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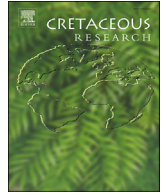
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Before and after the K/Pg extinction in West Antarctica: New marine fish records from Marambio (Seymour) Island



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ABSTRACT

An ichthyofauna recovered from the López de Bertodano Formation at Units 9 (uppermost Maastrichtian) and 10 (lowermost Danian) and the Sobral Formation (Danian), in Marambio (Seymour) Island in the James Ross Basin is described and analyzed herein. A review of previously described taxa based on the new material and several new fish records for the López de Bertodano Formation is provided, including the youngest record of *Enchodus* and the first Cretaceous evidence of Pachycormiformes. We also identify the first Paleocene fishes for the continent. The new information and the reinterpretation of previous Cretaceous records show that there was no decline in fish diversity until the Cretaceous–Paleogene (K/Pg) boundary in the area and extinction event appears to have been rapid. Finally, we find that the distribution of some chondrichthyans and teleosts in the James Ross Basin appears to be climatically determined.

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1. Introduction

The fossil ichthyofaunas of Antarctica are poorly known in comparison with other continents (e.g. Europe, North and South America). Most of the Upper Cretaceous and Cenozoic remains come from a few islands located near the northern part of the Antarctic Peninsula (Cione, 1996; Cione and Reguero, 1998; Kriwet et al., 2006; Cione and Medina, 2009; Otero et al., 2014; Gouiric-Cavalli et al., 2015 and references therein). The better known Antarctic ichthyofaunas are Eocene in age (Reguero et al., 2013 and references therein) but, Cretaceous Antarctic reports consist of a few taxa and specimens identified mostly at generic or higher hierarchical levels (e.g., Eastman and Grande, 1986; Grande and Chatterjee, 1987; Cione and Medina, 1987; Cione, 1996; Kriwet et al., 2006; Otero et al., 2013a, 2014). In contrast, Paleocene taxa had not been identified until now.

The Cretaceous–Paleogene (K/Pg) transition is widely exposed on Marambio (Seymour) Island (Zinsmeister, 1998; Tobin et al., 2012) but only a few fishes were described from that area (Otero et al., 2013a). Conversely, invertebrates, small chorate dinoflagellate cysts, and some tetrapods were reported (Olivero, 2012; Reguero et al., 2013; Bowman et al., 2013, 2014).

In this paper, we provide a description of a new collection of chondrichthyan and teleost material (teeth and fin ray fragments) from upper Maastrichtian and Danian beds of Marambio Island. We also give a list of the Cretaceous and Paleocene fish record of Antarctica – with corrected geographical and stratigraphic locations – and a brief discussion about the biogeography and terminal Cretaceous extinction of the ichthyofauna of the Antarctic continent.

2. Localities and stratigraphic setting

Marambio (Seymour) Island is located near the northeastern sector of the Antarctic Peninsula (West Antarctica), at the West of Weddell Sea (Fig. 1), and within the back-arc James Ross Basin (Del Valle et al., 1992). Like on Vega, James Ross, and Snow Hill islands, Marambio Island contains sedimentary rocks deposited during the

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Late Cretaceous–Paleogene, belonging to the Marambio and Seymour Island groups (Marenssi et al., 2012).

The Upper Cretaceous–lower Paleocene Marambio Group constitutes a thick succession of sandstones and pelites deposited in shelf and transitional environments (Marenssi et al., 2012). It comprises, from bottom to top, the Santa Marta, Rabot (lateral equivalent of the uppermost part of Santa Marta), Snow Hill Island, Haslum Crag Sandstone, López de Bertodano (LBF), and Sobral (SF) formations (Marenssi et al., 2012; Olivero, 2012; Montes et al., 2013). Subsequent to the deposition of these units, deep canyons were eroded and filled with the sandstones and volcanoclastic conglomerates constituting the basal unit of the Seymour Island Group (Elliot and Trautman, 1982).

The middle Paleocene–lowermost Oligocene Seymour Island Group includes the Cross Valley, La Meseta, and Submeseta formations (Montes et al., 2013), deposited within incised valleys on an emerging offshore platform (Marenssi et al., 2012).

Fossils described here come from the Maastrichtian and Danian López de Bertodano Formation and Danian Sobral Formation (Fig. 2). A detailed cross section, illustrating the stratigraphic relationships of these units can be consulted in Marenssi et al. (2012) and Olivero (2012).

2.1. López de Bertodano Formation

The López de Bertodano Formation spans from the lower Maastrichtian up to the lowermost Danian in its upper unit. It is composed of ~1100 m of sandy to clayey siltstones, with occasional

well-cemented sandier layers, some of which contain post-depositional carbonate concretions. Macellari (1988) used biostratigraphic and lithostratigraphic constraints to identify a series of informal units in the LBF; the lower ‘*Rotularia* units’ (Units 1–6) and the upper ‘molluscan units’ (Units 7–10) are named after their characteristic macrofossils. Unit 1 of the ‘*Rotularia* units’ was reassigned to the underlying Haslum Crag Member of the Snow Hill Island Formation (SHIF) (Crame et al., 2004; Olivero, 2012), and is capped by a prominent unconformity (Olivero et al., 2007, 2008). The ‘molluscan units’ are extremely fossiliferous, especially Units 8 and 9. The upper ‘molluscan units’ include the K/Pg boundary, which is located close to the base of Unit 10 (Macellari, 1988; Elliot et al., 1994; Zinsmeister, 1998; Witts et al., 2016). The K/Pg boundary was inferred from the presence of a laterally continuous 40 cm thick glauconitic horizon, beneath which the last records of ammonites and *Rotularia* are found (Macellari, 1988). These ‘Molluscan Units’ represent a generally deepening upwards trend. Macellari (1988) suggested a transition from middle (Units 7–8) to outer (Units 9–10) shelf, though a short interval of regression may have occurred just prior to the K/Pg boundary (Macellari, 1988). Minor water depth changes are difficult to discern based on sedimentology or fossil assemblages (Bowman et al., 2013; Witts et al., 2015). However the ‘molluscan units’ clearly do show a marked increase in both abundance and diversity of macrofossils (Macellari, 1988; Crame et al., 2004; Witts et al., 2016). The uppermost ~300 m of the Cretaceous succession are also characterized by an increase in the prevalence of relatively sandy, glauconitic beds, ranging from tens of cm to several meters in thickness. These may represent

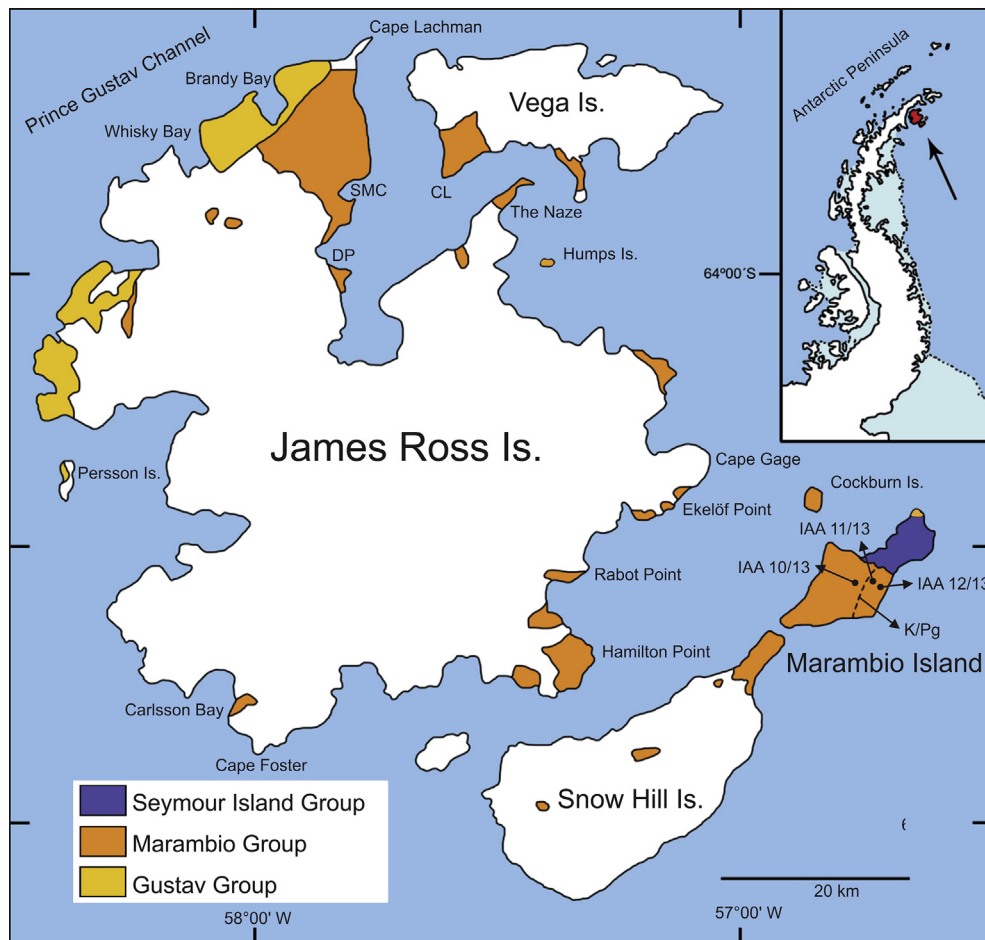


Fig. 1. Map of Antarctic islands (James Ross, Vega, Snow Hill, and Marambio). At Marambio (Seymour) Island the collection localities as well as the K/Pg boundary are indicated.

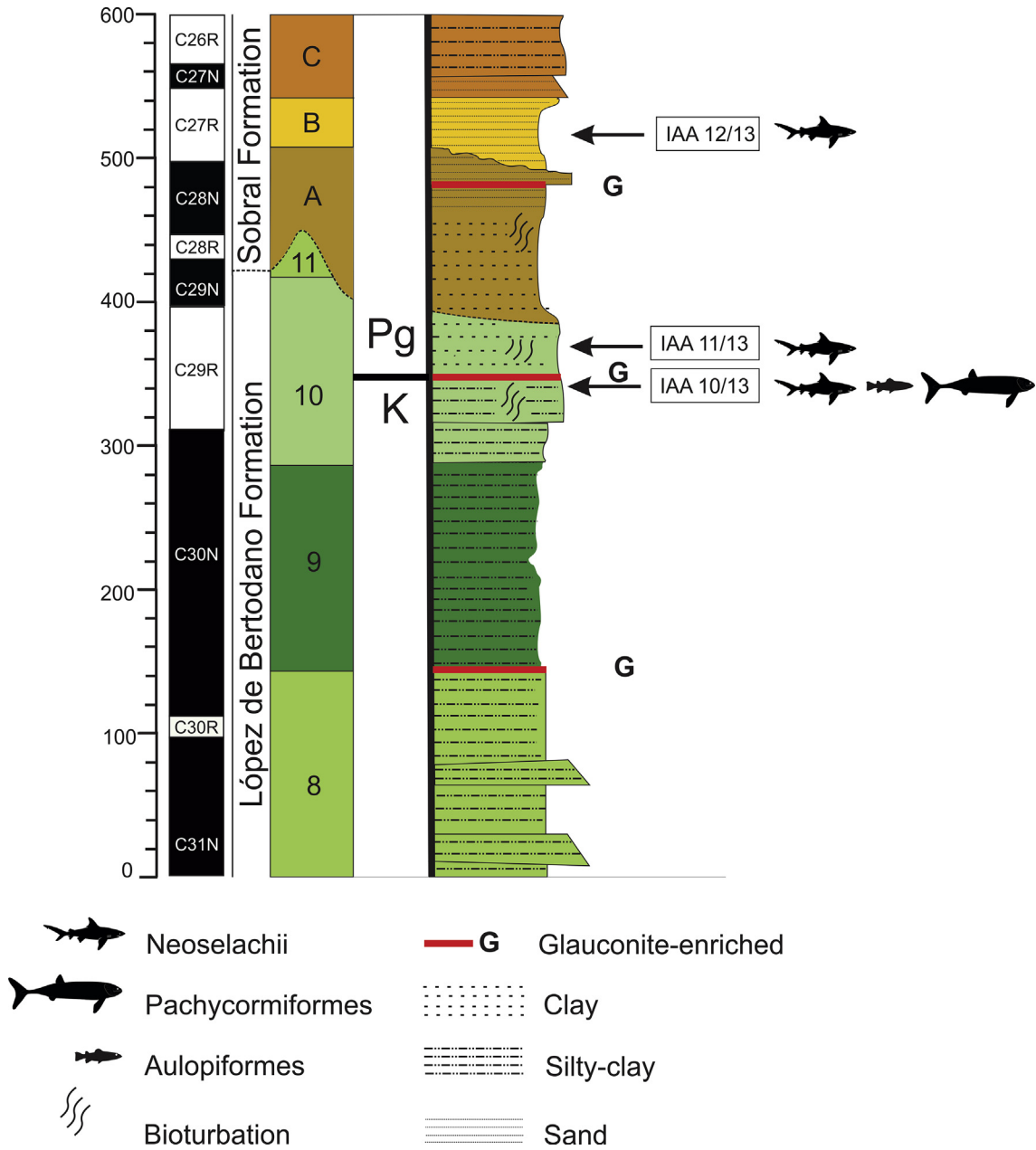


Fig. 2. Stratigraphic profile with localities on Marambio (Seymour) Island.

periods of reduced deposition and reworking, or lateral facies variability (Bowman et al., 2016).

The vertebrate distribution of Units 8 and 9 of LBF includes sharks, mosasaurs, and elasmosaurid plesiosaurs, which were recorded throughout the complete sequence. In contrast, cryptoclidid plesiosaurs, teleosts, and a gaviid bird are restricted to the ‘molluscan units’.

The fossils described herein come from two localities of the LBF IAA 10/13 in Unit 9 (64°16'18.5"S, 56°43'0.9"W) and IAA 11/13 (64°16'6.81"S, 56°42'34.33"W) in Unit 10 (Fig. 3). Otero et al. (2014) reported elasmobranch fishes from Unit 9 in a nearby locality (64°16'05"S, 56°42'38.8"W).

2.2. Sobral Formation

The Sobral Formation is assigned to the Danian (lower Paleocene) based on nano and microfossils (dinoflagellates, siliceous

microfossils, foraminifera, and palynomorphs) as well as geochemical data (Dingle and Lavelle, 1998; Marensi and Santillana, 2003; Santillana et al., 2007). The overlying Thanetian levels were considered as the top of the Sobral Formation (Bowman et al., 2016), but we follow the profiles of Montes et al. (2013) on which these levels were identified as the Cross Valley Formation.

The Sobral Formation overlies the lower Maastrichtian–Danian LBF and underlies the Selandian–Thanetian Cross Valley Formation (Montes et al., 2013). It comprises about 240 m of yellowish brown shales, marls, and sandstones. Siliceous volcanic fragments, lithic arkoses, and levels of feldspathic and glauconitic sandstones are frequent. This coarsening upward sequence of the SF is exposed in the east of Marambio Island between Punta Sobral and Bahía Pingüino and in a small outcrop in the northern sector of the island. The Sobral Formation was deposited in a marine environment during at least two transgressive-regressive cycles (Marensi et al., 2012).

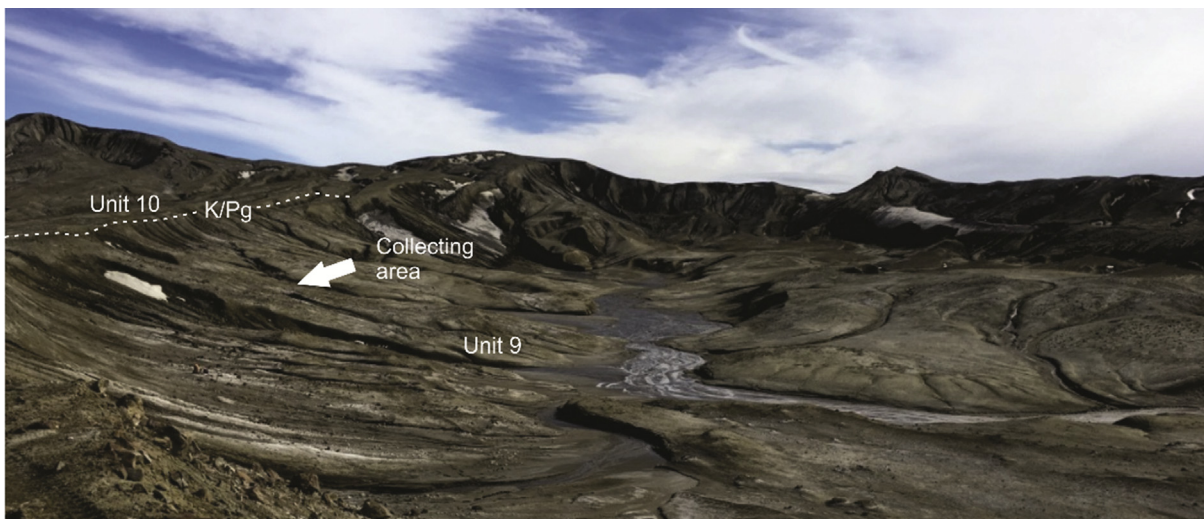


Fig. 3. Photograph of López de Bertodano Formation crops out at Marambio (Seymour) Island. Arrow indicates the collection area at Unit 9 (uppermost Maastrichtian) of LBF.

Sadler (1988) described four lithostratigraphic units for the SF. However, Santillana et al. (2007) recognized seven units – and based on the identification of two internal discontinuities – subdivided this formation into three sequential units, named Sobral A, B, and C allomembers (see Montes et al., 2013). The material from the SF we describe comes from the locality IAA 12/13 (64°16'10"S, 56°41'20.44"W).

3. Material and methods

The specimens were collected by surface prospection and from sieved sediment during the 2013–2014 Antarctic field-trip to Marambio Island by the authors CAH, MR, GML, SS and JNG. Sediment was dry sieved during field works in Marambio (Seymour) Island. The sediment was divided in three size fractions, coarse (>10 mm), middle (>4 mm < 10 mm) and a thin fraction (<4 mm). All specimens figured are housed at División Paleontología Vertebrados of the Museo de La Plata, La Plata, Argentina (MLP). Tooth terminology largely follows Cappetta (2012) for sharks, Slaughter and Springer (1968) for Pristiophorid, and Goody (1976) for Enchodontid. Pachycormiformes terminology follows Liston (2004). Open nomenclature follows Bengston (1988).

Pachycormiformes remains were photographed by SGC using a Canon® EOS T2i with a macro compact lens 2.5 and processed using Photoshop® CC. Measurements were taken using Vernier Calipers on the specimens and with the free software Fiji® using photographs. Statistics and graphs were done with R version 3.4.2 Copyright© 2017, The R Foundation for Statistical Computing, using the package 'plotrix' 3.6–6.

4. Systematic paleontology

Along this section we describe the new records and discuss some taxa previously reported by other authors. In the supplementary material a detailed Maastrichtian to Danian fish record of Antarctica is presented in Table 1 of Supplementary Material and complemented with the South American distribution in Table 2 of Supplementary Material. The complete list of new materials here described is included in Table 3 of Supplementary Material.

Class Chondrichthyes Huxley, 1880

Subcohort Neoselachii Compagno 1977
Order Squaliformes Goodrich 1909
Family Squalidae Bonaparte 1834
Genus *Protosqualus* Cappetta 1977

Protosqualus sp.

Fig. 4A–E

Referred material. Two lateral, almost complete teeth, MLP 13-XI-29-9, MLP 13-XI-29-33; one latero-posterior, complete tooth, MLP 13-XI-29-10.

Stratigraphic and geographic provenance and locality. Uppermost Maastrichtian LBF, Unit 9, IAA 10/13.

Description. Teeth are ca. 7 mm wide, not greatly labio-lingually compressed. The cusp is triangular, broad, and strongly inclined distally. The mesial cutting edge has a sigmoidal profile probably due to gynandric heterodonty. The distal cutting edge is straight (MLP 13-XI-29-10) or convex (MLP 13-XI-29-9) and smooth. The distal heel is short and strongly convex dorsally and joins the cusp in a notch. The mesial cutting edge of the cusp and the distal heel are undulated and/or feebly but widely serrated. The distal labial depression for interlocking is poorly developed in both teeth where this side of the teeth was well preserved (see MLP 13-XI-29-10). The base of enameloid in both faces is smooth.

The labial face presents a widely triangular apron (MLP 13-XI-29-33; Fig. 4C). There is a large medio-lingual twisted uvula. The root is not compressed and presents a very strong transversal bulge. In the middle, an infundibulum occurs in MLP 13-XI-29-9. The crown base overhangs labially the crown-root junction. The lingual crown-root junction is depressed. The inner face of the root is low and convex. Many foramina randomly open on all crown faces.

Discussion. The material closely resembles teeth of squalids such as *Protosqualus*, *Centrophoroides*, *Megasqualus*, and *Squalus*. *Protosqualus* includes several species that range from the Barremian to Coniacian (Cappetta, 2012). The Late Cretaceous genus *Centrophoroides* was synonymized with *Squalus* by Woodward (1889). However, it was considered valid by Cappetta (1980) who described thoroughly articulated skeletons from the type locality in Santonian beds of Lebanon (Cappetta, 1980) a criterion followed in the present contribution. There are other few reports elsewhere

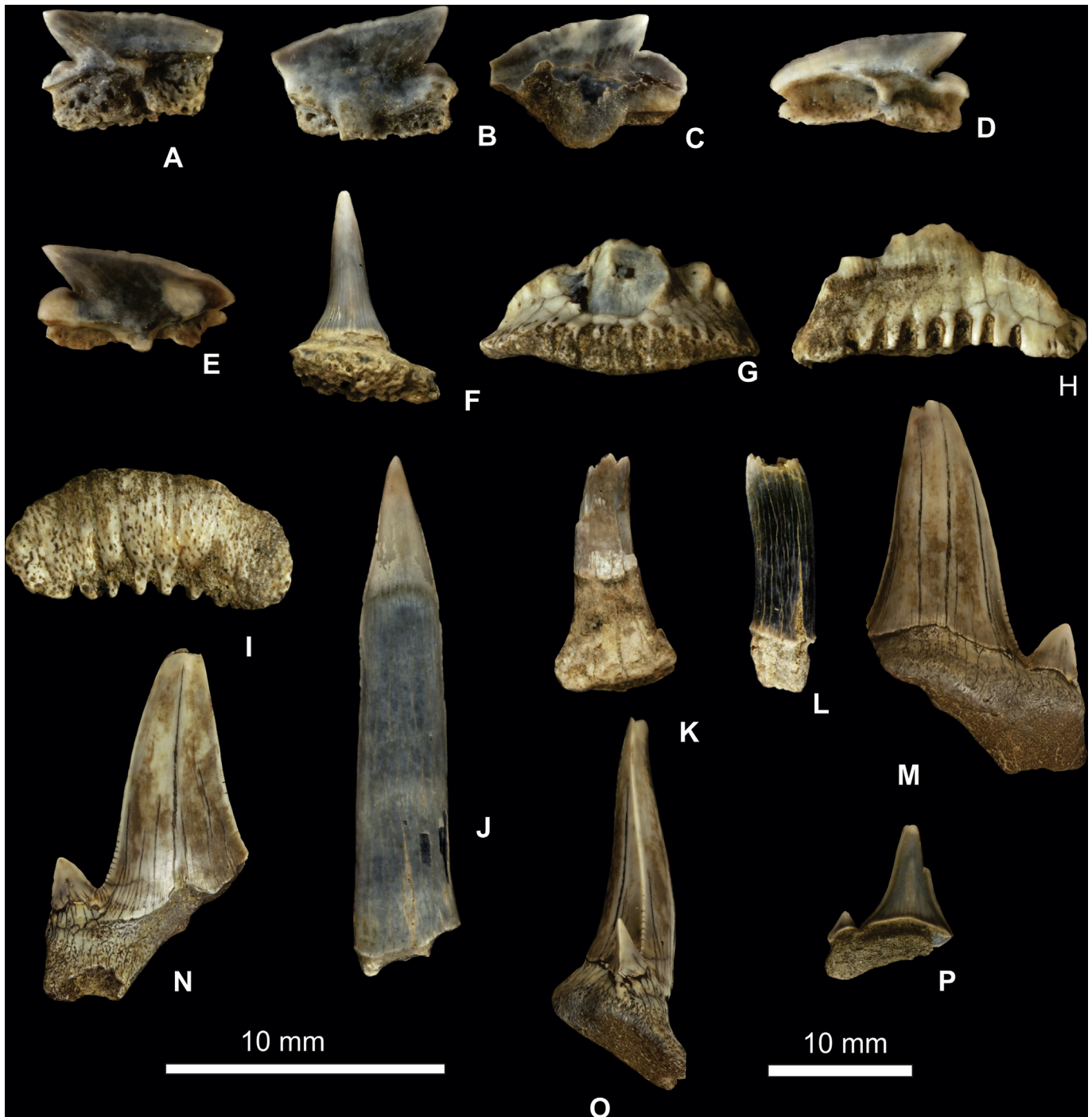


Fig. 4. Teeth of *Protosqualus* sp. (MLP13-XI-29-9) in lingual (A) and labial view (B); (MLP13-XI-29-33) in labial view (C); (MLP13-XI-29-10) in lingual (D) and labial view (E). Incomplete crown of *Paraorthacodus* sp. (MLP 13-XI-29-8) in lingual view (F). Fragmentary tooth base of *Paraorthacodus* sp. (MLP 13-XI-29-18) in occlusal (G), labial (H) and basal view (I); teeth of aff. *Propristiophorus* sp. (MLP13-XI-29-39) crown (J); (MLP 13-XI-29-40) lower middle portion of rostral tooth (K); (MLP 13-XI-29-41), middle part of crown (L); teeth of “*Cretolamna appendiculata*” (MLP 13-XI-29-47) fragmentary upper anterior tooth in lingual (M), labial (N), and mesial view (O); (MLP 13-XI-29-2), fragmentary lower lateral tooth in lingual view (P). All teeth from uppermost Maastrichtian LBF, Unit 9, locality IAA 10/13, except for MLP 13-XI-29-2 found in lowermost Danian LBF, Unit 10 locality IAA 11/13. Left scale: a-l. Right scale: m-p.

(see Cappetta, 2012; Guinot et al., 2013; Otero et al., 2013b, 2014). *Megasqualus* is a Selandian to Ypresian genus with only one species (Cappetta, 2012).

The material from Unit 9 could be differentiated from *Squalus*, *Megasqualus* and *Centrophoroides*. The mentioned specimens differ from *Squalus* in the absence of a long quadrangular apron with

parallel sides present especially in anterior, lateral, and antero-posterior rows. A triangular (but not a widely rounded) apron is only seen in *Squalus* in the more distal rows (e.g. *Squalus acanthias*; Herman et al., 1989; Pl.3).

In contrast to *Megasqualus* the material from Unit 9 has a much smaller (or none) infundibulum, concave basal root face, few labial root foramina, and being smaller (teeth of *Megasqualus* reach a

width of 13 mm) (Cappetta, 2012; Adolfssen and Ward, 2014). Besides, *Megasqualus* is rarely cited for the Cretaceous fossil record (Adolfssen and Ward, 2014).

The specimens from Unit 9 differ from *Centrophoroides* in the large and basally rounded apron and larger size. Otero et al. (2014, fig. 3.4) identified a natural mold preserving the labial surface of a small tooth from the Santa Marta Formation as pertaining to *Centrophoroides*. However, this material appears to be too fragmentary for identification. Previously, Otero and Suárez (2009) and Otero et al. (2013b) had identified this genus from the Dorotea Formation (Upper Cretaceous, southern Chile). Otero et al. (2014) mentioned the serrations as a character for all these specimens to be identified as *Centrophoroides*. However, all genera discussed here could present serrations of different kinds, weak (in *Squalus acanthias* Linnaeus 1758; extant; Herman et al., 1989) or strong (in *S. crenatidens*, Eocene, Arambourg, 1952; *Squalus weltoni*, Eocene, Long, 1992) serrations or slightly irregular cutting edges (*Squalus gabrielsoni*, late Maastrichtian–Paleocene, Adolfssen and Ward, 2014) are also present in *Squalus* and are not exclusive for *Centrophoroides*. Additionally, the material from the Cretaceous of Chile does not present a root notch such as shown for *C. latidens* (see Cappetta, 2012).

The material from Unit 9 can be assigned to *Protosqualus* because of the large, basally rounded, and short apron without parallel sides and the absence of a root notch (Fig. 4A–D). Recently, *P. argentinensis* was described for the Maastrichtian of Argentina being the first *Protosqualus* species for the Southern Hemisphere (Bogan et al., 2016). This new species differs from the Antarctic specimens in the presence of strong and irregularly denticulate cutting/edges, a festooned enameloid at the basal edge of the labial crown, and the root is apicobasally deeper. Bogan et al. (2016) suggested that teeth identified as *Centrophoroides* from Maastrichtian beds of southern Chile (Suárez and Otero, 2008; Otero et al., 2013b) also might be assigned to *Protosqualus*.

Order Hexanchiformes De Buen, 1926

Family Orthacodontidae Glikman, 1957

Genus *Sphenodus* Agassiz 1843

***Sphenodus* sp.**

Referred material. Two fragmentary teeth, MLP 13-XI-29-20, MLP 13-XI-29-11.

Stratigraphic provenance and locality. Uppermost Maastrichtian LBF Unit 9, IAA 10/13.

Remarks. Although fragmentary and worn out, the material can be easily referred to the monogeneric family Orthacodontidae. The tooth roots are similarly to those of late Kimmeridgian morphotype 3 of Böttcher and Duffin (2000, fig. 16A). Klug et al. (2008) suggested that the tooth identified as *Isurus* sp. by Grande and Eastman (1986) from indeterminate levels of LBF was assignable to the genus *Sphenodus*. Here, with a good stratigraphic control, we report the occurrence of *Sphenodus* in the uppermost Cretaceous levels (Unit 9) of LBF being the youngest documented record of orthacodontids for Antarctica.

Family Paraorthacodontidae Glikman, 1958

Genus *Paraorthacodus* Glikman, 1957

***Paraorthacodus* sp.**

Fig. 4F–I

Referred material. Four fragmentary teeth, MLP 13-XI-29-8, MLP 13-XI-29-18, MLP 13-XI-29-31, and MLP 13-XI-29-32.

Stratigraphic provenance and locality. Uppermost Maastrichtian LBF, Unit 9, IAA 10/13.

Description. Teeth relatively large, the medio-distal length reaching 9.5 mm and basoapical reaching at least 7.5 mm (the tooth illustrated by Otero et al., 2014; fig. 2.25 appears to have a mesio-distal length of 18 mm); pointed central main cusp flanked by at least 2 pairs of lateral cusplets diminishing in size laterally; lateral cusplets well separated from each other, only connected by a very low and smooth crown-band; labial face of main cusp faintly convex with very strong subparallel labial folds reaching 2/3 upwards of crown extending to the crown-root junction; cutting edges sub-parallel and prominent reaching the base of cusp and cusplets; no basal depression on labial face; cusplets with vertical labial irregular folds differing in length, not-bifurcating; lingual face of main cusp convex with strong vertical, densely and irregularly arranged ridges covering the face from side to side that reach about 70% of crown height; lingual tooth neck broad. The root is basally flat and presents up to 12 basal short labial folds.

Remarks. The validity of *Paraorthacodus* as different from *Synechodus* has been previously discussed (see comments in Klug et al., 2008; Cappetta, 2012). There is agreement about both representing different genera. Species of both genera differ in tooth characters: *Paraorthacodus* presents lateral cusplets rather high and acute, more or less well-developed vertical ridges on the labial and lingual crown faces, lateral cusplets well-defined and strongly separated from the main cusps and labial crown not overhanging crown-root junction (see Klug et al., 2008; Cappetta, 2012). Recently, Cappetta (2012) proposed that genera *Paraorthacodus* and *Synechodus* pertained to two unrelated families: the lamniform Palaeospinacidae (*Synechodus*) and the hexanchiform Paraorthacodontidae (*Paraorthacodus*). In addition to the dental characters, Cappetta (2012) stressed that the presence of only one dorsal fin in *Paraorthacodus* aligns it with Hexanchiformes.

The material from LBF clearly matches with *Paraorthacodus*. Otero et al. (2014; fig. 2.25) reported an isolated fragment of a tooth which is assignable to this genus in the Unit 9 level. We here report four additional fragmentary teeth. We found that these teeth differ from the only species described for Antarctica, *P. antarcticus* from the Upper Cretaceous Santa Marta Formation, in the following characters: no basal depression on labial face; very strong subparallel labial folds extending 2/3 up the crown and to the crown-root junction, lingual face of main cusp with strong vertical, densely and irregularly arranged ridges.

The LBF teeth also differentiate from *Paraorthacodus patagonicus* from the Cenomanian of the nearby Patagonia, in the smaller maximum size and maximum width observed, in having not more than three cusplets on each side, weaker basoapical ridges on lingual and labial faces of main cusp and cusplets, a more convex labial face of the main cusp, and the main cusp is slender and narrow.

The LBF teeth differ from the tooth identified as Palaeospinacidae indet. from the Lower Cretaceous of the Antarctic Alexander I Island (Kriwet, 2003) in the larger size of labial folds and the convexity of the labial face.

Collectively, these differences suggest that the teeth of *Paraorthacodus* from Unit 9 suggest that they might pertain to a new species, but the specimens are fragmentary and abraded in order to formalize it.

Order Pristiophoriformes Berg 1958

Family Pristiophoridae Bleeker 1859

Genus *Propristiophorus* Woodward 1932

aff. ***Propristiophorus* sp.**

Fig. 4J–L

Referred material. Three fragmentary rostral spines, MLP 13-XI-29-39, MLP 13-XI-29-40, and MLP 13-XI-29-41.

Stratigraphic provenance and locality. Uppermost Maastrichtian LBF, Unit 9, IAA 10/13.

Description. Our material and that of Otero et al. (2014) only include the long rostral spines of pristiophorids (see Slaughter and Springer, 1968). The material seems to correspond to one of the largest pristiophorid species known. On the basis of known morphology of recent rostral spines and dimensions, the longest rostral spines recovered from the LBF measured about 25 mm from the root base to the crown apex. The rostral spines have a basal peduncle and a long and compressed crown with an enameloid cap. The crown is straight and the anterior and posterior margins are almost parallel. The apex abruptly tapers because both cutting edges change their slope abruptly (Fig. 4J–L). The enameloid is partially smooth with basoapical subparallel folds in the basal portion in most specimens. Folds approximately occupy the basal 1/3 portion. The cutting edges are smooth and reach the base of the cap.

The peduncle is much shorter than the crown. The contact with the crown is circular but the proximal portion is antero-posteriorly elongate. There is a collar above it. The basal face has a large nutritive hollow that continues in a posterior sulcus.

Discussion. The absence of serrae in the cutting edges of the rostral spines separates the material from the pristiophorid genera *Ika-maiius* and *Pliotrema* and relates them to *Pristiophorus* and *Propristiophorus*. *Propristiophorus* has recently been resurrected as a valid Cretaceous genus by Herman and van Waes (2014). Cretaceous pristiophorids are extremely rare but in the Cenozoic they are much more common and abundant.

The rostral spines from Unit 9 are similar to those of *Propristiophorus tumidens* (the only so far recognized species of this genus) in the combination of the following characters: parallel sides of the rostral spines, pointed tip, and general presence of basoapical folds on the crown (see Cappetta, 1980, 2012; Herman and van Waes, 2014). The material from Unit 9 described by Otero et al. (2014) also has folds and parallel sides (no tips preserved; Otero, pers. comm., 2016). Other Cretaceous pristiophorids such as the putative *Pristiophorus* sp. from Japan (Nishimoto and Morozumi, 1979) and *Pristiophorus* sp. from Madagascar (Gottfried and Rabarison, 1997) also share the three features mentioned above. On the contrary, most Cenozoic species have rostral spines that gradually taper distally and have not parallel sides, no pointing tip, and no folds.

The hundreds of rostral spines collected in the Eocene of Antarctica and the Miocene of South America are all smooth (see also Engelbrecht et al., 2016). However, there are a few exceptional rostral spines with fine and few folds reported from the middle Eocene of France (Adnet, 2000), the Miocene species *Pristiophorus suevicus* (fide Engelbrecht et al., 2016), and a single rostral spine from the Eocene of New Zealand (Keyes, 1982). Also, some specimens of the recent species *P. cirratus* show a few basoapical folds (see Herman et al., 1992; Pl. 41, figs. 2a, 2b). *P. schoederi* possess some enameloid folds on the crown surface (Engelbrecht et al., 2016) and *Pristiophorus* sp. (Pollerspöck and Straube, 2016) shows very short folds at the crown base. A *Pristiophorus* tooth from the Miocene of Patagonia presents unusual tubercles in the base of the crown (Cione and Expósito, 1980).

The Antarctic material probably pertains to a new species because it differs from *Pristiophorus tumidens* in the presence of finer basoapical ridges that reach a lower height (2/3 of crown height in *P. tumidens* vs. 1/3 in the Antarctic teeth) and in the much larger size (about 6 times larger). Despite teeth from Unit 9 unit

being the largest pristiophorids reported from pre-Cenozoic rocks, the poor preservation of the material does not allow any specific identification. Nevertheless, Unit 9 unit teeth might represent the youngest known and the first Antarctic record of genus *Propristiophorus*.

Order Lamniformes Berg, 1958

Family Otodontidae Glikman, 1964

Genus *Cretolamna* Glikman, 1958

“*Cretolamna appendiculata*” (Agassiz, 1843) sensu lato
Fig. 4M–P

Referred material. One lateral lower tooth which lacks crown tip, distal lateral cusplet, and distal root branch (LBF, Unit 9), MLP 13-XI-29-47; one anterior upper tooth lacking the distal root branch, distal lateral cusplet, and crown tip (LBF, Unit 10), MLP 13-XI-29-2. **Stratigraphic provenance and localities.** uppermost Maastrichtian LBF, (Unit 9; IAA 10/13) and lowermost Danian LBF (Unit 10; IAA 11/13).

Description. MLP 13-XI-29-47 is a medium sized tooth (Fig. 4M–O). The cusp is triangular and relatively high, with convex and smooth labial and lingual faces. The base of the crown lingual face is flat and there is a depression of the tooth base of the labial face. The cutting edges are continuous down to the base of the main cusp and in the laterally preserved cusplet. There are no serrations in the base of cutting edge, only some parallel cracks in the flat, without undulations enamel. The cusp is slightly sigmoid in lateral view. The mesial lateral cusplet is large and mesially and lingually directed. Cusplets cutting edges are convex. The root is high and robust. The large lingual protuberance does not display a nutritive sulcus. The root lobe is relatively quadrangular and distally compressed.

MLP 13-XI-29-2 is small (Fig. 4P). The cusp is narrow, triangular and low, with convex labial and flat lingual faces. Both faces are smooth. The cutting edges are continuous down to the base of the cusp and with the laterally preserved cusplet. The main cusp is straight in lateral view. The preserved mesial lateral cusplet is large and parallel to the main cusp. The root is low and robust showing severe damage. The root lobe is relatively quadrangular and compressed distally.

Remarks. *Cretolamna appendiculata* (Agassiz, 1843) has been usually reported from beds ranging from Albian to Ypresian. Siversson et al. (2015) reviewed the species on the basis of thousands Cenomanian to Campanian specimens. This study demonstrated that teeth assigned to *C. appendiculata* actually represent a large species complex clustered into two genera and several species. Unfortunately, the authors did not discuss material from Maastrichtian to Ypresian stages.

Despite both teeth reported herein are too fragmentary for a good comparison in terms of the analysis by Siversson et al. (2015), it is possible to determine that MLP 13-XI-29-2 (Fig. 4P) from Unit 10 level is rather similar to lateral teeth of *Kenolamna* in the lingually directed cusp, the cusp being labially curved in profile view and being tall. However, the cusp is thicker and wider, and the labial face is strongly convex. The lateral cusplets present a concave outer cutting edge.

MLP 13-XI-29-2 from Unit 10 is also similar to an upper? anterior tooth of *Cretolamna hattini* (Siversson et al., 2015; his fig. 15A). However, the labial face of the crown is more convex and the lateral cusplets are much larger than in *Cretolamna hattini*.

Considering that the material is fragmentary and in the absence of a revision of Maastrichtian to Ypresian species of *Cretolamna* we

refer the Antarctic specimen as “*Cretolamna appendiculata*” sensu lato.

The lowermost Danian (Unit 10) tooth suggests that the taxon *Cretolamna* persisted in Antarctica into the Cenozoic. The clade Otodontidae is represented by *Otodus auriculatus* (Agassiz, 1843) in the Eocene of Marambio Island (Cione et al. 1977).

Family Odontaspidae Müller and Henle, 1839

Genus *Carcharias* Rafinesque 1810

cf. *Carcharias* sp.

Referred material. Two left upper lateral teeth preserving one root branch and lateral denticle, MLP 13-XI-29-35, MLP 13-XI-29-37; one right upper lateral tooth preserving one root branch and lateral denticle, MLP 13-XI-29-36; several fragmentary teeth, MLP 13-XI-29-4, MLP 13-XI-29-44 to 46, MLP 13-XI-29-16, MLP 13-XI-29-13 to 14.

Stratigraphic provenance and locality. Uppermost Maastrichtian LBF, Unit 9, IAA 10/13.

Description. The material is fragmentary. The enameloid of the crowns and lateral cusplets is smooth. The labial crown face is flat and the lingual face is moderately convex with a medial flattening. Cutting edges of crown and cusplets run from the tip to the base. MLP 13-XI-29-35 is preserved showing the basal margin of the crown to follow the root branch. Several isolated crowns (MLP 13-XI-29-44 to 46) are deep, slender, and sigmoid and correspond to anterior teeth.

Remarks. The material separates easily from teeth of mitsukurinids and other odontaspids and is assigned to cf. *Carcharias* on the basis of the flat labial crown, absence of basal labial folds, one pair of lateral cusplets, the base of the crown following on the root branch, and the extreme of root branches not expanded. The material is fragmentary but compares with *C. heathi*, *C. samhammeri*, and *C. aasenensis* in the smooth crown labial face. It is similar to the indeterminate odontaspids that Otero et al. (2014) described from the same unit.

Martin and Crame (2006) referred two teeth from the LBF as *Odontaspis* sp. and cf. *Odontaspis*. However, the characters mentioned and the photographs do not allow a specific assignment to this genus. We found that these teeth could be compared with *Carcharias* as well. Consequently, we do not include *Odontaspis* among the Cretaceous fishes from Antarctica. This might be the first report of *Carcharias* for the Mesozoic of Antarctica.

Lamniformes indet.

Referred material. Four crowns, MLP 13-XI-29-30. |

Stratigraphic provenance and locality. Lowermost Danian, SF, IAA 12/13.

Remarks. One of the crowns presents short and strong folds at the base of the labial cusp face and has a moderately convex labial cusp base. It resembles *Palaeohypotodus*, which is known since the early Paleocene (Cappetta, 2012). Despite being fragmentary, these teeth represent the first fish record for the Sobral Formation.

Class Actinopterygii Cope, 1887

Subclass Neopterygii Regan, 1923

Order Pachycormiformes Berg, 1937

Family Pachycormidae Woodward, 1895

Pachycormidae indet.

Fig. 5

Referred material. Isolated and fragmentary caudal fin-rays, MLP 13-XI-29-57.

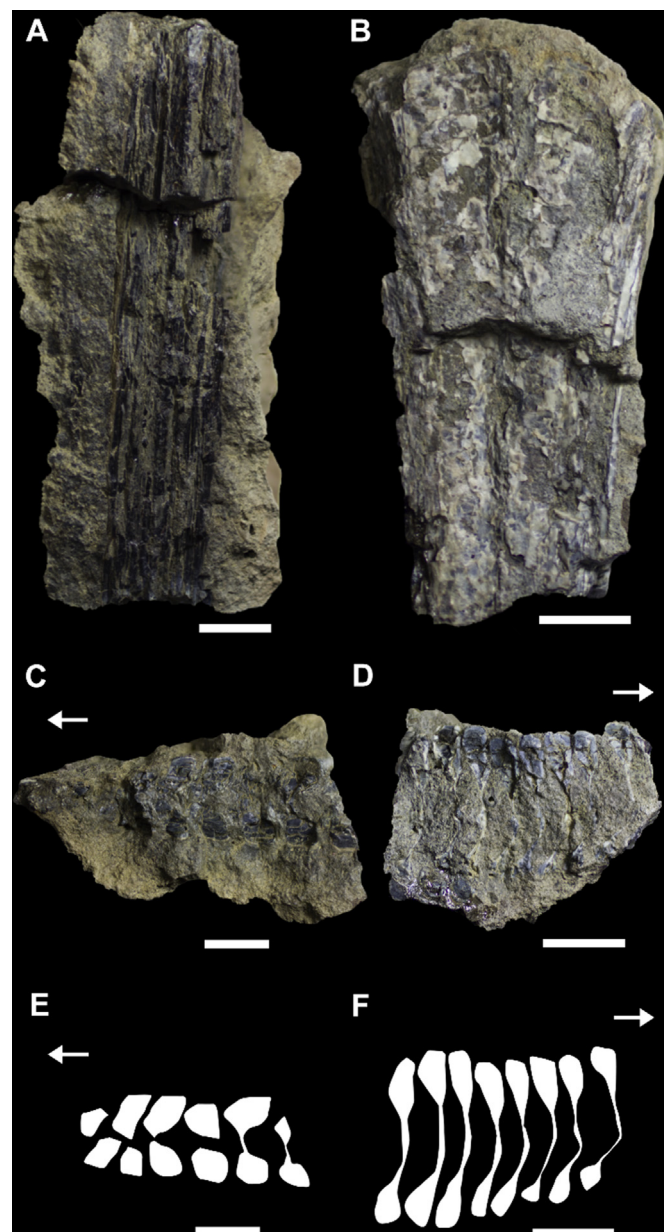


Fig. 5. Caudal? fin rays of Pachycormidae indet. (MLP 13-XI-29-57) lack of rays segmentation in lateral view (A), distally fused rays in ventral view (B), proximal portion with mostly not fused hemi-lepidotrichia (C) and distal portion of the fin rays figured in B with fused hemi-lepidotrichia (D); schematic drawing illustrating the progressive fusion of fin rays in C and D (E–F). The arrows indicate the ventral (or dorsal) portion of each fin lobe. Scale bar: 10 mm.

Stratigraphic provenance and locality. Uppermost Maastrichtian LBF, Unit 9, IAA 10/13.

Remarks. The material reported consists of two blocks of clustered lepidotrichia that belong to a single specimen. Both blocks measure about 70 mm height and each ray measures ca. 5 mm width, being more or less subcircular to rounded rectangular in cross-section (Fig. 5E). Although fragmentary, the material can be referred to the order Pachycormiformes because of the large size – considering that only the proximal portion of the rays are preserved – and lack of segmentation; being this last character a distinctive feature of caudal fin rays of large suspension-feeders pachycormids (e.g., *Leedsichthys*, *Asthenocormus*, and *Martillichthys*, see Liston et al.,

2013). The two blocks or clusters of lepidotrichia of the only Antarctic specimen found, show an unfused portion and a clearly fused one. The ray fusion gives the appearance of flattened structures overlying each other (Fig. 5D–F). Both cluster of rays does not show apparent bifurcations preserved (Fig. 5) but one block shows that are formed by paired structures which became flattened (Fig. 5B). It is probably that both blocks correspond to the proximal anterior and middle section of the fin.

Unfortunately, because the specimen is too incomplete, a better assessment and taxonomic comparison of the Antarctic material with other suspension-feeding pachycormids, is impossible to make. In the Jurassic, the suspension-feeding clade was diverse, being represented by *Asthenocormus*, *Leedsichthys*, *Martillichthys* (Lambers, 1992; Friedman et al., 2010; Liston, 2004, 2008) and indeterminate pachycormid remains (Gouiric-Cavalli and Rasia, 2014, 2016; Gouiric-Cavalli, 2017). However, in the Late Cretaceous, the group is only known by *Rhinconichthys* and *Bonnerichthys* (Friedman et al., 2010) and became extinct during the K/Pg transition (Friedman et al., 2010; Gouiric-Cavalli and Rasia, 2016; Gouiric-Cavalli, 2017). According to paleotemperature, suspension-feeding pachycormids inhabited warm and warm-temperate waters around continental shelves (Gouiric-Cavalli and Rasia, 2016). Apparently, the distribution of this clade was disjunct (amphitropical and bipolar), and similar to some extant mysticetes (e.g. *Eubalaena*) and filter-feeding sharks (i.e. *Cetorhinus*) (see Gouiric-Cavalli and Rasia, 2016).

Noteworthy, and despite of being isolated and fragmentary material, we report the first pachycormid in the uppermost Cretaceous levels (Unit 9) of the LBF and extend the distribution of filter-feeding pachycormids to the warm-temperate waters of Antarctic region (Gouiric-Cavalli and Rasia, 2016).

Subdivision Teleostei sensu Arratia, 1999
Order Aulopiformes Rosen, 1973
Family Enchodontidae Woodward, 1901
Genus *Enchodus* Agassiz, 1835

***Enchodus* sp.**
Fig. 6A–E

Referred material. One palatine tooth, MLP 12-XI-29-43; five teeth, MLP 12-XI-29-25 to 28; one tooth, MLP 12-XI-29-53; thirty-five teeth, MLP 12-XI-29-55; fifty-three teeth, MLP 12-XI-29-56.

Stratigraphic provenance and locality. Uppermost Maastrichtian LBF, Unit 9, IAA 10/13.

Description. All specimens recorded correspond to ectopterygoid large dentary “fangs” but a palatine “fang”.

Ectopterygoid and dentary teeth are slender, strongly labiolingually compressed, and measure up to 16 mm in height and 4 mm at the base. Teeth are strongly sigmoid in lateral view and straight in mesial view, not curved lingually. There is a single mesial unserrated posterior cutting edge that reaches the tip. The distal edge of the teeth is rounded, without a post-apical barb. The cross section is drop-like and became flatter to the tip. Both, labial and lingual faces are completely smooth.

The palatine tooth is straight and not sigmoid in lateral view. It is less compressed than ectopterygoid and mandibular teeth. There is a single medial unserrated cutting edge. The enameloid is smooth.

Some teeth are shorter, with a less marked sigmoid curvature (Fig. 6A–E).

Remarks. *Enchodus* has long been a challenge to paleontologists in view of the seemingly overwhelming task of reviewing all significant specimens of a putatively common cosmopolitan genus (Parris

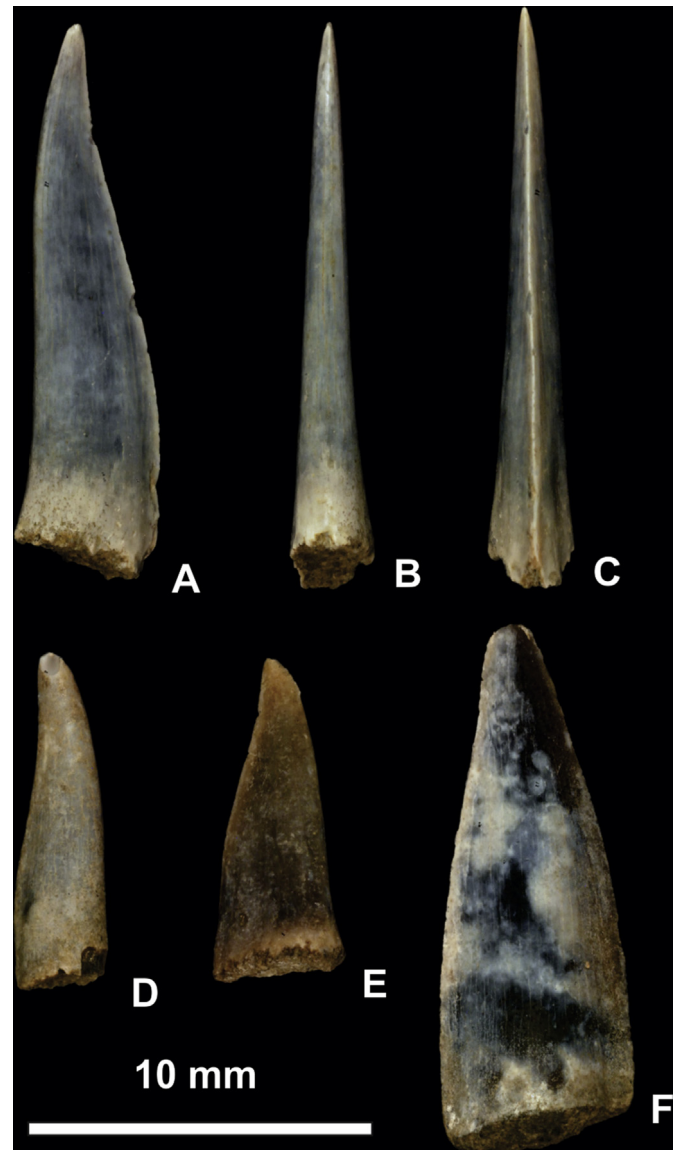


Fig. 6. Teeth of *Enchodus* sp. (MLP12-XI-29-43) in lateral (A), mesial (B) and commissural view (C); (MLP12-XI-29-53) lateral view (D); (MLP12-XI-29-55) lateral view (E); tooth of an Ichthyodectiformes indet (MLP12-XI-29-21) lateral view (F). All specimens from uppermost Maastrichtian LBF, Unit 9, locality IAA 10/13.

et al., 2007) which is mainly known by isolated teeth. Even when the species can be distinguished from tooth characters, we consider that additional material is needed in order to fund a new species. This is the youngest record of *Enchodus* for Antarctica.

Order Ichthyodectiformes Bardack and Sprinkle, 1969

Ichthyodectiformes indet.

Fig. 6F

Referred material. One tooth, MLP 12-XI-29-21; ninety-four teeth, MLP 12-XI-29-38; thirteen teeth, MLP 12-XI-29-51; seventy-eight teeth, MLP 12-XI-29-52; one tooth, MLP 12-XI-29-54.

Stratigraphic provenance and locality. Uppermost Maastrichtian LBF, Unit 9, IAA 10/13.

Remarks. The material is very similar to that figured by Kriwet et al. (2006) for the Herbert Sound Member of Snow Hill Formation. This is the first identification of Ichthyodectiformes for Unit 9. Notably, Cavin et al. (2013) suggested that from the Turonian to the

Maastrichtian, all ichthyodectiforms occurrences are located on northern continents. Unlike [Kriwet et al. \(2006\)](#), the former authors did not consider isolated teeth.

5. Some taphonomic considerations

Chondrichthyans and osteichthyans are comparatively few in the Upper Cretaceous and Paleocene units of the James Ross Basin (Figs. 7–9; Table 1 of Supplementary Material). This is particularly evident when compared with the Eocene record of Marambio Island, where many thousands of specimens were recovered. Most of the materials correspond to isolated teeth and many of them show signs of mechanical abrasion (e.g., in their cutting edges) or fracture. Therefore, the dearth of fish representation in Upper Cretaceous to Paleogene of James Ross Basin may suggest major taphonomic losses and do not favor the preservation of delicate teleostean bones. However, the nature of preservation of bony fish elements as well as other fossil remains and geological evidence attests to some environmental energy and/or reworking and consequent post-mortem mechanical destruction (see [Bazzi, 2014](#)).

The predominance of chondrichthyans over actinopterygians observed in LBF is probably attributed to taphonomic biases (Table 1 of Supplementary Material). Since fish postcranial material is scarce in these outcrops, most inferences rest in teeth. As mentioned by [Becker et al. \(2009\)](#) for an analogous sample from the Upper Cretaceous of South Dakota, while osteichthyan teeth have a thin outer sheath of hard enamel, chondrichthyans present teeth encased in a thick covering of highly durable enameloid. Thus, and due to the scant fish collected in Cretaceous and Paleocene beds of the James Ross Basin, it is difficult to assess the taxonomic proportions of the ancient biocenoses. Further studies are desirable to analyze properly if this proportional taxonomic differences could be explained by the taphonomic circumstances or, in contrast, are due to paleoecological conditions.

6. Antarctic Late Cretaceous fish diversity

We prepared two comparative charts. While Table 1 of Supplementary Material shows a comparison of the levels Units 9 and 10 of the LBF, and Sobral Formation with the other fish bearing units of the Cretaceous of James Ross Basin. Table 2 of Supplementary Material is a preliminary comparison with other Antarctic areas.

There are a relatively good fish representation in the Lachman Crags Member of the Santa Marta Formation, Herbert Sound

Member of the Snow Hill Island Formation, and Unit 9 of the LFB (Figs. 7–9; Table 1 of Supplementary Material). Thus, a good fish record extends from the Santonian to the upper Maastrichtian (see reference from Table 1 of Supplementary Material). Faunal diversity of the Santa Marta Formation is given in Fig. 7.

During the Late Cretaceous, Lamniforms, aulopiforms, and ichthyodectiforms are common in shelf environments ([Cicimurri and Everhart, 2001](#); [Cappetta, 2012](#)).

Primitive chlamydoselachiform, pristiophorid, orthacodontid, and palaeospinacid sharks are less frequent. Only few lamniform sharks of the families Otodontidae and perhaps Odontaspidae were found in Danian beds. Very rare are the demersal mitsukurinid *Scapanorhynchus*, the benthonic squatinid *Squatina*, and the small beryciform *Antarctiberyx*.

Suspension-feeding Pachycormiformes occur in the uppermost levels of Unit 9, representing the sole Cretaceous record of the clade in the Southern Hemisphere.

Remarkably, no batomorphs were reported, even those with large and robust teeth such as Sclerorhynchidae, Rhombodontidae, or *Igdabatis*, which are common in Upper Cretaceous beds (see [Cappetta, 2012](#)). Thus, the group might not have yet inhabited southern high latitudes. On the contrary, batomorphs with large and small teeth are abundant in Eocene beds of Marambio Island (the myliobatid *Myliobatis*, Rajidae; [Welton and Zinsmeister, 1980](#); [Long, 1994](#)).

Holocephalans show a significant diversity, perhaps one of the most diverse known ([Gouiric-Cavalli et al., 2015](#)). Yet, it is difficult to assess its frequency in the Cretaceous and Paleogene biocenoses because the potential number of specimens is much smaller than that of teleosteans and sharks due to their permanent dental plates. Based on the present evidence, holocephalan and in small number, squatinids and pristiophorids were the benthic chondrichthyans of the Late Cretaceous biocenoses of the James Ross Basin. Notably, holocephalan should have been the sole durophagous fishes in these associations.

Mosasaur, plesiosaurs, and large sharks were the largest predators in the Late Cretaceous marine environments of James Ross Basin. Since predation on plesiosaurs by *Notidanodon* was suggested in California, southern Patagonia, and Antarctica ([Cione and Medina, 1987](#); [Cione, 1996](#)), the recurrent presence of *Notidanodon* teeth in LBF thus could be related with plesiosaur remains.

Odontaspidid, *Enchodus* and ichthyodectiform species are considered to be predaceous fishes that fed on fast-swimming cephalopods and fish ([Nagrodski et al., 2012](#)). However, *Enchodus* also served as an important food resource for a variety of other

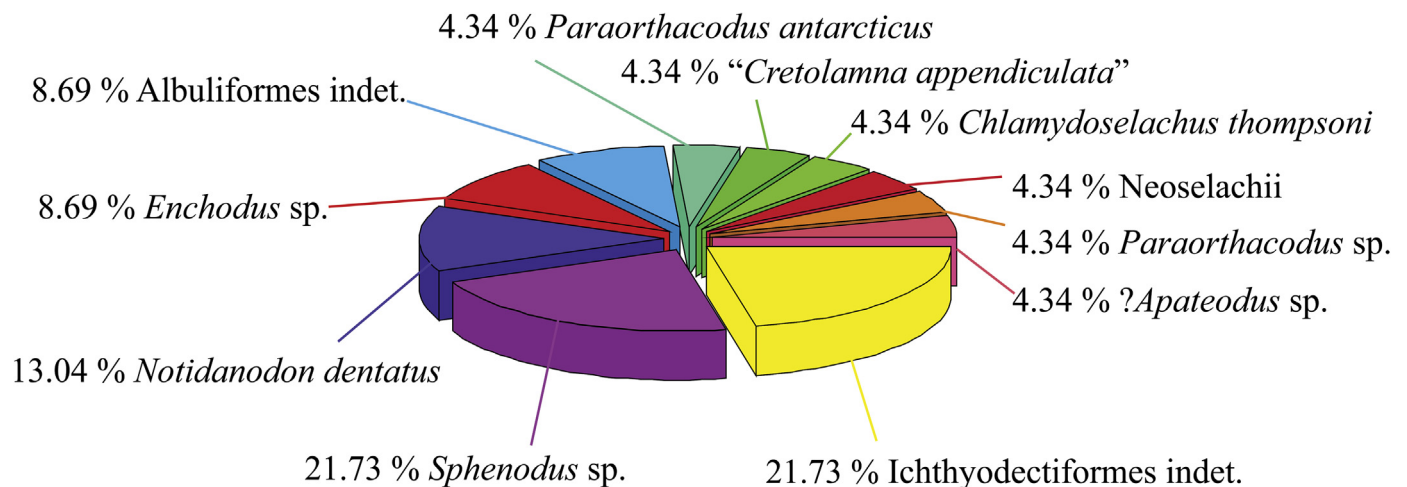


Fig. 7. Percentages of the ichthyofaunal diversity of the Lachman Crags of the Santa Marta Formation, Santonian-lower Campanian.

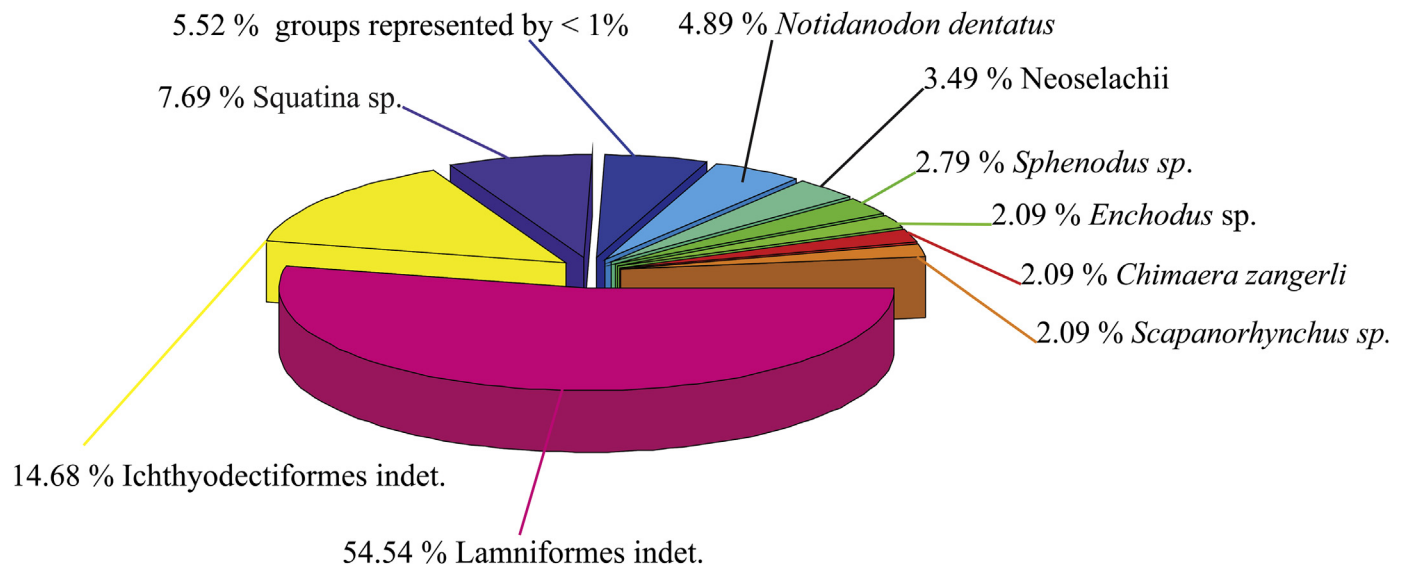


Fig. 8. Percentages of the ichthyofaunal diversity of Herbert Sound Member (=Gamma Member) of the Snow Hill Formation, upper Campanian. *Groups represented by only one tooth or 0.69% belong to: *Clamydoselachus thompsoni*, *Paraorthacodus sp.*, *Paraorthacodus antarcticus*, *Callorhynchus sp.*, *Edaphodon snowhillensis*, *Albuliformes indet.*, *Squaliformes indet.*, and *Rhinochimaeridae indet.*

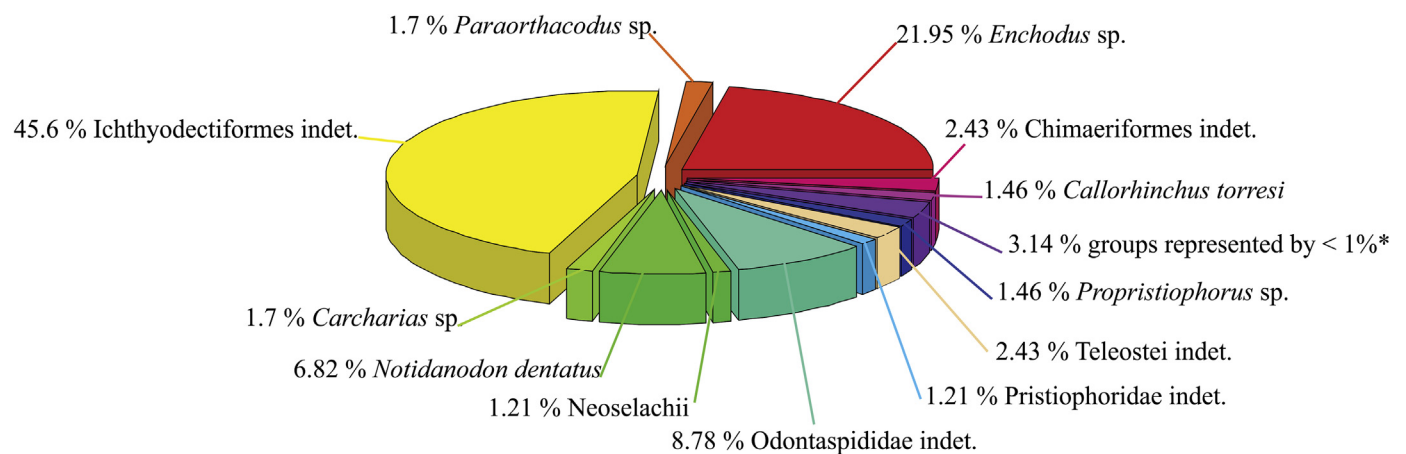


Fig. 9. Percentages of the ichthyofaunal diversity of the Unit 9 of the López de Bertodano Formation, Maastrichtian. *Groups represented by less than 1% belong to: *Callorhynchus sp.* 0.97%, *Protosqualus sp.* 0.73%, *Squatina sp.* 0.24%, *Clamydoselachus tateri* 0.48%, *Sphenodus sp.* 0.24%, "*Cretolamna appendiculata*" 0.48%.

animals such as other large-sized teleosts, sharks, and plesiosaurs (Nagrodski et al., 2012).

7. Fish and salinity

Preliminary the present evidence suggests that the Upper Cretaceous–lower Paleocene Marambio Group was deposited in shelf and transitional environments (Marenssi et al., 2012). The fish record –at all bearing units of the James Ross Basin– indicates normal marine (in salinity and oxygen content) water. This supports other sources of evidence (e.g., cysts, invertebrates, mosasaurs see Tobin et al., 2012; Bowman et al., 2014). The nature of preservation of fossil bony fish elements as well as other fossil remains attests to a relatively high energy in the environment or reworking. However, Units 9 and 10 might have been deposited in outer shelf settings (Tobin et al., 2012). The occurrence of some rare holocephalans, which are characteristics for continental slopes such as *Rhinochimaeridae* and *Chimaera* in Unit 9, supports this interpretation (Table 1 of Supplementary Material). However, these holocephalan remains were considered allochthonous (Otero et al., 2014).

The Upper Cretaceous–lower Paleocene Marambio Group did not provide freshwater or amphibiotic taxa. However, they should be present in nearby continental environments because closely related freshwater fishes (Dipnoi) inhabited South America and Australia during the Late Cretaceous (Cione and Gouiric-Cavalli, 2012).

8. Geographical distribution and climate

The present distribution of marine fishes is useful to infer ancient water temperatures and other variables during the Cenozoic, especially the Neogene. During the Cretaceous, however, it is difficult to hypothesize temperatures based on modern distributions because many dominant taxa became extinct at the K/Pg boundary and many ancestral forms had not yet evolved by then. The Late Cretaceous ichthyofaunas of the James Ross Basin include some widespread fish taxa such as *Carcharias*, *Scapanorhynchus*, *Ichthyodectiformes*, and *Enchodus*. However, no taxa indicative of supposedly warm or temperate latitudes (e.g., *Anacoracidea*, *Ptychodus*, *Cretoxyrhinidae*, *Serratolamnidae*, *Orectolobiformes*, or

Sclerorhynchidae) are known from the area (Table 1 of Supplementary Material).

Other taxa, such as the sharks *Notidanodon dentatus*, *Paraorthacodus*, and *Protosqualus*, as well as the holocephalan, *Edaphodon*, are widely distributed in middle and high latitudes but few or none were reported from tropical areas. This may be indicative of their temperature tolerance and sensitivity (Cione and Medina, 1987; Cione, 1996; Klug et al., 2008; Gouiric-Cavalli et al., 2015). Noteworthy, these taxa almost completely fail to occur in the well-known warm Late Cretaceous and early Paleogene marine ichthyofaunas from Morocco (Arambourg, 1952; Cappetta et al., 2014), “la Méditerrané américaine” (Lériche, 1938) or Niger (Cappetta, 1972), the Cretaceous of Egypt (Churcher and Russell, 1992), Brazil (Rebouças and Santos, 1956), or Lebanon (Cappetta, 1980).

Notidanodon is known from the Cretaceous of Australia, New Zealand, California, Antarctica, and southernmost South America (Cione and Medina, 1987; Cione, 1996; Bogan et al., 2016). Several species of *Protosqualus* are known from the Albian and Cenomanian of northern Europe and Russia but the genus is unknown from the North American Western Interior Seaway (see Cappetta, 2012). It has also not been reported from tropical Tethyan sites, but is present at several Albian sites and the Upper Cretaceous of Australia, India and southern South America (Kemp, 1991; Underwood et al., 2011; Bogan et al., 2016). *Notidanodon* in the Paleocene of Morocco and palaeospinacids in the Cretaceous of Israel are rare examples in warm areas (Lewy and Cappetta, 1989; Cappetta, 2012). *Edaphodon* species are widely distributed in the Northern Hemisphere in the Upper Cretaceous, but is only represented by *E. kawai* (New Zealand) and *E. snowhillensis* (Antarctica) in the Southern Hemisphere at this time (Gouiric-Cavalli et al., 2015).

A bipolar pattern appears evident in shelf areas for these taxa (Cione, 1996) and temperature might be responsible for this pattern. It is unknown if they were usual inhabitants of open ocean or deep waters.

The paleogeographic distribution of *Notidanodon dentatus*, *Paraorthacodus*, *Protosqualus*, and *Edaphodon* also partially agrees with the invertebrate pattern of a Boreal and an Austral Temperate Realms separated by a warmer Tethyan Realm (Kauffman, 1973; Aguirre Urreta et al., 2008).

Zinsmeister (1982; see also Harasewych et al., 2009) proposed a cold temperate Weddellian marine mollusk province for the shallow seas ranging from southern South America through Antarctica to Australia and New Zealand. Later, it was extended to land faunas and floras as well (see Reguero et al., 2013). Accordingly, Late Cretaceous ichthyofaunas of the James Ross Basin are related to coeval faunas of southern South America. A recent survey in the Maastrichtian Calafate Formation, Southwest of Santa Cruz Province (50°16'S) yielded teeth of *Notidanodon dentatus* and *Protosqualus* (Bogan et al., 2016), both sharks also occurring in the LBF. This latter also shares several taxa with the Maastrichtian Dorotea and Quiriquina formations of southern Chile: *Paraorthacodus*, *Carcharias*, *Edaphodon*, and *Callorhynchus* (see compilation by Suárez, 2015). However, in the Quiriquina Formation of Chile (30°–37°S) – deposited during a Pacific transgression rostral spines of the ray family Sclerorhynchidae, an inhabitant of warm Late Cretaceous seas, are common. Also, sclerorhynchids and the warm-temperate to warm water shark, *Serratolamna serrata*, occur in the upper Maastrichtian Dorotea Formation at Sierra Baguales, Chile (50° 48'S), being the southernmost record of both taxa (Otero et al., 2013b). The presence of the sclerorhynchid *Ischyrrhiza chilensis* in the Dorotea Formation might indicate a relatively direct connection with the Pacific (Otero et al., 2013b). Taxa of warm waters such as Anacoracidae and Serratolamnidae are abundant in the Maastrichtian Jagüel Formation, northern Patagonia (39°43'S) and Cuyo (36°12'S) in Argentina – deposited during an Atlantic

transgression – (Bogan and Agnolin, 2010; Prámparo et al., 2013). However, they are not – to date – present in the James Ross Basin. Yet, invertebrates from the Maastrichtian of Neuquén Basin have Weddellian affinities (Aguirre Urreta et al., 2008).

The temperature development of the James Ross Basin at the end of Cretaceous and beginning of the Paleogene is still debated (Kemp et al., 2014). Notably, the MBT/CBT (methylation index of branched tetrathers/cyclization ratio of branched tetrathers) paleothermometer, indicates that a predominantly cool temperate climate prevailed during the late Maastrichtian and Paleocene of the Antarctic Peninsula (Kemp et al., 2014). However, temperature oscillations were recognized for the late Maastrichtian (for a synthesis, see Witts et al., 2015). The palynomorph record of James Ross Basin is in agreement with a relatively cool early Maastrichtian time, a warm late Maastrichtian, and a possible cooling after the K/Pg event (see Bowman et al., 2013, 2014). The Maastrichtian fish record does not show any indication of a change in the temperature as it is not shown when we compare Unit 9 with older ones (Table 1 of Supplementary Material). The Paleocene fish record is very limited for a comparison, although some marine genera as ichthyodectiforms and aulopiforms show significant positive correlations with sea temperature, other actinopterygians such as pachycormiforms and marine beryciforms show no correlation with sea temperature (Cavin et al., 2007).

9. The K/Pg extinction event in the James Ross Basin

The global turnover in actinopterygian faunas occurred during Aptian – Cenomanian time (Poyato-Ariza and Martín-Abad, 2016). The K/Pg extinction was a comparatively minor event in the history of the osteichthyans, mostly affecting some important marine swift swimming and piscivorous predators (Poyato-Ariza and Martín-Abad, 2016). Certainly, the mass extinction greatly affected several groups of neoselachians and suspension-feeding actinopterygians (Kriwet and Benton, 2004; Cappetta, 2012; Gouiric-Cavalli and Rasia, 2016). In accordance with the direct observation of taxa diversity in the James Ross Basin there seems no to be a diversity drop at the K/Pg boundary. However, the fish diversity in the seas increased or tended to stagnate during the Late Cretaceous until the marked K/Pg extinction, followed by Paleocene–Eocene diversifications (see Guinot and Cavin, 2015, Belben et al., 2017 for discussion).

The stratigraphic and paleontological record of the transition between the upper Maastrichtian and lower Danian is very well preserved and documented in the James Ross Basin (Zinsmeister, 1998; Bowman et al., 2014). Thus, it is a remarkable area for studying the impact and tempo of the K/Pg extinction event in the high latitude marine fish biocenoses.

The boundary between the Maastrichtian and the Danian was identified between Unit 9 and Unit 10 in Marambio Island where a glauconitic bed with the iridium anomaly occurs, in the middle of paleomagnetic C29r zone (Zinsmeister, 1998; Tobin et al., 2012; Bowman et al., 2014). The fish fossils described here (along with plesiosaur and mosasaur teeth) were collected in Unit 9 very close below this bed (the uppermost 10 m; Fig. 3).

The Unit 9 fish association does not include several typical Cretaceous elasmobranch taxa such as Anacoracidae, the ptychodontid *Ptychodus*, most Cretoxyrhinidae, Serratolamnidae, and Sclerorhynchidae, more probably for temperature constraints than taphonomic biases (see above). Most of these groups became extinct during the K/Pg extinction event. However, in Unit 9 there are several other taxa that also became extinct during the event: *Notidanodon dentatus*, *Propriostrophus*, *Protosqualus*, *Callorhynchus torresi*, *Enchodus*, Pachycormiformes, and Ichthyodectiformes (Table 1 of Supplementary Material). Other chondrichthyans

became extinct in stratigraphic older Upper Cretaceous units: *Edaphodon snowhillensis* and perhaps *Chimaera zangerli* (Table 1 of Supplementary Material). The upper levels of Unit 9 yielded the most diverse and abundant ichthyofauna in the Cretaceous of Antarctica (Table 1 of Supplementary Material) comparable to the assemblages of the Lachman Crags Member of the Santa Marta Formation, Santonian–lower Campanian and the Herbert Sound Member of the Snow Hill Formation, upper Campanian (Table 1 of Supplementary Material). Consequently, no decrease in fish diversity and abundance was observed during the Maastrichtian before the K/Pg boundary. Otero et al. (2014) mentioned that mosasaurs of Unit 9 were diverse, with four different morphotypes. Reguero et al. (2015a) analyzed the diversity of mosasaurs in LBF and agreed that a rapid extinction occurred. Plesiosaurs are abundant until the K/Pg boundary as well. Some other authors working in the area proposed that the K/Pg extinction event would potentially be the sum of multiple, independent events, at least in high latitudes (see Tobin et al., 2012). However, the vertebrate pattern agrees with an abrupt pulse of cephalopod extinction at the end of the Cretaceous in the same section, when the final seven ammonite species disappeared, being consistent with lower latitude sections in the Tethyan and Boreal regions as well (Witts et al., 2015).

The Southern Hemisphere might have provided biodiversity refuges after the K/Pg mass extinction with a rapid recovery in both, continental and marine environments (Donovan et al., 2016). Unfortunately, very few fishes were reported from Unit 10 and the Sobral Formation. But, is this an actual representation of the high latitude earliest Danian ichthyofaunas after the K/Pg extinction or a matter of preservation? The Paleocene–Eocene interval witnessed a major fish radiation which is one of the two most important in vertebrate history (Guinot and Cavin, 2015). The Eocene ichthyofaunas of Marambio Island are very diverse and rich in specimens (Cione et al., 1977; Reguero et al., 2013 and references therein). They are dominated by taxa that were comparatively rare in the Cretaceous of the James Ross Basin such as mitsukurinid, odontaspimid, squatinid, and pristionphorid sharks, and myliobatid rays.

10. Conclusions

The review and analyses of previous and present collections allow us to arrive at the following conclusions.

Many of the Cretaceous Antarctic fishes were collected in the Santa Marta Formation of Vega and Ross islands (e.g., Richter and Ward, 1990). Most come from the Herbert Sound Member (=Gamma Member). Recently, Olivero (2012) assigned this member to the Snow Hill Island Formation. So, according to Olivero's lithostratigraphic scheme, the fish association assigned to the Santa Marta Formation becomes smaller and only is represented by *Clamydoselachus thompsoni*, *Notidanodon dentatus*, *Paraorthacodus antarcticus*, *Sphenodus* sp., "*Cretolamna appendiculata*," *Albuliformes* indet., *Ichthyodectiformes* indet., and *Enchodus* sp.

The present fish collection at LBF includes the first record of Squaliformes (*Protosqualus* sp.), the orthacodontid *Sphenodus*, probably the odontaspimid *Carcharias*, a member of the lamniform species group "*Cretolamna*," and the teleost *Enchodus* for the LBF; the first probable report of the pristionphorid, *Propristiophorus*, the youngest record of orthacodontids for Antarctica, and the first Cretaceous record of Pachycormiformes in Antarctica.

We consider the occurrence of the genera *Odontaspis* and *Centrophoroides* in Antarctica as well as the genus *Pristiophorus* in the Antarctic Cretaceous unsupported.

We also report the first fish remains identified from the Paleocene (the lowermost Danian Unit 10 of LBF and the Danian Sobral Formation) of Antarctica. The otodontid "*Cretolamna appendiculata*"

of Unit 10 is the oldest identified Cenozoic fish from Antarctica and the first Cenozoic report of the group "*Cretolamna*" in Antarctica.

The new material of *Paraorthacodus* along that collected by Otero et al. (2014) shows features that suggest that it might be a new species. It clearly differs from other close Cretaceous species such *P. antarcticus* from Antarctica and *P. patagonicus* from Patagonia.

Several fishes show a bipolar biogeographical pattern in the Late Cretaceous: *Notidanodon*, *Paraorthacodus*, *Protosqualus*, *Edaphodon*, and *Pachycormiformes*. They have not been documented in the warmest areas. At the same time, many Cretaceous taxa typical of warm water fail to occur in Antarctica.

The transition between the Cretaceous and the Paleogene occurs between the Unit 9 and Unit 10 of LBF. Fish remains of Unit 9 are relatively abundant in the last 10 m below the K/Pg boundary and include some typical Cretaceous taxa that became extinct: *Notidanodon dentatus*, *Scapanorhynchus*, *Propristiophorus*, *Enchodus*, and *Ichthyodectiformes* along with other taxa that transpired the extinction in other areas: *Squatina*, *Carcharias*, and *Sphenodus*. Above the K/Pg boundary, in Unit 10, the diversity and abundance dramatically drops, and only a few specimens of "*Cretolamna appendiculata*" and indeterminate odontaspimids were found. Danian beds of South America are dominated by these taxa (Cione, 1988; Cione et al., 2012). Consequently, the marine fish evidence of LBF supports a rapid extinction event at the very K/Pg boundary. However, additional exploration of the Paleocene beds in Antarctica is necessary for better understanding their poor fish record.

Remarkably, some of the Late Cretaceous Antarctic fish taxa are known only from the Paleocene in lower latitudes: the shark *Clamydoselachus tateri* and the holocephalian *Ischyodus dolloi*. It is clear that the Cretaceous Antarctic ichthyofauna showed certain endemism what is in agreement with the high latitude: *Clamydoselachus thompsoni*, *Paraorthacodus antarcticus*, *Edaphodon snowhillensis*, *Callorhynchus torresi*, *Chimaera zangerli*. All these taxa became extinct in the K/Pg or before along with *Enchodus*, *Pachycormiformes*, and *Ichthyodectiformes*. A possible scenario of heterochroneity could be represented by a migration of the chondrichthyans *C. tateri* and *I. dolloi* to the North, after being originated in Antarctica environments along with several invertebrate taxa.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.cretres.2018.01.004>.