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Ultimate Eocene (Priabonian) Chondrichthyans (Holocephali, Elasmobranchii) of Antarctica

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Abstract

The Eocene La Meseta Formation on Seymour Island, Antarctic Peninsula, is known for its remarkable wealth of fossil remains of chondrichthyans and teleosts. Chondrichthyans seemingly were dominant elements in the Antarctic Paleogene fish fauna, but decreased in abundance from middle to late Eocene, during which time remains of bony fishes increase. This decline of chondrichthyans at the end of the Eocene generally is related to sudden cooling of seawater, reduction in shelf area, and increasing shelf depth due to the onset of the Antarctic thermal isolation. The last chondrichthyan records known so far include a chimeroid tooth plate from TELM 6 (Lutetian) and a single pristiophorid rostral spine from TELM 7 (Priabonian). Here, we present new chondrichthyan records of *Squalus*, *Squatina*, *Pristiophorus*, *Striatolamia*, *Palaeohypotodus*, *Carcharocles*, and *Ischyodus* from the upper parts of TELM 7 (Priabonian), including the first record of *Carcharocles sokolovi* from Antarctica. This assemblage suggests that chondrichthyans persisted much longer in Antarctic waters despite rather cool sea surface temperatures of approximately 5°C. The final disappearance of chondrichthyans at the Eocene–Oligocene boundary concurs with abrupt ice sheet formation in Antarctica. Diversity patterns of chondrichthyans throughout the La Meseta Formation appear to be related to climatic conditions rather than plate tectonics.

Introduction

The modern Southern Ocean is delimited by the circum-Antarctic current (= Antarctic Convergence). The Antarctic continent is located within it, and these are amongst the most

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remote and coldest places in the world. They are key elements in any model of Earth processes and climatic change, as well as sites with unique scientific characteristics (Kriwet, 2005). The extant fish fauna within the Antarctic Convergence is striking in its low taxonomic diversity and high number of endemic taxa. Fishes that have evolved special morphological and physiological traits to survive in the extreme, low sea water temperatures are the dominant elements of this fauna (e.g., Eastman and Grande, 1989; Eastman, 1993; Albertson et al., 2010; Ingram and Mahler, 2011; Marshall, 2012; Near et al., 2012).

Chondrichthyans seemingly were major faunal components of pre-Oligocene Antarctic fish faunas, whereas chondrichthyan records from Neogene strata are still lacking. Similarly, the extant chondrichthyan fauna of the Southern Ocean surrounding Antarctica is extremely impoverished. Up to the present, only a few specimens belonging to three shark species have been reported, mostly off the Kerguelen Plateau (e.g., Gon and Heemstra, 1990), and it still is not established whether these sharks enter the Southern Ocean sporadically or represent permanent residents. Batoid diversity is slightly higher with eight described resident species (Gon and Heemstra, 1990; Long, 1994). Living holocephalans have not yet been recorded from Antarctic waters.

Post-Cretaceous and pre-Oligocene Antarctic fishes are mainly known from Seymour Island, which is located at the northern tip of the Antarctic Peninsula. Here, late early to late Eocene marine sediments of the La Meseta Formation yield the most diverse Paleogene ichthyofauna from the Southern Hemisphere to date, comprising cartilaginous and bony fishes (e.g., Welton and Zinsmeister, 1980; Jerzmanska, 1988; Eastman and Grande, 1989, 1991; Balushkin, 1994; Cione and Reguero, 1995, 1998; Doktor et al., 1996; Long, 1992a, 1992b, 1992c). The lack of post-Eocene fish records results in a gap of approximately 38 million years of unknown evolutionary history of Antarctic fishes between the Eocene–Oligocene boundary and the modern Antarctic fish fauna. Eocene Antarctic fishes consequently are very important for understanding evolutionary and adaptive processes in marine vertebrates related to abiotic causes such as plate-tectonically mediated dispersal and climatic perturbations, including the ‘Early Eocene Climatic Optimum’ and the onset of Antarctic ice-shield formation.

Chondrichthyan remains have previously only been reported from Ypresian to Lutetian (early–middle Eocene) strata, with most Eocene fish specimens occurring within Ypresian horizons, especially the *Cucullea* allomembers (late Ypresian) of the La Meseta Formation on Seymour Island (Reguero et al., 2012). Long and Stilwell (2000) reported additional selachian teeth from Eocene deposits of Mount Discovery in East Antarctica. All available data from published records imply a consistent increase in species richness of elasmobranchs and holocephalans from the earliest to the latest Ypresian (Tertiary Eocene La Meseta [TELMs] 2–5; Sadler, 1988) followed by rapid declines in both taxonomic diversity and abundance of specimens (e.g., Kriwet, 2005). Remains of chondrichthyans seemingly are very rare in the lower parts of the middle Eocene (Lutetian; TELM 6) and completely absent from upper parts of the middle Eocene (Bartonian; TELM 7) and the late Eocene (Priabonian; TELM 7) of the La Meseta Formation according to our current knowledge. Bony fish remains are quite abundant throughout the La Meseta Formation, including middle and late Eocene strata (e.g., Jerzmanska, 1988, 1991; Eastman and Grande, 1989, 1991; Jerzmanska and Swidnicki, 1992; Long, 1992a; Kriwet and Hecht, 2008). The disappearance of elasmobranchs and holocephalans towards the end of the Eocene in Antarctica generally is thought to be related to progressive cooling, reduction in shelf area, and increasing shelf depth due to the onset of Antarctic isolation through the establishment of the circum-Antarctic current (e.g., Grande and Eastman, 1986). The objective of this study is to describe the stratigraphically youngest and ultimate elasmobranch and chimeroid remains from the uppermost parts of the La Meseta Formation, which is ‘Layer 38’ according to the geological map of Montes et al. (2013). This new assemblage provides new information about Antarctic chondrichthyan diversity patterns during the Eocene and their final disappearance in relation to thermal changes at the Eocene–Oligocene boundary.

Locality and Stratigraphic Setting

Seymour Island is situated northeast of the Antarctic Peninsula in the Weddell Sea (Fig. 1A–B). It is a rather small island, about 20 km long and 9 km wide, which is not covered by glaciers and is considered one of the most productive Paleogene vertebrate sites in the Southern Hemisphere. Here, Paleogene fossils occur in the La Meseta Formation, which represents the top of the sedimentary infill of the Late Jurassic–Cenozoic James Ross Basin (e.g., Del Valle et al., 1992). Deposition of the La Meseta Formation took place from the Ypresian to the Priabonian according to Sr isotope dating (Dingle and Lavelle, 1998). The mostly unconsolidated sediments of this formation are subdivided into three transgressive-regressive cycles (Units I to III; Elliot and Trautman, 1982), or seven major lithofacies (TELMs 1 to 7), or six allomembers based on erosionally based internal units (Marenssi et al., 1998). These units represent different depositional environments ranging from deltaic and estuarine to shallow marine settings (Marenssi et al., 1998). The chondrichthyan remains described herein are from the uppermost parts of the depositional sequence of the La Meseta Formation and are referred to the upper part (‘Layer 38’ according to the Geological Map of Montes et al., 2013) of the Submeseta Allomember or TELM 7 (Fig. 1B). These sediments are of Priabonian age (late Eocene; TELM 7) and were deposited in a shallow marine, coastal environment (Stilwell and Zinsmeister, 1992, Reguero et al., 2013).

Materials and Methods

Argentinian-Swedish field parties from a joint project of the Instituto Antártico Argentino (DNA-IAA) and the Swedish Polar Research Secretariat (SPFS) collected the material that forms the focus of this study during three Antarctic summer campaigns between 2011 and 2013. The material consists exclusively of isolated shark teeth and two chimeroid tooth plate remains. The specimens were obtained by surface collecting at three sites exposed in the northern part of Seymour Island, south, southeast, and north of Marambio Base. All specimens described here are deposited in the palaeozoological collections of the Swedish Museum of Natural History (Department of Palaeobiology), with registration numbers prefixed by ‘NRM-PZ.’ The single recovered fin spine was scanned using a Skyscan 1173 (Bruker) desktop micro-CT device at the Department of Paleontology, University of Vienna, at 100 kV, 80 μA for 750 ms with Al filter and an image pixel size of 19.93 μm. Manual segmentation with unconstrained smoothing of digital μCT tiff images, 3D rendering, and analyses were performed using Amira version 5.4.1 (Visualization Sciences Group).

The terminologies and systematic scheme used here for the sharks essentially follows Cappetta (2012). We use the term ‘selachian’ when referring to sharks and ‘batomorph’ when referring to rays. Terms used in the description of the fin spine are according to Jerve et al. (2014). We refer to the saw shark specimen as ‘rostral spine’ rather than ‘rostral tooth’ to clearly distinguish this element from dental structures within the mouth cavity. The terminology employed for the chimeroid specimen follows Stahl (1999). References for fossil occurrences are not exhaustive.

Systematic Paleontology

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order SQUALIFORMES Goodrich, 1909

Family SQUALIDAE Bonaparte, 1834

Genus *SQUALUS* Linnaeus, 1758

Type Species—*Squalus acanthias* Linnaeus, 1758; extant.

Stratigraphic Range—Campanian (Late Cretaceous)–Recent.

Fossil Occurrences (Selected)—Europe (Lawley, 1876; Brozobathy and Kalabis, 1970; LeDeux, 1972; Hermann, 1977; Cappetta, 2012); Russia (Glikman, 1964); North and South America (Fitch, 1968; Welton, 1972); Asia (Itoigawa and Nishimoto, 1974; Itoigawa et al., 1985).

Squalus Sp. (Figs. 2–3)

Material—Single dorsal fin spine, NRM-PZ P16000.

Horizon and Locality—Level 38 within the Submeseta Allomember, close to locality DPV 13/84, Plateau SE Marambio Base, S64°14.650′, W056°36.620′.

Age—Upper TELM 7, Priabonian, late Eocene.

Description—The single specimen of this taxon recovered from the uppermost parts of the La Meseta Formation measures 50.98 mm in height, 8.98 mm in width, and 11.10 mm in depth (Fig. 2A–F). It is slender, elongated, and slightly curved posteriorly (Fig. 2A–B). The apex and the base are damaged and incompletely preserved. This damage allows for the distinction of the cap, trunk, and associated individual layers (Fig. 2F). Most of the preserved fin spine is covered with a continuous and completely smooth enamel-like (= enameloid) superficial layer anterolaterally, but which is lacking posteriorly. The enameled portion and associated tissues form the so-called ‘cap’ (e.g., Maisey, 1979, 1982). The external enameloid layer is preserved in the lower 50% of the total length of spine (TLS) but is secondarily lost in the upper 50% TLS due to abrasion.

The basal edge of the enameled cover is oblique, and the underlying grayish dentine is visible. Numerous grayish bands of variable width are arranged parallel to the basal edge of the cap. These bands result from melanocyte staining, which represents the original cap pigmentation (Fig. 2D). Mantle cavities are present directly beneath the enameloid, implying the occurrence of a mantle dentine (= mantle primordium of Maisey, 1979) (see supplementary movie online). There is some evidence of a transitional layer that separates the enameloid cover and the mantle dentine from the inner trunk dentine layers (Fig. 2F).

Two layers of trunk dentine can be distinguished in the micro-CT scan (Fig. 3). It is not possible to detect their thickness with confidence, because both layers are characterized by the same gray value and the separating layer is difficult to identify. Based on the micro-CT scan and the respective three-dimensional (3D) reconstruction, the diameter of the cartilage rod decreases in size towards the spine tip and disappears in the last 25% TLS.

Posteriorly, the trunk is depressed along its entire height, forming a sulcus between the posterior margins of the lateral enameloid surfaces (Fig. 2F). The trunk itself forms a hollow cone that opens basally. The trunk cavity is displaced posteriorly and extends almost three quarters up along the posterior trunk wall (Fig. 3A).

Remarks—Fin spines are present in many extinct and some extant chondrichthyans, such as holocephalans and several basal squalomorphs (e.g., *Centrophorus*, *Centroscymnus*, *Deania*, *Etmopterus*, *Euprotomicrus*, *Oxynotus*, *Squalus*) and galeomorph (*Heterodontus*) selachians (e.g., Maisey, 1974, 1979, 1982; Cione and Pandolfi, 1984; Jerve et al., 2014). The fossil record of chondrichthyans mainly consists of isolated teeth, whereas fin spines are comparatively rare. Up to the present, chondrichthyan fin spines have not been recovered from sediments of the La Meseta Formation on Seymour Island. Consequently, this specimen is an important new contribution because the presence of fin spines suggests that the animal died more or less at the place of fossilization (depending on transportation processes) because fin spines are deeply inserted within the body wall and are not shed, whereas teeth are continuously replaced throughout life, wherever the animal might have lived.

The fin spine is characterized by a smooth and continuous anterolateral enameloid cover, parallel pigmented bands, a posterior non-enameled sulcus, and a posteriorly displaced trunk cavity that extends far up the posteriorly curved trunk. This character combination is very distinctive for fin spines of *Squalus* and readily distinguishes the Antarctic fin spine from those of *Heterodontus*, in which the enameled surface covers a smaller area of the fin spine and the trunk cavity is considerably shorter (Maisey, 1979). The presence of an enameloid cover differentiates the specimen from those of *Deania* and *Euprotomicrus*, which do not have apical enameloid (Cione and Pandolfi, 1984). In *Centrophorus*, *Deania*, and *Etmopterus*, the enameloid cover is not continuous but only consists of ribs. Fin spines of hybodonts and holocephalans differ from those of selachians in the presence of apicobasally arranged hook-like structures along the posterior margin, and they often have strongly ornamented enameloid surfaces (Maisey, 1982).

The fin spine described herein is apically strongly abraded but still preserves the original pigmentation in the lower half of the enameloid cap. The size of the fin spine and the basal margin of the enameloid cap, which is continuous without any irregularities or gnarled patterns, indicate a healthy adult rather than a senile specimen (Maisey, 1979).

The internal structure as revealed in the micro-CT scan displays the characteristic composition, although distinction of the trunk dentine layers is very difficult. The fin spine from the late Eocene of Antarctica seemingly displays a reverse pattern to what is seen in fin spines of extant *Squalus* spp. in that the inner trunk layer is narrower than the outer trunk layer (cf. Maisey, 1979:fig. 4B). The importance of this reversal in structure remains unclear.

So far, only teeth assigned to two different species of *Squalus*, *S. woodburnei* Long, 1992a, and *S. weltoni* Long, 1992a, have been described from the La Meseta Formation on Seymour Island (Long, 1992a). Assignment of the fin spine to either of these two species remains impossible at present.

Order SQUATINIFORMES Compagno, 1973

Family SQUATINIDAE Bonaparte, 1838

Genus *SQUATINA* Duméril, 1806

Type Species—*Squalus squatina* Linnaeus, 1758.

Stratigraphical Range—Valanginian (Early Cretaceous)–Recent.

Fossil Occurrences (Selected)—Africa (Noubhani and Cappetta, 1997); Antarctica (Kriwet, 2005; Kriwet et al., 2006); Asia (Itoigawa and Nishimoto, 1974); Europe (Cappetta, 2012); North America (Meyer, 1974; Cappetta and Case, 1975); Russia (Glikman, 1964); South America (Suárez et al., 2006).

Squatina Sp. (Fig. 4)

Material—A single tooth, NRM-PZ P16005.

Horizon and Locality—Level 38 within the Submeseta Allomember, locality NRM 2, Slope S Marambio Base, S64°14.778′, W056°37.169′.

Age—Upper TELM 7, Priabonian, late Eocene.

Description—The single specimen displays the characteristic features of teeth attributable to *Squatina* (Fig. 4A–C). It measures ca. 6.52 mm in mesiodistal width and ca. 3.95 mm in height. The tooth crown is laterally expanded and displays well-developed lateral heels without lateral cusplets or indentations (Fig. 4A). The main cusp is rather bulky basally but slender apically, upright, and slightly bent lingually (Fig. 4B). The cutting edges of the main cusp and lateral heels are strong and continuous. The lateral heels are low in labial and lingual views, with rounded lateral edges (Fig. 4A) that are not curved lingually in occlusal view (Fig. 4C).

The labial face of the crown is convex from side to side and overhangs the root basally with a well-developed prominent and knob-like protuberance (Fig. 4A–B). The protuberance is narrow in labial view and rather short in lateral views, not reaching the root base. The lateral edges of the labial protuberance are smooth and converge medially, forming a rounded basal edge. The tooth crown is completely smooth labially and lingually, and the basal margin of the labial face is continuous and forms a clear boundary between crown and root.

The lingual face of the crown is strongly convex and continues into a very short but broad tongue-shaped uvula that covers the lingual protuberance of the root almost completely (Fig. 4C). The occlusal surface of the uvula is rather flat and slightly damaged. The boundary between crown and tooth is well demarcated lingually but slightly furrowed and marked by a neck collar.

The root is rather massive and mesiodistally elongated. It is hemiaulacorhize, with a central foramen that is connected to a second and smaller foramen by a shallow canal on the lingual surface of the root, forming the mediolingual foramen that opens onto the lingual face of the protuberance just below the neck collar. There are four small marginolingual foramina on each side of the uvula (Fig. 4C).

The root lobes are flared and marginally protrude below the crown in labial view (Fig. 4A). Lingually, they meet to form a broad protuberance. In basal view, the root has a heart-shaped outline. The root lobes are well separated and broadly divergent, forming a shallow labial trough. The basal surfaces of the root lobes are flat and pierced by many very small and incipient foramina.

Remarks—Living angel (or sand devil) sharks represent a peculiar group of bottom-dwelling sharks of moderate body size (total length about 1–2 m) that superficially resemble rays. Twenty-two extant species are known, and the genus is probably globally distributed in tropical and temperate seas (e.g., Compagno et al., 2005; Last and White, 2008; Kriwet et al., 2010; Stelbrink et al., 2010; Klug and Kriwet, 2013). Most living species are highly endemic, with only a few species displaying wider distribution patterns.

The fossil record of squatinids mainly consists of isolated teeth and only rare skeletal remains (Klug and Kriwet, 2013). The oldest remains are isolated teeth from the Valanginian (Early Cretaceous), and 34 fossil species have been described up to now. The sister group of squatinids are the extinct pseudorhinids, which are known by numerous well-preserved complete (holomorphic) specimens from the Jurassic and Early Cretaceous (see Klug and Kriwet, 2013).

Paleogene Gondwana records of *Squatina* consist of isolated teeth reported from India (late Paleocene–early Eocene; Rana et al., 2005), Antarctica (early–middle Eocene; Welton and Zinsmeister, 1980; Case, 1992; Long, 1992a), Chile (middle–late Eocene; Otero et al., 2012, 2013), North Africa (late Eocene; Underwood et al., 2011), and the Oligocene of Australia (Pfeil, 1984). All previous Antarctic *Squatina* records were recovered from TELMs 4 and 5 on Seymour Island, and the single *Squatina* tooth from TELM 7 extends the known stratigraphic range of this taxon into the Priabonian. It displays the general squatinid morphology (e.g., mesiodistally enlarged teeth with lateral heels lacking lateral cusplets, smooth tooth crowns, a labial, knob-like protuberance of the crown extending basally almost to the basal level of the root, hemiaulacorhize root vascularization). The straight cutting edges of the lateral heels in occlusal view, which are not curved lingually, and the distally inclined cusp identify the tooth as coming from a lateral jaw position. It is, however, not possible to assign this tooth to either the upper or lower jaw.

Teeth of squatinids, unfortunately, are morphologically very generalized and display only a few distinct characters for species discrimination (see Klug and Kriwet, 2013, for a detailed discussion of dental characters). Therefore, assignment of the single specimen from TELM 7, as well as all other records from TELMs 4 and 5 to any particular species, would be premature without more complete material. We assume that the teeth from Seymour Island might represent a distinct species considering today's distribution patterns of squatinids. This, however, requires detailed morphological analyses of all squatinid remains throughout the La Meseta Formation.

Order PRISTIOPHORIFORMES Berg, 1958

Family PRISTIOPHORIDAE Bleeker, 1859

Genus PRISTIOPHORUS Müller and Henle, 1837

Type Species—*Pristis cirratus* Latham, 1794; extant.

Stratigraphic Range—Albian (Early Cretaceous)–Recent.

Fossil Occurrences (Selected)—Africa (Herman, 1973); Antarctica (Grande and Eastman, 1986; Long, 1992a); Australia and New Zealand (Keyes, 1982); Europe (Jaekel, 1890; Herman et al., 1974; Cigala-Fulgosi, 1986); Near East (Woodward, 1932); North America (Welton, 1972; Barnes et al., 1981; Long, 1992a); Pacific region (Nishimoto and Morozumi, 1979); South America (Cione and Exposito, 1980; De Muizon and De Vries, 1985).

Pristiophorus Lanceolatus (Davis, 1888) (Fig. 5A–C)

Material—A single rostral spine, NRM-PZ P16006.

Horizon and Locality—Level 38 within the Submeseta Allomember, locality NRM 2, Slope S Marambio Base, S64°14.778′, W056°37.169′.

Age—Upper TELM 7, Priabonian, late Eocene.

Description—The specimen recovered from the uppermost parts of the La Meseta Formation is a slightly abraded rostral spine with the basal margin of the basal peduncle being damaged (Fig. 5A–C). The crown, conversely, is completely preserved and shows only minor weathering damage near the tip (Fig. 5A). It measures 15.73 mm in height, 2.62 mm dorsoventrally, and 3.58 mm anteroposteriorly. The spine is elongate, lanceolate in dorsal and ventral views, and weakly curved posteriorly with an almost straight anterior cutting edge that is slightly convex apically, and has a slightly concave posterior cutting edge (Fig. 5A– B). In anterior view, the crown is laterally compressed with apically tapering margins

(Fig. 5C). The dorsal and ventral faces are slightly convex transversely, with this convexity increasing towards the base. The surfaces are completely smooth and lack any ornamentation. The crown considerably overhangs the basal peduncle, with a well-developed bulge with almost straight margins in anterior and posterior views but with convexly curved and posteriorly oblique basal margins in dorsal and ventral views. The cutting edges are quite sharp and extend from the apex almost to the base. They fade out a short distance above the bulge.

The basal peduncle is considerably shorter than the crown and only takes up ca. 28% of total spine length. In dorsal and ventral views, the lateral margins of the peduncle are flaring and thus give the basal portion of the peduncle an anteroposteriorly elongated appearance. In anterior view, the lateral margins are concave. Basally, remnants are preserved of the anteroposteriorly directed nutritive canal in which the pulp cavity opens broadly.

Remarks—Living saw sharks of the order Pristiophoriformes are arranged into two genera, *Pliotrema* Regan, 1906, and *Pristiophorus* Müller and Henle, 1837, with eight valid species according to Militante (2012).

Saw sharks occur in temperate regions on continental and insular shelves, and upper slopes of the northwest and southeast Atlantic, west Indian Ocean, and west Pacific Ocean, but also in deeper water in the tropics (Compagno et al., 2005). Fossil saw sharks, conversely, seem to have been geographically more widespread but relatively uncommon (Gottfried and Rabarison, 1997). The fossil record extends back to the Albian, but most species have been described from Cenozoic deposits (e.g., Keyes, 1982). *Pristiophorus lanceolatus* occurs in TELMs 3, 4, 5, and 7. Tambussi et al. (2006) previously indicated the presence of *P. lanceolatus* in the *Anthropornis nordenskjoeldi* biozone from the uppermost part of TELM 7.

The smooth and completely unornamented crown readily distinguishes the rostral spine described here from those of *Pristiophorus tumidens* Woodward, 1932, from the Santonian of Lebanon, and from the Miocene species *Pristiophorus suevicus* Jaekel, 1890. In Oligocene *Pristiophorus lineatus* Applegate and Uyeno, 1968, the cutting edges are parallel and the apex is blunt in comparison with *P. lanceolatus*. Rostral spines of extant *Pliotrema* and extinct *Ikamauius* spp. differ in having serrated cutting edges. However, rostral spines of other described and still undescribed species resemble those assigned to *P. lanceolatus*, and we consider this species an artificial taxon that includes multiple species with similar morphologies. Dental morphologies might provide a better estimate of the real taxonomic assignment and diversity of fossil *Pristiophorus* spp.

Order LAMNIFORMES Berg, 1958

Family ODONTASPIDIDAE Müller and Henle, 1839

Genus *STRIATOLAMIA* Glikman, 1964

Type Species—*OTODUS MACROTUS* Agassiz, 1843.

Stratigraphic Range—Danian (Early Paleocene) to Priabonian (later Eocene).

Fossil Occurrences (Selected)—Africa (Priem, 1907; Arambourg, 1952); Antarctica (Long, 1992a); Europe (Agassiz, 1843; Siverson, 1995; Adnet, 2006; Dutheil et al., 2006; Van den Eeckhaut and De Schutter, 2009; Diedrich, 2012); North America (Leriche, 1942; Ward and Wiest, 1990; Padilla et al., 2014); Russia (Glikman, 1964; Zhelezko and Kozlov, 1999).

Striatolamia Sp. Cf. *S. Macrota* (Agassiz, 1843) (Fig. 5D–U)

Material—Seven teeth, NRM-PZ P15895, NRM-PZ P15924–15925, NRM-PZ P16001–16004.

Horizon and Localities—Level 38 within the Submeseta Allomember, locality NRM 2, Slope S Marambio Base, S64°14.778′, W056°37.169′; underneath locality NRM 5, Ridge N Marambio Base, S64°13.985′, W056°36.851′.

Age—Upper TELM 7, Priabonian, late Eocene.

Description—All seven specimens are more or less abraded and lack varying portions of the root or cusp apex (Fig. 5D–U). Mesial and distal lateral cusplets are preserved on only three teeth (Fig. 5G–L, S–U). The teeth are of typical odontaspidid appearance, with anterior teeth being long and slender with a sigmoidal profile, whereas the single assignable lateral tooth is less sigmoidal and has more divergent root lobes. The cutting edges are not serrated.

Specimen P15925 (Fig. 5D–F) displays the characteristic crown morphology of a first upper anterior tooth. It is high with a slender central cusp having almost parallel margins in labial view. The apex is acute and slightly bent distally. In profile, the main cusp is slightly sigmoidal and does not jut out labially over the root. In labial view, the cusp is slightly spatulate. The labial crown face is only faintly convex mesiodistally and is devoid of any ornamentation. The labial crown base exhibits a small central depression.

The lingual crown face of the central cusp is weakly convex mesiodistally with a median flattening and displays weak and fine striations, which start at the crown-root junction but do not reach the apex. Apically, the striations become more flexuous. The lateral cutting edges are not well developed (probably due to abrasion) and continuous, extending from the crown tip to almost the central cusp base. The basal crown neck separating the crown from the root is very narrow.

The root is very incompletely preserved, and only a part of the mesial root lobe is preserved. The lingual root protuberance is not well developed, not extending far lingually below the crown, and slightly abraded.

Specimen P15924-2 (Fig. 5G–I) is a second upper anterior tooth. It measures 26.86 mm in total height, 11.26 mm in mesiodistal width, and 7.97 mm labiolingually. The central cusp is inclined distally and sigmoidal in labial and lingual views, with the apex being twisted mesially. In labial view, the central cusp is slightly shorter in height but basally broader than specimen P15925. The enameloid of the labial face is almost completely smooth, lacking vertical striations, except a very short one extending from the base of the labial face a short way apically to the level where the lateral cutting edges fade out. The lateral cutting edges are rather sharp but incomplete and not continuous with the only preserved lateral cusplet, extending from the central cusp apex to the cusp base but fading out distinctly above the cusp-root junction. In profile, the main cusp is sigmoidal, with the apex being twisted labially.

The lingual face of the central cusp is convex mesiodistally with a medial flattening as in specimen P15925. Fine and flexuous striations are present, which start at the crown-root junction. They are rather short on the lingual medial flattening of the crown; but extend very far up the crown laterally, almost reaching the apex. The crown neck is very narrow.

Only one very small but acute lateral cusplet is preserved distally (Fig. 5H). It is separated from the central cusp and has a circular cross-section basally. Cutting edges are not identifiable. The apex is curved towards the central cusp and slightly inclined lingually. The lateral cusplet is positioned lingually with respect to the level of the cutting edge of the central cusp in profile view.

The root is damaged, with only parts of the mesial root lobe remaining. The preserved portion is rather short and is slightly depressed mesiodistally. The lingual protuberance is rather well developed and almost shelf-like. Remnants of the labiolingual nutritive groove are preserved. A small lingual foramen opens on the lingual surface of the protuberance basally.

Specimen P15895 (Fig. 5J–L) comes from the second lower anterior tooth row. It measures 28.20 mm in height, 11.87 mm in mesiodistal width, and 7.91 mm labiolingually.

The central cusp is quite high, slender, and very weakly sigmoidal in labial and lingual views, with the mesial margin being almost straight and the distal one being slightly concave. The apex is lacking but appears to have been twisted mesially, as seen in specimen P15924. In profile view, the crown is slightly sigmoidal and the apex does not jut out over the lingual protuberance.

The labial crown face is very flat and only slightly convex mesiodistally at its base. The medial, vertical ridge originating on the labial face of the central cusp is not well marked but reaches further up than in specimen P15924. The cutting edges are well developed but also do not reach the base of the crown, ending clearly above the crown-root junction. Lingually, the central cusp face is only weakly convex mesiodistally with a pronounced medial flattening. Weak and fine, flexuous striations are present, which reach far up the cusp medially, but do not reach the apex.

A single, distal cusplet is preserved. It is very small and only weakly separated from the central cusp. It is devoid of well-defined cutting edges, and no ornamentation is detectable. The cross-section is circular basally, and the apex curves towards the central cusp.

The root is massive, bilobate, and only slightly damaged. The preserved part of the root constitutes approximately 42% of the preserved total tooth height. The root lobes are divergent and form an asymmetric acute angle. The mesial root lobe appears shorter and broader than the distal one. The distal root lobe is long, rather slender, and basally pointed.

Both lobes are mesio-distally compressed. The protuberance is well developed and shelf-like mesiodistally. The nutritive groove is very shallow, and a small foramen opens on the protuberance basally.

Three isolated central cusps (NRM-PZ P16002–16004; Fig. 5M–R) that display the same features are also assigned to this species. They are morphologically very similar and bear a high and slender, almost triangular main cusp, which is more or less sigmoidal in profile view. One crown, NRM-PZ P16002 (Fig. 5M), also displays complete cutting edges that reach the base of the cusp.

Specimen NRM-PZ P16001 (Fig. 5S–U), which probably represents a lower first lateral tooth, is only tentatively assigned to this taxon. It differs from the specimens described above by a more slender, weakly distally curved central cusp, and a vertical nutritive groove separating the rather shallow lingual protuberance into two parts. Additionally, the lateral cutting edges are complete and reach the crown-root junction basally. The basal edge of the labial face is medially concave and irregular, forming small crenulations. The labial face is very flat and completely devoid of any ornamentation, whereas the lingual face is convex mesiodistally with very strong, densely arranged striations extending from the crown neck far up the cusp but not reaching the acute apex. In profile, the cusp is sigmoidal and the apex is not jutting out above the level of the lingual protuberance. The mesial cusplet is small, well separated from the central cusp, devoid of any ornamentation and cutting edges, and inclined towards the central cusp. It is lingually displaced in relation to the cutting edge in profile view. The distal cusplet is lacking. There is no indication of an additional pair of lateral cusplets. The root is imperfect, with only the mesial root lobe being preserved. It is long and slightly mesiodistally flattened, with a pointed basal extremity. The root lobes seemingly are very divergent, forming a broad and shallow, 'U'-shaped concavity.

Remarks—The fossil genus *Striatolamia* is known from the early Paleocene up to the late Eocene (Cappetta, 2012). The taxonomic identity and systematic position of *Striatolamia* is still debated because of dental similarities to living sand tiger sharks of the genus *Carcharias* (cf. Cunningham, 2000). *Striatolamia* has traditionally been assigned to Odontaspididae (e.g., Compagno, 1984; Long, 1992a; Adnet, 2006).

Striatolamia was dismissed by Long (1992a) and Purdy (1998), who consider it conspecific with *Carcharias*. Alternatively, Siver son (1995), Cappetta and Nolf (2005), and Cappetta (2012) assign *Striatolamia* to Mitsukurinidae, because of similarities to teeth of *Anomotodon hermani*. We follow the more traditional view and consider *Striatolamia* a valid taxon (for reasoning, see next paragraph) within Odontaspididae because of the very close similarities to members of this family, as well as the differences in anterior teeth from *Anomotodon*. Odontaspididae includes *Carcharias* Rafinesque, 1810, *Odontaspis* Agassiz, 1838, *Palaeohypotodus* Glikman, 1964, *Brachycarcharias* Cappetta and Nolf, 2005, *Gluekmanotodus* Zhelezko in Zhelezko and Kozlov, 1999, *Hypotodus* Jaekel, 1895, *Jaekelotodus* Menner, 1928, *Mennerotodus* Zhelezko, 1989, *Orpodon* Cappetta and Nolf, 2005, *Sylvestrilamia* Cappetta and Nolf, 2005, and *Turania* Kozlov, 2001, according to Cappetta (2012).

Teeth of *Striatolamia* differ from those of *Carcharias* most notably in having very small, rounded, and medially inclined lateral cusplets, less pronounced sigmoidal profile view, cutting edges that are confined to the lateral margins of the central cusp rather than being displaced labiobasally, and more massive root lobes that form an acute divergent angle (see Ferrusquia-Villa-franca et al., 1999; Cunningham, 2000).

Teeth of *Odontaspis* and *Palaeohypotodus* are easily differentiated from teeth of *Striatolamia* by the smooth lingual face of the central cusp and the presence of two pairs of lateral cusplets, of which the first lateral ones closest to the central cusp are distinctly large. Additionally, teeth of *Palaeohypotodus* depart from teeth of *Striatolamia* in the presence of coarse, short, and vertical striations at the base of the labial crown face along the crown-root junction. The tooth NRM-PZ P16001 resembles teeth of *Palaeohypotodus* in the presence of labial crenulae along the labial crown base, but the very small lateral cusplet supports its assignment to *Striatolamia*. This tooth most likely represents a juvenile or subadult individual.

Teeth of *Brachycarcharias* have a more robust central cusp and generally larger lateral cusplets, generally accompanied by a second pair of incipient cusplets, whereas teeth of the odontaspidids *Gluekmanotodus*, *Hypotodus*, and *Jaekelotodus* easily can be distinguished by the lack of any labial or lingual crown ornamentation. Teeth of *Mennerotodus* and *Orpodon* lack any lingual ornamentation. Additionally, teeth of *Orpodon* are characterized by a pair of large and robust lateral cusplets and a second incipient pair. In *Sylvestrilamia*, the cutting edge is continuous between the central cusp and the lateral cusplets.

Teeth of *Turania* are very similar to those of *Carcharias* and *Striatolamia*, but Cappetta (2012) doubts the validity of *Turania*. Anterior teeth of *Turania* differ from those of *Striatolamia* in being comparatively short and less sigmoidal in profile view.

Teeth of *Mitsukurina* largely agree morphologically with those of Striatolamia. They differ, however, in lacking lateral cusplets in anterior teeth and in the striation pattern. Lateral cusplets are absent in all tooth position in *Alopias*, *Anomotodon*, and *Woellsteinia*. Incipient lateral cusplets occur in *Macrorhizodus*. Teeth of other lamniforms such as *Cretalamna*, *Isurolamna*, and *Usakia* are devoid of any ornamentation on the labial and lingual central cusp faces.

According to Cappetta (2012), five species of *Striatolamia* have been described, including *S. cederstroemi* Siverson, 1995, *S. macrota* (Agassiz, 1838), S. *siberica* Zhelezko in Zhelezko and Kozlov, 1999, S. *striata* (Winkler, 1876), and ‘S.’ *whittei* (Arambourg, 1952).

Striatolamia cederstroemi from the upper Danian of Sweden has poorly defined lateral cusplets, whereas they are well separated from the main crown in *S. striata* and *S. macrota*. Teeth of *S. striata*, which might represent the ancestor of *S. macrota* according to Cappetta (2012), differ from teeth of the latter in better-developed lingual striations in all tooth positions. Teeth of ‘*S.*’ *whittei* display a rather peculiar morphology of the lateral cusplets and the form of the root lobes, and it thus probably warrants placing this species in its own genus (Zhelezko, 1989; Cappetta, 2012). The teeth from TELM 7 of Seymour Island display the basic characters of *S. macrota* (Agassiz, 1835) but have a very distinct medial flattening of the lingual crown face and very weak striations, which cover the complete lingual face up to the cutting edges. In this, the teeth differ from typical teeth of *S. macrota*. However, more material is necessary to establish the significance of these differences, because the labial ornamentation is highly variable in *Striatolamia* and *Carcharias*. Therefore, we assign the teeth described here tentatively to this species.

Compared with Eocene Arctic representatives of *S. macrota* (cf. Padilla et al., 2014), the Antarctic specimens seem to be slightly larger with more pronounced striations. The appearance, nevertheless, is more or less similar in both locations. Teeth assigned to *S. macrota* from the Paleogene of Morocco resemble teeth from the Arctic and Antarctica but are more delicate in overall appearance and in the striations.

Striatolamia macrota is the dominant species within all TELMs (e.g., Kriwet, 2005; Reguero et al., 2012; Engelbrecht et al., 2014; Kriwet et al., 2014). Dental resemblances to *Carcharias* and *Mitsukurina* imply that this species probably occupied a similar trophic niche. A detailed analysis of palaeogeographic occurrences and dental patterns might provide a better understanding of its ecological role.

Genus †*PALAEOHYPOTODUS* Glikman, 1964

Type Species—*Odontaspis rutoti* Winkler, 1876; from the middle Paleocene, Selandian, of Belgium.

Stratigraphic Range—Early Paleocene–late Eocene.

Fossil Occurrences (Selected)—Antarctica (Long, 1992a); Europe (Leriche, 1951; Casier, 1967; Gurr, 1962; Herman, 1972; Ward, 1980; Cappetta, 1987; Rayner et al., 2009; Iserbyt and De Schutter, 2012); Greenland (Bendix-Almgreen, 1969); North America (Ward and Wiest, 1990); Africa (Herman, 1973; Cappetta, 2012); central Asia (Glikman, 1964).

†*Palaeohypotodus* Sp. Cf. *P. Rutoti* Winkler, 1876 (Fig. 5V–Y)

Material—Single lower lateral tooth, NRM-PZ P15896.

Horizon and Locality—Level 38 within the Submeseta Allomember, locality NRM 2, Slope S Marambio Base, S64°14.778′, W056°37.169′.

Age—Upper TELM 7, Priabonian, late Eocene.

Description—The single specimen is quite small and compact (Fig. 5V–Y). In labial view, the main cusp of P15896 is markedly triangular, with a broad base that uniformly tapers apically (Fig. 5V). The apex of the cusp is very acute. The labial crown face is flat and almost completely devoid of ornamentation except for very short, but rather faint vertical wrinkles along the basal margin of the enamel. The basal enameloid boundary is more or less straight with a slight median depression and does not extend onto the root lobes as in many odontaspidids, but instead overhangs the root medially.

Lingually, the crown face is very convex mesiodistally and completely devoid of ornamentation (Fig. 5W). The lateral cutting edges are noticeably blunt and reduced, accentuating the rounded cross-section of the main cusp. The edges do not reach the base of the crown as far as can be ascertained. Lateral cusplets are not preserved, but their broken bases indicate that they were very broad with rounded bases. The cusplets were closely placed next to the main cusp and seemingly not clearly separated.

In profile view, the crown is strongly inclined lingually but not sigmoidal, with the apex not extending over the lingual root protuberance (Fig. 5X). The crown broadens considerably basally, but in labial view it is slightly constricted above the wrinkles. The transverse section of the main cusp is ‘D’-shaped, from tip to base.

The root is damaged, and only one root lobe is preserved. The root was bilobate and is of holaulacorhize vascularization pattern. The preserved root lobe is slender and long with a vertical lateral margin, giving the root, as far as can be ascertained, a rectangular appearance in labial view. It is depressed mesiodistally, and the basal edge is slightly pointed. Apically, the root lobes are not coalescing but form a very wide and shallow divergence that results in a broad, trough-like appearance in labial view. The lingual protuberance is well developed and rather massive with a shallow and narrow nutritive groove. A small foramen opens into this shallow nutritive groove lingually.

Remarks—*Palaeohypotodus* was erected by Glikman (1964) for teeth from the Selandian of Belgium and was placed in his new family Jaekolodontidae. Herman (1975) included two other species, *P. bronni* (Agassiz, 1843) and *P. striatula* (Dalinkevicius, 1935), from Cretaceous deposits in this genus. Cappetta (1987) alternatively included *Palaeohypotodus* in Odontaspididae and transferred *P. striatula* to *Synodontaspis* (= *Carcharias*). Cappetta and Nolf (2005) and Cappetta (2012) consider *Palaeohypotodus* monospecific with only *P. rutoti* being valid.

Teeth of *P. rutoti* are characterized by short, vertical wrinkles along the basal edge of the labial crown face, a character that is also present in *Cenocarcharias* Cappetta and Case, 1999, and *Hispidaspis* Sokolov, 1978. The latter two, however, are only known from the Cretaceous. Short vertical wrinkles may be present on some teeth of *Odontaspis* and adult anterior but also juvenile teeth of *Striatolamia*. These are never as coarse as in *Palaeohypotodus*. The basolabial wrinkles depicted in the specimen described here resemble the pattern seen in NRM-PZ P16001. Nevertheless, the general morphology of a very convex lingual face, flat labial face with basal bulge overhanging the root, rectangular appearance of root in labial view, and vertical nutritive groove bisecting the lingual protuberance distinguish this specimen from teeth of *Striatolamia* and other odontaspidids.

It is always difficult to identify a taxon from just a single tooth, but P15896 seems to be very close to *Palaeohypotodus*. The number (two to three pairs) and size of the lateral cusplets cannot be established, and thus we only tentatively assign the tooth to *P. rutoti*. The triangular central cusp and the rectangular root indicate that this tooth is from a lower, lateral position. Various teeth of *P. rutoti* were previously described by Long (1992a). This species was recently described from the Bartonian–Priabonian of southern Chile (Otero and Soto-

Acuna, 2015). In the northern hemisphere, this species is restricted to Paleocene strata and the Southern Hemisphere occurrences might represent relict occurrences if one assumes that this species was cool-water adapted (Kriwet et al., 2014).

Family †OTODONTIDAE Glikman, 1964

Genus †*CARCHAROCLES* Jordan and Hannibal, 1923

Type Species—*Squalus auriculatus* Blainville, 1818, from the middle Eocene, Lutetian, of Belgium (no precise locality known).

Stratigraphic Range—Ypresian (early Eocene)–Burdigalian (early Miocene).

Fossil Occurrences (Selected)—Africa (Case and Cappetta, 1990; Underwood et al., 2011); Europe (Leriche, 1905, 1910); central Asia (Zhelezko and Kozlov, 1999); North America (Freile et al., 2001; Cicimurri and Knight, 2009); Pacific region (Ueyno et al., 1984; Yabumoto, 1989); Russia (Jaekel, 1895).

†*Carcharocles Sokolovi* (Jaekel, 1895) (Fig. 6A–B)

Material—A single incomplete tooth, NRM-PZ P16007.

Horizon and Locality—Level 38 within the Submeseta Allomember, locality DPV 13/84, Plateau SE Marambio Base, S64°14′47″, W56°36′12″.

Age—Upper TELM 7, Priabonian, late Eocene.

Description—The single specimen represents an upper lateral tooth of 54.34 mm height, 60.83 mm mesiodistal length, and 15.41 mm labiolingual width. The crown is labiolingually flattened, quite slender, and slightly inclined distally (Fig. 6A–B). The labial face of the central cusp is very flat, the lingual face, conversely, is very convex mesiodistally, resulting in an almost ‘D’-shaped cross-section of the crown at its base. Unfortunately, the enameloid cover is heavily abraded due to weathering processes. Consequently, the serrated cutting edges, which are important for species identification, are not preserved. The enameloid is best preserved lingually where it is completely smooth apart from some cracks.

The distal lateral cusplet is almost completely lacking, whereas the mesial one is well preserved showing the serration. The cusplet is rather low compared with the central cusp, devoid of any ornamentation, and asymmetrically triangular in labial view, with a very broad base. Mesially, the cusplet is slightly incised, almost dividing it into a larger and a very incipient, smaller part. The serration is very fine and regular along the distal edge of the cusplet and somewhat more irregular and coarser along the mesial edge towards the incision.

The root is heavily damaged but still provides some information about its morphology. It is very low compared with the tooth crown and is best developed at the levels of the root lobes. The root lobes are rather mesiodistally elongated and broadly separated, forming a shallow and broad arc in labial view. The mesial root lobe is shorter and broader with a rounded extremity compared with the distal one, which is narrower and longer. The lingual protuberance is rather damaged but seemingly salient. Nutritive foramina are not discernable due to the state of preservation. The basal face of the root, as far as it can be ascertained, is flattened at the levels of the root lobes. The tooth neck separating the crown from the root lingually is broad and typically chevron-like.

Remarks—The systematic position of extinct macrophagous lamniform sharks represented by large teeth with serrated lateral cutting edges is still debated. The most prominent member of this group, *Megaselachus megalodon*, was originally assigned to *Carcharodon* by Agassiz (1835), a view that is still supported by various authors (e.g., Purdy et al., 2001). It was variously placed into *Otodus* (see Cappetta, 2012, for usage of this name for the lineage; Andrianavalona et al., 2015), *Procarcharodon* (Casier, 1960), *Carcharocles*, or *Megaselachus* (e.g., Jordan and Hanibal, 1923; Glikman, 1964). We follow the view of Cappetta (2012), who placed all extinct macrophagous sharks with serrated cutting edges in a single genus, *Otodus*, representing the family Otodontidae. Separation of species into different subgenera of *Otodus*, *Otodus* s.l., *Carcharocles*, and *Megaselachus*, by Cappetta (2012), however, is not reasonable for exclusively fossil groups. Therefore, we consider these subgenera to represent genera.

Members of Otodontidae are known from isolated vertebral centra and teeth, and associated tooth sets, with a fossil record ranging from the Paleocene to the Pliocene. The tooth from the uppermost Eocene of Antarctica described herein is similar to teeth of *Otodus*, but is distinguished by the presence of the single preserved, serrated lateral cusplet, which identifies it as belonging to a member of *Carcharocles*. Members of *Megaselachus* (late Oligocene–Pliocene) are characterized by very regular and fine serrations along the cutting edges and very low lateral cusplets, if any, compared with species of *Carcharocles*. Members of *Carcharocles* are geographically widely distributed during the Cenozoic, with several species that were described from Kazakhstan spanning the whole Eocene.

Identification of species within *Carcharocles* is generally based on serration patterns of the central cusp and the form and serration of lateral cusplets. Species assignment of the tooth presented here is difficult because the serrated cutting edges are not preserved. Two possible candidates known from Gondwana continents during the Eocene are *C. auriculatus*, which occurs in the Ypresian of Seymour Island (Long, 1992a), in the middle to late Eocene of Chile (Otero et al., 2013), and in the Oligo-Miocene of Australia (Pledge, 1967), and *C. sokolovi*, which has only been reported from the Priabonian of Egypt (Case and Cappetta, 1990; Underwood et al., 2011). The stratigraphic occurrence of the specimen presented here coincides with the general stratigraphic distribution of *C. sokolovi* (see above). The rather narrow central cusp, the distinctly mesiodistally elongated and rather low root with basally flattened root lobes, and the serration pattern of the mesially preserved cusplet also support its assignment to *C. sokolovi* rather than to *C. auriculatus*. Lateral teeth of *C. auriculatus* have sturdier roots, which are rather high with almost vertical, slightly concave lateral margins in labial and lingual views, not basally flattened root lobes, a more robust central cusp, and coarser serrated lateral cusplets. Thus, the specimen described here represents the southernmost record of *C. sokolovi*. The tooth from Antarctica corresponds in size and general morphological appearance to an upper lateral figured by Applegate and Espinosa-Arrubarrena (1996:fig. 9b), who consider the maximum body length of *C. sokolovi* to reach at least 6 m. This would make this shark one of the ultimate predators in the latest Eocene waters surrounding Antarctica.

Subclass SUBTERBRANCHIALIA Zangerl, 1981

Superorder HOLOCEPHALI Bonaparte, 1832

Order CHIMAERIFORMES Patterson, 1965

Suborder CHIMAEROIDEI Patterson, 1965

Family CALLORHYNCHIDAE Garman, 1901

Subfamily CALLORHYNCHINAE Stahl, 1999

Genus †*ISCHYODUS* Egerton, 1843

Type Species—*Chimaera townsendi* Buckland, 1835, from the Bathonian, Great Oolite (Middle Jurassic), Stonesfield, England.

Stratigraphic Range—Middle Jurassic–Miocene.

Fossil Occurrences (Selected)—Antarctic Peninsula (Ward and Grande, 1991); Europe (Leriche, 1902, 1909; Gurr, 1962; Ward, 1980); North America (Cvancara and Hoganson, 1993; Hoganson and Erickson, 2005); Russia (Popov and Ivanov, 1996).

†*Ischyodus Dolloi* Leriche, 1902 (Fig. 7A–E)

Material—A fragmentary mandibular tooth plate, NRM-PZ P15867, and a fragmentary palatine tooth plate, NRM-PZ P16008.

Horizon and Locality—Level 38 within the Submeseta Allo-member, locality NRM 2, Slope S Marambio Base, S64°14.778′, W056°37.169′; underneath locality NRM 5, Ridge N Marambio Base, S64°13.985′, W056°36.851′.

Age—Upper TELM 7, Priabonian, late Eocene.

Description—Both specimens from TELM 7 are very fragmentary (Fig. 7E). The mesial, distal, and lingual (= basal margin) portions of the mandibular tooth plate are broken off and missing (Fig. 7A–C). The preserved labial edge (= postocclusal margin of Ward and Grande, 1991) is straight and continuous. The symphyseal margin also is lacking.

Only portions of two heavily abraded tritorial pads are preserved, displaying the mesh-like appearance of the pleromic hard tissue that forms the hypermineralized tissue of the pads (Fig. 7A–C). The remnant of the posterior outer tritor is mesio-distally longer than high; the median tritor is rounded lingually and seems to taper mesially. The occlusal surface is undulating in lingual view, because of a depression between the posterior and median tritors.

The second specimen represents a very fragmentary, probably right palatine tooth plate (Fig. 7D–E). The fragment measures ca. 2.5 cm in anteroposterior length and ca. 1.4 cm in width, and is almost subrectangular in occlusal view. It seemingly is more depressed laterally than the mandibular tooth plate. A single tritor, the anterior inner tritor, is completely preserved; all other tritors are lacking. This tritor is elongated, with an anterior, narrow extremity, whereas the posterior part is more robust with a rounded posterior extremity. Basally, the pleromic hard tissue is exposed.

Remarks—Five chimeroids have thus far been recorded from Late Cretaceous and Paleogene strata of Antarctica: *Chimaera zangerli* Stahl and Chatterjee, 1999, and *Callorhinchus torresi* Otero et al., 2012, from Maastrichtian strata, and *Ischyodus dolloi, Chimaera seymourensis* Ward and Grande, 1991, and *Callorhinchus stahli* Kriwet and Gaździcki, 2003, from Eocene strata. Additionally, Martin and Crame (2006) indicated the presence of an additional, unidentified species of *Callorhinchus* in the Maastrichtian. The mandibular tooth plate reported here resembles those of *Ischyodus dolloi* in general appearance and arrangement of the tritorial pads, which are identified as posterior outer and median tritors in combination with the occlusal undulation caused by a depression between these two pads (see also Ward and Grande, 1991; Cicimurri and Ebersole, 2015).

Ischyodus dolloi was originally described from the late Paleocene of Belgium (Leriche, 1902). It occurs also in the Paleocene of France (Leriche, 1909), Paleocene of North America (Cicimurri and Ebersole, 2015), Paleocene–Eocene of Russia (Popov and Ivanov, 1996), and Eocene of England (Gurr, 1962; Ward, 1973). In Antarctica, this species occurs throughout the La Meseta Formation and so far is the only recorded chondrichthyan from TELM 6 (Ward and Grande, 1991; this study). Stahl and Chatterjee (2002) reported *I. dolloi* from the early Maastrichtian of Seymour Island based on a single right mandibular tooth plate. Hoganson and Erickson (2005) consider that specimen to be too abraded for unambiguous identification, a conclusion with which we agree. Thus, *I. dolloi* is restricted to the Eocene in Antarctica.

La Meseta Chondrichthyan Diversity Patterns

The chondrichthyan fauna from the La Meseta Formation on Seymour Island includes 29 species (two of which are probably new records: *Striatolamia* sp. cf. *S. macrota* and *Palaeohypotodus* sp. cf. *P. rutoti*; see above) and is the most diverse Paleogene ichthyofauna from the Southern Hemisphere during the Eocene greenhouse climate known to date. Consequently, this assemblage has the potential to provide important information about the influence of abiotic factors on diversity fluctuations of marine vertebrates in general. During the Eocene, major plate-tectonic and climatic changes occurred, including the Paleocene–Eocene Thermal Maximum, Early Eocene Climatic Optimum (EECO), and separation of Australia from Antarctica.

The overall paleotemperature trend throughout the La Meseta Formation is a decrease from the early to late Eocene (Ivany et al., 2008), and it was suggested that chondrichthyan diversity was influenced by this climatic shift, resulting in their final disappearance before the onset of ice sheet formation (ca. 40–30 Ma) (see Introduction). A detailed review of chondrichthyan occurrences throughout the La Meseta Formation based on published records and results presented here (early Ypresian–late Priabonian), however, shows that cartilaginous fishes did not disappear significantly before the onset of ice sheet formation as previously assumed, but that they occurred at least until the Priabonian, which coincides with the end of the sedimentary sequence of the La Meseta Formation and onset of Antarctic glaciation.

Detailed distribution data about chondrichthyans for TELM 1 (uppermost Thanetian) and TELM 2 (lowermost Ypresian) as reported by Long (1992a) are inconclusive, and we assume that most, if not all, of these remains come from the lowermost Ypresian, but further stratigraphic studies on Seymour Island are required. TELMs 1–3 are characterized by sediments deposited in deltaic settings under comparably high sea surface paleotemperatures, which reached their maximum of ca. 15°C during the EECO at the base of TELM 3 (ca. 51–53 Ma) according to Ivany et al. (2008). Chondrichthyan diversity, however, is lower than expected when compared with modern tropical environments with similar surface temperatures, with only two squaliform and two lamniform sharks and three chimeroids. This, however, also could represent a collecting bias. The occurrences of *Deania* sp. and *Carcharocles auriculatus* in the lowermost TELMs represent the oldest records of these species, implying that both probably evolved in the Southern Hemisphere.

Six remains of chondrichthyans were found in TELM 3, including the oldest batomorph record from Antarctica, but it lacks all records of squaliform sharks (Long, 1992a; Table 1). Living squaliform sharks generally live in the deeper waters but may enter shallow marine environments. Nevertheless, they are rather sensitive to seawater temperatures and avoid temperatures above 15°C. Long (1992b) suggested that squaliforms, which he considers to be deep-water/transitional forms, may have lived in adjoining deep-sea areas and conducted seasonal or cyclically diurnal migrations. Migrations into shallow waters in search for food also might be a possible explanation. Absence of squaliforms in TELM 3 thus might correlate with higher surface seawater temperatures, although collecting biases cannot be excluded here.

Towards the end of TELM 3, temperatures decline to 10–11°C, after which they remain stable throughout TELMs 4–5 (Ivany et al., 2008). The cooler waters probably allowed temperate and cool-temperate sharks, such as *Lamna* cf. *nasus* and *Palaeohypotodus rutoti*, to invade the near-coastal, shallow marine environments of the Antarctic continent and also enabled squaliform sharks to reenter the estuary depositional areas. This resulted in a significant increase in taxonomic diversity of TELM 4 and 5 chondrichthyan assemblages (28 and 21 species, respectively).

The last occurrence of *Odontaspis winkleri*, but not of *Palaeohypotodus rutoti*, as previously suggested by Long (1992b) (Table 1), is seen in TELM 5. Interestingly, this Eocene temperate chondrichthyan association is far more diverse than modern associations in comparable environments (see also Case, 1992). Recently published paleoclimatic data for the La Meseta Formation indicate significantly higher mean sea surface temperatures of ca. 16.8°C at 45 Ma, corresponding more or less to the base of the Lutetian, ca. 12.6°C at 42 Ma corresponding to TELM 6, and ca. 14.1° C and 11.3°C for TELM 7 (Douglas et al., 2014). These temperature records correlate much better to a highly diverse chondrichthyan association similar to those found in the tropics today. Nonetheless, the La Meseta

Formation associations are dominated by cool- to warm-temperate chondrichthyans or those living in deeper, cooler waters during warmer seasons, and thus it is in good accordance with sea water temperatures as proposed by Ivany et al. (2008). Notably, this Eocene temperate chondrichthyan fauna is more diverse than modern temperate ones.

Douglas et al. (2014) also present an age model for the La Meseta Formation indicating that the Ypresian (TELMs 1, 2, 3, 4, and parts of TELM 5) is missing. This model, however, is not generally accepted and needs further evaluation, because it would have tremendous impacts on all previous biotic considerations.

In the lower parts of TELM 6, a short warming event occurred and temperatures were similar to those at the base of TELM 3 (approximately 15°C), but subsequent cooling throughout the end of TELM 6 and TELM 7 ended with minimum seawater temperature of approximately 5°C at ca. 37 Ma according to Ivany et al. (2008). Temperatures returned to ca. 7–8°C shortly before the end of the Eocene and the onset of Antarctic ice sheet formation. A single chondrichthyan, *Ischyodus dolloi*, was noted from the upper part of TELM 6 (Ward and Grande, 1991), corresponding with cool-temperate climatic conditions, whereas no chondrichthyans have previously been recorded from the upper parts of TELM 7 (Priabonian). This indicates that chondrichthyans might have disappeared from Antarctic near-coastal waters due to decreasing sea surface temperatures and changing environments before establishment of the circum-Antarctic current (~40–30 Ma) (see also Kriwet, 2005).

The new shark and chimeroid finds from the Priabonian (upper TELM 7) reported herein are thus of great importance, because they verify that several chondrichthyan lineages persisted much longer in the waters surrounding the Antarctic continent. Taxonomic diversity was higher despite rather cool sea surface temperatures of approximately 5°C. All sharks reported here occupied upper trophic levels and represent either littoral-epipelagic or shelf overlapping taxa (Table 2). The chimeroid, *Ischyodus*, occupied the lowest trophic level and generally is considered to have lived in deeper waters of the oceans and only migrated inshore for spawning (Kriwet and Klug, 2011). *Carcharocles sokolovi* was a large coastal shark that probably occupied the top-most position within the latest Eocene Antarctic food web. The tooth tentatively assigned to *Palaeohypotodus* sp. cf. *P. rutoti* here possibly represents the last record of this cool-temperate shark. The angel shark, *Squatina* sp., represents a benthic taxon that today inhabits the upper continental and insular shelves down to more than 100 m. The occurrence of this taxon in TELM 7 implies that favorable benthic habitats around the Antarctic continent must have been present.

The final disappearance of chondrichthyans seemingly concurs with abrupt ice sheet formation on Antarctica, which occurred 34 Ma (Goldner et al., 2014). Decreasing sea temperatures and glaciation resulted in reduced shelf areas, which not only influenced the decrease of chondrichthyans before the end of the Eocene in Antarctica, but also most likely was the driving force behind their ultimate disappearance in the latest Eocene (Priabonian). Diversity patterns of chondrichthyans throughout the La Meseta Formation most likely followed climatic conditions rather than paleogeographic constellations, pending further analyses.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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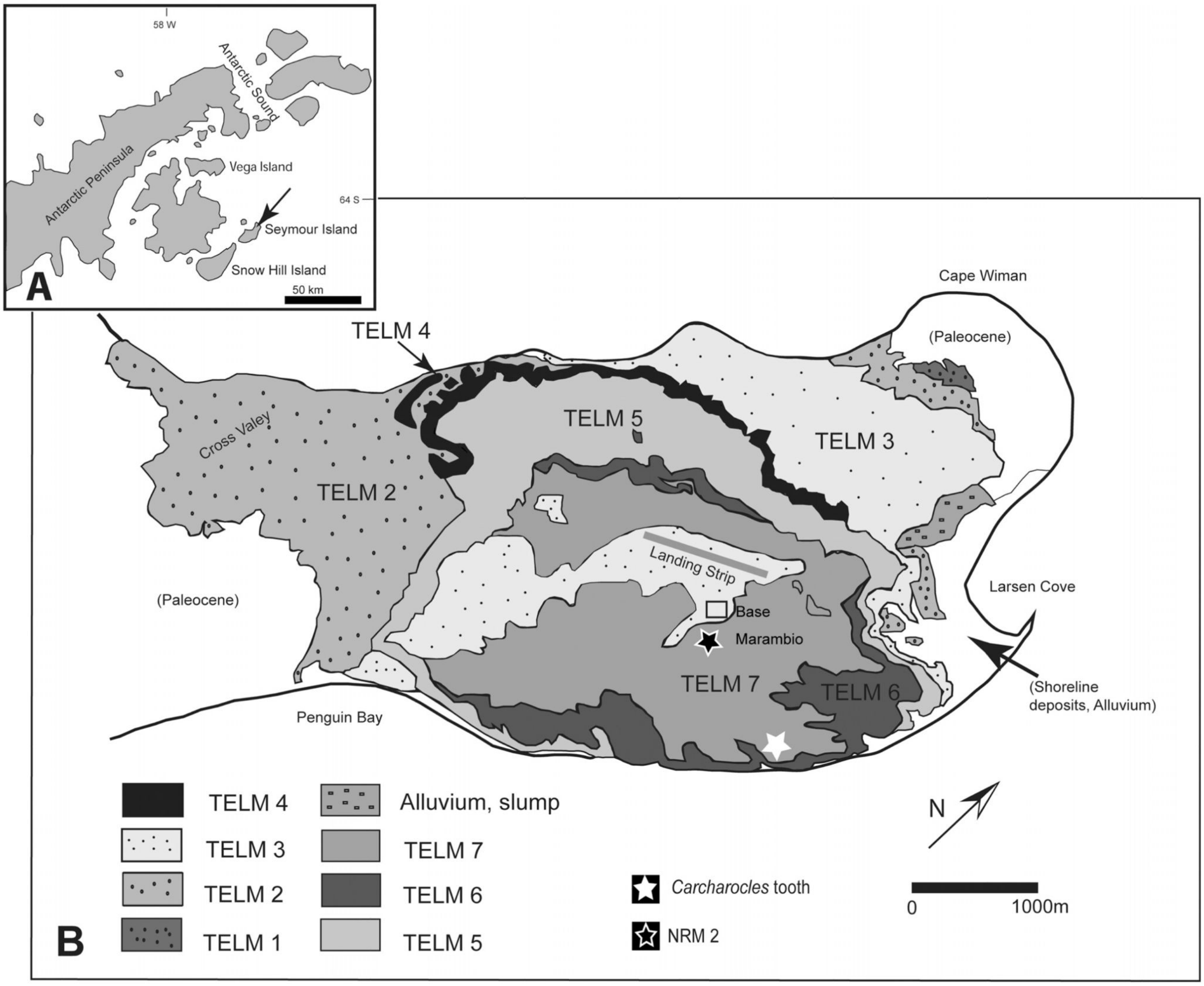

Figure 1. Geological maps of Seymour Island, Antarctica.

A, index map of Seymour Island; **B**, geological map of Seymour Island, showing units of the Eocene La Meseta Formation. Asterisks indicate localities from where the material described here was obtained.

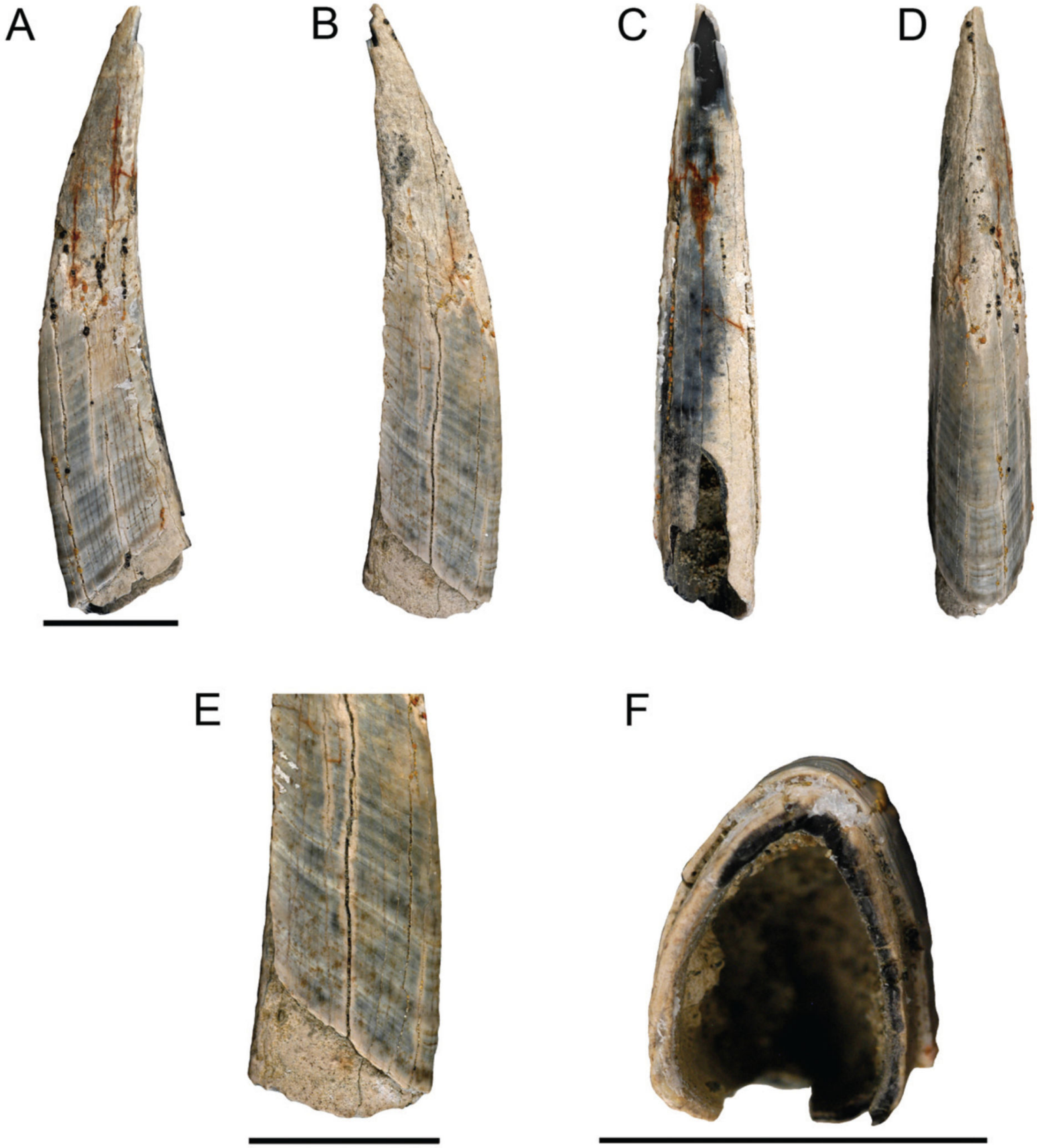

Figure 2. Isolated dorsal fin spine of Squalus sp., NRM-PZ P16000.

A, left lateral view; **B**, right lateral view; **C**, posterior view; E, enlargement showing growth bands with original pigmentation; **D**, anterior view; **F**, basal view. Scale bars equal 5 mm.

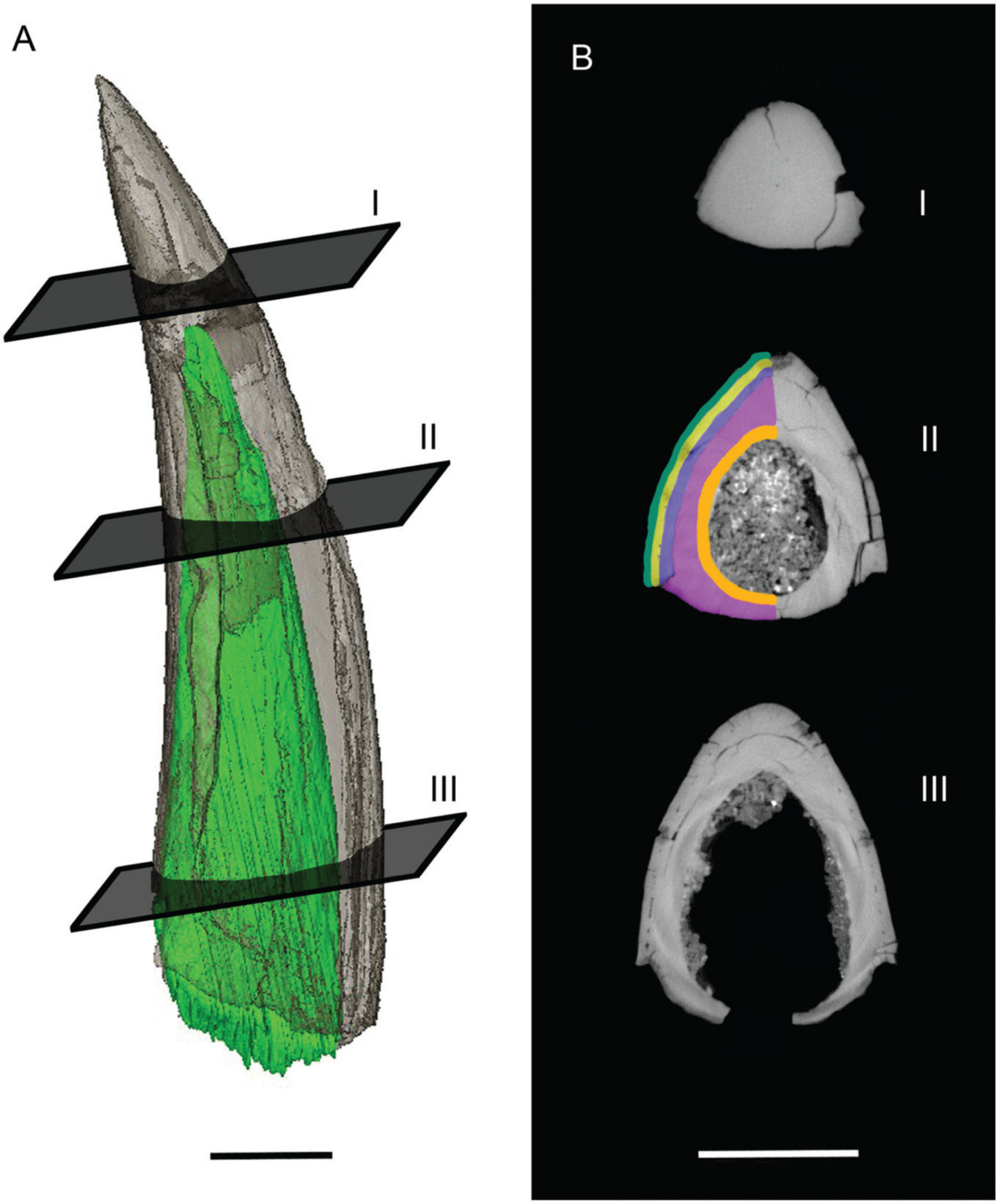

Figure 3. Micro-CT scan of the *Squalus* sp. fin spine depicted in Figure 2. Hard tissue organization is colored according to Jerve et al. (2014).

A, semitransparent fin spine with 3D reconstruction of the internal cartilage rod (green); **B–D**, representative horizontal micro-CT slides at different levels of the fin spine (from top to base). Scale bars equal 10 mm.

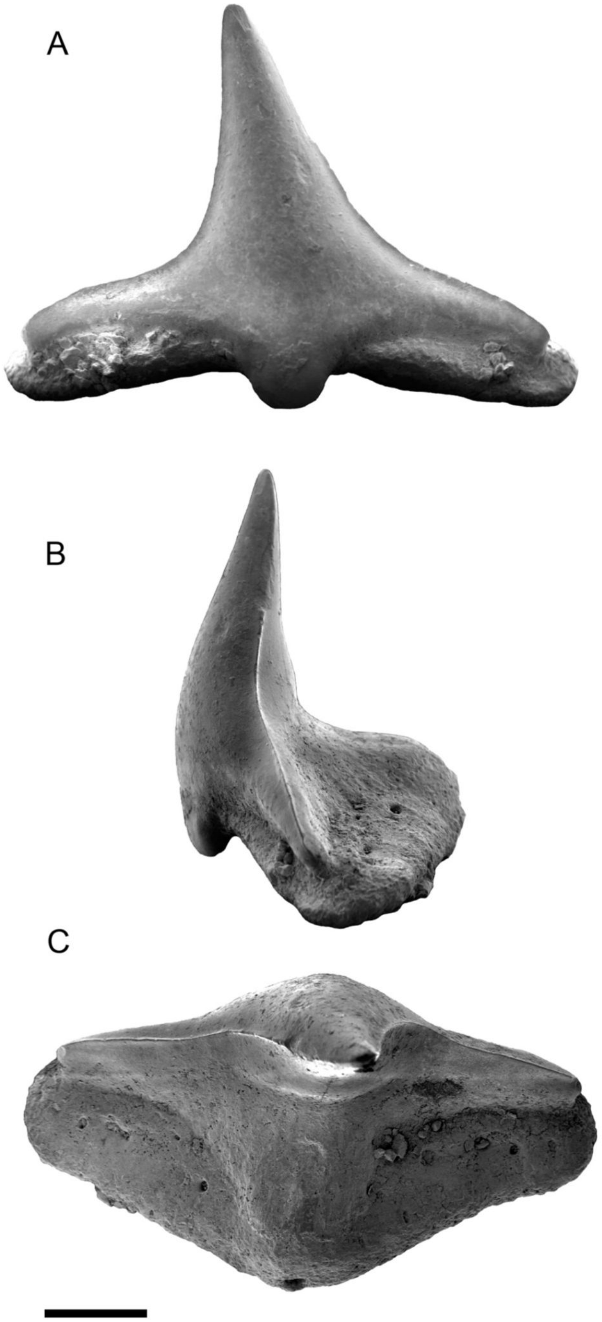

Figure 4. Isolated lateral tooth of *Squatina* sp. (NRM-PZ P16005).

A, labial view; **B**, mesial view; **C**, occlusal view. Scale bar equals 1 mm.

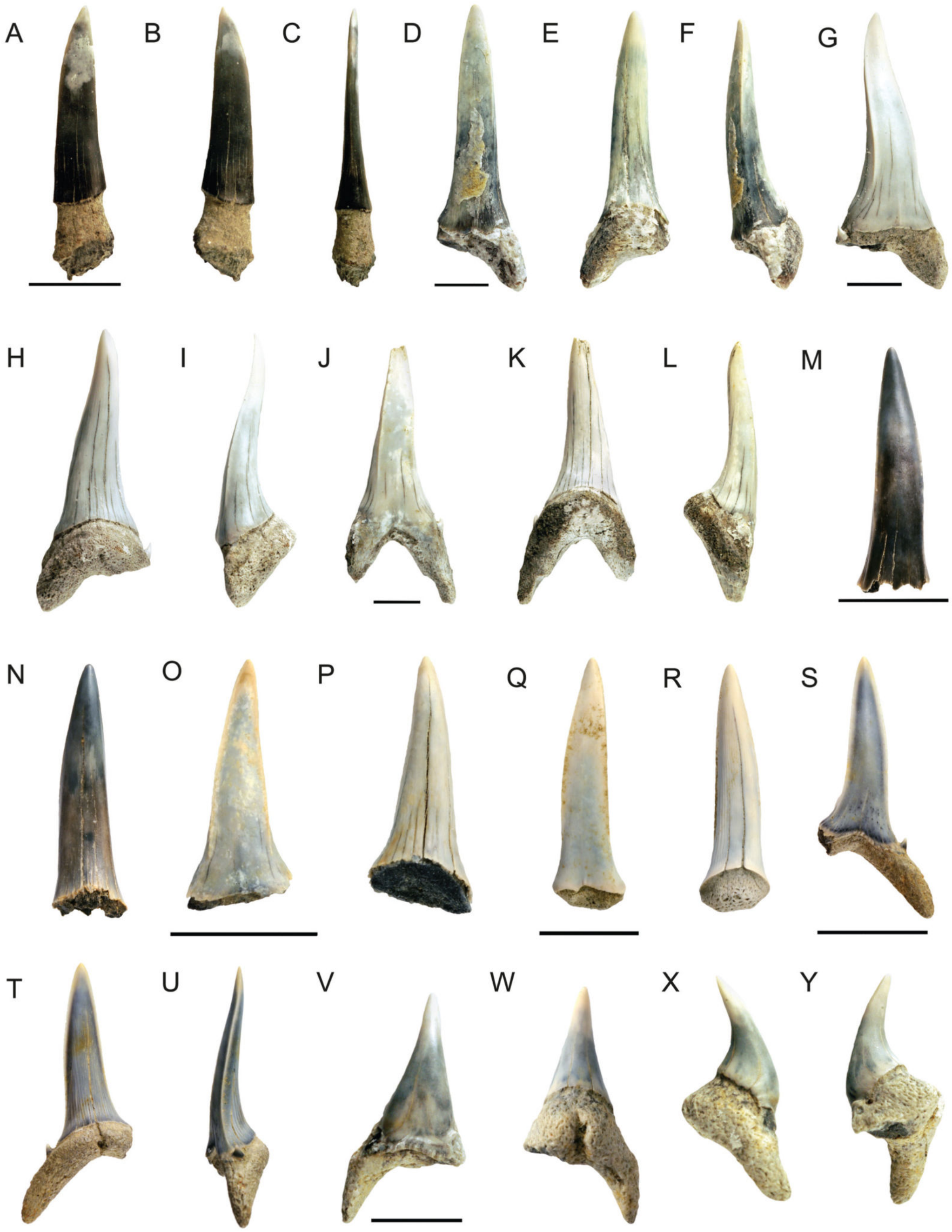

Figure 5. Isolated shark teeth from TELM 7.

A–C, single rostral spine of *Pristiophorus lanceolatus*, NRM-PZ P15924-1; **A**, ventral view, **B**, dorsal view; **C**, anterior view. **D–U**, seven teeth of *Striatolamia* sp. cf. *macrota*. **D–F**, NRM-PZ P15925; **D**, labial view; **E**, lingual view; **F**, profile view. **G–I**, NRM-PZ P15924-2; **G**, labial view; **H**, lingual view; **I**, mesial view. **J–L**, NRM-PZ P15895; **J**, labial view; **K**, lingual view; **L**, mesial view. **M–N**, NRM-PZ P16002; **M**, labial view; **N**, lingual view. **O–P**, NRM-PZ P16003; **O**, labial view; **P**, lingual view. **Q–R**, NRM-PZ P16004; **Q**, labial view; **R**, lingual view. **S–U**, NRM-PZ P16001; **S**, labial view; **T**, lingual view; **U**, mesial view. **V–Y**, single lower lateral tooth of Palaeohypotodus sp. cf. rutoti, NRM-PZ P15896; **V**, labial view; **W**, lingual view; **X**, lateral view; **Y**, profile view. Scale bars equal 5 mm.

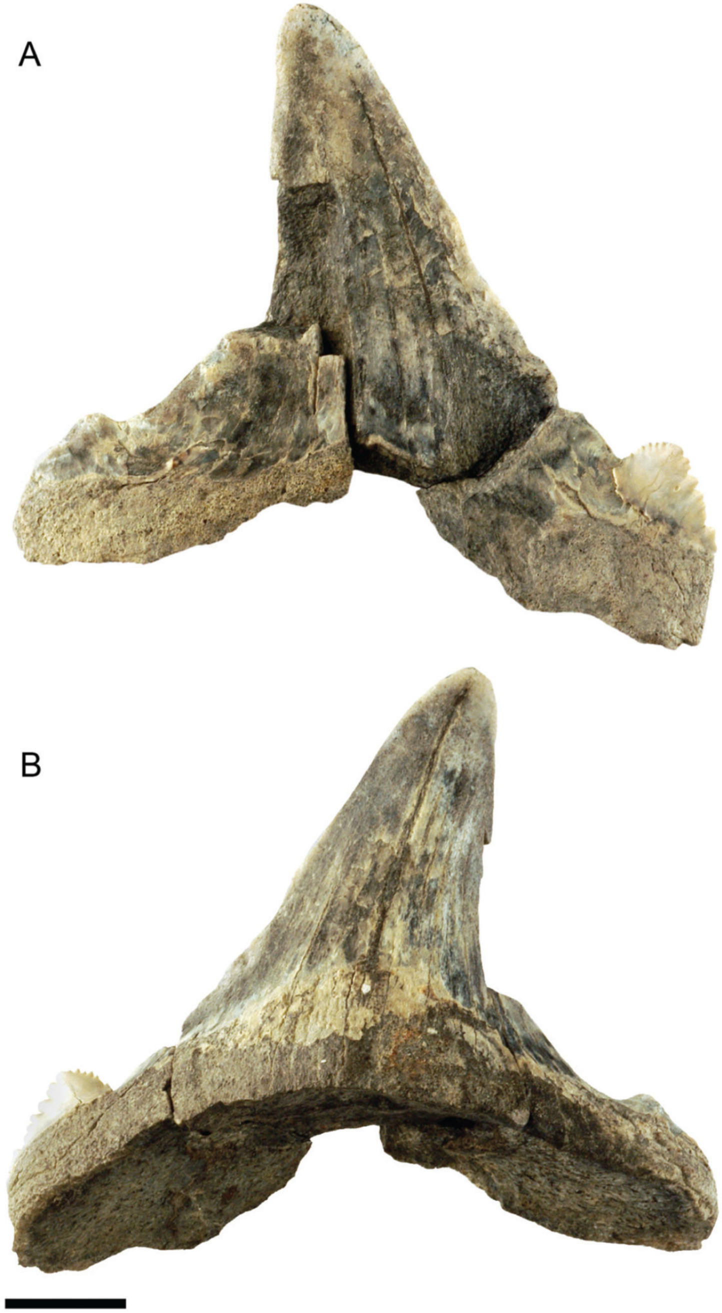

Figure 6. Upper lateral tooth of *Carcharocles sokolovi*, NRM-PZ P16007.
A, labial view; **B**, lingual view. Scale bar equals 5 mm.

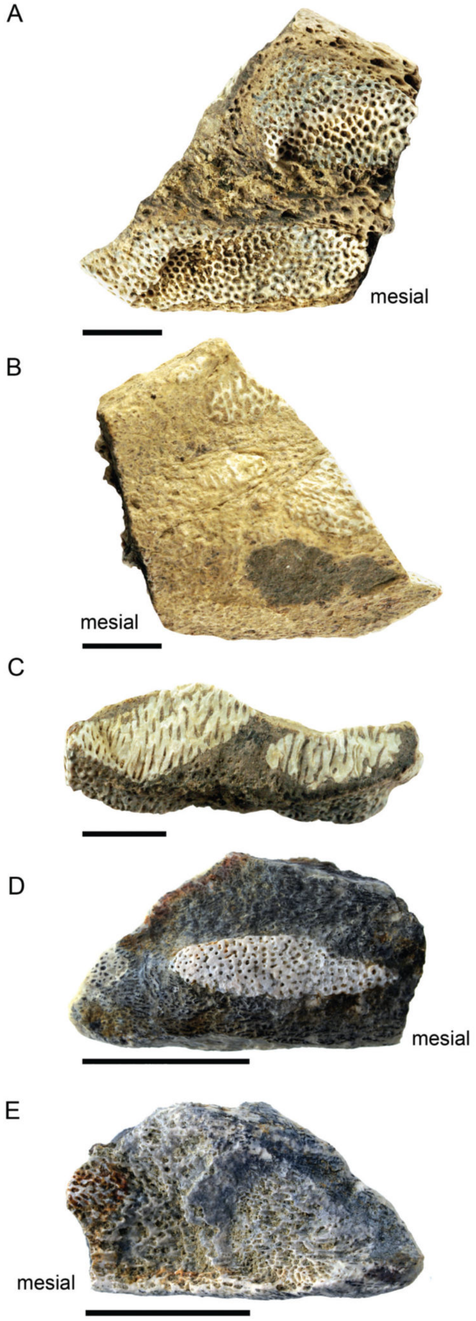

Figure 7. Fragmentary tooth plates of *Ischyodus dolloi*.

A–C, mandibular tooth plate NRM-PZ P15867; **A**, occlusal view; **B**. basal view; **C**, lingual view. **D–E**, palatine tooth plate, NRM-PZ P16008; **D**, oral view; **E**, aboral view. Scale bars equal 5 mm.

Table 1

Stratigraphic occurrences, facies distribution, and climatic conditions of Eocene La Meseta chondrichthyan associations of Seymour Island (Antarctica) based on published records (see the text for references).

TELM	Facies	Sea surface temperatures	Association
7	Shallow marine	ca. 7–8° C	*Squalus* sp., *Squatina* sp., *Pristiophorus lanceolatus, Carcharocles sokolovi, Palaeohypotodus* sp. cf. *rutoti, Striatolamia* sp. cf. *macrota, Ischyodus dolloi*
	Inner estuary channels	ca. 5° C	
6	Estuary	ca. 7° C	*Ischyodus dolloi*
		ca. 15° C	
5	Estuary	ca. 10–11°C	*Heptranchias howelli, Hexanchus* sp., *Centrophorus* sp., *Dalatias licha, Squalus weltoni, Squalus woodburnei, Pristiophorus lanceolatus, Squatina* sp., *Pseudoginglymostoma* cf. *brevicaudatum, Stegostoma* cf. *fasciatum, Anomotodon multidenticulata, Cetorhinus* sp., *Isurus praecursor, Lamna* cf. *nasus, Odontaspis winkleri, Palaeohypotodus rutoti, Striatolamia macrota, Scoliodon* sp., *Myliobatis* sp., *Raja/Bathyraja* sp., *Ischyodus dolloi*
4	Estuary	ca. 10–11°C	*Paraorthacodus* sp., *Heptranchias howelli, Hexanchus* sp., *Centrophorus* sp., *Dalatias licha, Deania* sp., *Squalus weltoni, Squalus woodburnei, Pristiophorus lanceolatus, Squatina* sp., *Pseudoginglymostoma* cf. *brevicaudatum, Stegostoma* cf. *fasciatum, Anomotodon multidenticulata, Carcharocles auriculatus, Cetorhinus* sp., *Isurus praecursor, Lamna* cf. *nasus, Odontaspis winkleri, Palaeohypotodus rutoti, Striatolamia macrota, Carcharhinus* sp., *Scoliodon* sp., *Myliobatis* sp., *Pristis* sp., *Raja/Bathyraja* sp., *Chimaera seymourensis, Ischyodus dolloi*
3	Delta plain–estuary	ca. 10–11°C	*Pristiophorus lanceolatus, Carcharocles auriculatus, Lamna* cf. *nasus, Striatolamia macrota, Myliobatis* sp., *Ischyodus dolloi*
		ca. 15° C	
2	Delta front		*Callorhinchus stahli, Chimaera seymourensis, Ischyodus dolloi*
1–2	Prodelta?/inner estuarine?		*Centrophorus* sp., *Deania* sp., *Carcharocles auriculatus, Striatolamia macrota*

Facies interpretation according to Marenssi et al. (2002); sea surface temperatures according to Ivany et al. (2014). For occurrence references, see the text.

Table 2

Environmental distribution and trophic level of late Bartonian Antarctic chondrichthyans.

Taxon	**Living analogue**	**Zonation**	**Trophic level**
Squalus sp.	*Squalus acanthias*	Shelf overlap species	4.1 / 4.4*
Squatina sp.	*Squatina squatina*	Continental shelves	4.1 / 4*
Pristiophorus lanceolatus	*Pristiophorus cirratus*	Shelf overlap species	4.2 / 4.2*
Striatolamia sp. cf. *macrota*	*Carcharias taurus*	Littoral-epipelagic	4.4 / 4.5*
Palaeohypotodus sp. cf. *rutoti*	*Odontaspis ferox*	Littoral-epipelagic	4.4 / 4.2*
Carcharocles sokolovi	*Carcharodon carcharias*	Littoral-epipelagic	4.3 / 4.5*
Ischyodus dolloi	*Chimaera* spp.	Deep slope/open marine	3.5–4.1*

Inferences are based on comparisons with extant analogues displaying similar structures. Zonations according to Compagno (1984) and Compagno et al. (1991); trophic-level assignment according to Ebert and Bizzaro (2007) and www.fishbase.org (asterisk).