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SHARK (NEOSELACHII) VERTEBRAL CENTRA FROM THE QUATERNARY OF SOUTHERN BRAZIL

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ABSTRACT – In the southern coast of Brazil, shark fossil remains are commonly found along the current beach line. Most of these fossils are represented by fossilized teeth, while fossilized vertebral centra are less frequently found. In the present study, 26 fossilized vertebral centra of sharks (Neoselachii) from the Quaternary period were analyzed and described. The vertebral centra collected *ex situ* in the Coastal Plain of Rio Grande do Sul (CPRS) were analyzed using X-ray to observe internal structures. Two morphotypes based on their morphological structure were identified: the first was Lamnoid, identified in 17 vertebral centra, and the second was Carcharhinoid, identified in eight centra. The analyzed materials represented the first records of fossil vertebral centra of Neoselachii found in the region. The morphotypes are characterized based on the morphological structure of the vertebral centrum, allowing for differentiation and correlation with the genera of sharks in which a morphotype occurs. The study showed a direct correlation between the identified morphotypes and the lineages that make up the faunal diversity of Neoselachii occurring in the CPRS, both in the fossil record and currently. The Lamnoid morphotype occurs within Lamniformes sharks, such as the species *Carcharias taurus*, *Carcharodon carcharias*, *Isurus oxyrinchus*, among others. The Carcharhinoid morphotype, on the other hand, is characteristic of Carcharhiniformes sharks, such as *Carcharhinus leucas*, *C. brachyurus*, *Galeocerdo cuvier*, *Galeorhinus galeus*, and others.

Keywords: Chondrichthyes, paleoichthyology, taxonomy, marine, vertebrae.

RESUMO – Na costa sul do Brasil, fósseis de tubarões são comumente encontrados ao longo da linha atual da praia. A maioria desses fósseis é representada por dentes fossilizados, enquanto as vértebras fossilizadas são encontradas com menos frequência. No presente estudo, 26 vértebras fossilizadas de tubarões (Neoselachii) do período Quaternário foram analisadas e descritas. As vértebras coletadas *ex situ* na Planície Costeira do Rio Grande do Sul (PCRS) foram analisados utilizando raios-X para observar as estruturas internas. Foram identificados dois morfotipos com base em sua estrutura morfológica: o primeiro foi o Lamnoide, identificado em 17 vértebras, e o segundo foi o Carcharinoide, identificado em oito vértebras. Os materiais analisados representaram os primeiros registros de vértebras fossilizadas de Neoselachii encontradas na região. Os morfotipos são caracterizados com base na estrutura morfológica do centro vertebral, viabilizando a diferenciação e a correlação com gêneros de tubarões em que um morfotipo ocorre. O estudo mostrou uma correlação direta entre os morfotipos identificados e as linhagens que compõem a diversidade faunística de Neoselachii que ocorre na PCRS, tanto no registro fóssil quanto atualmente. O morfotipo Lamnoide ocorre em tubarões Lamniformes, como as espécies *Carcharias taurus*, *Carcharodon carcharias*, *Isurus oxyrinchus*, entre outros. O morfotipo Carcharhinoide, por outro lado, é característico de tubarões Carcharhiniformes, como *Carcharhinus leucas*, *C. brachyurus*, *Galeocerdo cuvier*, *Galeorhinus galeus* e outros.

Palavras-chave: Chondrichthyes, paleoictiologia, taxonomia, marinho, vértebras.

INTRODUCTION

The fossil record of the neoselachian sharks is mainly represented by fossilized teeth, used to identify species, diversity, classifications, and taxonomic analyses (Shimada, 1997, 2008; Ehret *et al*., 2009; Cook *et al*., 2010; Fialho *et al*., 2020). This is mainly due to the low mineralization and fossilization potential of their cartilaginous skeletal elements (Shimada, 2007; Ehret *et al*., 2009; Kardong, 2016; Fialho *et al*., 2020). However, despite being rarer, fossilized shark vertebral centra are also excellent material for taxonomic and taphonomic analyses, and paleoecological reconstructions (Ridewood, 1921; Applegate, 1967; Shimada, 1997; Blanco-Piñón *et al*., 2005).

Fossil vertebral centra of sharks usually consist of the main body of the vertebrae, after all less mineralized parts (neural and hemal archs) have been decomposed or lost (Ridewood, 1921; Applegate, 1967; Welton & Farish, 1993; Ehret *et al*., 2009; Kardong, 2016). In terms of structure, shark and ray vertebral centra consist of double cones joined at the centrum by their apexes. Each cone consists of a phosphatic cartilage body, where growth rings can be found on the outer edge, while the inner region consists of either radial lamella or is completely mineralized (intermedialia) (Ridewood, 1921; Applegate, 1967; Welton & Farish, 1993; Shimada, 2008). These centra can be morphologically different among various lineages and even different among genus within a single family (Applegate, 1967; Burris, 2004).

Applegate (1967) proposed eight morphotypes based on the morphological structure of the vertebral centra. They were named after the genus in which a particular morphotype was firstly observed and are classified as follows: (a) Heterodontoid morphotype: characterized by a thick, mineralized phosphatic body, with the inner portion of the double cones surrounded by thick, well-spaced lamellae that bifurcate from the inner centrum of the double cone. This vertebral centrum has a hexagonal shape; (b) Squatinoid morphotype: displays an almost completely mineralized phosphatic body, filling the center of the double cone with calcifications arranged in numerous concentric lines. The outer part of the double cone has areas divided by irregularly arranged straight lines; (c) Pristiophoroid morphotype: identified by a thicker calcified phosphatic body and a more rectangular shape, with small projections expanding outward from the phosphatic body (one in the region of the neural arch, one in the hemal arch, and two laterally); (d) Squaloid morphotype: small vertebral centra characterized by a well-mineralized and thick double cone, but the surrounding portion of the intermedialia is weak and rudimentary. The intermedialia lack cavities; (e) Lamnoid morphotype: characterized by a thicker phosphatic body, with the inner portion of the double cones surrounded by several thin, calcified radial lamellae, originating from the meso-dorsal foramen in the dorsal portion; (f) Pristiuroid morphotype: characterized by a well-mineralized phosphatic double cone body, with the intermedialia region being poorly mineralized and lacking internal cavities. The phosphatic body has four extensions in its structure (two in the dorsal region and two in the ventral region of the vertebral centrum); (g) Atelomyeteroid morphotype: features a well-mineralized and thick phosphatic body, with strongly developed cavities emerging from the centrum of the double cone. The outer portion of the double cones is surrounded by a mineralized sheath, which has four pairs of cavities around it, originating from the inner cavities; and (h) Carcharhinoid morphotype: characterized by a thinner phosphatic body, and the outer portion of the double cones is surrounded by a mineralized sheath. Although all morphotypes present a basidorsal insertion of the neural arch and a basiventral insertion of the hemal arch, these cavities are thicker and more prominent in the intermedialia of the Lamnoid and Carcharhinoid morphotypes. However, a given morphotype can occur in more than one lineage.

The primary objective of this study was to identify and classify the morphotypes of isolated Quaternary fossil shark vertebral centra found in the Coastal Plain of Rio Grande do Sul (CPRS). Additionally, the study aims to describe the distinct morphological characteristics associated with each morphotype. This research seeks to contribute to a deeper understanding of the shark species that inhabited the coastal region of Rio Grande do Sul, Brazil, during the Quaternary period.There are no previous records of fossilized shark vertebrae in the CPRS; however, archaeological studies indicate the presence of these materials associated with shell mounds on the coast of the states of Santa Catarina and Rio de Janeiro (Lopes *et al*., 2016; Mayer *et al*., 2022, 2023).

GEOLOGICAL AND PALEONTOLOGICAL CONTEXT

The CPRS is a physiographic province that represents the younger strata of the Pelotas Sedimentary Basin, located in the eastern portion of the state of Rio Grande do Sul. It stretches across 620 km, between the municipalities of Torres and Chuí, and consists of sediments from the Neogene through to the Quaternary (Tomazelli *et al*., 1997; Tomazelli & Dillenburg, 2007). The formation and origin of the CPRS is directly related to mean sea-level (MSL) transgression and regression events that occurred during the past 400 ka due to glacial and interglacial cycles (Corrêa, 1990; Villwock & Tomazelli, 1995; Tomazelli & Villwock, 2000; Dillenburg *et al*., 2004; Lowe & Walker, 2014).

These events caused a lateral overlapping of sedimentary deposits, originating four Lagoon-Barrier-type depositional systems that comprise the current coastal plain, called, respectively, I, II, III (older, Pleistocene), and IV (earlier, Holocene) (Villwock *et al*., 1986; Villwock & Tomazelli, 1995). Because Barrier IV is the most recent, it presents a better preservation state compared with the other systems and has important records regarding physical processes related to the origin and development of the CPRS, as well as body and trace fossil records of marine and terrestrial organisms (Buchmann *et al*., 2009). Due to the wide climatic variation of this period and sea-level changes, several terrestrial and marine paleoenvironments were formed and most of them

are currently submerged on the continental shelf, containing submerged fossil deposits (Figueiredo, 1975; Ângulo & Souza, 2014). These underwater fossil deposits are correlated with old shorelines that are currently submerged, formed after the Last Glacial Maximum (LGM; ~21 ka BP) due to oscillating sea level events. Paleo-shorelines are estimated to be between 17.5 ka and 3 ka old (Kowsmann *et al*., 1977; Corrêa, 1990; Calliari & Klein, 1993). The erosion and reworking of these underwater deposits led to the deposition of biodetrital gravel in some beaches of Rio Grande do Sul. Because these deposits are not time structured, fossils found along beaches present a significant time and spatial mixture, originating from several moments within the Quaternary (Buchmann, 1994; Buchmann & Rincon, 1997; Cruz *et al*., 2016).

In the southernmost portion of the CPRS there is a region known by the occurrence of high concentrations of biodetrital gravel and fossils, forming accumulations known as "*Concheiros do Albardão*" (or Albardão shell deposits) (Richter, 1987; Buchmann *et al*., 2009). This region is highly targeted by studies; however, other regions, such as Hermenegildo beach (Santa Vitória do Palmar, RS) and Cassino beach (Rio Grande, RS), are also fossil-rich (Figure 1).

Recently, Medeiros *et al*. (2023) identified teeth of 13 taxa of fossilized shark from the coast of Rio Grande do Sul. Among them *Carcharhinus brachyurus*, *Carcharhinus leucas*, *Carcharhinus longimanus*, *Carcharhinus* sp., *Carcharias taurus*, *Carcharodon carcharias*, *Galeocerdo cuvier*, *Galeorhinus galeus*, *Isurus oxyrinchus*, *Notorynchus cepedianus*, *Rhizoprionodon* sp., *Sphyrna* sp. and *Squatina* sp. In addition, the taxa *Carcharhinus brachyurus*, *Carcharhinus longimanus*, *Galeorhinus galeus*, *Rhizoprionodon* sp. and *Squatina* sp. were recognized for the first time.

MATERIAL AND METHODS

A total of 26 fossil shark vertebral centra were analyzed, all belonging to the collection of the Laboratório de Geologia e Paleontologia (**LGP**) of the Universidade Federal do Rio Grande (**FURG**) and collected from the current shoreline along the Coastal Plain of Rio Grande do Sul (CPRS), Brazil.

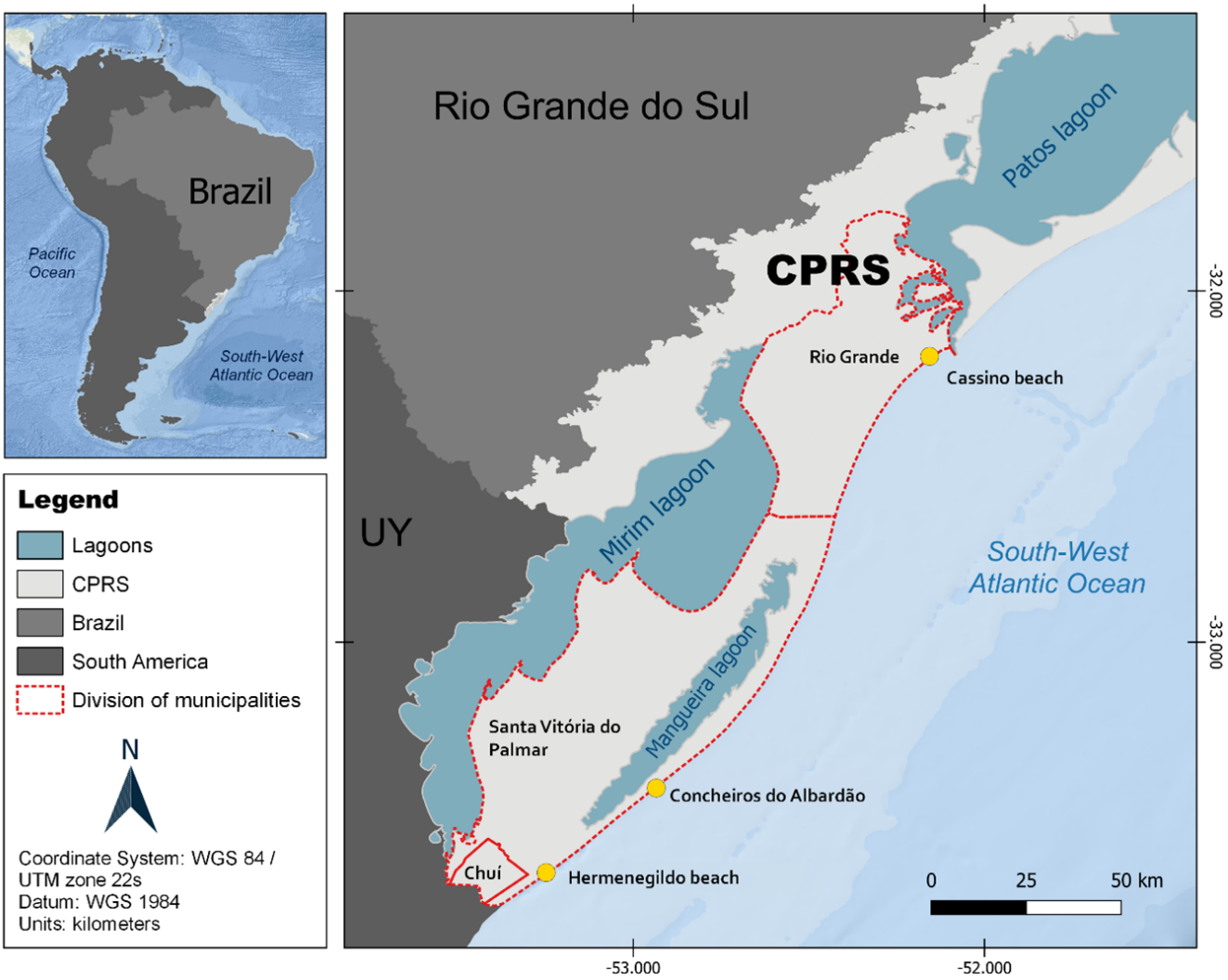

Figure 1. Location map of the study area within the Coastal Plain of Rio Grande do Sul (CPRS, represented in light grey). The study area encompasses a region that stretches between Cassino beach (Rio Grande, RS) and Hermenegildo beach (Santa Vitória do Palmar, RS). Red symbols indicate the location where samples were collected.

In order to describe and identify morphotypes of fossil vertebral centra, 30 modern vertebrae were used for comparison. They were preserved in polyester resin blocks, given that recent material consists of cartilage and can easily be deteriorated. These vertebrae belonged to *Isurus oxyrinchus* (Lamniformes) and *Prionace glauca* (Carcharhiniformes) and were obtained by necropsy of three individuals by the authors (SM and HF). In addition, images and/or photos found in the literature (*e.g.*, Kozuch & Fitzgerald, 1989; Burris, 2004; Lopes *et al*., 2016; Mayer *et al*., 2022) were used for further identification. Morphological terminology used to describe morphotypes followed those proposed by Kozuch & Fitzgerald (1989), Welton & Farish (1993), and Burris (2004) as indicated on Figure 2.

In order to observe the position of the basiventral insertion for the hemal arch without destroying the material, X-ray radiography was conducted using Dr Tech© equipment in all 26 vertebral centra (specimens: LGP/C337, LGP/C338, LGP/C339, LGP/C341, LGP/C342, LGP/C343, LGP/C344, LGP/C345, LGP/C346, LGP/C347, LGP/C348, LGP/C351, LGP/C352, LGP/C353, LGP/C355, LGP/C356, LGP/C357, LGP/C358, LGP/C359, LGP/C360, LGP/C363, LGP/C415, LGP/C434, LGP/C531, LGP/C531 and LGP/C609). In the anterior vertebrae, the basiventral insertions for the hemal arches are positioned more laterally in the centra; however, there is a progressive migration of these insertions to the ventral face of the centrum along the column, following the antero-posterior axis (Figure 3).

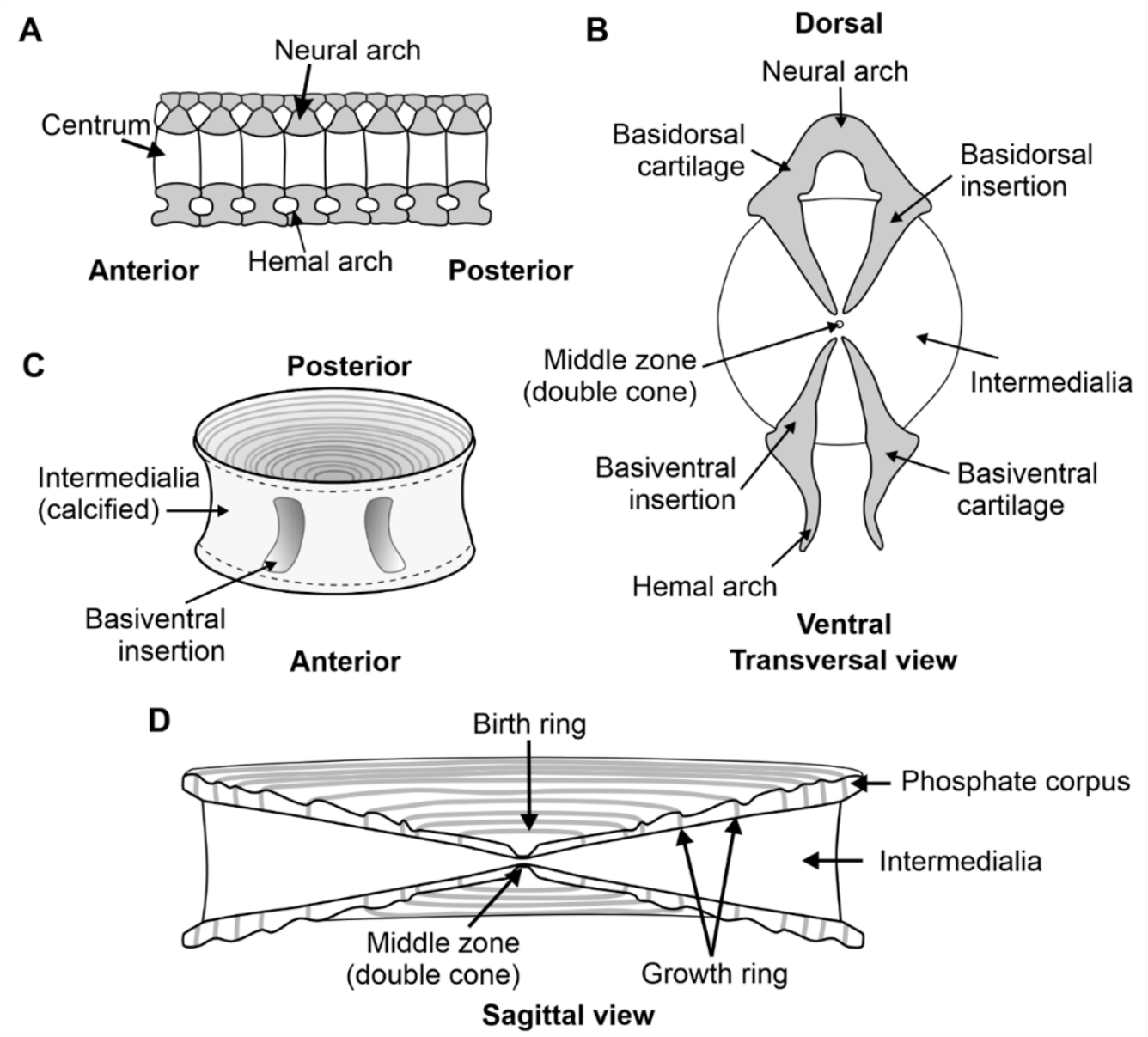

Figure 2. Orientation and terminology of a hypothetical shark vertebral centra including the most common features, adapted from Applegate (1967), Welton & Farish (1993), Burris (2004) and Moreira *et al*. (2019). **A**, left lateral view of a shark vertebral column showing a series of vertebral centra and associated cartilages of neural and hemal arches; **B**, transversal view of a cross sectioned hypothetical anterior caudal vertebra, showing the terminology; **C**, ventral-oblique view of a in; **D**, sagittal cut of a vertebral centrum.

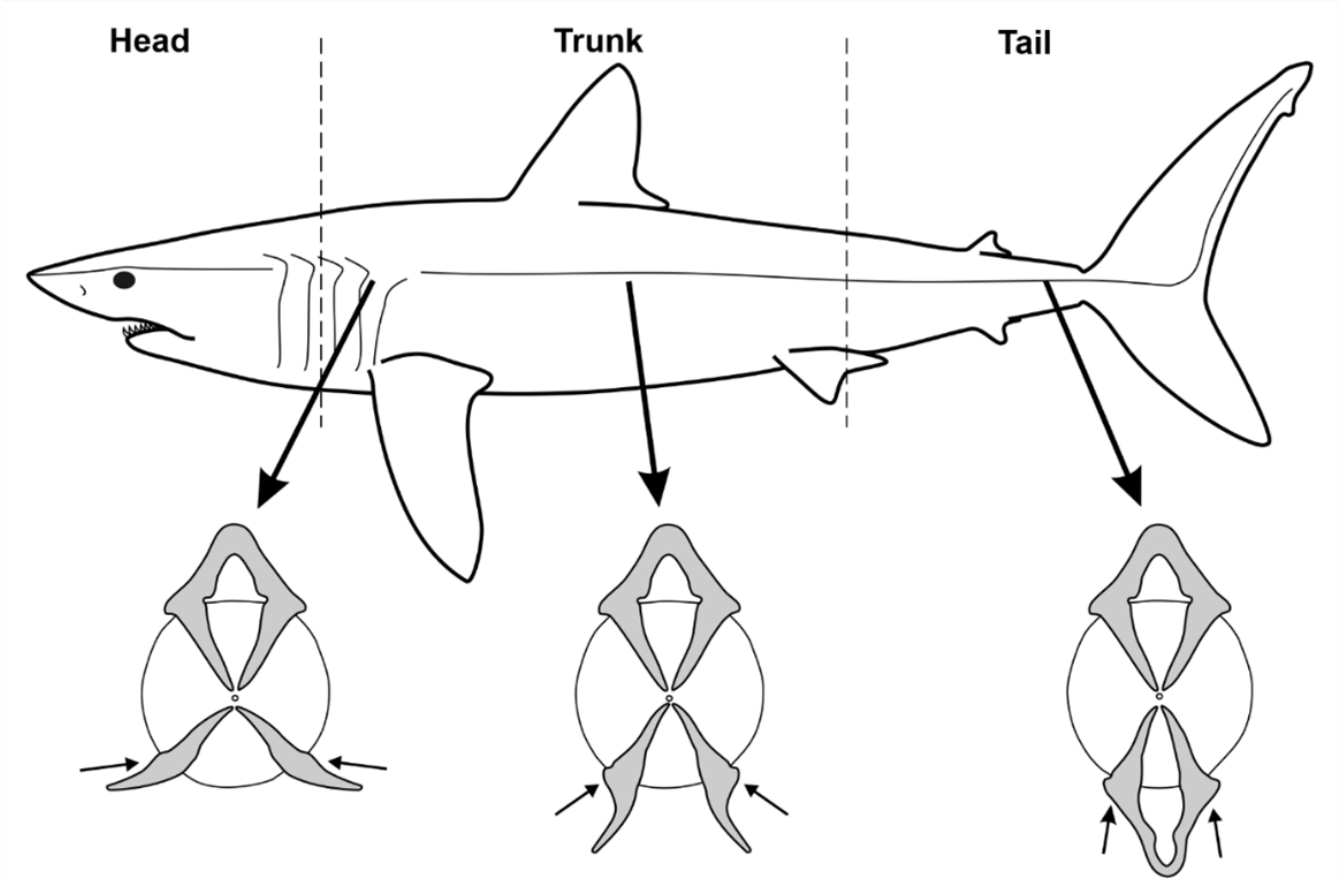

Figure 3. Illustration indicating the progressive ventral migration of the basiventral insertions for the hemal arches in the anteroposterior axis of a hypothetical shark column.

RESULTS

Most of the material presented is well preserved, allowing the identification of morphotypes and their description. However, part of the material exhibited some degree of fragmentation or the presence of attached concretions around the vertebral centra, precluding the identification at a more specific level. Two lineages of sharks were identified: (1) Lamniformes (Lamnoid morphotype), with 17 vertebral centra (65.38%); and (2) Carcharhiniformes (Carcharhinoid morphotype), with eight vertebral centra (30.77%). A single vertebral centrum (3.85%) could not be classified due to its high degree of abrasion and fragmentation.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880
ELASMOBRANCHII Bonaparte, 1838
NEOSELACHII Compagno, 1970
CARCHARHINIFORMES Compagno, 1973
CARCHARHINIDAE Jordan & Evermann, 1896

Carcharhinus Blainville, 1816

Carcharhinus leucas Valenciennes *in* Müller & Henle, 1839
(Figure 4A)

Specimen. LGP/C358.
Description. This vertebral centrum presents a well-defined and spacious phosphatic core and the intermedialia is surrounded by a mineralized band. The basidorsal insertions of the neural arch in the dorsal portion are large and have a rectangular shape, occupying almost the entire intermedialia region. In the ventral portion, the basiventral insertions for the hemal arch follow the same pattern. Throughout the circumference of the mineralized band, there are small pores and striations. The total width of the vertebral centrum is greater than the thickness, thus making this material wide and narrow compared to centra of other species of the same genus (Figure 4A).
Remarks. A single specimen was identified for this species, due to its good state preservation including some diagnostic characteristics. This is the first record of a fossilized vertebral centrum of this species on the southern coast of Brazil, since only fossilized teeth of this species have been identified previously in the region (Lopes *et al*., 2016; Medeiros *et al*., 2023), and also no record of the of this type of material from other regions of Brazil was found in the literature.

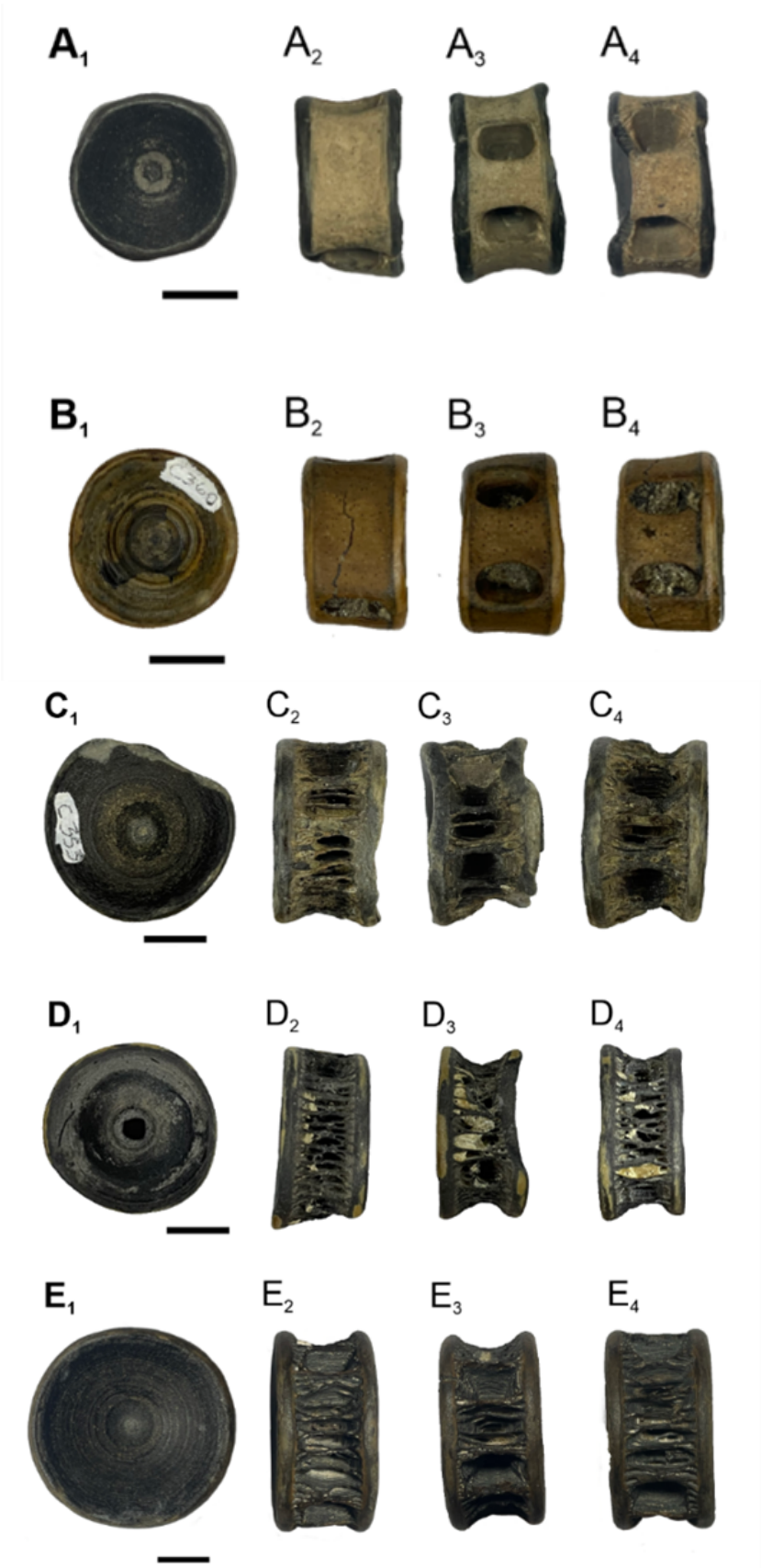

Figure 4. Fossilized vertebral centra of sharks collected in the Coastal Plain of Rio Grande do Sul (Brazil). **A–B**, Carcharhinoid morphotype; **C–E**, Lamnoid morphotype. $\mathbf{A}_{1\text{-}4}$, *Carcharhinus leucas* LGP/C358; $\mathbf{B}_{1\text{-}4}$, *Carcharhinus* indet. LGP/C360; $\mathbf{C}_{1\text{-}4}$, *Carcharias taurus* LGP/C353; $\mathbf{D}_{1\text{-}4}$, *Carcharodon carcharias* LGP/351; $\mathbf{E}_{1\text{-}4}$, Lamniformes indet. LGP/C415. $\mathbf{A}_1$–$\mathbf{E}_1$, anterior and posterior views. $\mathbf{A}_2$–$\mathbf{E}_2$, left lateral view. $\mathbf{A}_3$–$\mathbf{E}_3$, dorsal view. $\mathbf{A}_4$–$\mathbf{E}_4$, ventral view. Scale bars = 10 mm.

Carcharhinus sp. indet.
(Figure 4B)

Specimens. LGP/C342, LGP/C355, LGP/C356, LGP/C359, LGP/C360, LGP/C434, and LGP/C531.
Description. The vertebral centra identified as *Carcharhinus* have a generally well-defined and spacious phosphatic core, and the intermedialia region is surrounded by a mineralized solid band. In the dorsal portion, the basidorsal insertions for the neural arch are long and narrow, and they have a rectangular or oval shape, occupying almost the entire intermedialia region. In the ventral portion, the basiventral insertions for the hemal arch follow the same pattern. Throughout the circumference of the mineralized band, there may or may not be the presence of small pores. The specimens have a total width of the vertebral centrum approximately equal to the thickness, differing from vertebral central attributed to *Carcharhinus leucas* (Figure 4B).
Remarks. The specimens described above were assigned to the genus *Carcharhinus* based on features still present in the material, such as the shape of the vertebral centrum, width, thickness, and the shape of the neural and hemal arch insertions. However, it is not possible to assert whether all of them are conspecific or not. The absence of distinct diagnostic characters and the high morphological similarity of vertebral centra within this group hinder the process of more specific identification.

LAMNIFORMES Berg, 1937
ODONTASPIDIDAE Müller & Henle, 1838

Carcharias Rafinesque, 1810

Carcharias taurus Rafinesque, 1810
(Figure 4C)

Specimens. LGP/C348 and LGP/C353.
Description. The vertebral centra identified for this species have a less thick and less defined phosphatic core, which is surrounded by several thick and well-connected calcified radial lamellae. In dorsal view, there are two large basidorsal insertions for the neural arch that have a rectangular shape and are nearly the size of the vertebral centrum's thickness, extending to the edges of the phosphatic core. The meso-dorsal fenestra has a small opening. In ventral view, the basiventral insertion for the hemal arch have a similar shape to the basidorsal insertion for the neural arch (Figure 4C).
Remarks. The occurrence of vertebral centra from *Carcharias taurus* is noteworthy, as there are no records in the literature of vertebral centra related to this species in the CPRS up to this point. The only fossil record for this species in the region, previously reported in the literature, consists of isolated fossil teeth, as reported by Richter (2000), Buchmann (2002), Cruz *et al*. (2016) and Medeiros *et al*. (2023). However, the presence of fossilized vertebral centra of this species has already been reported in archaeological shell mound sites along the coasts of Rio de Janeiro and Santa Catarina states of Brazil (Lopes *et al*., 2016; Mayer *et al*., 2022). Thus, the specimens described here represent the first fossil record of vertebral centra of this species for the region.

Carcharodon Smith, 1838

Carcharodon carcharias Linnaeus, 1758
(Figure 4D)

Specimens. LGP/C341, LGP/C346, and LGP/C351.
Description. The vertebral centra identified for this species are characterized by a thicker and well-defined phosphatic corpus, surrounded by thin calcified radial lamellae with greater spacing between them. In dorsal view, the basidorsal insertion for the neural arch has a square shape and are smaller than the thickness of the vertebral centrum, therefore, they do not come into contact with the phosphatic core. The meso-dorsal fenestra, located between the basidorsal insertions for the neural arch, has a larger opening. In ventral view, the basiventral insertions for the hemal arch are also smaller than the thickness of the vertebral centrum and have a square outline (Figure 4D).
Remarks. The three vertebral centra described here exhibit a similar morphology, with the presence of well-preserved diagnostic features. The specimens described here represent the first fossil record of vertebral centra of this species for the region, once only fossilized teeth of this species previously identified (Richter, 2000; Buchmann, 2002; Lopes *et al*., 2016; Medeiros *et al*., 2023). However, there are records of fossilized vertebral centra from this species in shell mound archaeological sites along the coast of Rio de Janeiro and Santa Catarina states of Brazil (Lopes *et al*., 2016; Mayer *et al*., 2022).

LAMNIFORMES indet.
(Figure 4E).

Specimens. LGP/C337, LGP/C338, LGP/C339, LGP/C343, LGP/C345, LGP/C347, LGP/C352, LGP/C357, LGP/C359, LGP/C415, and LGP/C609.
Description. These vertebral centra are characterized by a thicker phosphatic body, with the inner part of the double cones surrounded by narrow calcified radial lamella. They present the basidorsal insertions for the neural arch varying in shape and size, and one meso-dorsal foramen in the dorsal portion, located between the two basidorsal insertions for the neural arch. In the ventral portion are located the two basiventral insertions for the hemal arch (Figure 4E).
Remarks. These specimens have a high degree of fragmentation, and many of them are concretioned in their surroundings, which makes it difficult and unfeasible to identify them at the level of species or even of genus. Furthermore, since they were collected individually and without any other associated material (*e.g*., teeth), taxonomic identification becomes uncertain. However, due to the presence of the phosphatic body and radial lamellae, they fit in the Lamnoid morphotype (Applegate, 1967).

BODY LOCATION

The results of the X-ray analyses conducted in 26 vertebral centra allowed to identify, based on inner structures, that 12 of these centra belonged to the thoracic region of the vertebral column (as illustrated in Figure 5A; Table 1), while another ten were assigned to the caudal region (as depicted in Figure 5B; Table 1). The remaining three vertebral centra were categorized as "indeterminate" (Figure 5C; Table 1).

DISCUSSION

The material analyzed in this study represents the first fossil record of Neoselachii vertebra centra found in the study area, given that there are no records in the scientific literature of these fossils for the CPRS. The identification of fossil vertebral centra revealed the presence of two lineages: Lamniformes, which have vertebral centra of the Lamnoid morphotype (Ridewood, 1921; Applegate, 1967; Kozuch & Fitzgerald, 1989; Burris, 2004; Jambura *et al*., 2021), with the highest number of identified specimens, attributed to the species *Carcharias taurus*, *Carcharodon carcharias*, and indeterminate Lamniformes; and Carcharhiniformes, which has vertebral centra of the Carcharhinoid morphotype (Ridewood, 1921; Applegate, 1967; Kozuch & Fitzgerald, 1989; Burris, 2004; Jambura *et al*., 2021), where a low number of vertebral centrum was identified, attributed to the species *Carcharhinus leucas* and indeterminate Carcharhiniformes. The Lamnoid morphotype (LGP/C337, LGP/C338, LGP/C339, LGP/C341, LGP/C343, LGP/C344, LGP/C345, LGP/C346, LGP/C347, LGP/C348, LGP/C351, LGP/C352, LGP/C353, LGP/C357, LGP/C415, LGP/C531 and LGP/C609) was recognized due the presence of thin and radial lamellae around the phosphatic body, typical of Lamniformes sharks. Regarding the Carcharhinoid morphotype (LGP/C342, LGP/C355, LGP/C356, LGP/C358, LGP/C359, LGP/C360, LGP/C434 and LGP/C531) it is recognized due a unique combination of features typical of Carcharhiniformes sharks: an intermedialia region surrounded by a solid mineralized band, the presence of fissures in the intermedialia region, the shape of the phosphatic body (which can be thin or thick, with a round or oval shape), and the shape of basidorsal and basiventral insertions, generally rectangular, but some genera have an oval shape, and often the size of these insertions varies among genera (Ridewood, 1921; Applegate, 1967; Burris, 2004).

The higher abundance of fossil vertebral centra belonging to Lamniformes compared to Carcharhiniformes is also observed in the fossil tooth record of the CPRS (Medeiros *et al*., 2023). However, some studies conducted in other regions along the Brazilian coast have identified fossilized shark vertebrae at the genus/species level and the results indicate an opposite situation, in which there is a predominance of vertebral centra belonging to Carcharhiniformes (Lopes *et al*., 2016; Mayer *et al*., 2022, 2023). In the present study, the majority of identifications were limited to the taxonomic levels higher than genus, with only a few materials identified at the specific level, due to the presence of taphonomic signatures such as fragmentation, abrasion, and the presence of attached concretions, which makes difficult or even unfeasible to identify them at lower taxonomic levels. Additionally, these materials were collected individually throughout the CPRS, without any other associated body parts of the organism (*e.g*., teeth). Currently, there are four lineages (orders) of elasmobranchs (Lamniformes, Carcharhiniformes, Hexanchiformes, and Squatiniformes) identified in the fossil record of the CPRS (Buchmann & Rincon, 1997; Richter, 2000; Buchmann, 2002; Lopes *et al*., 2020; Medeiros *et al*., 2023), and the Lamniformes is the most abundant and representative.

Complementarily, Medeiros *et al*. (2023) described and identified fossil teeth found in the CPRS and based on their identification, it is expected that vertebrae of the Lamnoid morphotype belong to the following species: *Carcharias taurus*, *Carcharodon carcharias*, and *Isurus oxyrinchus*. On the other hand, the Carcharhinoid morphotype should occur in the following taxa: *Carcharhinus brachyurus*, *Carcharhinus leucas*, *Carcharhinus longimanus*, *Carcharhinus* sp., *Galeocerdo cuvier*, *Rhizoprionodon* sp., *Sphyrna* sp., and *Galeorhinus galeus*. The relatively larger fossil record of Lamnoid vertebral centra, compared with fossil teeth of the group Lamniformes, can indirectly indicate a higher occurrence of either populations or taxa of this lineage in comparison to Carcharhiniformes during the Quaternary. Statistically, this can be best observed when percentages of fossil vertebral centra are compared with fossil teeth of the Lamniformes (66.18%) and Carcharhiniformes (22.73%) lineages, as stated by Medeiros *et al*. (2023), presenting a similarity in percentages between these materials.

X-ray images revealed the morphological features described along with inner structures and the distance between hemal arch insertions allowed to identify to which body region these vertebral centra belonged as pointed by several authors (*e.g*., Kozuch & Fitzgerald, 1989; Kardong, 2016; Mayer *et al*., 2022). This distance could be measured in most fossilized vertebral centra found in the CPRS. However, even using X-ray, the body region could not be identified in a small portion of the samples because of loss of morphological features, thus resulting in taphonomic processes and presence of rock around and inside the material. Furthermore, morphological variation between vertebral centra is subtle along the vertebral column, therefore, the transition between thoracic and caudal vertebrae is difficult to determine.

In addition, in both morphotypes, size (width) and robustness of each vertebral centrum varied, some of them being large and thin while others were smaller and thicker. These differences in size and robustness indicate that these materials originate from different groups of Neoselachii (Kozuch & Fitzgerald, 1989) because each taxon, regardless of its morphotype, will have vertebral structural features according to its size and body structure (Ridewood, 1921; Applegate, 1967; Newbrey *et al*., 2015). However, due to loss in diagnostic features caused by the abrasion these materials

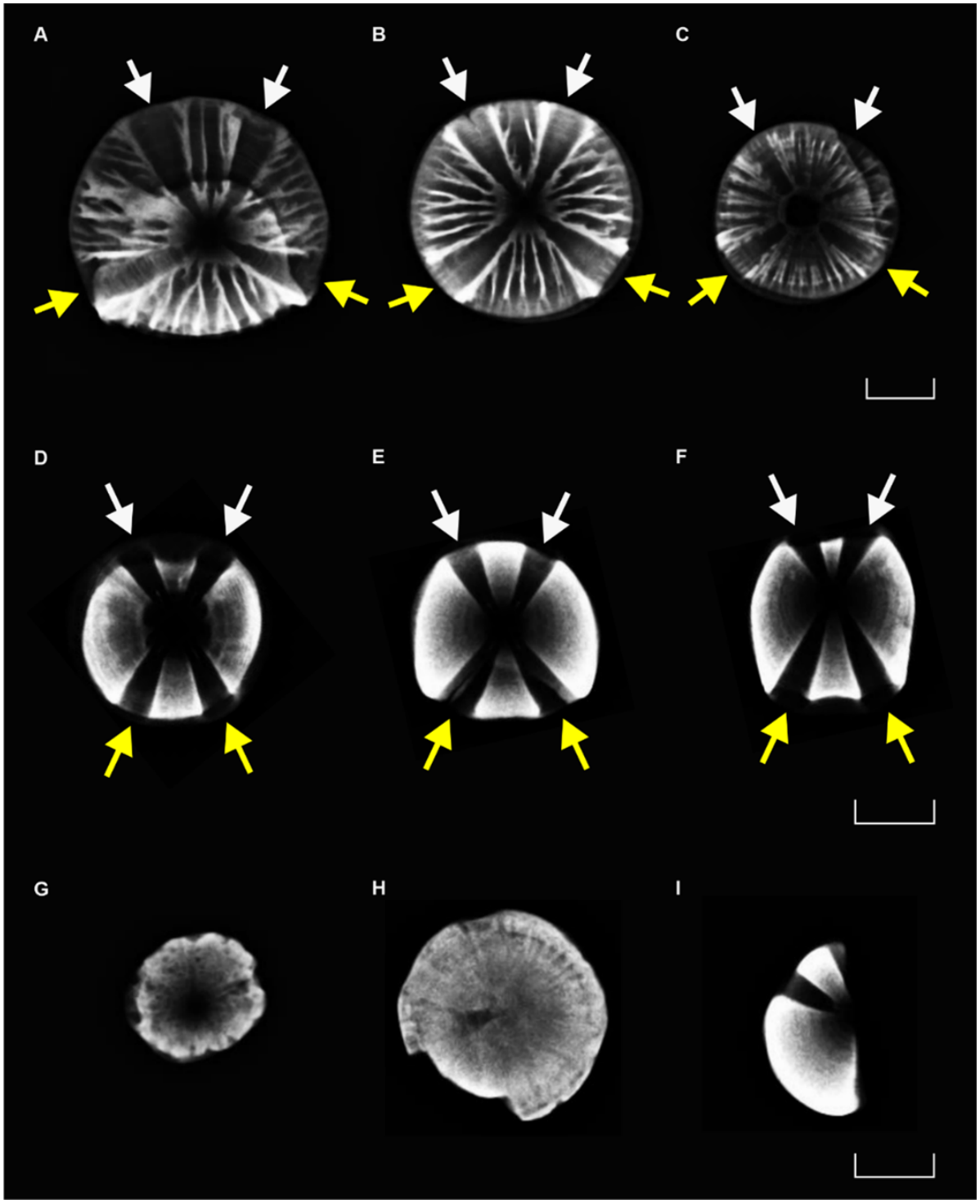

Figure 5. X-ray images of vertebral centra from CPRS. **A–C**, Lamnoid vertebral centra from the thoracic region (LGP/C338, LGP/C415, and LGP/C351); **D–F**, Carcharhinoid morphotype vertebral centra from the caudal region, (LGP/C434, LGP/C358, and LGP/C342); **G–I**, vertebral centra whose body location or inner structures could not be identified (LGP/C344, LGP/C359, and LGP/C356). White arrow indicates basidorsal insertions for the neural arches and yellow arrow indicates basiventral insertions for hemal arches. Scale bars = 10 mm.

Table 1. Fossil shark vertebral centra in relation to the body regions.

Body location	Specimens
Thoracic region	LGP/C337, LGP/C338, LGP/C339, LGP/C343, LGP/C34, LGP/C346, LGP/C347, LGP/C351, LGP/C352, LGP/C357, LGP/C363, LGP/C415, and LGP/C609.
Caudal region	LGP/C341, LGP/C342, LGP/C348, LGP/C353, LGP/C355, LGP/C358, LGP/C360, LGP/C434, LGP/C531, and LGP/C531.
Indeterminate	LGP/C344, LGP/C356, and LGP/C359.

suffered and the interspecific homogeneity of shark vertebrae, a species-level identification using them is unfeasible, thus being restricted to morphotypes.

FINAL REMARKS

Lamniformes and Carcharhiniformes compose most of the neoselachian faunistic diversity of the CPRS, both in modern and ancient ecosystems. Shark fossil vertebral centra present good potential for identification and provide complementary information on the Neoselachii occurrence in the CPRS during the Quaternary. However, the lack of information on the subject is an obstacle to a more precise identification at a species and/or genus level.

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