



## A NEW SYMMORIIIFORM SHARK AND OTHER CHONDRICHTHYAN TEETH FROM THE EARLIEST PERMIAN OF SOUTHERN BRAZIL

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**ABSTRACT** – The Lontras Shale (Itararé Group, Paraná Basin) is a relevant late Paleozoic fossil stratum in western Gondwana known as a *Lagerstätte*, as it presents a great diversity that includes plants, invertebrates, ichnofossils and a rich ichthyofauna, mainly composed by exceptionally well-preserved actinopterygians. The chondrichthyan remains reported here are represented by three isolated teeth, collected in dark gray levels of the Lontras Shale from an outcrop known as Campaleo, located in Mafra municipality, northeastern region of the Santa Catarina State, south Brazil. One of these teeth is considered a new genus and species, which represents the first Brazilian Symmoriiformes species known so far, while the other two are attributed to undetermined Chondrichthyes. These chondrichthyans lived alongside brachiopods, poriferans, conodonts, actinopterygians, and crossopterygian fishes in cold waters of a periglacial environment during the earliest Asselian (Cisuralian, Permian) that represents the terminal stage of the Gondwanan Glaciation.

**Keywords:** Cisuralian, Asselian, Paraná Basin, Campo Mourão Formation, Lontras Shale.

**RESUMO** – O Folhelho Lontras (Grupo Itararé, Bacia do Paraná) é um relevante estrato fossilífero do final do Paleozoico no Gondwana ocidental, conhecido por ser um *Lagerstätte* pela sua grande diversidade que inclui plantas, invertebrados, icnofósseis e uma rica ictiofauna, composta principalmente por actinopterígeos excepcionalmente bem preservados. Restos de condrictes reportados aqui são representados por três dentes isolados, coletados em níveis cinza-escuros do Folhelho Lontras em um afloramento conhecido como Campaleo, localizado no Município de Mafra, região nordeste do Estado de Santa Catarina, sul do Brasil. Um desses dentes é considerado um novo gênero e espécie, que representa a primeira espécie de Symmoriiformes brasileira conhecida até o momento, enquanto os outros dois são atribuídos a Chondrichthyes indeterminados. Estes condrictes viveram junto com braquiópodes, poríferos, conodontes e peixes actinopterígeos e crossopterígeos em águas frias de um ambiente periglacial durante o início do Asseliano (Cisuraliano, Permiano) que representa a fase final da Glaciação Gondwânica.

**Palavras-chave:** Cisuraliano, Asseliano, Bacia do Paraná, Formação Campo Mourão, Folhelho Lontras.

## INTRODUCTION

At the end of the twentieth century, the knowledge on chondrichthyans from the upper Paleozoic strata of Western Gondwana, especially in the Paraná Basin, was limited to a few records (*e.g.*, Silva-Santos, 1947; Barcellos, 1975; Würdig-Maciél, 1975; Ragonha, 1989a, b, 1990; Richter & Langer, 1998), with only three formally described species: *Sphenacanthus gondwanus* (Silva-Santos, 1947), *Xenacanthus pricei* Würdig-Maciél, 1975 and *Xenacanthus santosi* Würdig-Maciél, 1975.

New studies have been published, substantially increasing substantially the number of occurrences of paleozoic chondrichthyans in the Paraná Basin. These occurrences are reported from the following geological units: Lontras Shale (Sedor *et al.*, 2009; Pauliv *et al.*, 2014a), Irati Formation (Chahud, 2018; Chahud & Petri, 2009, 2010a, b, 2012, 2014; Chahud *et al.*, 2010), Teresina Formation (Richter, 2004, 2005, 2007), Corumbataí Formation (Bertini & Toledo, 2008; Campanelli & Fernandes, 2008) and Rio do Rasto Formation (Malabarba *et al.*, 2003; Horn *et al.*, 2009; Laurini *et al.*, 2009, 2010, 2011; Pauliv *et al.*, 2012, 2013, 2014a, b, 2017). As a consequence, the occurrence of at least four higher taxa are now known (Xenacanthiformes, Orodontiformes, Eugeneodontiformes and Sphenacanthidae) and eight species were described: *Wurdigneria obliterated* Richter, 2005; *Tiaraju tenuis* Richter, 2007; *Orodus ipeunaensis* Chahud *et al.*, 2010; *Sphenacanthus sanpauloensis* Chahud *et al.*, 2010; *Sphenacanthus riorastoensis* Pauliv *et al.*, 2012; *Xenacanthus ragonhai* Pauliv *et al.*, 2014; *Triodus richterae* Pauliv *et al.*, 2017; and *Taquaralodus albuquerquei* (Silva-Santos, 1946) redescribed by Chahud & Petri (2010b). Finally, shark coprolites were described by Ragonha (1987) and later by Dentzien-Dias *et al.* (2013).

The aim of the present work is the description of a new genus of a symmoriiform shark, as well as to discuss two undetermined chondrichthyan teeth, all collected at Mafra, Santa Catarina State, in the Campaleo outcrop of the Lontras Shale, Itararé Group, Paraná Basin, which were briefly presented by Sedor *et al.* (2009) and Pauliv *et al.* (2014b). These are the only three chondrichthyan specimens known

so far from the Lontras Shale, as well as the first identified species of this clade from the Itararé Group and the first symmoriiform species from Brazil.

## GEOLOGICAL SETTING

The Paraná Basin is an intracratonic sedimentary basin with almost 1,700,000 km<sup>2</sup> deposited on the South American platform, covering parts of Brazil, Argentina, Paraguay, and Uruguay (Holz *et al.*, 2010). The rocks of this basin were divided by Milani *et al.* (2007) into six supersequences: Rio Ivaí (Ordovician to Silurian), Paraná (Devonian), Gondwana I (Carboniferous to Lower Triassic), Gondwana II (Middle to Upper Triassic), Gondwana III (Upper Jurassic to Lower Cretaceous), and Bauru (Upper Cretaceous).

The Gondwana I Supersequence was deposited under a transgressive–regressive cycle and is subdivided into three groups: the Itararé (glacial to transgressive beds), Guatá (transgressive beds), and Passa Dois Group (regressive beds) following Milani *et al.* (2007). The Itararé Group is comprised of both continental and marine facies, which are mainly composed of clastic lithologies including diamictites and other conglomerates, sandstones, rhythmites, mudstones, shales, and minor coal seams (Holz *et al.*, 2008). The Itararé Group was deposited during the terminal glacial paleoclimatic stage of the Gondwanic Glaciation (Limarino *et al.*, 2014). This unit is considered by Holz *et al.* (2010) to be of late Carboniferous to early Permian age, spanning from the Bashkirian–Moscovian limit to the early Sakmarian.

Historically, the Itararé Group was lithostratigraphically subdivided by many authors, including Schneider *et al.* (1974), França & Potter (1988), Holz *et al.* (2010), and Vesely *et al.* (2021), with some differences between them, as synthesized in Figure 1. Following Holz *et al.* (2010), it is divided into four formations: Lagoa Azul, Campo Mourão, Taciba, and Rio do Sul. However, based on studies of the Itararé Group outcrops in the Paraná State, Vesely *et al.* (2021) proposed another arrangement of the formations: Lagoa Azul, Campo do Tenente, Campo Mourão, and Taciba, and considered the Lontras Shale as an upper member of the Campo Mourão

	Schneider <i>et al.</i> (1974)	França & Potter (1988)	Holz <i>et al.</i> (2010)	Vesely <i>et al.</i> (2021)
Itararé Group	Rio do Sul Formation	Taciba Formation	Taciba Formation Rio do Sul Fm. Suspiro Mb. Rio do Sul Fm. Budó Mb.	Taciba Formation
	Lontras Shale	Lontras Shale	Lontras Shale	Lontras Shale
	Mafra Formation	Campo Mourão Formation	Campo Mourão Formation	Campo Mourão Formation
	Campo do Tenente Formation	Lagoa Azul Formation	Lagoa Azul Formation	Campo do Tenente Formation
				Lagoa Azul Formation

**Figure 1.** Schematic representation of the different proposed lithostratigraphic subdivisions for the Itararé Group according to Schneider *et al.* (1974), França & Potter (1988), Holz *et al.* (2010), and Vesely *et al.* (2021) highlighting the position of the Lontras Shale.

Formation, which agrees with França & Potter (1988) and Weinschütz & Castro (2005, 2006).

The age of the Lontras Shale is also a matter of debate. U-Pb zircon dating for a further south Brazilian locality (which is not directly correlated to Campaleo outcrop) by Cagliari *et al.* (2016) indicated an age of  $307.7 \pm 3.1$  Ma (Moscovian–Kasimovian, Middle–Upper Pennsylvanian) for the upper layers of the Itararé Group in the Rio Grande do Sul State. However, Griffis *et al.* (2018) recalculated this age to  $302.0 \pm 4.9$  Ma (Gzhelian, Upper Pennsylvanian) based on U-Pb single zircon crystal CA-TIMS (chemical abrasion–thermal ionization mass spectrometry) analysis. Based on palynological data and glacial events, Valdez Buzo *et al.* (2019) placed the Lontras Shale on the Kasimovian–Gzhelian boundary (Upper Pennsylvanian), while Valdez Buzo *et al.* (2020) placed it in the Kasimovian. Koester *et al.* (2016) presented a radiometric date of  $287 \pm 10$  Ma (Artinskian, Cisuralian) for the Lontras Shale itself based on the analysis of clay minerals Rb-Sr content of the Campaleo outcrop. Based on the *Vittatina costabilis* palynological biozone, the Lontras Shale seems to be Cisuralian (Permian) just above the Carboniferous–Permian boundary (*e.g.*, Souza & Marques-Toigo, 2003, 2005; Souza, 2006; Holz *et al.*, 2008; 2010; Iannuzzi, 2013). Based on the presence of the conodont *Mesogondolella*, Wilner *et al.* (2016) also considered the Lontras Shale as Cisuralian. Therefore, the stratigraphic and geochronological positions of the Lontras Shale and the Campaleo outcrop remain disputed. A simplification of the age based on traditional palynology and conodont dating is used in this work, and therefore the Lontras Shale is considered as earliest Permian.

The fossils presented here were collected in the Lontras Shale, interpreted as marine transgressive facies of the Itararé Group related to the deglaciation process (Weinschütz & Castro, 2005; Vesely & Assine, 2006), corresponding to the maximum flooding surface of the entire glacial sequence of this group (França & Potter, 1988; Holz *et al.*, 2008). Consequently, this shale is considered a *datum* in some attempts to correlate outcrop and well cores mostly based on its palynological content (Holz *et al.*, 2008). This shale was mainly deposited in very quiet and dysoxic environmental conditions, as evidenced by the absence of current-driven preferential disposition of skeletons and by a very high total organic matter content respectively (Hamel, 2005), and the organic matter had mixed marine and terrestrial origin, with a marine dominance (Mouro *et al.*, 2017). Recently, Saldanha *et al.* (2023) pointed to a temperate external paleofjord environment for the Lontras Shale at the Campaleo outcrop, including both near coast and deeper conditions, mainly based on the revision of faunal content, geological features and new taphonomical data. The dysoxic floor conditions were probably related to increased productivity caused by relatively higher temperatures during deglaciation, marine transgression, and the increased input of nutrients from the land. The long-lasting periods of anoxia resulted in the exclusion of potential scavengers and bioturbators (Mouro *et al.*, 2017). These conditions combined with the cold temperatures of the

glacial paleoclimate probably slowed down the local bacterial activity during the sediment deposition that produced this shale (Hamel, 2005) and permitted exceptional preservation of specimens (including soft tissues and whole articulated specimens), which led to a *Konservat-Lagerstätte* status for the Campaleo site (Mouro *et al.*, 2020; Saldanha *et al.*, 2023). Despite these particular conditions, some fossils in this shale are found isolated and disarticulated including the shark specimens described here. Following Hamel (2005), Mouro *et al.* (2017) and Saldanha *et al.* (2023), this disarticulation might have been caused by episodic turbidity currents (evidenced by diamictites and rhythmites) that mechanically dispersed some skeletal elements and rapidly buried them together with more complete specimens. These turbidity currents also caused mass mortality of organisms by the abrupt saturation of sediments in the water column (Richter, 1991; Saldanha *et al.*, 2023) and by the production of sulfidric acid (a result of the bacterial decomposition process) that accumulated on the sea floor (Hamel, 2005). These dysoxic conditions allowed for pyrite formation which is common in/on the fossils (Hamel, 2005).

## FOSSIL DIVERSITY OF THE LONTRAS SHALE

The diversity of the Lontras Shale includes: palynomorphs (*e.g.*, Dino & Rösler, 2001; Holz *et al.*, 2008); wood fragments (*e.g.*, Gnaedinger *et al.*, 2012; Urban *et al.*, 2012); ichnofossils (*e.g.*, Balistieri *et al.*, 2002); exceptionally preserved invertebrates such as complete sponges, scolecodonts, brachiopods, bivalves, crustaceans, and insects (*e.g.*, Ruedemann, 1929; Oliveira, 1930; Pinto & Sedor, 2000; Adami-Rodrigues *et al.*, 2011; Mouro *et al.*, 2011, 2014, 2016, 2017, 2020; Ricetti *et al.*, 2012, 2016; Simões *et al.*, 2012) and vertebrates mostly represented by actinopterygians, but also sarcopterygians, conodonts and chondrichthyans. The actinopterygian fauna includes *Santosichthys mafrensis* Malabarba, 1988, *Roslerichthys riomafrensis* Hamel, 2005, *Irajapintoseidon uruguayensis* Beltan, 1975, *Daphnaechelus* sp., as well the actinopterygian fishes reported by Richter (1991, 2004) and Figueroa *et al.* (2018). Isolated sarcopterygian scales reported by Richter (1991) were later identified as *Coelacanthus* sp. by Richter (2004). Conodonts are represented by several associated feeding apparatus arranged in parallel and perpendicular planes that were preliminarily attributed to *Mesogondolella* spp. (Wilner *et al.*, 2016). The chondrichthyan remains were briefly reported by Sedor *et al.* (2009) and Pauliv *et al.* (2014a), mentioned in Mouro *et al.* (2020) and Saldanha *et al.* (2023), and are detailed in the present contribution.

**Institutional abbreviations.** CENPALEO-UNC, Centro de Paleontológico da Universidade do Contestado, Mafra, Santa Catarina State; CP, Coleção Paleontológica, Universidade do Contestado, Mafra, Santa Catarina State; LaFMA-UFPR, Laboratório de Foraminíferos e Micropaleontologia Ambiental, Universidade Federal do Paraná, Curitiba, Paraná State, Brazil; LAMIR-UFPR, Laboratório de Análise de

Minerais da Universidade Federal do Paraná, Curitiba, Paraná State, Brazil; **MCN.P.**, Coleção de Paleontologia do Museu de Ciências Naturais do Setor de Ciências Biológicas da Universidade Federal do Paraná, Curitiba, Paraná State, Brazil; **MCN-SCB-UFPR**, Museu de Ciências Naturais do Setor de Ciências Biológicas da Universidade Federal do Paraná; **LM-UP**, Laboratório de Microtécnica da Universidade Positivo, Curitiba, Brazil.

## MATERIAL AND METHODS

The studied material, consisting of three isolated shark teeth, is housed in the collection of CENPALEO-UNC with the numbers CP-142 (a–b) and CP/E-2995, and in MCN-SCB-UFPR with the number MCN.P.1077 (a–b). They were collected in dark gray shales attributed to the Lontras Shale, which belongs to the uppermost portion of the Campo Mourão Formation according to França & Potter (1998), Weinschütz & Castro (2005, 2006) and Vesely *et al.* (2021). The specimens were recovered from an outcrop known as the Campaleo site (Mouro *et al.*, 2016, 2017, 2020; Ricetti *et al.*, 2016; Saldanha *et al.*, 2023), located near the margin of the BR-280 federal highway, Municipality of Mafra, northeastern of the Santa Catarina State, coordinates 26°09'29.29" S, 49°48'51.95" W (Figure 2). For a detailed lithological profile of the Campaleo site, see Ricetti *et al.* (2016).

The specimens were prepared under a stereomicroscope using mechanical techniques with steel tips and impregnated with polystyrene dissolved in xylol to increase the fossil resistance. All specimens were photographed with an Olympus SZX9 stereomicroscope at LM-UP and with Zeiss Discovery V20 stereomicroscope at LaFMA-UFPR. The

anatomical terminology used follows Ginter *et al.* (2010, figs. 1B–C).

Because of the difficulty in preparing and extracting the fossils from the rock due to their fragility and rareness, and to avoid damage to the specimens, there was an attempt to analyze them via CT-scan at the LAMIR-UFPR using Skyscan 1172 microscan, but unfortunately, this analysis was inconclusive, because both matrix and fossil present similar x-ray opacity under the limits of the equipment used, which is probably due to a high concentration of pyrite as Mouro *et al.* (2020) has demonstrated.

## SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Superorder CLADODONTOMORPHI Ginter, Hampe & Duffin, 2010

Order SYMMORIIFORMES Zangerl, 1981

Family ?SYMMORIIDAE Dean, 1909

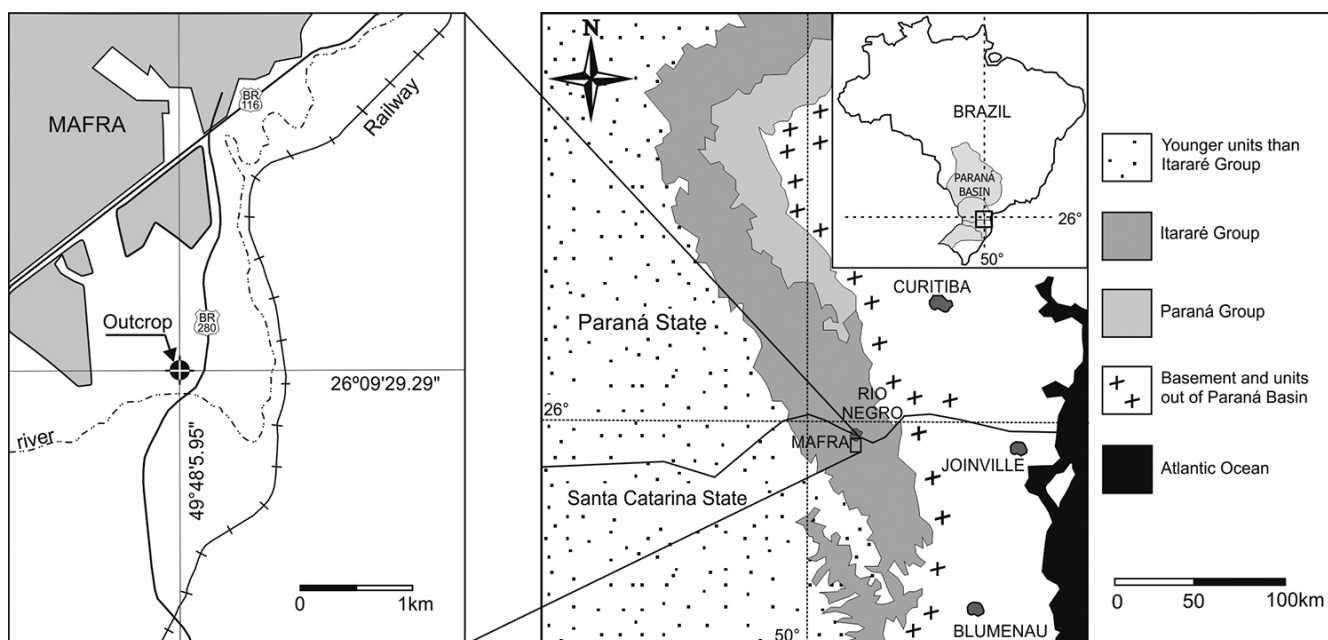
*Crioselache* gen. nov.

urn:lsid:zoobank.org:act:5A34C71B-746E-444D-A4EF-4ED5C21CFDFA

**Type species.** *Crioselache wittigi* sp. nov.

**Etymology.** From Gr. *kryos* = cold, ice + *sélakhos* = cartilaginous fish, in reference to the cold waters that this shark lived in during the Carboniferous–Permian glaciation/ deglaciation that resulted in the deposition of the Itararé Group.

**Diagnosis.** As for the species by monotypy.



**Figure 2.** Location of the Campaleo outcrop in the Municipality of Mafra and distribution of the Itararé Group in the Paraná and Santa Catarina states. Modified from Weinschütz & Castro (2005).

*Crioselache wittigi* gen. et sp. nov.

urn:lsid:zoobank.org:act:87BAF42D-237A-4A37-B837-1ED48452CFEC

(Figure 3)

**Etymology.** In honor of the neurologist and paleontology enthusiast Prof. Dr. Ehrenfried Othmar Wittig, who collected and recognized this fossil as a shark tooth.

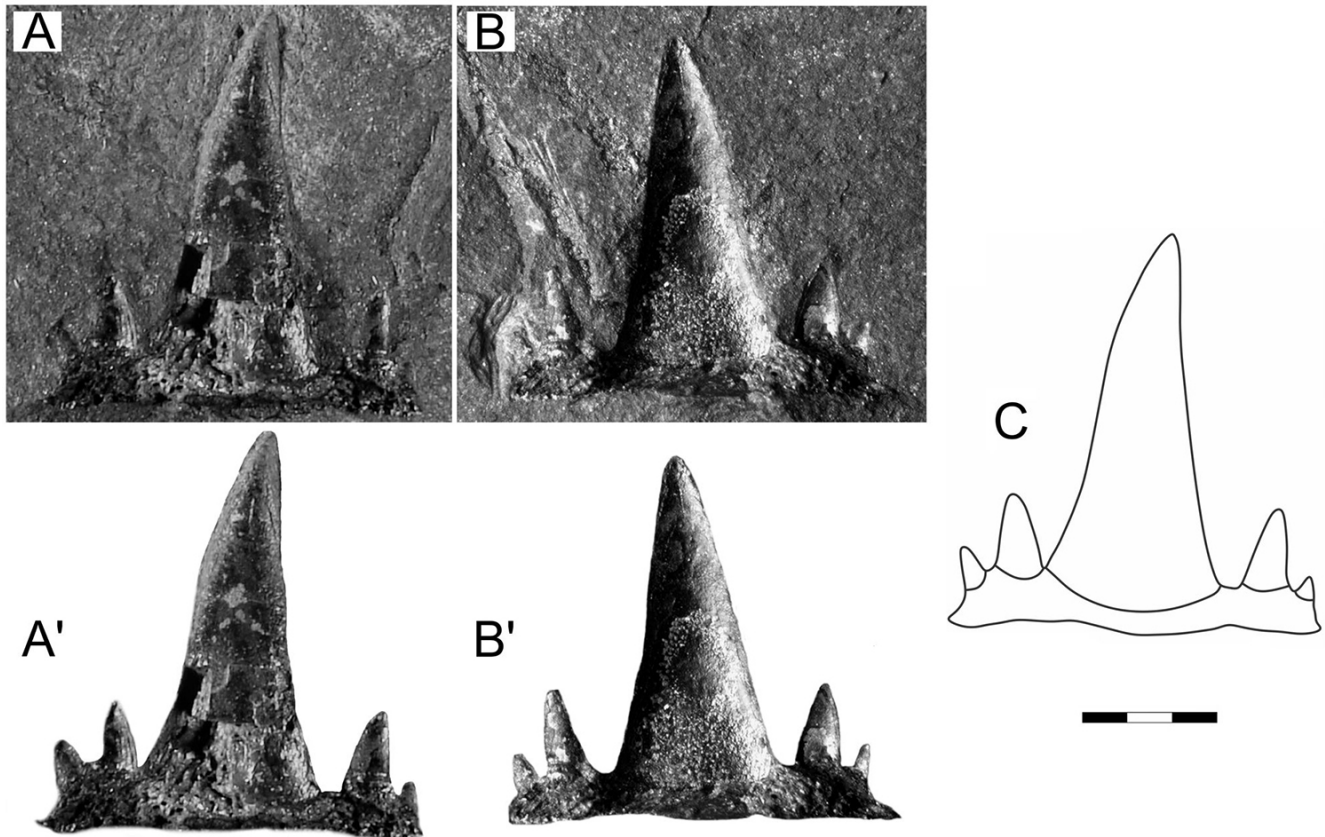
**Holotype.** CP-142, part and counterpart of an isolated tooth.

**Type-locality and horizon.** Campaleo site, Mafra Municipality, northeastern region of Santa Catarina State, Brazil (Figure 2), coordinates 26°09'29.29" S, 49°48'51.95" W, Lontras Shale, uppermost portion of the Campo Mourão Formation according to França & Potter (1998), Weinschütz & Castro (2005, 2006) and Vesely *et al.* (2021).

**Diagnosis.** A symmoriiform shark only known from an isolated tooth, distinguished from other species of this clade by the following unique combination of characters: tooth with a mesio-distally broad base with a single basolabial projection on its aboral-labial margin and five cusps on its oral-labial margin; median cusp taller than the others and laterally flanked by four accessory cusplets (two on each side), in which the innermost cusplets are taller than the outermost; median cusp with a smooth surface, while the accessory cusplets presents longitudinal and discontinuous smooth cristae; labiolingually

compressed median cusp with two smooth lateral carinae on its lateral edges.

**Description.** The specimen CP-142 (a–b) corresponds to a part and counterpart of a tooth with only its labial side visible which has a broad base, 9.2 mm in width (mesio-distally) and 9.8 mm in height (Figure 3). On the border between the labial and the aboral portion, the base presents a small basolabial projection, which is single and slightly smaller mesio-distally than the base of the median cusp, while the orolabial margin of the base has a crown with five cusps. The median cusp is bigger than the others, measures 9.0 mm in height and with its base occupying about a half of the tooth base width. This cusp has a smooth surface, without evidence of longitudinal cristae, being slightly distally curved and labiolingually compressed, forming two carinae on its lateral edges, without evidence of serrations. In lateral view, this cusp has a slightly sigmoidal curvature, being projected labially in its proximal third, lingually curved in its median third and very smoothly curved labially in its distal third. The median cusp is laterally flanked by four accessory cusplets (two on each side), all positioned along the labial margin of the base, in which the mesial cusplet pair measures 2.1 mm and 1.2 mm in height (innermost and outermost cusplet, respectively), while the distal pair measures 2.3 mm and 0.8 mm. Therefore, the innermost cusplets are taller than the outermost. The surface



**Figure 3.** Holotype of *Crioselache wittigi* gen. et sp. nov. (CP-142). A, part; B, counterpart; A' and B', photograph of corresponding view in which the rock matrix has been digitally removed; C, schematic outline drawing. Scale bars = 3 mm.

of these accessory cusplets presents some longitudinal and discontinuous smooth cristae.

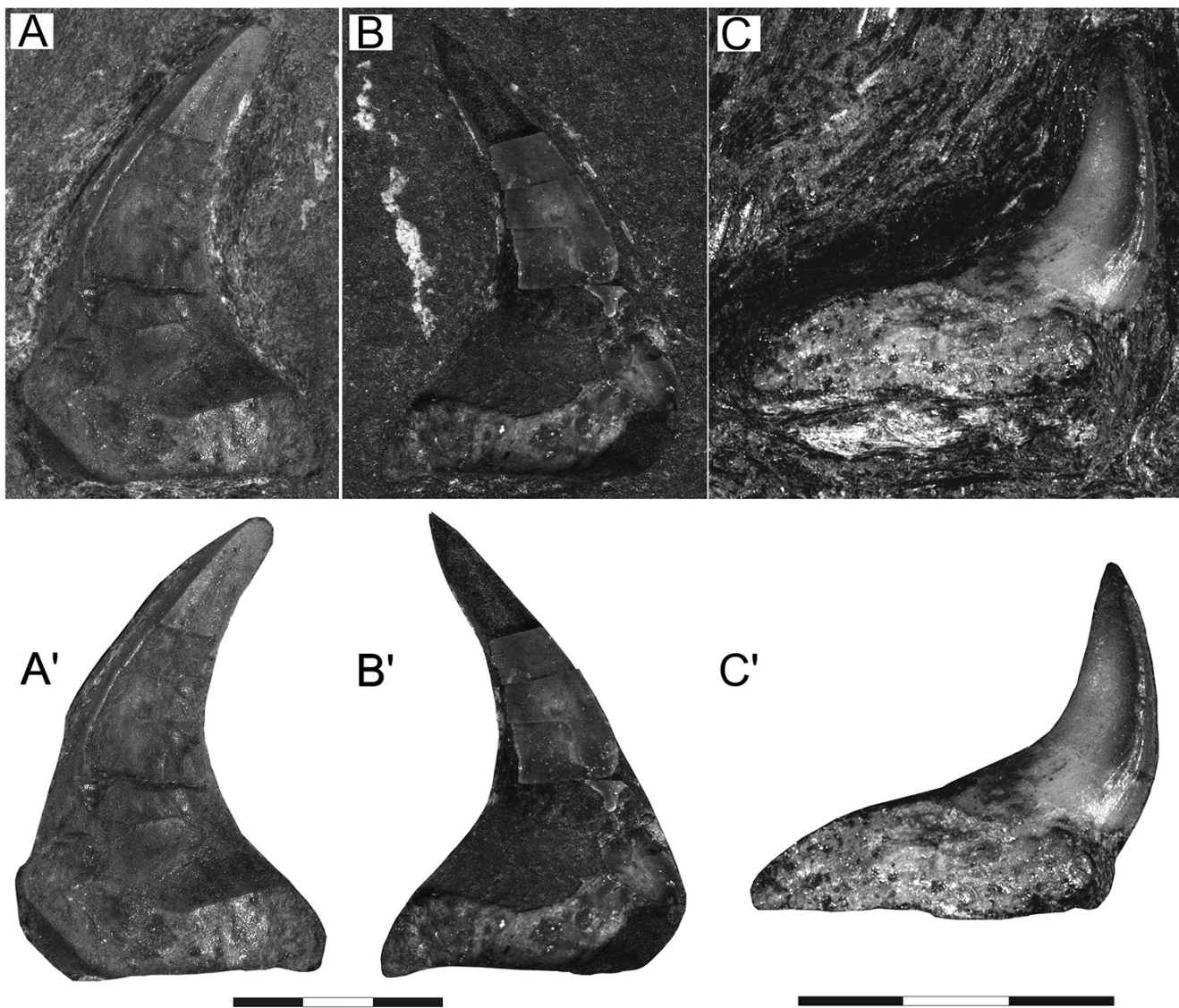
*Chondrichthyes incertae sedis*  
(Figure 4)

**Material.** MCN.P.1077 (a–b), isolated tooth (Figures 4A, B); CP/E-2995, isolated tooth (Figure 4C).

**Description.** The specimen MCN.P.1077 (a–b) is represented by part and counterpart of an isolated tooth preserved in lateral view, measuring 6.7 mm in height and 4.0 mm labiolingually (Figures 4A, B). The base of this tooth is relatively narrow labiolingually, without a lingual projection, coronal button, or basal tubercle, having a flat aboral surface. The visible portion of the base presents only one cusp that is strongly curved lingually, measuring 5.5 mm in height. This cusp has a

marked lateral carina on its distal third, while on its proximal third at least six smooth cristae are present. A small lateral portion of the base is preserved on the counterpart as well as the medial third of the cusp.

The specimen CP/E-2995 is preserved in lateral view, measuring approximately 3.7 mm in height and 3.9 mm labiolingually (Figure 4C). This specimen has a broad base that is lingually elongated, without any evidence of a coronal button. The aboral portion of the base is relatively flat, with a smooth concavity. This tooth has only one visible cusp, labially placed on the tooth base, measuring almost 2.5 mm in height. This cusp is strongly curved lingually, almost smooth and presents a strong lateral carina without any evidence of serrations. This carina runs from the most apical portion down to its proximal portion, dichotomizing proximally.



**Figure 4.** *Chondrichthyes incertae sedis*. A, Specimen MCN.P.1077, part; B, counterpart; C, Specimen CP/E-2995. A'–C', photograph of corresponding specimens in which the rock matrix has been digitally removed. Scale bar = 3 mm.

## DISCUSSION

Symmoriiformes is a clade of fossil chondrichthyans well known from isolated teeth and denticles, but also from partially complete and complete specimens, including those described by Lund (1974, 1984, 1985a, b, 1986) from the Bear Gulch Limestone, Montana (U.S.A.), as well as Sequeira & Coates (2000) and Coates & Sequeira (2001) from Scotland, contrasting with most of the other Paleozoic shark groups, which are mainly known from isolated teeth or spines.

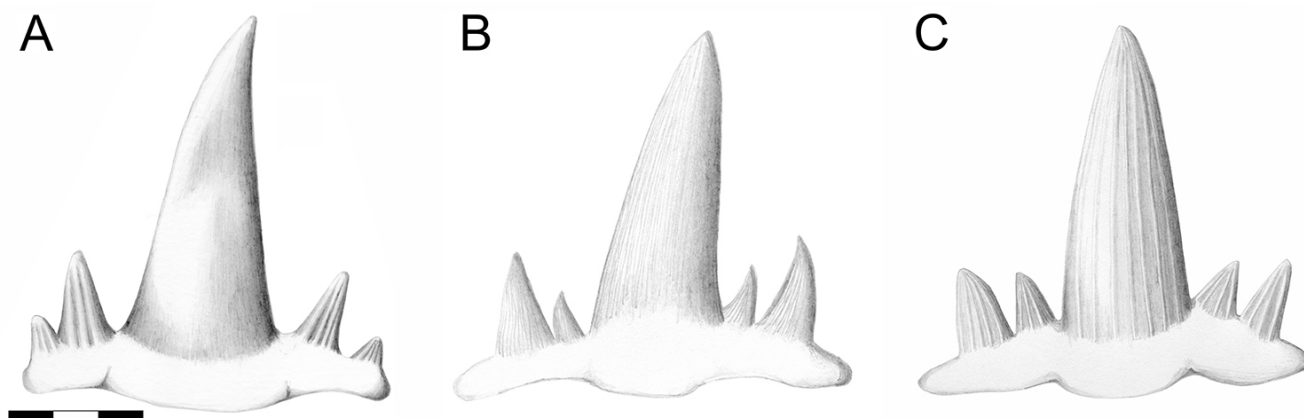
The most remarkable feature found in many symmoriiform genera, found primarily in males, is the presence of its distinctive “spine-brush complex”, a modification of the first dorsal fin, as seen in *Stethacanthus* Newberry, 1889, *Orestiacanthus* Lund, 1984, *Falcatus* Lund, 1985, *Damocles* Lund, 1986 and others. This group is also characterized by its distinctive teeth with a cladodont design. According to Ginter *et al.* (2010), symmoriiform teeth are characterized by a suit of features seen in labial view that includes: a biconvex median cusp (except large teeth of *Symmorium reniforme* Cope, 1893, in which it is labially flattened); shallow or complete absent basolabial depression; single basolabial projection usually no wider (mesio-distally) than the base of the median cusp. All these features are present in *Crioselache wittigi* gen. et sp. nov., which allows its assignment to Symmoriiformes.

Following Ginter *et al.* (2010) and Ginter (2018), the Symmoriiformes are subdivided into two families: the Symmoriidae Dean, 1909, which are represented by *Stethacanthus* Newberry 1889, *Symmorium* Cope, 1893, *Orestiacanthus* Lund, 1984, and *Cobelodus* Zangerl, 1973; and the Falcatidae Zangerl, 1990, which includes *Danaea* Pruvost, 1922, *Falcatus* Lund, 1985, *Damocles* Lund, 1986, *Stethacanthulus* Zangerl, 1990, and *Ozarcus* Pradel *et al.*, 2013. Another two genera are attributed to Symmoriiformes, *Kawichthys* Pradel *et al.* (2011) and *Kunguroodus obliquus* Ivanov (2016), but both are classified as *Incertae sedis* at the familial level.

According to Ginter (2018) the Symmoriiformes are distributed from the Fammenian (Upper Devonian) to Capitanian (Guadalupian, Permian). Nevertheless, the occurrence of a unique tooth attributed to Falcatidae indet. described by Guinot *et al.* (2013) from an outer platform deposit of the latest early Valanginian (Early Cretaceous) of France, extended the range of this clade by nearly 120 Ma. Guinot *et al.* (2013) suggested that the 120 Ma fossil gap in this group could be related to the occupation of a refuge environment (such as the deep-sea) during the long-lasting hostile environmental conditions in the post-Permian neritic habitats and by the scarcity of known deep-sea vertebrate assemblages from this time interval. Ginter (2018) considered this occurrence dubious, stating that the specimen described by Guinot *et al.* (2013) resembles those of Falcatidae (see Ginter *et al.*, 2010, p. 64–67), suggesting an affinity with this family or a remarkable morphological convergence.

Notwithstanding, the fact that dental features seem to be of little help for distinguishing Symmoriidae from Falcatidae (Ginter *et al.*, 2010), *Crioselache wittigi* gen. et sp. nov. closely resembles two genera within the Symmoriidae: *Symmorium* and *Stethacanthus*. A comparison with these genera is presented in Figure 5 and detailed below.

*Symmorium* has only one valid species, *Symmorium reniforme* Cope, 1893, described from the Moscovian (Middle Pennsylvanian, Carboniferous) of Illinois and Indiana, U.S.A., based on several partially articulated skeletons (*e.g.*, Cope, 1893; Williams, 1985). Whereas *Stethacanthus* is known from the Famennian up to the Gzhelian (Upper Devonian to Upper Pennsylvanian, Carboniferous) of Scotland (*e.g.*, Sequeira & Coates, 2000; Coates & Sequeira, 2001; Ginter *et al.*, 2010) and the U.S.A. in Montana, Nebraska, Ohio, Illinois, Iowa, and Oklahoma (*e.g.*, Lund, 1974; Williams, 1985; Zidek, 1993, Ginter *et al.*, 2010; Ginter, 2018). According to Ginter *et al.* (2010) and Ginter (2018), this genus has three valid species: *Stethacanthus altonensis* (St. John & Worthen, 1875) (probable synonym: *Akmonistion zangerli* Coates & Sequeira, 2001), *Stethacanthus neilsoni* (Traquair, 1898) (= *Gutturensis*



**Figure 5.** Comparison between *Crioselache wittigi* gen. et sp. nov. with other Symmoriidae. **A**, Interpretative reconstruction of *Crioselache wittigi* gen. et sp. nov. in labial view. Scale bar = 3 mm; **B**, *Symmorium*: based on *Symmorium reniforme* Cope, 1893 FMNH UF 574 (Field Museum of Natural History, Chicago, Illinois, USA) after Ginter *et al.* (2010 fig. 56); **C**, *Stethacanthus*: based on *Stethacanthus neilsoni* (Traquair, 1898) NMS 1911.62.521 (National Museum of Scotland, Edinburgh, Scotland) after Ginter *et al.* (2010, fig. 58). **B–C**, not to scale. Drawing by Nadaline, M.J.

*neilsoni* Sequeira & Coates, 2000) and the recently described *Stethacanthus concavus* Ginter, 2018. Comparing *Symmorium* and *Stethacanthus* with *Crioseleche wittigi* gen. et sp. nov., they share a very similar tooth morphology, mainly in the base shape, with a well-distinguished basolabial projection and a slight sigmoidal curvature of the median cusp in lateral view, which is seen in *Stethacanthus* and in the new Brazilian species. *Symmorium* and *Stethacanthus* exhibit an outermost pair of accessory cusplets that are always bigger than the innermost pair and have several narrowly spaced longitudinal cristae on all cusp surfaces, whereas *Crioseleche wittigi* gen. et sp. nov. lacks these cristae on the median cusp and the outermost pair of cusplets are smaller than the innermost ones.

Another Brazilian symmoriiform occurrence was reported by Barcellos (1975) from the Bagé Municipality, Rio Grande do Sul State, also from the Itararé Group, but from a younger unit, the Budó Member of the Rio do Sul Formation (see Figure 1), with an age between the late Asselian and the early Sakmarian (Holz *et al.*, 2010). This occurrence is represented by an impression of a complete tooth preserved in labial view, measuring 5.0 mm in height and almost 4.1 mm in width (mesio-distally), presenting the typical symmoriiform pattern: a broad base with a conspicuous basolabial projection and a crown with five cusps, in which the median cusp is taller and flanked by two pairs of cusplets (see Barcellos 1975, fig. 15). All cusps are elongated and slender. The median cusp is almost 4.2 mm tall, showing marked longitudinal smooth cristae mainly at the base, while the outermost pair of cusplets are almost twice higher than the innermost pair, with no evidence of longitudinal cristae. Barcellos (1975) mentioned that this tooth impression closely resembles those of *Danaea*, matching with the teeth descriptions of this genus. Unfortunately, this specimen seems to have been lost, precluding new comparisons.

Another Brazilian undetermined symmoriiform was described by Duffin *et al.* (1996) from the uppermost Bashkirian–Moskavian (Pennsylvanian, Carboniferous) (following Cunha *et al.*, 2007) Itaituba Formation of the Amazon Basin (northern Brazil). It corresponds to an isolated fragmentary tooth missing one of its lateral cusplets, comprising a broad base lingually extended with a multi-cusped crown placed in its labio-coronal portion (see Duffin *et al.*, 1996, figs. 7a–c). The preserved portion of the crown has a large median cusp laterally flanked by three cusplets, in which the median cusplet is larger than the other two cusplets. All these cusplets have longitudinal and non-bifurcated cristae on both labial and lingual surfaces, but their extent is not evident. These features allowed Duffin *et al.* (1996) to ascribe this specimen to ?*Danaea* sp. Nevertheless, a similar crown pattern also occurs in the genus *Stethacanthulus*.

Concerning the other two undetermined specimens described here, their fragility does not allow better preparation and consequently, precludes the exposure of additional diagnostic features and a more precise identification. As previously mentioned, specimen CP/E-2995 (Figure 4C) has a labiolingually elongated base, described as aulacorhize by Ginter *et al.* (2010), which occurs in chondrichthyan stem-

groups including the Phebodontiformes, Bransoneliiformes, Xenacanthiformes, Cladoselachiformes, Symmoriiformes, Ctenacanthiformes and Squatinactiformes. On the other hand, specimen MCN.P.1077 (Figure 4A, B) presents a relatively narrow base (labiolingually), without a lingual projection or basal tubercle, and with a flat aboral surface, which is compatible with anaulacorhize (“euselachian base”) as defined by Ginter *et al.* (2010). Following these authors, this kind of base is a synapomorphy of the crown-group of Chondrichthyes, which includes the Hybodontiformes, Neoselachii, Euselachii *incertae sedis*, such as the Sphenacanthidae and the Euchondrocephali (that includes the Eugeneodontiformes, Orodontiformes, Petalodontiformes and Holocephali). Therefore, as these two specimens (CP/E-2995 and MCN.P.1077) do not allow an in-depth discussion from both systematic and paleoecological point of views, this discussion is focused on the occurrence of the new Symmoriiformes *Crioseleche wittigi* gen. et sp. nov.

These are the first occurrences of chondrichthyans in the Lontras Shale, as well as the oldest record of Symmoriiformes for the Paraná Basin. The scarceness of symmoriiform teeth or any other cladodontomorph teeth in the Lontras Shale, could be the result of species rarity or could be related to a possible long-term tooth retention and lower rates of tooth replacement. Some cladodont sharks, including the two Symmoriiformes *Symmorium* and *Stethacanthus*, present this type of tooth retention and replacement as suggested by Williams (2001). It is possible that the same pattern also occurred in *Crioseleche wittigi* gen. et sp. nov. as these two genera closely resembles the new species.

The new chondrichthyan remains described from the Lontras Shale of the Campo Mourão Formation, Itararé Group, Paraná Basin (earliest Asselian age, earliest Permian) include the first species of Symmoriiformes described from Brazil, *Crioseleche wittigi* gen. et sp. nov and two Chondrichthyes *incertae sedis*. These sharks lived in the cold marine waters of a temperate periglacial paleofjord environment.

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