



CROSSING THE BOUNDARY: AN ELASMOBRANCH FAUNA FROM STEVNS KLINT, DENMARK

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Abstract: The chondrichthyan faunas from the Danish Maastrichtian chalk and the K/T boundary clay, the Fiskeler, are described for the first time. The rich and diverse fauna discovered in the late Maastrichtian chalk experienced a massive drop in diversity prior to the boundary. However, the fauna started to recover immediately after the deposition of the impact layer during earliest Danian times and had regained much of its diversity during the first few millennia after the bolide impact. Precision sampling has made it possible to document the recovery of the fauna, which did not suffer an extinction event of the same magnitude,

as apparently observed in Morocco. At Stevns Klint, only 33 per cent of the chondrichthyan fauna became extinct compared with the 96 per cent in Morocco. The drop in diversity before the boundary is attributed to a sudden change in sea level. Among the sharks found in the chalk and Fiskeler are rare species such as *Parasquatina* and *Echinorhinus* and the first representative of *Nebrius* in Europe.

Key words: K/T boundary, extinction, Chondrichthyes, Stevns Klint, Denmark.

LATE Maastrichtian chalk is exposed at several localities in northern Jutland, Zealand and Møn, and although most of the localities have been extensively studied for both micro- and macroinvertebrates, the vertebrate fauna has received little or no attention. This is equally true of the famous boundary clay, the Fiskeler (literally ‘Fish Clay’), which received much publicity following the detection of an iridium anomaly in it by Alvarez *et al.* (1980). Although its vertebrate remains have been known for almost two centuries, they have not been studied in any detail. The name ‘Fiskeler’ was coined by Forchhammer (1849), due to its content of fish debris and sharks’ teeth. In 1825, Forchhammer had already noticed that the clay was stratified and could be subdivided. Although shark teeth are scarce in the Danish Cretaceous chalk, they have been found at Møns Klint, Stevns Klint and northern Jutland, more specifically from Kjølbj Gaard and Vokslev kalkgrav (Jessen and Ødum 1923; Bonde *et al.* 2008; Gravesen and Jakobsen 2012). The Maastrichtian fauna bears similarities with the faunas found in the Campanian of Sweden (Siverson 1993a) and with those described from the Maastrichtian of North Germany (Herman 1982b) and the Netherlands (Herman 1977). Sharks’ teeth are more abundant in the Fiskeler, especially so at some localities at Stevns Klint, where they are quite common; teeth are rather scarce at other localities. The fauna from the Fiskeler at Stevns Klint covers the time immediately during and

a little after the impact (Kyte *et al.* 1985). It offers a unique opportunity to study how a shark fauna in the boreal realm was affected by the K/T boundary within a comparatively short period of time. Only a handful of papers include information on Danian shark faunas (Herman 1977; Siverson 1995; Noubhani and Cappetta 1997; Mannering and Hiller 2008), but none of these authors included boundary material in their descriptions, leaving a big gap in the understanding of how chondrichthyans coped with this catastrophic event.

GEOLOGICAL SETTING

The Maastrichtian chalk is present in most of the Danish subsurface, except the islands of Anholt and Bornholm, and may attain a thickness of up to 700 m (Stenestad 1972). The chalk is only exposed in northern Jutland, the islands of Zealand, Møn and Lolland-Falster, due to salt tectonics in northern Jutland and regional uplift in the south-eastern areas. Fiskeler has been deposited within a wide belt from Thy in the north-west to the cliffs at Stevns Klint in the south-east. It is accessible at several localities, mainly in Thy (Fig. 1A) and along Stevns Klint (Fig. 1B–C). The Fiskeler is usually about 5–10 cm thick, but can reach a maximum of 35 cm at the locality of Kulstirenden near Stevns Klint.

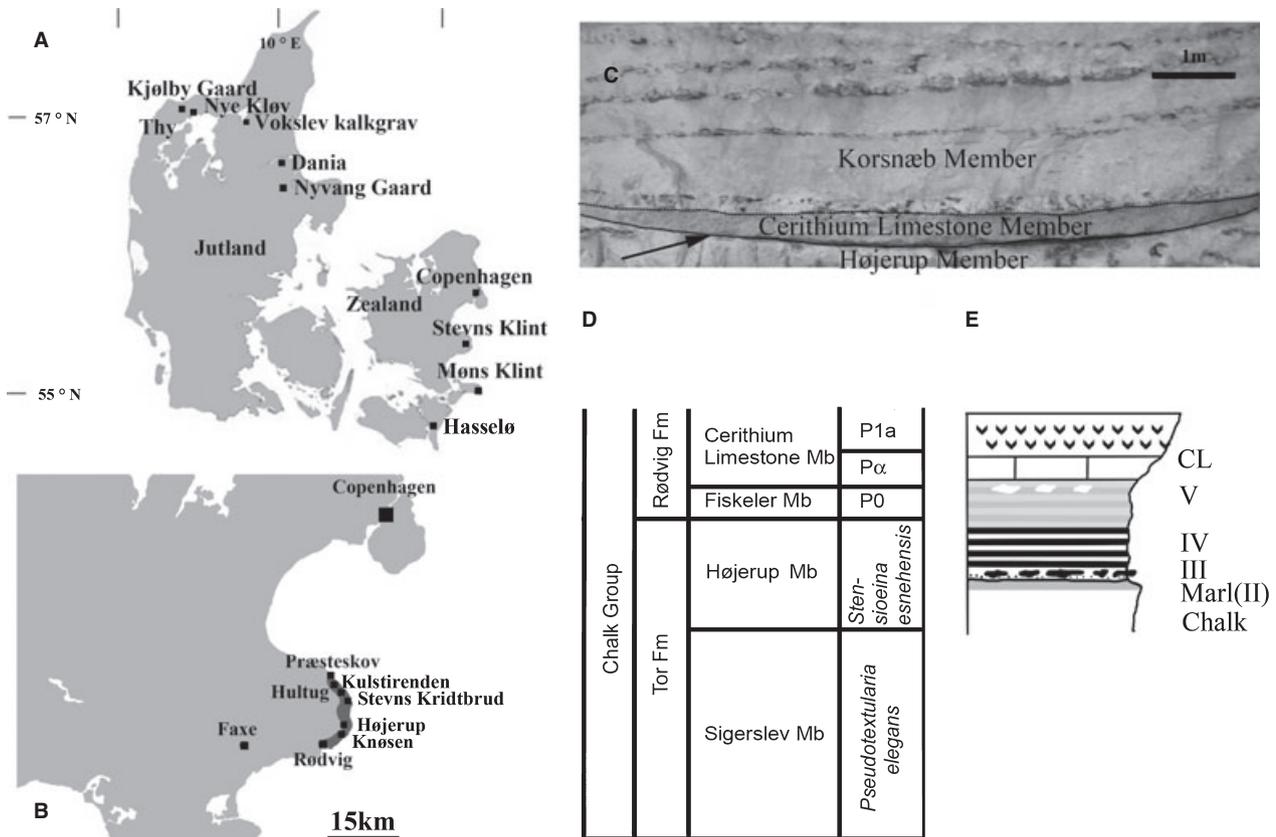


FIG. 1. A, map of Denmark marked with localities mentioned in the text. B, localities on a map of eastern Zealand, the dark area indicates the extent of the coastal cliffs of Stevns Klint. C, an image of the trough-shaped basins at Højerup in which both the Fiskeler and the Cerithium Limestone are deposited. The arrow indicates the Fiskeler with the underlying Maastrichtian Chalk and the overlying Danian Cerithium Limestone. D, stratigraphical scheme of the succession at Stevns Klint. E, section from the K/T boundary with the numbered layers (modified from Christensen *et al.* 1973). Scale bar represents 1 m.

Stevns Klint. The cliffs at Stevns Klint encompass the area from Præsteskov in the north to Rødvig in the south, a distance of 14.5 km. A thickness of up to 40 m of Maastrichtian chalk of the Tor Formation (Deegan and Skull 1977; Fig. 1D) is exposed here. The lower part of the exposed chalk belonging to the Sigerslev Member is a bryozoan-rich wackestone with a coccolith chalk matrix with layers of flint nodules deposited in large mound-like structures. The mounds pass gradually into a heavily bioturbated benthos-poor chalk, which was probably deposited during a period of deep water (Surlyk and Håkansson 1999). Two slightly phosphatized, incipient hardgrounds, 10 cm apart, 4–5 m below the Fiskeler marks the beginning of the Højerup Member, often referred to as the ‘grey chalk’ (Gråkridt in Danish literature; Rosenkrantz 1924). The Højerup Member is rich in bryozoans, brachiopods and bivalves. It was deposited in asymmetric mounds reaching a height of about 1 m and a width of 20–30 m, with slightly steeper southern than northern flanks, indicating a migrational direction towards the south (Surlyk and Håkansson 1999; Surlyk *et al.* 2006). Between the Fiskeler and the Cretaceous

chalk is a thin grey transitional layer of marl only a few centimetres thick, with a well-developed Maastrichtian dinoflagellate assemblage (Hultberg 1986). This marl layer was assumed to be part of the Fiskeler by Christensen *et al.* (1973) during their detailed description of the Fiskeler, and they numbered it as layer II (Fig. 1E). The K/T boundary was later moved up one bed due to the iridium anomaly found in layer III (Alvarez, *et al.* 1980) and is no longer included in the Fiskeler Member (Surlyk, *et al.* 2006). The Maastrichtian chalk consists of almost pure carbonate at Stevns Klint with only around 0.5 per cent clay, mainly smectite and illite (Thomsen 1995). The Fiskeler Member of the Rødvig Formation is deposited in trough-shaped basins between the Maastrichtian bryozoan mounds and the overlying early Danian Cerithium Limestone, indicating an abrupt cessation of calcareous sedimentation. The Fiskeler may attain an exceptional thickness up to 35 cm at Kulstirenden, but is usually <10 cm thick in the centre of the troughs wedging out towards their margins. The most basal part of the Fiskeler is a dark red and black layer, layer III of Christensen *et al.* (1973), based on the first occurrence of the iridium

anomaly. This is followed by a laminated black and white layer (layer IV) overlain by a grey marl layer, V. Layer III was further subdivided by Schmitz (1985) into a red lower layer and an upper layer or as IIIA and IIIB in Elliott (1993). The few millimetres thick reddish layer, IIIA, is regarded as 'impact layer' and consists mainly of smectite with a high content of goethite-rich microspherules. These have been identified as pseudomorphosed microtektites (Smit and Klaver 1981; Montanari *et al.* 1983; Smit and Romein 1985; Bauluz *et al.* 2000) or of volcanic origin as suggested by Naslund *et al.* (1986) and are regarded to be comparable with the spherule layers found worldwide (Premović 2011). A more controversial theory was proposed by Hansen *et al.* (1986) who proposed that the spherules were the result of diagenetic infill of prasinophyte algae. This was partly supported by Schmitz *et al.* (1988), but opposed by others (Bohor and Betterton 1988; Bohor 1990). The amount of biogenic calcite is less than 20 per cent in the impact layer, increasing to over 60 per cent in the upper part of the Fiskeler (Premović 2009). The impact layer also includes clasts of granite, small quartz grains and biotite, presumably originating from the nearby southern Scandia penplain (J. S. Adolfsen pers. obs.). Layer IIIB is black marl with a high content of smectite, also containing spherules, but to a lesser extent than layer IIIA. Layer IV is a fine, unbioturbated, laminated black-grey marl, which together with layer V comprises the main part of the Fiskeler. Layer V is light grey and can, in its upper part, include angular clasts of reworked Maastrichtian chalk (Ravn 1903; Rosenkrantz 1924, 1937; Surlyk and Håkansson 1999). Whereas the transition from the Maastrichtian chalk to the clay was abrupt, the transition from layer V into the overlying cream-coloured Cerithium Limestone is gradual.

The origin of the Fiskeler has been subject of debate for decades. Rosenkrantz (1955) suggested that it could have been a diagenetic alteration of volcanic ash, a theory which since has been supported by several authors (Valton 1959; Rampino and Reynolds 1983; Elliott *et al.* 1992; Elliott 1993; Premović *et al.* 1993; Drits *et al.* 2004; Premović 2004; Premović *et al.* 2008). Others have suggested that the clay is derived from ejecta fallout (Alvarez *et al.* 1980; Kyte *et al.* 1980; Kastner *et al.* 1984; Bauluz *et al.* 2004; see Premović *et al.* 2008, for thorough review of the literature on the origin of the Fiskeler). It has also been suggested that the Fiskeler resulted from the dissolution of carbonate, the clay content being a residual condensed deposit (Ekdale and Bromley 1984), similar to the English Frindsbury Clay (Ward and Cooper 1976). This is, however, not the case as pointed out by Hansen *et al.* (1986).

Although it is difficult to guarantee that a deposit is completely free of reworking, with the exception of the Maastrichtian chalk clasts in the upper part of layer V, the

lower and middle part of the Fiskeler appears to be authigenic as supported by Hultberg (1986, 1987), who reported that the dinoflagellates are primary. Likewise, Hart *et al.* (2004) confirmed that the carbonates at both Højerup and Kulstirenden are primary and, like Hultberg (1986), they did not find any signs of bioturbation in layer IV. During the earliest Danian, Stevns Klint was situated within a narrow straight, around 100 km wide east-west, which stretched from the newly opened North Atlantic and presumably further south-east towards the Crimean Basin and the Tethys Sea (Håkansson and Thomsen 1999).

Besides sharks' teeth, bony fish remains have been found, mainly vertebrae, bone fragments and teeth. The Fiskeler yields a very foraminiferan fauna, only benthic, and an abundance of dinocysts (Gwozdz *et al.* 2001). Premović *et al.* (2000) estimated that the duration of sedimentation for the lowermost layer of the Fiskeler (layer III) was within 30 years, which was comparable with that of Mukhopadhyay *et al.* (2001), which was 60 ± 12 years. The total duration of the deposition of the Fiskeler was estimated to be 40 ky (Hansen *et al.* 1992) or between 5 and 15 ky (Kyte *et al.* 1985). If these estimates are correct, the Fiskeler offers us a rare opportunity to observe the impact on the shark fauna within a geologically short period of time.

Møns Klint. The chalk at Møns Klint (Fig. 1A) is correlated with the late Cretaceous Tor Formation (Frykman 2001) and is overlain by Quaternary deposits due to an unconformity. The cliff itself is heavily distorted by glaciotectonic thrusting (Pedersen and Gravesen 2009). Most of the collected material from this locality has been surface-collected, so its specific stratigraphical position is unknown.

Kjølby Gaard. A small privately owned abandoned quarry in Thy (Fig. 1A) with 10 m of Maastrichtian chalk and a 10-cm-thick boundary marl, which is superimposed by 4 m of early Danian bryozoan limestone.

Hasselø By Kalkværk. A small abandoned quarry on Falster. The late Maastrichtian material from this locality was collected by J. Wind during fieldwork in the 1950s (Fig. 1A).

Nyvang Gaard. Small abandoned quarry in northern Jutland (Fig. 1A).

MATERIALS AND METHODS

Material was mainly collected from the 14.5-km-long Stevns Klint and from the adjacent Stevns Kridtbrud quarry, 45 km south of Copenhagen, Møns Klint, Hasselø By Kalkværk, on the island of Falster and from Kjølby Gaard, Thy. Material from Stevns Klint was collected from Rødvig, Knøsen and Højerup. At the working quarry

'Stevns Kridtbrud', close to Mandehoved, the majority of material was collected at Eskesti, which now has been totally excavated. 1068 kg of chalk was collected *in situ* at the Stevns Kridtbrud by Jan Rees (Karlstad) from the uppermost part of the Maastrichtian chalk and dissolved with buffered acetic acid (Jeppsson *et al.* 1999) at the Microfossil Laboratory of the University of Lund, Sweden. Smaller samples (10 kg) were collected in Jutland and 50 kg at Rødvig by one of the authors (JSA) and prepared at the Natural History Museum in Copenhagen (SNM). The remaining material has been either hand-picked by private collectors along the cliffs at Stevns Klint, at Møns Klint, in the quarries close by, or donated to the SNM.

More than 240 kg of Fiskeler was collected by the authors at Højerup, Knøsen and Rødvig and a further 200 kg by the Rasmussen family (Faxe, Denmark) from the Stevns Kridtbrud.

The Fiskeler was bulk-sampled where the overlaying Cerithium limestone had been completely removed so as to avoid contamination. The clay was dried and then disaggregated in water before being mechanically wet-sieved (Ward 1981). All sieved fractions above 500 µm were picked for selachian remains, and some samples were searched at fractions down to 250 µm. Using a 250-µm sieve, even dermal denticles could be recovered, although, in retrospect, the mesh may not have been fine enough to collect juvenile teeth of *Centroscyrnus*. The remains are, in general, well preserved without signs of wear, although teeth from larger specimens, particularly the larger Lamniformes, are almost always broken.

The clay collected by the authors was carefully sampled layer by layer, making it possible to investigate the succession after the impact, whereas the Fiskeler collected by the Rasmussen family was a bulk-sampled mixture of layers III–IV.

The specimens were coated with gold in a Polaron sputter coater and imaged with either a JEOL JSM-6335F or a FEI Quanta 200 Inspect scanning electron microscope. Larger specimens were imaged with a Nikon D7000 DSLR with a Carl Zeiss Makro-Planar T 2/100 lens. The specimens were lightly coated with an ammonium chloride (NH₄Cl) sublimate to enhance surface detail and reduce light reflection. In some cases, the depth of focus was extended by image stacking using Helicon Focus Pro© software.

Repository. The majority of the specimens figured in the article are deposited in the collection in The Natural History Museum of Copenhagen, Denmark, or at GeoMuseum Faxe, Denmark.

Institutional abbreviations. GMV, Geological Museum, Copenhagen – vertebrate collection; MGUH, Museum Geologicum Universitatis Hafniensis; OESM, Østsjællands Museum, Faxe, Denmark; SNM, The Natural History Museum, Denmark.

SYSTEMATIC PALAEOLOGY

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Cohort EUSELACHII Hay, 1902

Subcohort NEOSELACHII Compagno, 1977

Superorder INCERTAE SEDIS

Order SYNECHODONTIFORMES Duffin and Ward, 1993

Remarks. We have chosen to follow Klug (2010), so have included Orthacodontidae and Paraorthacodontidae within the Synechodontiformes, rather than within Hexanchiformes as suggested by Cappetta (2012).

Family ORTHACODONTIDAE Glickman, 1957

Genus SPHENODUS Agassiz, 1843

Type species. *Lamna longidens* Agassiz, 1843 from the Late Jurassic of Switzerland.

Sphenodus lundgreni (Davis, 1890)

Figure 2A–B

Material. Chalk: A single tooth from Stevns Kridtbrud (MGUH 29885).

Description. A tall narrow cusp bending lingually with a pointed apex. The tooth is sigmoid in lateral view. Both the labial and the lingual faces are convex, the lingual face strongly so. The lower half of the labial face has several strong folds, but is otherwise smooth. The lingual face is also smooth with the exception of the base, which has numerous small short folds. The labial face does not jut out over the root. The cutting edges are continuous and reach the base of the crown, which is 31 mm high and 10 mm wide at the base. The root is only partly preserved, but is low, wide with sloping shoulders and a flat basal face and is labio-lingually expanded.

Remarks. The tooth is morphologically very close to the specimen of *S. lundgreni* figured by Davis (1890) and displays same distinctive folds on both labial and lingual faces. The species *S. lundgreni* is common in the Danian of both Denmark and Sweden. The tooth differs from the Cretaceous *Sphenodus* sp. described by Kriwet *et al.* (2006) from Antarctica and by Antunes and Cappetta (2002) from Angola, as it has strong, long folds on the labial face and short strong folds on the lingual face. As noted by Böttcher and Duffin (2000), in the Late Jurassic species *Sphenodus macer*, the dentition exhibits monognathic heterodonty. Based on their reconstructed tooth set, the specimen described here appears to be an anterior

tooth. Duffin and Ward (1993) list 29 species of *Sphenodus*, several of which are synonymous, and only four of them are from the Cretaceous. These four species are *S. salandianus* (Gervais 1859), *S. subaudianus* (Pictet 1858), *S. planus* (Agassiz 1843) and *S. sennesi* (Leriche 1936). Kriwet *et al.* (2006) considered most late Cretaceous species of *Sphenodus* as dubious. This is further supported by the fact that *S. sennesi* described by Leriche (1936) is not a *Sphenodus*, but more probably an *Anomotodon* and that *S. salandianus* is a typographical mistake in Gervais (1859) for *S. subaudianus* according to Cappetta (2006, p. 201). Cappetta (2006) further rejected both *S. subaudianus* and *S. planus*, as both species were described on poorly preserved material. Thus, *S. lundgreni* is probably the only valid species of *Sphenodus* described from the Cretaceous. However, an undescribed robust species of *Sphenodus* is present in the mid-Cretaceous Cambridge Greensand of England (D. J. Ward pers obs.).

Family PARAORTHACODONTIDAE Klug, 2010

Remarks. The family Paraorthacodontidae consists of the two genera; *Paraorthacodus* Glickman 1957 and *Macrourogaleus* Fowler 1947. The family ranges from the Late Jurassic, Kimmeridgian to the Late Paleocene, Thanetian (Klug 2010).

Genus PARAORTHACODUS Glickman, 1957

Type species. *Sphenodus recurvus* Trautschold, 1877 from the Cenomanian, late Cretaceous, of Russia.

Paraorthacodus andersoni (Case, 1978)

Figure 2C–G

Material. Chalk: Five teeth from Stevns Kridtbrud (MGUH 29886, MGUH 29887, MGUH 29888, GMV2012–21 and GMV2012–22).

Description. A tall and slender principal cusp with a flat to slightly convex labial face. The lingual face of the cusp is so convex that it is visible in labial view. The labial face is smooth in anterior and lateral teeth, and the lingual face is ornamented with short fine folds. The cutting edges are continuous and reach the base of the cusp. The labial face does not jut out over the root. The principal cusp is flanked by two pairs of cusplets, both tall and acute with fine ridges on both the labial and lingual faces reaching half the height of the cusplet. The cross-section of the cusplets mimics that of the principal cusp. The cutting edges on the cusplets are similarly also continuous. The root is low and wide and labio-lingually expanded, with flat to

slightly concave basal face. The labial face is showing a pseudo-polyaulacorhize root vascularization pattern on the lowermost part. A smaller tooth with strong ridges on both the lingual and labial faces and with very acute cusplets could be regarded either as a tooth from a juvenile as mentioned by Siverson (1992b) or as a posterior tooth.

Remarks. Two species of *Paraorthacodus* are known from the late Maastrichtian in Scandinavia *P. andersoni* and *P. conicus*. The species *P. conicus* was described by Davis (1890), but Davis' material is badly preserved and can hardly be used for comparison, although Siverson (1992b) figured several specimens which he referred to that species. The specimens of *P. andersoni* figured by Case (1978) from Montana, USA, differ from those figured by Siverson (1992b) from Sweden, in both shape and ornamentation, although Siverson also illustrates specimens from the type locality of Case's *P. andersoni*. It would be useful to compare the types of *P. andersoni* with the specimens collected by Siverson from the type locality, to resolve any differences.

Family PALEOSPINACIDAE Regan, 1906

Remarks. The family Paleospinacidae consists of the genera *Palidiplospinax* Klug and Kriwet 2008 and *Synechodus* Woodward 1888b.

Genus SYNECHODUS Woodward, 1888b

Type species. *Synechodus dubrisiensis* (Mackie, 1863) from the Cenomanian of England.

Synechodus faxensis (Davis, 1890)

Figure 2H–R

Material. Chalk: one almost complete tooth (MGUH 29889); Fiskeler: three teeth (MGUH 29890, MGUH 29891, MGUH 29892).

Description. Teeth measuring up to 8 mm in height and width. The principal cusp is tall, biconcave in labial view and strongly lingually curved, flanked by up to five pairs of cusplets on wide, low shoulders. The cusplets are small, acute and connected by a continuous cutting edge. The labial face is concave and smooth except for the fine short folds below the shoulders and some vertical folds on the principal cusp. The folds on the principal cusp extend from the base of the cusp to halfway up. The basal edge of the crown is concave and overhangs the root. The lingual face of the crown is strongly convex and bears fine vertical folds on both the principal cusp and the cusplets. On the labial surface of the principal cusp, the folds also reach only halfway

up. The pseudopolyaulacorhize root has labial deep grooves; basally, the root is scattered with foramina, and the lingual face of the root is high with several grooves. A well-developed dental band is present above the root on the lingual face. The crown overhangs the labial surface of the root. The posterior tooth is mesial–distally elongated with a low strongly ornamented crown with a medially situated low cusp on a transverse ridge. The ornamentation on both labial and lingual faces of the crown is strongly reticulated. The labial face of the root is low and elongated with several deep grooves; the basal face is flat with numerous foramina.

Remarks. Contrary to the description in Davis (1890), the specimen described and figured by him is not smooth, but folded on both the labial and the lingual faces. Davis' specimen lacks the root and part of the crown, so comparison is difficult. The largest specimen described here is from the chalk and is less ornamented and more closely resembles the specimen figured by Davis (1890) as *S. faxensis*. The smaller specimens possess heavier ornamentation, suggesting that ornamentation is a juvenile character.

Super order SQUALOMORPHII Compagno, 1973

Order HEXANCHIFORMES Buen, 1926

Family HEXANCHIDAE Gray, 1851

Genus HEXANCHUS Rafinesque, 1810

Type species. *Squalus griseus* Bonnaterre, 1788, Recent.

Hexanchus microdon (Agassiz, 1835)

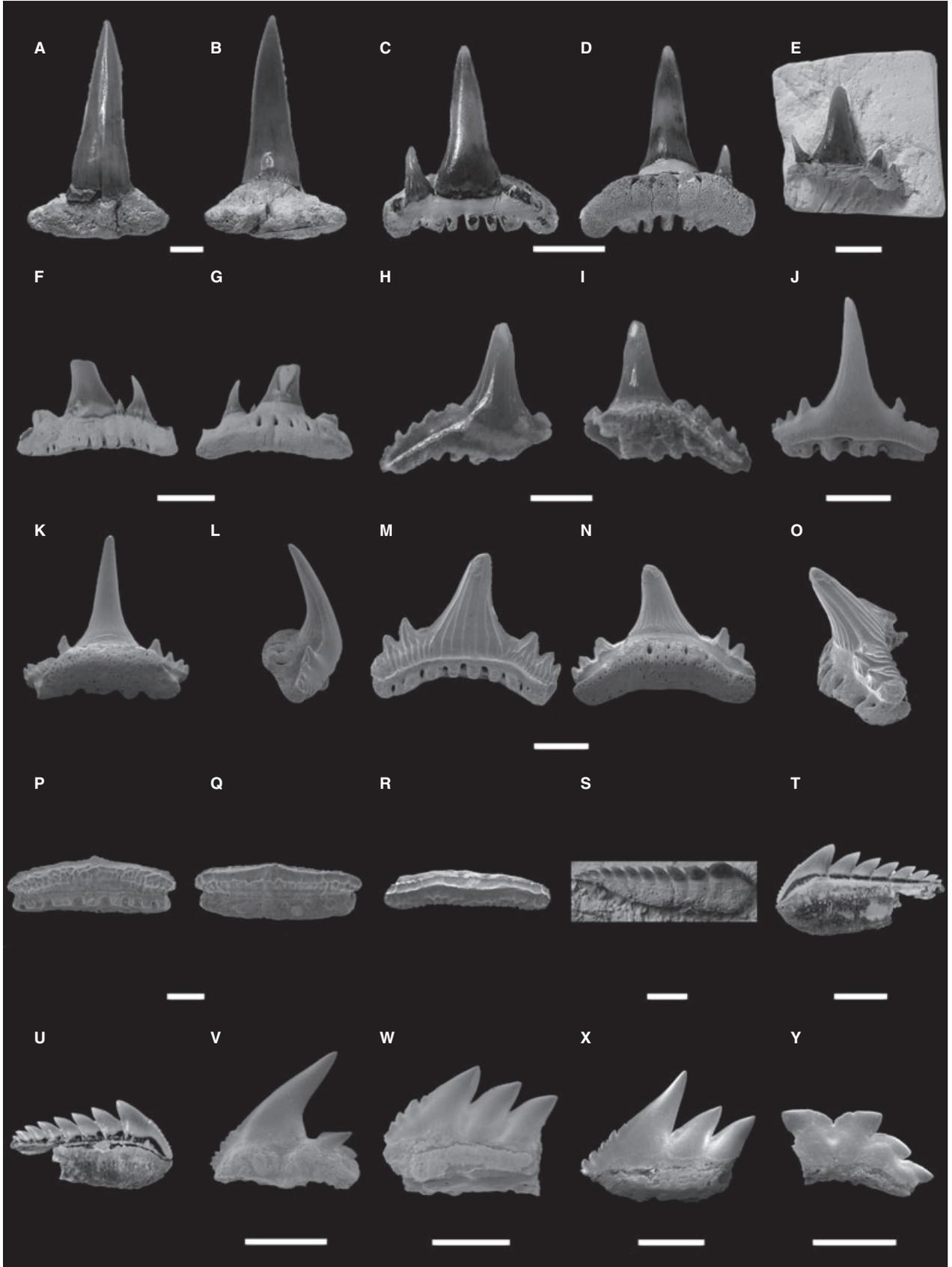
Figure 2S–Y

Material. Chalk: five partly preserved lower teeth and additional fragments (MGUH 29893, MGUH 29894, GMV2012–23, GMV2012–24 and GMV2012–26); Fiskeler: 43 broken specimens (MGUH 29895, MGUH 29896, MGUH 29897, MGUH 29898 and GMV2012–25 (batch number)).

Description. *Hexanchus* displays monognathic, dignathic and gynandric heterodonty. Teeth from the upper jaw are labio-lingually compressed with a prominent principal and a pair of distal accessory cusps. The principal is elongated and slanted towards the commissure, strongly convex on the mesial face and concave on the distal. The lower part of the mesial face has strong serrations, whereas the remaining part of the cusp is smooth, as are the two small distally slanted accessory cusps. All the upper jaw specimens lack roots. Teeth from the lower jaw are labio-lingually compressed with a prominent principal, except for the symphyseal tooth, which is almost symmetrical. Teeth from the lower jaw may attain up to 25 mm in length and at least 9 mm high. The symphyseal teeth have at least three cusps on both the mesial and the distal faces and are all slanted towards the commissure; no teeth were observed with a median erect cusp. Anterolateral teeth of the lower jaw have a prominent principal. The principal has serration on the lower part of the mesial cutting edge, whereas the remainder of the cusp is smooth. The distal accessory cusps are all inclined towards the commissure and diminish in size distally. In the specimens where the principal is more elongated than the first accessory cusp, the apex is more triangular and pointed than in those specimens with a shorter acrocone. The root is labio-lingually compressed, but lacking complete specimens, and it is not possible to comment further on the morphology of these teeth.

Remarks. The ontogenetic and gynandric heterodonty is well developed, but generally underestimated within the Hexanchidae. Tooth size and the number of accessory cusps are ontogenetically variable (Adnet 2006). In the teeth of mature males of recent *Hexanchus*, the principal cusp is elongated, a character also seen in fossil species. The misinterpretation of this character as being of specific significance has led to the description of *H. hookeri* Ward 1979, which subsequently proved to be a junior synonym of *H. agassizi* Cappetta 1976 and perhaps *H. gracilis* Davis 1887 a likely junior synonym of *H. microdon* Agassiz 1835 (Adnet 2006). *H. microdon* is a name usually applied to small, wide fossil teeth, resembling those of the Recent species *H. nakamurai* Teng 1962, from the late Cretaceous worldwide and from the Palaeogene in North Africa. Similar, if not identical, teeth from the European

FIG. 2. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–B, *Sphenodus lundgreni* (Davis, 1890); MGUH 29885, Højerup Member, an anterior tooth in A, labial and B, lingual views. C–G, *Paraorthacodus andersoni* (Case, 1978); C–D, MGUH 29886, Højerup Member, an anterior tooth in C, labial and D, lingual views. E, MGUH 29887, Højerup Member, an anterior tooth in labial view. F–G, MGUH 29888, Højerup Member, a lateral tooth in F, labial and G, lingual views. H–R, *Synechodus cf. faxensis* (Davis, 1890); H–I, MGUH 29889, Højerup Member, an adult lateral tooth in H, labial and I, lingual views; J–L, MGUH 29890, Fiskeler Member, a subadult anterior tooth in J, labial, K, lingual and L, lateral views. M–O, MGUH 29891, Fiskeler Member, a juvenile lateral tooth in M, in labial, N, lingual and O, lateral views. P–R, MGUH 29892, Fiskeler Member, a juvenile posterior tooth in P, labial, Q, lingual and R, occlusal views. S–Y, *Hexanchus microdon* (Agassiz, 1835); S, MGUH 29893, Højerup Member; an adult lower lateral tooth. T–U, MGUH 29894, Højerup Member, an adult lower lateral tooth in T, lingual and U, labial views. V, MGUH 29895, Fiskeler Member, an adult upper tooth, in lingual view. W, MGUH 29896, Fiskeler Member, an adult lower tooth, in lingual view. X, MGUH 29897, Fiskeler Member, an adult lower tooth, in lingual view. Y, MGUH 29898, Fiskeler Member, an adult symphyseal tooth. Scale bars represent 5 mm (A–I, S–U); 2 mm (J–L, V–Y); 1 mm (M–O); and 0.5 mm (P–R).



Tertiary are referred to as *H. agassizi* (Cappetta 1987, 2012; Siverson 1995).

Genus NOTIDANODON Cappetta, 1975

Type species. *Notidanus pectinatus* Agassiz, 1843 from the 'white chalk' (Cenomanian to Campanian)–Maastrichtian of Sussex, England.

Notidanodon pectinatus (Agassiz, 1843) Figure 3A–B

Material. Chalk: One almost complete specimen (OESM-10046-1) and one fragmentary tooth (MGUH 29899) both still embedded in matrix and collected in Stevns Kridtbrud.

Description. Anterior teeth measuring up to 27 mm in length and 16 mm in height labio-lingually compressed with a principal cusp and up to four distal cusplets or five mesial cusplets. The principal cusp is elongated and erect, whereas the distal cusplets are slanted towards the commissure. The four most mesial cusplets are erect and almost symmetrical, whereas the fifth cusplet closest to the principal cusp is distally slanted. Both faces of the crown are convex and smooth. The basal face of the root is flat and large; the lingual face of the root is low.

Remarks. Cappetta (1975) mentioned three species of late Cretaceous *Notidanodon*: *N. lanceolatus* (Woodward, 1886) from the Gault of Britain; *N. dentatus* (Woodward, 1886) from the Campanian New Zealand; and *N. pectinatus* (Agassiz, 1843) late Cretaceous of southern England (Antunes and Cappetta 2002). In both *N. lanceolatus* and *N. dentatus*, the mesial cusplets are slanted towards the commissure, whereas in *N. pectinatus*, the mesial cusplets are more erect and separated. Additionally, *N. pectinatus* is smaller than both *N. lanceolatus* and *N. dentatus*. The difference in size and degree of separation of the mesial cusplets in *N. pectinatus* when compared with the Paleocene species *N. brotzeni* Siverson 1995 and *N. loozi* (Vincent 1876) suggests that the latter are generically distinct.

Order SQUALIFORMES Goodrich, 1909

Family SQUALIDAE Bonaparte, 1834

Remarks. The separation of the genera *Centrophoroides*, *Squalus* and *Centrosqualus* on their teeth can be difficult. Müller and Schöllmann (1989) defined them in the following way (based partly on Cappetta, 1980): '*Centrophoroides* has, in general, separated axial foramina and only an infundibulum in anterior teeth. The basal face is concave, lingually directed, the mesial cutting edge is slightly serrated. The teeth in *Centrosqualus* differ little from those of *Centrophoroides* but the apron is longer, with a narrow base and a very wide termination giving it a bulbous shape. In *Squalus*, the axial foramina are fused to an infundibulum, the basal face is less lingually turned and the mesial cutting edge is smooth.'

The usefulness of the fused axial foramina forming an infundibulum in defining *Squalus* is limited, as this character is absent in several of the squaloid specimens described by Siverson (1993b) and also the specimens described below.

Genus SQUALUS Linnaeus, 1758

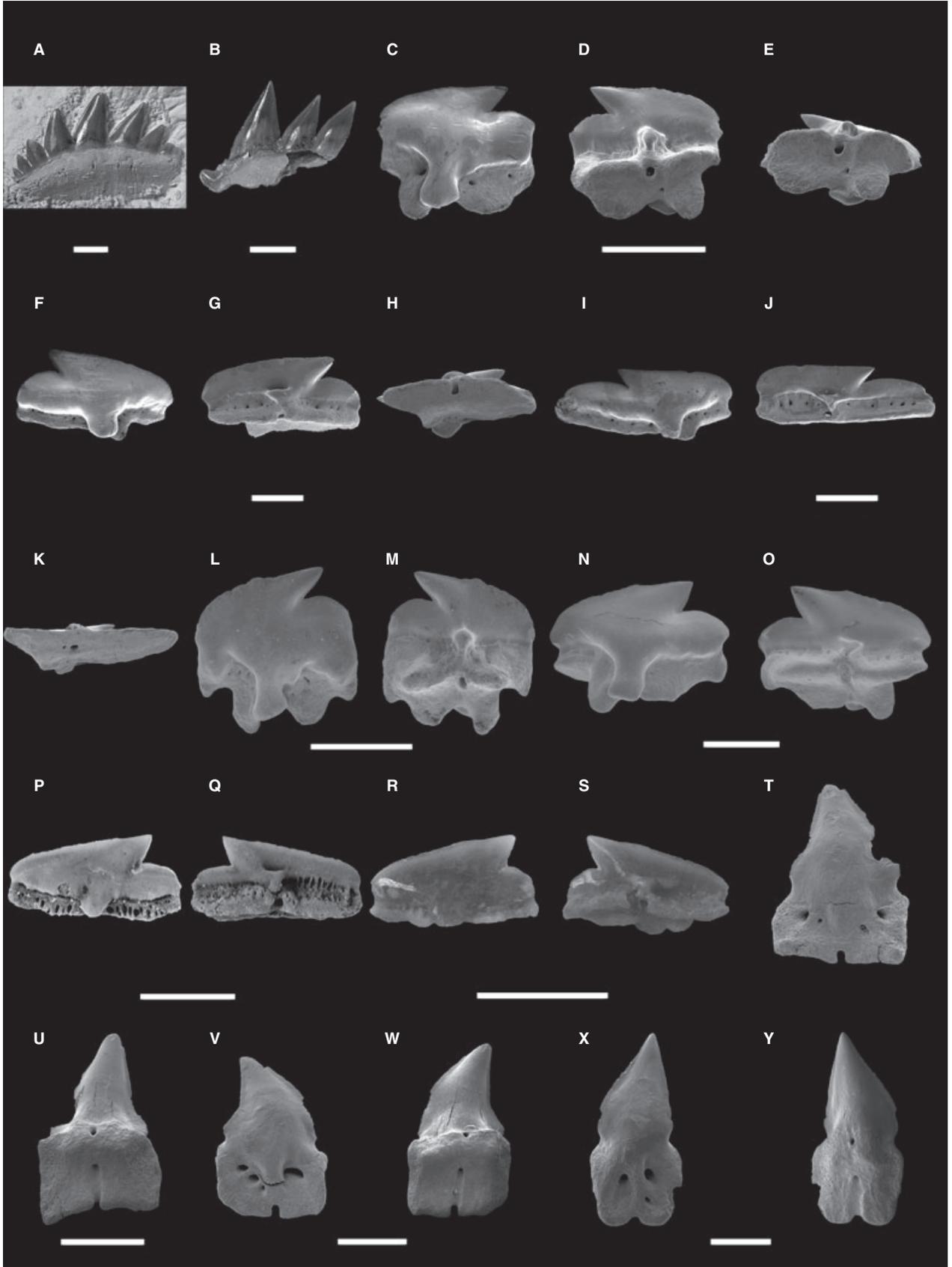
Type species. *Squalus acanthias* Linnaeus, 1758, Recent.

Squalus gabrielsoni Siverson, 1993b Figure 3C–O

Material. Chalk: 36 teeth from Stevns Kridtbrud (MGUH 29900, MGUH 29901, MGUH 29902, GMV2012-27 (batch)) and Rodvig; Fiskeler: 119 specimens (MGUH 29903, MGUH 29904, GMV2012-28 (batch)).

Description. The dentition of *Squalus* displays weak monognathic heterodonty with only the parasymphyseal teeth and the tooth closest to the commissure distinct from the remaining teeth. There is some ontogenetic and gynandric heterodonty. The teeth are labio-lingually compressed, with a single massive triangular cusp. The cusp is strongly slanted towards the commissure, but

FIG. 3. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–B, *Notidanodon pectinatus* (Agassiz, 1843); A, OESM-10046-1, Højerup Member, lateral tooth; B, MGUH 29899, Højerup Member, lateral tooth. C–O, *Squalus gabrielsoni* Siverson, 1993b; C–E, MGUH 29900, Højerup Member, anterior tooth in C, labial, D, lingual and E, basal views; F–H, MGUH 29901, Højerup Member, lateral tooth in F, labial, G, lingual and H, basal views; I–K, MGUH 29902, Højerup Member, tooth from a commissural position in I, labial, J, lingual and K, basal views; L–M, MGUH 29903, Fiskeler Member, symphyseal tooth in L, labial and M, lingual views; N–O, MGUH 29904, Fiskeler Member, lateral tooth in N, labial, O, lingual views. P–S, *Megasqualus* sp.; P–Q, MGUH 29905, Højerup Member, lateral tooth in P, labial and Q, lingual views; R–S, MGUH 29906, Højerup Member, lateral tooth in R, labial and S, lingual views. T–Y, *Centroscyminus praecursor* Müller and Schöllmann, 1989; T–U, MGUH 29907, Højerup Member, anterior upper jaw tooth in T, labial and U, lingual views; V–W, MGUH 29908, Højerup Member, upper jaw lateral tooth in V, labial and W, lingual views; X–Y, MGUH 29909, Højerup Member, anterior upper jaw tooth in X, labial and Y, lingual views. Scale bars represent 5 mm (A–B, P–S); 1 mm (C–O); and 0.5 mm (T–Y).



may be apically recurved in adult males, whereas the cusp is slanted towards the commissure in females and younger males (Ledoux 1970). The mesial cutting edge is long and convex and may carry some serration. The distal heel is short and convex and joins the principal cusp in a notch. The distal heel takes up around a quarter of the total length of most teeth, with the exception of the tooth closest to the commissure in which the heel may take up half the length of the tooth. The labial face of the tooth is convex and smooth with a median elongated apron. The apron is well developed with parallel face, a rounded basal edge, which extends to or beyond the base of the root. The apron is less regular in parasymphyseal teeth and in teeth close to the commissure. The lingual face of the tooth is slightly convex and smooth with a median uvula. This is, in general, large and mesially twisted, but smaller and less twisted in parasymphyseal teeth. The root carries both labially and lingually several foramina below the crown–root junction. The basal edge is almost straight, and the mesial expansion of the basal edge is well developed. The axial foramina are usually fused into an infundibulum.

Remarks. The distinction between some of the extinct species of *Squalus* is difficult, as one of the characters used for discriminating between species is the shape of the apron. This can vary in size and shape during ontogeny, probably as a result of the imbricating nature of the teeth. Contrary to the claims of Müller and Schöllmann (1989), *Squalus* does not necessarily have an unserrated mesial cutting edge (Herman *et al.* 1989). *Squalus gabrielsoni* differs from the Maastrichtian *S. ballingsloevensis* (Siverson 1993b) in its smaller size and more developed apron and from the Maastrichtian *S. balsvikensis* Siverson (1993b) in having a larger and a less united uvula and a more massive principal cusp. The teeth of early–middle Eocene species *S. smithi* (Herman 1982b) appear to be smaller, but the poor quality of the illustration makes any further comparison impossible. As noted by Müller and Schöllmann (1989), much of the material from the Cretaceous described as *Centrosqualus*, *Centrophoroides* and *Squalus* is in need of reinterpretation.

Genus MEGASQUALUS Herman, 1982a

Type species. *Squalus orpiensis* Winkler, 1874 from the Selandian, Middle Paleocene, of Belgium.

Megasqualus sp. Figure 3P–S

Material. Chalk: two teeth from Stevns Kridtbrud (MGUH 29905, MGUH 29906) and one from Møns Klint (DK564).

Description. Very large squaloid teeth up to 13 mm wide, with a long slightly irregular mesial cutting edge, but no sign of serra-

tion. The slightly erected short cusp is separated from the low and sloping distal heel by a notch. The centrally situated apron is short, barely reaching the basal edge of the root and slightly triangular. Both the mesial and distal basal edges of the crown are sinuous in labial view. The uvula is large and mesially twisted. The lingual basal edge of the crown displays microlobulation or buttressing. The root is not perfectly preserved, but appears to be low with only a slightly concave basal face and a centrally situated infundibulum. The apron is comparatively wider in juvenile specimens than in adults.

Remarks. The teeth differ from *Megasqualus orpiensis* (Winkler, 1874) in possessing a shorter, more triangular apron, lacking serration on the cutting edges, but have the characteristic buttressing on the lingual crown base. Although sharing some similarities with *Protosqualus* and *Centrophoroides worlandensis* Case (1987), they differ from the former by having a longer and lower distal heel and a much more developed apron and from the later by a much larger size. These teeth are very large, even larger than those belonging to the Albian *Protosqualus glickmani* (Adnet *et al.* 2008) and the Oligocene *Squalus alsaticus* (Andreae 1892), reaching the same size as Selandian specimens of *Megasqualus orpiensis* (Herman 1982a). They might be the largest squaloid teeth from the Cretaceous seen to date. Among the loose cusps found in the Fiskeler, there are several ‘*Squalus*-like’ fragments, which are of the same size or even larger. As squaloid teeth within both the chalk and the Fiskeler appear to be more prone to bioerosion than other teeth (J. S. Adolfssen pers. obs.), squaloids may have been more numerous than is apparent.

Family SOMNIOSIDAE Jordan 1888

Genus CENTROSCYMNUS Bocage and De Brito Capello, 1864

Type species. *Centroscymnus coelolepis* Bocage and De Brito Capello, 1864, Recent.

Centroscymnus praecursor Müller and Schöllmann, 1989 Figures 3T–Y, 4A–J

Material. Chalk: 31 lower and 5 upper teeth (MGUH 29907–MGUH 29911, GMV2012–29 (batch)); Fiskeler: 27 specimens (MGUH 29912, MGUH 29913, GMV2012–30 (batch)).

Description. The dentition displays monognathic and strong dig-nathic heterodonty. The teeth of the upper jaw are elongated with a pointed triangular cusp, erect in anterior teeth, but distally inclined in lateral and posterior teeth. The labial face is convex with a smooth surface and flat triangular median apron. The lingual face is strongly convex and smooth. The labial face

of the root is square with a straight basal edge. On either side of the apron are one or more foramina. The basal face of the root is large, covering around a third of the tooth's height. The basal face is concave, divided medially by an open median lingual duct, which is connected to the median lingual foramen. The lingual face of the root forms a narrow convex bulge with a median foramen.

Teeth of the lower jaw are quadrangular in shape with a single, almost horizontal slanted cusp. The cusp is short, massive and triangular. The mesial cutting edge is slightly convex and gently serrated, whereas the short distal shoulder is convex and smooth. The distal shoulder joins the cusp in a notch. The labial face of the crown, which covers almost two-thirds of the height of the tooth, is smooth and flat. It has a large, flat median apron with one or two foramina on each side. The basal edge is low and flat, almost straight with a median notch. The basal face of the crown is large, covering two-thirds of the height of the tooth and median divided by the open median lingual duct. The lingual face of the crown is smooth and slightly convex. The lingual face of the root has a narrow bulge with a mesio-lingual and a median foramen, but no disto-lingual foramen. Disto-lingual and mesial-labial interlocking hollows are apico-basally elongated and well developed. Anterior teeth are more elongated than lateral, and the last tooth closest to the commissure is lower and wider, with an expanded distal shoulder showing a disto-lingual hollow.

Remarks. *Centroscymnus praecursor* was first described by Müller and Schöllmann (1989) from the Campanian of Münster in the central Western Germany. Besides the German locality and Stevns Klint, this species is known from unpublished Maastrichtian material from the ENZI quarry in Maastricht, the Netherlands (J. S. Adolfssen pers. obs.). The species is one of the two known species from the Cretaceous, the other being *C. schmidii* (Herman 1982b). Müller (1989) and Müller and Schöllmann (1989) state that anterior teeth have three labial foramina, whereas lateral teeth only have two; this appears to be a variable character in our specimens, but this may be due to the limited amount of material. Our specimens appear to be slightly larger than the German material. Müller (1989) wrote that a distinct serration on the cutting edges was not detectable. He does not say whether the material was studied under an SEM, without which the serration may not have been detected. Further differences are the extension of the interlocking hollows and the basal edge of the root, which is round in *C. schmidii*, but straight in *C. praecursor*. The upper jaw in *C. schmidii* is tricuspid and easily separated from the monocuspid teeth of *C. praecursor*.

Family ETMOPTERIDAE Fowler, 1934

Genus PROETMOPTERUS Siverson, 1993b

Type species. *Etmopterus hemmooriensis* Herman, 1982b from the Maastrichtian of northern Germany.

Proetmopterus hemmooriensis Siverson, 1993b

Figure 4K–M

Material. Chalk: two well-preserved upper teeth (MGUH 29914 and MGUH 29915).

Description. Very small teeth measuring 1.2 mm high and 0.8 mm wide. Upper teeth with one large triangular principal cusp bent slightly towards the commissure, flanked by two pairs of acute elongated cusplets diminishing in size laterally. The base of the basal face is slightly concave with a median apron. Both the labial and the lingual faces are smooth and convex, more so in the latter. On the labial surface, several foramina open up below the crown–root junction. The labial face of the root is flat, and the basal edge of the root is concave or slightly irregular with a median furrow. The basal face of the root is concave and divided by a median groove. The lingual face of the root is a low, transverse bulge with a medio-internal foramen.

Remarks. No lower teeth were recovered, even though the material was thoroughly examined. This might be due to rareness of the species and their fragility or they might have been mistaken for the lower teeth of *C. praecursor*.

Order ECHINORHINIFORMES Buen, 1926

Family ECHINORHINIDAE Gill, 1862

Genus ECHINORHINUS Blainville, 1816

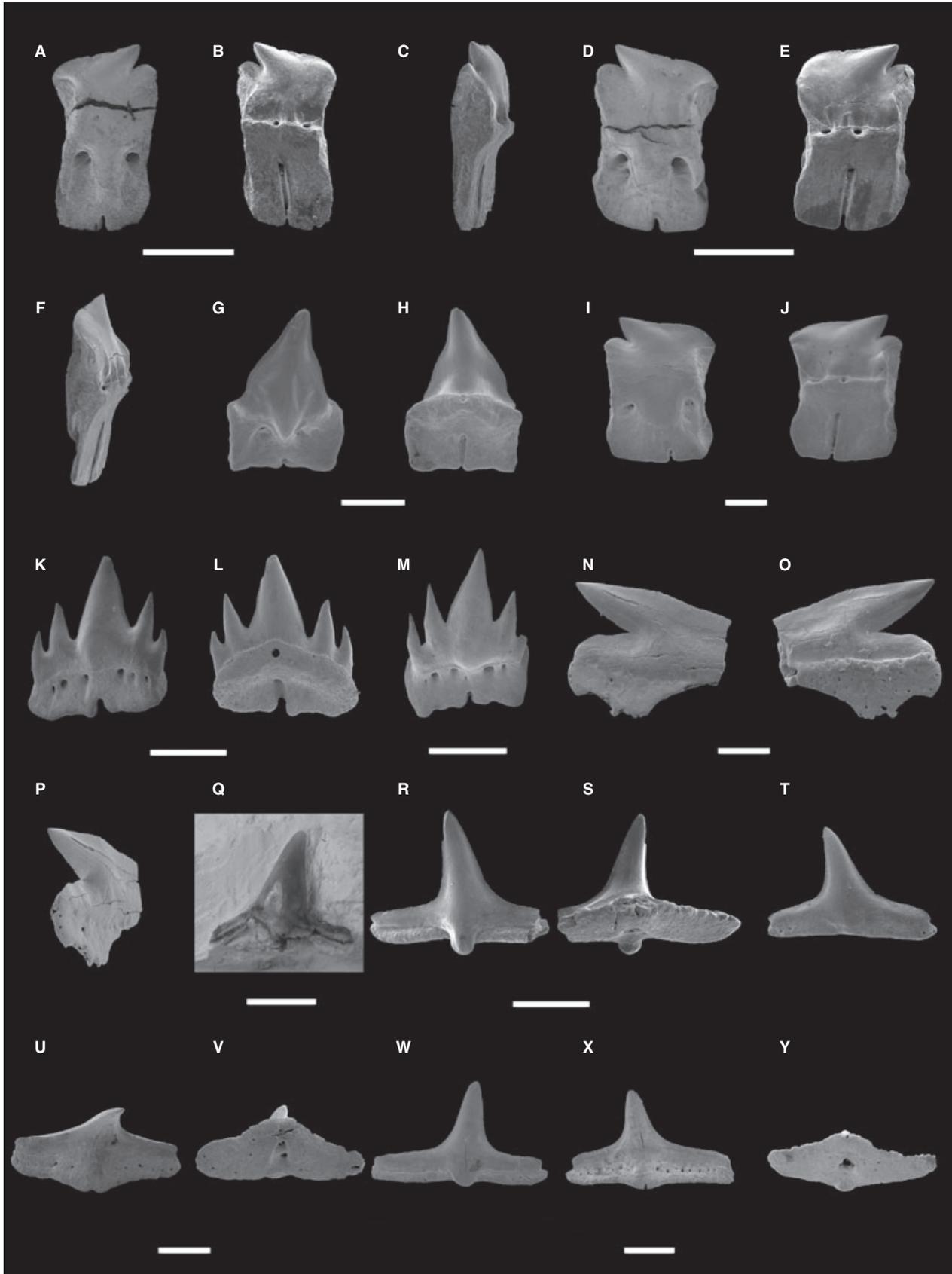
Type species. *Squalus brucus* Bonnaterre, 1788, Recent.

Echinorhinus sp.

Figure 4N–P

Material. Fiskeler: A single broken specimen (MGUH 29916), collected at Rødvig.

Description. The dentition in *Echinorhinus* displays diagenathic, gradient monognathic and strong ontogenetic heterodonty, but there is no evidence for gynandric heterodonty (Pfeil 1983). The tooth is strongly labio-lingually compressed and has a large principal cusp slanted towards the commissure, forming an 18 degrees angle with the base of the crown. The principal cusp, which is distally offset, has a median kink turning the triangular apex slightly downward. The apex of the cusp is closer to the commissure than the short, low, horizontal shoulder, which joins with the cusp in a notch. Both the labial and the lingual faces of the crown are slightly convex and smooth. The labial crown–root junction is indented. The root is largely missing, but the labial face appears to be flat with a few foramina. The basal edge is missing, but the distal edge of the root is present and slightly rounded. The basal face of the root is flat to gently labio-lingually concave with numerous scattered foramina. The lingual face of the root is limited to a narrow band.



Remarks. Although *Echinorhinus* is thought to have originated in the Jurassic (Underwood 2006), the oldest known species is from the early Cretaceous of France (Adnet *et al.* 2011). The mid-Cretaceous species, *E. australis* (Chapman 1909), is abundant in Albian limestones and mudstones in Queensland, Australia (D. J. Ward pers. obs.). The Maastrichtian species, *E. eyerensis* Pledge 1992, known from a single specimen, appears to be based on a corroded upper lateral tooth of *Cretalamna*. A few species are known from the Palaeogene: *E. priscus*, *E. caspius*, *E. weltoni* and *E. schoenfeldi*. *Echinorhinus* appears to have changed little since its first appearance, suggesting that it was specialized for deep water from an early stage.

The closest species to this is *E. priscus* Arambourg, 1952, poorly known from the Early Eocene of Morocco. It is, however, quite common in the Danish Early Eocene plastic clays (D. J. Ward pers. obs.). Large specimens of *E. priscus* often bear a single small accessory cusp on mesial cutting edge, suggesting that this is an adult character. Thus, its absence in our specimen suggests that this is from a juvenile individual. All the species prior to the Oligocene appear to have had only one accessory cusp in contrast to the two Recent species *E. brucus* and *E. cookei*, which have up to three or four cusps (Pfeil 1983). In the two Recent species, single cusps are only observed in the dentition of juveniles or in posterior teeth of adults.

Order SQUATINIFORMES Buen, 1926
Family SQUATINIDAE Bonaparte, 1838

Genus SQUATINA Dumeril, 1806

Type species. *Squalus squatina* Linnaeus, 1758, Recent.

Squatina sp.
Figure 4Q–Y

Material. Chalk: four partly preserved teeth from Stevns Kridtbrud (MGUH 29917, MGUH 29918, GMV2012–31 (batch)); Fiskeler: 13 specimens (MGUH 29919, MGUH 29920, GMV2012–32 (batch)).

Description. The teeth are monocuspid with an elongated acute cusp. In anterior teeth, the principal cusp is almost vertical, whereas in lateral and posterior teeth, it may incline slightly towards the commissure. The elongated principal cusp forms an almost perpendicular angle to the basal face of the root. The shoulders are low and wide and of almost equal length, with the exception of the third upper tooth, where the mesial shoulder is comparatively shorter than the distal. The shoulders carry a continuous cutting edge. Both the labial and the lingual faces are smooth and strongly convex; there are no signs of ornamentation on any of the specimens. A large cambered median labial apron is present with a rounded termination, which may project below the basal face of the root. A median prominent lingual uvula is present. Both the labial and the lingual faces of the root are low and wide with numerous foramina below the crown–root junction, more numerous on the lingual face than the labial. The basal face is wide and flat with central foramina.

Remarks. *Squatina* species are notoriously difficult to identify, usually due to inadequate descriptions and diagnoses, especially when the material is limited, as noted by several authors: Dalinkevičius (1935), Cappetta (1987), Underwood and Mitchell (1999) and Rees (2005). This is mainly due to the simple very conservative morphology of the teeth. Using articulated material, Guinot *et al.* (2012b) demonstrated that *S. decipiens* and *S. cranei*, the two most commonly recorded Cretaceous species of *Squatina*, were synonymous, *S. cranei* being the senior synonym. The dentition in Recent species of *Squatina* displays weak dignathic heterodonty and some gradient heterodonty. *S. cranei*, however, displays a far greater degree of heterodonty than is seen in the teeth of Recent species of *Squatina*. Anterior teeth of *S. cranei* have a broad, triangular crown and a narrow heart-shaped root with few lingual foramina. Anterolateral teeth have a taller, narrower crown. Lateral teeth are wider with a distally inclined crown. This degree of heterodonty prompted Guinot *et al.* (2012b) to refer *S. cranei* to a new subgenus: *Cretascyllium* Müller and Diedrich, 1991. The limited Danish material does not display this heterodonty, and although we cannot exclude the possibility that the teeth do belong to *S. cranei*, we think it more prudent that they currently remain in open nomenclature.

FIG. 4. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–J, *Centroscyrmnus praecursor* Müller and Schöllmann, 1989; A–C, MGUH 29910, Højerup Member, lower jaw tooth in A, labial, B, lingual and C, distal views; D–F, MGUH 29911, Højerup Member, lower jaw tooth, in D, labial, E, lingual and F, mesial views; G–H, MGUH 29912, Fiskeler Member, anterior upper jaw tooth, in G, labial and H, lingual views; I–J, MGUH 29913, Fiskeler Member, lower jaw tooth in I, labial and J, lingual views. K–M, *Proetmopterus hemmooriensis* Siverson, 1993b; K–L, MGUH 29914, Højerup Member, upper jaw tooth in K, labial and L, lingual views; M, MGUH 29915, Højerup Member, upper jaw tooth in labial view. N–P, *Echinorhinus* sp. MGUH 29916, Fiskeler Member, tooth in N, labial, O, lingual and P, distal views. Q–Y, *Squatina* sp. Woodward, 1888a; Q, MGUH 29917, Højerup Member, anterior lower jaw tooth, in labial view; R–S, MGUH 29918, Højerup Member, lateral tooth in R, labial and S, lingual views; T–V, MGUH 29919, Fiskeler Member, lateral tooth in T labial, U, lingual and V, basal view; W–Y, MGUH 29920, Fiskeler Member, lateral tooth in W, labial, X, lingual and Y, basal views. Scale bars represent 1 mm (A–F, I–J, R–Y); 0.5 mm (G–H, K–P); and 5 mm (Q).

Leriche (1927) described a large anterior tooth of the angle shark *S. hassei*, which differs from *S. cranei* by size alone. One tooth from the chalk, Figure 4Q, is strongly reminiscent of this specimen.

Family †SQUATINIDAE Bonaparte, 1838

Genus PARASQUATINA Herman, 1982b

Type species. Parasquatina cappettai Herman, 1982b from the Maastrichtian of Northern Germany.

Remarks. See Guinot *et al.* (2012a, b) for discussion.

Parasquatina cappettai Herman, 1982b
Figure 5A–I

Material. Chalk: two teeth (MGUH 29921 and MGUH 29922); Fiskeler: a single tooth (MGUH 29923).

Description. Very small teeth with a single triangular massive cusp, which is slightly slanted towards the commissure. The mesial cutting edge is gently sigmoidal, whereas the distal cutting edge is mesio-distally concave. As a result, the mesial shoulder is a bit higher than the distal one. The cutting edge appears to be continuous. The labial face is smooth and convex, which is also the case of the lingual face. There is no sign of an apron. A median uvula is present on the lingual face, which appears to have been covered with enameloid. The root is bilobed with a triangular flat basal face and a median lingual protuberance. The lingual face of the root is high with several scattered foramina.

Remarks. *Parasquatina* is a rather rare genus in the literature, only mentioned in the description by Herman (1982b), briefly commented upon by Underwood and Ward (2008), described from North America by Bourdon *et al.* (2011) and from France and Britain by Guinot *et al.* (2012b). Herman (1982b) did not assign it to any order, but due to its morphology, it is assigned to Squatiniformes following Guinot *et al.* (2012b). The teeth are very small, around 1 mm wide, and due to its small size, it

may have been overlooked and be more common than apparent from the very limited literature.

Superorder GALEOMORPHII Compagno, 1973

Order ORECTOLOBIFORMES Applegate, 1972

Family HEMISCYLLIIDAE Gill, 1862

Genus HEMISCYLLIUM Müller and Henle, 1837 (in Smith, 1837) and Müller and Henle, 1838

Type species. Squalus ocellatus Bonnaterre, 1788, Recent, northern Australasia.

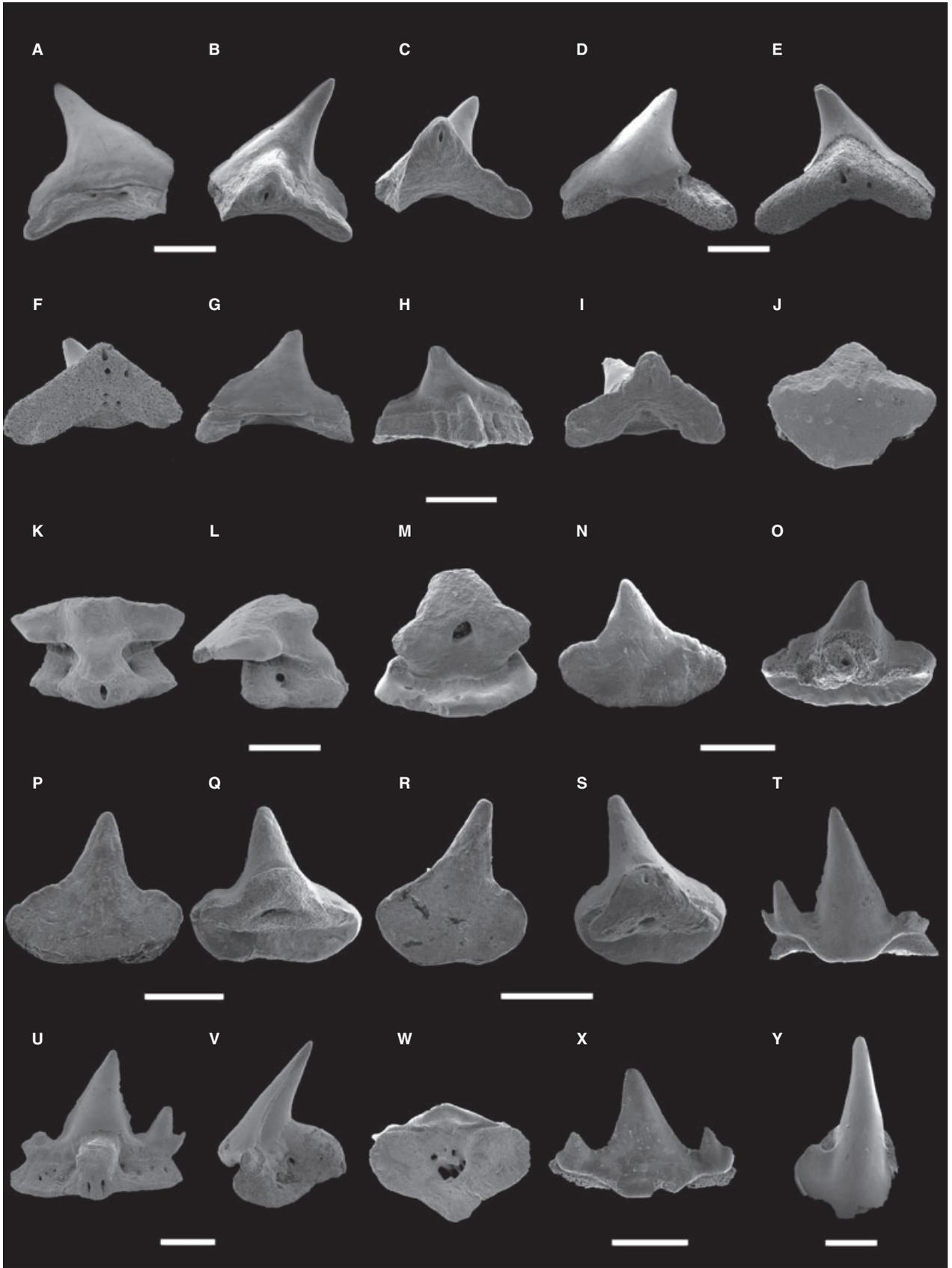
Hemiscyllium hermani Müller, 1989
Figure 5J–S

Material. Chalk: 22 poorly preserved teeth from the Stevns Kridtbrud lacking roots and a single tooth from Rødvig (MGUH 29924, MGUH 29925, GMV2012–33 (batch)); Fiskeler: 11 specimens (MGUH 29926, MGUH 29927, GMV2012–34 (batch)).

Description. Very small teeth, often less than a millimetre wide, that display gradient monognathic heterodonty. The teeth are monocuspid with a short erect triangular cusp in anterior teeth and an elongated cusp, slanted towards the commissure in laterals. In posteriors, the crown is more asymmetric than in anteriors, and the size of the cusp progressively diminishes in more distal files. The shoulders are wide in all teeth, although slightly sloping in laterals and posteriors. The crown of the tooth is large, slightly convex, smooth and strongly overhanging the root with a broad bifid apron. The lingual face of the tooth is convex and smooth. A median lingual uvula is present. The root is bilobed with a large flat triangular basal face and a medium-sized central foramen in a labially directed depression. The lingual face of the root is high with a central protuberance, which has a median foramen. None of the specimens show signs of lateral cusplets or ornamentation.

Remarks. As mentioned by Müller (1989), there are many similarities between *H. hermani* and the Recent bamboo

FIG. 5. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–I, *Parasquatina cappettai* Herman, 1982b; A–C, MGUH 29921, Højerup Member, tooth in A, labial, B, lingual and C, basal views; D–F, MGUH 29922, Højerup Member, tooth in D, labial, E, lingual and F, basal views; G–I, MGUH 29923, Fiskeler Member, tooth in G, labial, H, lingual and I, basal views. J–S, *Hemiscyllium hermani* Müller, 1989; J–M, MGUH 29924, Højerup Member, anterior tooth in J, labial, K, lingual, L, lateral and M basal views; N–O, MGUH 29925, Højerup Member, lateral tooth in N, labial and O, basal views; P–Q, MGUH 29926, Fiskeler Member, anterior tooth in P, labial and Q, lingual views; R–S, MGUH 29927, Fiskeler Member, anterior tooth in R, labial and S, lingual views. T–Y, *Palaeobrachaelurus* sp.; T–W, MGUH 29928, Højerup Member, lateral tooth in T, labial, U, lingual, V, lateral and W, basal views; X, MGUH 29929, Højerup Member, lateral tooth in labial view; Y, MGUH 29930, Højerup Member, anterior tooth in labial view. Scale bars represent 0.5 mm (A–I, T–Y) and 0.4 mm (J–S).



shark *H. ocellatum*, with the only minor difference being the size of the central foramen, which is much enlarged in *H. ocellatum*. The specimens figured by Müller (1989) tend to have shorter cusps in anterior teeth than the specimens figured here. *H. hermani* has been described from the Maastrichtian of northern Germany and the Campanian of central western Germany (Müller 1989). It may have had a larger distribution than revealed by the present literature as, due to its very small size, it can easily be overlooked. The first known Hemiscylliidae or a very close relative of that family appears in the Albian (Underwood and Mitchell 1999), in which lateral cusps were still present, but by the Campanian, species with an almost modern monocuspid dental morphology were already present. The referral of *H. hermani* to *Pseudospinax* (= *Protospinax* Woodward, 1918) by Underwood and Mitchell (1999, p. 31) lacks convincing evidence.

Family *Incertae familiae*

Genus PALAEOBRACHELURUS Thies, 1983

Type species. *Palaeobrachaelurus bedfordensis* Thies, 1983 from the Jurassic of England.

Palaeobrachaelurus sp.

Figure 5T–Y

Material. Chalk: four teeth from Stevns Kridtbrud (MGUH 29928, MGUH 29929, MGUH 29930, GM2012–35).

Description. Teeth with a high degree of monognathic heterodonty. Anterior teeth have a semi-circular crown with an elongated biconvex principal cusp and a pair of cusplets. The labial face is smooth and convex and strongly overhanging the root. The lingual face is strongly convex with some sculpturing below the broad apron. The root is only partially preserved, but appears bilobate with a lingual protuberance with a foramen. Lateral teeth are broad with a large triangular principal cusp and one or two pairs of lateral cusplets. A very large and semi-circular apron is present overhanging the root, projecting below the basal face of the root. The inner lateral cusplets are erect and triangular, whereas, if present, the outer pairs of cusplets are minute. The labial face is smooth and convex. A continuous cutting edge is present. The lingual face is smooth and very convex. The basal face of the root is flat and heart-shaped. The root is hemiacorhize.

Remarks. The anterior tooth (Fig. 5Y), closely resembles the tooth figured by Underwood and Ward (2004, fig. 4d) from the Bathonian of England.

These teeth differ from *Paraginglymostoma* Herman 1982b as its apron is broader, and there are no long

parallel ridges present on its labial face. It is possible that *Palaeobrachaelurus* Thies, 1983 may be a junior synonym of *Paraginglymostoma* Herman, 1982b, but the current lack of material of the latter, combined with the size difference and presence of ornamentation in the latter make a decision unreliable. *Palaeobrachaelurus* was erected by Thies in 1983 on material from the Toarcian to the Callovian of Germany and Britain. Subsequently, material from the Toarcian of Luxembourg (Delsate and Weis 2010) and Belgium (Delsate and Lepage 1990), Bajocian of France (Delsate 1993), Callovian of Poland (Kriwet 2003; Rees 2010) and the Kimmeridgian and Tithonian of France (Landemaine 1991; Candoni 1993) was described. As mentioned by Landemaine (1991), it can be difficult to distinguish between *Palaeobrachaelurus* and *Cretorectolobus*, and they might be synonymous. Underwood *et al.* (1999) suggested that *Brachaelurus roklumensis* (Thies, 1981) from the Barremian of Germany might belong to *Palaeobrachaelurus*, and together with *Palaeobrachaelurus mitchelli* from the Barremian of England (Underwood and Ward 2004), they were the youngest representatives of this genus until now. With the presence of *Palaeobrachaelurus* in the late Cretaceous of Denmark, its stratigraphic range has been expanded quite significantly.

Family PARASCYLLIIDAE Gill, 1862

Genus PARARHINCODON Herman, 1976 (in Cappetta 1976)

Type species. *Pararhincodon crochardi* Herman, 1977 from the Campanian of Belgium.

Pararhincodon groessensi Herman, 1982b

Figure 6A–J

Material. Chalk: three specimens, two from Stevns Kridtbrud and one from Rødvig (MGUH 29931, MGUH 29932, GM2012–36 (batch)); Fiskeler: seven specimens from Rødvig and Højerup (MGUH 29933, MGUH 29934, MGUH 29935, GM2012–37 (batch)).

Description. The dentition of *Pararhincodon* displays gradient monognathic heterodonty. The anterior teeth are very elongated and mesially distally compressed, slightly asymmetrical with an offset towards the commissure. The principal cusp is elongated, triangular and acute. Anterior teeth have also two small shoulders in which the distal may turn into a small cusp. The labial one is flat to convex and free of ornamentation. The crown is rather high with a deep median indentation. The lingual face of the crown is smooth and very convex. Lateral and posterior teeth tend to be much more asymmetrical, and the principal cusp is slanted towards the commissure. There is often a distal cusp, and the base of the crown may be strongly sculptured

especially in posterior teeth. The basal face of the root is flat and mostly hemiaulacorhize, strongly asymmetrical with an extended mesial lobe and short distal lobe. The lingual face of the root is high with a median protuberance with a foramen. There is a depression on both sides of the lingual protuberance bearing foramina. As many of the roots are either missing or damaged, it is difficult to see whether or not the tooth is at the hemiaulacorhized or holaulacorhized stage.

Remarks. Herman (1982b) described this species from the north German Maastrichtian locality of Hemmoor based on four very small teeth. *P. groessensi* has also been described from the Campanian of Texas (Welton and Farish 1993), although the specimens figured are significantly different in morphology and may very well be a new species, as may the specimens figured by Müller (1989) from the Campanian of Germany. As Herman (1982b) only figured two lateral teeth, the precise morphology of the anterior teeth is unknown. The teeth of *P. groessensi* differ from those of *P. lehmani* (Cappetta 1980) and *P. crochardi* (Herman 1977) as *P. groessensi* possesses sculptured distal cusplets.

Family GINGLYMOSTOMATIDAE Gill, 1862

Genus NEBRIUS Rüppell, 1837

Type species. *Nebrius concolor* Rüppell, 1837, Recent from the Indo-Pacific, Australasia to Japan.

Nebrius sp. Figure 6K–N

Material. Fiskeler: one incomplete specimen lacking its root and with a damaged principal cusp from Stevns Kridtbrud (MGUH 29936).

Description. The specimen is multicuspid with a triangular principal cusp slightly larger than the cusplets curved towards the commissure and flanked by three mesial and two small distal cusplets. The cusplets are short, acute and curving towards the principal cusp. The crown of the tooth is slightly asymmetrical, wide and low with a smooth, convex labial face. The basal edge of the crown is markedly overhanging the root, and the apron is wide and bifid. The lingual face is smooth and convex. The lingual face of the basal part of the crown is labio-lingually concave.

Remarks. The asymmetrical shape of the crown and the low principal cusp suggest *Nebrius* rather than *Ginglymostoma*, although the literature mentions some confusion between the two genera (Cappetta 1987). The smooth labial face suggests that this particular tooth does not belong to *Plicatoscyllium* (Case and Cappetta 1997). The

low crown and the limited number of cusplets suggest a lateral–posterior tooth. The tooth has some similarities with the late Maastrichtian specimen figured by Case and Cappetta (1997) from the Kemp Formation, in Texas, and the specimens figured by Purdy (1998) from the Paleocene of South Carolina. Both specimens appear to have a less developed apron than the Eocene *N. thielensi* and *N. obliquus*.

The above-mentioned specimen from Texas appears to be the oldest known member of the genus. The modern *Nebrius* is monospecific and limited to the Indo-Pacific area. However, fossil *Nebrius* have been found in North America, Europe and North Africa and appear to have suffered a huge decrease in habitat in post-Eocene times (Ferrusquia-Villafranca *et al.* 1999).

Order HETERODONTIFORMES Berg, 1937

Family HETERODONTIDAE Gray, 1851

Genus HETERODONTUS Blainville, 1816

Type species. *Squalus philippi* Bloch and Schneider, 1801, Recent.

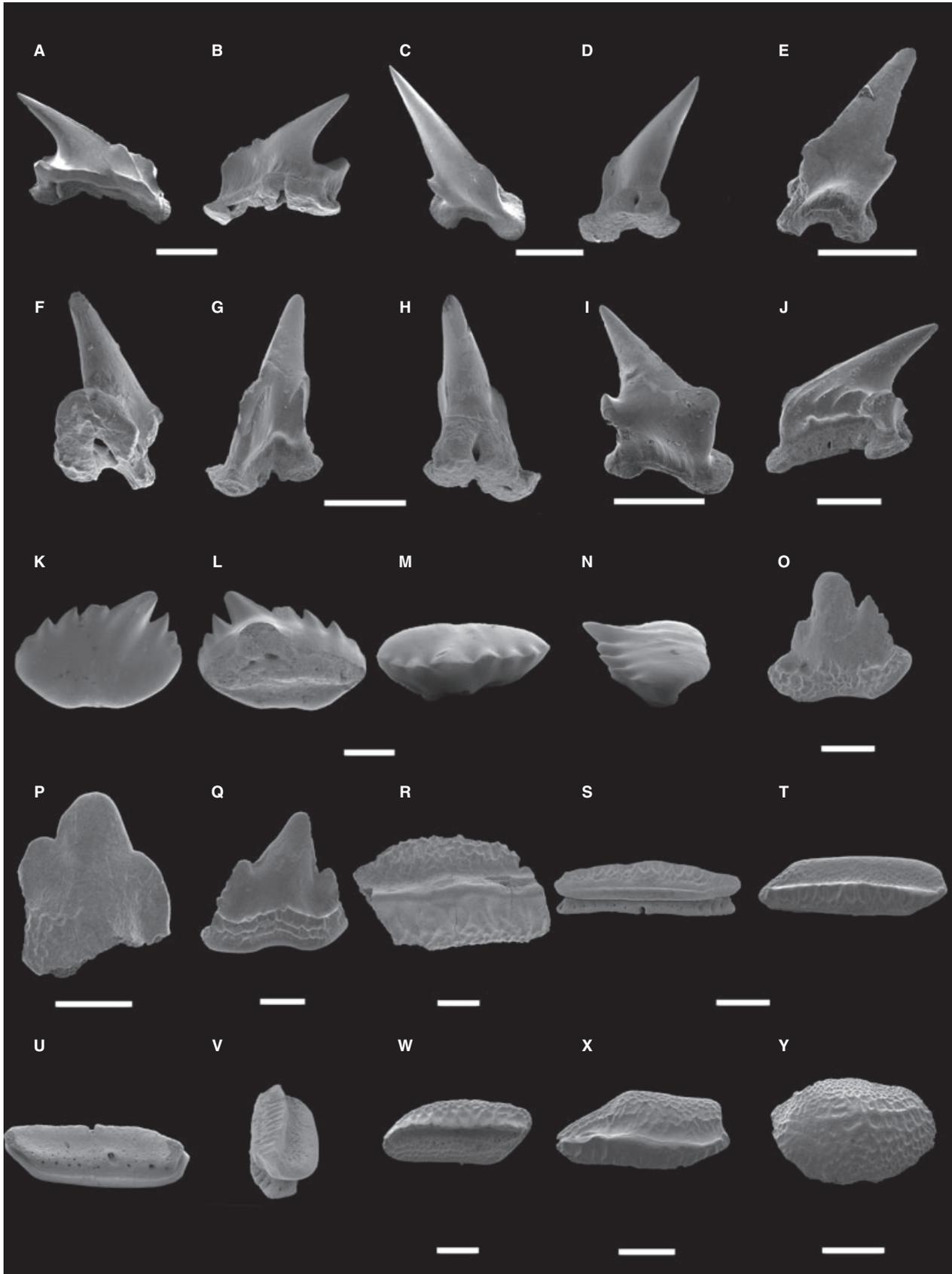
Heterodontus rugosus (Agassiz, 1839)

Figure 6O–Y

Material. Chalk: six anterior teeth and three laterals, all of which are fragmentary (MGUH 29937, MGUH 29938, GMV2012–38 (batch)); Fiskeler: one complete tooth and 30 incomplete teeth (MGUH 29939, MGUH 29940, MGUH 29941 and GMV2012–39 (batch)).

Description. A dentition with a disjunct monognathic heterodonty. Anterior has a large round principal cusp flanked by a pair of indistinctive cusplets. Labial face is convex, and the bifid basal part is carrying a strongly puckered ornamentation. Lingual face is convex and smooth. Lateral teeth have a strong, slightly undulating transverse crest. Both mesial and distal parts of the crown have a strongly puckered ornamentation. The roots are generally very badly preserved. Juvenile anterior teeth have up to five cusps, which decrease in number with size and age to only three.

Remarks. The specimens are in general badly preserved, but the ornamentation and size fit the description by Agassiz (1843) and Herman (1977). The presence of cusped anterior teeth and the lack of or differences in ornamentation differentiate these teeth from *H. canaliculatus* (Egerton in Dixon, 1850) and *H. upnikensis* (Dalinkevičius, 1935). The difference between *H. rugosus* and *H. lonzeensis* (Herman, 1977) is minimal, and they could be conspecific. The Eocene *H. vincenti* (Leriche, 1905) is based on an anterior tooth which makes comparison difficult. A



few specimens lack the transverse keel on the lateral and posterior teeth and probably belong to another species.

Order LAMNIFORMES Berg, 1937

Family CARCHARIIDAE Jordan and Gilbert, 1883

Genus CARCHARIAS Rafinesque, 1810

Type species. *Carcharias taurus* Rafinesque, 1810, Recent.

Remarks. The use of folds or striae as a taxonomic character in *Carcharias* should be used with care, as many modern specimens of *C. taurus* can have folds on some of the teeth, but lack them in others (J. S. Adolfssen pers. obs.). Similarly, Taniuchi (1970) has demonstrated the difficulties in using lateral cusplets as an identification character for *Carcharias*. As correctly stated by Underwood and Cumbaa (2010), the Odontaspidae must be presumed to be polyphyletic, and a major revision of the relationship between the numerous genera and species of this family is needed.

Carcharias aff. *gracilis* Davis, 1890

Figure 7A–T

Material. Chalk: 10 complete teeth from Stevns Kridtbrud (MGUH 29945, MGUH 29946, MGUH 29947, MGUH 29948, MGUH 29949, GMV2012–40 (batch), GMV2012–41 and GMV2012–42); Fiskeler: five specimens and additional fragments (MGUH 29950, MGUH 29951, MGUH 29952, MGUH 29953, MGUH 29954, GM2012–43 (batch) and GMV2012–44 (batch)).

Description. Dentition displaying gradient monognathic heterodonty and weak dignathic heterodonty. The teeth have a large triangular principal cusp with a flat to slightly convex smooth labial face with the exception of the posterior teeth, which have short strong coarse folds above the crown–root junction. The principal cusp is flanked by a pair of tall erect triangular cusplets. The lingual face is smooth and convex, less so in laterals and posteriors than in anteriors. The cutting edge is continuous in laterals and posteriors, but not in anteriors. Some intermediate teeth lack cusplets, which may be a juvenile character (Applegate 1965). The root is bilobed and elongated with rounded

extremities. Both the labial and the lingual faces of the root are low; the lingual face of the root has a median protuberance with a deep groove. The basal face is flat to concave.

Remarks. The specimens collected at Stevns Klint have smooth crowns or have labial short strong folds. The size and smooth lingual face compares well with *C. gracilis* (Davis 1890), but differ from the later having labial folds and shorter root lobes. The use of folds or striae on the labial face to characterize *Carcharias* and Odontaspidae should be used cautiously. In Recent *C. taurus*, laterals and posteriors can carry coarse folds, which are not found in the anterior and intermediate teeth. This was not mentioned by Applegate (1965), but addressed by Cunningham (2000). The value of this character is therefore questionable. The typical *Carcharias* tooth design and dentition is extremely conservative. Intraspecific variation is slight, but still sufficient to make it very difficult to identify species-level characters. The differences between several species of late Maastrichtian to early Palaeogene of *Carcharias* are often minor and based on the absence/presence of folds and on size, both of which characters may be too variable for diagnostic use.

Family MITSUKURINIDAE Jordan, 1898

Genus ANOMOTODON Arambourg, 1952

Type species. *Anomotodon plicatus* Arambourg, 1952.

Anomotodon plicatus Arambourg, 1952

Figure 8A–B

Material. Chalk: a single almost perfectly preserved tooth from Møns Klint (MGUH 29958).

Description. Tooth measuring 9 mm high and 8 mm wide with a single large elongated principal cusp. The mesial cutting edge is slightly concave and the distal cutting edge slightly convex. The labial face is flat to slightly convex except for the basal border, where there is a gentle medio-basal depression in which a

FIG. 6. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–J, *Pararhincodon groessensi* Herman, 1982b; A–B, MGUH 29931, Højerup Member, lateral tooth in A, labial and B, lingual view; C–D, MGUH 29932, Højerup Member, anterior tooth in C, labial and D, lingual views; E–F, MGUH 29933, Fiskeler Member, anterior tooth in E, labial and F, lingual views; G–H, MGUH 29934, Fiskeler Member, lateral tooth in G, labial and H, lingual views; I–J, MGUH 29935, Fiskeler Member, lateral teeth in labial view. K–N, *Nebrius* sp., MGUH 29936, Fiskeler Member, lateral tooth in K, labial, L, basal, M, occlusal and N, mesial views. O–Y, *Heterodontus rugosus* (Agassiz, 1839); O, MGUH 29937, Højerup Member, anterior tooth in labial view; P, MGUH 29938, Højerup Member, anterior tooth in labial view; Q, MGUH 29939, Fiskeler Member, anterior tooth in labial view; R, MGUH 29940, Fiskeler Member, lateral tooth in occlusal view; S–V, MGUH 29941, Fiskeler Member, lateral tooth in S, labial, T, occlusal, U, basal and V, lateral view; W, MGUH 29942, Fiskeler Member, lateral tooth in occlusal view; X, MGUH 29943, Fiskeler Member, lateral tooth in occlusal view; Y, Fiskeler MGUH 29944 lateral tooth in occlusal view. Scale bars represent 0.5 mm (A–J, O–Q) and 1 mm (K–N, R–Y).

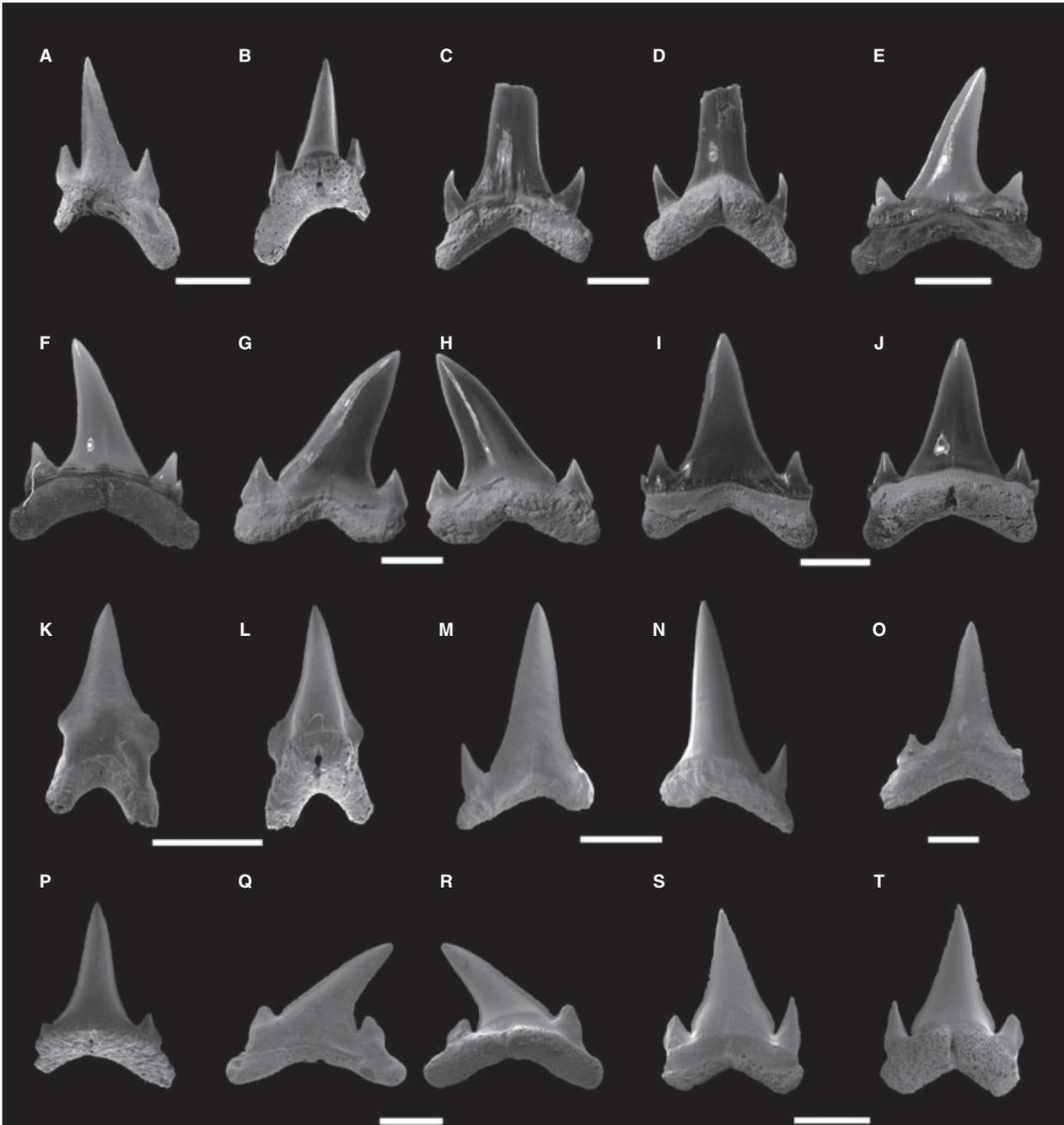


FIG. 7. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–T, *Carcharias* aff. *gracilis* (Davis, 1890); A–B, MGUH 29945, Højerup Member, lower symphyseal tooth in A, labial and B, lingual views; C–D, MGUH 29946, Højerup Member, anterior tooth in C, labial and D, lingual views; E–F, MGUH 29947, Højerup Member, upper lateral tooth in E, labial and F, lingual views; G–H, MGUH 29948, Højerup Member, an upper lateral tooth in G, labial and H, lingual views; I–J, MGUH 29949, Højerup Member, lower lateral tooth in I, labial and J, lingual views; K–L, MGUH 29950, Fiskeler Member, lower symphyseal tooth in K, labial and L, lingual views; M–N, MGUH 29951, Fiskeler Member, anterior tooth in M, labial and N, lingual views; O–P, MGUH 29952, Fiskeler Member, lower lateral tooth in O, labial and P, lingual views; Q–R, MGUH 29953, Fiskeler Member, upper lateral tooth in Q, labial and R, lingual views; S–T, MGUH 29954, Fiskeler Member, lower lateral tooth in S, labial and T, lingual views. Scale bars represent 1 mm (A–B, K–L); 5 mm (C–J); and 3 mm (M–T).

few folds are situated. Two equally well-developed shoulders are present. The lingual face is convex with flexuous folds covering the lower half of the crown. The cutting edge is prominent and continuous. The principal cusp is sigmoid in lateral view. The two root lobes are short and rounded. The mesial lobe is shorter than the distal one. The lingual face has a low protuberance with a deep nutrient groove. The basal face is concave.

Remarks. The size corresponds with teeth of *A. plicatus*. The Danish specimen differs from *A. hermani* Siverson, 1992a due to size and the presence of well-developed heels. *A. senessei* (Leriche, 1936) is based on fragmentary material and therefore comparison is difficult, even more so is *A. laevis* Herman, 1982b, from the Maastrichtian of Germany.

Family OTODONTIDAE Glikman, 1964

Genus CRETALAMNA Glikman, 1958

Type species. *Otodus appendiculatus*, Agassiz, 1838, from the Turonian of Lewes, England.

Remarks. A form genus *par excellence*. Conventionally, *Cretalamna* is loosely used for a series of species that have little in common with Agassiz's *Otodus appendiculatus*.

Cretalamna appendiculata (Agassiz, 1843)

Figure 8C–D

Material. Chalk: one almost complete upper lateral tooth, from Hultug, Kalkbrud (Tor Fm) (MGUH 29959); Fiskeler: a single cusp but the largest tooth found in the Fiskeler (MGUH 29960).

Description. A large tooth measuring 30 mm high and 30 mm wide with a large principal cusp, with a convex mesial cutting edge and a concave distal cutting edge. The principal cusp is flanked by a pair of almost separated acute divergent cusplets. Both the labial and the lingual faces are smooth and convex. The root is bilobed with short terminating lobes. The basal face is flat and the lingual face is low with a small protuberance with a centrally placed median foramen.

Remarks. Herman (1977) divided *Cretalamna appendiculata* into three subspecies. This practice is at best problematic and should be avoided. Herman's subspecific differences might be ontogenetic (Siverson 1992a) or actually different species (Cappetta and Case 1999; Cappetta and Corral 1999). The 'species' *C. appendiculata* would appear to be cosmopolitan and long-lasting, as it is reported from almost all over the world from the Albian–Eocene. It most likely represents a number of independently evolving lineages.

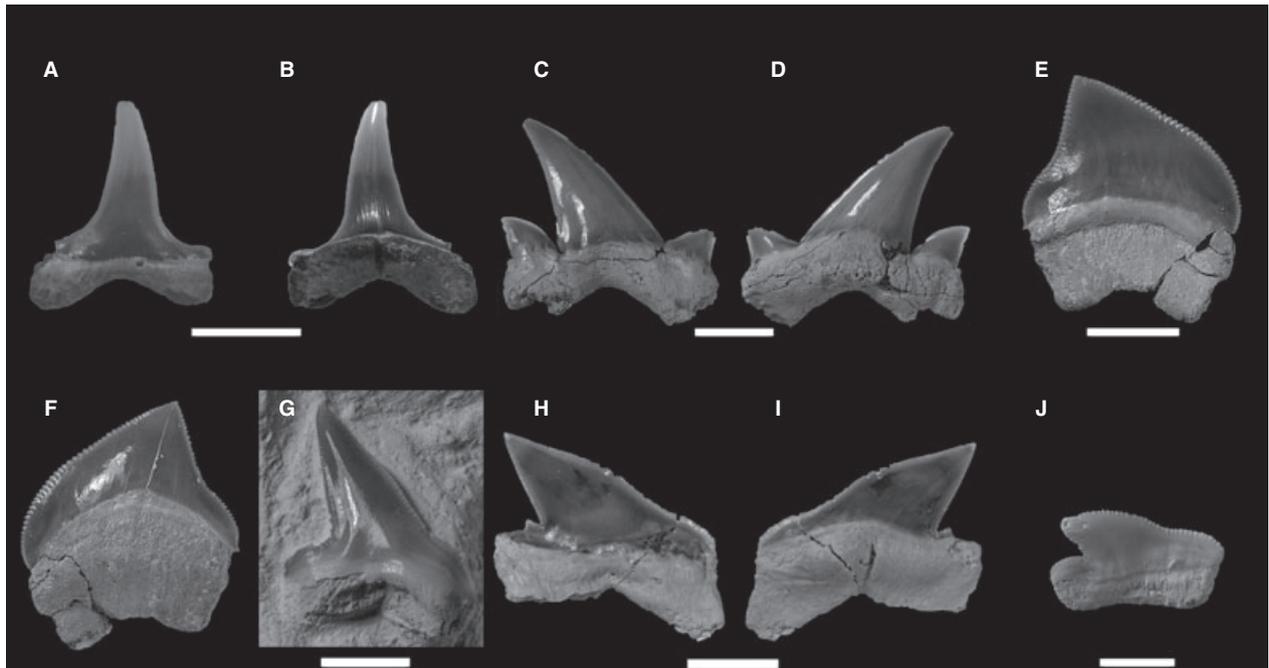


FIG. 8. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–B, *Anomotodon plicatus* Arambourg, 1952, MGUH 29958, Højerup Member, lateral tooth in A, labial and B, lingual views. C–D, *Cretalamna appendiculata* (Agassiz, 1835), MGUH 29959, Højerup Member, upper lateral tooth in C, labial and D, lingual views. E–F, *Squalicorax pristodontus* (Agassiz, 1843), MGUH 29961, Højerup Member, lateral tooth in E, labial and F, lingual views. G–J, *Pseudocorax affinis* (Agassiz, 1843); G, MGUH 29962, Højerup Member, anterior tooth in labial view; H–I, MGUH 29963, Højerup Member lateral tooth in H, labial and I, lingual views; J, MGUH 29964, posterior tooth in labial view. Scale bars represent 1 mm (A–B); 10 mm (C–F); and 5 mm (G–I).

We have chosen to follow Siverson (1999, p. 59) regarding the spelling of *Cretalamna* as originally used in the type description by Glickman (1958, p. 570) as opposed to *Cretolamna*, as recommended by Cappetta (2012).

Family ANACORACIDAE Casier, 1947

Genus SQUALICORAX Whitley, 1939

Type species. *Corax (Galeus) pristodontus* Agassiz, 1843 from the Maastrichtian of the Netherlands.

Squalicorax pristodontus (Agassiz, 1835)

Figure 8E–F

Material. Chalk: one almost complete tooth (MGUH 29961) and one fragment (GMV2012–45) surface-collected in Stevns Kridtbrud (Tor Fm).

Description. Teeth up to 26 mm high and 22 mm wide. Labio-lingually strongly compressed tooth with an asymmetrical crown, convex mesial cutting edge, a straight distal cutting edge and a convex distal heel. The cutting edges are continuous and strongly serrated. The labial face is slightly convex and smooth. The lingual face is strongly convex and smooth. Both labial and lingual crown–root junctions are convex. The labial face of the crown overhangs the root. The labial face of the root is flat; the basal edge is incomplete, but appears to be indented. The basal face of the root is large and flat.

Remarks. *Squalicorax pristodontus* differs from *S. kaupi* by lacking a distal notch. Crown shapes in the remaining species of *Squalicorax* generally show a marked distal notch (except in some anterior teeth) and would rarely be confused with *S. pristodontus*. The Anacoracidae is, as several other families of extinct selachians, in need of revision (Siverson 1992a; Siverson 1996; Cappetta and Case 1999; Siverson *et al.* 2007; Shimada 2008). The species *S. pristodontus* appears to have been cosmopolitan and is recorded from Europe (Herman 1977; Vullo 2005; Jagt *et al.* 2006) North Africa (Arambourg 1952; Cuny *et al.* 2012), North America (Cappetta and Case 1975; Welton and Farish 1993), India (Verma 1965) and Madagascar (Gottfried *et al.* 2001).

Family PSEUDOCORACIDAE Cappetta, 2012

Genus PSEUDOCORAX Priem, 1897

Type species. *Corax affinis* Münster in Agassiz, 1843 from the Maastrichtian in of the Netherlands.

Pseudocorax affinis (Agassiz, 1843)

Figure 8G–J

Material. Chalk: four teeth, of which three are from Stevns Kridtbrud (Tor Fm) (MGUH 29962, MGUH 29963, GMV2012–46) and one is from Kjølbj Gaard (MGUH 29964).

Description. Teeth up to 17 mm high and 13 mm wide, displaying a moderate degree of monognathic heterodonty, with the anteriors more symmetrical than distal teeth. Labio-lingually compressed teeth with a single elongated and acute principal cusp. The mesial face is deflected towards the commissure with a kink half way up the cusp. The distal face is either straight or also has a slight kink. Two deflected or convex shoulders are present, and there is no sign of cusplets. The cutting edge is continuous and serrated. The labial face is smooth and slightly convex and overhangs the root; the lingual face is also smooth and convex. The root is bilobed, with an elongated mesial lobe and a short square distal lobe. The basal face is flat to concave depending on the position of the tooth, with posterior teeth being flat. The root has a nutrient groove with pores. Anterior teeth are more erect and are less labio-lingually compressed than lateral and posterior teeth.

Remarks. *P. affinis* is known from the Maastrichtian of Europe and Africa (Geyn 1937a; Arambourg 1952; Albers and Weiler 1964; Herman 1977; Bless *et al.* 1991; Ladwig 2000; Antunes and Cappetta 2002), so its presence in Scandinavia is not unexpected.

Order CARCHARHINIFORMES Compagno, 1973

Family SCYLORHINIDAE Gill, 1862

Genus SCYLORHINUS Blainville, 1816

Type species. *Squalus canicula* Linnaeus, 1758, Recent.

Remarks. We are using the Recent genus *Scyliorhinus* in its loose, traditional palaeontological sense, but in quotes, indicating a lack of taxonomic certainty, rather than prematurely erecting a new fossil genus. There are in the region of 20 Recent genera with *Scyliorhinus*-like dentitions, any of which could prove more closely related to these fossil genera than *Scyliorhinus s.s.* (Compagno 1984).

In the case of *Scyliorhinus*, with approximately 34 Recent species (<http://fishbase.org>, 2011), our knowledge of the inter- and intraspecific variation is limited. This leaves us with the choice of either assigning fossil species to a modern genus or erecting a new genus to contain the fossils with a morphology close to a modern genus. Either solution is undesirable and has taxonomic repercussions. This problem was aired by Müller and Diedrich (1991) who saw the use of *Scyliorhinus* as a last resort rather than a desirable solution.

'Scyliorhinus' elongatus (Davis, 1887)

Figure 9A–P

Material. Chalk: 11 mostly incomplete teeth from Stevns Kridtbrud and Rødvig (MGUH 29965, MGUH 29966, MGUH 29967, MGUH 29968 and GMV2012–47 (batch)); Fiskeler: Around 200 complete and fragmentary specimens Rødvig and Højerup (MGUH 29969, MGUH 29970, MGUH 29971, MGUH 29972 and GMV2012–48 (batch)).

Description. Teeth up to 4 mm high and 2 mm wide. The teeth have an elongated biconvex principal cusp flanked by a pair of slightly incurving acute cusplets. The labial face is convex with strong vertical folds covering the whole face in lateral teeth, whereas the medial part of the labial face is smooth in anterior teeth. The labial crown–root junction has a deep medial indentation in anterior teeth, less so in lateral and posterior teeth. The lingual face of the crown is strongly convex with strong vertical folds. The root is low with several foramina medially below the labial crown–root junction. The basal face of the root is flat, bilobed and in general symmetrical. The lingual face of the root has a strong protuberance with foramina.

Remarks. *'Scyliorhinus' dubius* is slender and has a smooth labial face; the cusp and cusplets are bent lingually (Woodward 1911; Ward 2010). *'S. antiquus'* differs by having a shallower median indentation and more marked labial folds (Cappetta 1977). *'S. elongatus'* has been recorded from several late Cretaceous locations in England (Underwood and Ward 2008), Belgium (Herman 1977), Lebanon (Davis 1887), Morocco (Noubhani and Cappetta 1997) and now Denmark. Cappetta and Case (1999) described *'S. arlingtonensis'* from the Cenomanian of Texas, which differs very little from the *'S. elongatus'* from the above-mentioned localities and may be a junior synonym.

'Scyliorhinus' biddlei Halter, 1995

Figure 9Q–X

Material. Chalk: four teeth from Stevns Kridtbrud, all lacking roots (MGUH 29973, MGUH 29974, GMV2012–49 (batch)); Fiskeler: 31 specimens from Rødvig and Højerup (MGUH 29975, MGUH 29976, GMV2012–50 (batch)).

Description. Dentition displaying monognathic heterodonty. Anterior teeth are elongated, triangular and slightly slanted towards the commissure with a deep indentation in the crown base. The principal cusp is triangular and acute, with a straight mesial face, whereas the distal face is mesio-distally concave. The labial face is convex and smooth with the exception of the overhanging basal edge, which may carry folds, as well as on the sloping shoulders. The lingual face is strongly convex and can be either smooth or carry folds, on both the cusp and below the shoulders. The roots on our specimens are in almost all cases badly

preserved, but the following can be deduced: the root is low and wide, labially deeply indented with several foramina below the crown–root junction. The root is bilobed with a prominent lingual protuberance, which has a median foramen. The basal face is flat with a partly closed median groove. Lateral and posterior teeth are lower and wider than anteriors, the principal cusp is slanted towards the commissure, and the shoulders are less sloping. Both of the heels may carry cusplets or at least on the distal heel. The convex labial face is rather smooth with the exception of the basal edge, which may be heavily ornamented. The lingual face in lateral and posterior teeth appears to always carry folds of which some are flexuous. The root lobes tend to be more separated.

Remarks. Halter (1995) stated that it was not possible to differentiate upper from lower teeth as there are no fossils or modern species to compare with. The presence of labial folds are, according to Halter (1995), only found in juveniles, which may be supported by the fact that it tends to be present in slightly smaller teeth. The specimens figured as *Pararhincodon groessensi* (Hübner and Müller 2010; fig. 5H–I) presumably belong to *S. biddlei*, although the quality of the drawings does not allow further conclusions to be drawn.

Genus CRASSESCYLORHINUS Underwood and Ward, 2008

Type species. *Scyliorhinus germanicus* Herman, 1982b from the Maastrichtian of North Germany.

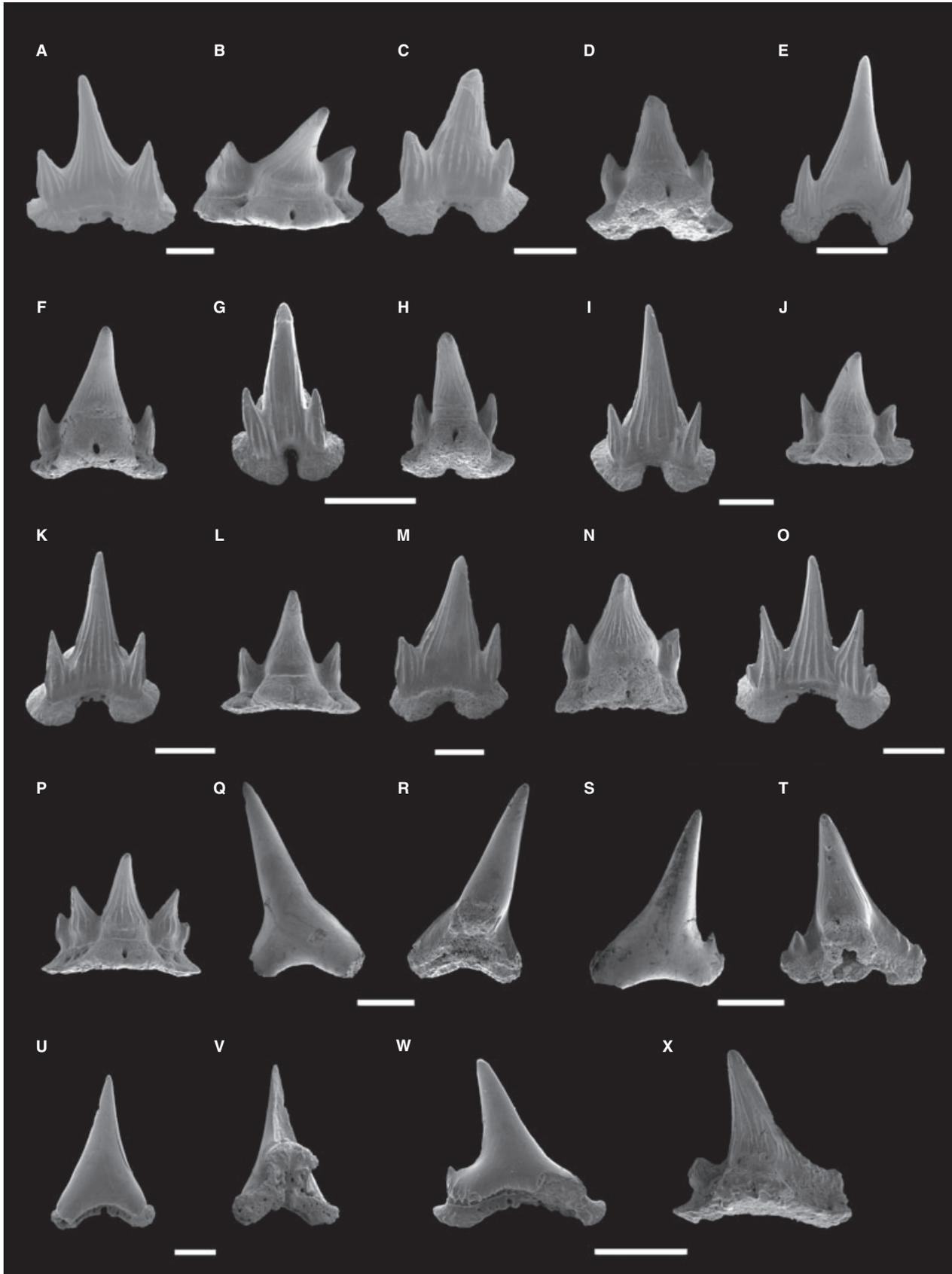
Crassescyliorhinus germanicus (Herman, 1982b)

Figure 10A–H

Material. Chalk: Seven teeth from Stevns Kridtbrud (MGUH 29977, MGUH 29978 and GMV2012–51 (batch)); Fiskeler: 62 specimens from Rødvig and Højerup (MGUH 29979, MGUH 29980 and GMV2012–52 (batch)).

Description. Dentition displaying monognathic heterodonty with the anterior teeth being taller and having more elongated cusps than the lateral and posterior teeth. Anterior teeth have an elongated principal cusp flanked by two pairs of cusplets. All cusps are massive with a flat to slightly convex labial face carrying vertical folds. The basal ledge is median indented, overhangs the root and is carrying coarse reticulated folds. The lingual face is strongly convex with vertical folds reaching the apex of the cusps. Lateral and posterior teeth have shorter cusps, and the basal edge of the crown is less indented or straight. The principal cusp is slanted towards the commissure in lateral teeth. The root is high and bilobed with a flat basal face and a large median lingual protuberance. Several foramina are present below the crown–root junction on the labial face.

Remarks. The cusps and roots in *Crassescyliorhinus* are massive compared with other genera of Scyliorhinidae and



could indicate a specialization towards a tougher diet. The genus appears to have been indigenous to north-western Europe in the late Cretaceous and early Danian and the Bartonian/Priabonian of Egypt (Underwood *et al.* 2011). As suggested by Underwood and Ward (2008), *S. mustiliformis* should be included into *Crassescyliorhinus*.

Family TRIAKIDAE Gray, 1851

Genus PARATRIAKIS Herman, 1977

Type species. *Paratriakis bettrechiensis* Herman, 1977.

Paratriakis curtirostris (Davis, 1887)

Figure 10I–O

Material. Chalk: 18 specimens from Stevns Kridtbrud (MGUH 29981, MGUH 29982 and GMV2012–53 (batch)); Fiskeler: 56 specimens from Rødvig and Højerup (MGUH 29983, MGUH 29984, GM2012–54 (batch)).

Description. Dentition with weak gradient monognathic heterodonty. The teeth are almost twice as wide as they are tall, with an acute principal cusp strongly slanted towards the commissure. The mesial edge of the cusp is straight or slightly sinuous at an angle to the basal edge of the crown. The distal edge of the cusp is mesially inclined and meets the distal shoulder in a notch. The distal shoulder is well developed and almost angular. The labial face is smooth and slightly convex with a median transverse depression. A horizontal transverse narrow ledge is present along the basal edge of the crown. The lingual face of the crown is convex and smooth. The root is low with an irregular basal edge and several foramina scattered on the labial face. The root is flat and as wide as the crown with a median protuberance. Lateral teeth tend to have a shorter cusp than anteriors. There are no signs of dignathic heterodonty.

Remarks. *Paratriakis* is known from the late Cretaceous of the Middle East (Lebanon; Davis 1887; Cappetta 1980), Germany (Herman 1982b) and north-western Europe

(France, Belgium, the Netherlands and Britain; Herman, 1977; Underwood and Ward, 2008).

Genus PALAEOGALEUS Gurr, 1962

Type species. *Galeocerdo vincenti* Daimeries, 1888 from the Paleocene of Belgium.

Palaeogaleus aff. *faujasi* (Geyn 1937a)

Figure 11A–Y

Material. Chalk: 38 specimens from Stevns Kridtbrud and four specimens from Nyvang Gaard (MGUH 29985, MGUH 29986, MGUH 29987 and GMV2012–55 (batch)); Fiskeler: 92 specimens from Rødvig and Højerup (MGUH 29988, MGUH 29989, MGUH 29990, MGUH 29991, MGUH 29992, MGUH 29993, MGUH 29994, MGUH 29995, MGUH 29996, MGUH 29997, MGUH 29998, MGUH 29999 and GMV2012–56 (batch)).

Description. The dentition displaying gradient monognathic and dignathic heterodonty. Parasymphyseal and anterior teeth are almost symmetrical with an elongated principal cusp flanked by two pairs of small cusplets. Both the labial and the lingual faces are smooth and convex, with the lingual face being the most convex. The labial face may carry some strong vertical folds above the basal edge of the crown that overhangs the root. In lateral and posterior teeth, the mesial cusplets are lacking in teeth from the upper jaw, whereas they are present in the lower jaw. The principal cusp in the laterals and posteriors of the upper jaw has a strongly curved mesial edge, whereas the mesial edge is straight in teeth of the lower jaw. The root is high and bulky with a flat basal edge, well-separated lobes and a deep median groove, which almost separates the lingual protuberance into two.

Remarks. The *Palaeogaleus* from Stevns Klint is close to *P. faujasi* (Geyn 1937b,c) from the Maastrichtian of the Netherlands, but the Danish material has more developed cusps and folds than those observed in *P. faujasi*. The specimens differ from the late Cretaceous *P. dahmanii* in having blunter and thicker cusplets and a higher crown and from *P. havreensis* in having less folds and blunter cusps.

FIG. 9. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–P, ‘*Scyliorhinus*’ *elongatus* (Davis, 1887); A–B, MGUH 29965, Højerup Member, lateral tooth in A, labial and B, lingual views; C–D, MGUH 29966, Højerup Member, lateral tooth in C, labial and D, lingual views; E–F, MGUH 29967, Højerup Member, lateral tooth in E, labial and F, lingual views; G–H, MGUH 29968, Højerup Member, anterior tooth in G, labial and H, lingual views; I–J, MGUH 29969, Fiskeler Member, anterior tooth in labial I, and J, lingual views; K–L, MGUH 29970, Fiskeler Member, anterior tooth in K, labial and L, lingual views; M–N, MGUH 29971, Fiskeler Member, lateral tooth in M, labial and N, lingual views; O–P, MGUH 29972, Fiskeler Member, posterior tooth in O, labial and P, lingual views; Q–X, ‘*Scyliorhinus*’ *biddlei* Halter, 1995; Q–R, MGUH 29973, Højerup Member, anterior tooth in Q, labial and R, lingual views; S–T, MGUH 29974, Højerup Member, anterior tooth in S, labial and T, lingual views; U–V, MGUH 29975, Fiskeler Member, anterior tooth in U, labial and V, lingual views; W–X, MGUH 29976, Fiskeler Member, lateral tooth in W, labial and X, lingual views. Scale bars represent 0.5 mm (A–D, I–X) and 1 mm (E–H).

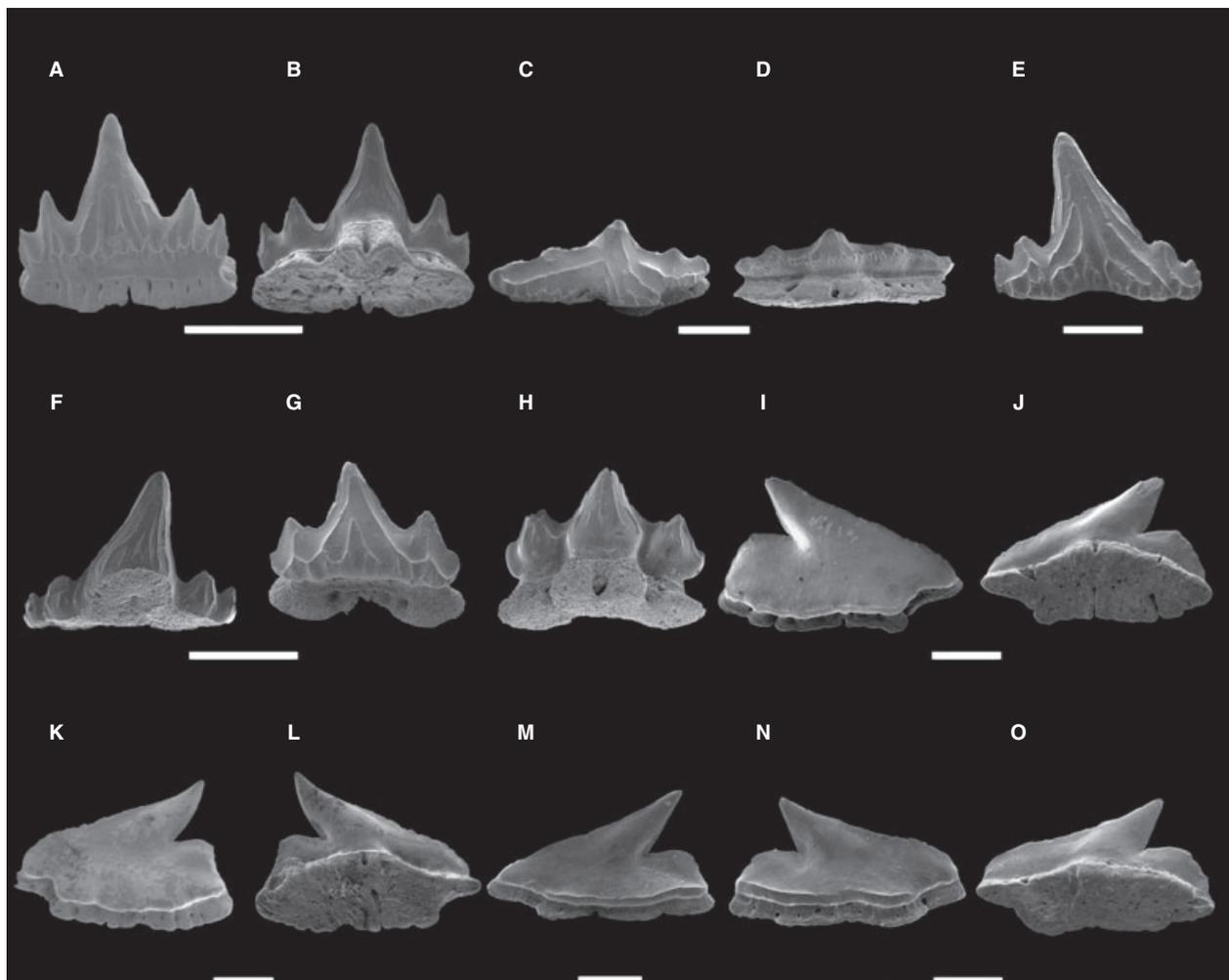


FIG. 10. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–H, *Crassescyliorhinus germanicus* (Herman, 1982b); A–B, MGUH 29977, Højerup Member, lateral tooth in A, labial and B, lingual views; C–D, MGUH 29978, Højerup Member, posterior tooth in C, labial and D, lingual views; E–F, MGUH 29979, Fiskeler Member, anterior tooth in E, labial and F, lingual views; G–H, MGUH 29980, Fiskeler Member, anterior tooth in G, labial and H, lingual views. I–O, *Paratriakis curtirostris* (Davis, 1887); I–J, MGUH 29981, Højerup Member, anterior tooth in I, labial and J, lingual views; K–L, MGUH 29982, Højerup Member, anterior tooth in K, labial and L, lingual views; M, MGUH 29983, Fiskeler Member, lateral tooth in labial view; N–O, MGUH 29984, Fiskeler Member, posterior tooth in N, labial and O, lingual views. All scale bars represent 0.5 mm.

Superorder and Order INCERTAE SEDIS
Family PROTOSPINACIDAE Woodward, 1918

Genus PROTOSPINAX Woodward, 1918

Type species. *Protospinax annectens* Woodward, 1918 from the Late Jurassic of southern Germany.

Protospinax sp.
Figure 12A–C

Material. Chalk: a single damaged tooth from Stevns Kridtbrud (MGUH 30000).

Description. Very small, less than 1 mm wide tooth with a flat asymmetrical oval-shaped crown and a single small triangular cusp. The mesial shoulder is much enlarged and convex, whereas the distal shoulder is very short and declined, giving the tooth an almost vertical straight distal face. The cutting edges appear to be continuous. The labial face is convex and smooth with a slightly irregular basal edge, which would have overhung the root. The lingual face is smooth and very convex, and the uvula is small and triangular. The root is missing, and the lingual face is strongly eroded.

Remarks. The state of preservation of the tooth has not left many useful characters, so the identification is only tentative. The morphology compares well with the Albian specimen figured in Ward (2010).

Superorder BATOMORPHII Cappetta, 1980
 Order RAJIFORMES Berg, 1940
 Suborder: RHINOBATOIDEI Fowler, 1941
 Family *Incertae familiae*
 ‘*Rhinobatos*’ sp.
 Figure 12D–J

Material. Fiskeler: two complete specimens from Stevns Kridtbrud (MGUH 30001, MGUH 30002).

Description. Dentition displaying gynandric, ontogenetic and gradient monognathic heterodonty. The wide, shallow labial face is smooth and convex and is limited lingually by an almost straight transverse crest. The marginal angles are obtuse, rounded, and the labial visor is indented and irregular with a narrow and short median expansion. The lingual face of the crown is convex and is apico-basally narrow with a prominent, well-developed, median lingual uvula with almost parallel vertical faces and rounded termination. The lingual marginal uvulae are hardly developed at all. There are no signs of ornamentation on the lingual face. The root is holaulacorhize with a flat basal face, which is almost as wide as the crown. A distinct V-shaped median groove with a large median foramen divides the basal face into two.

Remarks. The basic ‘*Rhinobatos*’ tooth morphology is shared with a number of genera, some closely related (*Platyrrhina* Bloch and Schneider 1801 and *Zapteryx* Jordan and Gilbert 1880) and some less so (*Pristis* Linck 1790, *Anoxypristis* White and Moy-Thomas 1941). Numerous fossil species have been assigned to the Recent genus *Rhinobatos*, but few are likely to belong to it (Cappetta and Case 1999; Kriwet *et al.* 2007; Guinot *et al.* 2012a). Furthermore, the dentitions in several of the extinct *Rhinobatos* species are so morphologically similar that distinguishing between the different species can be difficult (Kriwet *et al.* 2007). The Danish specimens differ from other late Maastrichtian and early Palaeogene species by lacking lingual marginal uvulae, being wider than high and by having a fairly straight transverse crest. This sets them apart from other late Cretaceous species, such as *R. incertus*, *R. uvulatus* and *R. craddocki* (Case and Cappetta 1997) from North America. The two Danish specimens have a close affinity with *R. mariannae* from Europe (Bor 1983), but differ in having the much more prominent median uvula. Several species of fossil ‘*Rhinobatos*’ that either lack or have a weakly developed marginal uvulae (see Cuny *et al.* 2004 for a review) presumably belong to an undefined genus (Cappetta and Case 1999; Underwood and Rees 2002; Cuny *et al.* 2004). The fossil ‘*Rhinobatos*’ species are in need of revision, which is beyond the scope of this article. We have tentatively referred our two specimens to ‘*Rhinobatos*’ sp., but we feel that there is a strong likelihood that they represent an undescribed genus.

Family INCERTAE SEDIS

Genus *Squatirhina* Casier, 1947

Type species. *Squatirhina lonzeensis* Casier, 1947 from the Late Cretaceous of Belgium.

Squatirhina kannensis Herman, 1977
 Figure 12K–O

Material. Chalk: one tooth from Stevns Kridtbrud (MGUH 30003).

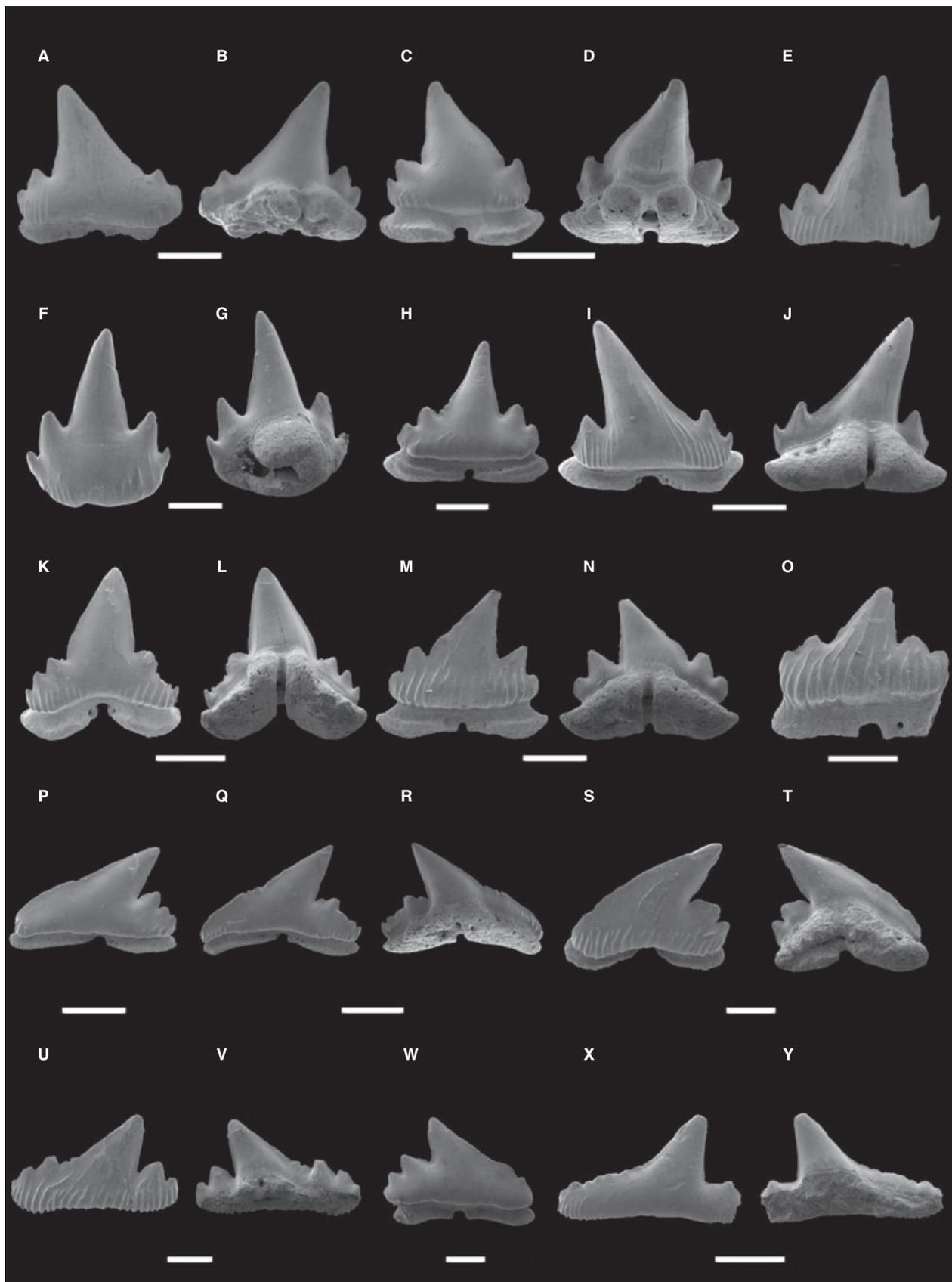
Description. Tooth measuring 3.5 mm in width, with a rhomboid labial face and a short massive cusp. The labial face is strongly convex and smooth with a median elevation from the cusp and reaching almost to the apron, which is bifid and strongly overhangs the root. The lingual face is low and vertical and slightly convex with a large protruding median lingual uvula. The lingual basal edge is strongly ornamented with vertical folds as is the lower part of the labial basal edge. The lateral and basal edges of the uvula are also strongly ornamented. The holaulacorhize root is of the same width as the crown. The two lobes are separated by a deep groove. A central foramen and a pair of paracentral foramina are present. The basal face of the root is flat and has several multiple small foramina. The lingual face of the root has a pair of large marginal foramina in the indentations below the lingual face and a notch below the median uvula.

Remarks. Four species of *Squatirhina* have been described from the Late Cretaceous of Europe: *S. thiesi* Biddle, 1993 (Albian of France); *S. westfalica* Müller and Diedrich, 1991 (Cenomanian of Germany); *S. lonzeensis* Casier, 1947 (Santonian of Belgium); and *S. kannensis*, Herman, 1977 (Maastrichtian of Belgium). *S. thiesi* have a well-developed apron, and the crown is labio-lingually expanded (Biddle 1993). In *S. westfalica*, the crown is smooth with a developed apron and folds on the lingual face (Müller and Diedrich 1991). The apron is rounded or bifid in *S. lonzeensis* as in *S. kannensis*. *S. lonzeensis* differs from *S. kannensis* in having median folds on the uvula, whereas *S. kannensis* has folds only on the lateral and basal edges (Guinot *et al.* 2012a), and in *S. lonzeensis*, the marginal foramina are smaller (Vullo 2005).

DISCUSSION

The Maastrichtian chalk and the Fiskeler have yielded a chondrichthyan fauna of 32 species of sharks and rays (Fig. 13).

The result is somewhat biased, as the majority of the material comprises fragments of ‘Odontaspid-like’ cusps,



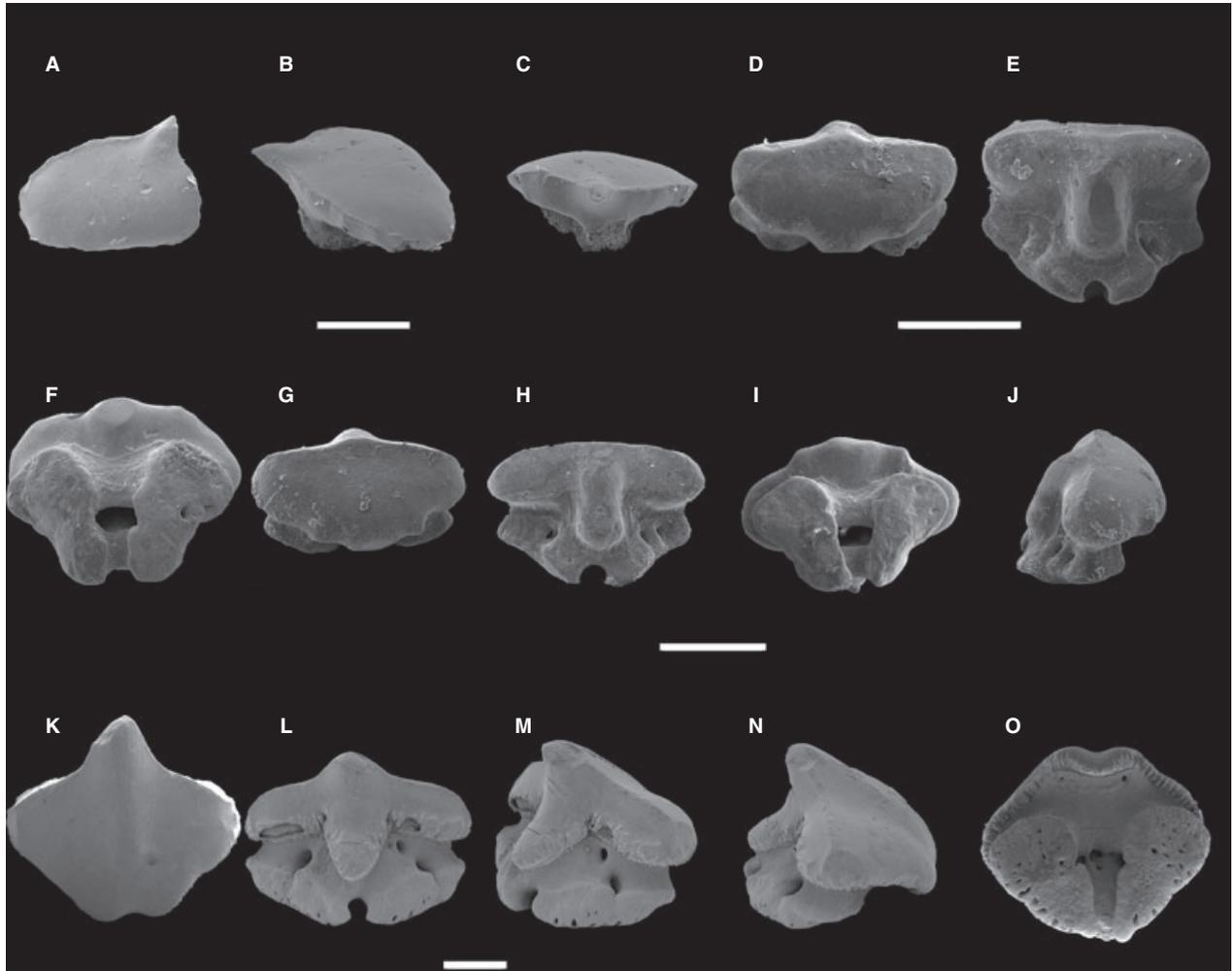


FIG. 12. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–C, *Protospinax* sp., MGUH 30000, Højerup Member, lateral tooth in A, labial, B, lateral and C, lingual views; D–J, '*Rhinobatos*' sp.; D–F, MGUH 30001, Fiskeler Member, tooth in D, labial, E, lingual and F, basal views; G–J, MGUH 30002, Fiskeler Member, tooth in G, labial, H, lingual, I, basal and J, lateral views. K–O, *Squatirrhina kannensis* Herman, 1977; K–O, MGUH 30003, Højerup Member, lateral tooth in K, labial, L, lingual, M–N lateral and O, basal views. All scale bars represent 0.5 mm

which are indeterminate. The fragments do not show signs of wear due to, for example, reworking, but are clearly fragments of cusps which in general are fractured vertically. This phenomenon is common in some horizons in the English chalk, usually on or just above hard-

grounds (D. J. Ward pers. obs.). It is likely that these tooth shards represent several species.

The fauna listed in Figure 13 compares well with that described by Herman (1982*b*) from the Maastrichtian of North Germany and briefly mentioned by Siverson

FIG. 11. Neoselachian teeth from the Højerup Member and the Fiskeler Member, Stevns Klint, Denmark. A–Y, *Palaeogaleus* aff. *faujasi* (Geyn 1937*a*); A–B, MGUH 29985, Højerup Member, lateral tooth in A, labial and B, lingual views; C–D, MGUH 29986, Højerup Member, anterior tooth in C, labial and D, lingual views; E, MGUH 29987, Højerup Member, lateral tooth in labial view; F–G, MGUH 29988, Fiskeler Member, symphyseal tooth in F, labial and G, lingual views; H, MGUH 29989, Fiskeler Member, anterior tooth in labial view; I–J, MGUH 29990, Fiskeler Member, lateral tooth in I, labial and J, lingual views; K–L, MGUH 29991, Fiskeler Member, anterior tooth in K, labial and L, lingual views; M–N, MGUH 29992, Fiskeler Member, lateral tooth in M, labial and N, lingual views; O, MGUH 29993, Fiskeler Member, lateral tooth in labial view; P, MGUH 29994, Fiskeler Member, posterior tooth in labial view; Q–R, MGUH 29995, Fiskeler Member, lateral tooth in Q, labial and R, lingual views; S–T, MGUH 29996, Fiskeler Member, posterior tooth in S, labial and T, lingual views; U–V, MGUH 29997, Fiskeler Member, posterior tooth in U, labial and V, lingual views; W, MGUH 29998, Fiskeler Member, posterior tooth in labial view; X–Y, MGUH 29999, Fiskeler Member, posterior tooth in X, labial and Y, lingual views. Scale bars represent 1 mm (A–E, I–L) and 0.5 mm (F–H, M–Y).

(1993a) from the early Campanian chalks of Scandia in southern Sweden. Among the genera he mentioned are *Scyliorhinus* (*Crassescyliorhinus*), *Palaeogaleus*, *Galeorhinus*, *Squatirhina*, *Rhinobatos* and specimens resembling *Paratriakis*. Palaeogeographically, the Scandinavian localities belonged to the boreal realm; similarly, most of the species found here appear to have been indigenous to the Boreal Sea of north-western Europe.

There are, however, some species that had a larger distribution, for example *Paratriakis curtirostris*, *Scyliorhinus elongatus*, *Anomotodon plicatus*, the cosmopolitan species *Cretalamna appendiculata* and *Squalicorax pristodontus*. The presence of *P. curtirostris* and *S. elongatus* supports a connection to the Tethyan realm during the late Maastrichtian (Cappetta 1980). Besides yielding information on the relationships with other faunas, Figure 13 offers a rare opportunity to observe how a chondrichthyan fauna responded to the K/T boundary event. This appears to be the only study of this nature yet attempted.

In Figure 13, a major change in the fauna can be observed prior to the K/T boundary, where the late Maastrichtian fauna (layer I) changes dramatically from at least 27 species to only 5 in layer II. In the absolute earliest part of the Danian (Fiskeler layer III), at least 8 species reappeared, suggesting that the fauna had started to recover. The chondrichthyan diversity continued to increase during the deposition of Fiskeler layers IV and V with the reappearance of at least 12 and 14 species, respectively. Nine species of 27 disappeared (33.3 per cent of the species and 23 per cent of the genera) before the K/T boundary, depending whether or not the very fragmentary squaloid teeth from the Fiskeler are conspecific with the *Megasqualus* sp. from the chalk. It is important not to interpret these disappearances as extinctions because three of the genera, *Paraorthacodus*, *Notidanodon* and *Anomotodon*, survive into the late Paleocene elsewhere.

The only other detailed study conducted on chondrichthyan faunas on either side of the K/T boundary is by Noubhani and Cappetta (1997) and deals with the fauna from Morocco. Their data suggested that 96 per cent of the species and 72.5 per cent of genera that were present in the late Maastrichtian were absent in the Paleocene (Noubhani and Cappetta 1997, table 4; Kriwet and Benton 2004). Taken at face value, this would appear to be a very different result that requires some explanation. The Moroccan Maastrichtian deposit is an inshore, shallow water, phosphorite, rich in small sharks and rays, which has been extensively studied (Arambourg, 1952; Noubhani and Cappetta, 1997). There is clearly a sedimentary and temporal hiatus at the K/T discontinuity, but currently no means of estimating its duration. In the Moroccan Paleocene and Early Eocene, there is no formal lithostratigraphic nor chronostratigraphic framework, and ages are deduced from the faunal composition, most of which is

restricted to North Africa. The Selandian is not formally recognized, and Selandian-aged sediments are referred to as Danian or Thanetian. Reworking is usually present at the base of each phosphatic interval. Danian samples are often rich in Maastrichtian species (D. J. Ward pers. obs.). However, there would appear to be an assumption that 'Cretaceous' species did not cross the K/T boundary and if encountered in the Danian are regarded as having been reworked. This would eliminate any record of Moroccan species crossing the K/T boundary, whereas we have demonstrated that the majority of the Danish species did so. It would be a useful exercise to resample Moroccan latest Maastrichtian and basal Danian sediments and determine either geochemically or by faunal composition whether some 'reworked' species were actually K/T survivors, as is most likely.

If the Moroccan data are reviewed in terms of genera rather than species and we exclude the genera that we know survive into the Paleocene, a very different result is obtained. The generic loss in Morocco decreases to 57 per cent. This is still biased by the loss of number of monospecific genera known only from Morocco, but gives a more reasonable indication of the extent of the faunal change.

How reliable are the Danish records? Sampling issues, as in the meagre diversity in the Fiskeler layer II, could be an artefact of sample size. The chalk samples were much larger than the Fiskeler layer II samples. The results from two localities, 5 km apart (Rødvig and Højerup, respectively) did, however, yield the same species, supporting the validity of the results from Stevns Klint. Reworked specimens can alter the fauna signal and conceal the true fauna. This can be hard to detect, unless older reworked specimens show distinct signs of wear, but this might not always be the case. Discarding material as being reworked and the acceptance of material as being *in situ* can bias the result towards either a greater extinction or survival rate. Specimens from the different layers of the Fiskeler, however, yielded different oxygen isotopic values (J. S. Adolfsson *et al.* in prep.) strongly suggesting that the specimens from Stevns Klint were not reworked. This conclusion is further supported by results of studies conducted by Hultberg (1986, 1987) on dinoflagellates and by Hart *et al.* (2004) on foraminifera.

What do the Danish sharks tell us about the environment?

The sea level during the late Maastrichtian at Stevns Klint was probably at least 150 m deep or more (Håkansson *et al.* 1974). The palaeobathymetry of the Fiskeler has been a subject of discussion. Ekdale and Bromley (1984) suggested that the sea level fell at the boundary, whereas Schmitz *et al.* (1992) argued that it rose. The fossil shark fauna may offer some clues regarding the palaeobathymetry by

FIG. 13. Distribution of shark and ray species of this study. The vertical black line marks the K/T boundary. I, Late Maastrichtian chalk; II, uppermost Maastrichtian marl (II); III, Fiskeler (layers IIIA and IIIB); IV, Fiskeler (layer IV); V, Fiskeler (layer V); III–V, species whose precise occurrence in the Fiskeler is uncertain; GS, genera which survived the K/T boundary; †, species going extinct at the boundary; ?, species may be present, but is indeterminate due to state of preservation of the fossil teeth. Shannon H diversity indices were calculated with PAST 2.14 (Hammer *et al.* 2001).

Order	Taxa	I	II	III	IV	V	III-V	GS
Synechodontiformes	<i>Sphenodus lundgreni</i>	+						+
	† <i>Paraorthacodus andersoni</i>	+						+
	<i>Synechodus faxensis</i>	+		+		+	+	+
Hexanchiformes	<i>Hexanchus microdon</i>	+			+	+	+	+
	† <i>Notidanodon pectinatus</i>	+						+
Squaliformes	<i>Squalus gabrielsoni</i>	+	+	+	+	+		+
	<i>Megasqualus</i> sp.	+		?	?	?		+
	<i>Centroscymnus praecursor</i>	+	+			+		+
	† <i>Proetmopterus hemmooriensis</i>	+						+
Echinorhiniformes	<i>Echinorhinus</i> sp.						+	+
Squatiformes	<i>Squatina</i> sp.	+			+	+		+
	<i>Parasquatina cappelletai</i>	+					+	+
Orectolobiformes	<i>Pararhincodon groessenssi</i>	+		+	+	+		+
	<i>Nebrius</i> sp.						+	+
	<i>Hemiscyllium hermani</i>	+	+		+	+	+	+
	† <i>Palaeobrachaelurus</i> sp.	+						+
Heterodontiformes	<i>Heterodontus rugosus</i>	+			+	+	+	+
Lamniformes	<i>Carcharias</i> aff. <i>gracilis</i>	+				+	+	+
	Indet		+	+				
	<i>Palaeohypotodus</i> cf. <i>bronni</i>						+	+
	† <i>Anomotodon plicatus</i>	+						+
	<i>Cretalamna appendiculata</i>	+					+	+
	† <i>Squalicorax pristodontus</i>	+						
	† <i>Pseudocorax affinis</i>	+						
	<i>'Scyliorhinus' elongatus</i>	+	+	+	+	+		+
	<i>'Scyliorhinus' biddlei</i>	+		+	+	+		+
	<i>Crassescyliorhinus germanicus</i>	+		+	+	+		
<i>Paratriakis curtirostris</i>	+		+	+	+		+	
<i>Palaeogaleus</i> aff. <i>faujasi</i>	+		+	+	+			
Incertae Sedis	† <i>Protospinax</i> sp.	+						
Rajiformes	<i>'Rhinobatos'</i> sp.						+	+
	† <i>Squatirhina kannensis</i>							
Sum:		27	5	9	12	14		
Shannon H diversity indices:								
	Højerup		1.561	1.2	1.999	1.121		
	Rødvig	1.729	1.321	2.084	2.151	2.051		

comparing it with the occurrence and behaviour of related living forms. Of the sharks encountered in the chalk and Fiskeler, 10 of 29 genera have close modern representatives.

Hexanchus griseus lives in a wide range of water depths, from the surface down to 1875 m (Compagno *et al.* 2005). They are vertical migrators, feeding in shallow water and resting in deeper water during the day (Andrews *et al.* 2009). *Squalus acanthias* is epipelagic in cool water, but lives closer to the bottom in warm water and can be found as low as 1400 m. *S. acanthias* also performs seasonal migration (Vince 1991) and forms schools segregated by sex and size (Alonso *et al.* 2002). Pregnant females migrate to give birth in shallow water nursing grounds (Simpson and Wardle 1967; Compagno *et al.* 2005). *Centroscymnus* live close to or on the bottom, generally in deep water, mostly more than 400 m. *C. coelolepis* inhabits deep water at depths of 270–3675 m (Compagno *et al.* 2005). *Echinorhinus* normally lives in deep water down to 1100 m, but may be encountered close to the surface (Compagno *et al.* 2005). *Squatina* lives on continental shelves, down to 300 m (Compagno *et al.* 2005). *Hemiscyllium* tends to live in shallow water (Compagno *et al.* 2005), as does *Nebrius ferrugineus*, but may be found as low as 70 m (Compagno *et al.* 2005). *Heterodontus* species tends to live in shallow water, but *H. portusjacksoni* can be found down to 275 m. *Carcharias*

inhabits shallow warm to temperate waters from the surf zone to the offshore reefs (1–190 m of depth), but mainly occur within 15–25 m (Compagno *et al.* 2005). *Scyliorhinus* generally lives close to the bottom. *S. canicula* lives down to 110 m on continental shelves and upper slopes, but other species of *Scyliorhinus* inhabit both shallower and deeper waters (Compagno *et al.* 2005). Of the extinct species, *Paraorthacodus* may have preferred cool shallow water (Siverson 1992b), and *Proetmopterus* has been found in a shallow water deposit (Siverson and Cappetta 2001).

Although care should be taken when inferring the palaeoecology from the behaviour of the modern species, as the behaviour of modern relatives may not correspond to their extinct relatives. If, however, the behaviour of modern species is used as a proxy and we accept the dangers of an actualistic approach, we can conclude that the chalk and the Fiskeler were deposited in intermediate to deep water. Recent species of *Hemiscyllium* and *Nebrius* tend to prefer shallow water, but the majority of the other species lived in or above deep water.

This leaves us with the question, 'Why did the fauna change before the K/T boundary?' The boundary event is placed at the Iridium Anomaly, which occurs at the bottom of the Fiskeler layer III (Alvarez, *et al.* 1980; Alvarez *et al.* 1984), so a misinterpretation of the position of the boundary is unlikely. The cause for the massive drop in

diversity before the boundary could be an artefact of sample size, but is more likely attributed to a change in palaeobathymetry. Evidence for such a change in the palaeobathymetry comes from an oxygen isotope analysis (J. S. Adolfsson *et al.* in prep.), which suggests that an increase in sea level occurred in the latest Maastrichtian. This was followed by a fall in sea level during the early Danian, resulting in a return of the majority of the species that had disappeared prior to the boundary. This hypothesis is supported by studies of foraminifera conducted by Schmitz *et al.* (1992) at Stevns Klint and Keller *et al.* (1993) from Nye Kløv. O'Dea *et al.* (2011) also concluded that environmental changes occurred prior to the boundary in a study of bryozoans from Nye Kløv, which may also be related to the local relative changes in sea level.

CONCLUSIONS

This study has demonstrated that the majority of species present in the Danish Maastrichtian chalk did not become extinct and clearly persisted across the boundary into the Danian. It does not cast any light on the mechanism of the extinctions and, due to its stratigraphic precision, cannot be meaningfully compared with other tables quantifying faunal change at the boundary.

The Maastrichtian chalk and the Fiskeler appear to have been deposited in an intermediate to deep water environment, and the specimens collected from the individual beds are not reworked. The diverse chondrichthyan fauna at Stevns Klint experienced a massive drop in diversity prior to the K/T boundary, possibly due to an increase in sea level. The fauna recovered quickly, and the majority of species that disappeared prior to the boundary reappeared during the early Danian, so they must have had a refugium nearby. The chondrichthyans in the Danish Basin experienced a much lower generic extinction rate (23 per cent) than the 57 per cent reported from Morocco by Noubhani and Cappetta (1997). The cause of this difference is probably a combination of differences in sea level, with the Moroccan localities representing shallow water environments, which according to Kriwet and Benton (2004) were more seriously affected than faunas from deeper water settings. The absence of accurate dating and the degree of systematic attention received by the Moroccan fauna also make any comparisons uninformative. The results from Stevns Klint do support an extinction event, although much less than previously reported. However, some of the species, which became extinct, may have already disappeared prior to the boundary. *Notidanodon pectinatus*, *Pseudocorax affinis* and *Squalicorax pristodontus* were collected several metres below the uppermost Maastrichtian marl, so the exact timing of their disappearances remains uncertain. In a study conducted by Håkansson

and Thomsen (1999) at Nye Kløv on the reappearance of the invertebrate fauna following the extinction event, it was concluded that the early Danian fauna was an impoverished version of that of the late Maastrichtian, in keeping with our results with the sharks and rays.

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APPENDIX 1

Geographical coordinates of localities cited in the text

Dania: Active quarry in northern Jutland [56°41'15"N, 010°03'09"E].

Hasselø By Kalkværk: A small abandoned quarry on Falster [54°43'31"N, 011°54'24"E].

Højerup: Sea cliffs in central stretch of the Stevens Klint section [55°16'45"N, 012°26'46"E].

Kjølby Gaard: An abandoned quarry in Thy [57°1'59"N, 008°48'21"E].

Knøsen: Sea cliffs at southern end of the Stevens Klint section [55°16'32"N, 012°26'31"E].

Kulstirenden: Sea cliffs at northern end of the Stevens Klint section [55°21'00"N, 012°26'30"E].

Møns Klint: Sea cliffs [54°57'59"N, 012°33'03"E].

Nye Klov: Abandoned quarry in northern Jutland [57°0'49"N, 008°49'37"E].

Nyvang Gaard: Small abandoned quarry in northern Jutland [c. 56°31'N, 010°03'E].

Praesteskov: Sea cliffs at northern end of the Stevens Klint section [55°21'50"N, 012°25'08"E].

Rødvig: Sea cliffs at southern end of the Stevens Klint section [55°15'16"N, 012°23'20"E].

Stevns Kridtbrud quarry: Active quarry [55°19'20"N, 012°26'30"E].

Vokslev kalkgrav: Abandoned quarry in northern Jutland [56°57'49"N, 009°40'11"E].