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## Eocene squalomorph sharks (Chondrichthyes, Elasmobranchii) from Antarctica

Andrea Engelbrecht<sup>a,\*</sup>, Thomas Mörs<sup>b</sup>, Marcelo A. Reguero<sup>c</sup>, and Jürgen Kriwet<sup>a</sup>

<sup>a</sup>Department of Palaeontology, University of Vienna, Geozentrum, Althanstraße 14, 1090 Wien, Austria

<sup>b</sup>Department of Palaeobiology, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden

<sup>c</sup>División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina, CONICET

### Abstract

Rare remains of predominantly deep-water sharks of the families Hexanchidae, Squalidae, Dalatiidae, Centrophoridae, and Squatinidae are described from the Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula, which has yielded the most abundant chondrichthyan assemblage from the Southern Hemisphere to date. Previously described representatives of *Hexanchus* sp., *Squalus weltoni*, *Squalus woodburnei*, *Centrophorus* sp., and *Squatina* sp. are confirmed and dental variations are documented. Although the teeth of *Squatina* sp. differ from other Palaeogene squatinid species, we refrain from introducing a new species. A new dalatiid taxon, *Eodalatias australis* gen. et sp. nov. is described. This new material not only increases the diversity of Eocene Antarctic elasmobranchs but also allows assuming that favourable deep-water habitats were available in the Eocene Antarctic Ocean off Antarctica in the Eocene. The occurrences of deep-water inhabitants in shallow, near-coastal waters of the Antarctic Peninsula agrees well with extant distribution patterns.

### Keywords

La Meseta Formation; Seymour Island; Antarctic Peninsula; Hexanchiformes; Squaliformes; Squatiniformes

## 1 Introduction

Today's Southern Ocean, which is delaminated by the Antarctic Circumpolar Current and the Antarctic continent, is amongst the most remote and coldest places in the world and is both a key element in any model of Earth processes and climatic changes as well as a site with unique scientific characteristics (Kriwet, 2005). The extant chondrichthyan fauna of the Southern Ocean surrounding Antarctica is extremely impoverished compared to pre-

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\*Corresponding author. Department of Palaeontology, University of Vienna, Geozentrum, Althanstraße 14, 1090 Vienna, Austria. andrea.engelbrecht@univie.ac.at.

Oligocene times. Up to now, only five extant shark taxa *Squalus acanthias* (Linnaeus, 1758), *Centroscymnus* sp., *Lamna nasus* (Bonnaterre, 1788), *Somniosus* cf. *microcephalus* (Bloch and Schneider, 1801) and *Etmopterus* cf. *granulosus* (Günther, 1880) were reported from few specimens mostly off the Kerguelen Plateau (e.g., Gon and Heemstra, 1990) and it still is not established whether these sharks enter the Antarctic Convergence only sporadically or represent permanent residents. Batoid diversity, conversely, is slightly higher with eight resident species having been described (Stehmann and Bürkel, 1990; Gon and Heemstra, 1990; Long, 1994). Holocephalans have not been recorded from Antarctic waters so far. The Swedish South Polar Expedition (1901–1903) collected the first chondrichthyan fossils, which were subsequently described by Woodward (1908). New chondrichthyan fish material was collected by many different expeditions during the 20th century. Grande and Eastman (1986), Eastman and Grande (1989) and Eastman (2005) provided comprehensive and updated reviews of fossil fishes from Antarctica. Fossil remains of sharks are well known from extensive Cretaceous marine deposits of Antarctica (e.g., Kriwet et al., 2006; Otero et al., 2014; Gouiric Cavalli et al., 2015). Accordingly, Antarctic fossil fishes occur in Devonian, Early Triassic, Middle – Late Jurassic, Late Cretaceous, Eocene, and Holocene deposits (Stilwell and Long, 2011). This enumeration exemplifies the rather patchy knowledge of fossil fishes from this high-latitude area.

Cenozoic Antarctic chondrichthyans mainly are known from Seymour Island. Here middle and upper Eocene marine sediments of the La Meseta Formation. yielded the most diverse Palaeogene ichthyofauna comprising cartilaginous and bony fishes from the Southern Hemisphere to date (e.g., Balushkin, 1994; Cione and Reguero, 1995, 1998; Doktor et al., 1996; Eastman and Grande, 1989, 1991; Jerzmanska, 1988; Long, 1992a,b,c; Welton and Zinsmeister, 1980; Kriwet, 2005; Kriwet et al., 2016; Engelbrecht et al., 2016a,b; Schwarzhan et al., 2016). Long and Stilwell (2000) additionally reported rare selachian teeth from Eocene deposits of Mount Discovery in East Antarctica. This material includes the first record of the school shark, *Galeorhinus* for Antarctica. Long (1994) discussed the origin of Antarctic rajids and presented the first unambiguous record of a skate from the Eocene of Antarctica. Recently, Engelbrecht et al. (2016b) revised the sawsharks (Pristiophoriformes) from the Eocene of Antarctica, which are member of Squalomorphi.

Squalomorph sharks represent a monophyletic group of cartilaginous fishes, which is sister to Galeomorphi including four orders, Hexanchiformes, Squaliformes, Squatiniformes, and Pristiophoriformes. About 125 squalomorph species out of about 150 species are considered deep-sea inhabitants with more than 40 species occurring below 200 m depth. The goal of the present paper is to present a revision of the remaining squalomorph sharks belonging to Hexanchiformes, Squatiniformes and Squaliformes from Eocene near-coastal, shallow marine deposits of Seymour Island, Antarctica. Based on new and numerous material to establish their taxonomic diversity throughout the La Meseta Formation and review their distributions.

## 2 Locality and geological setting

Located at the northern tip of the Antarctic Peninsula (64°15' S, 56°45' W), Seymour Island (see Fig. 1) represents the uppermost part of the sedimentary infill of the James Ross Basin

(Del Valle et al., 1992). The fossiliferous strata of Seymour Island belongs to two groups, the lower Marambio Group (late Cretaceous to Paleocene) including the Lopez de Bertodano and Sobral formations and the overlying Seymour Island group comprising the Cross Valley (middle to earliest late Paleocene), La Meseta (late Paleocene to early middle Eocene), and Submeseta (middle Eocene to early Oligocene) Formations (e.g. Zinsmeister, 1982; Grande and Chatterjee, 1987; Marensi, 2006; Montes et al., 2013). The La Meseta Formation is subdivided into six allomembers, which are named Valle de las Focas (TELM 1), Acanitlados I and II (TELMs 2 and 3 in partem), Campamento (TELMs 3 in partem and TELM 4) and *Cucullaea* I and II (TELMs 5 and 6 in partem). Montes et al. (2013) subdivided the overlying Submeseta Formation into three allomembers, which are named Submeseta I (TELMs 6 in partem and 7 in partem), Submeseta II (TELM 7 in partem) and Submeseta III (upper TELM 7). We use both schemes to indicate where the material was sampled.

The middle part of the La Meseta Formation, the *Cucullaea* I Allomember (TELMs 4 and 5), from which most material comes, is composed of well-sorted sands with thick shelly conglomerates and interlaminated sand/mud channel fills. TELM 4 was characterized by Sadler (1988) by its thickness, coarseness and the high amount of teeth and bones. This horizon is dominated by the pelecypod *Cucullaea* and darwinellid gastropods (Reguero et al., 2012). Generally, sediments of TELM 5 consist of laminated fine-grained sandstones and silty clays with interbedded conglomeratic sandstones (Sadler, 1988), *Cucullaea* shells are characteristic for this unit, which characterizes a near-shore, shallow-marine environment (Stilwell and Zinsmeister, 1992). The “*Natica*-Horizon” (TELM 5) of the *Cucullaea* I allomember yielded abundant material of marine mollusks, sharks, skates, and rays (see Stilwell and Zinsmeister, 1992; Long, 1992a; Kriwet et al., 2016) together with teeth and bones of teleosts, basilosaurid whales, penguins, and mammals such as gondwanatheres, marsupials, and ungulates (Woodburne and Zinsmeister, 1984; Goin and Carlini, 1995; Bargo and Reguero, 1998; Goin et al., 2006; Gelfo et al., 2009, 2015; Bond et al., 2011; Reguero et al., 2013; Schwarzhan et al., 2016; Buono et al., 2016). The deposits are characterized by parallel laminations, climbing ripples, flaser- and wavy bedding, small-scale channels, invertebrate burrows and shell lenses (Elliot and Trautman, 1982; Sadler, 1988; Stilwell and Zinsmeister, 1992). The “*Natica*-Horizon” is a 1 m thick lens that is exposed at several sites along the western margin of the Seymour Island plateau. Generally, TELM 5 consists of laminated fine-grained sandstones and silty clays with interbedded conglomeratic sandstones (Sadler, 1988), *Cucullaea* shells are characteristic for this unit, which represents a nearshore, shallow-marine environment (Stilwell and Zinsmeister, 1992).

TELM's 6 and 7 (Submeseta Allomember) consist of medium to fine-grained sandstones, with intervals of laminated fine-grained sands and silty clays and were deposited in a low energy and shallow marine environment (Sadler, 1988). Sediments of the La Meseta Formation were deposited in estuarine, deltaic and marine environments (Marensi et al., 1998).

### 3 Material and methods

The material was collected on Seymour Island, Antarctic Peninsula, by an Argentine-Swedish field party as a joint project of the Instituto Antártico Argentino (DNA-IAA) and the Swedish Polar Research Secretary (SPFS) during three summer campaigns from 2011 to 2013. All material described here consists exclusively of isolated teeth and is deposited in the collections of the Swedish Museum of Natural History (Department of Palaeobiology) and the Museo de La Plata (División Paleontología de Vertebrados), with registration numbers prefixed by “NRM-PZ” and “MLP”, respectively. Approximately 1100 kg of dry-screened sediments (mesh sizes 10 mm, 5 mm, 2.5 mm) were collected in the field for further processing in the laboratory. Of these 1100 kg, about 350 kg of concentrated sediment from localities IAA 2/95 (“Marsupial Site”), IAA 1/90 (“Ungulate Site”) and IAA 1/93 were further processed with mesh sizes of 2 mm, 0.5 mm and 0.1 mm and subsequently sorted for shark teeth. All shark teeth were cleaned with Rewoquat® before photographing. Smaller teeth were mounted on stubs for taking pictures with a JEOL-6400 Scanning Electron Microscope (SEM). From every specimen four pictures were taken in occlusal, labial, lingual and profile views. Larger specimens were photographed with a microscope camera, Keyence VHX-1000D. The morphological terminologies and the systematic scheme used here follow that of Cappetta (2012).

### 4 Systematic palaeontology

Supraclass Chondrichthyes Huxley (1880)

Class Elasmobranchii Bonaparte (1838)

Cohort Euselachii Hay (1902)

Subcohort Neoselachii Compagno (1977)

Superorder Squalomorphii Compagno (1973)

Order Hexanchiformes Compagno (1973)

Family Hexanchidae Gray (1851)

Genus *Hexanchus* Rafinesque (1810)

*Type species.* *Squalus griseus* Bonnaterre (1788); Recent

*Hexanchus* sp.

(Fig. 2A–D)

*Material.* NRM-PZ P15880, a single upper and NRM-PZ P15894, a single lower fragmentary tooth.

*Stratigraphic and geographic range.* TELM 4 (Ypresian, Early Eocene), Punta Sergios (GPS data: 64°14.168' S, 056°40.264' W), lower tooth fragment, NRM 1 (GPS data: 64°14.285' S, 56°40.182' W), upper tooth.

*Description.* The upper tooth is well preserved and nearly complete, only the apex of the main cusp (acrocone) is missing, whereas the second specimen, a lower tooth, is heavily damaged. The upper tooth measures 10 mm in mesio-distal length and approximately 11 mm in preserved height (Fig. 2A–B). The main cusp is transversally convex in lingual view, whereas the labial crown face only is slightly convex and bent labially. The cutting edges are sharp, with the mesial one being slightly sigmoid and crenulated, while the distal one is straight and smooth. The mesial cutting edge is longer than the distal one. The root is broad, rectangular with a convex basal edge in labial view, and relatively high. A narrow and shallow furrow is developed.

The lower tooth is incomplete and consists of only three cusps, where the main cusp (acrocone) is higher than the two preserved accessory cusps (Fig. 2C–D). All three cusps are slightly bent lingually. The labial crown face is slightly convex. The root of the tooth is markedly damaged.

*Remarks.* Teeth of the Antarctic *Hexanchus* sp. differ from teeth of Heptranchidae in the slightly distally decreasing size of accessory cusps (Cappetta, 2012). Teeth of *Notorynchus* (Ayes, 1855) can be separated from teeth of *Hexanchus* in displaying well-developed mesial serrations, whereas this mesial serration is less developed or even missing in teeth of *Hexanchus* (Ward, 1979). Antarctic *Hexanchus* teeth can be separated from *Weltonia* (Ward, 1979) in lacking a very elongated first cusp.

The fossil record of *Hexanchus* ranges back into the early Late Cretaceous, all Jurassic hexanchiforms belong to other taxa (Kriwet and Klug, 2011). The only fossil skeletal material comes from the Santonian of Lebanon and belongs to *Hexanchus gracilis* Davis (1887); otherwise members of this genus are exclusively known by isolated teeth. So far, seven fossil species have been described: *H. gracilis* Davis (1887) (Late Cretaceous, Palaeogene), *H. microdon* Agassiz (1843) (Late Cretaceous), *H. casieri* Kozlov in Zhelezko and Kozlov (1999) (Palaeogene); *H. agassizi* Cappetta (1976) (Palaeogene), *H. collinsonae* Ward (1979) (Palaeogene), *H. hookeri* Ward (1979) (Eocene), and *H. tusbairicus* Kozlov in Zhelezko and Kozlov (1999) (Palaeogene). Teeth of *Hexanchus* are widespread in Late Cretaceous and Cenozoic sediments of Europe, northern Africa, central Asia, Near East and North America (e.g., Cappetta, 1990; Davis, 1887; Adolfssen and Ward, 2014, 2015; Adolfssen et al., 2017; Reinecke et al., 2014; Adnet, 2000, 2006; Zhelezko and Kozlov, 1999; Takakuwa, 2006).

Cione and Reguero (1994) presented the first record of *Hexanchus* from the Eocene of Antarctica, which is the southern-most occurrence. The single specimen comes from TELM 5 of Seymour Island and represents a nearly complete lower anterolateral tooth. The lower tooth described here resembles the previously described one and we assume that both belong to the same species. However, we refrain from assigning these specimens to a species because of the small number and incomplete nature of teeth.

Order Squaliformes Goodrich (1909)

Family Squalidae Bonaparte (1834)

Genus *Squalus* Linnaeus (1758)

*Type species.* *Squalus acanthias* Linnaeus (1758); Recent

*Squalus weltoni* Long (1992a)

(Fig. 3A-BB)

*Material.* NRMP-PZ P15803, NRM-PZ P15810, NRM-PZ P15800, NRM-PZ P15809, NRM-PZ P15830, NRM-PZ P15819 and NRM-PZ P15831.

*Additional Material.* TELM 6 (Lutetian, Middle Eocene): IAA 1/93, NRM-PZ P15898 (one specimen). TELM 5 (Ypresian, Early Eocene): South of Marsupial Site, NRM-PZ P15945 (one specimen); Pass Site, NRM-PZ P15794 (one specimen); *Natica*-Horizon, NRM 10, NRM-PZ P15937 (six specimens), *Natica*-Horizon, NRM 11, NRM-PZ P15813 (five specimens), IAA 1/90, 'Ungulate Site', NRM-PZ P15822 (15 specimens), IAA 2/95, 'Marsupial Site', NRM-PZ P15818 (47 specimens).

*Stratigraphic and geographic range.* TELM 5 (Ypresian, early Eocene), *Natica*-Horizon, NRM 11, (GPS data: 64°13.849'S; 056°37.193'W), IAA 1/90, 'Ungulate Site' (GPS data: 64°14'04.67''S; 56°39'56.38''W), IAA 2/95, 'Marsupial Site' (GPS data: 64°13'58''S; 56°39'06''W), Pass Site (GPS data: 64°14.144'S; 056°39.917'W); *Natica*-Horizon, NRM 10 (GPS data: 64°13'950'S, 56°37'768'W).

TELM 6 (Lutetian, middle Eocene): IAA 1/93 (GPS data: 64°14.144'S, 056°39.917'W).

*Description.* The teeth have a short mesio-distal crown. The principal cusp is triangular shaped and slightly to strongly bent towards the rear. In upper teeth, the principal cusp can be slightly recurved upwards and the distal cutting edge is more perpendicular than in lower teeth. The mesial cutting edge is slightly sigmoidal to straight, and serrated. The distal cutting edge is vertical to sub-vertical and also bears pronounced serrations. The distal heel is clearly separated from the principal cusp by a notch in lateral and posterior teeth forming an acute angle. In anterior view, the distal heel is very oblique. In labial view both, distal cutting edge and distal heel, form an obtuse angle, because the notch is less well developed. The labial edge of the crown face is slightly convex, whereas the lingual edge of the crown face is more or less straight (e.g. Fig. 3C, S, W, AA). The apron is broad and elongated, but is not reaching the basal edge of the root in profile views (Fig. 3C, G, K, O, S, W, AA). In labial view, some specimens have a strongly indented or undulated basal limit below the distal heel almost forming a bulbous extensions (e.g., Fig. 3I, M, Q). The mesial basal crown margin is less undulating (e.g., Fig. 3U).

The prominent lingual uvula is triangular shaped, long and covered with enameloid. In most teeth the uvula ends at the upper part of the infundibulum. The upper part of the uvula bears a rather deep depression at the meeting point to the crown.

The root is low and mesio-distally shorter than or as wide as the crown. The mesial root margin is concave, in labial view, whereas the distal one is more salient. The labial and lingual root faces bear numerous rounded to oval-shaped, small to rather large foramina (e.g., Fig. 3I, M, R, V). The root base is concave in most of the specimens. The infundibulum is rounded, heart-shaped or triangular shaped and is rather big in size.

*Remarks.* Upper and lower teeth in extant *Squalus* species are morphologically very similar. However, lower teeth are noticeable larger than upper jaw teeth. Identification and distinction of fossil *Squalus* species is difficult, as one of the characters used for distinguishing between species is the shape of the apron. However, the apron varies in shape and size during ontogeny (Adolfssen and Ward, 2014). According to Kriwet and Klug (2009) the most useful character for identifying isolated *Squalus* Linnaeus (1758) teeth is the morphology of the root. Also the form and angle of the basal root face could represent a useful character for separating fossil *Squalus* species (Siverson, 1993). However, extant species of *Squalus* are very difficult to separate even if complete sets of teeth are available using these characters, which exemplifies how difficult it is to identify fossil species, when only isolated teeth are available (Cappetta et al., 2016).

The fossil record of squalid dogfishes consists exclusively of isolated teeth and rare fin spines and ranges back into the Cenomanian (Underwood and Mitchell, 1999). These teeth resemble those of the extant *S. acanthias*. So far, 14 fossil *Squalus* species have been described (compare Kriwet and Klug, 2009) with seven species occurring in the Late Cretaceous. In the Palaeogene, *Squalus* species are wide-spread but mainly known from Europe, USA, and Morocco (Kriwet and Klug, 2009). Most Palaeogene teeth are assigned to *S. minor* (Daimeries, 1888), *S. crenatidens* (Arambourg, 1952), or *S. alsaticus* (Andreae, 1892). A species closely related to *S. acanthias* was reported from the Eocene of North America (Müller, 1999).

Isolated teeth of *Squalus* previously were known from Seymour Island. Long (1992a) described *Squalus weltoni* based on few teeth that easily can be separated from other serrated species such as *S. crenatidens* Arambourg (1952), *S. occidentalis* Jordan and Hannibal (1923) and *Megasqualus orpiensis* Herman (1982) by a mesio-distally short crown, vertical to sub-vertical distal cutting edges, serrations on mesial and distal cutting edges as well as on the cutting edge of the distal heel, and the moderately concave root base. The newly recovered Antarctic material compares very well with the specimen described by Long (1992a), and we therefore assign the material described here to *Squalus weltoni*.

*Squalus woodburnei* Long (1992a)

(Fig. 4A-T)

*Material.* NRMP-PZ P15913 lower teeth, NRM-PZ P15799, NRMP-PZ P15907, NRMP-PZ P15919, and NRMP-PZ P15917 upper teeth.

*Additional material.* TELM 6 (Lutetian, Middle Eocene): IAA 1/93, NRM-PZ P15921 (five specimens). TELM 5 (Ypresian, Early Eocene): IAA 1/90, 'Ungulate Site', NRM-PZ

P15944 (50 specimens); IAA 2/95, 'Marsupial Site', NRM-PZ P15820 (55 specimens); Pass Site, NRM-PZ P15936 (one specimen).

*Stratigraphic and geographic range.* TELM 5 (Ypresian, early Eocene), IAA 1/90, 'Ungulate Site' (GPS data: 64°14'04.67" S; 56°39'56.38" W), IAA 2/95, 'Marsupial Site' (GPS data: 64°13'58" S; 56°39'06" W), Pass site (GPS data: 64°14.144' S, 056°39.917' W); and TELM 6 (Lutetian, middle Eocene), IAA 1/93 (GPS data: 64°14'25" S; 56°35'51" W).

*Description.* The teeth are wider than high, with a principal cusp slightly shifted towards the rare. The mesial cutting edge of the crown is convex to straight, but in its upper part slightly sigmoid. In upper teeth, the tip of the principal cusp slightly twists upwards (e.g., Fig. 4A, Q). The labial crown face is weakly convex, whereas the lingual crown face is slightly convex. The mesial cutting edge is longer than the distal one, both being smooth as well as the cutting edge of the distal heel. This heel is mesio-distally short, with a slightly convex upper crown edge and is separated from the principal cusp by a shallow and narrow notch (e.g., Fig. 4E, M). In some specimens one can observe an incipient cusplet on the distal heel. This cusplet may be well separated from the principal cusp and from the rest of the more rounded distal heel by a notch. The well-developed apron varies in size being narrow to rather broad labially. In some specimens a vertical ridge on the apron is present. In lateral view, the apron does not reach the basal edge of the root (e.g., Fig. 4G, O, K).

Along the lower labial crown edge numerous small foramina are present (e.g., Fig. 4B, R). The lingual uvula is triangular shaped, short, convex and bears a shallow depression in its upper portion close to the crown. The uvula is covered with enameloid on the upper part and ends slightly before the edge of the basal root face. The lingual root face, mesial and distal from the uvula, is strongly indented and concave (e.g., Fig. 4F, R). It bears also some large and numerous smaller foramina on the lingual root face directly under the horizontal line of the crown. The basal root face is flat to slightly concave and bears a large basal foramen (infundibulum) right below the short uvula.

*Remarks.* Long (1992a) also erected the species *Squalus woodburnei* for teeth from the Eocene La Meseta Fm. of Seymour Island. According to this author, a lingually directed uvula, a triangular and basally wide crown, a shallow depression on the apical surface of the uvula, and a slightly widened labial apron characterize teeth of *S. woodburnei*. The unserrated teeth of this species are very similar to teeth of the Palaeocene species *Squalus minor* Leriche (1902), but can be easily distinguished in that the uvula of the Antarctic teeth has the appearance of being curved mesially in occlusal view (see Long, 1992a, Fig. 4H and C). Additionally, the uvula of the Antarctic species is relatively wider than in *Squalus minor*.

*Squalus* sp.

(Fig. 4U–X)

*Material.* NRM-PZ P15920, lateral tooth.

*Stratigraphic and geographic range.* TELM 6 (Lutetian, middle Eocene), IAA 1/93 (GPS data: 64°14'25" S; 56°35'51" W).



*Description.* This specimen slightly differs from the other species in this study (Fig. 4U–X). The principal cusp of the single specimen is triangular and slightly pointing upwards. The principal cusp is shifted towards the distal part of the crown. The mesial cutting edge is elongated and slightly concave. The distal cutting edge is considerably shorter than the mesial one and nearly almost perpendicular. The mesial and distal cutting edges are lacking any serrations. The labial crown face is completely smooth and slightly convex. The apron is rather broad (mesio-distally) but not very elongated and its distal portion is eroded. The distal heel is rather short (mesio-distally), not very high, and separated from the principal cusp by a distinct notch. The lingual face of the tooth as well as the root is considerably damaged.

*Remarks.* This tooth differs distinctly from the other described specimens of *Squalus* in this study. Teeth of *Squalus weltoni* differ most significantly in the strongly serrated cutting edge, the shorter mesio-distal width and the undulated basal labial crown edge. The single tooth of *Squalus* sp. shares the smooth cutting edge with teeth of *Squalus woodburnei* but differs in the higher labial crown face, and the slightly convex cutting edge. Teeth of *Megasqualus orpiensis* disagree in their size, their nearly straight to convex mesial cutting edges, and the lower labial crown face. The tooth of *Squalus* sp. differs from teeth of the Paleocene species *Squalus minor* in the shape of the distal heel, the concave mesial cutting edge and the slightly lower labial crown face. Teeth of *Squalus smithi* Herman (1982) can be distinguished by the slightly shorter mesio-distal width and the mesial cutting edge being slightly convex.

Teeth of centrophorids, such as *Deania* (Jordan and Snyder, 1902) and *Centrophorus* (Müller and Henle, 1837), easily can be distinguished from the here described teeth of *Squalus* sp. in being more labio-lingually compressed. The principal cusp in *Deania* and *Centrophorus* is more elongated and prominent. The basal edge of the enameloid crown in the here described teeth of *Squalus* sp. is more or less straight, which differs from *Deania* and *Centrophorus* having an undulated edge or strongly concavely bent edge.

The single tooth shown in Fig. 4U–X most likely represents yet another species, but the true affinities of the specimen cannot be properly resolved with only one not completely preserved specimen recovered so far.

Family Dalatiidae Gray (1851)

Subfamily Dalatiinae sensu Shirai (1992)

*Eodalatias* gen. nov.

*Type species.* *Eodalatias australis* gen. et sp. nov.

*Etymology.* Named after the greek word ‘eos’ for “new, extraordinary”, referring to the Eocene epoch in combination with ‘dalatias’ in reference to dental similarities of the genus *Dalatias*.

*Diagnosis.* Extinct dalatiid shark defined by the following combination of lower tooth characters: very compressed lower teeth, with a low, convex and rather broad crown, which

slightly is inclined towards the rear; mesial and distal cutting edges coarsely serrated; distal heel also with coarse serrations; distal cutting edge nearly vertical; mesial cutting edge comparatively longer than distal cutting edge and slightly concave to more or less straight; the distal heel is convex and low; short, broad, convex, and bifid apron; uvula absent; root mesio-distally compressed, with well separated root lobes; articular facets are restricted to upper part of root.

*Differential Diagnosis.* Lower teeth of *Eodalatias* gen. nov differ from teeth of *Angoumeius* in being higher than wide. The short, broad and triangular shaped principal cusp distinguishes the new described taxon from *Eosqualiolus*, *Isistius*, and *Acrosqualiolus*. Teeth of *Euprotomicroides*, *Angoumeius*, *Isistius* and *Squaliodalatias* differ from the new taxon in having a high, convex and prominent distal heel. Coarse serrated mesial and distal cutting edges as well as serrations on the distal heel, separate teeth of the new taxon from teeth of *Euprotomicroides*, *Isistius* (sometimes weakly serrated), *Squaliodalatias* (mesial edge smooth to finely serrated), *Oligodalatias* (lower teeth with smooth to finely serrated cusp and distal heel). *Isistius*, *Euprotomicroides*, *Squaliolus*, *Eosqualiolus*, *Squaliodalatias*, *Acrosqualus*, and *Dalatias* differ in having well-developed articular facets over the complete or nearly the complete height of the root. Teeth of *Eodalatias* gen. nov. differ from all other squaliform sharks in having strongly compressed, elongated and separated root lobes.

*Eodalatias australis* sp. nov.

(Fig. 5A–J)

1992 *Dalatias licha*; Long, pp. 19, fig. 3A-B

*Holotype.* NRM-PZ P15815 (Fig. 5C, D), a lower lateral tooth.

*Paratypes.* Two lower lateral teeth, NRM-PZ P15801 and NRM-PZ P15903.

*Type horizon.* TELM 5, *Natica*-Horizon, La Meseta Formation.

*Type locality.* IAA 2/95, ‘Marsupial Site’.

*Geographic and stratigraphic range.* TELM 5 (Ypresian, early Eocene): IAA 2/95, ‘Marsupial Site’ (GPS data: 64°13′58″S; 56°39′06″W); TELM 4 (Ypresian, early Eocene): IAA 1/11 (GPS data: 64°14′03″S; 56°39′13″W), Antarctica.

*Etymology.* The species name is derived from the Latin word “australis” meaning “Antarctic”, in reference to their Antarctic occurrence.

*Diagnosis.* As for genus by monotypy.

*Description.* The teeth are higher than broad with a triangular shaped principal cusp, which is slightly inclined distally. The labial and lingual crown faces are smooth and convex transversally, with the labial crown face being more convex than the lingual one. The lingual boundary between cusp and root is rather horizontal to slightly undulating. The distal heel has a slightly rounded edge and is distinctly separated from the principal cusp. The mesial

and distal cutting edges of the crown are coarsely serrated continuing onto the distal heel, with upwardly directed serrae (e.g., Fig. 5A, C). In labial view, the apron is well-developed, broad, occupying a large percentage of the tooth width (Fig. 5A, C, E). The apron is slightly convex transversally and short, and forms short mesial and distal extensions on the upper part of the root lobes.

No uvula is present. An oval to drop-shaped medio-lingual foramen is present directly below the crown-root junction (e.g. Fig. 5B). The root is mesio-distally flattened and longer than the crown. The root lobes are well separated, with the distal root lobe being shorter than the mesial one (e.g, Fig. 5C). The articular facets are well developed but are limited to the upper part of the root.

*Remarks.* Dalatiidae include seven living genera, five of which are monotypic, *Dalatias*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, and *Mollissquama*. The genera *Isistius* and *Squaliolus* include two species each. *Squaliolus laticaudus* is one of the smallest known sharks, reaching only about 25 cm in total length (Compagno, 1984). Most species within this family are tiny, oceanic, pelagic sharks, with *Dalatias licha* being an exception.

The Antarctic dalatiid teeth described here resemble those of *Somniosus crenulatus* described by Arambourg (1952) from the Thanetian of Morocco to some extent. The Moroccan teeth, however, differ in having coarser serrations and the principal cusp is less strongly inclined distally. Teeth of the new taxon differ from those of other *Somniosus* species mostly in the different shape and appearance of the root and the inclination of the cusp. Cappetta (2012) indicated the close similarities of teeth of *Somniosus crenulatus* from Morocco to those of the genus of *Dalatias* but assumed that it also could be referred to a different genus.

Teeth of the new taxon *Eodalatias austrinalis* gen. et sp. nov differ from rather similar teeth of *Angoumeius paradoxus* (Adnet et al., 2006) in having serrated cutting edges and a distal heel. The inclination of the principal cusp differs between this two taxa – teeth of *Angoumeius paradoxus* are more distally inclined than teeth of *Eodalatias austrinalis* gen. et sp. nov. Also the shape of the apron differs in the two taxa, in being more elongated basally in *Angoumeius paradoxus*. The separated root lobes of *Eodalatias austrinalis* gen. et sp. nov. are more slender and more elongated than in *Angoumeius paradoxus*. The root in teeth of *Eodalatias austrinalis* gen. et sp. nov. additionally differ from those of *Angoumeius paradoxus* in lacking labial foramina.

Long (1992a) described an incomplete tooth from the La Meseta Fm. that he identified as belonging to the species *Dalatias licha*. This specimen, nevertheless, differs from teeth of the extant *Dalatias licha* in the comparably lower crown, the straight distal cutting edge, and the rather short apron. These characteristics distinguish this tooth readily from teeth of *Dalatias licha* but concur well with teeth of *Eodalatias austrinalis* gen. et sp. nov. However, teeth of the new taxon described here resemble slightly lower teeth of *Dalatias* in the bifid apron, the upwardly directed serrations and to some extent the shape of the root, but differ significantly in the shape and length of the crown and the separated root lobes.

Lower teeth with a low, convex, and rather broad crown, which has coarsely serrated cutting edges, a nearly upright directed crown, lacking a uvula, and well-separated root lobes characterize the new taxon. As indicated above, these are characteristics only for lower teeth, since no corresponding upper teeth have been found up to now. We nevertheless assign the teeth to the new taxon, *Eodalatias australis* gen. et sp. nov., which is member of the Dalatiidae based on their general resemblance to teeth of *Dalatias*.

Dalatiidae indet.

(Fig. 5G–J)

*Material.* NRM-PZ P15821 and NRM-PZ P15814.

*Stratigraphic and geographic range.* TELM 5 (Ypresian, early Eocene), IAA 2/95, ‘Marsupial Site’ (GPS data: 64°13′58″S; 56°39′06″W).

*Description.* The crown of the two preserved teeth is triangular shaped and short. The labial and lingual crown faces are transversally convex and completely smooth. In labial view, the mesial and distal cutting edges are well-demarcated and serrated. The mesial cutting edge is slightly longer than the distal one and weakly sigmoidal, whereas the distal cutting edge is slightly convex. The serrated cutting edge of the very low distal heel is nearly horizontal. The apron is poorly preserved, the uvula is absent, and the root is incomplete.

*Remarks.* A very strong dignathic heterodonty characterizes the dentition of *Dalatias*, in which the upper teeth are slender and conical, whereas lowers are broad and blade-like, the cutting edges are finely serrated and teeth overlap. Dalatiid teeth reported from Neogene species are identical to those of the extant *Dalatias licha* Bonnaterre (1788). The oldest reliable record of *Dalatias licha* is known from the middle Eocene of New Zealand (Keyes, 1984; Kriwet and Klug, 2009). The presence of *Dalatias* in the Palaeocene of Turkmenistan is based on only a single tooth crown and needs to be confirmed (Glikman, 1964, p. 162, pl. 10, fig. 6). Nevertheless, the genus *Dalatias* is assumed to range from the Lower Paleocene to the Recent (see Kriwet and Klug, 2009; Cappetta, 2012).

Teeth of the here described Dalatiidae indet differ from those of *Squaliolus*, *Heteroscymnoides*, *Euprotomicroides*, *Acrosqualiolus*, *Mollisquama* in having a short and almost erect cusp. *Acrosqualiolus*, *Angoumeius*, *Eosqualiolus*, *Euprotomicroides*, *Squaliodalatias*, *Euprotomicrus*, *Heteroscymnoides*, *Mollisquama* vary from the two Antarctic specimens in having a rather high and rounded distal heel. Lower teeth of *Dalatias* have a higher and more coarsely serrated cusp with a short and rounded distal heel. Additionally, the labial crown face seems to be flatter in *Dalatias* than in the specimens described here. The here described teeth share a serrated cutting edge with the genus *Dalatias*, but the serration seem to be coarser in *Dalatias*. The teeth therefore probably represents an as yet undescribed genus or species, but with only two not complete specimens recovered so far, the true affinities of the specimens cannot be properly resolved until more teeth are discovered. Teeth of *Eodalatioas australis* gen. et sp. nov. can be separated from teeth of Dalatiidae indet in the higher and more inclined crown and the higher and slightly smaller lateral cusplet.

Family Centrophoridae Bleeker (1859)

Genus *Centrophorus* Müller and Henle (1837)

*Type species. Centrophorus granulatus* Müller and Henle (1837); Recent

*Centrophorus* sp.1

(Fig. 5K–L)

*Material.* NRM-PZ P15804, a single lower lateral tooth.

*Stratigraphic and geographic range.* TELM 5 (Ypresian, early Eocene), IAA 2/95, 'Marsupial site' (GPS data: 64°13'58"S; 56°39'06"W).

*Description.* The single lower tooth is slightly higher than mesio-distally broad, and labio-lingually compressed. The principal cusp is triangular and distinctly distally inclined. The labial and lingual crown faces are slightly convex transversally and completely smooth. The distal crown edge has two indentations directly below the distal heel. The mesial cutting edge is slightly sigmoid and coarsely serrated, whereas the distal one is oblique and devoid of any serration. The distal heel is low, more or less horizontal with a convex cutting edge. It is well separated from the crown by a deep notch. The labial apron is rather flat, triangular shaped with distinct edges and extends downward on the root but without reaching its base (Fig. 5K). The lingual uvula is narrow, triangular and only slightly elongated. A rounded and small foramen opens close to the basal edge of the uvula. An infundibulum is present, right below the uvula.

The root is labio-lingually compressed. The basal edge of the root is slightly damaged. The lingual root face bears a large and deep articular depression mesially and directly below the basal limit of the crown (Fig. 5L). The preserved basal part of the root is strongly convex and labio-lingually more compressed than the rest of root.

*Remarks.* The fossil record of centrophorids, unfortunately, consists predominantly of isolated teeth with some questionable skeletal remains from the Late Cretaceous of Lebanon. Therefore, the evolutionary significance of different adaptations seen in extant species (Compagno, 1990) as well as assignment of taxa based on isolated teeth to any of extant groups thus remains ambiguous. The known fossil record of *Centrophorus* ranges back into the Late Cretaceous (Adnet et al., 2008; Kriwet and Klug, 2009) and the genus occurs in Europe, Asia, North America, New Zealand and Antarctica (see Cappetta, 2012).

Teeth of *Deania* are morphologically very close to teeth of *Centrophorus*, but are more compressed labio-lingually, have narrower cusps, unserrated mesial cutting edges, and comparably narrower roots. The main differences are the two root foramina, which are distinctly present in *Deania*, but fused together in *Centrophorus* forming a distinct infundibulum (Ledoux, 1970). The single tooth described here thus can be undoubtedly assigned to *Centrophorus*.

The material in the Woodburne collection, housed in the University of California Museum of Paleontology (UCMP), might confirm the occurrence of *Centrophorus* sp. and *Deania* sp. in TELMs 1 and 2. *Centrophorus* sp. (material examined at the UCMP) and *Centrophorus* sp. 1 (this study) also appear in TELMs 4 and 5 (Ypresian in age), which represents estuarine deposits. Welton and Zinsmeister (1980) and Long (1992a) indicated the presence of *Deania* sp. and *Centrophorus* sp. in TELM 4 of the La Meseta Formation on Seymour Island. The teeth ascribed to *Centrophorus* by Long (1992a) are lowers with fine and coarse serrations on the mesial and distal cutting edges, respectively. In the material described in this study, no additional material of the genus *Deania* had been discovered.

*Centrophorus* sp. 2

(Fig. 5M–N)

*Material.* A single lower tooth, NRM-PZ P15807.

*Stratigraphic and geographic range.* TELM 5 (Ypresian, early Eocene), IAA 2/95, ‘Marsupial Site’ (GPS data: 64°13′58″S; 56°39′06″W).

*Description.* The single lower tooth is slightly higher than broad and labio-lingually compressed with a triangular principal cusp that is slightly inclined distally (Fig. 5M). The labial and lingual crown faces are smooth and transversally convex. The crown overhangs the root labially and lingually. The mesial cutting edge is longer than the distal one and both are irregularly and rather coarsely serrated (Fig. 5N). The distal heel is low, slightly convex, and separated from the principal cusp by a deep notch. The elongated and low distal heel bears very fine serrations compared to the mesial and distal cutting edges. The labial apron is well-developed, narrow, convex from side to side, and extends basally over the root but without reaching the root base. The lingual uvula is short and rather broad mesio-distally. Lingually, the interlocking hollow is semi-circular and rather large.

The root is labio-lingually compressed, and basally convexly curved. The labial root face is flat and a lingual foramen, which is oval-shaped and rather large, opens directly below the uvula. An infundibulum is present.

On the lingual mesial root face some small and one larger foramen is visible. Below the basal limit of the labial crown face, the root bears mesially some additional small foramina. Mesially a foramen is present on the labial root face half way down the apron (Fig. 5M). The lower part of the root is more labio-lingually compressed than the rest of the root.

*Remarks.* Teeth of *Centrophorus* sp. 2 can easily be distinguished from the former described *Centrophorus* sp. 1 by its larger overall size, a broader triangular-shaped and more erect main cusp. The distal heel in *Centrophorus* sp. 1 is higher and convex compared to a low and more or less straight distal heel in the second species. The surface for interlocking with the next tooth is formed differently in both specimens. It is bigger in the second specimen and slightly triangular shaped. The *Centrophorus* teeth described by Long (1992a), have a shorter triangular cusp, which is slightly more inclined and steeper than in *Centrophorus* sp. 2. The mesial and distal cutting edges of the specimen described here are coarser than of the

specimen described by Long (1992a). The morphology of teeth in *Centrophorus* changes with growth and a sexual dimorphism can be recognized (White et al., 2008). Female dentitions differ from the dentition of males in having teeth pointing more strongly distally (Garrick, 1959; Ledoux, 1970). Therefore, the teeth described by Long (1992a) may represent female teeth of this species.

Order Squatiniformes Compagno (1973)

Family Squatinidae Bonaparte (1838)

Genus *Squatina* Duméril (1806)

*Type species: Squalus squatina* Linnaeus (1758); Recent.

*Squatina* sp.

(Fig. 6A–X)

*Material.* NRM-PZ P15802, NRM-PZ P15811, NRM-PZ P16237 to NRM-PZ P16240 (6 teeth).

Additional material (not figured): TELM 6 (Lutetian, middle Eocene): IAA 1/93, NRM-PZ P15923 (17 teeth); TELM 5 (Ypresian, Early Eocene): Monotreme Site, NRM-PZ P15797 (one specimen), *Natica*-Horizon, NRM 11 NRM-PZ P15823 (six specimens); *Natica*-Horizon, NRM 10, NRM-PZ P15834 (one specimen); IAA 1/90, 'Ungulate Site', NRM-PZ P15832 (559 specimens); IAA 2/95, 'Marsupial Site', NRM-PZ P15833 (642 specimens); TELM 4 (Ypresian, Early Eocene): NRM 1, NRM-PZ P15881 (four specimens).

*Stratigraphic and geographic range.* TELM 4 (Ypresian, early Eocene); NRM 1 (GPS data: 64°14.284'S; 056°40.182'W), TELM 5 (Ypresian, early Eocene): *Natica*-Horizon, NRM 10, (GPS data: 64°13.950'S; 56°37.768'W), *Natica*-Horizon, NRM 11 (GPS data: 64°13.849'S; 056°37.193'W), IAA 1/90, 'Ungulate Site' (GPS data: 64°14'04.67''S; 56°39'56.38''W), IAA 2/95, 'Marsupial Site' (GPS data: 64°13'58''S; 56°39'06''W), Monotreme Site (GPS data: 64°14.679'S; 056°40.567'W); TELM 6 (Lutetian, middle Eocene): IAA 1/93 (GPS data: 64°14'25''S; 56°35'51''W).

*Description.* The teeth display the characteristic features of teeth attributed to *Squatina* (Fig. 6A–X). They are conspicuously wider than high with a slender, high, erect, and triangular shaped cusp. The lateral heels are strong and low, with the upper edge of the mesial and distal heels being straight, sigmoid or slightly convex. In some specimens the crown is not as high as the root lobes are long. The labial crown face is slightly convex transversally and straight to sigmoid (in profile view) and devoid of any ornamentation. The lingual crown face is slightly sigmoid or concave in profile view and also completely smooth. The labial crown face continues basally into a prominent apron. The apron is knob-like, rather small in most specimens (e.g., Fig. 6E, M, U) and narrow to rather broad in labial view. In profile view, the apron does not reach the root base (e.g., Fig. 6C, K, O). The cutting edges are strong, sharp, continuous, and expand over the long and low heels. The basal margin of the crown forms a clear boundary between the crown and the root (e.g., Fig. 6A, E, M).

Assumed lower teeth are more robust (Fig. 6A–H) and larger than those most likely coming from the upper jaw when compared with dentitions of extant squatiniids. Anterior teeth are mesio-distally shorter than lateral and posterior teeth. As the teeth become wider, the principal cusp becomes slightly reduced in height.

The root corresponds to the hemiaulacorhize vascularization pattern of Casier (1947) with broadly divergent and well-separated root lobes and a central basal foramen that is connected to a second smaller medio-lingual foramen below the neck collar. In some teeth, the root lobes meet lingually to form a shallow labial trough in which a large median foramen opens. In occlusal view, the root is rather massive, protruding lingually and laterally below the crown (e.g., Fig. 6D, L, R).

The basal root face is strongly concave in labial view, whereas in lateral and posterior teeth the basal root face is more or less straight. Lingually, the root face bears numerous small rounded or oval foramina located mesially and distally from the lingual protuberance (e.g., Fig. 6F, N, R). The root lobes protrude below the crown in labial view in most specimens (e.g., Fig. 6A).

*Remarks.* Klug and Kriwet (2013) reviewed the fossil record of squatiniiforms and concluded that the group originated in the Jurassic. The fossil record of *Squatina* mainly consists of isolated teeth but only rare skeletal remains (Klug and Kriwet, 2013). The oldest unambiguous remains of *Squatina* are isolated teeth from the Valanginian (Early Cretaceous) (Cappetta, 2012; Kriwet and Klug, 2013). Isolated teeth of *Squatina* in the Palaeogene of Gondwana were reported from India (Rana et al., 2005), Chile (Otero et al., 2012, 2013), Northern Africa (e.g. Noubhani and Cappetta, 1997), and from Australia (Pfeil, 1984; Oligocene). Welton and Zinsmeister (1980) first described two incomplete teeth of *Squatina* from Unit II sensu Elliot and Trautman (1982) (= TELM 4) of Seymour Island and Kriwet et al. (2016) described one isolated tooth from the uppermost part of the Submeseta Fm. (=TELM 7).

Most squatiniid teeth from Palaeogene deposits are assigned to *Squatina prima*, which is supposed to be characterized by a distinct slender crown and low crown shoulders (Casier, 1966; Adnet, 2006). Rather robust teeth characterize, conversely, the Pliocene-Miocene species, *Squatina subserrata* Münster, 1846. This separation, however, seemingly is very unsubstantiated and artificial, because it is based on stratigraphic rather than morphological reasons. Unfortunately, teeth are very plesiomorphic and morphologies are conserved over long periods in squatiniids (Klug and Kriwet, 2013). Recent attempts to separate Cretaceous *Squatina* species based on dental characters (Siverson, 1993; Guinot et al., 2012) have provided a wealth of new information. However, dental variations (ontogenetic and sexual dimorphisms, different morphologies in upper and lower jaws) observed in extant *Squatina* species might account for many characters used for species discrimination and need to be validated using larger samples of extant species. Since separation of species based on isolated teeth seems to be ambiguous, we refrain from assigning the teeth from the Eocene of Antarctica to any species.



## 5 Discussion and conclusions

Squalomorph sharks (Hexanchiformes, Echinorhiniformes, Pristiophoriformes, Squatiniformes, Squaliformes) are seemingly less diverse and abundant than galeomorph sharks (Heterodontiformes, Orectolobiformes, Lamniformes, Carcharhiniformes) in the Eocene La Meseta and Submeseta formations of Seymour Island (z.B. Kriwet, 2005; Kriwet et al., 2016; Engelbrecht et al., 2016a,b). Intriguingly, several sharks that could have been expected have not been found up to now, such as remains of frilled sharks (represented by an endemic species in the Late Cretaceous of Ross Island, Antarctic Peninsula; Richter and Ward, 1990) and heterodontids. The absence of these two groups might be related either to climatic or environmental conditions.

Modern squalomorph sharks are mostly found in cold and deep waters, where they generally are bottom-dwelling and only few species are meso- or bathypelagic (Compagno et al., 2005). Fig. 7 provides a summary of depth ranges of living squalomorph sharks that also occur in the La Meseta and Submeseta formations. All squalomorph records from the Eocene of Seymour Island come from marine shallow water or estuarine deposits, which is in general agreement with current distributions.

Within squalomorphs, squaliform sharks (dogfish sharks) represent the most species-rich group today with more than 120 described species (Compagno et al., 2005) representing approximately 27% of all extant elasmobranchs (Straube et al., 2015). They also display a large range of body sizes from only few centimetres representing some of the smallest sharks (Dwarf Lanternshark, *Etmopterus perryi* Springer and Burgess, 1985; Spined Pygmy Shark, *Squaliolus laticaudus* Smith and Radcliffe, 1912) to species of over 6 m in length (Greenland Shark, *Somniosus microcephalus* Bloch and Schneider, 1801). Squaliform sharks are generally considered to represent deep-water sharks and thus corresponding fossil deposits, in which squaliform sharks occur are interpreted as representing deep-water environments. This provoked Long (1992b) to suggest that deep-water/transitional squaliforms inhabited adjoined deep-sea areas and may have invaded the shallow water environments of the Antarctic Peninsula seasonal or during cyclical diurnal migrations to search for food. Nevertheless, the occurrence of squaliform (and as that of squalomorph sharks) in the Eocene La Meseta Fm. of Seymour Island is not contradicting the depositional interpretations of the TELMs. For instance, living dogfish sharks are circum-globally distributed in tropical to cold temperate waters but are most species-rich in cold-temperate polar environments (Ebert and Winton, 2010). They are, conversely less diverse and dominant in warmer environments, where they generally occur in comparably deeper waters, because most squaliforms are sensitive to seawater temperatures and avoid sea temperatures above 15 °C, which not only constrains their geographic but also their depth ranges (Musick et al., 2004).

Independent of geographic ranges, extant squaliform sharks normally occur in deeper waters but they may enter shallow marine environments less than 200 m deep (e.g., Yano et al. 2017) and even very shallow waters (e.g. Serena et al., 2009). Members of the Squalidae generally occur from the intertidal zone near the surface of the epipelagic zone to about 1400 m on the deep continental slope. Most species, however, occur on the shelves and

uppermost slopes down to about 600 m (Kyne and Simpfendorfer, 2010). Many dogfish sharks also are known to change their lifestyle as they grow and mature, inhabiting mid-waters as neonates and develop a more benthic lifestyle as they grow in size (Ebert and Winton, 2010). Living squalids also often co-occur with more deep-dwelling squaloids (e.g. Centrophoridae, Dalatiidae, Somniosidae) on the slopes (Ebert and Stehmann, 2013), which agrees with the composition of squaliform sharks in the La Meseta Fm. In contrast to squalids, living centrophorids are most diverse in warm waters of the Indo-west Pacific. The main depth range of this group is between approximately 1000–1500 m (see Fig. 7) and are thus considered deep-water, bottom-dwelling species. However, few records from shallow occurrences of about 50 m are known (Compagno et al., 2005). Living taxa are, however, absent from very high latitudes and in the north-eastern Pacific (Compagno et al., 2005; Nelson et al., 2016). Adaptation of squaliform sharks to deep-water environments seemingly already occurred in the Cretaceous and they were abundant and diverse in deep-water environments in the Late Cretaceous and Cenozoic (e.g., Klug and Kriwet, 2010; Straube et al., 2010; Sorenson et al., 2014), but their fossil record is biased among others by the rarity of suitable deep-water facies. From the Cretaceous (Müller, 1989; Siverson, 1993), Eocene (Adnet, 2006), Miocene (Ledoux, 1972; Underwood and Schlögl, 2013) and Pliocene (e.g., Cigala-Flugosi, 1996; Marsili and Tabanelli, 2007) diverse faunas including fossil squaliforms are known. Many extant squaliform genera are already present in the Eocene (Adnet, 2006), while several genera are now extinct. Unfortunately, only little is known of Cenozoic squaliform diversity outside of southern Europe (Underwood and Schlögl, 2013).

Angel shark (Squatinae) remains represented by isolated teeth are very abundant (>1000 teeth) in the Eocene deposits of Seymour Island. Unfortunately, it is not possible to identify or distinguish species due to the insufficient knowledge of dental variations in living species. The occurrence of *Squatina* teeth within the La Meseta Fm. and the geographic distribution on Seymour Island that includes all environmental types is in good accordance with distribution patterns in living species. Living *Squatina* species inhabit upper continental and insular shelves down to more than 100 m and occur in the Atlantic, Pacific and southwestern Indian oceans (Nelson, 2006).

The living Bluntnose Sixgill Shark, *Hexanchus girseus*, occurs on shelves and slopes of continents, islands, seamounts, and mid-oceanic ridges. Young sharks may occur close inshore in cold waters, whereas adults can be found in shallow waters to submarine canyons. *Hexanchus griseus* is usually found in depths ranging from 500 to 1100 m and at least 1875 m (Compagno et al., 2005). In contrast, the Bigeye Sixgill Shark, *Hexanchus nakamurai*, is widely but patchy distributed in warm temperate to tropical seas, on continental and island shelves and slopes. It can be found on or near the bottom in depths between 90 and 621 m (Compagno et al., 2005). The occurrence of rare hexanchiform shark remains in the shallow water deposits of Seymour Island is not in conflict with their current spatial and depth distribution patterns.

Nevertheless, the remains of squalomorph sharks are unevenly distributed throughout the La Meseta and Submeseta formations on Seymour Island, with most representatives occurring in TELMs 4 and 5. Teeth of *Squatina* sp. are the most in terms of individual numbers within the Squalomorphii in the La Meseta and Submeseta formations and are the most abundant

shark remains in TELMs 5 (35,91%) and 6 (29,03%) of the total chondrichthyan quantity. Odonataspidid sharks like *Striatolamia macrota* (Agassiz, 1843) and *Palaeohypotodus rutoti* (Winkler, 1876) conversely dominated the other TELMs. Moreover, the species of *Squatina* and *Squalus* include a wide range of sizes from very small to large ones indicating that different ontogenetic stages, juvenile to adult (probably even senile) occurred in shallow waters during the Eocene in Antarctica. This might be interpreted that squatinids and squalids may have used these waters as breeding and/or nursing grounds.

More precisely, teeth of *Squatina* sp. occur in TELMs 4, 5, 6 and 7 (Ypresian, Lutetian, Bartonian and Priabonian in age, respectively) of the La Meseta and Submeseta Formations, where TELMs 4 to 6 represent estuarine deposits and TELM 7 shallow marine deposits. The occurrence of this taxon in TELMs 4 to 7 implies that favourable benthic habitats around the Antarctic continent must have been present. *Squalus weltoni* and *Squalus woodburnei* are present in TELMs 4 to 6, which are early to middle Eocene in age. In the upper most part of the Submeseta Formation a fin spine of *Squalus* sp. was found and described by Kriwet et al. (2016), extending the range of *Squalus* into the Priabonian, late Eocene. *Hexanchus* sp. occurs in TELMs 4 and 5 (Ypresian in age), with an estimated sea-surface temperature of about 10–11 °C. Conversely, *Centrophorus* were recovered from TELMs 4 and 5, which are interpreted as estuary deposits. The records of this taxon from the Antarctic Peninsula are the southernmost occurrences in the Cenozoic. The new taxon, *Eodalatias australis* gen. et sp. nov. also occurs in TELMs 4 and 5 (Ypresian in age). It is not possible to infer its depth range since it has no extant relatives (see Table 1).

The occurrence and distribution patterns of extant squalomorphs, especially those considered deep-water taxa do not contradict the presence of squalomorph sharks within near-coastal to estuary deposits of Antarctica during the Eocene as outlined above. Consequently, the taxa are not transitional forms as suggested by Long (1992b). The taxonomic diversity of squalomorph sharks gradually decreased during the Eocene and they seemingly retreated from the shallow-water environments by the end of the sedimentary succession in TELM 7 when ice-shield formation started and the shelf areas surrounding Antarctica where successively reduced.

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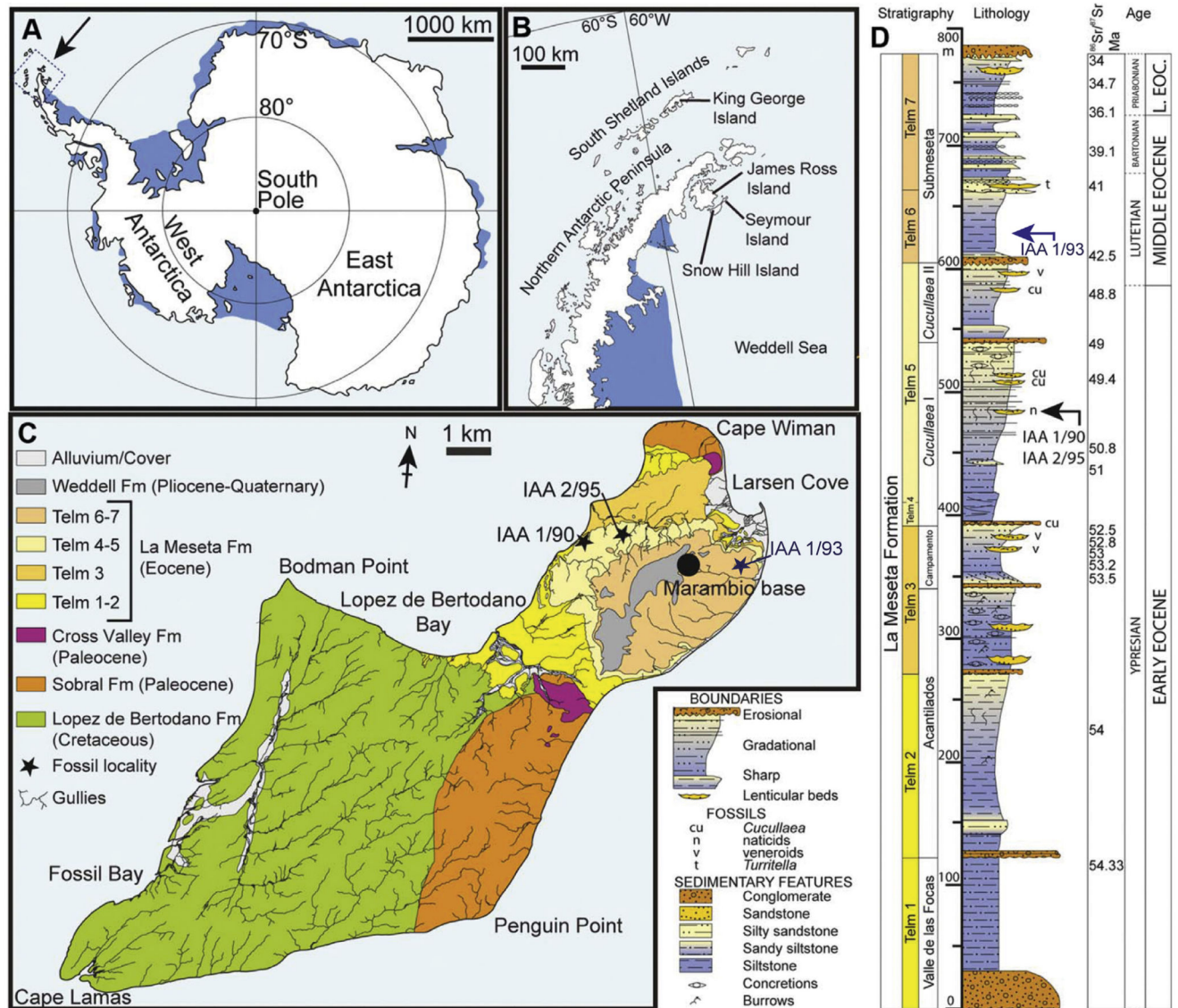
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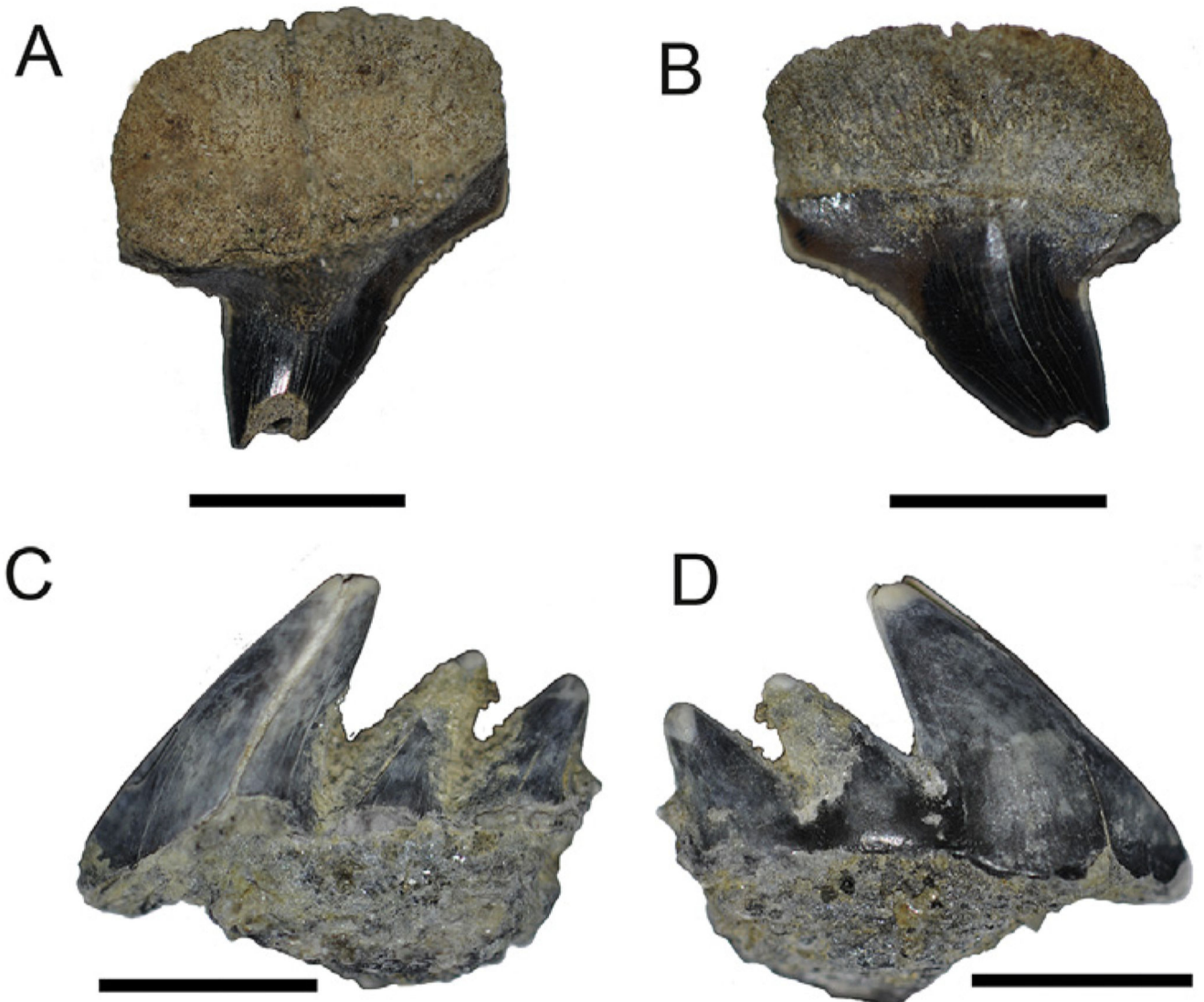


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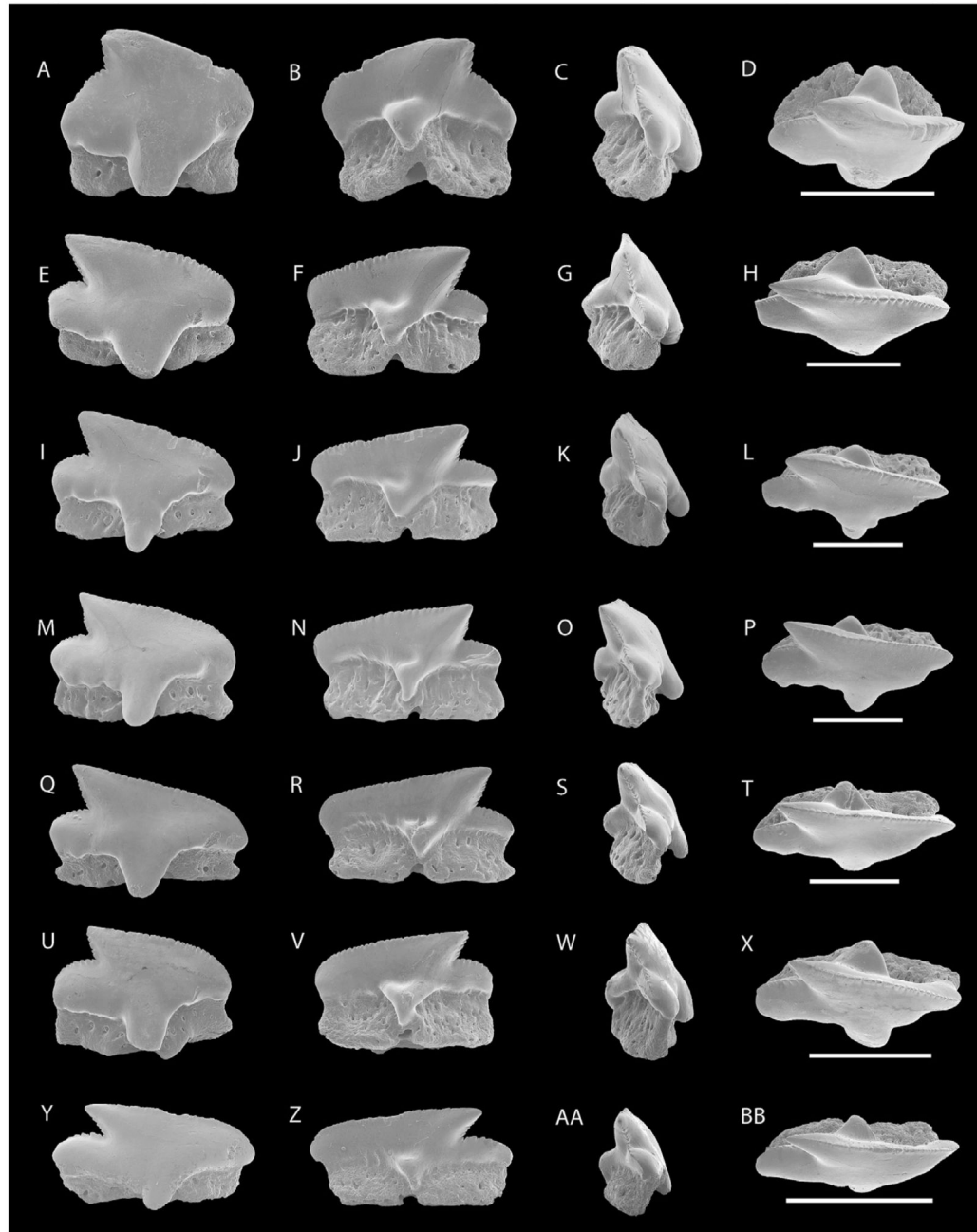
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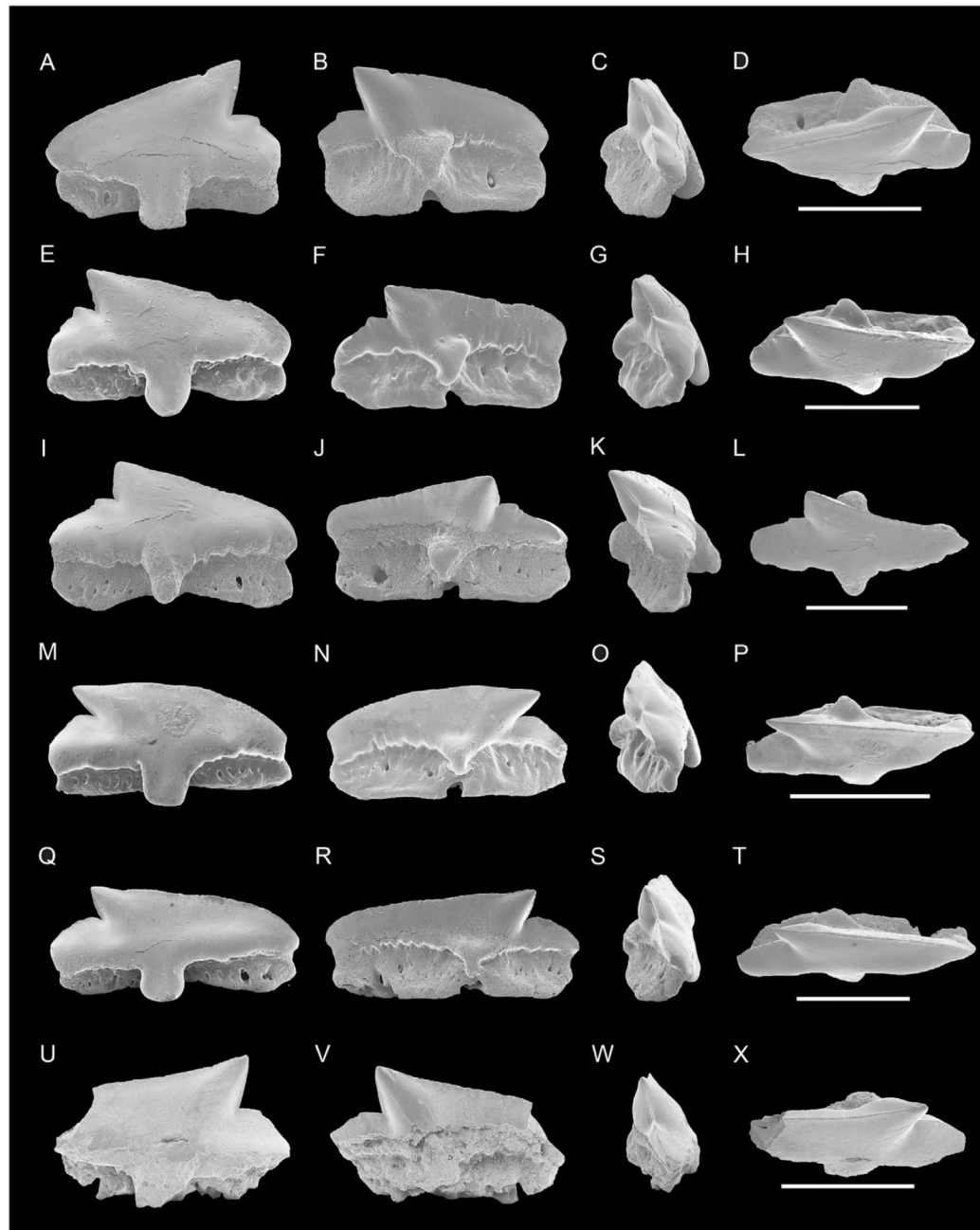
**Fig. 1.** Location and stratigraphy of Seymour Island, Antarctica. **A**, map of Antarctica, showing the position of the Antarctic Peninsula; **B**, map of the Antarctic Peninsula, showing the location of Seymour Island; **C**, Geological map of Seymour Island, showing the outcrop of TELMs 5–6 with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



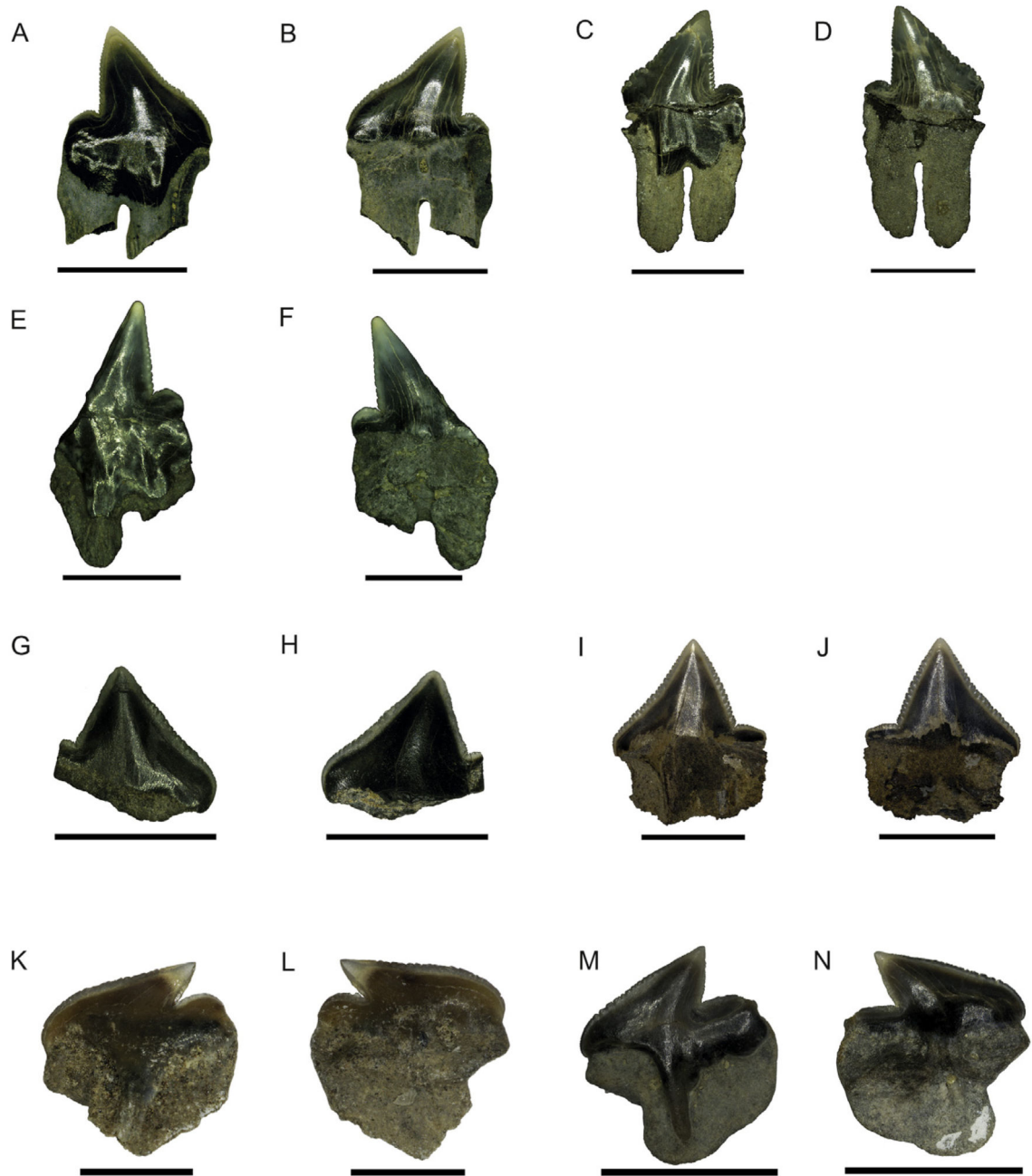
**Fig. 2.** Pictures of *Hexanchus* sp. taken with a Keyence VHX-1000D of NRM-PZ P15880, **A**, labial; **B**, lingual; NRM-PZ P15894, **C**, labial; **D**; Scale bar equals 1 mm.



**Fig. 3.** SEM photographs of teeth of *Squalus weltoni*. NRM-PZ P15803, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P15810, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P15800, ?upper tooth, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P15809, ?upper tooth, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P15830 **Q**, labial; **R**, lingual; **S**, profile; **T**, profile views; NRM-PZ P15819, ?upper tooth, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views; NRM-PZ P15831, **Y** labial; **Z**, lingual; **AA**, profile; **BB**, occlusal views; Scale bar equals 3 mm.

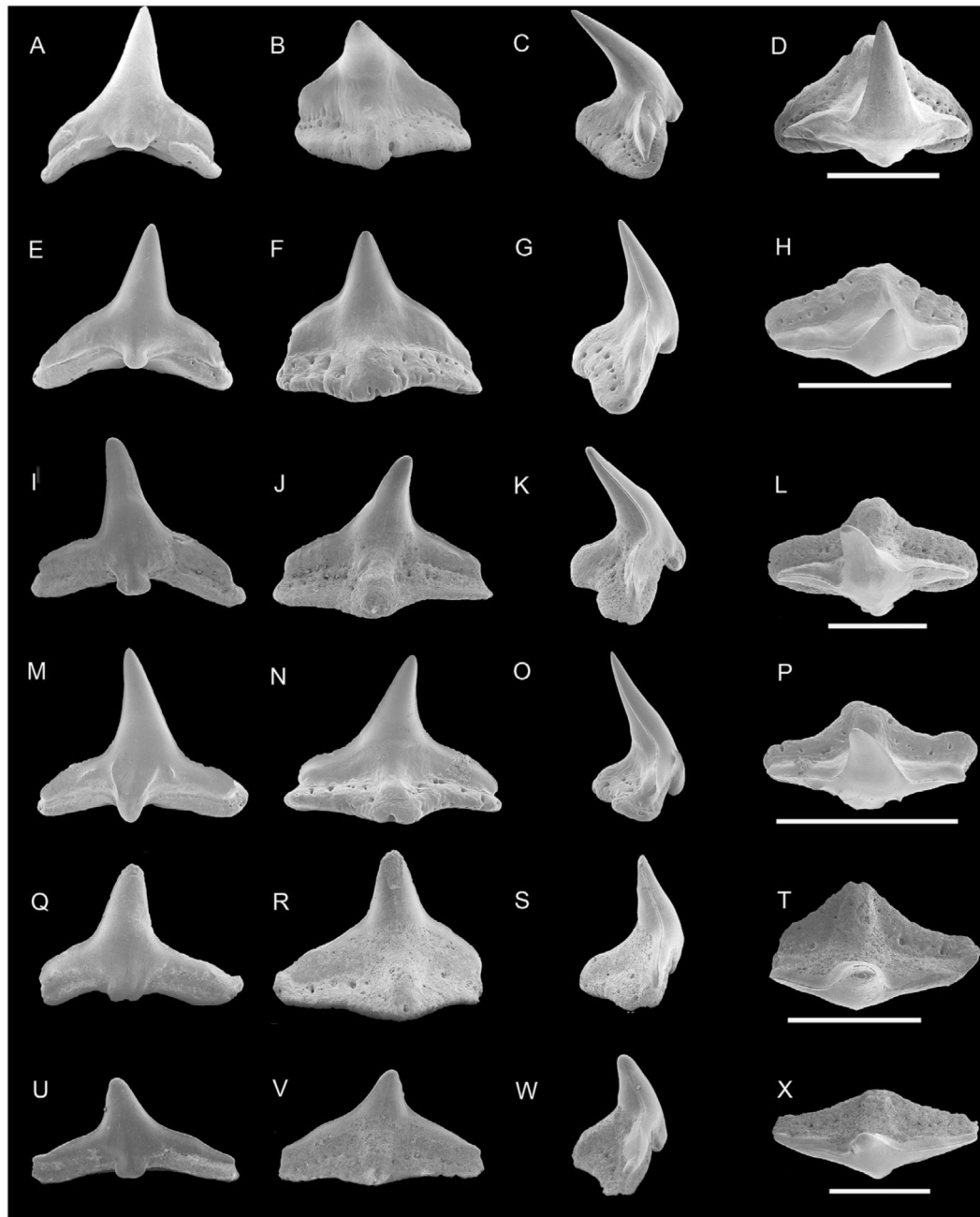


**Fig. 4.** SEM photographs of teeth of *Squalus woodburnei*. NRM-PZ P15799, ?upper tooth, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P15907, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P15919, ?upper tooth, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P15918, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P15917, ?upper tooth, **Q**, labial; **R**, lingual; **S**, profile view; **T**, profile views; NRM-PZ P15920, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views. Scale bar equals 3 mm.



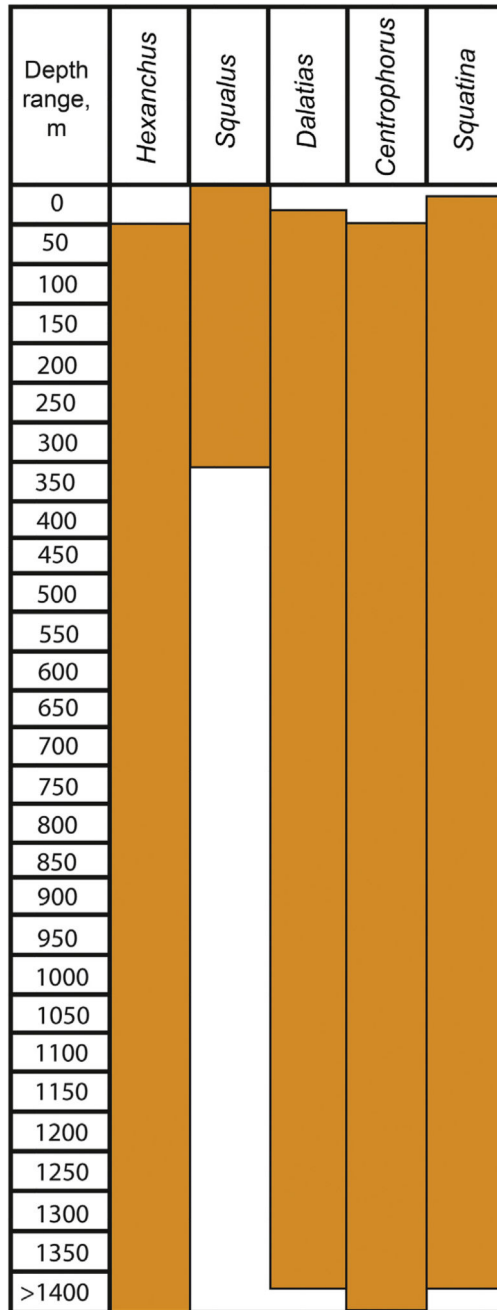
**Fig. 5.**

Pictures taken with a Keyence VHX-1000D. *Eodalatias australis* gen. et sp. nov, NRM-PZ P15801, A, labial; B, lingual views; holotype, NRM-PZ P15815, C, labial; D, lingual views; NRM-PZ P15903, E, labial; F, lingual views, scale bar equals 5 mm; Dalatiidae indet, NRM-PZ P15821, G, labial; H, lingual views; NRM-PZ P15814, I, labial; J, lingual views, scale bar equals 5 mm; *Centrophorus* sp. 1, NRM-PZ P15804, K, labial; L, lingual views, scale bar equals 1 mm; *Centrophorus* sp. 2, NRM-PZ P15807, M, labial; N, lingual views, scale bar equals 5 mm.



**Fig. 6.** SEM photographs of teeth of *Squatina* sp., NRM-PZ P15802, **A**, labial; **B**, lingual; **C**, profile; **D**, occlusal views; NRM-PZ P16237, **E**, labial; **F**, lingual; **G**, profile; **H**, occlusal views; NRM-PZ P16238, **I**, labial; **J**, lingual; **K**, profile; **L**, occlusal views; NRM-PZ P16239, **M**, labial; **N**, lingual; **O**, profile; **P**, occlusal views; NRM-PZ P16240, **Q**, labial; **R**, lingual; **S**, profile; **T**, occlusal views; NRM-PZ P15811, **U**, labial; **V**, lingual; **W**, profile; **X**, occlusal views. Scale bar equals 1 mm.





**Fig. 7.** Present-day bathymetrical ranges of taxa that were found in the La Meseta and Submeseta Formations.

**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). 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.

TELM	Facies	Temp.	Association
7	shallow marine inner estuary channels	ca. 7 –8 °C ca. 5 °C	<b>Squalus sp.</b> , <b>Squatina sp.</b> , <i>Pristiophorus laevis</i> , <i>Carcharocles sokolovi</i> , <i>Palaeohypotodus cf. rutoti</i> , <i>Striatolamia cf. macrota</i> , <i>Ischyodus dolloi</i>
6	estuary	ca. 7 °C ca. 15 °C	<b>Squatina sp.</b> , <b>Squalus woodburnei</b> , <b>Squalus weltoni</b> , <i>Pristiophorus laevis</i> , <i>Ischyodus dolloi</i> , <i>Coelometlaouia pannucea</i> , <i>Notoramphoscyllium woodwardi</i>
5	estuary	ca. 10 –11 °C	<i>Hepranchias howelli</i> , <b>Hexanchus sp.</b> , <b>Centrophorus sp. 1</b> , <b>Centrophorus sp. 2</b> , <b>Eodalatias austrinalis gen. et sp. nov.</b> , <b>Squalus weltoni</b> , <b>Squalus woodburnei</b> , <i>Pristiophorus laevis</i> , <b>Squatina sp.</b> , <i>Anomotodon multidenticulata</i> , <i>Cetorhinus sp.</i> , <i>Macrorhizodus praecursor</i> , <i>Lamna cf. nasus</i> , <i>Odontaspis winkleri</i> , <i>Palaeohypotodus rutoti</i> , <i>Striatolamia macrota</i> , <i>Notoramphoscyllium woodwardi</i> , <i>Coelometlaouia pannucea</i> , <i>Scoliodon sp.</i> , <i>Myliobatis sp.</i> , <i>Raja/Bathyraja sp.</i> , <i>Ischyodus dolloi</i>
4	estuary	ca. 10 –11 °C	<i>Paraorthacodus sp.</i> , <i>Hepranchias howelli</i> , <b>Hexanchus sp.</b> , <i>Centrophorus sp.</i> , <b>Eodalatias austrinalis gen. et sp. nov.</b> , <i>Deania sp.</i> , <b>Squalus weltoni</b> , <b>Squalus woodburnei</b> , <i>Pristiophorus laevis</i> , <b>Squatina sp.</b> , <i>Anomotodon multidenticulata</i> , <i>Carcharocles auriculatus</i> , <i>Cetorhinus sp.</i> , <i>Macrorhizodus praecursor</i> , <i>Lamna cf. nasus</i> , <i>Odontaspis winkleri</i> , <i>Palaeohypotodus rutoti</i> , <i>Striatolamia macrota</i> , <i>Carcharhinus sp.</i> , <i>Scoliodon sp.</i> , <i>Myliobatis sp.</i> , <i>Pristis sp.</i> , <i>Raja/Bathyraja sp.</i> , <i>Chimaera seymourensis</i> , <i>Ischyodus dolloi</i>
3	delta plain – estuary	ca. 10 –11 °C ca. 15 °C	<i>Pristiophorus laevis</i> , <i>Carcharocles auriculatus</i> , <i>Lamna cf. nasus</i> , <i>Striatolamia macrota</i> , <i>Myliobatis sp.</i> , <i>Ischyodus dolloi</i>
2	delta front		<i>Callorhynchus stahli</i> , <i>Chimaera seymourensis</i> , <i>Ischyodus dolloi</i>
1–2	prodelta?/inner estuarine?		<b>Centrophorus sp.</b> , <b>Deania sp.</b> , <i>Carcharocles auriculatus</i> , <i>Striatolamia macrota</i>