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New Carcharhiniform Sharks (Chondrichthyes, Elasmobranchii) from the Early to Middle Eocene of Seymour Island, Antarctic Peninsula

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Abstract

Seymour Island, Antarctic Peninsula, is known for its wealth of fossil remains. This island provides one of the richest fossiliferous Paleogene sequences in the world. Chondrichthyans seemingly dominate this Eocene marine fauna and offer a rare insight into high-latitude faunas during the Palaeogene. So far, only a few isolated teeth of carcharhinid sharks have been reported from Seymour Island. Bulk sampling in the well-exposed La Meseta and Submeseta formations yielded new and abundant chondrichthyan material, including numerous teeth of carcharhinid and triakid sharks. Here, we present a reevaluation of the previously described carcharhinid remains and a description of new taxa: *Meridiogaleus cristatus*, gen. et sp. nov., *Kallodentis rythistemma*, gen. et sp. nov., *Abdounia richteri*, sp. nov., and *Abdounia mesetae*, sp. nov. The carcharhiniforms *Mustelus* sp. and *Galeorhinus* sp. are reported based on rare material, whereas teeth previously assigned to *Scoliodon* represent a nomen dubium.

Introduction

Carcharhiniformes (ground sharks) are the most speciose and widespread clade of extant elasmobranchs, containing about 225 species arranged into eight families. Their

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evolutionary history extends back some 160 Ma into the Middle Jurassic. Scyliorhinidae seemingly is the most plesiomorphic clade within this order (Underwood and Ward, 2004; Cappetta, 2012). Most extinct and extant carcharhiniforms are small, but some extant members such as the tiger and bull sharks are amongst the largest marine predators. Today, carcharhiniforms are distributed worldwide, from tropical to cold-temperate and even arctic waters (Compagno et al., 2005), occupying all environments from the intertidal to the open sea and are even adapted to deep ocean conditions. Some species have restricted geographic ranges, whereas others are effective long-distance swimmers and highly migratory (Musick et al., 2004; Compagno et al., 2005).

Carcharhiniformes represent the sister group to Lamniformes (Musick et al., 2004) and the monophyly of Carcharhiniformes is widely accepted, and is here supported by three morphological synapomorphies: (1) suborbital with two divided heads; (2) presence of nictating lower eyelid; and (3) accessory terminal cartilage of the pelvic fin not spinous or modified into the external mesorhipidion (Shirai, 1996), and by molecular data (e.g., Douady et al., 2003; Winchell et al., 2004; Naylor et al., 2012; Gkafas et al., 2015). However, relationships within the order are still largely unresolved, because molecular and morphological studies suggest that some families are paraphyletic (Maisey, 1984, 2012; Iglésias et al., 2005; Human et al., 2006). For instance, the triakid genera *Triakis* Müller and Henle, 1838, and *Mustelus* Linck, 1790, are paraphyletic, or probably polyphyletic in the case of *Triakis*, according to López et al. (2006), which would be in agreement with the different tooth morphologies already noted by Herman et al. (1988).

The family Scyliorhinidae (catsharks) is by far the largest family, with at least 160 species in 17 genera (Ebert et al., 2013). Triakidae (houndsharks) and Carcharhinidae (requiem sharks) are among the most diverse carcharhiniforms occurring in warm to temperate seas. Triakids and carcharhinids are known since the Early Cretaceous (Cappetta, 2012; Maisey, 2012; Guinot et al., 2014). In Antarctica, chondrichthyan remains are very common and occur in the early Eocene to ?earliest Oligocene La Meseta and Submeseta formations on Seymour Island (e.g., Case, 1992; Long, 1992a, 1992b; Cione and Reguero, 1994, 1998; Kriwet, 2005, Kriwet et al., 2016), including rare records of carcharhinids and triakids (Long, 1992a; Long and Stilwell, 2000; Kriwet, 2005). Fossil shark remains have been predominantly surface-collected until now, and our knowledge about chondrichthyan diversity patterns during the Eocene of Antarctica might present serious taxonomic biases because teeth of small taxa generally are not recovered. Microvertebrate remains, including abundant shark remains, however, have been collected only recently at some fossil sites by screen-washing of bulk samples. Here, we report on new triakid and carcharhinid records from the Eocene of Seymour Island, Antarctic Peninsula, discuss their extant and extinct occurrences, and comment on previous records.

Locality and Stratigraphic Settings

The Eocene La Meseta Formation is exposed on Seymour and Cockburn islands, which are situated approximately 100 km southeast of the northern tip of the Antarctic Peninsula (Fig. 1). The sedimentary sequence exposed on Seymour Island represents the uppermost part of the infill of the James Ross Basin (del Valle et al., 1992). The fossiliferous sediments belong to two groups, the lower Marambio Group of Late Cretaceous to Paleocene age, comprising the Lopez de Bertodano and Sobral formations, and the overlying Seymour Island group, including the Cross Valley (middle–earliest late Paleocene), La Meseta (late Paleocene–early middle Eocene), and Submeseta (middle Eocene–early Oligocene) formations (e.g., Zinsmeister, 1982; Grande and Chatterjee, 1987, Marenssi, 2006; Montes et al., 2013). Here, the La Meseta Formation is an unconformity-bound unit (La Meseta Alloformation of Marenssi et al., 1998a) comprising mostly poorly consolidated clastic fine-grained sediments, which were deposited in deltaic, estuarine, and shallow marine environments (Marenssi, 1995; Marenssi et al., 1998a, 1998b). The La Meseta Formation is further subdivided into six allomembers, which are named Valle de las Focas (Tertiary Eocene La Meseta [TELM] 1), Acatnilado I and II (TELMs 2 and 3 in part), Campamento (TELM 3 in part and TELM 4), and *Cucullaea* I and II (TELMs 5 and 6 in part) and range from the Thanetian (58.8 Ma) to the Lutetian (43.4 Ma).

The Submeseta Formation is organized in three allomembers, which are named Submeseta I (TELMs 6 and 7 in part), Submeseta II (TELM 7 in part), and Submeseta III (upper TELM 7). Montes et al. (2013) placed the base of this unit at 43.4 Ma (late Lutetian) and the top at 33.9 Ma (Priabonian/Rupelian). We use both schemes, allomembers and TELMs, to indicate where the material was sampled to provide as much stratigraphic information as possible.

The material that forms the focus of this study was recovered from three different localities in two different TELMs. Most of the material described here was collected from the *Cucullaea* I allomember of TELM 5, which is Ypresian, Early Eocene, in age, at locality IAA 1/90 (all positions of localities are Global Positioning System [GPS] data; 64°14′04.67″S, 56°39′56.38″W), informally known as ‘Ungulate site.’ The second-most material was collected at IAA 2/95 (64°13′58″S, 56°39′06″W), informally known as ‘Marsupial site.’ Four teeth were collected in TELM 6, Submeseta I, which is Lutetian, Middle Eocene, in age at locality IAA 1/93 (64°13′51.8″S, 56°35′53.14″W).

The *Cucullaea* I allomember crops out all around the foothill of the meseta, with a maximum thickness of 90 m (Marenssi et al., 1998a), and consists of laminated fine-grained sandstones and silty clays with interbedded conglomeratic sandstones (Sadler, 1988). Marenssi (1995) described the depositional setting as estuarine to shallow marine of the mouth of the estuary. It corresponds to level 35 of Montes et al. (2013) and belongs to the informal biozone, TELM 5, of Sadler (1988).

Localities IAA 1/90 and IAA 2/95 are located in thin shell lenses on the north side of Seymour Island that are dominated by naticid gastropods informally referred to as the ‘*Natica* horizon’ (Bomfleur et al., 2015). This conglomeratic lens is less than 1 m thick and was interpreted as a nearshore, shallow-marine environment by Stilwell and Zinsmeister (1992).

The Submeseta Formation (Montes et al., 2013) is about 160 m thick and crops out continuously around the uppermost flanks of the meseta. The depositional and lithological environments are similar to the *Cucullaea* I and *Cucullaea* II allomembers, with the uppermost part of the sedimentary sequence being thicker and including very fine sandstones, mudstones, and gravel sheets (Marenssi et al., 1998a, 2001; Marenssi, 2006). These lens-shaped units represent different stages related to sea level fluctuations as described by Marenssi et al. (2002), that were deposited in deltaic, estuarine, and shallow marine environments (Porebski, 1995; Marenssi et al., 1998b).

Materials and Methods

Bulk samples were collected by an Argentinian-Swedish field party as a joint project of the Instituto Antártico Argentino (DNA-IAA) and the Swedish Polar Research Secretariat (SPFS) during three summer campaigns in 2011, 2012, and 2013 from three sites, IAA 1/90, IAA 2/95, and IAA 1/93, of the La Meseta and Submeseta formations (see above). Sediment samples were dry sieved in the field, and subsequent specimen picking in three different size fractions (2, 0.5, and 0.2 mm) was done in the laboratory. The vertebrate material also comprises numerous isolated shark teeth (e.g., Engelbrecht et al., 2016a, 2016b; Kriwet et al., 2016), including oral teeth of carchariniform sharks that form the focus of this study.

All teeth were cleaned with Rewoquat and mounted on stubs before sputter coating (Sputter Coater SC 500) for scanning electron microscopy (SEM) studies with a JEOL-6400 scanning electron microscope at the Department of Palaeontology, University of Vienna. Additional photos were taken with a 3D digital microscope (Keyence VHX-1000D 3D). The systematic framework and morphological terminologies used here largely follow those of Cappetta (2012), but we additionally distinguish between ‘costule’ (rib-like sculpture) and ‘stria’ (less pronounced, wrinkle-like folds). ‘Enameloid folds’ are equivalent to ‘striae.’ The described material is housed in the Swedish Museum of Natural History with the prefix NRM-PZ P.

Systematic Paleontology

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Cohort EUSELACHII Hay, 1902

Subcohort NEOSELACHII Compagno, 1977

Superorder GALEOMORPHII Compagno, 1973

Order CARCHARHINIFORMES Compagno, 1973

Family TRIAKIDAE Gray, 1851

Subfamily TRIAKINI Gray, 1851

Genus *MUSTELUS* Linck, 1790

Type Species—*Squalus mustelus* Linnaeus, 1758.

MUSTELUS SP.

(Figs. 2A–BB, 3A–P)

Material—Four teeth are considered to be anteriors (NRM-PZ P16235, NRM-PZ P16226–16228), three are considered to be anterolaterals (NRM-PZ P16229–16230, NRM-PZ P16233), and three are laterals (NRM-PZ P16231–16232 and NRM-PZ P16234). NRM-PZ P16220–16221: unfigured lateral teeth from localities IAA 1/90 (one specimen) and IAA 2/95 (one specimen), respectively.

Geographic Range—IAA 1/90, 'Ungulate site' (64°14′04.67″S, 56°39′56.38″W); IAA 2/95, 'Marsupial site' (64°13′58″S, 56°39′06″W); IAA 1/93(64°13′51.8″S, 56°35′53.14″W); Seymour Island, Antarctica.

Stratigraphic Range—TELM 5, *Natica* horizon, *Cucullaea* I allomember, Ypresian, Early Eocene; TELM 6, Submeseta I, Lutetian, Middle Eocene.

Description—The genus is characterized by a crushing-type dentition, which resembles that of rhinobatoids to some degree. A total of 12 isolated teeth are here assigned to *Mustelus* sp. All teeth are very well preserved and are from anterior, anterolateral, and lateral positions of the jaw.

Anterior and anterolateral teeth (Figs. 2A–I, 3A–D, I–L) are about 2 mm wide and more or less symmetrical. The crown is slightly broader than the root and overhangs it on all four sides. A waist-like circumferential belt-like furrow separates the crown from the root. Anterolateral teeth are more elongated than anteriors, and the uvula is slightly shifted distally. The crown is higher than the root in profile view (Fig. 2 K, S, N, AA). No lateral cusplets are present. The occlusal crown face is flat and smooth but with short and well-separated vertical striae along the basal edge of the crown (Fig. 2D, T). Labially, additional undulating and slightly horizontally directed striae occur in the middle part of the crown. These striae are not regularly arranged and vary in length; some extend over the entire edge of the labial crown face, whereas others start at the base or at the top of the labial face but remain very short. Additionally, the labial crown face broadly overhangs the root in profile view (e.g., Fig. 2I, M, U).

In profile view, the uvula is concave and bears distinctive fine, vertical striations similar to those of the labial crown edge, which do not reach the occlusal surface and are rather unevenly distributed (Fig. 2 N, R, V). The enameloid of the lingual crown face bears some fine striae, most of which are vertically oriented, but a few horizontally directed ones occur medially. These striae are well separated from each other, not equal in length and slightly oblique.

The root is massive and slightly lower than the crown in profile view (e.g., Fig. 2S, W). The root consists of two rather blunt root lobes, which are well separated by a rather deep nutritive groove. Two to three marginal foramina open margino-lingually on both sides of the uvula. On the labial root face, two foramina open (e.g., Fig. 2M, Q).

Lateral teeth are asymmetric and transversely elongated; the distally directed cusp is reduced. The enameloid of the crown is wrinkled on both lingual and labial crown faces, with the labial enameloid folds being short, unequal in length, and vertically directed (Fig. 3E). The labial crown face significantly overhangs the root with a broad rim (Fig. 3G). The lingual crown face bears a salient uvula located below the cusp (e.g., Fig. 3F). The vertically directed enameloid folds on the lingual crown face are unequally distributed and never reach the top of the crown. No lateral cusplets are present. The occlusal crown face is smooth except for well-separated costules on the labial edge. The lingual protuberance is well developed.

The root is very high compared with the crown, and the root lobes are well separated by a broad nutritive groove. The root face bears labially two foramina on each root lobe and two to three marginal foramina on the lingual root face. The basal face of the root is slightly convex in basal view (Fig. 3M–P).

Remarks—Extant species of *Mustelus* are distributed worldwide in tropical to cold areas of the oceans (Compagno et al., 2005), and the genus is one of the most diverse groups among triakids, with about 28 species mainly inhabiting the neritic zone (e.g., *Mustelus canis* Mitchill, 1815), up to 200 m in depth (Compagno et al., 2005). Some species are widely distributed (e.g., *Mustelus mustelus* Linnaeus, 1758), whereas others have a very restricted distribution, like the endemic New Zealand species, *Mustelus lenticulatus* Phillipps, 1932 (Compagno et al., 2005).

The fossil record of the genus *Mustelus* is rather poor. This genus seems to be scarce in deposits until the Neogene, when it becomes more abundant (Herman, 1982; Baut and Genault, 1995). The oldest record, however, is reported from the Thanetian, late Paleocene, of the Paris Basin (Baut and Genault, 1995; Reinecke and Engelhard, 1997). The tooth morphology of *Mustelus* spp. is very general and hardly differentiable (Herman et al., 1988, 1990). Therefore, only three fossil species currently are considered valid (Cappetta, 2006): *Mustelus biddlei* Baut and Genault, 1995; *Mustelus whitei* Cappetta, 1976; and *Mustelus vanderhoefti* Herman, 1982. *Mustelus biddlei* Baut and Genault, 1995, is characterized by teeth that are generally larger in size compared with those of other fossil species. They have a low crown, and striae on the labial and lingual crown faces. Cappetta (1976) first described *Mustelus whitei* based on two teeth, which are characterized by their smaller overall size and a finer crown ornamentation compared with those of the other two fossil species. Teeth of *Mustelus* sp. from Seymour Island differ from those of *M. biddlei* in having a higher crown and ‘additional’ cusps mesially and distally from the uvula in labial view. *Mustelus whitei* differs from the Antarctic species in having a lower crown, a broader uvula with a different sculpture, and no obvious labial striae on the labial-occlusal crown face.

The described specimens here are morphologically close to *M. vanderhoefti* but differ in having a higher root, a less marked waist-like circumferential belt, which separates the crown from the root, and weaker striae compared with the described holotype of *M. vanderhoefti*. *Mustelus vanderhoefti* can be easily distinguished from the other two described species by its larger size, the strong and rather coarse striae on the labial crown face, and the distinct uvula.

Nevertheless, teeth of extant and extinct species appear very homogenous and can be easily confused on the basis of dental characters, making species identifications difficult (Herman et al., 1988, 1990; Adnet and Cappetta, 2008). According to Herman et al. (1988), the following differences are useful to distinguish between the various nominal species of *Mustelus*: (1) variability of the principal ornamentation; (2) discrete differences in the secondary ornamentation; (3) number of primary costules and their degree of development; and (4) size of the teeth and the perceptibility of the principal cusp. Nevertheless, these features vary ontogenetically, which makes a reliable identification hardly possible. As mentioned above, the described teeth resemble those of *M. vanderhoefti*, but differ in several characteristics from the described holotype. Therefore, we refrain from any species assignment but prefer to keep these specimens in open nomenclature.

MERIDIOGALEUS, gen. nov.

Etymology—The genus name combines the Latin word ‘meridionalis,’ meaning ‘south,’ with reference to its southerly occurrence, and the Greek word ‘galeus,’ meaning ‘shark.’

Type Species—*Meridiogaleus cristatus*, gen. et sp. nov.

Diagnosis—Fossil triakid shark characterized by the following combination of dental characters: tooth crown mesiodistally wider than high (anterior to posterior teeth); principal cusp well developed and displaced distally; lack of mesial and distal cusplets; mesial cutting edge on lateral teeth concave; distal cutting edge short; short and fine to coarse costules on the basal mesial heel (sometimes short and fine costules on distal shoulder present); lack of labial ornamentation; apron-like bulge at the basal labial crown face overhanging the root labially; and rather high root lobes, which are well separated from each other.

Taxonomic Comparison—The teeth of the new taxon differ from teeth of

- *Archaeotriakis* Case, 1978, in having mesial and distal heels without distinct lateral cusplets, having a concave mesial cutting edge on lateral teeth, lack of labial and lingual crown ornamentation, and presence of an apron-like bulge slightly overhanging the basal labial crown face;
- *Foumtizia* Noubhani and Cappetta, 1997, in having a taller and more slender principal cusp, elongated lateral heels that may can bear one to four pairs of rather low cusplets, which are largely united with the base, a more gracile crown, and a concave to strongly concave labial crown base;
- *Furgaleus* Whitley, 1951 (no cusplets on lateral teeth), in having mesial and distal heels without distinct lateral cusplets, having a concave mesial cutting edge on lateral teeth, lack of lingual crown ornamentation, and presence of an apron-like bulge slightly overhanging the basal labial crown face;
- *Galeorhinus* Blainville, 1816, in having mesial and distal heels without distinct lateral cusplets, lack of lingual crown ornamentation, and presence of an apron-like bulge slightly overhanging the basal labial crown face;

- *Gogolia* Compagno, 1973, in having mesial and distal heels without distinct lateral cusplets, having a concave mesial cutting edge on lateral teeth, and presence of an apron-like bulge slightly overhanging the basal labial crown face;
- *Gomphogaleus* Adent and Cappetta, 2008, in lacking strong lingual costules that start at the lower edge of the tooth cusplet and run until near the upper edge of the cusplet;
- *Hemitriakis* Herre, 1923, in having a crown that is broader than tall;
- *Hypogaleus* Smith, 1957, in having mesial and distal heels without distinct lateral cusplets, having a concave mesial cutting edge on lateral teeth, presence of an apron-like bulge slightly overhanging the basal labial crown face, and lack of lingual crown ornamentation;
- *Iago* Compagno and Springer, 1971, in having a concave mesial cutting edge on lateral teeth, lack of labial and lingual crown ornamentation, and presence of an apron-like bulge slightly overhanging the basal labial crown face;
- *Khouribgaleus* Noubhani and Cappetta, 1997, in having a crown that is broader than high, a concave mesial cutting edge on lateral teeth, and lack of labial tooth ornamentation;
- *Mustelus* Linck, 1790, in having teeth with a well-developed principal cusp, having a concave mesial cutting edge on lateral teeth, and lack of labial crown ornamentation;
- *Palaeogaleus* Gurr, 1962, in having a crown that is broader than tall, presence of mesial and distal heels without distinct lateral cusplets, presence of an apron-like bulge slightly overhanging the basal labial crown face, having a concave mesial cutting edge on lateral teeth, having a taller, more slender triangular cusp, and having labial and lingual fine, short to elongated (depending on species) enameloid striae;
- *Pachygaleus* Cappetta, 1992, in having a concave mesial cutting edge on lateral teeth, lack of any lingual crown ornamentation, presence of an apron-like bulge slightly overhanging the basal labial crown face, and well-separated root lobes;
- *Paratriakis* Herman, 1977, in having a concave mesial cutting edge on lateral teeth, lack of lingual crown ornamentation, and presence of an apron-like bulge slightly overhanging the basal labial crown face;
- *Scylliogaleus* Boulenger, 1902, in having teeth with a well-developed principal cusp and having a concave mesial cutting edge on lateral teeth;
- *Triakis* (*Cazon*) de Buen, 1959, in having a concave mesial cutting edge on lateral teeth, lack of lingual ornamentation, and presence of an apron-like bulge slightly overhanging the basal labial crown face;
- *Triakis* (*Triakis*) Müller und Henle, 1838, in having mesial and distal heels without distinct lateral cusplets, having a concave mesial cutting edge on lateral

teeth, and presence of an apron-like bulge slightly overhanging the basal labial crown face;

- *Squatigaleus* Cappetta, 1989, in having a concave mesial cutting edge on lateral teeth, presence of an apron-like bulge slightly overhanging the basal labial crown face, and lack of labial crown ornamentation; and
- *Xystrogaleus* Adnet, 2006, in having a concave mesial cutting edge on lateral teeth, having a distinct labial crown ornamentation, and presence of an apron-like bulge slightly overhanging the basal labial crown face.

Teeth of *Kallodentis*, gen. nov., differ from those of *Meridiogaleus*, gen. nov., in lacking any labial ornamentation and lateral cusplets, having a concave mesial cutting edge, and presence of an apron-like bulge of the basal labial crown face.

MERIDIOGALEUS CRISTATUS, gen. et sp. nov (Figs. 4 and 5)

Etymology—The species name is derived from the Latin word ‘cristatus,’ meaning ‘crested.’

Holotype—NRM-PZ P16243, an anterior tooth.

Paratypes—Three anterior teeth (NRM-PZ P16241–16242, NRM-PZ P 16244); three anterolaterals (NRM-PZ P16079– 16081); three lateral to posteriors (NRM-PZ P16133–16135); an unfigured anterior tooth (NRM-PZ P16222) from locality IAA 2/95 (one specimen); one lateral tooth (NRM-PZ P16223) from locality IAA 1/90.

Type Horizon and Locality—IAA 1/90, ‘Ungulate site,’ *Natica*-horizon, *Cucullaea* I allomember, TELM 5, La Meseta Formation.

Geographic Range—IAA 1/90, ‘Ungulate site’ (64°14′04.67″S, 56°39′56.38″W); IAA 2/95, ‘Marsupial site’ (64°13′58″S, 56°39′06″W); IAA 1/93 (64°13′51.8″S, 56°35′53.14″W); Seymour Island, Antarctica.

Stratigraphic Range—TELM 5, Ypresian, Early Eocene; TELM 6, Lutetian, Middle Eocene.

Diagnosis—As for the genus.

Description—A total of 11 teeth are assigned to this new species. The teeth are more or less well preserved and can be assigned to anterior, lateral, and posterior jaw positions. The teeth are mesiodistally wider than tall, with a taller crown compared with the root, which is rather massive in profile view. The labial and lingual crown faces are smooth with no ornamentation except for short vertical costules on the mesial lingual crown faces. The root is quite long, with well-separated root lobes. The basal face of the root lobes is almost completely flat. The nutrient groove is deep and divides the root longitudinally into two root lobes. In basal view, the root lobes are kidney-shaped and broad.

Anterior teeth have a short, erect, and triangular principal cusp with a blunt apex. The labial crown face is smooth and devoid of any ornamentation. In profile view, the labial crown face forms an apron-like convex basal bulge, which overhangs the root labially (e.g., Fig. 4K). The lingual crown face is almost completely smooth except for several short, vertical, and stout costules, which mostly occur on the mesial crown face portion (e.g., Fig. 4B, F, J). Rarely, short and vertical costules are present on the disolingual crown face. These enameloid costules are well separated from each other and are relatively thick. Lateral cusplets are not developed. The cutting edge runs over the mesial and distal lateral shoulders and reaches the apex of the principal cusp. In occlusal view, the tooth crown is concavely indented at the basal edge of the crown, and the basal labial edge of the crown is rather straight to slightly concave. The root is high, with several elliptically shaped margino-lingual foramina. The median lingual part of the root is very distinct. The root lobes are well separated by a broad nutrient groove (e.g., Fig. 4J). In labial view, the basal edges of the root lobes are rounded (Fig. 5M).

Lateral teeth are wider than tall. The principal cusp is well separated, not that tall, slightly displaced distally, and has a blunt apex. The mesial crown shoulder is longer than the distal one. In labial view, the mesial crown edge is straight to slightly concave (Fig. 4Q, U). In profile view, the labial crown face is smooth, slightly convex, and forms an apron-like basal bulge, which overhangs the root. The lingual crown face is smooth except for strong enameloid folds on the mesial crown shoulder, which is bent lingually. These enameloid folds are clearly separated, short, and do not reach the upper part of the crown shoulder. Some teeth display fine and weak, lingually directed enameloid folds on the distal crown shoulder (e.g., Fig. 4R). The cutting edge runs continuously from the apex of the principal cusp to the mesial and distal crown shoulders (e.g., Fig. 4X). In occlusal view, the base of the crown is concavely indented compared with anterior teeth. The nutritive groove is rather broad but not as deep as in anterior teeth and separates the two well-developed root lobes.

More posterior teeth have a distinctly low principal cusp, with smooth labial crown faces and displaying abrasions. The labial crown face slightly overhangs the root and is convex towards the base of the crown. The basal edge of the labial face bears fine wrinkles in the median part of the crown (Fig. 5I). In occlusal view, the labial crown base is more concave than in all other teeth in this sample. The lingual crown face bears strong but short vertical costules on the mesial part of the crown and is slightly bent lingually in profile view. The lingual and labial crown faces are slightly convex. The cutting edge is rather blunt compared with anterior and lateral teeth. The root is high, and the root lobes are well separated by a broad nutritive groove (e.g., Fig. 5F). One pair of margino-lingual foramina is present on the lingual root face.

One posterior tooth has a very low occlusal crown face with a strongly wrinkled labial crown base but a smooth upper portion, distinctly overhanging the root. The principal cusp is heavily worn (e.g., Fig. 5J, K). The lingual crown face bears strong and short enameloid folds on each side of the very low principal cusp, which is directed lingually, almost being horizontal, but the apex is broken off. The crown shoulders bear low and lingually directed cusplets. The distal cusplet is separated from the principal cusp by a deeper notch than the mesial one, and it is higher than the mesial cusplet. The lateral cusplets bear strong basal wrinkles in profile view. In occlusal view, the base of the labial crown face is slightly sigmoidal in lateral teeth. The root is tall but slightly damaged in two specimens. In lingual view, the nutritive groove divides the two root lobes (Fig. 5M). In profile view, the root face bears a rounded and rather large margino-lingual foramen. The basal face of the root is slightly concave to flat in more posterior teeth.

Remarks—The teeth of the new taxon described here to some extent resemble those of the extant *Hemitriakis japonica* Müller and Henle, 1939. They share a mostly smooth labial crown face with strong mesial costules (only present in lower lateral teeth) but differ most significantly in the position of the principal cusp and the number of distal lateral cusplets. The teeth of the new taxon differ from teeth of other Eocene carcharhiniforms most particularly in having more or less symmetrical anterior teeth, an apron-like bulge forming at the base of the labial crown face, which overhangs the root slightly, and the very pronounced labial enameloid ridges/costules. The new taxon is characterized by a unique combination of dental features, such as lacking lateral cusplets on anterior and lateral teeth, a distinct apron-like bulge at the labial basal crown face, and short and strong costules on the lingual mesial crown shoulder.

The phylogeny of extant Triakidae is not well resolved, whereas the monophyly of Carcharhiniformes (Compagno, 1973) is widely accepted and supported by three synapomorphies (see Iglésias et al., 2005). Using DNA sequences of four protein coding genes, López et al. (2006) tested the inter- and intrafamilial relationships of the family Triakidae. Their results rejected the hypotheses that the triakid genera *Mustelus* and *Triakis* are monophyletic. We nevertheless allocate *Meridiogaleus cristatus*, gen. et sp. nov., to the family of Triakidae and subfamily Triakinae because of its distinct tooth character combinations, despite the varied combination of characters that partly also are found in various other carcharhiniforms.

KALLODENTIS, gen. nov.

Etymology—The genus name *Kallodentis* is derived from the Greek words ‘Kallo,’ meaning ‘beauty,’ and ‘dentis,’ meaning ‘tooth.’

Type Species—*Kallodentis rhytistemma*, gen. et sp. nov.

Diagnosis—Fossil triakid shark characterized by the following combination of dental characters: tooth crown taller than broad in anteriors but mesiodistally broader than tall in anterolateral teeth to posterior teeth; well-developed main cusp; one to three distal cusplets in all teeth; mesial cutting edge longer than distal one and slightly sigmoidal in lateroposterior teeth; labial ornamentation present; rather coarse basal costules on the basal labial face; short and fine striae on the mesial lingual heel in most teeth; apron-like bulge of basal labial crown face absent; uvula absent; root slightly mesiodistally broader than crown; and root lobes very well separated, with flat basal faces.

Taxonomic Comparison—The new taxon described here is considered to belong to the family Triakidae because of the typical dental morphology. Teeth of the new taxon differ from teeth of

- *Archaeotriakis* Case, 1978, in having less than two distal cusplets in all anterior to posterior positions;
- *Furgaleus* Whitley, 1951, in having lingual ornamentation on the mesial crown shoulder, and having labial ornamentation;
- *Gogolia* Compagno, 1973, in having strong and short basal costules and mesial cusplets in anterior teeth, having a comparatively taller crown, and having more a robust main cusp with the upper part of the apex being turned upwards;
- *Gomphogaleus* Adnet and Cappetta, 2008, in having a strong basal labial ornamentation and fine lingual striations below the distal lateral heel;
- *Hemitriakis* Herre, 1923, in having a more pronounced labial ornamentation;
- *Hypogaleus* Smith, 1957, in having a lingual ornamentation on the mesial crown shoulder, and having labial ornamentation;
- *Galeorhinus* Blainville, 1816, in having fewer distal cusplets in all anterior to posterior positions, and having a slightly sigmoidal mesial cutting edge;
- *Iago* Compagno and Springer, 1971, in having a more distal cusplets in all anterior to posterior positions, having lingual ornamentation on the mesial crown shoulder, and having labial ornamentation;
- *Khouribgaleus* Noubhani and Cappetta, 1997, in having a crown that is broader than tall in almost all tooth positions (except the parasymphyseal positions), and having lingual ornamentation on the mesial crown shoulder;
- *Meridiogaleus*, gen. nov., in lacking an apron-like bulge at the basal labial crown face, having two to three lateral cusplets, and having a labial ornamentation;
- *Mustelus* Linck, 1790, in having a better-developed main cusp and lacking an uvula;
- *Pachygaleus* Cappetta, 1992, in having a lingual ornamentation on the mesial crown shoulder;
- *Palaeogaleus* Gurr, 1962, in having a crown that is broader than tall at almost all tooth positions (except the parasymphyseal positions), having a comparatively lower and more robust, not triangular cusp, and lack of labial and lingual fine, short to elongated (depending on species) enameloid striae;
- *Paratriakis* Herman, 1977, in having distal cusplets in all anterior to posterior positions;
- *Scylliogaleus* Boulenger, 1902, in having a better-developed main cusp;
- *Squatigaleus* Cappetta, 1989, in having distal cusplets in all anterior to posterior positions, and having a slightly sigmoidal mesial cutting edge;
- *Triakis* (*Cazon*) de Buen, 1959, in having less than two distal cusplets in all anterior to posterior positions;

- *Triakis* (*Triakis*) Müller and Henle, 1838, in having a distinctly lower and not triangular-shaped main cusp, and a lack of lateral cusplets in anterior teeth; and
- *Xystrogaleus* Adnet, 2006, in lacking the distinct labial crown ornamentation.

KALLODENTIS RHYTISTEMMA, gen. et sp. nov. (Figs. 6–12)

Etymology—The species name is composed of the Greek word ‘rhutis,’ meaning ‘wrinkled and/or ‘folded,’ and the Greek word ‘stemma,’ meaning ‘crown,’ referring to the typically wrinkled crown of this species.

Holotype—NRM-PZ P16143, an anterior tooth.

Paratypes—Eleven anterior teeth (NRM-PZ P16136–16142, NRM-PZ P16144–16147); 13 anterolateral to laterals (NRM-PZ P16181–16189; NRM-PZ P16190–16193); 12 more posteriors (NRM-PZ P16194–16205). Not figured specimens: NRM-PZ P16224 from locality IAA 1/90: anterior, lateral, and posterior teeth (seven specimens); NRM-PZ P16225 from locality IAA 2/95 (two specimens).

Type Horizon and Locality—IAA 1/90, ‘Ungulate site,’ *Natica*-horizon, *Cucullaea* I allomember, TELM 5, La Meseta Formation.

Geographic Range—IAA 1/90, ‘Ungulate site’ (64°14′04.67″S, 56°39′56.38″W); IAA 2/95, ‘Marsupial site’ (64°13′58″S, 56°39′06″W); IAA 1/93 (64°13′51.8″S, 56°35′53.14″W); Seymour Island, Antarctica.

Stratigraphic Range—TELM 5, Ypresian, Early Eocene; TELM 6, Lutetian, Middle Eocene.

Diagnosis—As for the genus.

Description—This new species is known only from isolated teeth, which are comparatively small (<2 mm high). Although the teeth are very variable in shape, a number of characteristic morphological features are present in all teeth. The teeth are mesiodistally wider than tall, with a well-developed principal cusp. The labial face of the lateral cusplets is slightly convex from side to side and separated from the straight to gently convex lingual crown face by a well-developed cutting edge that almost reaches the apex of the crown. The crown bears a smooth upper labial crown face with short costules near the base. They are strong in anterior teeth and are typically found on the distal and mesial parts of the crown or form a continuous band from one side of the tooth to the other.

In lateral and postlateral teeth, the costules are weaker than in anterior teeth. The basal edge of the crown weakly overhangs the upper part of the root. The root is of similar shape in all teeth, differing mainly in height, resulting in longer roots in anterior teeth than in lateral and postlateral teeth. The root comprises two clearly separated lobes and is nearly symmetrical in labial view.

Despite the overall similarities in the morphology of all teeth, there is considerable variation in the form of the tooth crown depending on jaw position. The parasymphyseal tooth is symmetrical, with a rather tall and slender principal cusp, compared with the other teeth (Fig. 7U–X). The principal cusp makes up half of the height of the complete crown. The tooth is slightly taller than wide (mesiodistally), with a triangular principal cusp and a rounded apex, which is slightly worn. The labial and lingual crown faces are smooth except for very short and fine striae at the base of the labial crown face. These striae span over the entire basal crown width (mesiodistally) (Fig. 7U). The basal part of the crown is convex and slightly overhangs the root labially. The cutting edge starts at the median part of the crown and runs down the basal part of the lateral cusplet, but does not reach the basal edge of the crown (Fig. 7W).

Upper anterior teeth tend to have a stronger ornamentation than lower anterior teeth (e.g., compare Fig. 6E, M with Fig. 7A, E, Q). In profile view, the crown is labiolingually rather massive compared with lateral teeth. The lingual crown face bends lingually slightly and is smooth except for short and fine, vertically arranged striae on the mesial heel in most teeth. The labial and lingual crown faces are separated by a short but well-developed cutting edge. The principal cusp is flanked by a pair of small incipient cusplets on each side, which are not well separated from the principal cusp. The root is rather long, with root lobes being clearly separated by a broad nutrient groove. This nutrient groove is rather long on the lingual root face, nearly reaching the basal part of the crown (Fig. 12B, F). One pair of margino-lingual foramina is generally present (Fig. 12B, F).

Anterolateral teeth are slightly wider mesiodistally than tall, with a rather low and triangular principal cusp that is displaced towards the distal edge of the crown. In occlusal view, the base of the crown can be strongly wrinkled to nearly smooth (Fig. 8D, L, P, T). The mesial edge of the principal cusp is straight to slightly convex. A very small mesial cusplet may be present, but it is absent in most tooth positions (Fig. 8U). Distally, there are one to two lateral cusplets, which are well separated from the principal cusp but weakly separated from each other.

Lateral to posterior teeth appear to show a gradation in crown morphology, but all teeth are wider than tall, with a distally inclined principal cusp (Figs. 9I–X, 11A–P). The principal cusp is rather broad at the base, with a rounded apex. In profile view, the labial crown face is straight to slightly convex (e.g., Fig. 9G, W). The basal labial costules tend to be stronger in upper lateral to posterior teeth, but the labial crown face can be completely smooth in presumed lower teeth.

Most lateral to postlateral teeth have short and fine striae on the lingual-mesial crown face. In profile view, the labial crown is slightly convex (Fig. 11L). These teeth possess one to three distal lateral cusplets, which are slightly divergent and directed distally, whereas the principal cusp is more or less distally inclined. Lateral cusplets are well separated from the principal cusp by a deep and long notch. Towards the posterior teeth the cusplets become less well separated from each other. The mesial edge of the crown is straight to slightly convex. Compared with anterior teeth, the crown of lateral and postlateral teeth is finer and the cutting edge nearly reaches the apex of the crown. The distal cutting edge is short, and towards the crown base it is replaced by a series of two to three cusplets that are gradually reduced in height (Figs. 10E, 11A). In occlusal view, the basal edge of the labial crown face is straight to slightly convex. The root is rather long, with two or more foramina on the labial root face (e.g., Fig. 11A, I, M). Two to five small foramina are located on the lingual root face (e.g., Fig. 11B, N). The root lobes are well separated from each other by a rather wide nutritive groove. The basal parts of the root bear a distinct rim in labial view (e.g., Fig. 11A, M).

Remarks—The character combination is very similar to that of *Triakis* (*Triakis*), *Hemitriakis*, and *Palaeogaleus*. Teeth of *Triakis* (*Triakis*) differ from those of *Kallodentis*, gen. et sp. nov., in the following combination of characters: upper anterior teeth with tall and triangular principal cusp, more lateral teeth almost symmetrical with only a single pair of slightly divergent cusplets, mesial cutting edge regularly convex; lower anterior teeth symmetrical with a pair of large and divergent cusplets; and bulge-like apron present. In all anterior to posterior teeth, only a single distal cusplet is present. *Hemitriakis* differs most notably in having only a weak labial ornamentation, more mesiodistally elongated lower anterolateral teeth, and lower crown height. Anterior teeth differ most significantly from other Eocene triakids in having a rather low principal cusp and strong and short basal costules. In occlusal view, the labial basal edge of the crown is often strongly incised. *Palaeogaleus* is characterized by having tall teeth with a broad, tall, and distally bent cusp. Anterior teeth have two to three pairs of divergent lateral cusplets. Teeth of *Kallodentis rhytistemma*, gen. et sp. nov., differ most significantly in lacking the elongated mesial heel that bears up to four cusplets. The rather strong labial enameloid folds of *Palaeogaleus* (length depends on the species) are elongated and finer than in *Kallodentis rhytistemma*, gen. et sp. nov.

Teeth of *Meridiogaleus cristatus*, gen. et sp. nov., can be easily distinguished from *Kallodentis rhytistemma*, gen. et sp. nov., in lacking distal lateral cusplets, labial basal costules, and a very pronounced apron-like bulge on the basal labial crown face. Both taxa seemingly are endemic Eocene Antarctic triakids.

Genus *GALEORHINUS* Blainville, 1816

Type Species—*Squalus galeus* Linnaeus, 1758.

GALEORHINUS sp. (Fig. 13)

Material—NRM-PZ P16212, one ?posterior tooth.

Geographic Range—IAA 1/90, ‘Ungulate site’ (64°14′04.67″S, 56°39′56.38″W); Seymour Island, Antarctica.

Stratigraphic Range—TELM 5, Ypresian, Early Eocene.

Description—The single tooth is slightly broader than tall, with a rather broad triangular principal cusp, which is bent distally. On the labial crown face, short and fine striae occur at the level of the heels, and the labial crown face overhangs the root. Lingually, the crown face is smooth. The mesial cutting edge is rather straight and longer than the distal one. The principal cusp is flanked by approximately six distal lateral cusplets, but only the first lateral cusplet is broad and well separated from the main cusp and from the other cusplets. The lateral cusplets decrease in size towards the rear. Labially, the root is low and the basal root edge is concave. The root lobes are short and rounded at the edges.

Remarks—The morphology of the single tooth is congruent with the basic diagnosis of Triakidae, and it is very similar to representatives of the genus *Galeorhinus* Blainville, 1816. Teeth of *Galeorhinus* can be distinguished from other morphologically similar teeth, by the smaller size (less than 5 mm), five to 10 well-separated cusplets of decreasing size, principal cusp bent towards the rear (from anterior files distally), and mesial cutting edge distinctly longer than distal cutting edge. The fossil record of *Galeorhinus* extends back to the Cenomanian (Upper Cretaceous) of the Lower Volga River Basin, Russia (Popov and Lapkin, 2000), and the genus is additionally known from many Late Cretaceous and Cenozoic sites in Europe, North Africa, and North America (Maisey, 2012). The described specimen differs from *G. minutissimus* Arambourg, 1935, *G. goncalvesi* Antunes et al., 1999, and *G. louisi* Adnet and Cappetta, 2008, in lacking an upturned cusp apex. *Galeorhinus mesetaensis* Noubhani and Cappetta, 1997, is characterized by small teeth of about 3.5 mm total width, two to five distal cusplets, which decrease in size distally, and strong folds on the labial crown face. The main cusp of *G. mesetaensis* is considerably taller and more slender than the main cusp of the here-described tooth of *Galeorhinus*. Additionally, the Antarctic specimen is lacking distal cusplets and only a heel is developed. Teeth of *Galeorhinus duchaussoisi* Adnet and Cappetta, 2008, can be distinguished from the Antarctic *Galeohrinus* specimen by its medium-sized teeth (up to 7 mm in total width), the rather thick cusp, and the more robust root. *Galeorhinus ypresiensis* Casier, 1946, differs from the Antarctic *Galeorhinus* teeth in the slightly taller labial crown face, the slender and more elongated main cusp, and the presence of mesial cusplets.

The differences from other fossil species (e.g., lack of distal serrae or cusplets) may indicate a distinct, hitherto unknown Antarctic Eocene species. However, with only one tooth found in the La Meseta Formation and its presumed posterior jaw position, it is identified to the generic level only and we refrain from erecting a new taxon. Long and Stilwell (2000) first reported *Galeorhinus* from the Eocene of Antarctica at Mount Discovery. Comparing the specimen described here with the one from Mount Discovery, some differences can be observed. Our tooth is smaller; the basal edge of the root is more convex than in the Mount Discovery specimen, whereas the lateral cusplets are more clearly separated from each other in the specimen described by Long and Stilwell (2000) than in the present specimen.

Family CARCHARHINIDAE Jordan and Evermann, 1896 Genus *ABDOUNIA* Cappetta, 1980

Type Species—*Eugaleus beaugei* Arambourg, 1935.

ABDOUNIA MESETAE, sp. nov. (Fig. 14A–R)

Etymology—The new species name ‘mesetae’ is in reference to the La Meseta Formation, from which the material was collected.

Holotype—NRM-PZ P15808, anterior tooth.

Paratypes—Two upper teeth (NRM-PZ P16213–16214); six lower teeth (NRM-PZ P16215–16216, NRM-PZ P15915, NRM-PZ P16217–16219).

Type Horizon and Locality—IAA 1/95, ‘Marsupial site,’ *Cucullaea* I allomember, TELM 5, La Meseta Formation.

Geographic Range—IAA 1/90, ‘Ungulate site’ (64°14′04.67″S, 56°39′56.38″W); IAA 2/95, ‘Marsupial site’ (64°13′58″S, 56°39′06″W); Seymour Island, Antarctica.

Stratigraphic Range—TELM 5, Ypresian, Early Eocene (nine teeth).

Diagnosis—Species of *Abdounia* differing from all other species of this genus by the following combination of characters: principal cusp blade-shaped; labial and lingual crown faces smooth; one pair of low and broad lateral cusplets in anterior teeth; in upper anterior teeth, no lateral cusplets present; in upper lateral teeth, mesial cusplet very reduced; distal cusplet broad and rather low; mesial cusplet reduced in lower lateral teeth; one or two distal cusplets; lingual protuberance well developed in upper teeth and less developed in lower teeth; and low labial root face.

Taxonomic Comparison—*Abdounia mesetae*, sp. nov., can be easily distinguished from

- *A. belselensis* (Mollen, 2007), *A. enniskellini* (White, 1956), *A. lapierrei* (Cappetta and Nolf, 1981), *A. africana* (Arambourg, 1952), and *A. vassilyevae* (Malyshkina, 2012) by a blade-like, prominent principal cusp;
- *Abdounia claibornensis* (White, 1956) and *A. recticona* (Winkler, 1874) in having a smaller number of lateral cusplets;
- *A. minutissima* (Winkler, 1874) and *A. vassilyevae* (Malyshkina, 2012) in lacking a labial ornamentation;
- *Abdounia furimsky* (Case, 1980) in having better developed lateral cusplets;
- *A. beaugei* (Arambourg, 1935) in having fewer lateral cusplets (two pairs in *A. beaugei*) in lateral teeth, which are divergent, taller, and more slender in *A. beaugei*;
- *Abdounia lata* (Malyshkina, 2012) taller and more pointed lateral cusplets;
- *Abdounia vassilyevae* (Malyshkina, 2012) in having lower, more robust, and blunt lateral cusplets;
- *A. biauriculata* (Casier, 1946), in having a lower and more robust principal cusp, and lower and more robust lateral cusplets (up to two pairs in *A. biauriculata*), which are less well separated from the main cusp in the new taxon; and
- *A. richteri*, sp. nov., in having comparably lower and more robust lateral cusplets and a more slender principal cusp.

Description—In anterior teeth, the principal cusp is prominently blade-shaped but comparativey low (Fig. 14A). The labial and lingual crown faces are devoid of any ornamentation except for one tooth that displays short and fine basal striae on the labial crown face. The labial crown face is slightly concave. One pair of low, triangular lateral cusplets is present. The lateral cusplets are well separated from the principal cusp by a rather low, triangular notch. The cutting edge is sharp and continuous. The root is labially low and labiolingually broad, with root lobes slightly projecting outwards. The basal edge of the root is slightly concave. The lingual protuberance is well marked, with a deep nutrient groove and a small central foramen.

Upper lateral teeth also have a blade-shaped principal cusp, which is straight to slightly curved towards the rear (Fig. 14G, I). One pair of lateral cusplets flanks the rather broad principal cusp. The mesial cusplet is broad and pointed, whereas the distal one is reduced to a low heel (e.g., Fig. 14I). One lateral tooth also has a mesial heel. The labial and lingual crown faces are smooth. The lingual crown face is flat, whereas the labial crown face is concave. The root is massive compared with lower lateral and anterior teeth (Fig. 14C, A). The basal face of the root is flat, with a deep nutrient groove dividing the root lobes (Fig. 14A, E). The root lobes project outwards and slightly downwards. The basal edge of the root is concave (e.g., Fig. 14A, C).

In lower lateral teeth, the principal cusp is slender compared with upper lateral teeth, which are bent towards the rear. The mesial cutting edge is straight to slightly convex. The labial and lingual crown faces are smooth without any ornamentation. One or two lateral cusplets on the distal side and one on the mesial side flank the principal cusp. The cutting edge is continuous. The root is low, with a longer mesial than distal root lobe. The lingual central protuberance is not well developed compared with upper lateral teeth. The basal edge of the root is slightly concave.

Remarks—*Abdounia richteri*, sp. nov., differs from *A. mesetae*, sp. nov., in having a slender and straight principal cusp, which is flanked by taller and narrower lateral cusplets. Teeth of *A. richteri*, sp. nov., have one pair of lateral cusplets in all jaw positions, whereas *A. mesetae*, sp. nov., has one pair of lateral cusplets in anterior teeth and only one cusplet in lateral teeth.

The genus *Abdounia* had a relatively wide geographic range within the Northern Hemisphere. *Abdounia beaugei* has a comparable paleodistribution to that of numerous extant carcharhinids with a high vagility (Musick et al., 2004). It has the widest distribution and has been recorded from Europe, northern Africa, Asia, and North America (e.g., Arambourg, 1952; Case et al., 1996; Noubhani and Cappetta, 1997). *Abdounia clabornensis* and *A. enniskilleni* are known from the middle and upper Eocene of Alabama. *Abdounia africana* is only known from the Eocene of Africa (Noubhani and Cappetta, 1997). Malyshkina (2012) described two new species of *Abdounia* (*A. lata* and *A. vassilyevae*) from the upper Eocene of the trans-Ural region. Two Oligocene species are known from North Carolina (Case, 1980) and Belgium (Mollen, 2007).

Case et al. (2015) noted that in the Ypresian Fishburne Formation of South Carolina, only one species of *Abdounia* is present, which is somewhat unexpected, because multiple species occurrences were reported from other North American deposits. In Antarctica two co-occurring new species are described herein. The co-occurrence of two nominal *Abdounia* species in most localities is very peculiar and might indicate a case of sexual dimorphism rather than taxic differences. However, this is impossible to establish without skeletal material.

ABDOUNIA RICHTERI, sp. nov. (Fig. 15A–L)

Etymology—Named after Martha Richter (Natural History Museum, London, U.K.) for her contributions to paleoichthyology.

Holotype—NRM-PZ P16209, lateral tooth.

Paratypes—Two anterior teeth (NRM-PZ P16206–16207); anterolateral to lateral teeth (NRM-PZ P16208–16211).

Type Horizon and Locality—IAA 1/90, 'Ungulate site,' *Natica*-horizon, *Cucullaea* I allomember, TELM 5, La Meseta Formation.

Geographic Range—IAA 1/90, 'Ungulate site' (64°14′04.67″S, 56°39′56.38″W) and IAA 2/95 (= IAA 1/95), 'Marsupial site' (64°13′58″S, 56°39′06″W); Seymour Island, Antarctica.

Stratigraphic Range—TELM 5, Ypresian, Early Eocene (six teeth).

Diagnosis—A species of *Abdounia* characterized by the following combination of dental characters: anterior teeth with slender and straight principal cusp; smooth lingual crown face; short and fine striae at the base of the labial crown face; one pair of rather slender lateral cusplets with rounded apices; well-developed central lingual protuberance; short root with poorly separated root lobes in anterior teeth; root lobes slightly projecting outwards; and the basal edge of the root is straight to slightly concave.

Taxonomic Comparison—Teeth of *Abdounia richteri*, sp. nov., differ from teeth of

- *A. clairbornensis* (White, 1956) and *A. recticona* (Winkler, 1874) in having only one pair of lateral cusplets;
- *Abdounia enniskilleni* (White, 1956) in having comparatively lower and more blunt lateral cusplets;
- *A. lapierrei* (Cappetta and Nolf, 1981) and A. *africana* (Arambourg, 1952) in having a comparatively lower cusp;
- *Abdounia minutissima* (Winkler, 1874) and *A. vassilyevae* (Malyshkina, 2012) in lacking labial crown ornamentation;
- *A. beaugei* (Arambourg, 1935) and *A. belselensis* (Mollen, 2007) in having a comparatively higher principal cusp;
- *Abdounia biauriculata* Casier, 1946, in having lower lateral cusplets, which are separated by a deep and broad notch from the principal cusp in *A. biauriculata*;
- *Abdounia furimsky* (Case, 1980) in having distinct distal cusplets; and

- *A. recticona* (Winkler, 1874), *A. claibornensis*, and *A. lata* (Malyshkina, 2012) in having distinctly fewer lateral cusplets.

Description—The principal cusp is slender, straight, and tall in anterior teeth. The lingual crown face is smooth. Short and fine striae are present at the base of the labial crown face (Fig. 15B). The upper part of the labial crown face is smooth. In profile view, the main cusp is slightly sigmoidal (Fig. 15C, G). The principal cusp is flanked by one pair of short, rather slender, and rounded lateral cusplets. The cutting edge is well developed, sharp, and continuous. The root is low with poorly separated root lobes (Fig. 15C, D, I, J). The central lingual protuberance is well developed, with a deep nutrient groove, which separates the two root lobes. The root lobes project slightly outwards.

Lateral teeth are broader than anterior teeth (e.g., Fig. 15K). In profile view, lateral teeth are slightly sigmoidal. The principal cusp is slender and straight to slightly distally inclined in more lateral files. The labial and lingual crown faces are smooth without any ornamentation (e.g., Fig. 15G, H, K, L). The lingual crown face is flat to somewhat convex. The lateral cusplets are slender, rather low, and are not acuminate. Lateral cusplets are well separated from the principal cusp by a deep notch (e.g., Fig. 15C, I).

In more lateral teeth, the mesial cusplets are larger and more triangular than in distal teeth. The root is low, with not well-separated root lobes, which project slightly outwards. The lingual protuberance is well developed, with a prominent nutrient groove and a deep central foramen. The nutrient groove is not as deep as in anterior teeth. The basal edge of the root is straight to slightly concave.

Remarks—*Abdounia* is a rather common Paleogene carcharhiniform with a wide distribution in the Northern Hemisphere. The new species represents (together with the other new species described here) the southernmost record of this genus. The oldest record is from the Danian (early Paleocene), whereas the stratigraphically youngest record is from the Rupelian (early Oligocene; Cappetta, 2012). The genus reached its greatest diversity and widest geographical range in the middle Eocene (Malyshkina, 2012). *Abdounia* was very abundant in the Eocene but disappeared at the end of the Eocene/beginning of the Oligocene (Müller, 1999). *Abdounia*, like *Galeorhinus* is considered a small-sized predatory shark, which might be considered a generalist feeder, preying on active food such as bony fishes (Underwood et al., 2011).

The two new Antarctic species of *Abdounia* can be easily separated by the shape of the principal cusp and the lateral cusplets, and the prominent lingual protuberance in *A. mesetae*, sp. nov.

Discussion and Conclusions

Chondrichthyans probably are the most diverse and abundant fish remains in the Eocene La Meseta and Submeseta formations. Long (1992a) was the first to describe two carcharhiniform shark teeth, which he identified as *Scoliodon* sp. by comparison with teeth of extant *Scoliodon* Müller and Henle, 1837, *Loxodon* Müller and Henle, 1838, and *Rhizoprionodon* Whitley, 1929, from these formations. Teeth of extant *Scoliodon* spp. are, however, more gracile compared with the specimens that Long (1992a) described. Moreover, the principal cusp is more slender, distally displaced, and is more lingually curved in *Scoliodon*. The described prominent lingual root protuberance is absent in *Scoliodon* and *Rhizoprionodon*. The root is taller in Long's (1992a) specimen than in typical teeth of *Scoliodon* and the material described by Long (1992a) thus is very different from teeth of *Scoliodon*. The root depicted in Long's figured specimen could even indicate closer relationships to lamniforms. Unfortunately, it was not possible to locate the original material that Long (1992a) described in his work for detailed comparison. Therefore, we consider the material assigned to *Scoliodon* by Long (1992a) to be indeterminate.

In 2005, Kriwet described the southernmost representative of *Carcharhinus* sp. from TELM 3 of the La Meseta Formation. In the examined material for this study, no additional specimens that could be assigned to *Scoliodon* or to *Carcharhinus* were recovered, and the only valid carcharhiniform shark from the Eocene La Meseta Formation of Antarctica has been *Carcharhinus*. Therefore, the new carcharhiniform material described here provides important information about the southern distribution of carcharhiniform sharks in the Eocene and also contributes to our general understanding about their paleogeographic distribution during the Cenozoic.

The two new species of *Abdounia* Cappetta, 1980, described here belong to a widespread and common Paleogene group of small carcharhinids known in the Eocene from European (e.g., Belgium, England, France), North American (e.g., Alabama, North Carolina, Virginia; Mexico), African (e.g., Angola, Bas-Congo, Enclave de Cabinda, Morocco), and Asian (e.g., east Jordan; Uzbekistan) deposits (e.g., Casier 1946, 1957; Arambourg, 1952; White, 1956; Mustafa and Zalmout, 2002; Malyschkina, 2012; Otero et al., 2012; Maisch et al., 2014; Case et al., 2015; Cappetta and Case, 2016). Consequently, the two new species extend the paleogeographic range of this genus into the Southern Hemisphere and also indicate the presence of highly endemic species, which are only known from Antarctica up to now.

The single tooth of *Galeorhinus* presented here, in addition to the one from Mount Discovery, indicates that this genus was probably more common in the Antarctic Eocene and thus in high southern latitudes during the Paleogene than suggested by their currently known fossil record.

So far, only members of Triakidae (houndsharks) and Carcharhinidae (groundsharks) have been reported from the Eocene of Antarctica; scyliorhinids (catsharks) that might have been expected seemingly are not present. The same applies to Hemigalidae (weasel sharks) and the rather rare Sphyrinidae (hammerhead sharks), which otherwise occur in Eocene faunas around the world. Representatives of the Carcharhinidae and Triakidae are the most abundant members of Carcharhiniformes found in Eocene deposits of Asia, Africa, Europe and the U.S.A., whereas Sphyrinidae are the least abundant sharks found. Fossil charcharinids and triakids are predominantly known from the Northern Hemisphere (e.g., Casier, 1946; Arambourg, 1952; Case and Cappetta, 1990; Li, 1995; Noubhani and Cappetta, 1997; Mustafa and Zalmout, 2002; Adnet and Cappetta, 2008; Adnet et al., 2010; Carlson and Cuny, 2014; Case et al., 2015; Cappetta and Case, 2016), with only a few records from the Southern Hemisphere (e.g., Dartevelle and Casier, 1943, 1959; Casier, 1957, 1958; Keyes, 1984; Wallett, 2006; Otero et al., 2012, 2013; Otero and Soto-Acuna, 2015). Most representatives of extant families of Carcharhinidae first appeared in the Eocene (Cappetta, 2012; Maisey, 2012). Recently, Guinot et al. (2014) reported on a Valanginian elasmobranch assemblage from southern France, setting the first occurrence of Carcharhinidae into the Lower Cretaceous. This would imply that, in comparison with most other living sharks, this group might have evolved rather long ago. Carcharhinids only became abundant in the Paleocene, and they are seemingly most abundant in the Miocene of Europe, U.S.A., Africa, and Asia (Underwood and Ward, 2008; Cappetta, 2012). The triakids and carcharhinids from the Eocene described here are the southernmost records known, indicating that these carcharhiniform groups attained global distributions early in their evolutionary history after the K/P boundary event.

The two new triakid taxa, *Meridiogaleus cristatus*, gen. et sp. nov., and *Kallodentis rhytistemma*, gen. et sp. nov., and the triakid *Mustelus* sp. occur in TELMs 5 and 6 (Ypresian and Lutetian in age, respectively) of the La Meseta Formation on Seymour Island, which represent estuarine deposits (Table 1). The two new carcharhinids, *Abdounia richteri*, sp. nov., and *Abdounia mesetae*, sp. nov., and the traikid, *Galeorhinus* sp., are restricted to TELM 5. The standing diversity of chondrichthyans is the same in TELMs 4 and 5 (25 species each) and represents a mixed cool- and warm-temperature association. The faunal composition correlates well with rather low temperatures of 10–11°C that were established in TELM 4. A short temperature increase is recognizable at the base of TELM 6 (ca. 15°C), with subsequent cooling at the end of TELM 6 that continues into TELM 7 (see Table 1). The lower chondrichthyan diversity in TELM 6 (five taxa) does not correlate with the temperature increase, however. This indicates that cool-temperate taxa vanished from the near-coastal shallow waters of Antarctica and were not replaced by warm-temperate or even subtropical taxa. All taxa recovered from TELM 6 also occur in TELMs 3 and/or 4. However, the occurrence of several taxa in TELMs 5 and 7 that are absent from TELM 6 (e.g., *Squalus* sp., *Squatina* sp., *Palaeohypotodus* cf. *rutoti, Striatolamia* cf. *macrota*) also could represent a collecting bias rather than a real pattern.

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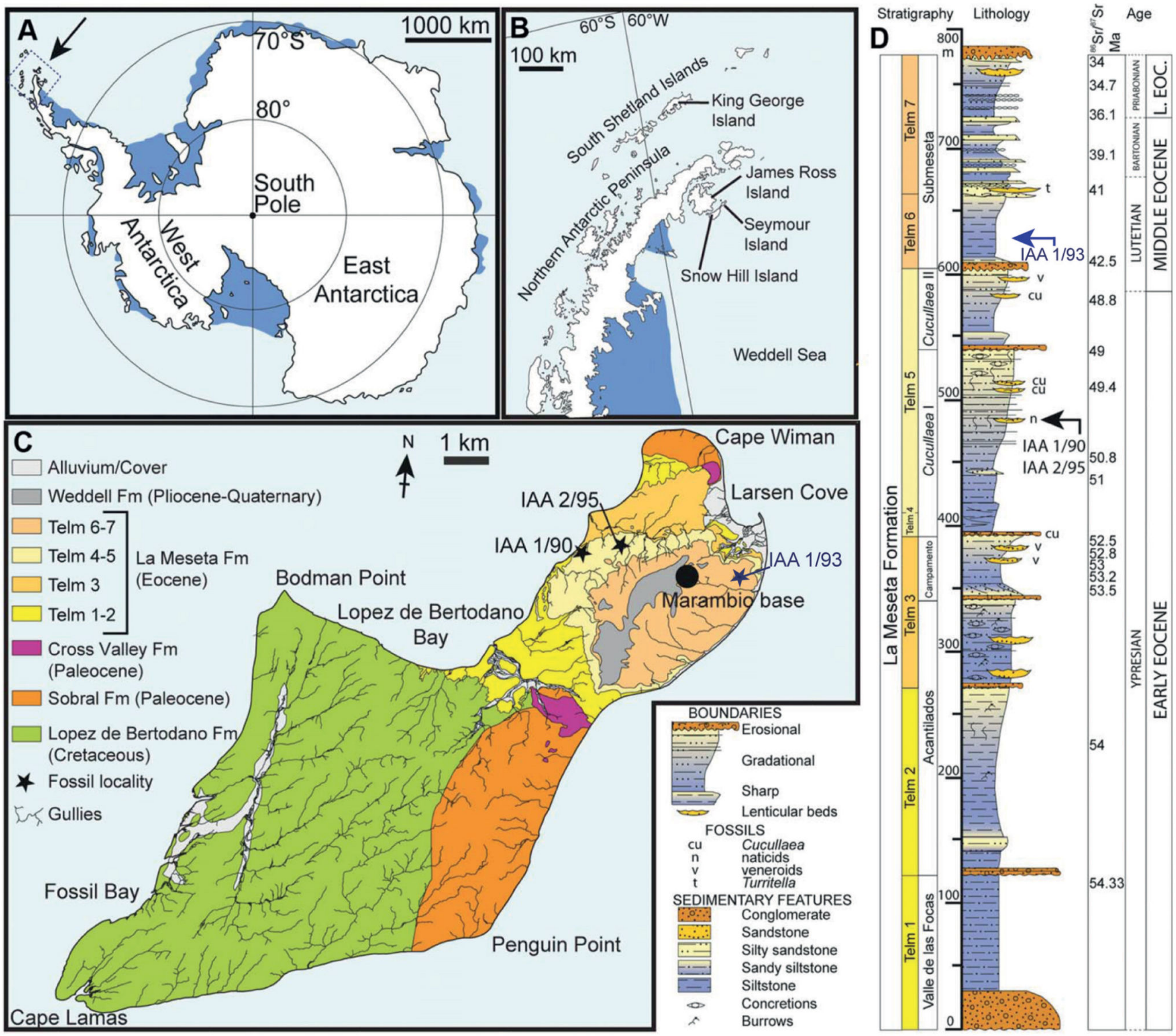

Figure 1.

Location and stratigraphy of Seymour Island, Antarctica. **A**, map of Antarctica, showing the position of the Antarctic Peninsula; **B**, map of the Antarctic Peninsula, showing the location of Seymour Island; **C**, geological map of Seymour Island, showing the outcrop of TELMs 5 and 6 with the localities IAA 1/90, IAA 2/95, and IAA 1/93 of the Eocene La Meseta Formation; **D**, composite measured section trough the La Meseta and Submeseta formations, showing the stratigraphical positions of the sampled localities IAA 1/90, IAA 2/95, and IAA 1/93. Modified from Schwarzhans et al. (2016). Strontium date values from Dingle and Lavelle (1998), Dutton et al. (2002), Ivany et al. (2008), and Reguero et al. (2013).

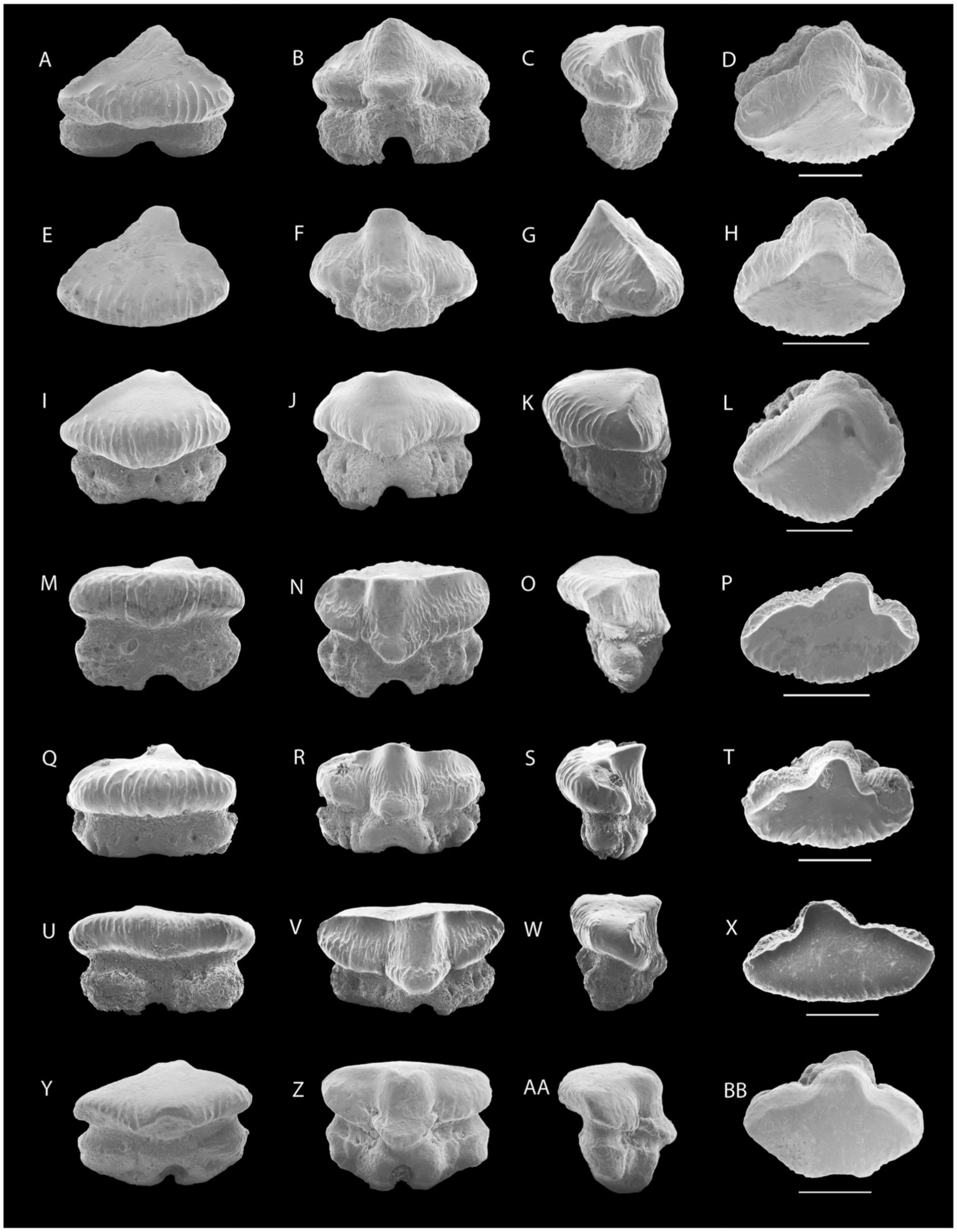

Figure 2.

SEM images of *Mustelus* sp., NRM-PZ P16226, **A**, labial; **B**, lingual; **C**, profile **D**, occlusal views; NRM-PZ P16227, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16228, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16229, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P16230, **Q**, labial; **R**, lingual; **S**, profile; **T**, occlusal views; NRM-PZ P16231, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views; NRM-PZ P16232, **Y**, labial; **Z**, lingual; **AA**, profile; **BB**, occlusal views. All scale bars equal1 mm.

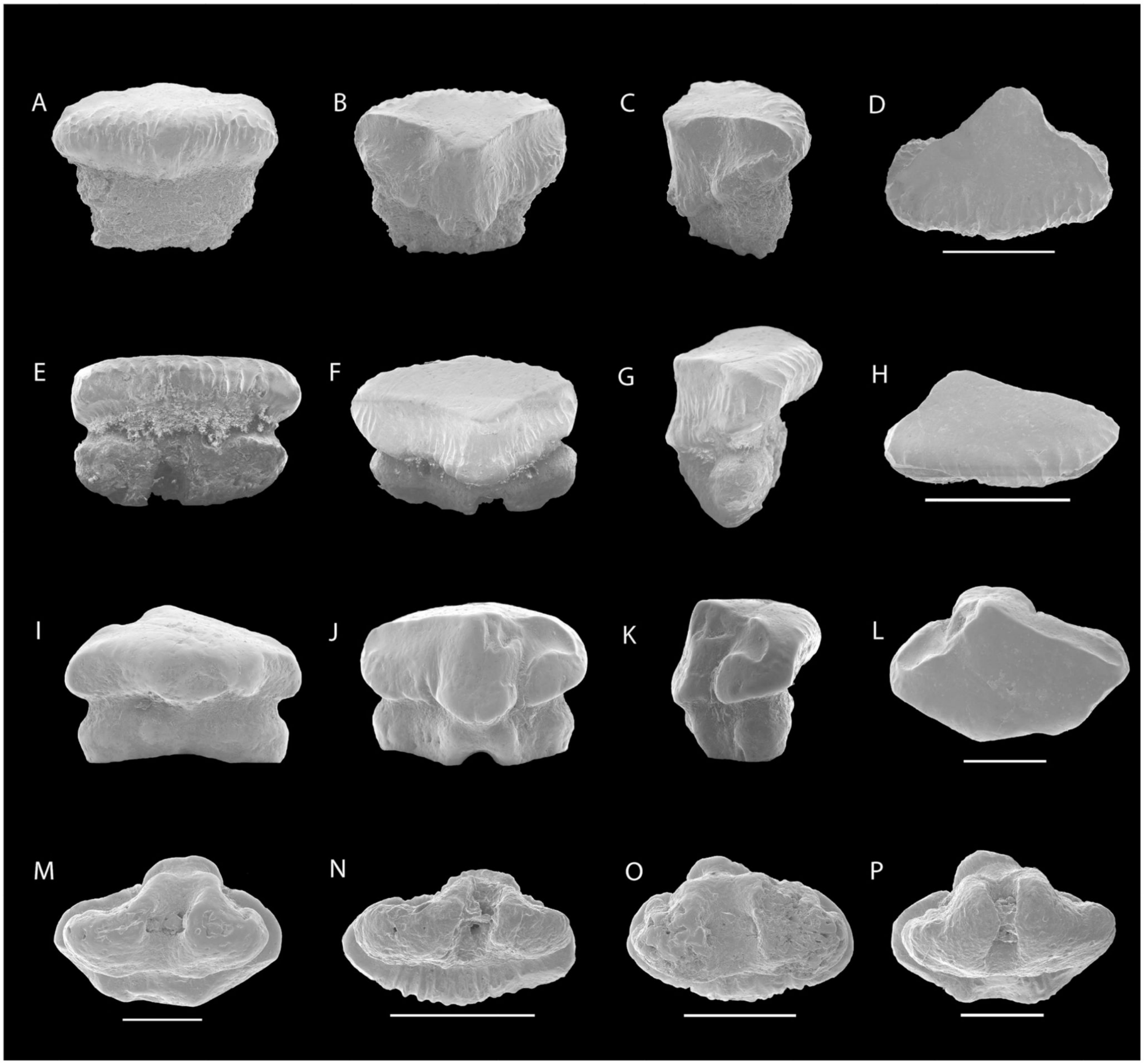

Figure 3.

SEM images of *Mustelus* sp., NRM-PZ P16233, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16234, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16235, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16235, **M**, basal view; NRM-PZ P16234, **N**, basal view; NRM-PZ P16088, **O**, basal view; NRM-PZ P16232, **P**, basal view. All scale bars equal 1 mm.

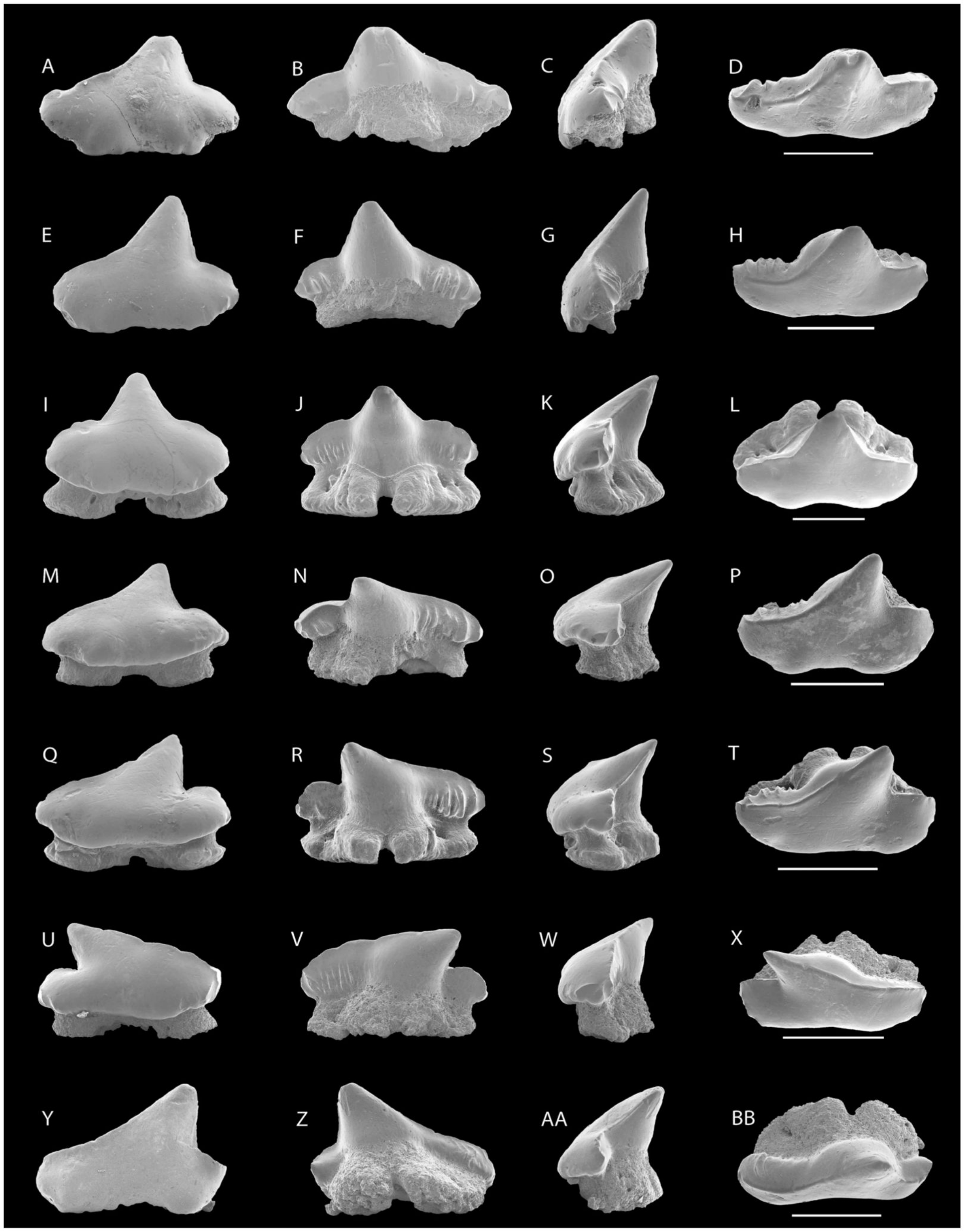

Figure 4.

SEM images of *Meridiogaleus cristatus*, gen. et sp. nov., NRM-PZ P16241, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16242, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16243 (holotype), **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16244, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P16079, **Q**, labial; **R**, lingual; **S**, profile; **T**, occlusal views; NRM-PZ P16080, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views; NRM-PZ P16081, **Y**, labial; **Z**, lingual; **AA**, profile; **BB**, occlusal views. All scale bars equal 1 mm.

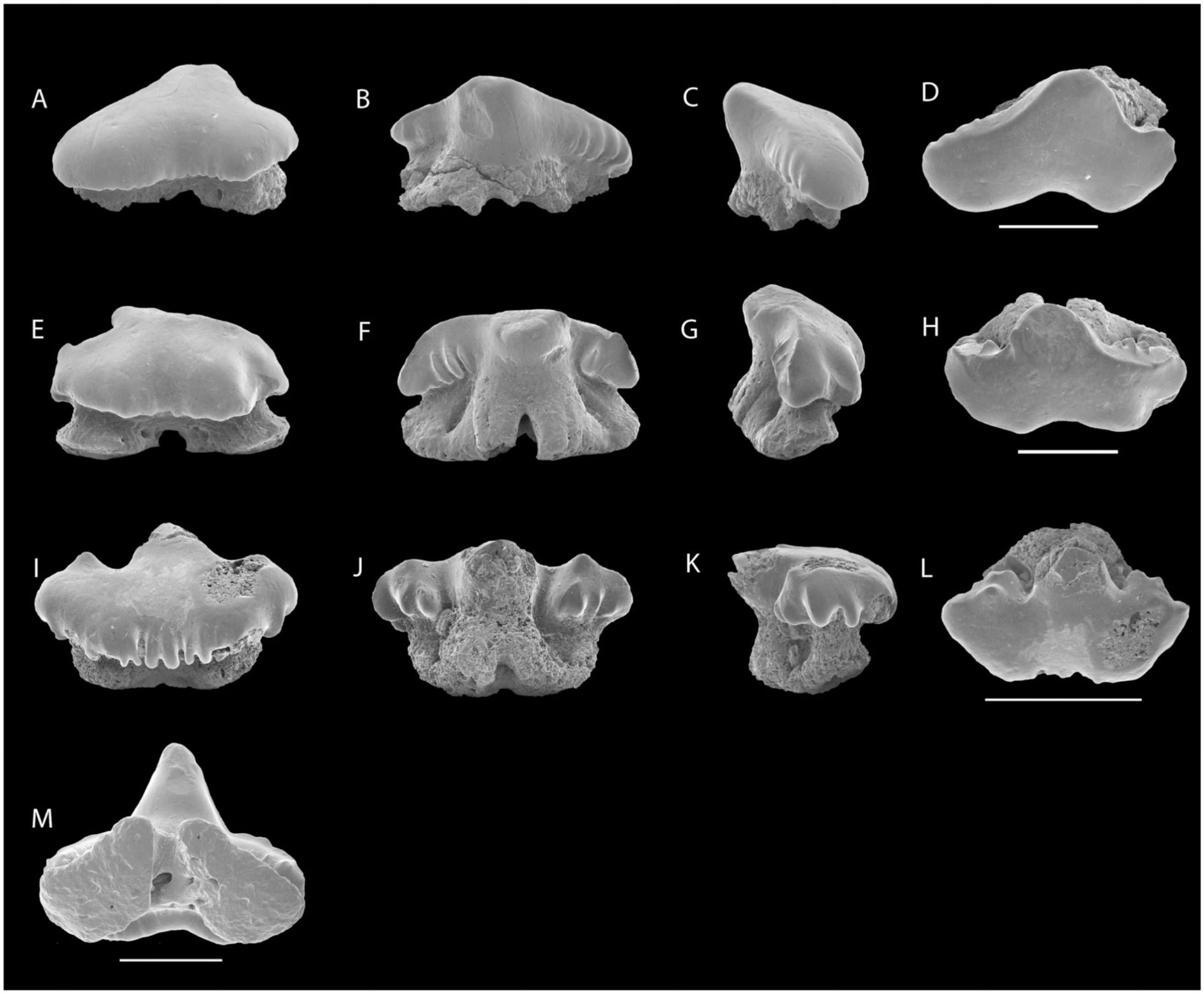

Figure 5.

SEM images of *Meridiogaleus cristatus*, gen. et sp. nov., NRM-PZ P16133, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16134, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16135, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16077, **M**, basal view. All scale bars equal 1 mm.

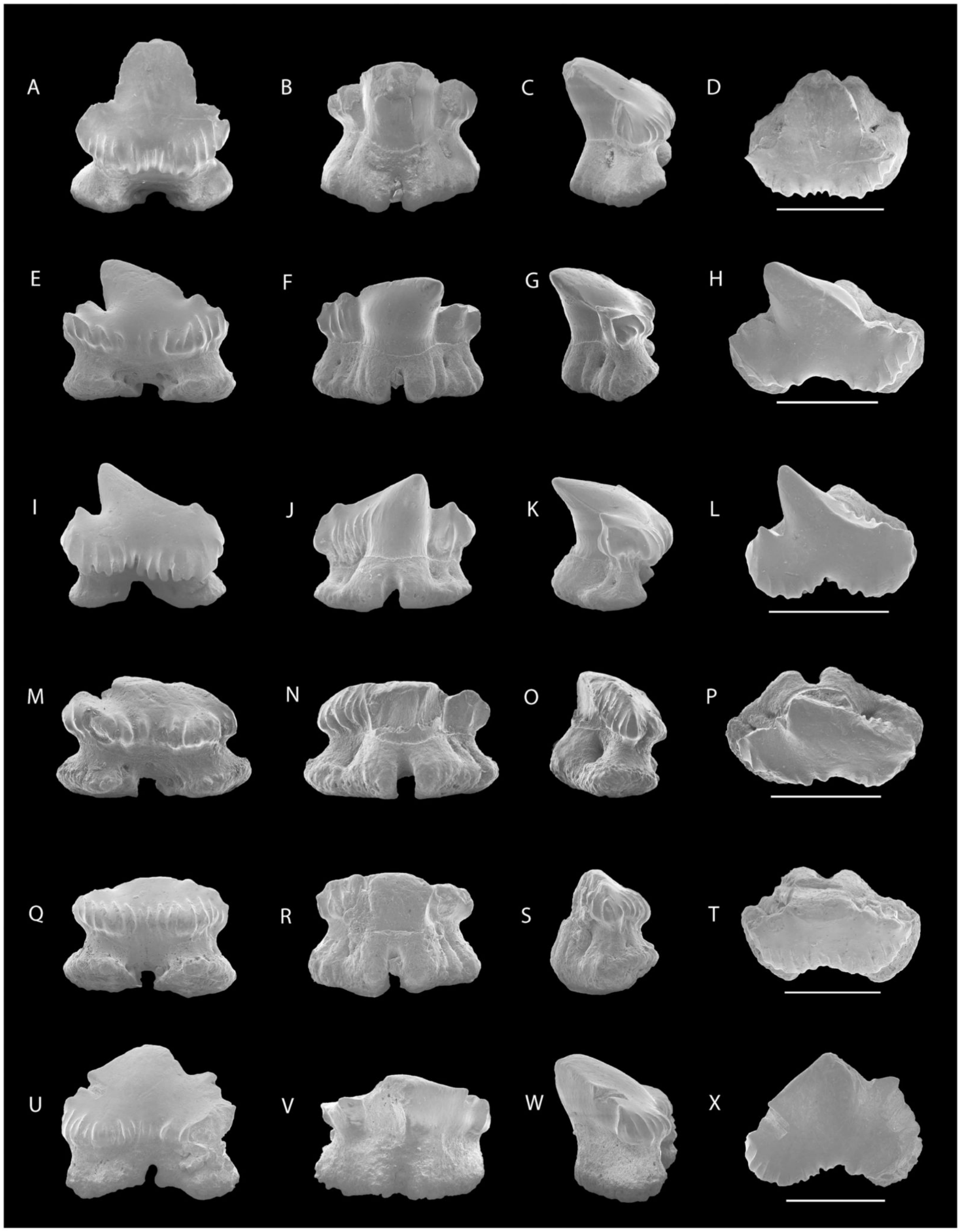

Figure 6.

SEM images of *Kallodentis rhytistemma*, gen. et sp. nov., anterior teeth, NRM-PZ P16136, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16137, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16138, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16139, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal; views; NRM-PZ P16140, **Q**, labial; **R**, lingual; **S**, profile; **T**, occlusal views; NRM-PZ P16141, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views. All scale bars equal 1 mm.

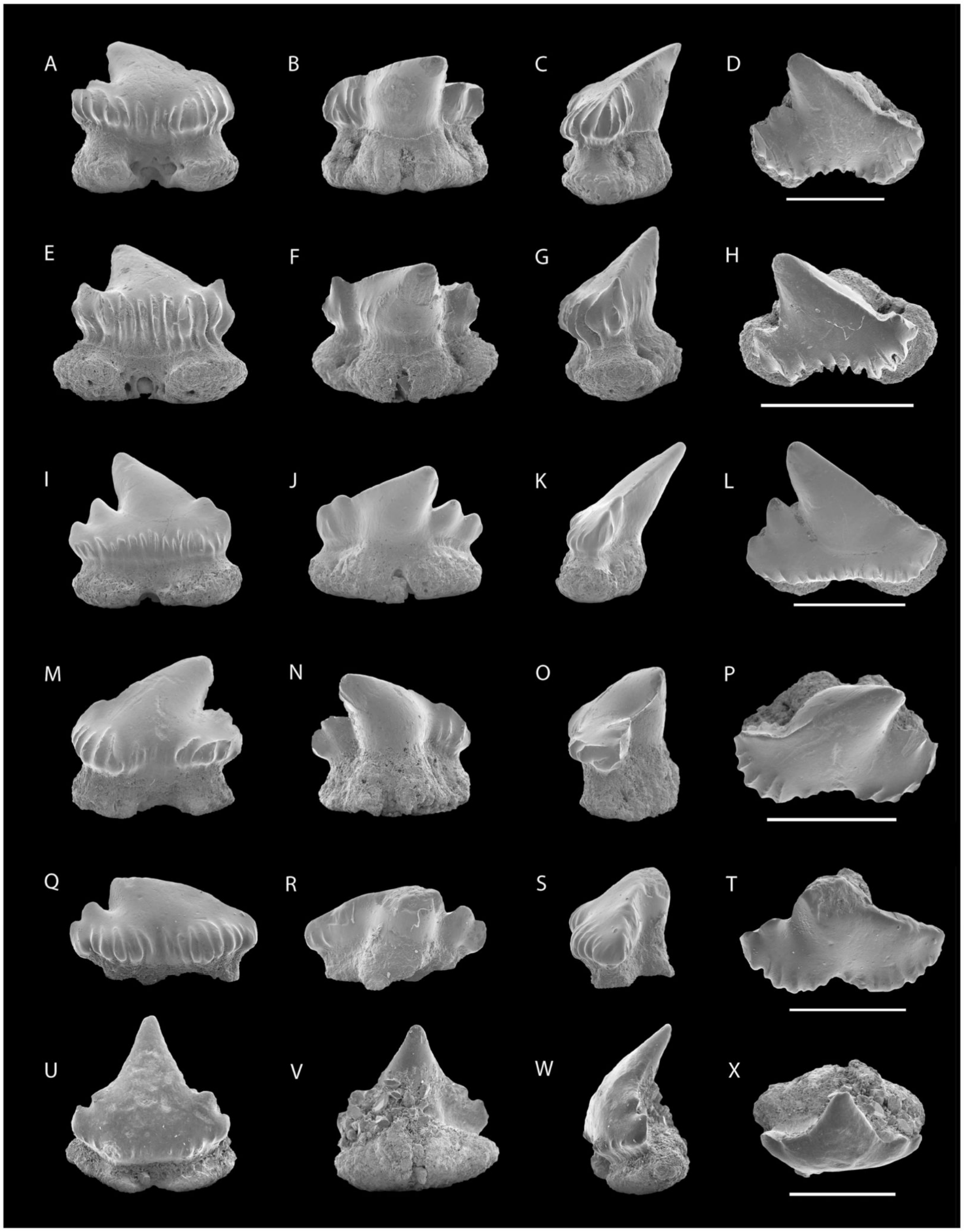

Figure 7.
SEM images of *Kallodentis rhytistemma*, gen. et sp. nov., anterior teeth, NRM-PZ P16142, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16143 (holotype), **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16144, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16145, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal; views; NRM-PZ P16146, **Q**, labial; **R**, lingual; **S**, profile; **T**, occlusal views; NRM-PZ P16147, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views. All scale bars equal 1 mm.

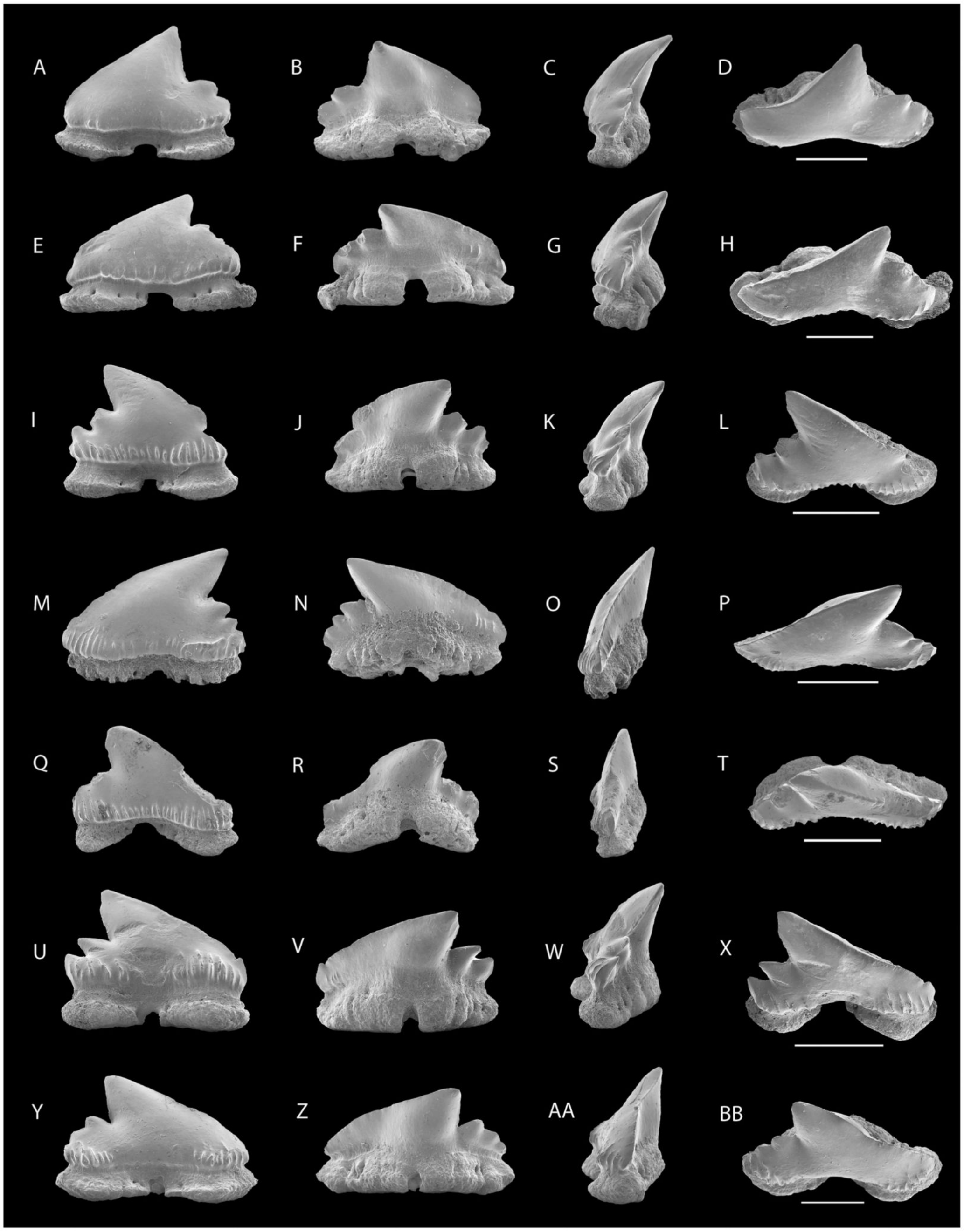

Figure 8.

SEM images of *Kallodentis rhytistemma*, gen. et sp. nov., NRM-PZ P16181, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16182, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16183, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16184, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P16185, **Q**, labial; **R**, lingual; **S**, profile; **T**, occlusal views; NRM-PZ P16186, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views; NRM-PZ P16187, **Y**, labial; **Z**, lingual; **AA**, profile; **BB**, occlusal views. All scale bars equal 1 mm.

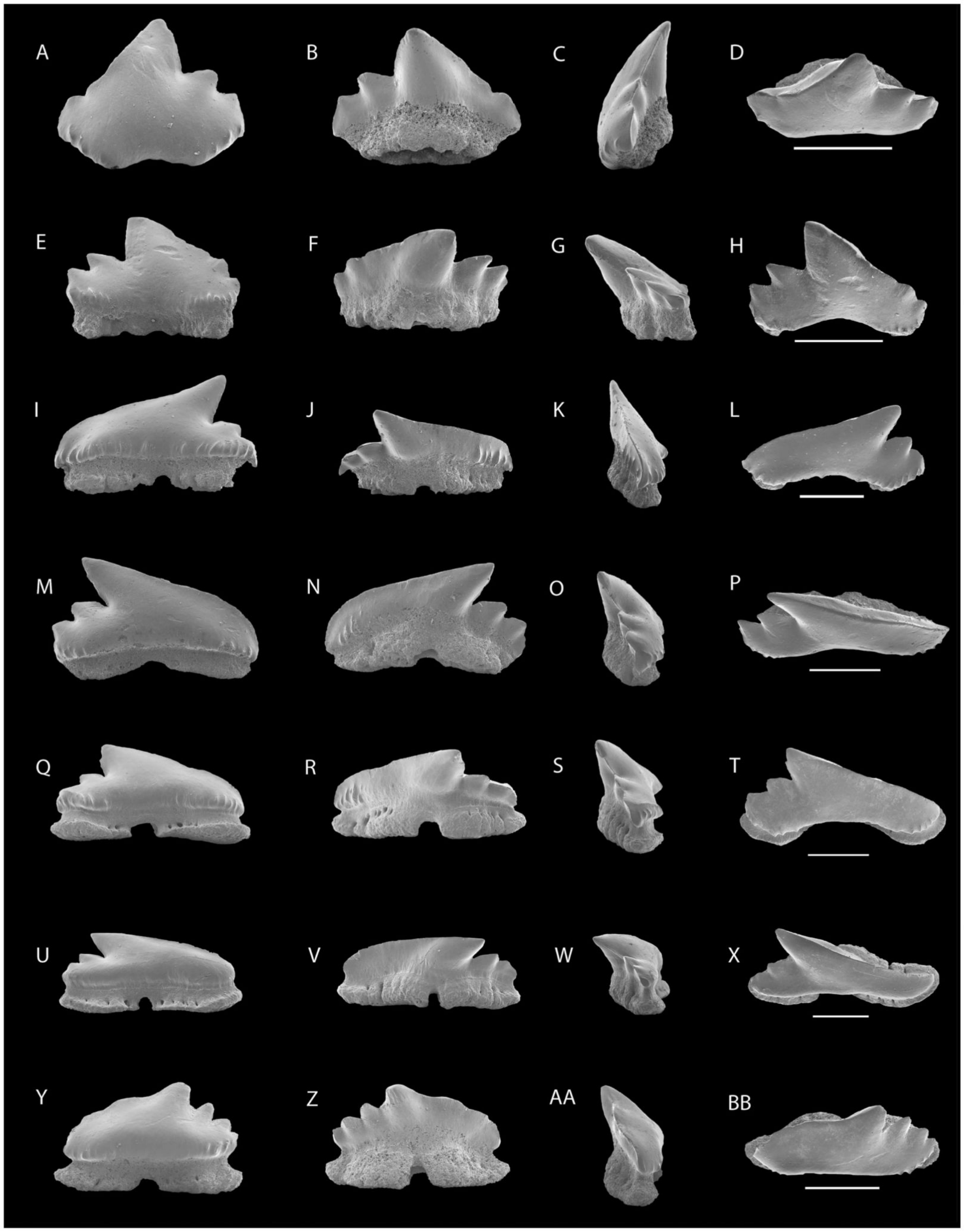

Figure 9.

SEM images of *Kallodentis rhytistemma*, gen. et sp. nov., NRM-PZ P16188, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16189, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16190, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16191, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P16192, **Q**, labial; **R**, lingual; **S**, profile; **T**, occlusal views; NRM-PZ P16193, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views; NRM-PZ P16194, **Y**, labial; **Z**, lingual; **AA**, profile; **BB**, occlusal views. All scale bars equal 1 mm.

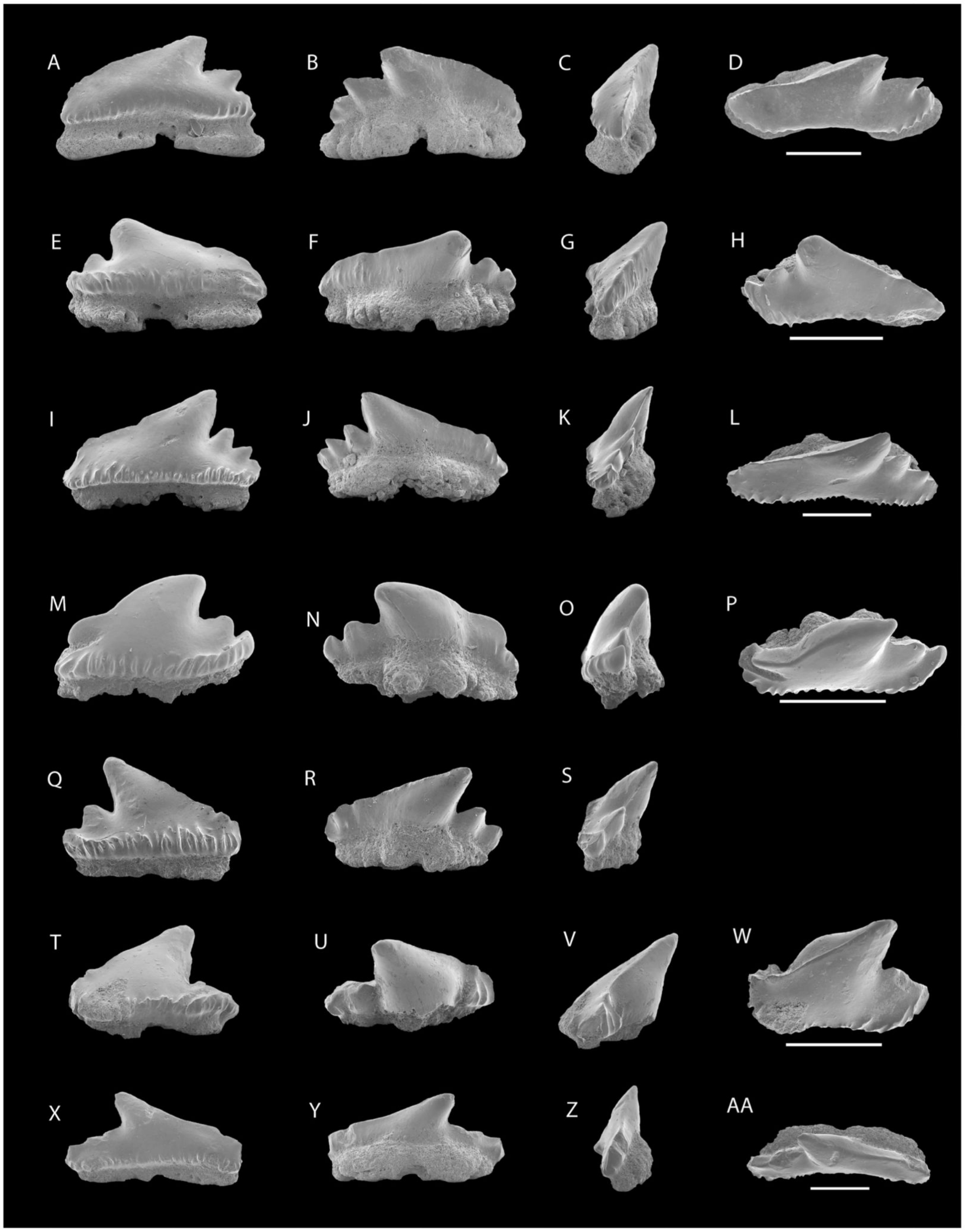

Figure 10.

SEM images of *Kallodentis rhytistemma*, gen. et sp. nov., NRM-PZ P16195, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16196, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16197, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16198, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P16199, **Q**, labial; **R**, lingual; **S**, profile views; NRM-PZ P16200, **T**, labial; **U**, lingual; **V**, profile; **W**, occlusal views; NRM-PZ P16201, **X**, labial; **Y**, lingual; **Z**, profile; **AA**, occlusal views. All scale bars equal 1 mm.

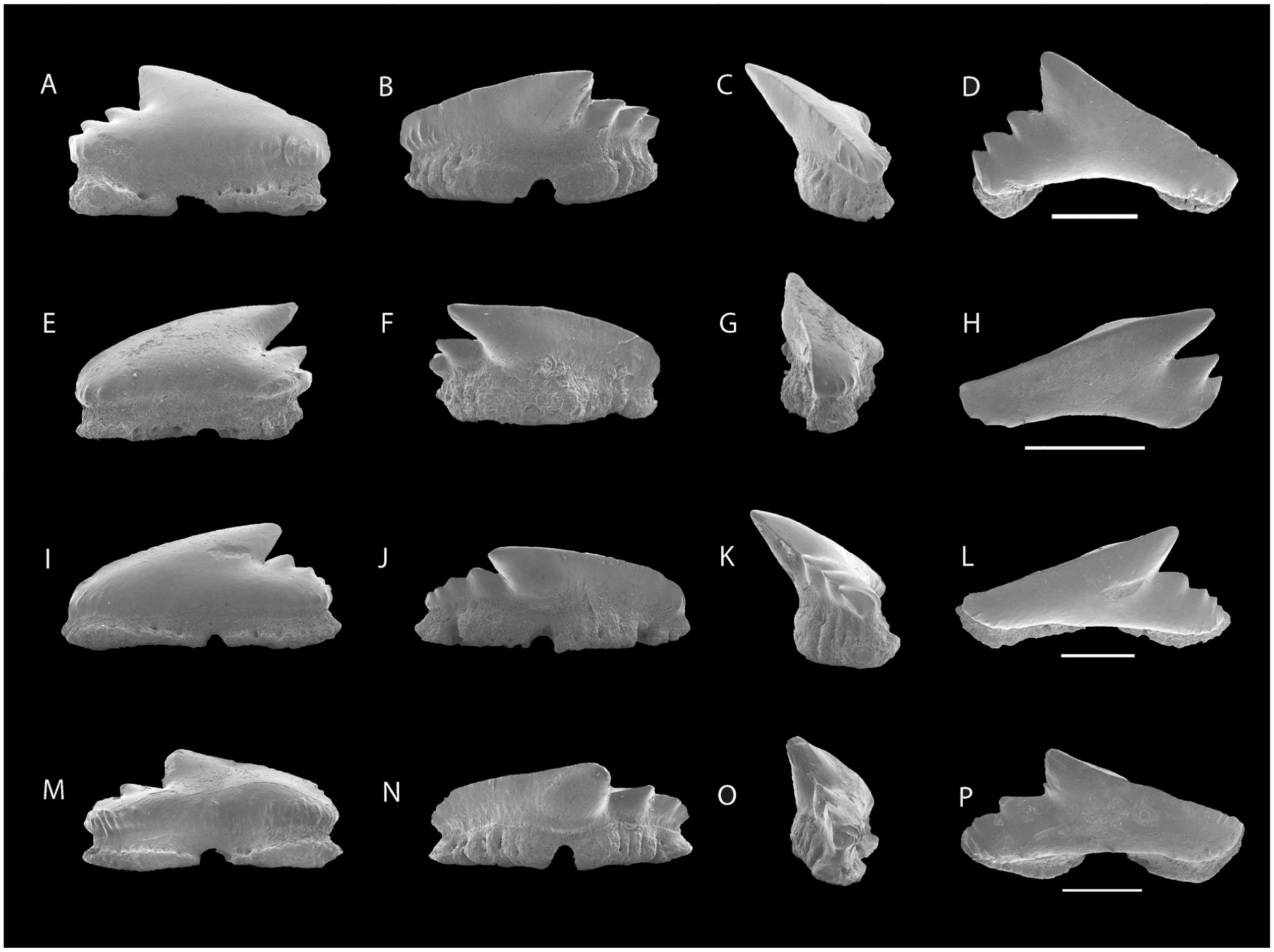

Figure 11.
SEM images of *Kallodentis rhytistemma*, gen. et sp. nov., NRM-PZ P16202, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16203, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16204, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16205, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views. All scale bars equal 1 mm.

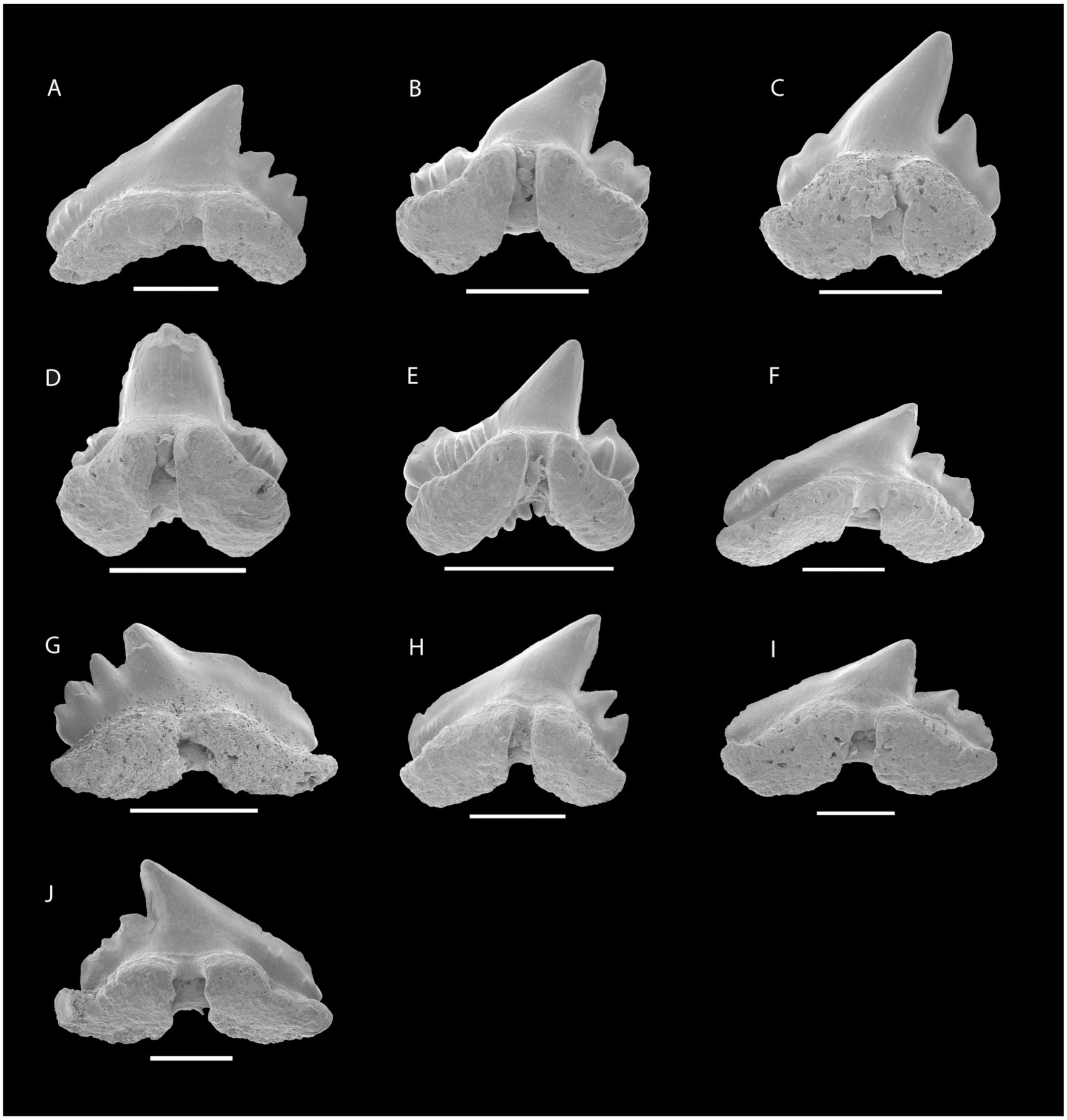

Figure 12.

SEM images of *Kallodentis rhytistemma*, gen. et sp. nov., NRM-PZ P16202, **A**, linguobasal view; NRM-PZ P16137, **B**, linguobasal view; NRM-PZ P16144, **C**, linguobasal view; NRM-PZ P16141, **D**, linguobasal view; NRM-PZ P16139, **E**, linguobasal view; NRM-PZ P16192, **F**, linguobasal view; NRM-PZ P16194, **G**, linguobasal view; NRM-PZ P16186, **H**, linguobasal view; NRM-PZ P16205, **I**, linguobasal view; NRM-PZ P16182, **J**, linguobasal view. All scale bars equal 1 mm.

Figure 13.

Photograph taken with a 3D digital microscope (Keyence VHX-1000D 3D), of *Galeorhinus* sp. NRM-PZ P16212 in labial view. Scale bar equals 1 mm.

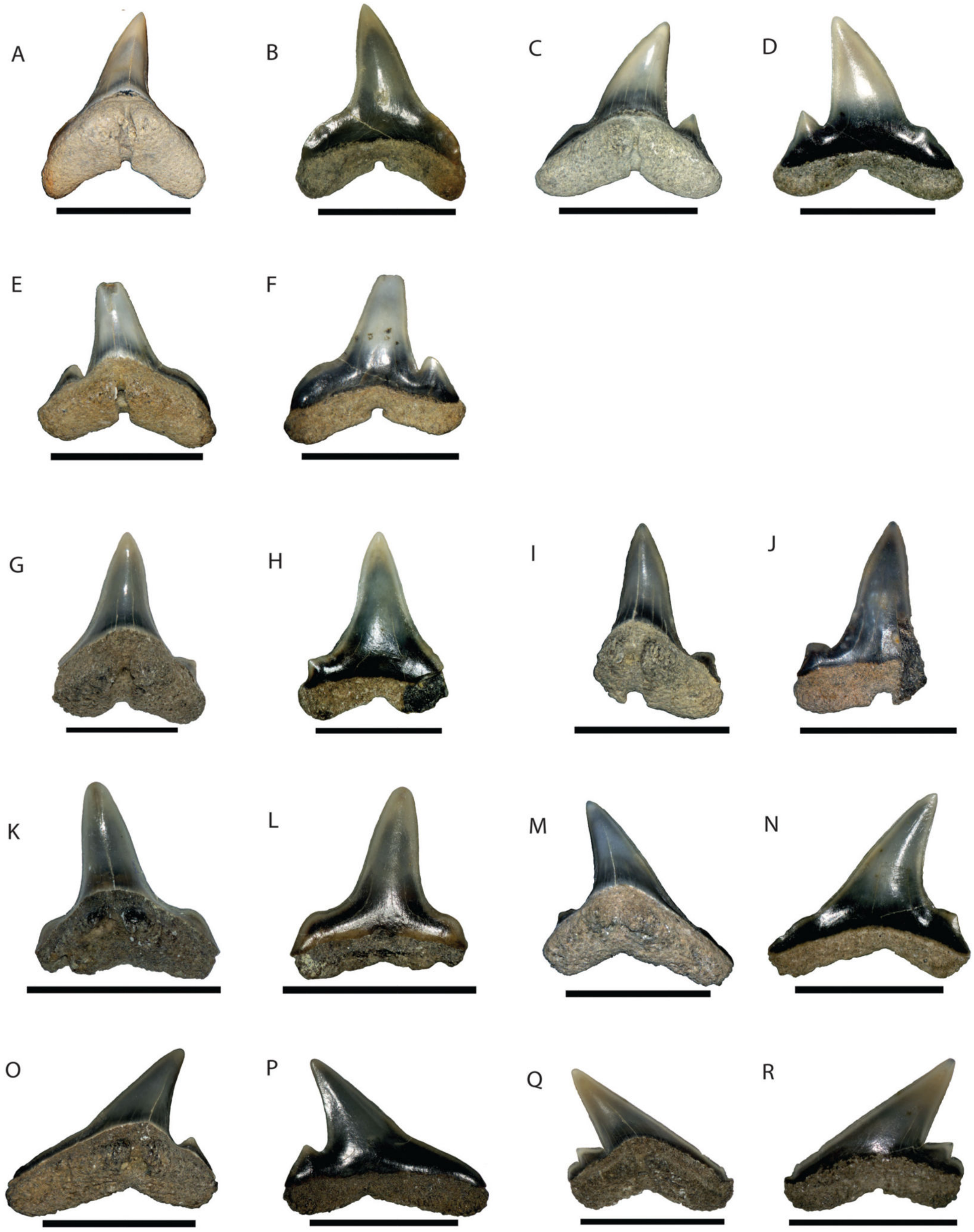

Figure 14.

Photographs of *Abdounia mesetae*, sp. nov., taken with a digital microscope camera, Canon PowerShot G 15, NRM-PZ P16213, **A**, labial; **B**, lingual views; NRM-PZ P15808 (holotype), **C**, labial; **D**, lingual views; NRM-PZ P16214, **E**, labial; **F**, lingual views; NRM-PZ P16215, **G**, labial; **H**, lingual views; NRM-PZ P16216, **I**, labial; **J**, lingual views; NRM-PZ P15915, **K**, labial; **L**, lingual views; NRM-PZ P16217, **M**, labial; **N**, lingual views; NRM-PZ P16218, **O**, labial; **P**, lingual views; NRM-PZ P16219, **Q**, labial; **R**, lingual views. All scale bars equal 5 mm.

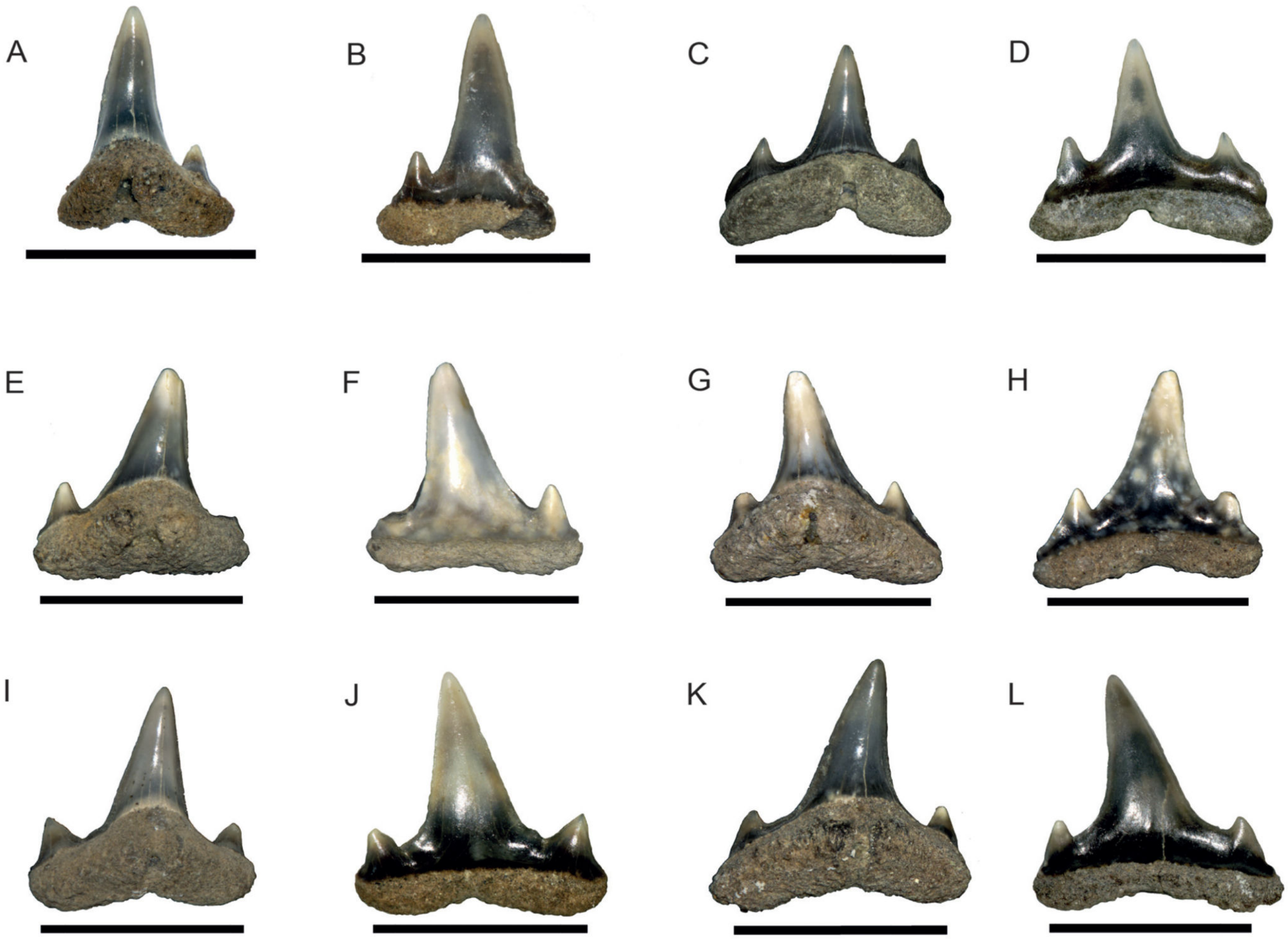

Figure 15.

Photographs of *Abdounia richteri*, sp. nov., taken with a digital microscope camera, Canon PowerShot G15, NRM-PZ P16206, **A**, labial; **B**, lingual views; NRM-PZ P16207, **C**, labial; **D**, lingual views; NRM-PZ P16208, **E**, labial; **F**, lingual views; NRM-PZ P16209 (holotype), **G**, labial; **H**, lingual views; NRM-PZ P16210, **I**, labial; **J**, lingual views; NRM-PZ P16211, **K**, labial; **L**, lingual views. All 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 text for references).

TELM	Facies	Temp.	Association
7	Shallow marine Inner estuary channels	ca. 7–8° C ca. 5° C	*Squalus* sp., *Squatina* sp., *Pristiophorus laevis, Carcharocles sokolovi, Palaeohypotodus* cf. *rutoti, Striatolamia* cf. *macrota, Ischyodus dolloi*
6	Estuary	ca. 7° C ca. 15° C	*Coelometlaouia pannucea, Pristiophorus laevis,* **_Mustelus_ sp., _Meridiogaleus cristatus_, gen. et sp. nov.,** *Notoramphoscyllium woodwardi,* **_Kallodentis rhytistemma_, gen. et sp. nov.,** *Ischyodus dolloi*
5	Estuary	ca. 10–11° C	*Heptranchias howelli, Hexanchus* sp., *Centrophorus* sp., *Dalatias licha, Squalus weltoni, Squalus woodburnei, Pristiophorus laevis, Squatina* sp., *Anomotodon multidenticulata, Cetorhinus* sp., *Macrorhizodus praecursor, Lamna* cf. *nasus, Odontaspis winkleri, Palaeohypotodus rutoti, Striatolamia macrota,* **_Mustelus_ sp., _Meridiogaleus cristatus_, gen. et sp. nov., _Kallodentis rhytistemma_, gen. et sp. nov., _Galeorhinus_ sp., _Abdounia richteri_, sp. nov., _Abdounia mesetae_, sp. nov.,** *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 laevis, Squatina* sp., *Anomotodon multidenticulata, Carcharocles auriculatus, Cetorhinus* sp., *Macrorhizodus praecursor, Lamna* cf. *nasus, Odontaspis winkleri, Palaeohypotodus rutoti, Striatolamia macrota, Carcharhinus* sp., *Myliobatis* sp., *Pristis* sp., *Raja*/*Bathyraja* sp., *Chimaera seymourensis, Ischyodus dolloi*
3	Delta plain to estuary	ca. 10–11° C ca. 15° C	*Pristiophorus laevis, Carcharocles auriculatus, Lamna* cf. *nasus, Striatolamia macrota, Myliobatis* sp., *Ischyodus dolloi*
2	Delta front		*Callorhinchus stahli, Chimaera seymourensis, Ischyodus dolloi*
1–2	Prodelta? /Inner estuarine?		*Centrophorus* sp., *Deania* sp., *Carcharocles auriculatus, Striatolamia macrota*

Taxa described here are in bold. Facies interpretation according to Marenssi et al. (2002); sea surface temperatures (Temp.) according to Ivany et al. (2008). For occurrence references, see text.