes & Buchmann, 2008; Lopes *et al*., 2024a).

The oldest known fish fossils from the Pelotas Basin consist of one skeleton and partial skulls of holocentrid, dercetid, and protacanthopterygians of Cretaceous (Albian-Turonian) ages recovered from shales of the Atlântida Formation sampled by cores obtained offshore of Rio Grande do Sul (Gallo-da-Silva & Figueiredo, 1999; Figueiredo & Gallo, 2006; Gallo *et al*., 2006; Figueiredo *et al*., 2012). Undescribed otoliths, scales, and teeth of Miocene age were sampled from boreholes made in onshore areas of the CPRS (Closs, 1970). The Quaternary records include cranial and postcranial elements of sciaenids and ariids, teeth of several shark species and dental plates of stingrays, all found on the *concheiros* (Cunha & Nunan, 1980; Richter, 1987, 2000; Buchmann & Rincón Filho, 1997; Medeiros *et al*., 2023; Britto *et al*., 2024). Some Quaternary fossils of marine fishes were found in onshore areas, in Holocene storm-generated shell deposits on the eastern shore of Mirim Lagoon (Lopes *et al*., 2020a). Although Pleistocene fossils of mollusks and other invertebrates are found in marine deposits on continental settings, either in subsurface or exposed on outcrops (Lopes & Bonetti, 2012; Lopes & Simone, 2012; Lopes *et al*., 2013; Bettinelli *et al*., 2018), these have not yielded fish remains so far.

Here we present descriptions of new marine fish fossils from the Pelotas Basin, found on beaches in the central and southern (*concheiros*) CPRS and Mirim Lagoon, besides the first fossils from marine and fluvial deposits on continental areas in the southernmost CPRS, exposed along the banks of Chuy Creek, with comments on taphonomic aspects of the remains and its

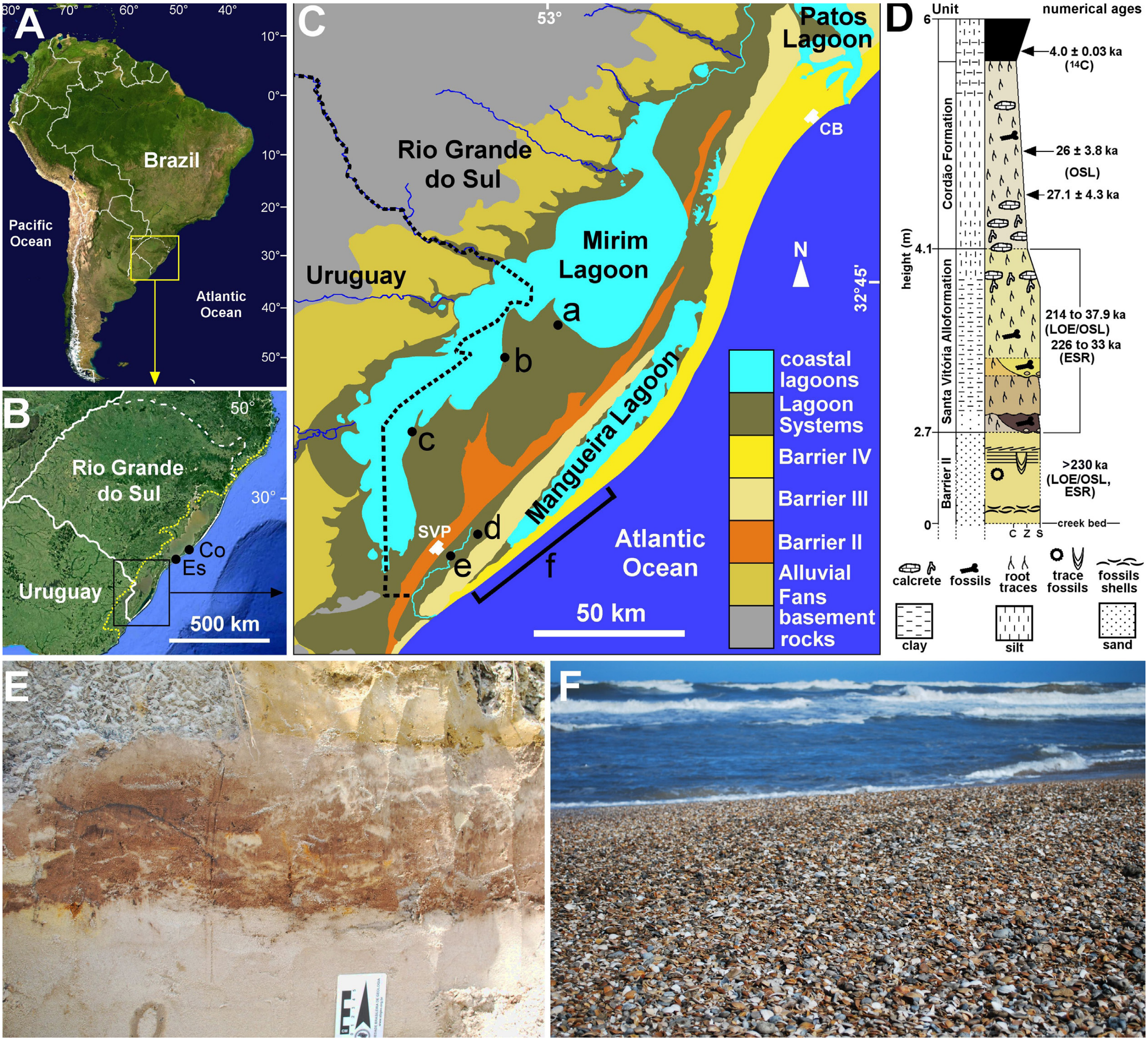

Figure 1. A, Blue Marble satellite image of South America, showing the location of Rio Grande do Sul; **B**, Google Earth image of southernmost Brazil with the Pelotas Basin indicated by the yellow dotted line and the location of the fossiliferous sites mentioned in the text; **C**, geological map of the southernmost CPRS, showing the localities and sites mentioned in the text; **D**, stratigraphic succession exposed along Chuy Creek; **E**, detail of the base of the Santa Vitória Alloformation outcropping on Chuy Creek with a fluvial deposit represented by the brown layer in the middle; **F**, a fossiliferous concentration (the *concheiros*) at the beach on the southern CPRS. **Abbreviations: a**, Latinos Spit; **b**, Santiago Spit; **c**, Afogados Spit; **CB**, Cassino Beach; **Co**, Conceição; **d**, borehole G02A09; **e**, Chuy Creek; **Es**, Estreito; **f**, *concheiros*; **SVP**, Santa Vitória do Palmar.

implication for the representativity and known diversity of fossil fishes in the basin. These finds increase the knowledge about the fossil record of fishes from the Pelotas Basin, which are poorly documented and scarcer in comparison with mollusks and mammal remains from the basin, which seems to be a general pattern in the Cenozoic fossil record of southern South America (SSA, Arratia & Cione, 1996).

GEOLOGICAL SETTING

The CPRS is composed of an Alluvial Fans System of Miocene-Pliocene age (Closs, 1970) and four Barrier-Lagoon systems developed during the Pleistocene by successive eustatic oscillations (Villwock & Tomazelli, 1995; Rosa *et al*., 2017). Each barrier-lagoon system includes long sandy coastal barriers with lagoon/lacustrine deposits developed on the backbarrier lowlands (Villwock & Tomazelli, 1995). In the southern sector of the CPRS, the Pleistocene Barrier-Lagoon Systems II and III and the Holocene System IV are preserved (Figure 1C).

The fossils from continental areas described here were collected within the Lagoon System III, in sediments outcropping along the banks of Chuy Creek (Figure 1D) interpreted as the marine facies of the Barrier System II (Rosa, 2012), and from the fluvial facies (Figure 1E) of the overlying Santa Vitória Alloformation (**SVA**) (Lopes *et al*., 2021b). Ages obtained in sediments and shells using thermoluminescence (**TL**) and electron spin (or paramagnetic) resonance (**ESR**) indicate the marine sediments were deposited by a sea-level transgression during the penultimate interglacial, or marine isotope stage (**MIS**) 7 (Lopes *et al*., 2014a, b, 2020b). The foraminiferan and molluskan assemblages, and ichnofossils *Ophiomorpha nodosa* and *Rosselia socialis* (Lopes & Bonetti, 2012; Lopes *et al*., 2013, 2020c) found in the ~2.7-meter-thick marine sediments exposed above the mean water level of Chuy Creek indicate a shallow marine (shoreface-foreshore) environment.

The SVA encompasses aeolian deposits, paleosols, and fluvial systems (Lopes *et al*., 2021b). Luminescence and ESR ages from sediments and mammalian fossils show that the SVA was deposited between ~226 and 33 ka (Lopes *et al*., 2010, 2014b, 2019). The only fossils from the SVA described so far belong to mammals and a stork (Lopes *et al*., 2019), preserved in fluvial facies composed of sand with 20–24% of silty mud, usually massive but sometimes with poorly developed lamination. These facies are represented by lens- and tabular-shaped deposits measuring <50 cm in thickness and sometimes reaching >10 meters across (Lopes *et al*., 2021b).

The fossils collected along the central CPRS in the localities of Estreito and Conceição (Figure 1B) and the *concheiros* to the south (Figure 1C) are found stranded on the beach. As these remains are removed from submarine deposits and thrown onto the beach by storm waves, they do not have a precise stratigraphic provenance or age determination. Dated shells collected on the continental shelf provided ^{14}C ages ranging from >30 to ~10.6 ka (Figueiredo Junior, 1975; Kowsmann *et al*., 1977; Ritter *et al*., 2023), whereas the ages of ESR-dated fossil mammals from the shelf range from ~18 to >600 ka (Lopes *et al*., 2010). These ages imply that the fossiliferous assemblages of the continental shelf and *concheiros* are highly time-averaged, representing faunas that lived between the Middle Pleistocene and the Middle Holocene.

MATERIAL AND METHODS

The fossils described here have been collected along the central-southern CPRS over the last 20 years, both on the shoreline and also on ancient marine deposits formed by Pleistocene marine transgression and now located on continental settings. The fossils from the central CPRS were found on the beach near the localities of Estreito and Conceição (Figure 1B). The fossils from the southern CPRS (Figure 1C) were collected along the *concheiros* (Figure 1F), in fluvial sediments of the SVA, and at the bottom of Mirim Lagoon close to the Afogados Spit. One specimen was also collected in subsurface deposits of the Lagoon System III west of Chuy Creek.

The fossils belong to the vertebrate collection of Tancredo Fernandes de Mello Museum, in the town of Santa Vitória do Palmar, and to the paleontological collection of Universidade Federal do Rio Grande (**FURG**). The samples were identified by comparison with recent specimens and descriptions in the literature (Cuvier, 1837; Chao, 1978; Corrêa & Vianna, 1993; Carpenter, 2002). The systematic classification is based on Nelson (2006). The nomenclature of otoliths follows Takeuchi & Huddleston (2008).

Abbreviations: LGP, Laboratório de Geologia e Paleontologia (FURG), Rio Grande, RS; **MCTFM-PV**, Museu Coronel Tancredo Fernandes de Mello-Paleontologia de Vertebrados, Santa Vitória do Palmar, RS; **MN-UFRJ**, Museu Nacional, Universidade Federal do Rio de Janeiro.

SYSTEMATIC PALEONTOLOGY

CHORDATA Haeckel, 1874
CHONDRICHTHYES Huxley, 1880
MYLIOBATIFORMES Compagno, 1973
DASYATIDAE D.S. Jordan, 1888

cf. *Bathytoshia* Whitley, 1933

aff. *Bathytoshia centroura* (Mitchill, 1815)
(Figure 2A–D)

Material. Dermal bucklers MCTFM-PV1091 (Figure 2A), MCTFM-PV1092 (Figure 2B); MCTFM-PV1093 (Figure 2C); MCTFM-PV1094 (Figure 2D).

Provenance. *Konzentratt-Lagerstätten* (*concheiros*) on the southern coastline of the CPRS, age unknown but estimated to be of Middle Pleistocene to Middle Holocene.

Description. The four specimens are strongly mineralized and somewhat abraded, as other vertebrate fossils found in marine settings along the CPRS (Lopes & Ferigolo, 2015). All have flattened, dorsoventrally biconvex basal plates with low, blunt spines at the center of the dorsal side. The specimen MCTFM-PV1091 is light brown-colored, measuring 22 mm

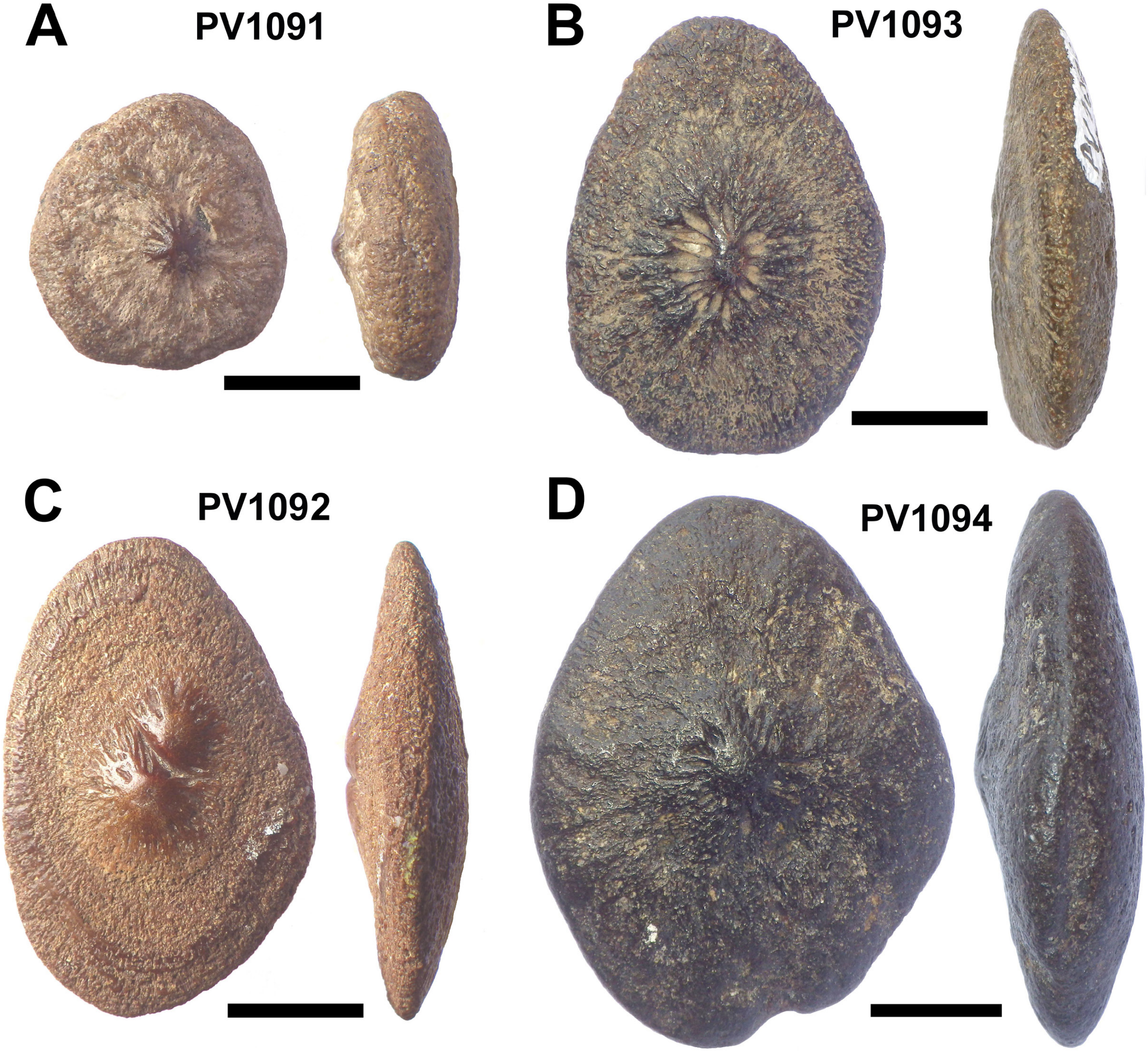

Figure 2. A-D, dermal bucklers of cf. *Bathytoshia centroura* from the *concheiros* in dorsal and lateral views. **A**, MCTFM-PV1091; **B**, MCTFM-PV1093; **C**, MCTFM-PV1092; **D**, MCTFM-PV1094. Scale bars = 10 mm.

in length, 21 mm in width and 10 mm in thickness. Its basal plate exhibits a subcircular outline, with a less acute and more rounded margin than the bucklers. It has a low dorsal crown with the central spine surrounded by ridges and furrows emanating radially from it. The specimen MCTFM-PV1092 is also light brown-colored and measures 39 mm in length, 25 mm in width and 19 mm in thickness. Compared to MCTFM-PV1091, its basal plate is oval-shaped, thicker at the center, and tapering towards the margin. Its slightly raised crown exhibits two blunt spines, surrounded by radial ridges and furrows less developed than MCTFM-PV1091. Shorter radial furrows also form a ring surrounding the crown. The specimen MCTFM-PV1093 is a dark brown-colored, oval-shaped buckler measuring 31 mm in length, maximum width of 22 mm and a thickness of 8 mm. Its basal plate also tapers marginally, and the dorsal surface exhibits a central depressed area with a low blunt spine in the middle, surrounded by radial ridges emanating from it. The specimen MCTFM-PV1094 is black-colored, larger, measuring 39 mm in length, 30 mm in width, and 11 mm in thickness. It also has an oval-shaped, marginally tapering basal plate, but compared to MCTFM-PV1093, its crown is more raised, with the central blunt spine surrounded by shorter and less evident radial furrows.

Remarks. The dorsoventrally biconvex aspect, oval or subcircular outline, and relatively large size of the basal plates, and the low crown with the central spine surrounded by radial furrows/ridges, indicate they belong to dasyatid rays, probably adults of the species

Bathytoshia centroura or a similar species (Bigelow & Schroeder, 1953; Deynat & Brito, 1982; P. Deynat, pers. comm., 2016). By comparison with *B. centroura*, the more evident ridges on MCTFM-PV1091 (together with its subcircular base) and MCTFM-PV1093 indicate that these may be from the base of the tail. In contrast, the poorly developed ridges, oval outline and and larger sizes of the specimens MCTFM-PV1092 and MCTFM-PV1094 suggest that they may be from the scapular or metapterygial series of the dorsum (Bigelow & Schroeder, 1953; Deynat, 1998). The species *B. centroura* and *Hypanus say* (Le Sueur, 1817) (*sensu* Last *et al*., 2016, formerly *Dasyatis say*) occur along the coast of southern Brazil only during summer months (Vooren, 1997), but *H. say* lacks dorsal bucklers or spines, exhibiting only small tubercles along the dorsal midline and scapula (Le Sueur, 1817; Bigelow & Schroeder, 1953).

The species *Bathytoshia centroura* occurs along the Atlantic coast of the Americas from Argentina (41°S) up to the United States of America (42°N) (Bigelow & Schroeder, 1953; Menezes *et al*., 2003; Cousseau *et al*., 2007; Menni *et al*., 2007). Together with another fossil buckler possibly belonging to *B. centroura* found on the eastern margin of Mirim Lagoon at Santiago Spit (Figure 1C) (Lopes *et al*., 2020a), the four specimens described here increase the representativity of Dasyatidae in the fossil assemblages of the CPRS, being the first specimens described from the *concheiros*. Other fossils of Dasyatidae are known from Early Miocene (Aquitanian-Burdigalian) deposits of the Pirabas Formation in northern Brazil (Aguilera *et al*., 2017a), and Holocene specimens were described from archaeological sites in the southeastern Brazilian coast (Lopes *et al*., 2016). Fossils of dasyatids also occur in Miocene deposits in the Entre Ríos Province of northern Argentina (Arratia & Cione, 1996).

OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII Klein, 1885
SILURIFORMES Cuvier, 1817
PIMELODIDAE Swaison, 1838

Pimelodidae indet.
(Figure 3A–G)

Material. Left opercles (MCTFM-PV0874 and PV0875, Figure 3A–B), right frontal (MCTFM-PV0872, Figure 3C), right sphenotic? (MCTFM-PV0873, Figure 3D), pterotic? (MCTFM-PV0866, Figure 3E), right dentary (Figure 3F) and

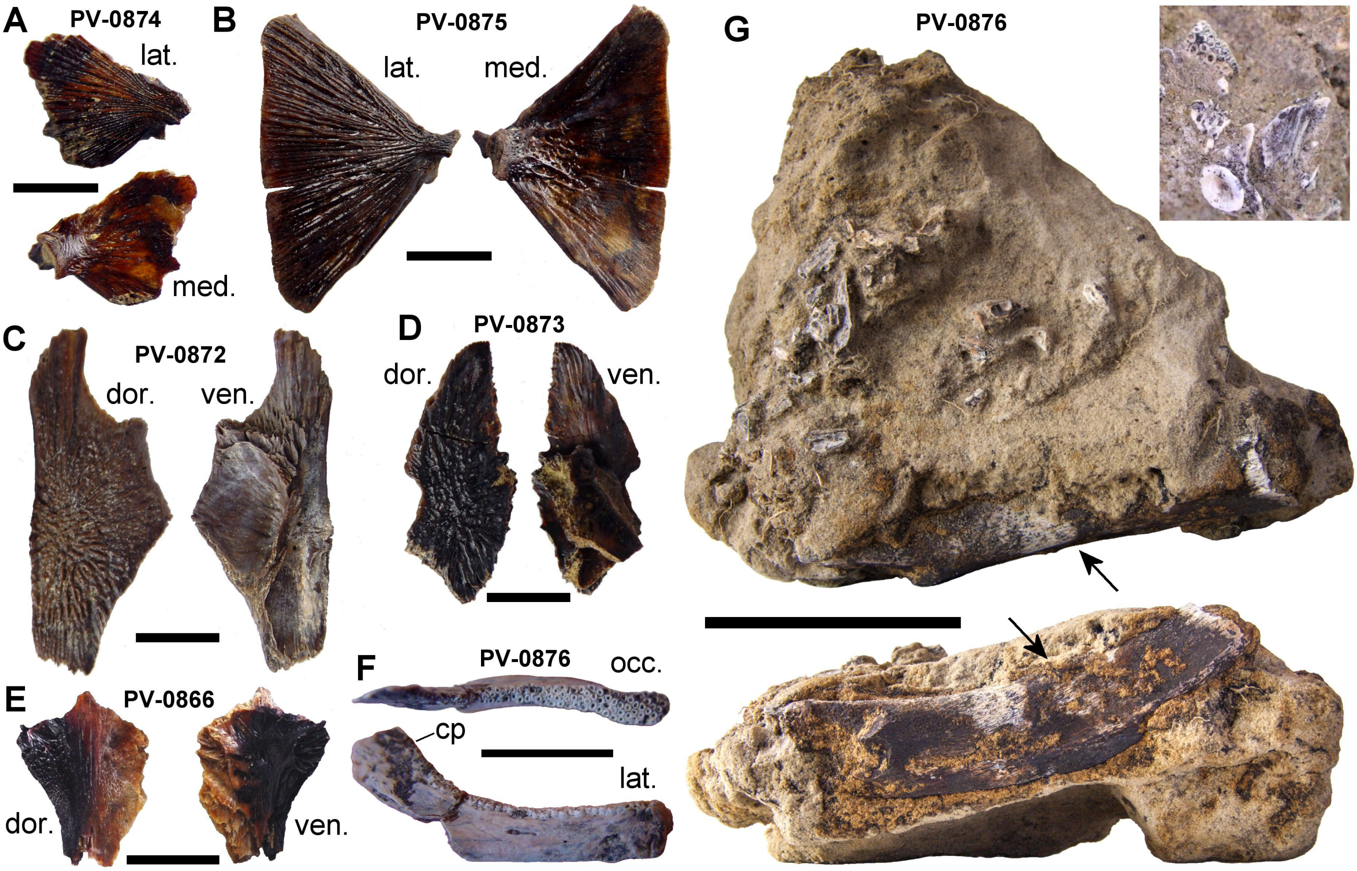

Figure 3. Fossils of pimelodid fishes. **A–B**, left operculars in lateral (**lat.**) and medial (**med.**) views; **C**, right frontal in dorsal (**dor.**) and ventral (**ven.**) views; **D**, right sphenotic? in dorsal and ventral views; **E**, pterotic?; **F**, right dentary extracted from the remains embedded in the sediment block (**G**) in occlusal (**occ.**) and lateral (**lat.**) views; **cp**, coronoid process. The inset shows a close-up view of teeth and a vertebra in the sediment; the arrows indicate the fragment of a vertebrate (mammalian?) rib. Scale bars: A–F = 10 mm; G = 50 mm.

disarticulated but associated bones of the same individual (MCTFM-PV0876, Figure 3G).

Provenance and age. Fluvial facies of the SVA, Middle or late Pleistocene.

Description. The specimens MCTFM-PV0872 and MCTFM-PV0875 consist of disarticulated but closely associated remains found within a fluvial deposit outcropping on the banks of Chuy Creek and thus may belong to the same individual. The specimens MCTFM-PV0873 and MCTFM-PV0874 were found nearby within the same deposit; therefore, they may belong to other individuals, whereas MCTFM-PV0866 was found on another outcrop. These specimens are identified as skull elements of pimelodid catfishes based on the flattened shape, morphology, and surface ornamentation (Rocha, 2012).

The specimen MCTFM-PV0876 consists of several disarticulated but associated bones of the same individual, preserved in muddy sand with a rib fragment, presumably from a mammal (Figure 3G). Diagnosed as a pimelodid catfish based on the dorsally projected coronoid process of the dentary (Figure 3F), and dentition characterized by numerous small viliform teeth arranged along the dentary in a band of more than three rows (Cuvier, 1837; Hildebrand, 1930; Lundberg *et al*., 1991; Rocha, 2012).

Remarks. These remains are the first record of Pleistocene freshwater fishes from the SVA. The disarticulated state of the skeletal elements is similar to the mamalian fossils found within this unit (Lopes & Ferigolo, 2015), although the latter are usually isolated. The larger vertebrate rib fragment preserved in close association with MCTFM-PV0876 exhibits crusts of sand coated with iron oxide (see the lower photo of Figure 3G), not observed in the fish remains.

PERCIFORMES Ludwing, 1883
SCIAENIDAE Owen, 1846

Micropogonias Cuvier, 1830

Micropogonias furnieri (Desmarest, 1823)
(Figure 4A)

Material. Left (LGP-B0002, B0004, B0009, B0088, MCTFM-PV1083) and right (B0001, B0003, B0005, B0006, B0019, B0087, MCTFM-PV1085, PV1086, PV1087, PV1088) otoliths (sagittae) (Figure 4A).

Provenance and age. *Konzentratt-Lagerstätten* (*concheiros*) in the southern coastline of the CPRS, age unknown but estimated to be of Middle Pleistocene-Middle Holocene.

Description. The smaller size, oblong shape, sinuous margins and absent or poorly developed lateral concrescences of the otoliths LGP-B0002, LGP-B0003 LGP-B0004 and LGP-B0006 (Figure 4A), indicate that these belonged to juveniles

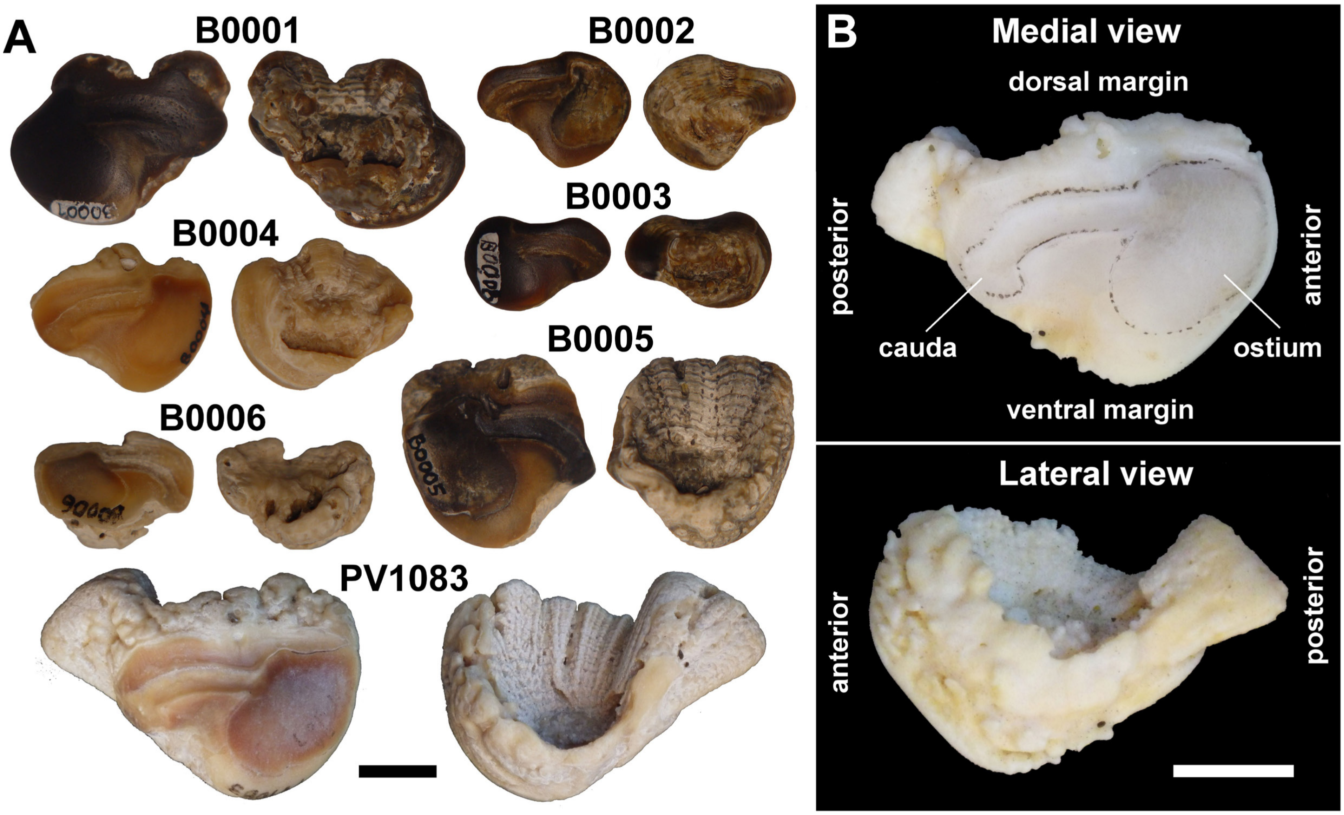

Figure 4. A, fossil otoliths of *Micropogonias furnieri* found in the concheiros in medial and lateral views; **B**, recent otolith of the species showing diagnostic morphological features according to Chao (1978). Scale bars = 10 mm.

(Waessle *et al*., 2003), whereas the other specimens are from adult individuals, based on comparison with recent otoliths (Figure 4B). The morphological features that allow identifying these specimens as *Micropogonias furnieri* (Figure 4B) include the 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, and the cauda has a disc-like distal end and is bent toward the ventral margin (Chao, 1978; Corrêa & Vianna, 1993). The specimens exhibit variable degrees of preservation, ranging from complete to broken, and/or abraded. The dark brown color and the broken and/or abraded state of LGP-B0001, LGP-B0002, LGP-B0003, and LGP-B0005, similar to other fossils from the continental shelf (Lopes & Ferigolo, 2015), indicate preservation in marine settings. The comparatively lighter color and good preservation of LGP-B0004, LGP-B0006 and MCTFM-PV1083 suggest that these may be subfossils and/or were originally preserved in lagoon settings (see Discussion).

Remarks. *Micropogonias furnieri* is widely distributed along the Atlantic coast of South America, reaching latitudes up to 40°S. It is a common species along the coast of Rio Grande do Sul, being exploited commercially (Haimovici, 1997; Fischer *et al*., 2011). The only other known published fossil record of *M. furnieri* from the southern CPRS is a left otolith of a juvenile individual from deposits on the shore of Mirim Lagoon (Lopes *et al*., 2020a).

Pogonias cromis Linnaeus, 1766

(Figure 5A–E)

Material. Hyperostotic pterygiophore (MCTFM-PV1082, Figure 5A), lower (LGP-B0092, Figure 5B) and upper (LGP-B0078, Figure 5C) pharyngeal jaws, isolated molariform teeth (MCTFM-PV1339, Figure 5D) and partial skeleton (MCTFM-PV1099, Figure 5E).

Provenance and age. Middle Pleistocene marine deposits exposed along Chuy Creek (MCTFM-PV1082). The other fossils are from the *concheiros* and are estimated to be of early-Middle Holocene (MCTFM-PV1099), and presumably Pleistocene to Holocene (LGP-B0092, LGP-B0078, and MCTFM-PV1339) ages.

Description. The specimen MCTFM-PV1082 is one of the pterygiophores, or interspinal bones, located between the spinous processes of the vertebrae and the fin rays (Cuvier, 1837). It exhibits a medial keel on the anterior side and a concavity along the posterior midline, giving it a triangular transversal outline. The distal portion is wider than the proximal one, and it has articular processes for insertion of the fin rays. The elongated morphology indicates that it is probably the 1st pterygiophore of the anal fin, similar in shape and size to the specimens from the *concheiros* described by Souza Cunha & Nunan (1980), and its robust aspect is due to hyperostosis. It is dark-colored and strongly mineralized, as the vertebrate fossils found in the concheiros and continental shelf (Lopes & Ferigolo, 2015).

The specimen LGP-B0092 (Figure 5B) consists of the right half of the lower pharyngeal jaw, formed of a dental plate fused to the 5th ceratobranchial (Helfman *et al*., 2009). It is diagnosed as *Pogonias cromis* by the large alveoli for pharyngeal teeth arranged in rows, and the presence of a ventral longitudinal ridge with forward projecting strut that buttresses this element against the lower region of the cleithrum (Cuvier, 1837; Hildebrand, 1930; Gregory, 1959; Chao, 1978; Grubich, 2003; Ziv *et al*., 2020). The alveoli range from 1.5 to 6.5 mm in maximum diameter; the larger ones are located close to the midline of the dental plate. Compared to LGP-B0092, the upper pharyngeal jaw LGP-B0078 has similar dental alveoli, ranging in diameter from 3 to 6 mm, and a more rounded outline in occlusal view (Figure 5C). This is one of the two dental plates that are fused to the pharyngobranchial 3 and attached to the posterior epibranchial and pharyngobranchial bones (Helfman *et al*., 2009). The dorsal side of the plate is highly abraded but has a projection that may be a remnant of the longitudinal ridge that buttresses this element against the parasphenoid (Grubich, 2003). The isolated molariform teeth (Figure 5D) are identified as *P. cromis* based on the blunt occlusal surface, with smooth texture and large pulpar cavity (Gregory, 1959; Chao, 1978; Deng *et al*., 2022). The shape of the teeth in occlusal view is comparable to the alveoli of the pharyngeal jaws (Figure 5B–C).

The specimen MCTFM-PV1099 (Figure 5E) consists of skeletal elements cemented together by indurated, light gray mud, and includes two vertebrae, three pterygiophores, scales, teeth, and several spines/ribs. It is identified as *Pogonias cromis* by the blunt molariform teeth (Figure 5F), similar in size and shape to the isolated specimens. The bones are light brown-colored, not strongly mineralized as the vertebrate fossils from the continental shelf (Lopes & Ferigolo, 2015), and the spines/ribs are thickened. Parts of the bones are encrusted with colonies of marine cheilostomate bryozoans (cf. *Biflustra arborescens*, Figure 5G), also found in other fossils preserved on the continental shelf (Lopes, 2012; Ramalho & Calliari, 2015).

Remarks. The pterygiophore MCTFM-PV1082 (together with the vertebral centrum MCTFM-PV1095, see below) are the first vertebrate remains from marine deposits located on continental settings in the southern CPRS. The pterygiophore was found on the right bank of Chuy Creek close to the outcrop M03 on the left bank, which also had yielded several marine fossil shells (Lopes *et al*., 2013). The hyperostosis observed in this specimen is an ontogenetic condition common in pterygiophores and other bones of sciaeanids, including *Pogonias cromis*, *P. courbina* and *Micropogonias furnieri*, besides other fish groups (Gervais, 1875; Barcellos, 1962; Konnerth, 1966; Pilleri, 1973; Aguilera & Rodrigues de Aguilera, 1999; Aguilera *et al*., 2017b; Agnolín *et al*., 2024). This specimen is similar to the pterygiophores from the *concheiros* described by Cunha & Nunan (1980). By comparison with the measurements and estimates from living specimens presented by these authors (Table 1), its dimensions (86.5 mm in length and 27 mm in maximum diameter) would indicate an individual with >800 mm of body length and a weight of ~10 kg. These dimensions indicate it was probably an adult, considering that individuals found on the coast of Rio Grande do Sul today reach up to 1.4 m in length and weigh ~40 kg (Fischer *et al*., 2011).

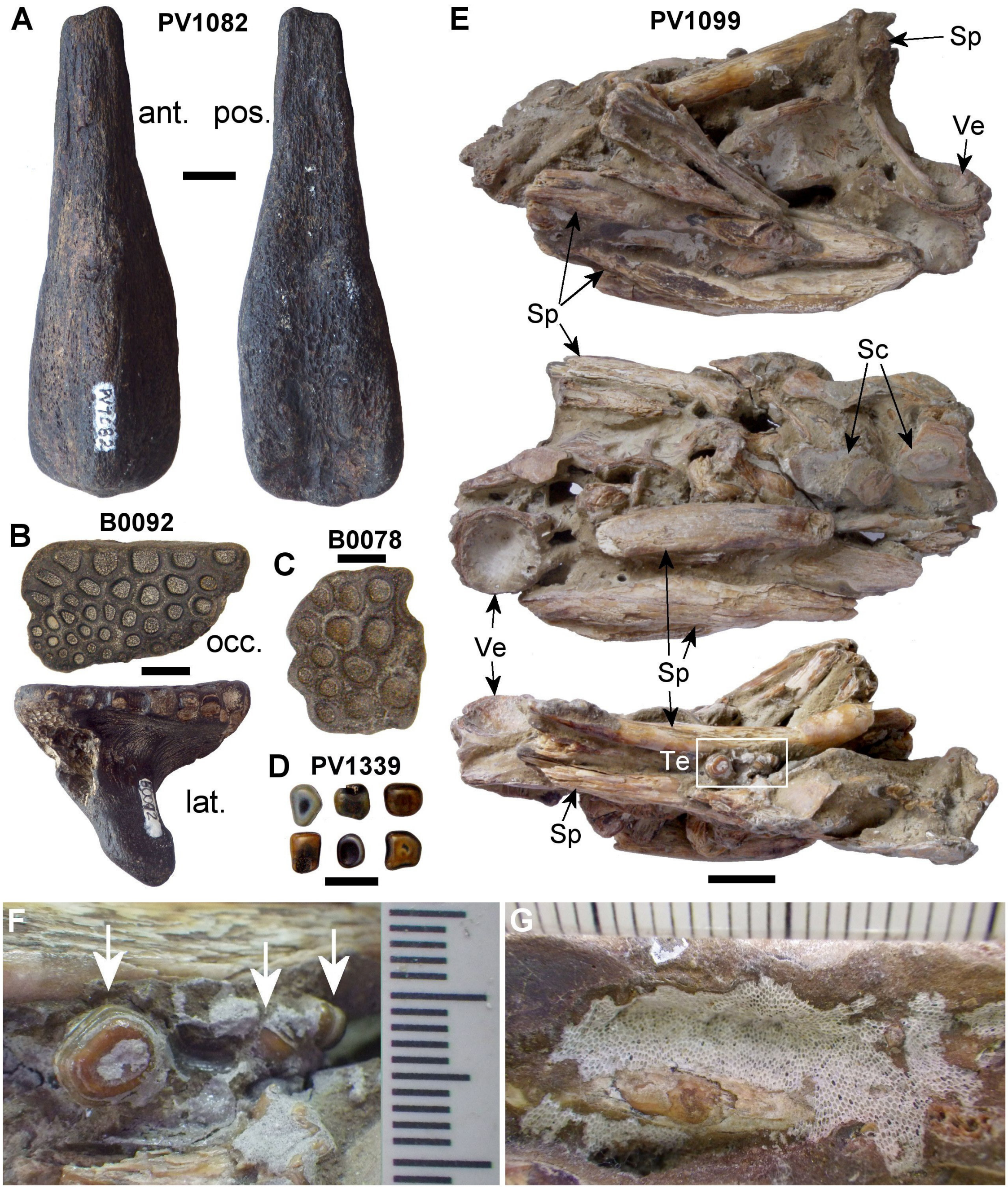

Figure 5. Fossils of *Pogonias cromis*. **A**, interspinal of the 1$^{\sigma\tau}$? ray of the anal fin in anterior (**ant.**) and posterior (**pos.**) views; **B**, occlusal (**occ.**) and lateral (**lat.**) view of a lower pharyngeal jaw; **C**, dental plate of an upper pharyngeal jaw in occlusal view; **D**, isolated molariform teeth; **E**, different views of a disarticulated partial skeleton; **F**, close-up view of the teeth shown in 4E; **G**, detail of a spine showing encrustation by ceilostomate bryozoans. **Abbreviations: Sc**, scales; **Sp**, spines; **Te**, teeth; **Ve**; vertebral centrum. Scale bars: A–D = 10 mm; E = 20 mm; F–G = 1 mm (each division of the scale).

Table 1. Estimated (*****) length (in mm) of fossil *Pogonias cromis* from the *concheiros* based on the dimensions of the 1$^{\sigma\tau}$ pterygiophores of the anal fin and corresponding size of recent individuals (Cunha & Nunan, 1980). **Abbreviations: BL**, body length; **ML**, maximum length; **MW,** maximum width.

Type	Number	ML	MW	BL
recent	MN-UFRJ 307-V	170	29.5	1,000
recent	unnumbered	132.5	21.5	915
fossil	MN-UFRJ 307-V	86	22.5	809*
fossil	MCTFM-PV1082	86.5	27	810*

The pharyngeal jaws evolved from modified branchial arches and derived dermal pharyngeal plates (Helfman *et al.*, 2009). The large, blunt molariform pharyngeal teeth and arrangement of the pharyngeal jaw apparatus of *Pogonias cromis* are adaptations to molluscivory that confer to this species the strongest bite force among bony fishes (Hildebrand, 1930; Grubich, 2000, 2003; Ziv *et al.*, 2020; Deng *et al.*, 2022). Although *Micropogonias furnieri* also has a similar apparatus, it is formed of three upper and two lower dental plates that are unfused, smaller than in *P. cromis*, and bear conical teeth (Ruiz *et al.*, 2001). *P. cromis* occurs between 45°N and 40°S, and in southern Brazil it is found at depths of less than 40 m, near the estuary of Patos Lagoon where it breeds, although it was much reduced in abundance due to overfishing (Haimovici, 1997; Fischer *et al.*, 2011). Besides the pterygiophore described by Cunha & Nunan (1980), other fossils attributed to this species found on this area include thoracic and caudal vertebrae from Cassino Beach (Buchmann & Rincón Filho, 1997), and a large pterygiophore from Mirim Lagoon (Lopes *et al.*, 2020a). Remains of this species were also found in one Holocene archaeological site close to the town of Santa Vitória do Palmar (Schmitz *et al.*, 1997).

The specimen MCTFM-PV1099 is remarkable for the association of bones of the same individual. The disarticulated state indicates that it was subject to some degree of *postmortem* reworking, similar to the pimelodids from Chuy Creek described above. However, the bones were probably kept together by soft tissues prior to the final burial. The gray indurated mud binding the bones together suggests that it died and/or was buried in a low-energy environment (see Discussion). The thickened elements suggest hyperostosis due to periosteal ossification (Aguilera *et al.*, 2017b).

TETRAODONTIFORMES Regan, 1929
DIODONTIDAE Bonaparte, 1835

cf. *Chilomycterus spinosus spinosus* (Linnaeus, 1758)
(Figure 6A)

Material. Fused beak-like jaw bones (LGP-B0034 and B0035, Figure 6A)

Provenance and age. Central sector of the CPRS (Figure 1B), near the Conceição lighthouse (31°43’46”S / 051°28’53”W, B0034) and Estreito (31°51’05”S / 051°42’45”W, B0035). Probably Middle Pleistocene to early Holocene ages.

Description. Both specimens are similar, black-colored and strongly mineralized, and consist of the medially fused tooth elements of the upper and lower jaws, forming a characteristic beak-like crushing structure with cutting margins (Hildebrand, 1930; Tyler, 1980; Carpenter, 2002). The specimen LGP-B0034 is tentatively identified as the upper premaxilla based on the wide spacing between the marginal (anterior) teeth and the dental plate, by comparison with the upper and lower jaws (Figure 6B) of a recent diodontid *Chilomycterus spinosus spinosus* (Linnaeus, 1758) found at Cassino Beach (Figure 6C). The marginal (premaxillary) teeth in LGP-B0034 are anteroposteriorly elongated and dorsoventrally compressed, arranged in 16 columns (Figure 6A1). In LGP-B0035, the marginal teeth are less defined, which could result from abrasion or indicate this specimen may be the anterior portion of the dentary (Figure 6B). The crushing surface behind the marginal teeth of the two specimens consists of paired mediolaterally elongated flat dental sheets (Figure 6A2–A3), which, together with stacked inner sheets, form a battery united by a medial suture (Aguilera *et al.*, 2017b). Although both specimens exhibit four sheet pairs on the crushing surface, the number of inner sheet pairs in LGP-B0034 is six, whereas in LGP-B0035, the number could not be determined due to abrasion. Nevertheless, the shape and number of plates are consistent with those observed in *Chilomycterus* (Aguilera *et al.*, 2017c). Although the jaw elements of *Diodon* have similar morphologies and sizes, this taxon has more sheets and a higher battery than *Chilomycterus* (Aguilera *et al.*, 2017c). The surface sheets become narrower anteriorly, resulting in a subtriangular-shaped plate in occlusal view (Figure 6A2), and in the specimen LGP-B0035, the sheets exhibit small, rounded tubercles on the occlusal surface.

Remarks. The Diodontidae are commonly known as porcupine fishes (Leis, 2002), and the fossils found in tropical South America consist mainly of the beak-like fused jaw elements, which are adapted to crush mollusks and crustaceans (Aguilera *et al.*, 2017c). The morphologies of both specimens are more similar to *Chilomycterus* than to *Diodon*, probably belonging to the species *C. spinosus spinosus* (Figure 6C). This species is distributed along the western Atlantic, from northern South America (Venezuela) up to the coast of the Buenos Aires Province in Argentina (Menni *et al.*, 1984), being the only diodontid found living today along the coast of Rio Grande do Sul (Haimovici, 1997; Fischer *et al.*, 2011). Although the species *C. antillarum* was recorded living in marine waters off the State of Santa Catarina to the north (Caires et al, 2008), its presence in Rio Grande do Sul has not been recorded so far.

The crushing battery of the upper jaw (Figure 6B) removed from the ~150 mm-long individual measured from the tip of the snout to the base of the caudal fin (Figure 6C) has a maximum width of 9 mm, whereas the plates of LGP-B0034 and LGP-B0035 have maximum widths of 15.5 and 14 mm, respectively. This could indicate that the fossils belong to adults, considering that recent individuals from Rio Grande do Sul reach maximum lengths of ~250 mm (Fischer *et al.*, 2011), or may represent a larger extinct species that once inhabited this area. The two specimens described here are the southernmost fossils of this group found so far along the Brazilian coast. The only other fossil records of diodontids from Brazil are jaw bones of Late Cretaceous (Maastrichtian) age from the Gramame Formation and of Early Miocene age from the Pirabas Formation (Gallo *et al.*, 2009). Jaw elements of *Chilomycterus spinosus spinosus* have also been found on archaeological sites (shell mounds) on the coast of Rio de Janeiro in southeastern Brazil (Lopes *et al.*, 2016). Fossilized crushing batteries of *C. spinosus* also occur in Holocene deposits on the shore of the La Plata River in the Province of Buenos Aires (Agnolín *et al.*, 2022).

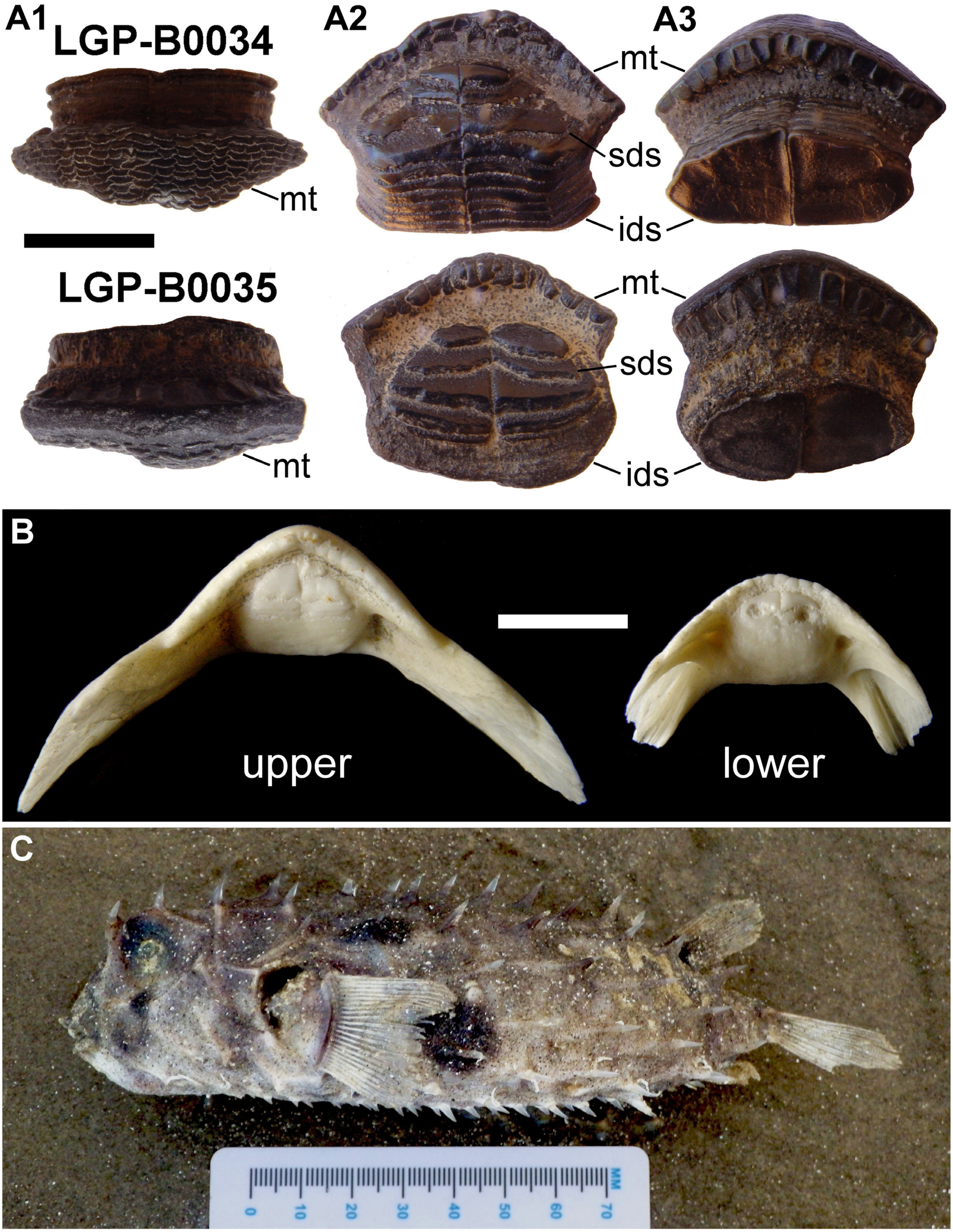

Figure 6. Fossil jaws of cf. *Chilomycterus spinosus spinosus* in anterior (**A1**), occlusal (**A2**) and dorsal (**A3**) views; (**B**) jaw bones of a recent ~150 mm-long *C. spinosus spinosus* (**C**). **Abbreviations: ids**, inner dental sheets; **mt**, marginal teeth; **sds**, surface dental sheets. Scale bars = 10 mm.

Actinopterygii indet.
(Figure 7A–I)

Several fish fossils are difficult to assign to any specific group or species due to the fragmented or abraded state or the lack of diagnostic features.

Material. Broken vertebral centrum (MCTFM-PV1095, Figure 7A), precaudal vertebra (MCTFM-PV1341, Figure 7B), hyperostotic precaudal vertebra (MCTFM-PV1343, Figure 7C), isolated scales (LGP-B0009, 0012, 0013, 0014, 0015, 0017, 0018, 0019, 0033, 0035, 0040, Figure 7D) and opercles (LGP-B0047, LGP-B0073, MCTFM-PV1084, MCTFM-PV1340 and MCTFM-PV1344, Figure 7E–I).

Provenance and age. MCTFM-PV1095: subsurface deposits within the Lagoon System III, presumably of late (Barrier III) or possibly Middle (Barrier II) Pleistocene age. MCTFM-PV1341: Mirim Lagoon (Figure 1C), probably Middle-Late Holocene age. MCTFM-PV1343, isolated scales and opercles: *concheiros*, probably Pleistocene to Early–Middle Holocene ages.

Description. The vertebral centrum MCTFM-PV1095 (Figure 7A) has one well-preserved concave articular facet, whereas half of the centrum and the opposite facet are broken and abraded. It is black-colored and strongly mineralized as the vertebrate fossils from the *concheiros* (Lopes & Ferigolo, 2015).

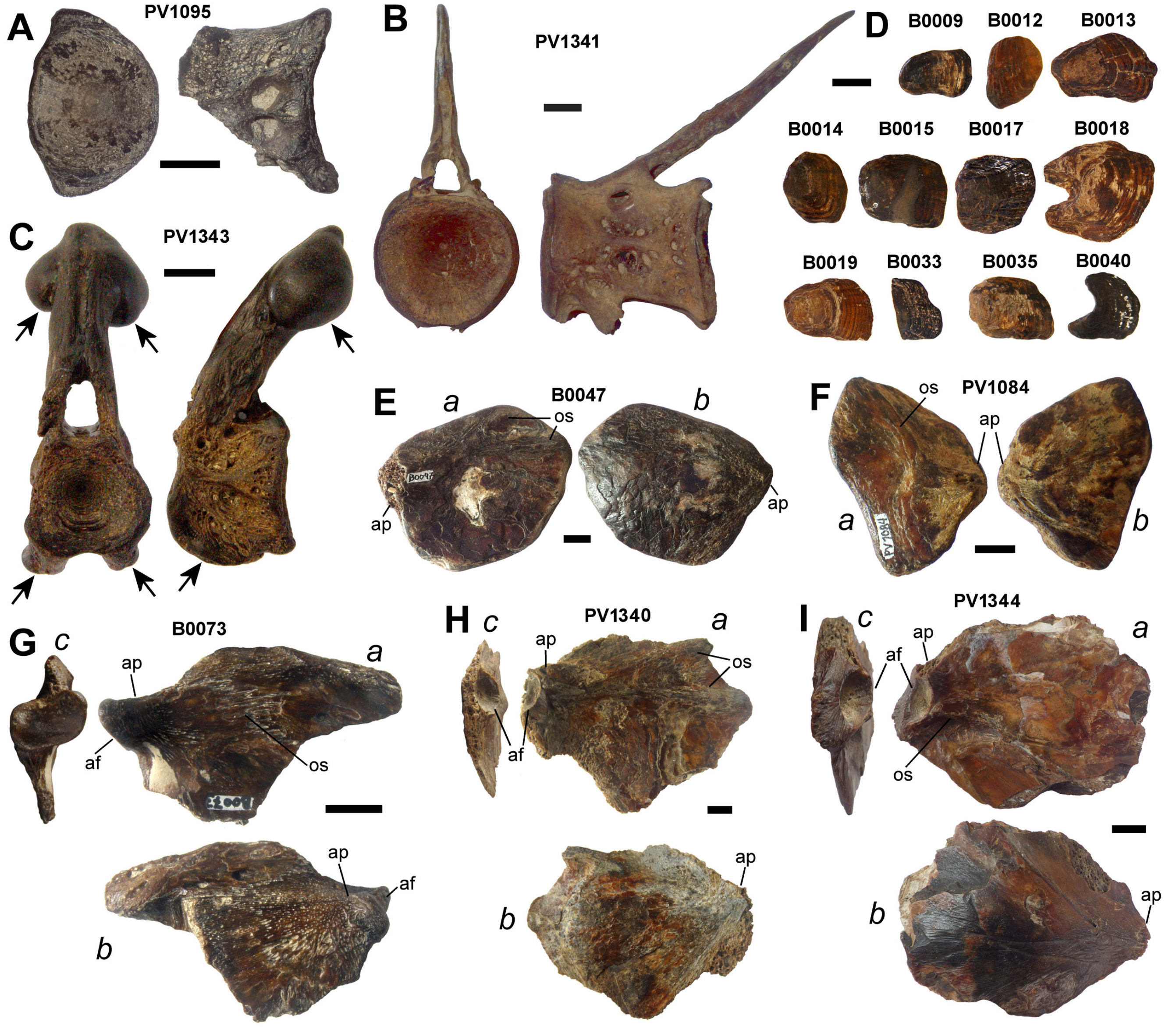

Figure 7. Fossils of unidentified actinopterygians. **A**, partial vertebral centrum from subsurface lagoon margin deposits in cranial or caudal and lateral views; **B**, precaudal vertebra form Mirim Lagoon in anterior and lateral views; **C**, precaudal vertebra in anterior and lateral views, with hyperostotic areas indicated by arrows; **D**, isolated scales in lateral view. Opercular bones (**E–I**) in medial (*a*), lateral (*b*), and anterior (*c*) views. **Abbreviations : af**, articular facet; **ap**, articular process; **os**, opercular spine. Scale bars = 10 mm.

The precaudal vertebra MCTFM-PV1341 was retrieved by a fisherman from the lagoon bottom close to the Afogados Spit, on the southeastern shore of Mirim Lagoon some 40 km to the north of the town of Santa Vitória do Palmar (Figure 1C). The specimen is complete, lacking the haemal spines, without other broken or abraded parts, and it is not dark-colored and mineralized as the fossils from the *concheiros*. The centrum has maximum height, width and length of 36.7 mm, 40.9 mm, and 42 mm, respectively, and the height of the neural spine is 54.2 mm (Figure 7B).

The specimen PV1343 is a dark brown-colored, strongly mineralized precaudal vertebra lacking the ventral spinous processes, exhibiting signs of hyperostosis such as the thickened dorsal spinous process, globose osseous overgrowths close to the tip of the process, and osseous overgrowths at the insertion of the neural arch and on the ventral area of the centrum (Figure 7C).

The isolated scales (Figure 7D) exhibit varying degrees of preservation; some are strongly mineralized, similar to other vertebrate fossils from the *concheiros*, whereas some are less mineralized, similar to the specimen MCTFM-PV1099. The scales are flattened, with a thin margin and a thicker central area. Although most are abraded, growth rings are clearly visible, especially on the anterior field. On specimens LGP-B0013, LGP-B0015, and LGP-B0019, the posterior field exhibits cteni partially preserved, showing these are ctenoid scales, similar in size to those of *Micropogonias furnieri* and *Pogonias cromis* (Isaac, 1988; Carpenter, 2002).

Although mostly incomplete, the opercles are characterized by a flattened shape, medially concave and laterally convex (Kimmel *et al*., 2017). The specimen LGP-B0047 (Figure 7E) is apparently a right opercle, dark brown-colored and strongly mineralized. The high degree of abrasion produced rounded margins and polished surfaces and obliterated most anatomical details such as the articular facet. Nevertheless, it seems it has two posteriorly oriented, divergent, opercular spines. The opercle MCTFM-PV1084 (Figure 7F) appears to be from the left side, strongly mineralized and mostly dark brown-colored. Although highly abraded and polished, it exhibits surface ornamentation (visible with a hand lens) in the form of tiny pits around the articular region and thin longitudinal striae radially emanating from it. The specimen LGP-B0073 (Figure 7G) is a dark brown fragment of the middle-anterior portion of a right opercle, strongly mineralized but not heavily abraded. Its articular facet is well-preserved, deeply concave, mediolaterally elongated at an angle of ~15° relative to the horizontal plane (Figure 7G*c*). Its surface ornamentation is similar but more evident than in MCTFM-PV1084, in the form of pits and radial longitudinal striae. The specimen MCTFM-PV1340 (Figure 7H) is not mineralized like the other opercles, being light brown-colored and softer, more similar to the bones of specimen MCTFM-PV1099 (Figure 5E). Its margins are irregular, and the surface is not strongly abraded, exhibiting a laminated structure. The articular surface is deeply concave and vertically oriented (Figure 7H*c*) and has two posteriorly oriented opercular spines (Figure 7Ha). Although similar to MCTFM-PV1340 in overall shape and vertically oriented articular facet, the specimen MCTFM-PV1344 (Figure 7I) is more mineralized and apparently has a single spine.

Remarks. The partial centrum MCTFM-PV1095 was recovered from sediments extracted by a rotating drill during the installation of a wind turbine. Although its exact stratigraphic position could not be determined, the location of the borehole G02A09 (Figure 1C) indicates that it may be from lagoon margin deposits of the late Pleistocene Barrier III. During MIS 5 Transgression III, substantial amounts of marine sediments and shells were transferred across Barrier III up to Lagoon III in the backbarrier lowlands through overwash and/or inlets, forming thick lagoon margin deposits (Bettinelli *et al*., 2018; Lopes *et al*., 2024b). However, the possibility that it was originally preserved in marine facies of the underlying Barrier II cannot be excluded, because deposits of this unit were seemingly reworked and its associated fossils were re-deposited in the lagoon environment of the System III (Lopes *et al*., 2020b). This specimen could belong to a sciaenid, based on the maximum diameter of ~30 mm, seemingly compatible with the large *Pogonias cromis* and *Micropogonias furnieri* that inhabit this area.

According to local fishermen, the large dimensions of the vertebra MCTFM-PV1341 indicate a fish larger than the freshwater species found in the lagoon today. It could possibly belong to *Pogonias cromis*, although this species does not inhabit the lagoon nowadays. However, the presence of this species in the lagoon in the past is evidenced by the large pterygiophore found at Latinos Spit (Figure 1C, Lopes *et al*., 2020a), which, together with other vertebrate and mollusk fossils, shows that Mirim Lagoon was flooded by seawater during past interglacial sea-level highstands. The fact that MCTFM-PV1341 was retrieved from the bottom surface indicates that this individual lived at a recent time, probably coeval with the Middle-Late Holocene flooding of the lagoon as a result of the post-glacial marine transgression (PMT) (Barboza *et al*., 2021b; Lopes *et al*., 2021a).

Hyperostosis, as observed in the vertebra MCTFM-PV1343, is common on vertebrae and pterygiophores of sciaenids (Gervais, 1875; Barcellos, 1962; Konnerth, 1966; Pilleri, 1973; Aguilera, 1988). Although thickening as observed on this specimen also occurs on neural arches of *Pogonias cromis* (Richter, 1987) and haemal arches of *P. courbina* (Agnolín *et al*., 2024), the globose osseous overgrowths on the dorsal process are similar to those found on vertebrae of *Micropogonias furnieri*, being more frequent from the 5TH precaudal vertebra backwards in adults of maximum length >75 mm (Aguilera, 1988). Hyperostotic bones are more common in populations of *M. furnieri* found in warm temperate areas off southern Brazil (29–33°S) than in warmer subtropical areas to the north (Vazzoler, 1971).

Similar to the isolated scales, the opercles exhibit variable degrees of preservation, making it difficult to conclusively assign these bones to any species. Nevertheless, the double opercular spines in LGP-B0047 and MCTFM-PV1340 indicate that they may belong to sciaenids (Gregory, 1959), whereas the surface ornamentation in MCTFM-PV1084 and LGP-B0073 seems consistent with siluriform species.

DISCUSSION

The temporal range of the known paleoichthyofauna of the Pelotas Basin (Appendix 1) encompassing Cretaceous and Quaternary fossils, is characterized by a significant gap in the fossil record and shows how little is known about the vertebrate faunas that inhabited marine and coastal aquatic environments of southern Brazil between the late Mesozoic and virtually the entire Cenozoic. Because most of that interval is preserved only in subsurface (Closs, 1970), the gap can be attributed mainly to the fact that the Pelotas Basin is not oil- and gas-rich as the Santos and Campos marginal basins to the north, and therefore its subsurface deposits have not been as extensively sampled. Nevertheless, of the eight boreholes made by PETROBRAS S/A in onshore areas of the CPRS in the 1950s, four made in the central-southern area (Figure 8) reached marine deposits located at depths between ~108 and 522 m that yielded undescribed fish scales, otoliths and teeth and were dated to the Late Miocene based on associated foraminiferal assemblages (Closs, 1970). These deposits probably represent the 'Entrerriense' or 'Paranense' marine transgression recorded in Argentina, Uruguay, Paraguay and Bolivia (Cione *et al*., 2011).

The fossils described here increase the known diversity of fish species and fossil types found on Quaternary deposits of the basin, and although not all specimens could be conclusively identified to the species level, all recognized fossils belong to groups that still inhabit the coastal waters off southern Brazil nowadays. Despite the lack of precise chronological data of these fossils, the putative Middle Pleistocene to Middle Holocene ages of the specimens described here, plus the fact that all belong to living species, suggest a relative uniformity of the marine fish faunas of southern Brazil during the Quaternary. In fact, such uniformity at the generic level and above can be traced back to the Neogene (Miocene) according to fossil records of Argentina (Arratia & Cione, 1996; Cione *et al*., 2011, 2013; Gouiric-Cavalli *et al*., 2021).

The modern marine faunas of the southwestern Atlantic were established in the Late Miocene and are characterized by warm-temperate taxa of the Argentinean biogeographic province, such as *Myliobatis*, *Carcharias taurus*, *Carcharhinus* sp., and *Galeocerdo* (Cione *et al*., 2011). This indicates that marine environmental conditions along the southwestern Atlantic did not change much between the Neogene and the present, although the Quaternary glacial-interglacial climate fluctuations probably favored the episodic southward expansion of tropical fish species during warmer periods (see below). The scarce fossils of Pimelodidae found in the CPRS make it difficult to establish temporal and faunal correlations, but as the fossil records of this group in Argentina date back to the Miocene (Arratia & Cione, 1996), it is possible that it has lived in southern Brazil since that time as well.

Most of the identified fossils of actinopterygians belong to sciaenids (Appendix 1), which may in part be related to the abundance and diversity of this group. However, preservation biases may have influenced this pattern (see Taphonomy below).

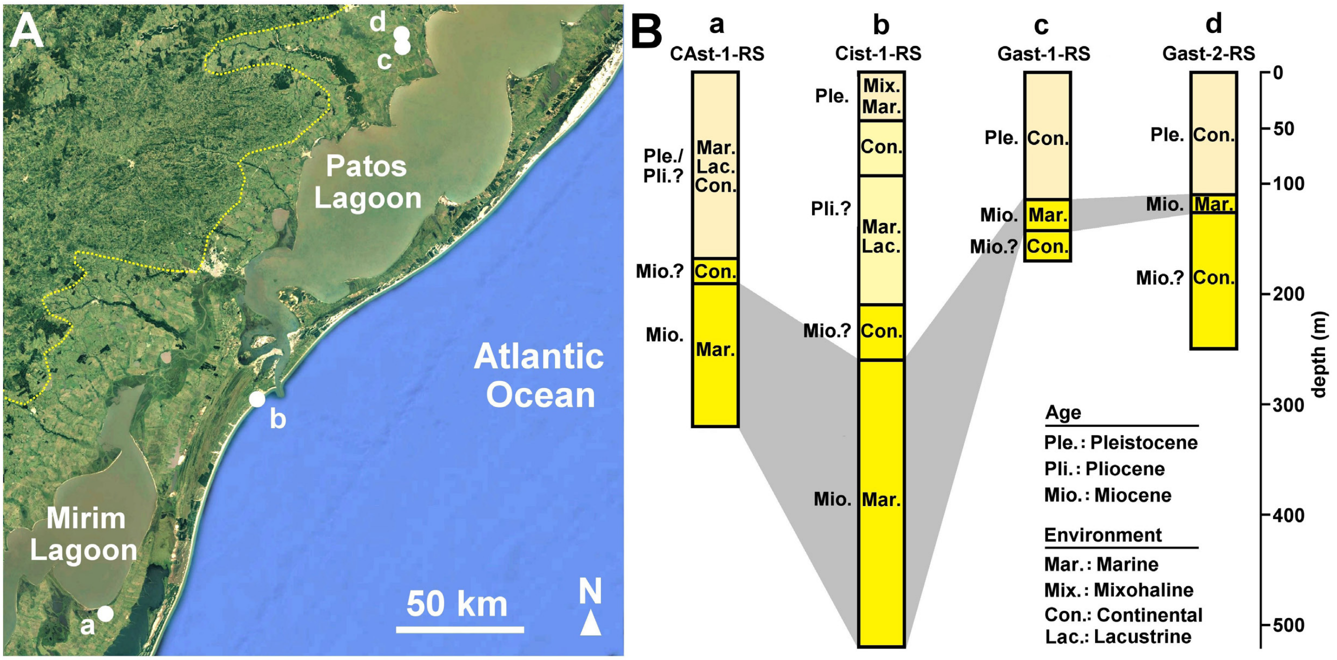

Figure 8. A, Google Earth image showing the location of the boreholes made in onshore areas of the Pelotas Basin in the central-southern CPRS that yielded fish fossils: **a**, Curral Alto (CAst-1-RS); **b**, Cassino (Cist-1-RS); **c**, Graxaim 1 (Gast-1-RS); **d,** Graxaim 2 (Gast-2-RS); **B**, stratigraphy of the boreholes, the grey area shows the Miocene deposits with fish fossils (from Closs, 1970).

The Sciaenidae originated in the New World, and all genera from the southwestern Atlantic are monospecific (Sasaki, 1989). The fossil records of *Micropogonias* and *Pogonias* in coastal waters of SSA date back to the Miocene (Cione *et al*., 2013; Noriega *et al*., 2024). On the coast of Rio Grande do Sul this is one of the richest groups at depths up to 120 meters, represented by twelve species. Most of these are fully marine, but *P. cromis* and *M. furnieri* are estuarine dependent; the adults live close to the estuary of Patos Lagoon, where they spawn. Juveniles inhabit coastal waters throughout the year, while the adults migrate to deeper waters during winter (Haimovici, 1997; Fischer *et al*., 2011).

Fossils of Myliobatiformes are relatively common along the *concheiros*, represented mainly by tail spines and dental plates of Myliobatidae (Richter, 1987; Cruz *et al*., 2016; Britto *et al*., 2024), and one incomplete dental plate was found on Mirim Lagoon at the same site (Santiago Spit, Figure 1C) where a buckler of cf. *Bathytoshia centroura* was found (Lopes *et al*., 2020a). The dermal bucklers described here are the first records of Dasyatidae fossils from the *concheiros*. Dasyatid rays are not residents of southern Brazilian waters today, being found along Rio Grande do Sul only during summer (Vooren, 1997) when the meridional influence of warm tropical waters is increased. It is possible that dasyatids (and other tropical species) were more permanent residents of the southwestern Atlantic during the Neogene, as indicated by fossils of this group found in 'Entrerriense/Paranense' Late Miocene deposits of Argentina, whose aquatic fossil assemblages indicate coastal waters relatively warmer than today (Cione *et al*., 2013).

If that was the case, the contemporaneous seasonal occurrence of tropical marine species in southern Brazil may have been a response to the general cooling resulting from the cyclic Quaternary climate, characterized by long (cold) glacial periods intercalated with short (warm) interglacial periods. The cyclic interglacial warming along the southwestern Atlantic resulting from the stronger influence of tropical water masses would have favored periodic southward shifts in the distribution of tropical taxa. These shifts could have been especially favored (and relatively more frequent or permanent) during the warmest periods (hypsithermals) of the early part of interglacials, as occurred between the latest Pleistocene and Early Holocene, characterized in the Southern Ocean by sea surface temperatures 1–2°C warmer than today between ~12.5 and 6.2 cal ka BP (Nielsen *et al*., 2004). The influence of this hypsithermal (or Holocene climatic optimum, HCO) seems supported by the fossils of the bull shark *Carcharhinus leucas* and the bivalves *Anomalocardia flexuosa* and *Cyrtopleura costata*, which today inhabit areas to the north of Rio Grande do Sul, found in Holocene deposits of Mirim Lagoon (Lopes *et al*., 2020a, 2021a). Based on the presence of *A. flexuosa* and other tropical mollusks in Pleistocene marine deposits (*e.g*., Lopes & Simone, 2012; Lopes *et al*., 2013; Bettinelli *et al*., 2018), it is likely that such faunal shifts may have been recurrent in geological time scales since the establishment of the glacial-interglacial cycles with periodicity of ~100 ka in the Middle Pleistocene, so it is possible that tropical fish species may be eventually found in Pleistocene deposits as well.

The fossil records of both Dasyatidae and Diodontidae in northern-northeastern Brazil date back to the Miocene, although fossils of the latter were also found in Cretaceous deposits (Gallo *et al*., 2009). The Diodontidae seem to have originated during the Early Eocene in tropical waters of the Tethys Ocean (Santini & Tyler, 2003), which explains the high diversity, both fossil and extant, of this group in the Caribbean region (Aguilera *et al*., 2017c). The oldest fossils of Tetraodontiformes in SSA consist of beaks of Molidae of Early (Aquitanian–Burdigalian) and Tetraodontidae of Late (Tortonian–Messinian) Miocene ages from Argentina (Gouiric-Cavalli *et al*., 2021), which together with the beaks described by Agnolín *et al*. (2022) and the specimens presented here, are the only fossils of this group recorded along the southwestern Atlantic so far. Although the scarce fossil record makes difficult to understand the paleobiogeography of this group along the eastern-southwestern Atlantic, the presence of *Chilomycterus spinosus spinosus* as the only living Diodontidae in southern Brazil, Uruguay and Argentina may indicate a relatively recent (Pleistocene?) dispersal related to its eurihaline tolerance and capability to occupy different marine and coastal environments, being characterized as marine estuarine opportunist (Andrade *et al*., 2015).

One major problem for the understanding the patterns of temporal distribution of the Quaternary fossil ichthyofauna of southern Brazil is the high degree of time averaging of the continental shelf-beach fossil assemblages, which were mixed together by successive marine transgressions driven by glacioeustatic cycles during the Quaternary, as indicated by ages of fossil mammals and marine shells (Lopes *et al*., 2014b, 2020b). Although the specimens MCTFM-PV1082 (Figure 5A) and MCTFM-PV1095 (Figure 7A) were retrieved from marine units of Middle (Barrier II) or late (Barrier III) Pleistocene age in terrestrial settings, the fossils themselves may be from older deposits that were eroded, and its associated fossils were re-deposited on younger units by the marine transgressions that originated those barriers.

Another possible influence of past marine transgressions on the fossil record of fishes was through the changes in the coastal lagoons, creating dispersal corridors or barriers between lagoons (Beheregaray *et al*., 2002; Lopes *et al*., 2022), or changing the water characteristics (and consequently the associated fauna) from fresh, to brackish, and fully marine (Lopes *et al*., 2021a). If the large pterygiophore (Lopes *et al*., 2020a) and vertebra MCTFM-PV1341 (Figure 7B) from Mirim Lagoon belong to adults of *Pogonias cromis*, this could indicate that they died during spawning seasons during an early phase of the Holocene marine incursion into the lagoon around 7–8 ka, when it was still an estuarine environment, also indicated by the otolith of a juvenile *Micropogonias furnieri* (Lopes *et al*., 2020a, 2021a). Alternatively, these individuals could have inhabited the lagoon more permanently during the period of strongest marine influence due to the highest sea-level around 6–5 ka (Angulo *et al*., 2006). In this case, *P. cromis* could have been, at least on occasion, a potential fisheries source for the early humans that reached the area, as indicated by the presence of its bones in a Holocene archaeological site (*cerrito*) near Chuy Creek (Schmitz *et al*., 1997).

Contrary to the marine remains, the pimelodid fossils preserved on fluvial facies of the SVA have reasonable stratigraphic control. Although the SVA seemingly accumulated between the Middle and late Pleistocene, the fragmentary state of most mammalian fossils (Lopes & Ferigolo, 2015) and the late Pleistocene ages of the luminescence-dated fluvial deposits (Lopes *et al*., 2019, 2021b) indicate substantial reworking of the deposits and associated fossils by episodic variations in fluvial activity. The relatively good preservation and close association of the pimelodid bones indicate that *postmortem* reworking was minimal, and thus, a relatively young, late Pleistocene age of these remains, seems more likely. The fossil record of pimelodids in SSA is quite diverse, with several taxa recorded on Miocene to late Pleistocene fluvial deposits in Argentina (Ameghino, 1898; Arratia & Cione, 1996; Fucks *et al*., 2005; Azpelicueta & Cione, 2016; Vallone *et al*., 2017; Agnolín & Bogan, 2020; Schmidt *et al*., 2020; Brambilla *et al*., 2021).

Taphonomy

The fossil described here exhibits variable degrees of preservation, ranging from the complete and unabraded, such as the vertebra MCTFM-PV1341, to broken and/or highly abraded, as the centrum MCTFM-PV1095, scales, and opercles shown in Figure 7. These differences probably reflect the *postmortem* modifications controlled by hydrodynamics and physicochemical conditions in distinct environments (*i.e*., lagoon or wave-dominated shallow marine). Similar variations are observed in mammalian fossils found on the continental shelf and fluvial deposits (Lopes & Ferigolo, 2015). Besides producing variable physical (biostratinomic) features, those conditions can also result in preservation biases due to differential destruction of some skeletal elements.

One factor that probably contributed to the relatively high abundance of sciaenid fossils is the large sizes attained by *Micropogonias furnieri* (body length up to 750 mm) and *Pogonias cromis* (body length >1.4 m) (Fischer *et al*., 2011). Larger specimens, such as the vertebrae MCTFM-PV1095 and MCTFM-PV1341, some scales, and the operculi LGP-B0047, MCTFM-PV1340, and MCTFM-PV1344 (Figure 7) could belong to those sciaenids, but the possibility that they represent other taxa cannot be excluded. Species of other groups, such as Mugilidae, can unusually attain body sizes similar to the largest sciaenids (Figure 9A), but no fossils of these groups have been positively identified so far. One major problem with taxonomic assignment of some specimens was the lack of diagnostic characters, in many cases resulting from *postmortem* modification by biostratinomic processes, especially abrasion and breakage, as is the case with most mammalian fossils from the continental shelf and *concheiros* (Lopes & Ferigolo, 2015).

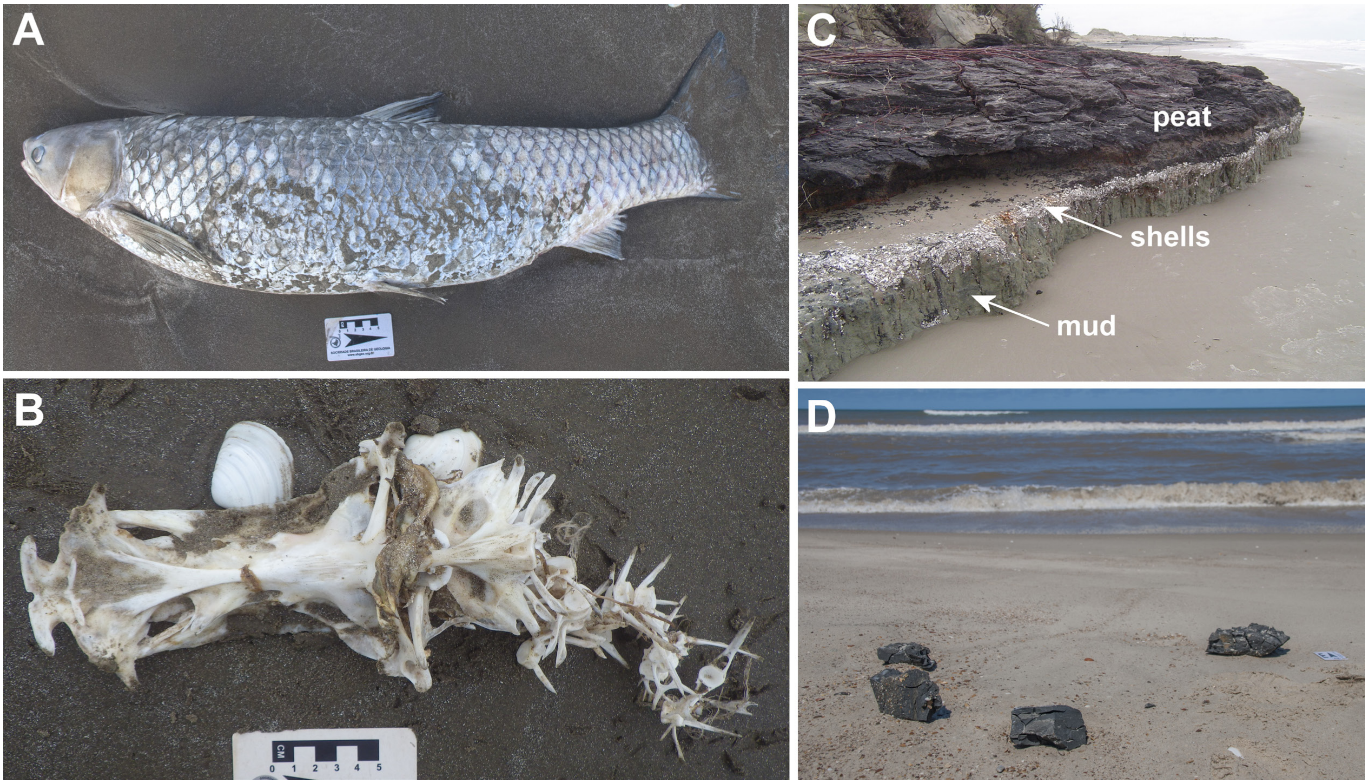

Figure 9. A, an exceptionally large specimen of *Mugil* sp. at Cassino Beach; **B**, partial skeleton of a catfish (cf. Ariidae) stranded at Cassino Beach, with the skull and vertebrae still articulated; **C**, Middle (>5 ka BP) Holocene layer of grey mud from the paleo-Mangueira Lagoon bottom outcropping at the beach on the southernmost CPRS; **D**, mudblocks similar to the mud layer shown in C, eroded and transported by waves from the shoreface to the *concheiros*. Scale bars: A–B = 5 cm.

The fossil fish assemblages of Quaternary marine deposits of the Pelotas Basin (Appendix 1) also seem biased toward more numerous and/or resistant skeletal elements (*e.g.*, vertebral centra, hyperostotic bones, otoliths, dental elements) with higher preservation potential. This is more evident on the fossil record of chondrichthyans, dominated by teeth and dental plates (Appendix 1), which are more mineralized than their cartilagenous skeletons. Together with the high number and continuous development of teeth throughout the life history of the shark species, the preservation potential results in a paleoichthyological record of the CPRS dominated both in diversity and abundance by chondrichthyan teeth (*e.g.*, Richter, 1987; Buchmann & Rincón Filho, 1997; Medeiros *et al.*, 2023; Britto *et al.*, 2024). Although the number of extant species of coastal and estuarine actinopterygians and chondrichthyans living in the southern CPRS is similar (Table 2; Seeliger *et al.*, 1997; Fischer *et al.*, 2011), the latter exhibits the highest relative abundance in fossil assemblages. The lower relative representativity of actinopterygians probably results from the absence of large teeth in most species, and the preferential taphonomic destruction of smaller taxa and more fragile elements such as skull bones, spines, and fin rays. Although spinous processes and pterygiophores are thin, long, and relatively fragile bones, the hyperostotic condition apparently increases the preservation potential of these bones (*e.g.*, Cunha & Nunan, 1980; Richter, 1987; Agnolín *et al.*, 2024). This possibility is supported by the hyperostotic vertebra MCTFM-PV1343 (Figure 7C) that has the thickened spinous process of the neural arch fused to the centrum, which is usually found without attached arches (*e.g.*, Richter, 1987), although Buchmann & Rincón Filho (1997) described vertebrae with fused arches.

Higher abundance of chondrichthyans compared to actinopterygians related to taphonomic processes is also observed on Early Miocene fossil assemblages of Patagonia (Cione *et al.*, 2011), thus implying that selective taphonomic loss may be recurrent across shallow marine environments, which may make the reconstruction of ancient fish communities difficult. On the other hand, that similarity indicates that the understanding of the mechanisms responsible for the taphonomic loss observed in recent marine fossil assemblages can aid in the reconstruction of ancient depositional environments.

The main agents of modification of the fossils from the marine deposits of the CPRS are the cyclic sea-level oscillations that occur on timescales of tens of thousands of years and erode the upper 6–10 m of the continental shelf sediments (Dillenburg, 1996). The wave regime is characterized by storm waves that episodically erode shelf fossiliferous deposits and transport the remains to the shore, and fair-weather waves that constantly move the fossils along and across the surf zone (Lopes *et al.*, 2024a). These processes result in taphonomic destruction of more fragile skeletal elements, not only of fishes but also of terrestrial mammals found on the continental shelf, resulting in fossil assemblages biased toward large-bodied taxa and more compact skeletal elements (Aires & Lopes, 2012; Lopes & Ferigolo, 2015). As the shelf sediments were reworked multiple times by the Quaternary marine transgression-regression cycles, many of the older fossils were probably broken and/or highly abraded beyond recognition, and the few fragile elements such as spines, skull parts (Richter, 1987), and scales (Figure 7D) found at the *concheiros* may be relatively young and/or were probably exhumed recently from the shelf deposits, thus exposed for a short time to waves and curents.

Besides mechanical destruction, other taphonomic features characteristic of the fossils from marine settings include the hardness and dark color, ranging from black to reddish, although the dasyatid specimens MCTFM-PV1091 and 1092 in Figure 2 and the otoliths LGP-B0004, LGP-B0006 and MCTFM-PV1083 in Figure 4A exhibit light brown color, and the disarticulation of the skeletal elements by sea-level oscillations, waves and currents (Lopes & Ferigolo, 2015). One notable exception (the only of its kind known so far from the CPRS) is the *Pogonias cromis* MCTFM-PV1099 (Figure 5E). The bones of this specimen are softer, more similar to the fish fossils from Mirim Lagoon (Lopes *et al.*, 2020a) and SVA, and exhibit distinct color than the other vertebrate fossils from the *concheiros*, thus indicating preservation in a depositional environment subject to physicochemical conditions not fully marine, but probably suitable for the survival of the individual. However, the possibility of *postmortem* transport of the carcass from its original habitat before the decomposition of soft tissues cannot be excluded. In fact, skeletons of large fishes can remain articulated while being transported by waves and currents, despite the total decomposition of most soft tissues (Figure 9B).

The indurated mud and the association of disarticulated elements on the specimen MCTFM-PV1099 point to preservation in an environment with weaker hydrodynamics than the high-energy, wave-dominated sandy nearshore setting along the CPRS, probably a lagoon bottom. The Quaternary depositional systems of the CPRS are characterized by long sandy barriers isolating large lagoons on the back barrier (Figure 1C), whose low-energy settings favor the accumulation of mud at the bottom (Villwock & Tomazelli, 1995). The presence of *Pogonias cromis* in such an environment could be explained by the life habit of this species, which spawns and remains in estuarine areas until reaching sexual maturity (Fischer *et al.*, 2011).

Table 2. Comparison of the number of fish species found living along the CPRS (Seeliger *et al.*, 1997; Fischer *et al.*, 2011) with the number and relative percentage of the species also represented in the fossil assemblages.

Groups	Living	Fossil	%
Chondrichthyes	60	17	14.0
Actinopterygii	61	4	3.3

The taphonomic features of MCTFM-PV1099 thus suggest that either it lived, died and was preserved in a lagoon setting, or it died at the sea and was transported as a dead carcass from the sea, possibly through overwash and/or inlets across the barrier, to the backbarrier lagoon where it settled at the bottom, either as disarticulated but associated elements (similar to Figure 9B) or as a complete carcass that decomposed and had its elements moved and partially disarticulated by water at the muddy bottom. Considering the location of the specimen in the southern CPRS, it is likely that it was preserved at the bottom of the paleo-Mangueira Lagoon (Figure 1C) when sea-level was still below the present and both the paleo-lagoon and Barrier IV were still located seaward of the modern coastline. If this were the case, the presence of this fossil on the modern marine setting would have resulted from the landward migration of the Barrier IV over lagoon bottom deposits, as indicated by cores and GPR data across the barrier (Caron, 2014), which caused the muddy lagoon bottom sediments to be exposed on the shoreface, and thus subject to erosion and onshore transport by waves and currents. That possibility is supported by the Holocene lagoon margin deposits of the paleo-Mangueira Lagoon outcropping at the shoreline of the southernmost CPRS as a result of the migration and complete erosion of the Barrier IV in this area (Dillenburg *et al*., 2000). These deposits (Figure 9C) exhibit a succession of a grey mud layer with marine and freshwater palynomorphs (Masetto & Lorscheitter, 2019) and shells of bivalve mollusks adapted to brackish conditions (*Tagelus plebeius*, *Erodona mactroides* and *Anomalocardia flexuosa*), one of latter dated as 5,840–5,580 cal yrs BP (Lopes *et al*., 2022), overlain by a peat layer accumulated between ~4 and 2 ka BP (Masetto & Lorscheitter, 2019). Grey mud with shells was also found at the bottom of deeper areas of the Mangueira Lagoon (Vassão, 1952). The colonization by bryozoans (Figure 5G) indicates exposure of MCTFM-PV1099 on marine environment for some time prior to transport to the beach. The process of erosion-exposure-transport of the fossil was likely the same as that responsible for the grey mudblocks thrown by waves onto the shore at the *concheiros* (Figure 9D), probably eroded from the paleo-Mangueira Lagoon bottom being exposed on the shoreface due to contemporaneous erosion.

The preservation of MCTFM-PV1099 in lagoon settings seems supported by the similar features (despite the disarticulated and isolated state) of fish fossils from Mirim Lagoon, including the vertebra MCTFM-PV1341 (Figure 7B), the large pterygiophore presumably of *Pogonias cromis* and the otolith of a juvenile *Micropogonias furnieri* (Lopes *et al*., 2020a), which are more similar to MCTFM-PV1099 than to the dark, strongly mineralized and broken/abraded fossils from marine settings. The good preservation and lighter color of the otoliths LGP-B004, LGP-B006 and MCTFM-PV1083 (Figure 4A), similar to the otolith from Mirim Lagoon (see Figure 4E in Lopes *et al*., 2020a), could indicate that these were also preserved in lagoon environments posteriorly exposed to marine environment as a result of the landward migration of coastal barriers over lagoon deposits. This possibility is consistent with the fact that smaller, juvenile individuals inhabit brackish-freshwater inner areas of the Patos Lagoon and La Plata River estuaries, whereas adults live in coastal marine waters but enter the estuaries to spawn (Jaureguizar *et al*., 2008; Fischer *et al*., 2011; Costa *et al*., 2014).

The fossils of pimelodids from the fluvial deposits of the SVA are also more similar to the remains from Mirim Lagoon. The close association of the specimens MCTFM-PV0872 and MCTFM-PV0875 (possibly also MCTFM-PV0873 and MCTFM-PV0874) and the different bones embedded in the sediment (Figure 3G) point to a lower degree of reworking, thus implying a parautochthonous origin. This is also indicated by the relatively good preservation of these small and fragile bones compared to the larger mammalian remains found in the SVA, which are mostly broken and/or abraded due to repeated episodes of burial and reworking by oscillating fluvial dynamics (Lopes & Ferigolo, 2015). The crust of iron oxide-coated sand grains on the rib fragment associated with the fish bones (Figure 3G) is absent on the latter, thus indicating that the rib was eroded from a preexisting deposit and buried in a fluvial channel together with the partially disarticulated carcass of the pimelodid. This association of relatively small and fragile vertebrate fossils with broken and abraded large mammalian fossils was also observed in a late Pleistocene (~38 ka) fluvial deposit containing one complete vertebra of a ciconiid together with several fragments of different species of mammals (Lopes *et al*., 2019).

CONCLUSIONS

The specimens described here contribute to the knowledge about the diversity and spatial distribution of both chondrichthyan and actinopterygian fossils across Quaternary depositional systems of the Pelotas Basin. The known fossil fish record of this basin exhibits a significant temporal gap between the Late Cretaceous and the Quaternary, probably due to the relatively small number of subsurface samples available. Most of the known fossils are from Quaternary deposits on the uppermost basin, but even these seem scarcer and are less studied in comparison to fossil mollusks and mammals from the same deposits.

The dominance of chondrichthyans over actinopterygians and the scarcity of identifiable fish fossils in the Quaternary assemblages probably result from the taphonomic destruction of most fossils preserved in marine settings by long-term (sea-level oscillations) and short-term (storm and fair-weather waves) processes that erode and rework the deposits and associated fossils. That destruction seems to affect mostly skeletal elements that are fragile and/or belong to smaller species, resulting in fossil assemblages biased towards elements that are more numerous, resistant, and/or belong to larger species or older individuals in the case of hyperostotic bones. Fish fossils preserved on lagoon and fluvial settings, on the other hand, are better preserved and even include disarticulated but associated skeletal elements, probably due to weaker hydrodynamics.

Despite the preservation bias of the fossil fish assemblages, the taxonomic affinities of the Quaternary fossils of Pelotas Basin with those from Neogene–Quaternary units of Argentina indicate a relative uniformity of subtropical warm-temperate environmental conditions along the southwestern Atlantic at least since the Miocene. Nevertheless, some tropical species indicate episodically warmer conditions, probably driven by glacial-interglacial climate oscillations. Besides contributing for the knowledge about the diversity of late Cenozoic marine faunas of the southwestern Atlantic and their possible relation with climate changes, the results presented here also highlight the importance of fossil fishes as tools for recognizing ancient depositional environments, based on the preservation patterns of the remains, thus providing additional elements for the interpretation of the geological history of coastal areas.

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AUTHOR CONTRIBUTIONS

Renato Pereira Lopes: conceptualization, writing – original draft, editing, visualization, investigation, formal analysis, resources. Jamil Corrêa Pereira: writing – review, investigation, formal analysis, data curation. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix 1. Fish fossils from the Pelotas Basin described in the literature.

Taxon	**Material**	**Reference**
CHONDRICTHYES		
MYLIOBATIFORMES		
MYLIOBATIDAE		
Myliobatidae indet.	dental plates, spines	Richter (1987)
	dental plate	Lopes *et al*. (2020a)
Myliobatis ridens	dental plates	Britto *et al*. (2024)
Myliobatis freminvillei	dental plates	Britto *et al*. (2024)
Myliobatis goodei	dental plates	Britto *et al*. (2024)
DASYATIDAE		
cf. *Dasyatis centroura*	dermal buckler	Lopes *et al*. (2020a)
	dermal bucklers	this paper
CARCHARHINIFORMES		
CARCHARHINIDAE		
Carcharhinus sp.	teeth, vertebrae	Richter (1987); Medeiros *et al*. (2024)
cf. *Carcharhinus brachyurus*	teeth	Medeiros *et al*. (2023)
cf. *Carcharhinus longimanus*	teeth	Medeiros *et al*. (2023)
Galeocerdo cuvieri	teeth	Buchmann & Rincón Filho (1997); Medeiros *et al*. (2023)
Rhizoprionodon sp.	teeth	Medeiros *et al*. (2023)
LAMNIDAE		
Isurus oxyrhynchus	teeth	Buchmann & Rincón Filho (1997); Medeiros *et al*. (2023)
TRAKIDAE		
Galeorhinus galeus	teeth	Medeiros *et al*. (2023)
ODONTASPIDIDAE		
Carcharodon carcharias	teeth, vertebrae	Richter (1987); Medeiros *et al*. (2023); Medeiros *et al*. (2024)
Carcharias taurus	teeth, vertebrae	Buchmann & Rincón Filho (1997); Medeiros *et al*. (2023); Medeiros *et al*. (2024)
Carcharhinus leucas	teeth	Lopes *et al*. (2020a); Medeiros *et al*. (2023)
HEXANCHIFORMES		
HEXANCHIDAE		
Heptranchias perlo	teeth	Buchmann & Rincón Filho (1997)
Notorynchus cepedianus	teeth	Medeiros *et al*. (2023)
SQUATINIFORMES		
SQUATINIDAE		
Squatina sp.	teeth	Medeiros *et al*. 2023
ACTINOPTERYGII	scales, vertebrae	this paper
SILURIFORMES	opercles?	this paper
ARIIDAE	spines	Richter (1987)
Netuma sp.	skull bones	Richter (1987)
	skull bones	Buchmann & Rincón Filho (1997)
PIMELODIDAE		
Pimelodidae indet.	skull bones, partial skeleton	this paper
PERCIFORMES		
SCIAENIDAE		
Pogonias cromis	pterygiophores	Cunha & Nunan (1980)
	pterygiophore, neural arches, vertebral centra	Richter (1987)

Appendix 1. Continued...

Taxon	Material	Reference
	vertebrae	Buchmann & Rincón Filho (1997)
	pterygiophore	Lopes *et al*. (2020a)
	pterygiophore, partial skeleton	this paper
Micropogonias furnieri	otolith	Lopes *et al*. (2020a)
	otoliths	this paper
	TETRAODONTIFORMES	
	DIODONTIDAE	
cf. *Chilomycterus spinosus*	dental plates	this paper
	BERYCIFORMES	
	HOLOCENTRIDAE	
Pelotius hesselae	skeleton	Gallo-da-Silva & Figueiredo (1999)
	ARGENTINIFORMES	
Parawenzichthys minor	skeleton	Figueiredo *et al*. (2012)
	AULOPIFORMES	
DERCETIDAE		
Brazilodercetis longirostris	skull, vertebrae	Figueiredo & Gallo (2006)