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Neoselachians from the Danian (early Paleocene) of Denmark

JAN S. ADOLFSSSEN and DAVID J. WARD



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A diverse elasmobranch fauna was collected from the early Danian Rødvig Formation and the early to middle Danian Stevns Klint Formation at Stevns Klint and from the middle Danian Faxø Formation at Faxø, Denmark. Teeth from 27 species of sharks are described including the earliest records of *Chlamydoselachus* and *Heptranchias howelli* from Europe. The fauna collected at the Faxø quarry is rich in large species of shark including *Sphenodus lundgreni* and *Cretalamna appendiculata* and includes no fewer than four species of Hexanchiformes. The species collected yield an interesting insight into shark diversity in the Boreal Sea during the earliest Paleogene. The early Danian fauna recorded from the *Cerithium* Limestone represents an impoverished Maastrichtian fauna, whereas the fauna found in the slightly younger bryozoan limestone is representative of a pronounced cold water fauna. Several species that hitherto have only been known from the Late Cretaceous have been identified, clearly indicating that the K–T boundary was not the end of the Cretaceous fauna; it lingered and survived into the early Danian.

Key words: Chondrichthyes, Faxø Formation, *Cerithium* Limestone, Danian, Paleocene, Denmark.

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Introduction

Invertebrates from the early Danian *Cerithium* Limestone in Denmark have been the subject of several studies (Rosenkrantz 1939, 1966; Heinberg 1999; Rasmussen et al. 2005) as have those from the middle Danian limestone, the bryozoan limestone (Floris 1980; Bernecker and Weidlich 1990; Wilumsen 1995; Bernecker and Weidlich 2005). The vertebrate remains, however, have been left almost untouched, with the exception of a few papers on otoliths and shark teeth and remains of crocodylians and turtles from middle Danian deposits of the Faxø quarry (Davis 1890; Schwarzhan 2003; Bonde et al. 2008; Milàn et al. 2011). This paper will address the selachian fauna in these early Danian limestone rocks, which were deposited just above the K–T boundary clay (the Fiskeler) and provide us with a unique insight into the fauna of the Boreal realm shortly after the global mass extinction event.

Danian selachian faunas have been described from Europe (Herman 1977; Siverson 1993a, 1995), North Africa (Noubhani and Cappetta 1997), New Zealand (Mannering and Hiller 2008; Consoli 2009), and North America (Case 1996; Wroblewski 2004), but only a few studies include the

lowermost Danian. The middle Danian selachian faunas of Denmark and Sweden have been studied by Davis (1890), but there are several problems, as mentioned by Siverson (1992, 1995) regarding the age, origin and locality of the specimens. These include the species *Sphenodus lundgreni*, *Archaeolamna (Odontaspis) kopingensis*, but also his *Carcharodon ron-deletti*, as commented upon by Ravn (in Milthers 1908) and Bendix-Almgreen (1983), as this tooth presumably is from the Miocene of Malta. These problems with the Davis (1890) material could be because he did not collect the material himself, but bought it from local quarry workers.

Institutional abbreviations.—GMV, Geological Museum-vertebrate collection, Copenhagen, Denmark; MGUH, Museum Geologicum Universitatis Hafniensis, Copenhagen, Denmark; OESM, Østsjælland Museum, Faxø, Denmark; SNM, The Natural History Museum, Copenhagen, Denmark (Danish abbreviation).

Other abbreviations.—Br1, lower bryozoan limestone (Korsnæb Member); Br2, intermediate bryozoan limestone (Faxø Formation); Ce, *Cerithium* Limestone Member; D and NP, nannoplankton zones.

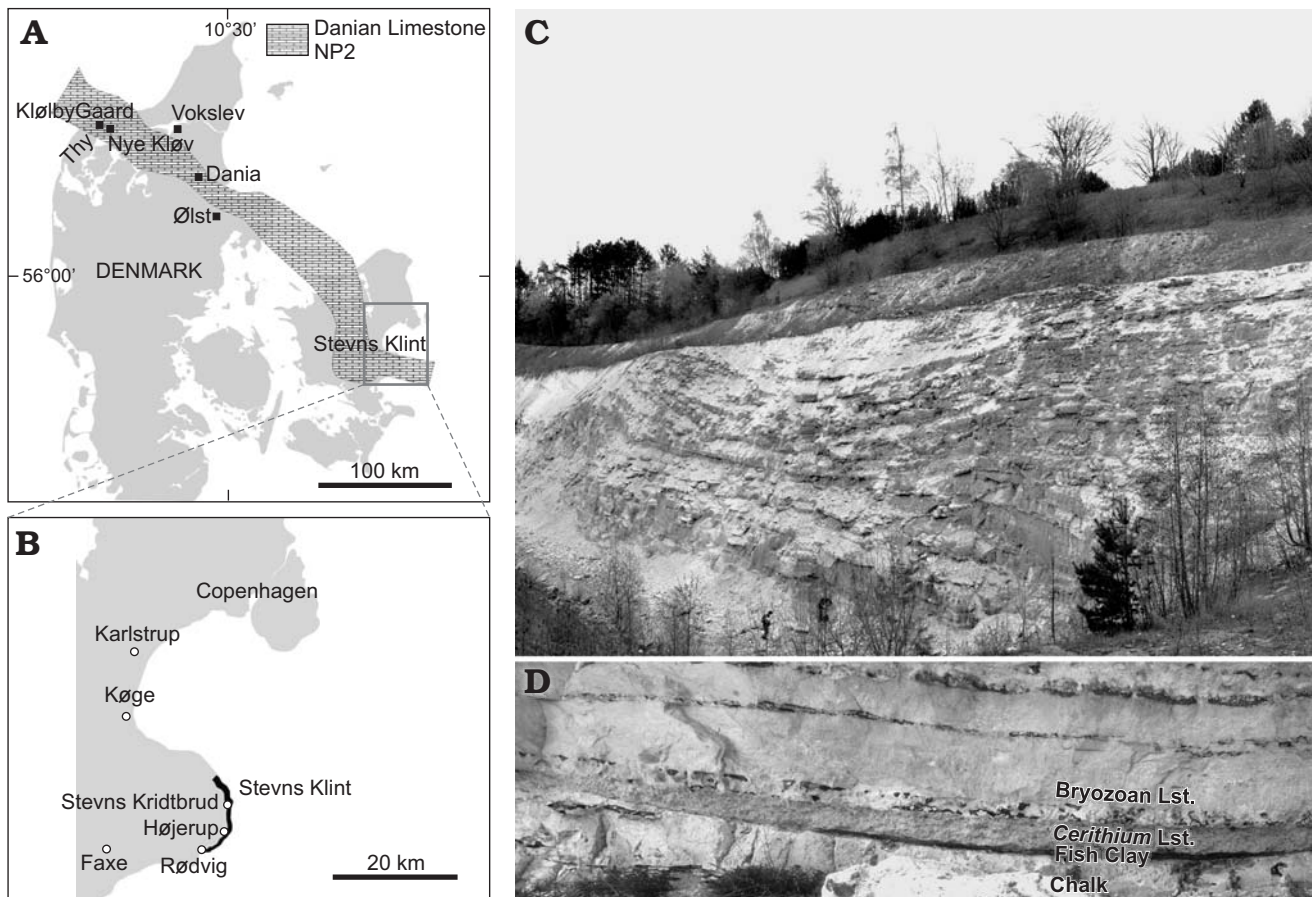


Fig. 1. **A.** Map of Denmark with the localities mentioned in the paper (black squares). The extent of the bryozoan limestone is based on Thomsen (1995). **B.** Map of south-eastern Sealand, with Stevns Klint marked as the dark grey line. **C.** View of coral bank south-western face of the Faxe quarry, the persons in the lower central part of the picture give an impression of the magnitude of the bank. **D.** Maastrichtian bryozoan inter-mound troughs, with the Maastrichtian Chalk, Fiskeler, *Cerithium* Limestone Member and the lowermost section of the middle Danian bryozoan limestone (Korsnæb Member). Picture from 50 m south of Højerup Church (thickness of the *Cerithium* Limestone 40 cm). Lst., limestone.

Geological setting

The *Cerithium* Limestone belongs to the Rødvig Formation and was named Ceritkalkstenen by Forchhammer (1825) from the presence of moulds of cerithiid-like gastropod *Metacerithium balticum*. Forchhammer (1835) later changed the name of this limestone to Faxekalken as he mistakenly took it to be the same as the middle Danian bryozoan limestone in the village of Faxe. The *Cerithium* Limestone was deposited in a wide belt from Stevns Klint in the south-east to Thy in the north-west, with a maximum width of around 100 km (Fig. 1A; Thomsen 1995), and with a thickness from around 0.3 m at Stevns Klint to 5.5 m at Nye Kløv, Thy. The limestone is well exposed along almost the entire 12.8 km of Stevns Klint and at Karlstrup kalkgrav and also at some localities in the north-western part of Denmark, Dania, Vokslev and Kjølbjgaard (Fig. 1A, B). The *Cerithium* Limestone is underlain by the Fiskeler, and overlain by the bryozoan limestone above an erosional hardground, indicating a hiatus. It should be noted that this hardground diminishes towards the west and is not present at Thy.

The *Cerithium* Limestone was deposited during the low-

ermost part of the Danian in the nannofossil fauna D1 and the lower part of D2 (Perch-Nielsen 1979) corresponding to NP1 of Martini (1971). The limestone is probably chemically precipitated according to Hansen (1990) and is mainly composed of uniform carbonate crystals in the silt fraction (Thomsen 1995). The fauna mainly consists of aragonite-shelled gastropods and bivalves preserved as moulds and calcite bivalves (Heinberg 2005; Machalski and Heinberg 2005). The limestone is heavily bioturbated by *Thalassinoides* and *Spongliomorpha*-type burrows and is interpreted to have been deposited in shallow water based on both its invertebrate fossils and on its ichnofossils (Ekdale and Bromley 1984). The limestone was deposited above the boundary clay, but in the same Maastrichtian bryozoan inter-mound troughs as the Fiskeler at Stevns Klint, where the limestone is at its thinnest. Both the Maastrichtian chalk and the limestone are truncated by the hardground (Fig. 1D) that separates the *Cerithium* Limestone from the bryozoan limestone. At Stevns Klint the *Cerithium* Limestone is slightly diachronous with the older part south at Rødvig and younger part further north as demonstrated by Rasmussen et al. (2005) using foraminiferal biozonation. In contrast, Nielsen (1917: 7) thought that it was

the reverse and that the *Cerithium* Limestone was reworked Maastrichtian chalk. The *Cerithium* Limestone is thought to have had a much larger distribution, but this is difficult to estimate following erosion. The *Cerithium* Limestone was thought to have been deposited in shallow water (Hansen 1990), but recent isotopic data suggests that it was deposited in a water depth in excess of 200 m (JSA unpublished data).

The precise extent of the hiatus below the bryozoan limestone (Korsnæb Member) is uncertain, but this unit was deposited during NP2–NP3 (Martini 1971) or coccolith zones D2–D3 of Perch-Nielsen (1979) and Thomsen (1995), the early Danian. At Stevns Klint, a thickness of up to 20 m is preserved, which is characterized by large asymmetrical bryozoan mounds reaching dimensions of 5–9 m high and 50–100 m long (Surlyk et al. 2006). Younger sections (early–middle Danian) of the bryozoan limestone are preserved and accessible at Faxø quarry, following a hiatus above the section at Stevns Klint. Within the quarry, bryozoan and coral mounds and bank mounds can attain very large size, of up to 200 m long and at least 30 m high (Bernecker and Weidlich 2005). The corals found in the quarry are low-diversity azooxanthellate coral communities of mainly dendroid scleractinians that are assumed to have flourished in a cool and deep water environment (Bernecker and Weidlich 2005). The bryozoan limestone is assumed to have been deposited at a depth of more than 200 m (Bernecker and Weidlich 1990), well below the photic zone. Bjerager and Surlyk (2007) have given a very detailed account of the bryozoan limestone at Stevns Klint, whereas our present understanding of the younger section of the unit at Faxø is still poor and needs further study.

Material and methods

Jan Rees (Karlstad, Sweden) collected 283 kg of *Cerithium* Limestone at Stevns Kridtbrud and JSA collected two samples of bryozoan limestone at Kulstirenden (100 kg) and at the Faxø quarry (160 kg) respectively. The samples of *Cerithium* Limestone, which was moderately lithified, were chopped into 5 cm blocks and processed in buffered acetic acid following the procedure of Jeppsson et al. (1999) at Lund University, Sweden. The samples of bryozoan limestone were processed by the method described by Nielsen and Jakobsen (2004). Residue from the 250 µm sieving was picked for vertebrate remains and yielded several thousand, mostly fragmented, but also some complete selachian teeth and dermal denticles. Small samples (5–10 kg) from Kjølbj Gaard (Thy) and the Dania Kridtgrav, were also collected and processed with acetic acid following the procedure of Jeppsson et al. (1999) and sieved through 250 µm sieves, but did not yield any teeth. In general, sieves with a mesh size of 500 µm should be adequate but to ensure that no dermal denticles were missed, a mesh size of 250 µm was used. Almost all teeth have been bioeroded by microbial organisms and a majority of the material is not identifiable due to either fracturing or erosion and only material that has been identified has been counted. In the majority

of the larger specimens from the bryozoan limestone, the root was either missing or preserved as a cast of chalk. However, smaller specimens were usually preserved with their roots intact. Most of the specimens have been gold-coated and imaged with a SEM (FEI Quanta 200 Inspect), but larger specimens were imaged with a Nikon D7000 DSLR with Carl Zeiss objectives and digitally stacked to obtain greater depth of field with Helicon Pro© software.

All specimens figured here are deposited at the Natural History Museum of Denmark, Copenhagen or at Geomuseum Faxø, Faxø, Denmark. Tooth terminology largely follows Cappetta (1987, 2012).

Systematic palaeontology

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

Family Paleospinacidae Regan, 1906 sensu Klug, 2010

Genus *Synechodus* Woodward, 1888

Type species: Synechodus dubrisiensis (Mackie, 1863) from the Late Cretaceous of England.

Synechodus faxensis (Davis, 1890)

Fig. 2A–C.

1890 *Odontaspis faxensis* sp. nov.; Davis 1890: 390, pl. 38: 26.

1929 *Synechodus faxensis* (Davis); Leriche 1929: 232.

1976 *Synechodus hesbayensis* (Davis); Glickman 1976: pl. 21: 19, 20, 34.

1977 *Synechodus faxensis* (Davis); Herman 1977: 36, pl. 1: 9.

Material.—One complete tooth from a juvenile (OESM-10046-17) and two incomplete teeth (MGUH 1401, OESM-10046-16) including the specimen depicted by Davis (1890) of the species from the Br2 in Faxø. A dozen more in private collections have been studied.

Description.—Teeth with a tall main cusp and two to four pairs of lateral cusplets on the deflecting shoulders. The main cusp has smooth labial and lingual faces, whereas the cusplets may carry a few irregular vertical folds on both faces. The cutting edge appears to be continuous and strong. The base of the crown overhangs the root and displays a strong concave indentation in anterior teeth but less so in laterals and posteriors. The labial face is convex and the lingual face is strongly so. Neither of the adult specimens has completely preserved roots, but the remnants of the roots exhibit a pseudopolyaulacorhize vascularization (Herman 1977). Juveniles have much coarser vertical folds on both the labial and lingual faces, with the folds covering the lower two thirds of the labial face and almost all of the lingual face.

Remarks.—Davis (1890) described this species as being smooth on both faces. This is incorrect, as the specimen depicted by Davis (1890: pl. 38: 26) does show weak folds on both faces. Anterior teeth may have fewer folds than observed in lateral teeth and the folds become weaker in larger specimens. Leriche (1927) commented that he has no doubt that the specimens from the Maastrichtian of Belgium and the Netherlands were the same species as Davis' (1890) tooth from Faxe.

Ward (2010) synonymised two mid-Cretaceous species of *Synechodus*, *S. nitidus* (Woodward, 1911) and *S. tenuis* (Woodward, 1889), with *S. dubrisiensis* (Mackie, 1863). This species has a similar distribution of folds as *S. faxensis*, that is anterior and presumed lower teeth display less folding.

The poorly known mid-Paleocene species *Synechodus hesbayensis* (Casier 1943), listed erroneously by Cappetta (2006: 105) as a junior synonym of *Paraorthacodus eoacenus* (Leriche 1902), differs from *S. faxensis* in having more developed vertical ridges on the labial crown face. Further study may demonstrate that this is a positional or ontogenetically variable feature and that *S. faxensis* is the senior synonym.

Stratigraphic and geographic range.—Late Maastrichtian of Denmark and the Netherlands to the Thanetian of the Urals (Herman 1977; Glickman 1957).

Family Orthacodontidae Glickman, 1957

Genus *Sphenodus* Agassiz, 1843

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

Sphenodus lundgreni (Davis, 1890)

Fig. 2D–G.

1890 *Oxyrhina lundgreni* sp. nov.; Davis 1890: 393, pl. 38: 9.
1957 *Eychlaodus lundgreni* (Davis 1890); Glickman 1957: pl. 1: 16.
1979 *Orthacodus lundgreni* (Davis 1890); Floris 1979: fig. 7.
1993 *Sphenodus lundgreni* (Davis 1890); Siverson 1993a: 28.

Material.—Four almost complete specimens (including the holotype), a further nine cusps in the collections of SNM (MGUH1406 holotype, MGUH 29822, MGUH 29823, MGUH 29824, GM1881-3326, GM1885-881, GMV2012-57 [batch number]), and dozens of specimens, many without roots, in private collections, all collected from the Br2 at Faxe.

Description.—Large monocuspid teeth (up to 60 mm high cusps). The cusp is tall, slender with strong deep folds covering the lower part of the labial face and with very short folds at the base of the lingual face, but folds may be lacking in some specimens. Both the faces are strongly convex. Anterior teeth are erect whereas lateral and posterior teeth are slanted towards the commissure, sometimes only in the upper part of the cusp. The majority of teeth display a strong sigmoidal curvature in lateral view, regardless of whether the anterior or posterior margin carries a strong cutting edge. The root is lacking in most teeth but most of the few preserved roots are low and wide with a concave base. Anterior teeth have much narrower roots (Fig. 2E).

Remarks.—By analogy with the Recent sand shark, *Carcharias taurus* Rafinesque, 1810, upper teeth are more likely to be sigmoid (Fig. 2D) and lower teeth more posteriorly recurved (Fig. 2E; Böttcher and Duffin 2000).

The teeth depicted by Mannering and Hiller (2008) from the Danian of New Zealand have much longer lingual folds and much more lingually protruding roots, characters which have not been observed in any of the Danish material. It is very likely that the material from New Zealand represents another species. None of the Danish specimens have lateral cusplets and the specimen depicted from New Zealand may be pathologic (Mannering and Hiller 2008: pl. 1: 6–9). Though *Sphenodus* may have been more common during the Jurassic, it has been found in the Maastrichtian of Antarctica (Richter and Ward 1990; Kriwet et al. 2006), but the material from Antarctica differs in that both the labial and lingual folds are very short compared to *S. lundgreni*, and is too poorly known to draw further conclusions on relationships.

The specimens depicted by Antunes and Cappetta (2002) from Angola appear to carry very similar folds as those in *S. lundgreni*, even though the Angolan material presumably is from the Campanian. The specimens depicted by Waldman (1971) from the early Paleogene of British Columbia, Canada are of too poor a quality for further comment.

Stratigraphic and geographic range.—*S. lundgreni* is known from the late Maastrichtian of Denmark to the middle Danian of Denmark and Sweden (Davis 1890). Teeth of *Sphenodus* sp. also occur in the Beltinge Fish Bed, basal Upnor Formation, Thanetian, in the UK and in the Thanetian at Shatrylisa, western Kazakhstan (DJW personal observation).

Order Hexanchiformes de Buen, 1926

Family Hexanchidae Gray, 1851

Genus *Hexanchus* Rafinesque, 1810

Type species: *Squalus griseus* Bonnaterre, 1788, Recent, worldwide distribution.

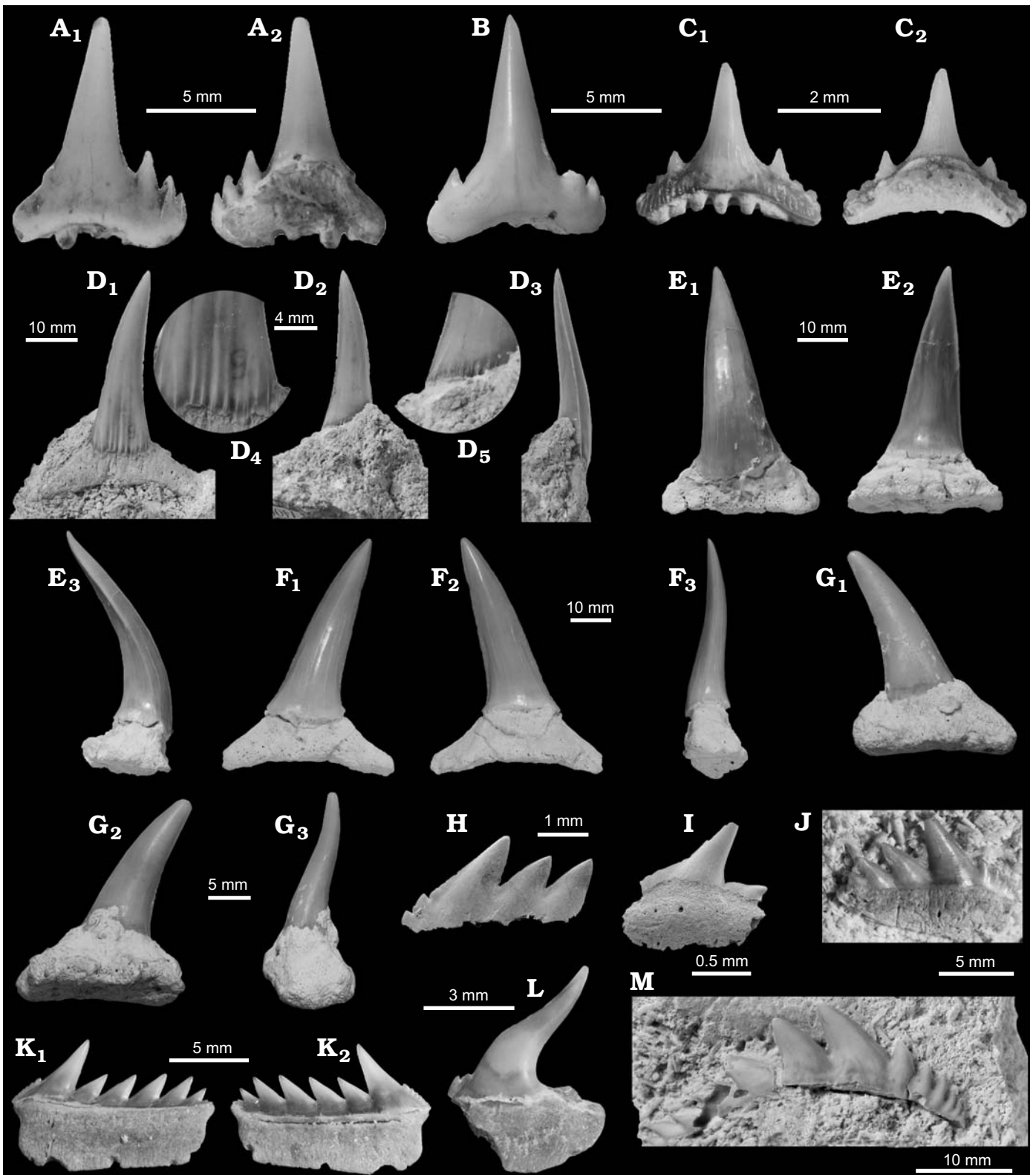
Hexanchus microdon (Agassiz, 1835)

Fig. 2H, I.

1835–44 *Notidanus microdon* sp. nov.; Agassiz 1835: 3, pl. 27: 1; 1843: 222; 1844: pl. 36: 1, 2.
1952 *Notidanus (Hexanchus?) microdon* Agassiz; Arambourg 1952: 40, pl. 1: 1–55.
1977 *Notidanus (Hexanchus?) microdon* Agassiz; Herman 1977: 98, pl. 3: 7.
2002 *Hexanchus microdon* (Agassiz); Antunes and Cappetta 2002: 108, pl. 4: 3, 4.

Material.—Three almost complete upper jaw teeth (MGUH 29825, MGUH 29826, GMV2012-58) and two fragmentary teeth from the lower jaw collected from the Ce in Stevns

Fig. 2. *Synechodontiformes* and *Hexanchiformes* from the Danian of Stevns Kridtbrud and Faxe Kalkbrud. A–C. *Synechodus faxensis* (Davis, 1890). A. MGUH 1401, Type (Br2) anterior tooth in labial (A₁) and lingual (A₂) views. B. OESM-10046-16 (Br2) anterior tooth in labial view. C. OESM-10046-17 (Br2) lateral tooth in a juvenile in labial (C₁) and lin- →



gual (C₂) views. **D–G.** *Sphenodus lundgreni* (Davis, 1890). **D.** MGUH1406, holotype (Br2) anterior lateral tooth in labial (D₁), lingual (D₂), and distal (D₃) views, with magnification of folds (D₄, D₅, respectively). **E.** MGUH 29822 (Br2) anterior tooth in labial (E₁), lingual (E₂), and distal (E₃) views. **F.** MGUH 29823 (Br2) lateral tooth in labial (F₁), lingual (F₂), and mesial (F₃) views. **G.** MGUH 29824 (Br2) rare posterior tooth in labial (G₁), lingual (G₂), and mesial (G₃) views. **H, I.** *Hexanchus microdon* (Agassiz, 1843). **H.** MGUH 29825 (Ce) fragment from a lower jaw tooth. **I.** MGUH 29826 (Ce) fragment from an upper jaw tooth in lingual view. **J.** *Gladioserratus* sp., MGUH 29827 (Br2) in lingual view. **K, L.** *Heptranchias howelli* Reed, 1946. **K.** OESM-10046-14 (Br2) lower jaw tooth in labial (K₁) and lingual (K₂) views. **L.** OESM-10046-15 (Br2) upper jaw tooth in labial view. **M.** *Notidanodon brotzeni* Siverson, 1995, MGUH 1399 (Br2) crown of tooth.

Kridtbrud. Incomplete teeth of *Hexanchus* are common in the Faxø quarry (Br2).

Description.—The dentition in *Hexanchus* is both monognathic disjunct, dignathic and gynandric heterodont. Teeth from the upper jaw are strongly labio-lingually compressed with a prominent main cusp that is slightly inclined towards the commissure, with a flat labial face and a convex lingual face. The mesial cutting edge of the main cusp is only partly preserved, but fine serration is visible. A single low distal cusplet is present and strongly inclined towards the commissure. The distal end of the tooth is missing, so it is unclear whether there was a second distal cusp or not. The root is high and wide and labio-lingually compressed.

Teeth from the lower jaw are strongly labio-lingually compressed with a distally inclined main cusp. The main cusp is serrated on the lower of its half mesial cutting edge and is either straight or slightly sigmoid mesially on the upper half. The distal cutting edge is convex. The distal cusplets are distally inclined with convex mesial and distal cutting edges. The maximal number of distal cusplets observed was five, but it was in a broken specimen with clear signs of having had more.

Remarks.—The teeth are not well preserved but do not differ significantly from those referred to *H. microdon* from the Late Cretaceous chalks and from the Fiskeler. Of the two Recent species, *H. griseus* (Bonnaterre, 1788) and *H. nakamurai* (Teng, 1962), the dentition of *H. microdon* closely resembles those of *H. nakamurai* in having lower teeth with lower crowns making them relatively wider than those of *H. griseus* (Herman, Hovestadt-Euler, Hovestadt, and Stehmann, 1994).

The name *H. microdon* is problematic as it is applied to almost any *H. nakamurai*-like *Hexanchus* from the Late Cretaceous and early Paleogene. In particular, in Morocco it is conventionally used for all *Hexanchus* specimens in the Maastrichtian, Paleocene, and early Eocene, whereas in NW Europe it is restricted to the Cretaceous and *H. agassizi* is used for Paleocene and early Eocene specimens. A revision is required but it is beyond the scope of this paper. Teeth of *H. agassizi*, as the name is currently used, differ from those of *H. microdon* by their smaller size. *H. microdon* differs from *H. gracilis* (Davis, 1887) mainly in having more distal cusplets, up to ten in *H. microdon* versus up to six in *H. gracilis* (Cappetta 1980). All these differences could be due to a combination of ontogenetic and sexual dimorphism.

Stratigraphic and geographic range.—Maastrichtian in northern Europe to the Ypresian in Morocco (Cappetta 1980, 1987).

Genus *Gladioserratus* Underwood, Goswami, Prasad, Verma, and Flynn, 2011

Type species: *Notidanus aptiensis* Pictet, 1865; Aptian, Early Cretaceous, Apt, France.

Stratigraphic and geographic range.—*Gladioserratus* is known from the mid-late Cretaceous to possibly the early Eocene (if “*N.*” *seratissimus* is included in the genus).

Gladioserratus sp.

Fig. 2J.

Material.—Two almost complete specimens embedded in matrix (MGUH 29827, GMV2012-59) and four incomplete in a private collection, all collected from the Br2 in Faxø.

Description.—Labio-lingually compressed teeth with a triangular main cusp slanted towards the commissure and three cusplets distally diminishing in size. Mesial to the main cusp are five or six small mesial cusplets, which increase in size towards the main cusp. The distal part is missing in one tooth, but it does not appear to have had more than three cusplets. The root is compressed, with a convex mesial face (partly missing in the figured specimen). The basal edge of the root is also rounded, leaving a slightly triangular outline of the root in lingual view.

Remarks.—The teeth found in the quarry of Faxø are very similar to the teeth described by Siverson (1995: 5) and are presumably conspecific. Underwood et al. (2011) erected the new genus *Gladioserratus* to contain the Cretaceous species *N. aptiensis* (Pictet, 1865), distinguishing it from *Notorynchus* by its lower and mesially “rounded” root and by having more massive cusps and an evenly mesial serration. The material from SNM is embedded in matrix and the thickness is difficult to estimate, but is presumably less than 3 mm, and two incomplete specimens in a private collection are both less than 2 mm thick. As noted by Underwood et al. (2011) the Scandinavian material lies somewhere between *Gladioserratus* and *Notorynchus* as the root is much like the former but the crown is more like the latter with its cockscomb-like serration. As material is limited, we refrain from erecting a new species and agree with Underwood et al. (2011) that more material is needed before such a decision can be made. Teeth of the early Eocene species *Notorynchus seratissimus* (Agassiz, 1843) more closely approach those of *Gladioserratus* than Recent *Notorynchus* and should probably be included in *Gladioserratus*. In particular they possess a similar mesially and distally rounded root profile as seen in *Gladioserratus* and have fewer distal cusplets than Recent teeth of *Notorynchus*. The mesial cusplets (cockscomb), however, resemble more closely those of *Notorynchus* in being distinct and increasing in size as they approach the main cusp. In this, they are similar to the Scandinavian material. This feature is much less developed in juvenile teeth, where the mesial cusplets are less developed or virtually absent as in *G. aptiensis*.

Genus *Notidanodon* Cappetta, 1975

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

Notidanodon brotzeni Siverson, 1995

Fig. 2M.

1977 *Notidanus? loozi* Vincent: Herman 1977; 99, pl. 3: 8a.

1993 *Notorynchus seratissimus* (Agassiz); Cvancara and Hoganson 1993: 3, fig. 2X, AA, non W, Z.

1995 *Notidanodon brotzeni* sp. nov.; Siverson 1995: 6, fig. 2I.

Material.—A single partly preserved specimen (MGUH 1399) from the Br2 at Faxe and two fragmentary specimens in a private collection.

Description.—A labio-lingually compressed tooth with a main cusp and six mesial cusplets and six distal cusplets. The mesial cusplets increase in size towards the main cusp and are apico-distally directed with convex mesial cutting edges and concave distal cutting edges; the later feature dwindles toward the main cusp and the sixth mesial cusp has an almost straight distal cutting edge. The main cusp is inclined toward the commissure with a convex mesial cutting edge and a straight distal cutting edge. The two following distal cusplets after the main cusp have a similar morphology whereas the remaining cusplets appear to have a concave distal cutting edge mimicking the mesial cusplets. The crown-root boundary is apically convex. None of the teeth are preserved with roots.

Remarks.—Siverson (1995) differentiated *N. brotzeni* from *N. loozi* (Vincent 1876) on the basis of the distal cutting edge of both the mesial cusps, the main cusp and the distal cusplets. They are straight or concave in the former and convex in the latter. None of the material from Kazakhstan (Kordikova et al. 2001), New Zealand (Mannering and Hiller 2008) and France (Dutheil et al. 2006) that has been associated with *N. brotzeni* is sufficiently well preserved to be identified with absolute certainty as this species. An almost complete tooth illustrated by Floris (1979) from the Danish Paleocene appears unfortunately to have been lost. Teeth of *N. brotzeni* (or a very similar species) are fairly commonly collected from the Paleocene (presumed Selandian) of the Sidi Chenane mine, near Houribga, Morocco (DJW, personal observation). The reference by Siverson (1995) to a fragment figured by Arambourg (1952) from the Danian of Morocco is therefore supported, but it is too fragmentary to refer to a species. The Cretaceous species of *Notidanodon* (*N. lanceolatus*, *N. pectinatus*, and *N. dentatus*) differ from the species from the Paleogene (*N. brotzeni* and *N. loozi*) by the reduced size of the mesial cusplets and by the more distally directed distal cusps. The morphology of the Paleocene species is much closer to *Hexanchus* than to the Cretaceous species. Whether or not the species *N. brotzeni* and *N. loozi* should be included within *Notidanodon* is a matter of debate because the lower teeth differ considerably from those of the type species, *N. pectinatus* (Agassiz 1843).

Stratigraphic and geographic range.—*N. brotzeni* is known from the middle Danian (early Paleocene) of Denmark (Faxe) and the contemporaneous Limhamn quarry in Southern Sweden (Siverson 1995) as well as from the Paleocene of Morocco (Arambourg 1952).

Family Heptranchidae Barnard, 1925

Genus *Heptranchias* Rafinesque, 1810

Type species: *Squalus perlo* Bonnatere, 1788; Recent in tropical to temperate seas. Mainly deep water, but can also occur in shallow water (Compagno et al. 2005).

Heptranchias howellii (Reed, 1946)

Fig. 2K, L.

- 1890 *Notidanus microdon* Agassiz: Davis 1890; 380, pl. 38: 5.
 1946 *Notidanion howellii* sp. nov.: Reed 1946; 1, figs. 1–4.
 1974 *Heptranchias howellii* Reed; Welton 1974, 7, pl. 2: A, B.
 2006 *Heptranchias howellii* Reed; Adnet 2006: 18, pl. 1: 3–8.
 2008 *Heptranchias howellii* Reed; Mannering and Hillier 2008: 1345, text-fig. 4A, B
 2009 *Heptranchias howellii* Reed; Bienkowska-Wasiluk and Radwański 2009: 238, pl. 1: 1–5.

Material.—An almost complete lower antero-lateral tooth and an incomplete upper lateral tooth (OESM-10046-14, OESM-10046-15). Two incomplete lower antero-laterals and one upper anterior specimen are kept in a private collection, all collected from the Br2 in Faxe.

Description.—An upper lateral tooth (Fig. 2L), labio-lingually compressed with a long and acute strongly sigmoid main cusp, with mesial serration and a distal cusplet. The root has a rounded basal edge, but it is mesially damaged so the outline is uncertain.

The lower tooth (Fig. 2K) is strongly compressed labio-lingually with a strong triangular main cusp and six cusplets. The main cusp carries eight reduced mesial cusplets on the lower mesial face, increasing upwards in size. The first distal cusplet after the main cusp is slightly lower than number two, three and four, but twice the size of number five. The sixth distal cusplet is very small. The root is tall and mesio-distally elongated with a slightly damaged basal edge.

Remarks.—The contemporaneous middle Danian *Heptranchias* sp. from the Limhamn quarry in Sweden (Siverson 1995) differs from the Faxe specimen by the presence of numerous reduced mesial cusplets in the latter. Numerous mesial cusplets are also present in another tooth held in the private collection of Alice Rasmussen in Faxe (JSA, personal observation). Since the teeth are of the same size, around 13 mm wide and appear to have been in the same position in the lower jaw, the differences can hardly be solely due to ontogeny. The tooth figured by Cappetta (1981) as *H. howellii* from the early Eocene of Morocco displays five poorly developed mesial cusplets, similar to the Faxe specimen. A further 10 specimens from Morocco of similar size (12–15 mm) in the DJW collection display between four and six reduced mesial cusplets, varying from poorly developed to robust. Lower *Heptranchias* teeth from the early Oligocene of Poland show a similar degree of variation (Bienkowska-Wasiluk and Radwański 2009). Clearly the number and degree of development of mesial cusplets in lower teeth is not a reliable taxonomic character. Currently *Heptranchias* teeth are too intraspecifically variable to identify trends or groupings in order to separate them into separate species. In the lower teeth of the Recent *H. perlo* the mesial face of the main cusp carries one to five cusplets (Welton 1974) and it appears to have been the same in *H. howellii* (Reed 1946; Welton 1974; Adnet 2006) and in the *Heptranchias* sp. described by Waldman (1971). The Danian material from New

Zealand (Mannering and Hiller 2008) is too poorly preserved for comparison.

Stratigraphic and geographic range.—Middle Danian (early Paleocene) of Denmark to early Oligocene of Poland (Bieñkowska-Wasiluk and Radwański 2009), Danian (early Paleocene) of New Zealand (Mannering and Hiller 2008), and the Eocene and Oligocene of Oregon, USA (Welton 1974).

Family Chlamydoselachidae Garman, 1884

Genus *Chlamydoselachus* Garman, 1884

Type species: *Chlamydoselachus anguineus* Garman, 1884; Recent, globally northern hemisphere.

Stratigraphic and geographic range.—*Chlamydoselachus* is known from the Late Cretaceous, Campanian of Antarctica (Richter and Ward 1990) and Angola (Antunes and Cappetta 2002) to Recent.

Chlamydoselachus sp.

Fig. 3A.

Material.—A single incomplete tooth (MGUH 29828) collected in the Ce in Stevns Kridtbrud.

Description.—Tooth with three elongated cups of almost equal length. The cusps are sigmoid in lateral view and rather divergent. The median cusp is slightly inclined toward the commissure, whereas the mesial and the distal cusp are at a 45° angle with the basal face of the root. The enameloid is smooth, but may have very small wide indistinct depressions at the base of the labial face of the cusps. The cutting edges do not reach the base of the crown and the enameloid is not continuous between the cusps. Both the labial and the lingual faces of the cusps are very convex. There is no sign of strong vertical folds on the main cusps and no sign of cusplets in between the main cusps. The root is badly preserved, but appears to be wide and low and linguallly reduced. A transverse notch is visible in the basal face of the root. The tooth is 24 mm wide and 14 mm high. The tooth is probably a lateral tooth, as lateral teeth have divergent cusps, whereas anterior teeth have less divergent and more erect cusps (Pfeil 1983).

Remarks.—Fossil frilled sharks are poorly known, owing to the rarity of deep-water sediments where teeth can be recovered. However, owing to their unique morphology they are more likely to be described and figured than a lamniform tooth. Specimens are known from Antarctica (Richter and Ward 1990), Africa (Antunes and Cappetta 2002), Asia (Goto and Research 2004), New Zealand (Consoli 2009), North America (Welton 1979), and Europe (Davis 1887; Pfeil 1983; Adnet 2006; Fulgosi et al. 2009). The oldest known specimens are from the Campanian of Antarctica and Angola. Three different species were described from Angola by Antunes and Cappetta (2002) of which one species, *C. gracilis*, appears to be similar to *Chlamydoselachus*, whereas *C. goliath* is more reminiscent of the genus *Proteothrinax* (Pfeil 2012). The two genera were separated by Pfeil

(1983) on the lack of intermediate cusplets between the main cusps, size and being less linguallly inclined. Richter and Ward (1990) argued that differences between *Thrinax* (*Proteothrinax*) and *Chlamydoselachus* were within the variation of *Chlamydoselachus* and regarded it as a junior synonym of *Chlamydoselachus*. Both the first discovered fossil *Chlamydoselachus* (Lawley 1876) as well as *C. gracilis* described by Antunes and Cappetta (2002) and *C. tatere* (Consoli 2009) may lack intermediate cusplets and the lingual projection of the root appears to vary. This makes the basis for a separation into two genera quite unreliable. As specimens described as *Proteothrinax* may just be older and larger individuals of a sturdy *Chlamydoselachus* species, this is more a question of ontogenetic heterodonty than of different genera.

Order Squaliformes Goodrich, 1909

Family Squalidae Blainville, 1816

Genus *Squalus* Linnaeus, 1758

Type species: *Squalus acanthias* Linnaeus, 1758; Recent, temperate waters worldwide.

Squalus gabrielsoni Siverson, 1993b.

Fig. 3B–E.

1993 *Squalus gabrielsoni* sp. nov.; Siverson 1993b: 8, pl. 2: 1–8.

Material.—Six teeth from the Ce of Stevns Kridtbrud (MGUH 29829, MGUH 29830, GMV2012-60 [batch number]), two teeth and 13 fragments from the Br1 at Kulstirenden (MGUH 29831, MGUH 29832, GMV2012-61 [batch number]), and two teeth from the Br2 at Faxe (GMV2012-62).

Description.—The heterodonty in Squalidae is moderately monognathic. Monocuspid teeth show a cusp strongly declined towards the commissure and a long slightly irregular mesial cutting edge. The cusp is triangular and may be gently turned upward in males. The distal heel is long and convex, joining the cusp in a notch. The labial face of the crown is smooth and convex with median apron. The apron is elongated with parallel edges reaching well below the basal edge of the root. The lingual face of the crown is smooth with a prominent mesially twisted uvula. The labial face of the root is low, with several foramina below the crown-root junction. The basal face of the root is in general almost flat with the axial foramina fused into an infundibulum. Anterior and upper teeth are narrower and higher than lateral and posterior teeth. Teeth reaching up to 3 mm in width and 2 mm in height.

Remarks.—Differs from *S. minor* (Leriche 1902) in having irregular cutting edges and a more demarcated apron and from *S. smithi* (Herman 1982) in having an apron with almost parallel faces, whereas *S. smithi* has a triangular apron. *S. crenatidens* (Arambourg 1952) differs from *S. gabrielsoni* in the shape of the apron, which is triangular in the former and the strongly serrated cutting edge of *S. crenatidens*. The specimens depicted as *S. minor* by Case (1996) from the Paleocene of New Jersey, USA resemble the Danish material

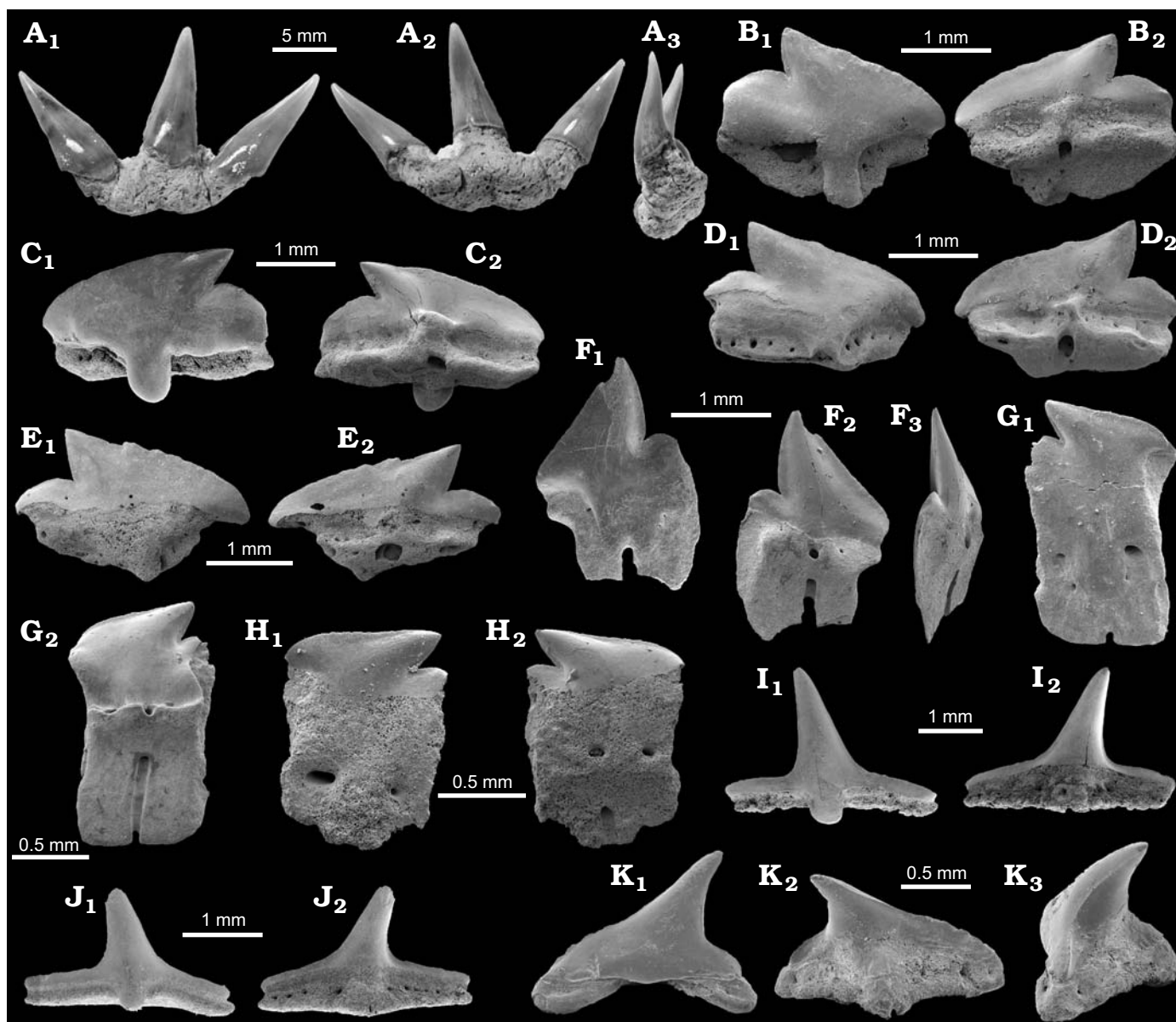


Fig. 3. Hexanchiformes, Squaliformes, and Squatiniformes from the Danian of Stevns Kridtbrud, Kulstirenden, and Faxe kalkbrud. **A.** *Chlamydoselachus* sp., MGUH 29828, DK635 (Ce) lateral tooth in labial (A₁), lingual (A₂), and distal (A₃) views. **B–E.** *Squalus gabrielsoni* Siverson, 1993. **B.** MGUH 29829 (Ce) lower anterior tooth in labial (B₁) and lingual (B₂) views. **C.** MGUH 29830 (Ce) lower lateral tooth in labial (C₁) and lingual (C₂) views. **D.** MGUH 29831 (Br1) lateral tooth in labial (D₁) and lingual (D₂) views. **E.** MGUH 29832 (Br1) lateral tooth in labial (E₁) and lingual (E₂) views. **F.** *Squaliodalatias* sp., MGUH 29833 (Ce) lateral tooth in labial view (F₁), lingual (F₂), and distal (F₃) views. **G, H.** *Centroscymnus praecursor* Müller and Schöllmann, 1989. **G.** MGUH 29834 (Ce) lower tooth in labial (G₁) and lingual (G₂) views. **H.** MGUH 29835 (Ce) lower tooth in labial (H₁) and lingual (H₂) views. **I, J.** *Squatina* sp. **I.** MGUH 29836 (Ce) lateral tooth in labial (I₁) and lingual (I₂) views. **J.** MGUH 29837 (Ce) lateral tooth in labial (J₁) and lingual (J₂) views. **K.** *Parasquatina cappettai* Herman, 1982, MGUH 29838 (Ce) tooth in labial view (K₁), lingual (K₂), and distal (K₃) views.

and may be conspecific. The separation of several species of *Squalus* is rather difficult owing to the very conservative morphology of the genus and ontogenetic heterodonty. In particular, the shape of the apron has been used as a character for defining species within Squalidae, which itself is subject to ontogenetic variation. The use of the fusion of the axial foramina into an infundibulum is also unreliable, as this appears to be a very variable character.

Stratigraphic and geographic range.—Mid-Maastrichtian (Siverson 1993b) to middle Danian of southern Scandinavia.

Family Dalatiidae Gray, 1851

Genus *Squaliodalatias* Adnet, Cappetta, and Reynnders, 2006

Type species: *Squaliodalatias weltoni* Adnet, Cappetta, and Reynnders, 2006; Lutetian (middle Eocene), southwest France.

Stratigraphic and geographic range.—Campanian (Late Cretaceous) of Lithuania (Dalinkevicius 1935), Paleocene of California (Welton 1978) and middle Eocene of France (Adnet 2006). Also probably in the Oligocene of California

and Miocene of France and Slovakia; see Underwood and Schlogl (2013).

Squaliodalantias sp.

Fig. 3F.

Material.—A single incomplete lower tooth from the Ce of Stevns Kridtbrud (MGUH 29833).

Description.—This tooth is strongly labio-lingually compressed, with a prominent principal cusp. The slightly triangular cusp has almost straight mesial cutting edge whereas the distal cutting edge is convex. The distal cutting edge and the small convex distal heel join into a notch. The labial face of the crown is slightly convex with a large and flat apron, the extremity of which is bifid, split by the labial marginal foramen and mesially delimited by the interlocking hollow. The lingual face is more convex than the labial face and the uvula is reduced to a small convexity in the crown-root junction. The mesial edge of the root is indented, the basal edge is damaged, but the labial marginal foramen is visible. The basal face of the root is large, labio-lingually concave and separated by the median lingual duct, which is connected to the median lingual foramen. The lingual face is limited to the minor transverse lingual bulge with the central foramen and a small mesio-lingual foramen. The distal lingual interlocking is apicobasally elongated and narrow. The tooth is 1.6 mm wide and 2.6 mm high.

Remarks.—Teeth described as *Centrophorus* (?) *balticus* by Dalinkevičius (1935) were referred to *Squaliodalantias* by Adnet et al. (2006) as were similar specimens from the Paleocene of California (Welton 1979). There are some differences between the specimens described here and the specimens described by Adnet (2006) and Adnet et al. (2006), Dalinkevičius (1935), and Welton (1979) and the assignment of the above mentioned specimens to the same genus is open to discussion, due to a lack of material.

Family Somniosidae Jordan, 1888

Genus *Centroscymnus* Bocage and Capello, 1864

Type species: *Centroscymnus coelolepis* Bocage and Capello, 1864; Recent with a wide distribution, found in the Atlantic, Indian, and Pacific oceans.

Centroscymnus praecursor Müller and Schöllmann, 1989

Fig. 3G, H.

1989 *Centroscymnus praecursor* sp. nov.; Müller and Schöllmann 1989: 15, pl. 2: 2–8, pl. 5, figs. 6–8.

1993 *Centroscymnus praecursor* Müller and Schöllmann; Thies and Müller 1993: 100, figs. 16, 17.

2010 *Centroscymnus praecursor* Müller and Schöllmann; Hübner and Müller 2010: 440, fig. 3f–k.

Material.—Two lower teeth and five fragments from the Ce of Stevns Kridtbrud (MGUH 29834, MGUH 29835, GMV2012-63 [batch number]).

Description.—Teeth with moderate monognathic heterodon-

ty and strongly dignathic heterodonty. Labio-lingually strongly compressed teeth in general rectangular and approximately twice as high as wide. The cusp is strongly inclined toward the commissure, with an irregular mesial cutting edge. The distal heel is short and convex joining the main cusp in a notch. The labial face of the crown is flat with a large flat apron. The lingual face of the crown is low and smooth. The labial face of the root is low with two pairs of marginal foramina on each side of the apron. The basal edge of the root is almost straight, and divided by a median notch. The basal face of the root is large, covering almost half of the entire tooth, and divided by the median lingual duct, which is connected to the median lingual foramen. The lingual face of the root is limited to the transverse bulge with the central foramen and a mesio-lingual foramen. The labial interlocking hollow is deep in the crown and decreases along the mesial face of the tooth, reaching almost the basal edge of the root. The lingual interlocking hollow is apically limited by the distal heel and reaches basally almost down to the basal edge of the root. Teeth reaching 2 mm in height and 1 mm in width.

Remarks.—Teeth of *Centroscymnus praecursor* are known from the Campanian of north-west Germany (Herman 1982; Müller and Schöllmann 1989). Whether the squaloids already were deep-water species in the early Late Cretaceous as stated by Klug and Kriwet (2010) is debated: although most living squaloids are deep-water, not all are (Compagno et al. 2005), nor are all the locations of fossil squaloids from deep-water facies (Siverson 1993b).

Stratigraphic and geographic range.—Campanian (Late Cretaceous) of North-West Germany (Herman 1982; Müller and Schöllmann 1989; Hübner and Müller 2010) to the Danian (early Paleocene) of Denmark.

Order Squatiniformes Buen, 1926

Family Squatinidae Bonaparte, 1838

Genus *Squatina* Duméril, 1806

Type species: *Squalus squatina* Linnaeus, 1758; Recent, North East Atlantic, Mediterranean, and Black Sea.

Squatina sp.

Fig. 3I–J.

Material.—Four teeth collected from the Ce of Stevns Kridtbrud (MGUH 29836, MGUH 29837, GMV2012-64 [batch number]) and a few specimens in private collections from the Br2 of Faxe.

Description.—Monocuspid teeth with a long narrow elongated main cusp with continuous cutting edges. The shoulders are almost horizontal and long and low. The labial face of the crown is convex and smooth, with a well-demarcated apron that projects below the basal face of the root. The lingual face of the crown is strongly convex and smooth. The labial face of the root is low and wide and the basal face of the root is flat. The lingual face of the root has a protuberance with a foramen

and several foramina below the crown-root junction on the shoulders. Teeth reaching 2.7 mm in height and 3 mm in width.

Remarks.—The separation of individual species of *Squatina* is extremely difficult (Dalinkevičius 1935; Cappetta 1987; Rees 2005). *Squatina cranei* (Woodward 1888) and *S. decipiens* (Dalinkevičius 1935) from the Late Cretaceous and earliest Paleocene were demonstrated to be synonyms (Guinot et al. 2012), the former being based on the teeth of juveniles and the latter, adults. This species demonstrates a higher degree of heterodonty than seen in Recent *Squatina* and was therefore placed in a separate subgenus, *Cretascyllium* Guinot et al. 2012. It is probable that these specimens belong to *S. cranei*, however, while evidence of the heterodonty is absent from these specimens, they are better left in open nomenclature.

Stratigraphic and geographic range.—*Squatina* ranges from the late Jurassic to Recent, Worldwide. It is most likely that it will be subdivided into separate genera or subgenera.

Genus *Parasquatina* Herman, 1982

Type species: *Parasquatina cappettai* Herman, 1982; Maastrichtian, Hemmoor North-West Germany.

Remarks.—Whether *Parasquatina* is a genus of Squatinidae is a matter of debate (see Guinot et al. 2012).

Parasquatina cappettai Herman, 1982

Fig. 3K.

1982 *Parasquatina cappettai* sp. nov.; Herman 1982: 132, text-fig. 1; pl. 1: 3; pl. 3: 2.

Material.—A single tooth from the Ce in Stevns Kridtbrud (MGUH 29838).

Description.—A monocuspid tooth, with the main cusp triangular and inclined towards the commissure and slightly distally twisted. The mesial shoulder is broader and more convex than the distal one. The labial face is smooth and convex, with a median protuberance that may be the remnants of an apron. The lingual face of the crown is smooth and very convex. The labial face of the root is low and the basal face is flat with a large central foramen. The lingual face of the root is high and broad with a protuberance with a central foramen. Three foramina are present below the mesial shoulder and a single foramen below the distal shoulder. It is not possible to confirm whether an uvula is present or not because of bioerosion.

Remarks.—Until the papers by Guinot et al. (2012) and Bourdon et al. (2011), *Parasquatina* was only known from Herman (1982) and in a short comment by Underwood and Ward (2008). Guinot et al. (2012) described two new species of *Parasquatina*; *P. justinensis* from the middle Turonian of France and *P. jarvisi* from the late Santonian of France and Britain. Guinot et al. (2012) separate *P. justinensis* from *P. cappettai* by the lack of a well-developed apron and the presence of a labial protuberance and more robust root branches in the latter and *P. jarvisi* from *P. cappettai* by a lesser marked cutting edge, a longer apron and stronger labial overhang.

The specimen found in the *Cerithium* Limestone resembles the specimen depicted by Herman (1982) and is the youngest known *Parasquatina* specimen.

Stratigraphic and geographic range.—Late Cretaceous: mid-Turonian of France (Guinot et al. 2012), Santonian of England, France, and the USA (Underwood and Ward 2008; Bourdon et al. 2011; Guinot et al. 2012), late Maastrichtian of Germany (Herman 1982); Danian (early Paleocene) of Denmark.

Order Orectolobiformes Applegate, 1972

Family Hemiscyllidae Gill, 1862

Genus *Hemiscyllium* Smith, 1837

Type species: *Squalus ocellatus* Bonattere, 1788; Recent, New Guinea and Australia.

Hemiscyllium hermani Müller, 1989.

Fig. 4A–E.

1982 *Hemiscyllium* sp.; Herman 1982: 141, pl. 2: 4.

1989 *Hemiscyllium hermani* sp. nov.; Müller, 1989: 35, pl. 7: 2–7.

Material.—28 teeth from the Ce of Stevns Kridtbrud (MGUH 29839, MGUH 29840, GMV2012-65 [batch number]) and eight teeth from the Br1 of Kulstirenden (MGUH 29841, MGUH 29842, MGUH 29843, GMV2012-66 [batch number]).

Description.—Dentition with monognathic heterodonty. Monocuspid teeth with a large crown and a triangular cusp. The cusp is elongated in anterior teeth and short in lateral and posterior teeth. The crown has a pair of prominent shoulders in anterior teeth whereas the shoulders are deflecting in lateral and posterior teeth. The labial face of the crown is flat and smooth and has a semicircular apron in anterior teeth, whereas it is often bifid in lateral and posterior teeth. The crown strongly overhangs the root. The lingual face of the crown is low and convex and may carry some short folds below the shoulders. The root is bilobed with widely diverging lobes. The basal face is flat with a foramen and the lingual face of the root is high with a median protuberance showing a small central foramen. One or several foramina may be present below the crown-root junction on the shoulders. Anterior teeth tend to be more symmetrical than lateral and posterior teeth and some anterior teeth may have small remnants of cusplets on the shoulders. Teeth reaching 1 mm in height and 0.8 mm in width.

Remarks.—It is not possible to make an informed comparison between this species and *Hemiscyllium daimeriesi* (Herman, 1972) due to the rarity and poor illustration of the latter. *Hemiscyllium bruxelliensi* (Herman and Crochard, 1977) can be separated from *H. hermani* as the former is more massive and has lateral cusplets.

Stratigraphic and geographic range.—From Campanian and Maastrichtian (Late Cretaceous) of North Germany (Herman 1982; Müller 1989) to Danian (early Paleocene) in Denmark.

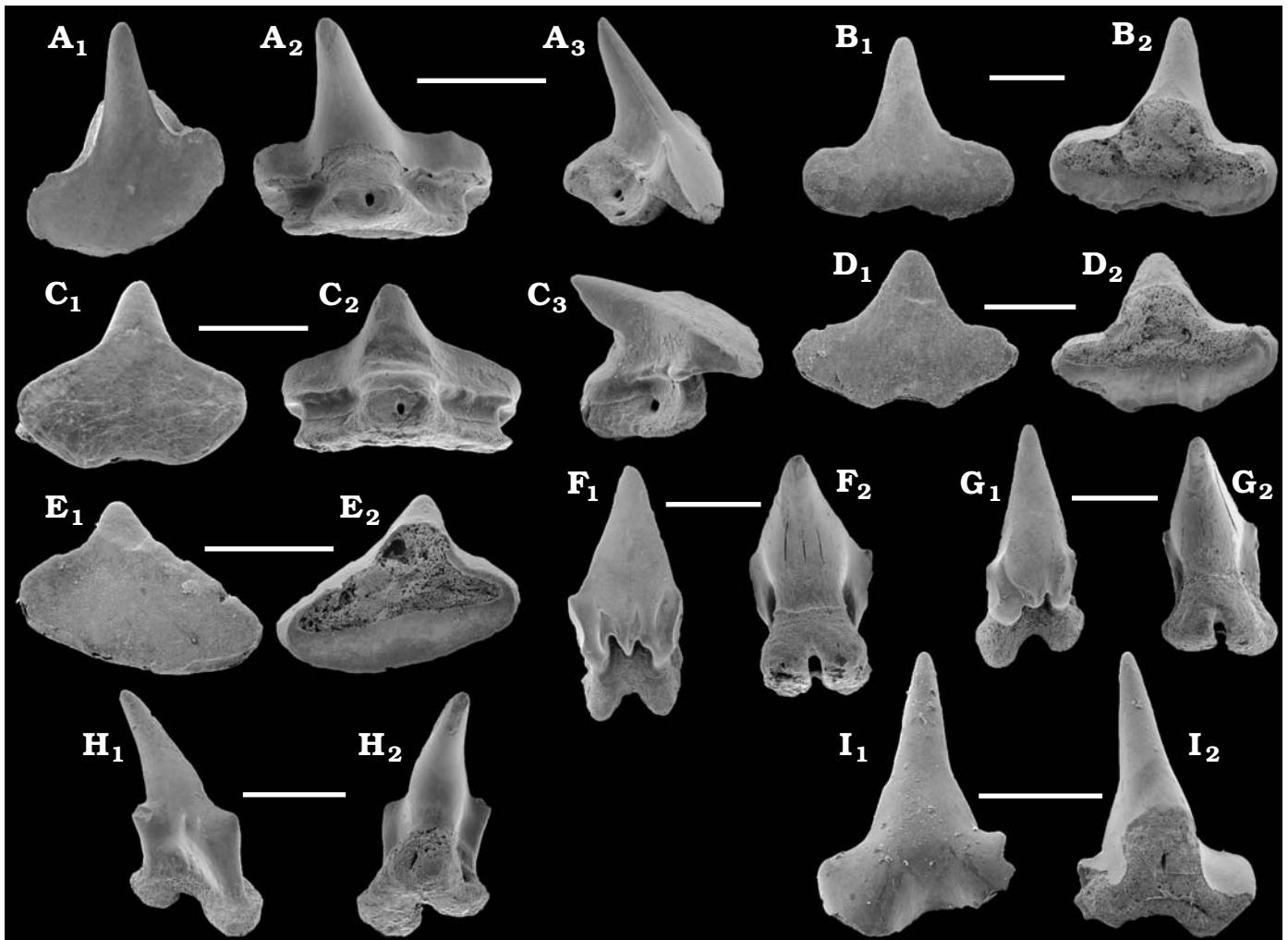


Fig. 4. Orectolobiformes from the Danian of Stevns Kridtbrud, Kulstirenden, and Faxø kalkbrud. **A–E.** *Hemiscyllium hermani* Müller, 1989. **A.** MGUH 29839 (Ce) anterior tooth in labial (A₁), lingual (A₂), and lateral (A₃) views. **B.** MGUH 29841 (Br1) anterior tooth in labial (B₁) and lingual (B₂) views. **C.** MGUH 29840 (Ce) lateral tooth in labial (C₁), lingual (C₂), and lateral (C₃) views. **D.** MGUH 29842 (Br1) lateral tooth in labial (D₁) and lingual (D₂) views. **E.** MGUH 29843 (Br1) posterior tooth in labial (E₁) and lingual (E₂) views. **F–H.** *Pararhincodon groessenssi* Herman, 1982. **F.** MGUH 29844 (Ce) anterior tooth in labial (F₁) and lingual (F₂) views. **G.** MGUH 29845 (Ce) anterior tooth in labial (G₁) and lingual (G₂) views. **H.** MGUH 29846 (Ce) lateral tooth in labial (H₁) and lingual (H₂) views. **I.** *Pararhincodon* sp., MGUH 29847 (Br1) anterior tooth in labial (I₁) and lingual (I₂) views. Scale bars 0.5 mm.

Family Parascyllidae Gill, 1862

Genus *Pararhincodon* Herman, 1977

Type species: *Pararhincodon crochardi* Herman, 1974; upper Campanian, South-West Belgium.

Pararhincodon groessenssi Herman, 1982

Fig. 4F–H.

1982 *Pararhincodon groessenssi* sp. nov.; Herman, 1982: 143, pl. 2: 9, pl. 4: 2, 3.

Material.—12 teeth from the Ce in Stevns Kridtbrud (MGUH 29844, MGUH 29845, MGUH 29846, GMV2012-67).

Description.—Dentition with monognathic heterodonty. Very small teeth with a prominent elongated main cusp, which is slightly inclined towards the commissure in anterior teeth, whereas it is strongly so in lateral teeth. The crown is small and convex with a pair of small shoulders. The shoulders car-

ry short strong folds, whereas the cusp and remaining crown is smooth. The lingual face of the crown is very convex and smooth. The root is slightly asymmetric in anterior teeth, but is much more so in lateral teeth. The root is bilobed, with the mesial lobe in general being longer than the distal, except in anterior teeth. The basal face is flat and the lingual face of the root is high. The lingual face bears a protuberance with central foramina. Foraminae are present lingually below the crown-root junction in each of the shoulders. Anterior teeth appear fairly symmetrical whereas the lateral teeth are strongly asymmetrical. In lateral teeth the distal shoulder carries a small cusplet. Teeth reaching 1.0 mm in height and 0.5 mm in width.

Remarks.—These teeth can be separated from the Cretaceous *P. crochardi* (Herman, 1977) and *P. lehmani* (Cappetta, 1980) and the Ypresian species *P. ypresiensis* (Cappetta, 1976) and *P. germaini* (Adnet, 2006) by being ornamented. All other species of *Pararhincodon* possess smooth teeth. The differ-

ence probably does not allow separation at the generic level. The species *P. bilizi* described by Reinecke and Engelhard (1997) is very similar to *Microscyliorhinus leggetti* (Case, 1994) and may be conspecific with the latter.

Stratigraphic and geographic range.—Campanian and Maastriichtian (Late Cretaceous) of North Germany (Herman 1982) to the Danian (early Paleocene) of Denmark and possibly also the Campanian (Late Cretaceous) of Texas (Welton and Farish 1993).

Family Ginglymostomatidae Gill, 1862

Genus *Delpitoscyllium* Noubhani and Cappetta, 1997

Type species: Ginglymostoma africanum Leriche, 1927.

Delpitoscyllium planum (Davis, 1890)

Fig. 5A–E.

1890 *Scyllium planum* sp. nov.; Davis 1890: 383, pl. 38: 9.

Material.—Davis' specimen from Terkelskov, Denmark (MGUH 1400), further four specimens from Faxø (OESM-10046-19, OESM-10046-20, OESM-10046-21, OESM-10046-22), and additional specimens in the collection of Alice Rasmussen, Faxø (Br2).

Description.—Symmetrical teeth with a prominent main cusp flanked by one to two pairs of cusplets. The teeth are sigmoidal in lateral view and the furrows between the cusplets and the main cusps create a median labial depression in the crown. The apron is weakly bifid and strongly overhangs the root.

In anterior teeth the crown is longer than wide with only one pair of converging cusplets, whereas lateral teeth are wider and the cusplets are either erect or diverging. Posterior teeth have a second pair of small cusplets and the crown becomes progressively wider and slightly asymmetrical. Both the labial and the lingual faces are smooth and convex, the lingual face particularly so. In none of the specimens is the root preserved. The lingual face has a well-developed median protuberance

Remarks.—Noubhani and Cappetta (1997) erected a new genus, *Delpitoscyllium*, for the species *Ginglymostoma africanum* Leriche, 1927 due to the lower number of cusps, “not exceeding two pairs” and a median labial keel on the main cusp. Though lacking the keel, present in the Moroccan material, we have transferred *Scyllium planum* Davis, 1890 to this genus. *D. planum* is regarded as a separate species and it is separated from the partly coeval species *Delpitoscyllium africanum* by the presence of a median keel on the apex of the labial crown. It could be that this character is variable among populations and that the two species of *Delpitoscyllium* are synonymous, in which case *D. planum* (Davis, 1890) is the senior synonym.

Amongst the Moroccan material depicted by Arambourg (1952: pl. 22: 8), there is a wide posterior tooth similar to what is observed in the Danish material. The median keel is present in specimens from the French Thanetian figured by Moreau and Mathis (2000).

Stratigraphic and geographic range.—Currently only recorded from the Danian (early Paleocene) of Denmark.

Order Heterodontiformes Berg, 1937

Family Heterodontidae Gray, 1851

Genus *Heterodontus* Blainville, 1816

Type species: Squalus philippi Schneider, 1801; Recent, South Australia.

Heterodontus rugosus (Agassiz, 1843)

Fig. 5F–H.

1843 *Acrodus rugosus* sp. nov.; Agassiz 1843: t. 3, 148, pl. 22: 28, 29.

1889 *Cestracion rugosus* Agassiz; Woodward 1889: 335.

1964 *Heterodontus rugosus* Agassiz; Albers and Weiler 1964: 7, fig. 41a–c.

1977 *Heterodontus rugosus* Agassiz; Herman 1977: 90, pl. 3: 5.

Material.—20 incomplete teeth from the Ce of Stevns Kridtbrud (MGUH 29848, MGUH 29849, MGUH 29850, GMV2012-68 [batch number]).

Description.—Dentition with strong ontogenetic heterodonty and disjunct monognathic heterodonty. Anterior teeth with six short and apical rounded cusps of lateral decreasing size. The lower crown of the labial face and the cusps are at an oblique angle to each other and whereas the cusps are smooth the lower crown has a strongly puckered ornamentation. The apron is broad and semicircular. The lingual face of the crown is smooth and convex, with a medio-lingual protuberance. The root is bilobed and slightly asymmetrical. The basal face is flat with a central foramen. The lingual face of the root has a protuberance and there is a foramen in each side of the lingual protuberance.

Lateral teeth are mesio-distally elongated, with a transverse crest. The transverse crest may have a cusp in anterior-lateral teeth. The labial face is more coarsely ornamented and steeper than the finer ornamented lingual face. The roots are missing in almost all of the lateral teeth, but appear to have been low and basally flat.

Remarks.—In Recent *Heterodontus*, there is strong ontogenetic heterodonty in all files but it is particularly evident in anterior files where the teeth undergo a reduction in lateral cusplets and likewise in the posterior teeth which loses their cusps and acquires a crushing morphology (Reif 1976). This is evident in the sampled anterior teeth, indicating the presence of both juveniles and adults. Reif (1976) divided Recent *Heterodontus* into two groups based on their dentitions. The *H. portusjacksoni* group possess several files of low-crowned inflated lateral files with a straight, poorly developed carina. The *H. francisci* group possess narrower lateral teeth with a centrally placed, often sigmoidal carina, and a low centrally placed cusp and coarse ornamentation. According to this scheme, *H. rugosus* would belong to the *H. francisci* group.

Stratigraphic and geographic range.—Late Cretaceous: Campanian of France and Germany (Thies and Müller 1993; Vullo 2005) and Campanian and Maastriichtian of Belgium (Agassiz 1843; Herman 1977; Bless et al. 1991) to the Danian (early Paleocene) of Denmark.

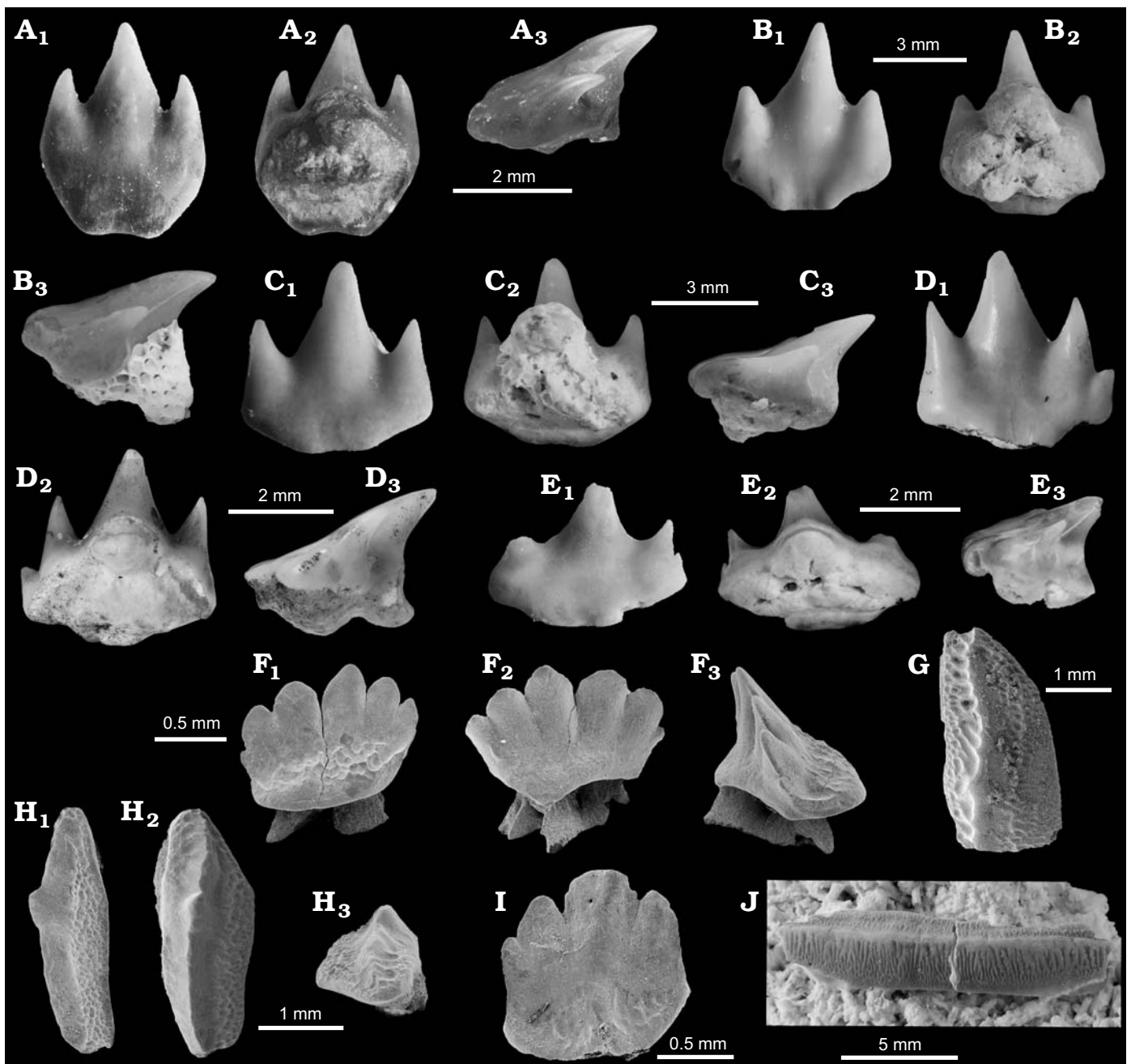


Fig. 5. Orectolobiformes and Heterodontiformes from the Danian of Stevns Kridtbrud, Kulstirenden, Faxe kalkbrud, and Terkelskov Kalkværk. A–E. *Delpitoscylidium planum* (Davis, 1890). A. MGUH 1400, holotype (Br2) anterior tooth in labial (A₁), basal (A₂), and lateral (A₃) views. B. OESM-10046-20 (Br2) anterior tooth in labial (B₁), basal (B₂), and lateral (B₃) views. C. OESM-10046-21 (Br2) anterior tooth in labial (C₁), basal (C₂), and lateral (C₃) views. D. OESM-10046-19 (Br2) lateral tooth in labial (D₁), basal (D₂), and lateral (D₃) views. E. OESM-10046-22 (Br2) posterior tooth in labial (E₁), basal (E₂), and lateral (E₃) views. F–H. *Heterodontus rugosus* (Agassiz 1843). F. MGUH 29848 (Ce) anterior tooth in labial (F₁), lingual (F₂), and lateral (F₃) views. G. MGUH 29849 (Ce) lateral tooth in occlusal view. H. MGUH 29850 (Ce) lateral tooth in labial (H₁), occlusal (H₂), and lateral (H₃) views. I, J. *Heterodontus* sp. I. MGUH 298451 (Br2) anterior tooth in labial view. J. OESM-10046-13 (Br2) lateral tooth in occlusal view.

Heterodontus sp.

Fig. 5I, J.

Material.—Anterior and lateral tooth from the Br2 at Faxe (MGUH 298451, OESM-10046-13).

Description.—The anterior tooth is poorly preserved. It has a single rounded principal cusp and a single mesial cusplet

and two distal cusplets, the more distal being very small. The labial crown base is only slightly ornamented. The lateral tooth bears a long straight carina, no central cusp, and is ornamented by a series of fine ridges originating from the carina and passing at right angles across the crown.

Remarks.—This large tooth, which probably represents an undescribed species, despite having a distinct carina, is

closer to the *H. portusjacksoni* grouping in ornamentation, consisting of fine striae rather than large pits. It is similar in morphology to the Late Cretaceous species *H. lonzeensis* (Herman, 1977) and less inflated than the Paleocene species *H. lerichei* (Casier, 1943). Case and Borodin (2000) published a new species *H. elongatus* from the middle Eocene of North Carolina (USA), which shares a similar morphology, with a faint ornamentation on the anterior teeth, but with less distinct ridges on the lateral teeth.

Order Lamniformes Berg, 1958

Family Carchariidae Jordan and Gilbert, 1883

Remarks.—Recent molecular studies have suggested that *Odontaspis* and *Carcharias* are only distantly related (Naylor et al. 1997; Vélez-Zuazo and Agnarsson 2011). Thus we have reverted to the Family Carchariidae Jordan and Gilbert, 1883.

Genus *Carcharias* Rafinesque, 1810

Type species: *Carcharias taurus* Rafinesque, 1810; Recent, warm-temperate to tropical waters.

Stratigraphic and geographic range.—Campanian (Late Cretaceous) of Sweden to the Danian (early Paleocene) of Denmark (Davis 1890; Siverson 1995), Maastrichtian (Late Cretaceous) of Spain (Cappetta and Corral 1999), and possibly the Ypresien–Lutetien (Eocene) of France (Adnet 2006).

Carcharias aff. *gracilis* (Davis, 1890)

Fig. 6A–C.

Material.—Five teeth from the Ce of Stevns Kridtbrud (MGUH 298452, MGUH 29853, MGUH 29854, GMV2012-69, GMV2012-70) and two in from the Br2 of Faxe in a private collection (Alice Rasmussen, Faxe).

Description.—The dentition in *Carcharias* displays both a monognathic and dignathic heterodonty. The main cusp is prominent and elongate, flanked by a pair of tall acute cusplets, which may or may not be divergent. Both the labial and lingual faces are generally smooth with the exception of the labial crown-root boundary which may carry short, strong folds. A median sulcus is present in the basal part of the crown above the dental band in both anteriors and laterals. In all teeth, the main cusp is interconnected with the cusplets and a continuous cutting edge extends over all cusps. The root is bilobed with short rounded lobes and has a median lingual protuberance divided by a deep nutrient groove.

Remarks.—The type series of *C. gracilis* (Davis 1890) are poorly preserved. Siverson (1995) figured better preserved specimens; *C. gracilis* is, however, still poorly defined. None of the specimens from the Ce and the Br carry lingual folds, which are common in the Moroccan *C. whitei* (Arambourg 1952), and this explains why we cannot assign the collected specimens to this species. Case (1996) depicted several specimens of *Carcharias teretidens* (*Sylvestrilamia teretidens*) which are similar to the specimens from Denmark. The latter, however, tend to be much smaller than the

teeth from New Jersey. There is still disagreement around the fossil species of *Carcharias*, and especially about the use of the Recent genus *Carcharias* in the late Mesozoic and early Paleogene. Some Late Cretaceous species have been transferred to *Eostriatolamia* (Glickman 1980), but the whole fossil Odontaspidae is generically more diverse than suggested in the current literature and is in a dire need of revision. Until then, our specimens will be kept within *Carcharias* sensu lato.

Genus *Striatolamia* Glickman, 1964

Type species: *Otodus macrotus* Agassiz, 1843, Eocene of France.

Striatolamia cederstroemi Siverson, 1995

Fig. 6D–H.

1995 *Striatolamia cederstroemi* sp. nov.; Siverson 1995: 9, fig. 3K–P. See Siverson (1995) for further synonymy.

Material.—Five specimens (OESM-10046-5, OESM-10046-6, OESM-10046-11, OESM-10046-12, OESM-10046-18) and several others in a private collection (Alice Rasmussen, Faxe), all from the Br2 of Faxe.

Description.—Teeth with an elongated main cusp, strongly sigmoid in anteriors, less so in laterals. Cusplets are only present in anterior teeth where they are small and blunt, often with an entirely flattened apex. In lateral teeth, the cusplets are lacking and instead the shoulders are mesio-distally very well developed. Both faces of the crown are in general smooth, but loose smaller cusps found at the same locality with similar affinity carry lingual folds. The root is low and bilobed and has elongated lobes. The lingual face of the root has a prominent median protuberance with a nutrition groove.

Remarks.—*S. cederstroemi* differs from *S. striata* by being smooth or lightly lingually striated and having more narrow root extremities, whereas the latter has strong lingual folds and wider root lobes.

Siverson (1995) tentatively assigned *Striatolamia* to Mitsukurinidae, a position that has been followed by Cappetta and Nolf (2005) and Cappetta (2012). He based his opinion on the similarity of the teeth of *Striatolamia* to those of a generalised *Anomotodon*. However, Siverson (1995: 9) also stated “I am not completely convinced that the latter genus [*Anomotodon*] is a true mitsukurinid taxon, hence the assignment of *Striatolamia* to Mitsukurinidae in a broad sense”. Cunningham (2000), using an artificial tooth set, conducted a detailed, position-by-position comparison of the teeth of *Striatolamia macrotus* (Agassiz, 1843) with those of Recent *Carcharias taurus*. His data demonstrated a very close similarity between the two, closer than between Recent *Carcharias* and *Odontaspis*. On the basis of its dental similarity to *C. taurus*, we prefer to group *Striatolamia* with *Carcharias* in the Carchariidae.

Stratigraphic and geographic range.—*Striatolamia cederstroemi* is only known from the Danian (early Paleocene) of Denmark and Sweden.

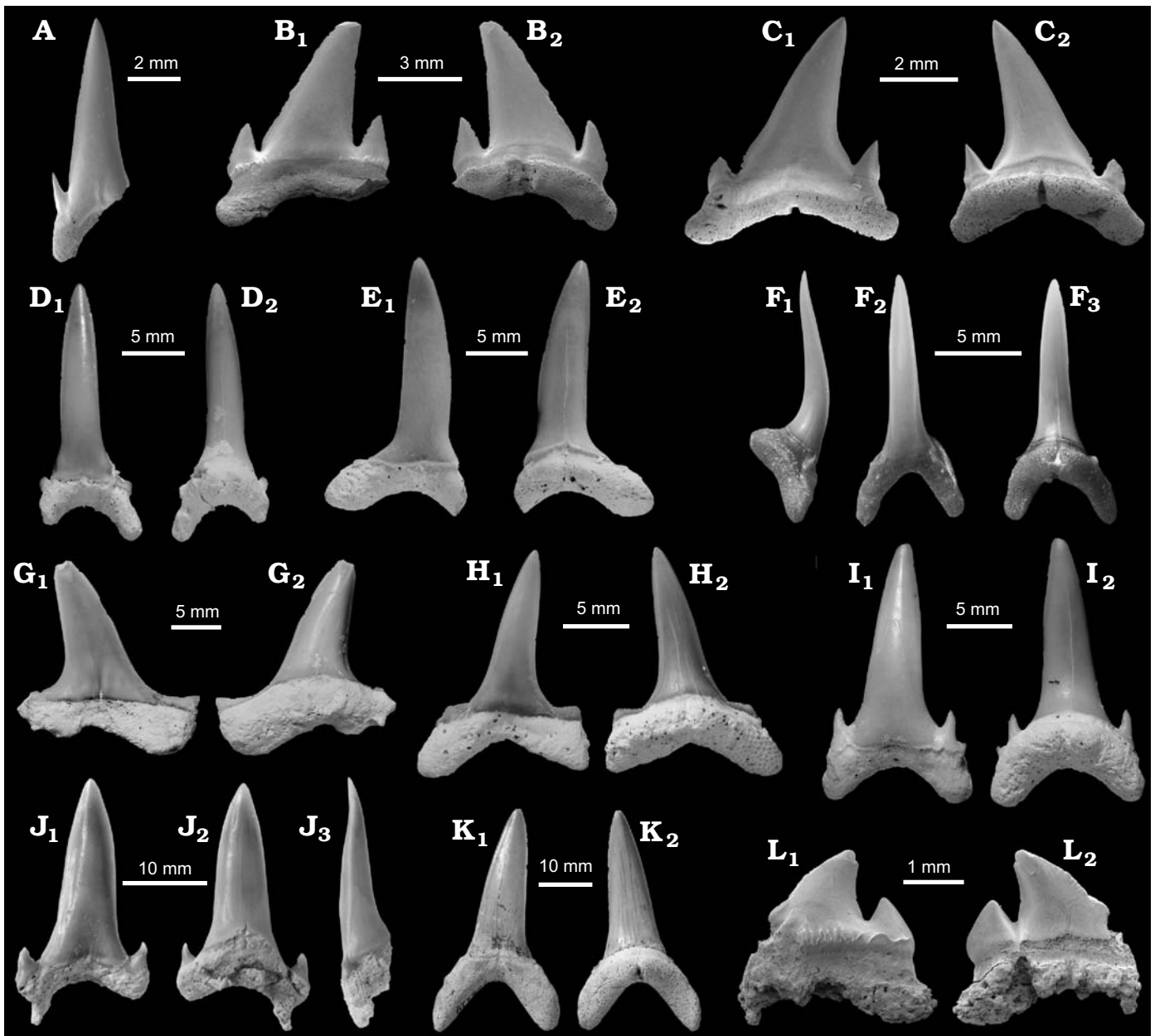


Fig. 6. Lamniformes from the Danian of Stevns Kridtbrud, Karlstrup kalkgrav, and Faxø kalkbrud. **A–C.** *Carcharias* aff. *gracilis* (Davis, 1890). **A.** MGUH 29852 (Ce) anterior tooth in labial view. **B.** MGUH 29853 (Ce) anterior tooth in labial (B₁) and lingual (B₂) views. **C.** MGUH 29854 (Ce) anterior tooth in labial (C₁) and lingual (C₂) views. **D–H.** *Striatolamia cederstroemi* Siverson, 1995. **D.** OESM-10046-5 (Br2) anterior tooth in labial (D₁) and lingual (D₂) views. **E.** OESM-10046-6 (Br2) anterior tooth in labial (E₁) and lingual (E₂) views. **F.** OESM-10046-18 (Br2) anterior tooth in lateral (F₁), labial (F₂), and lingual (F₃) views. **G.** OESM-10046-12 (Br2) lateral tooth in labial (G₁) and lingual (G₂) views. **H.** OESM-10046-11 (Br2) lateral tooth in labial (H₁) and lingual (H₂) views. **I.** *Odontaspis speyeri* Darteville and Casier, 1943, OESM-10046-8 (Br2) anterior tooth in labial (I₁) and lingual (I₂) views. **J–L.** *Palaeohypotodus* aff. *bronni* (Agassiz, 1843). **J.** MGUH 29855 (Ce) anterior tooth in labial (J₁), basal (J₂), and lateral (J₃) views. **K.** MGUH 298457 (Br1) lower anterior tooth in labial (K₁), lingual (K₂) views. **L.** MGUH 29856 (Ce) posterior tooth in labial (L₁) and lingual (L₂) views.

Family Odontaspidae Muller and Henle, 1839

Genus *Palaeohypotodus* Glickman, 1964

Type species: *Lamna* (*Odontaspis*) *bronni* Agassiz, 1843; Maastrichtian of Maastricht, the Netherlands.

Palaeohypotodus aff. *bronni* (Agassiz, 1843)

Fig. 6J–L.

Material.—One anterior and one posterior tooth from the Ce

of Stevns Kridtbrud (MGUH 29855, MGUH 29856) and one anterior tooth from the Br1 of Karlstrup kalkgrav (MGUH 298457).

Description.—An anterior tooth with a strongly elongated erect main cusp flanked by a pair of small but thick, acute, inwardly twisted cusplets. The labial face of the crown is convex and smooth with a large triangular sulcus originating from the base of the main cusp and reaching almost a third

of the cusp length. The lingual face is strongly convex and smooth without any signs of folds or ornamentation. The crown is slightly sigmoid in lateral view and the cutting edge is prominent and reaches the base of the cusp, but is not continuous with the cusplets. The root is almost absent and cannot provide any useful information. The tooth measures 28 mm in height and 15 mm in width. Posterior teeth are low, with a triangular cusp and cusplets and carry strong irregular folds at the crown-root boundary.

Remarks.—These teeth correspond reasonably to those of *Palaeohypotodus*. Maastrichtian teeth of *P. bronni* (Agassiz 1843) often have basal striation or folds on the labial crown base and often two pairs of cusplets. However, the latter has not been observed in these specimens. Because of this, and the limited material, this determination must be regarded as tentative. The genus *Palaeohypotodus* is kept within Odonaspidae, following Cappetta (1987, 2012).

Stratigraphic and geographic range.—Maastrichtian (Late Cretaceous) of northern Spain (Kriwet et al. 2007), the Paris Basin (Priem 1897), Belgium, the Netherlands (Agassiz 1843; Herman 1977; Geyn 1937b), and the north of Germany (Herman 1982) to the Danian (early Paleocene) of Denmark.

Genus *Odontaspis* Agassiz, 1838

Type species: *Squalus ferox* Risso, 1810; Recent.

Odontaspis speyeri Darteville and Casier, 1943

Figs. 6I, 7A, B.

1943 *Odontaspis speyeri* sp. nov.; Darteville and Casier 1943: 146, pl. 4: 1–13.

See Siverson (1995: 7), for additional synonymy.

Material.—Three teeth (OESM-10046-7, OESM-10046-8, OESM-10046-10) and several others in a private collection, all from the Br2 in Faxe.

Description.—Elongated teeth with a prominent main cusp flanked by one to two pairs of small hook-shaped cusplets. The main cusp is very elongated and strongly convex on both the labial and lingual face. The faces are smooth, with no signs of ornamentation. The first pair of cusplets are larger than the second pair and both pairs are connected with the main cusp. The crown-root boundary appears in general to be smooth with only some bulking in anterior teeth. The cutting edge reaches the base of the crown and connects with the cusplets. The roots are bilobed and have elongate and tapered extremities. The basal face of the root is flat and the root has a well-developed lingual protuberance.

Remarks.—*O. speyeri* has been described from West Africa (Darteville and Casier 1943) and Morocco (Arambourg 1952) and is characterized by its smooth faces and small twisted lateral cusplets. The teeth collected at Faxe are very close to the size and morphology of the specimens depicted by Arambourg (1952).

Stratigraphic and geographic range.—*Odontaspis speyeri* appears to have had a fairly wide distribution as it is known

from West Africa (Darteville and Casier 1943), Morocco (Arambourg 1952; Cappetta 1987) and in Scandinavia during the Paleocene (Siverson 1995).

Family Otodontidae Glickman, 1964

Genus *Cretalamna* Glickman, 1958

Type species: *Otodus appendiculatus* Agassiz, 1843; Turonian of Lewes, England.

Cretalamna appendiculata (Agassiz, 1843)

Fig. 7C–I.

1843 *Otodus appendiculatus* sp. nov.; Agassiz 1843: 270, pl. 32: 10.

1889 *Lamna appendiculata* (Agassiz); Woodward 1889: 392.

1958 *Cretalamna appendiculata* (Agassiz); Glickman 1958: 530.

Material.—One incomplete specimen from the Ce of Stevns Kridtbrud (MGUH 29858) and numerous teeth from the Br2 of Faxe at the SNM (MGUH 29858, MGUH 29859, MGUH 29860, MGUH1408, GM1992-1 to 6, GM1992-16, GM1992-17) and at Østsjælland Museum in Faxe (OESM-10046-3, OESM-10046-2, OESM-10046-4) and in private collections. A majority are, however incomplete.

Description.—Teeth with a broad triangular main cusp, erected in anterior and lower laterals and slanted toward the commissure in upper laterals. The main cusp is elongate and broad, with a convex labial face and convex at the crown-root boundary lingually and tends to flatten apically. Both faces are smooth, with the only exception of the median basal part of the labial face, which displays one or two deep vertical furrows. The cutting edges are continuous down to the base of the main cusp and may be continuous in the lateral cusp, but rarely so in upper laterals. The teeth appear to be slightly labio-lingually curved or flat, with the exception of anteriors, which can be slightly sigmoid in lateral view. The cusplets are often triangular and are either erect or divergent depending on their dental position in the mouth. A few teeth display a small denticle at the lateral extremities, but this is not common. The remaining cusplet is triangular and diverging from the main cusp. The root is only partly preserved, but was bilobed with short rounded lobes. There is a deep basal concavity and the basal face appears to have been flat. The largest specimen, a lower lateral, measured 45 mm in height.

Remarks.—*Cretalamna appendiculata* is a very long-ranging species, known from the Albion of the Anglo-Franco-Belgian basin to the Lower Eocene of Morocco and with a wide distribution. It is evident that in its current usage it comprises several lineages and a number of species (Underwood and Cumbaa 2010; Underwood et al. 2011). The high crowned anterior teeth (Fig. 7C, D) closely resemble those from the Maastrichtian of Kanne, Belgium, figured by Herman (1977: pl. 9: 3a, b) as *C. appendiculata* var. *pachyrhiza*. However, the more lateral teeth (Fig. 7G–I) appear more robust than those figured by Herman (1977) and may represent an undescribed species. In the light of this, we use the name *C. appendiculata* in a loose sense, pending a revision and cannot make any accurate conclusions on its specific distribution and evolution.

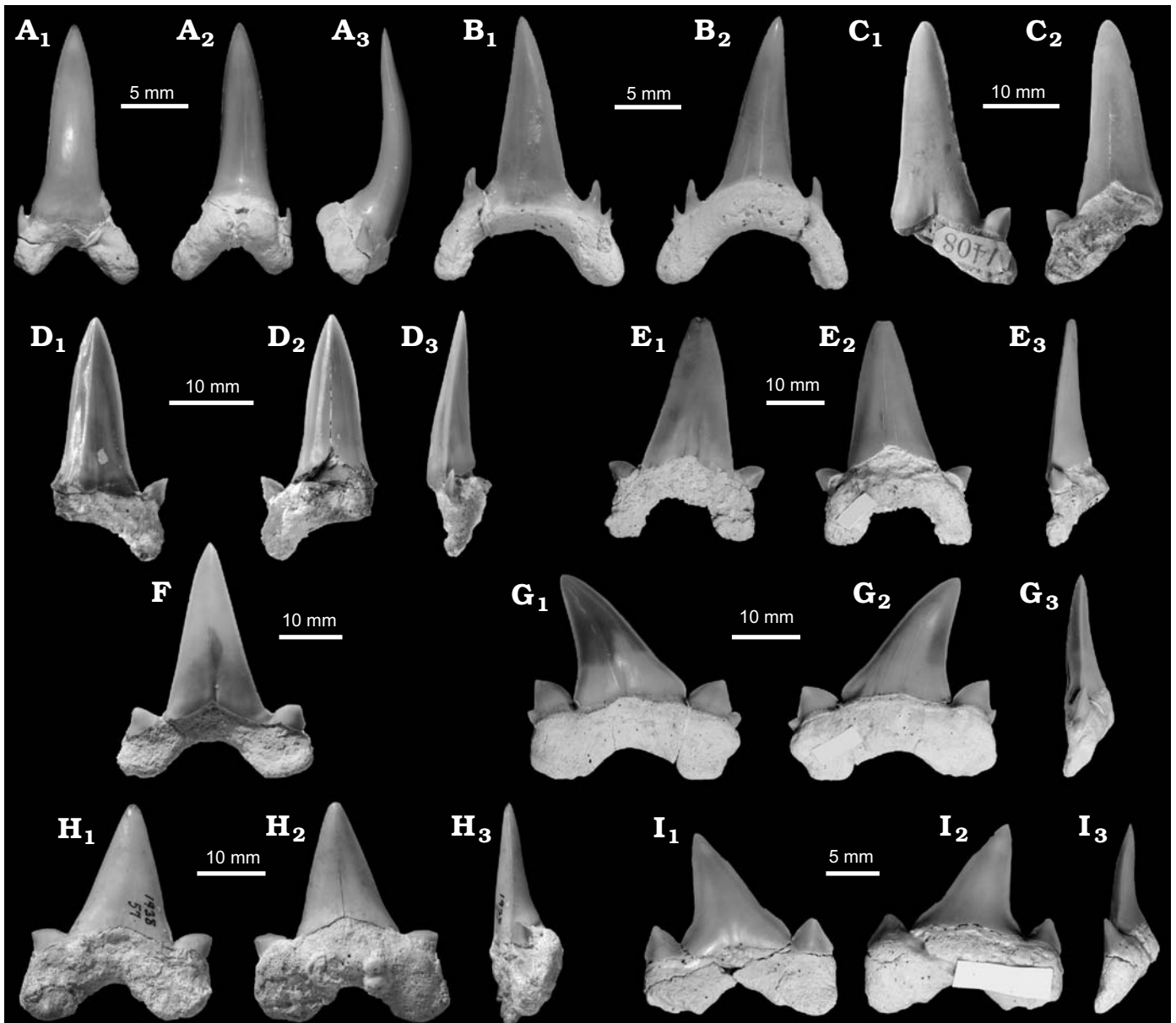


Fig. 7. Lamniformes from the Danian of Stevns Kridtbrud and Faxe kalkbrud. **A, B.** *Odontaspis speyeri* Darteville and Casier, 1943. **A.** OESM-10046-7 (Br2) anterior tooth in labial (A₁), lingual (A₂), and lateral (A₃) views. **B.** OESM-10046-10 (Br2) lower lateral tooth in labial (B₁) and lingual (B₂) views. **C–I.** *Cretalamna appendiculata* (Agassiz, 1843). **C.** MGUH1408 (Br2) anterior tooth in labial (C₁) and lingual (C₂) views. **D.** MGUH 29858 (Ce) anterior tooth in labial (D₁), lingual (D₂), and lateral (D₃) views. **E.** OESM-10046-3 (Br2) anterior tooth in labial (E₁), lingual (E₂), and lateral (E₃) views. **F.** MGUH 29859 (Br2) lower lateral tooth in labial view. **G.** OESM-10046-2 (Br2) upper lateral tooth in labial (G₁), lingual (G₂), and distal (G₃) views. **H.** MGUH 29860 (Br2) lower lateral tooth in labial (H₁), lingual (H₂), and distal (H₃) views. **I.** OESM-10046-4 (Br2) upper posterior tooth in labial (I₁), lingual (I₂), and distal (I₃) views.

The spelling of *Cretalamna* or *Cretalamna* has been discussed by Siverson (1999: 59) and although Glickman (1958: 570) did spell the name *Cretalamna*, Cappetta (2012) suggests *Cretalamna* should be used to avoid confusion, an opinion which we have chosen not to follow here.

Stratigraphic and geographic range.—*Cretalamna appendiculata* sensu lato occurs in Late Cretaceous: Japan (Goto et al. 1996), Cenomanian of Spain (Vullo et al. 2009), Santonian and Campanian of Georgia (Case et al. 2001), Campanian of Delaware (Lauginiger and Hartstein 1983), Cenomanian,

Campanian–Maastrichtian of Southern France (Vullo 2005; Vullo et al. 2007), Northern Spain (Kriwet et al. 2007), and Germany (Hübner and Müller 2010), Maastrichtian of Madagascar (Gottfried et al. 2001). Selandian (early Paleocene) of New Jersey (Case 1996) and Denmark.

Order Carcharhiniformes Compagno, 1977

Family Scyliorhinidae Gill, 1862

Genus *Scyliorhinus* Blainville, 1816

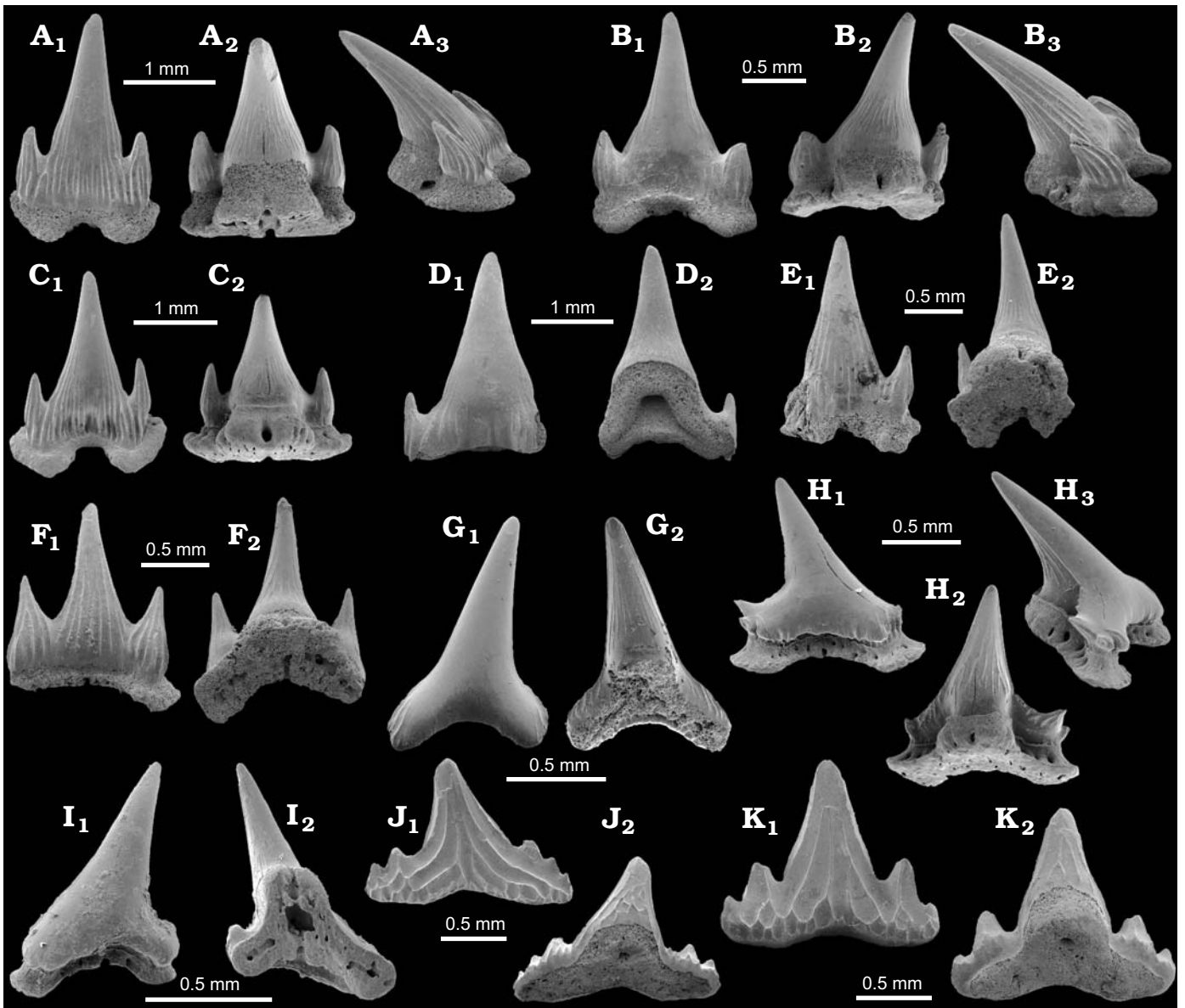


Fig. 8. Carcharhiniformes from the Danian of Stevns Kridtbrud and Kulstirenden. **A–F.** “*Scyliorhinus*” *elongatus* (Davis, 1887). **A.** MGUH 29861 (Ce) anterior tooth in labial (A₁), lingual (A₂), and lateral (A₃) views. **B.** MGUH 29862 (Ce) anterior tooth in labial (B₁), lingual (B₂), and lateral (B₃) views. **C.** MGUH 29863 (Ce) lateral tooth in labial (C₁) and lingual (C₂) views. **D.** MGUH 29864 (Ce) lateral tooth in labial (D₁) and lingual (D₂) views. **E.** MGUH 29865 (Ce) lateral tooth in labial (E₁) and lingual (E₂) views. **F.** MGUH 29866 (Ce) posterior tooth in labial (F₁) and lingual (F₂) views. **G–I.** “*Scyliorhinus*” *biddlei* Halter, 1995. **G.** MGUH 29867 (Ce) anterior tooth in labial (G₁) and lingual (G₂) views. **H.** MGUH 29868 (Ce) lateral tooth in labial (H₁), lingual (H₂), and lateral (H₃) views. **I.** MGUH 29869 (Br1) lateral tooth in labial (I₁) and lingual (I₂) views. **J, K.** *Crassescyliorhinus germanicus* (Herman, 1982). **J.** MGUH 29870 (Ce) lateral tooth in labial (J₁) and lingual (J₂) views. **K.** MGUH 29871 (Br1) anterior tooth in labial (K₁) and lingual (K₂) views.

Type species: *Squalus canicula* Linnaeus, 1758; Recent, Northeast Atlantic, Mediterranean, Canary Islands, and Ivory Coast.

Remark.—Many fossil sharks have been affiliated with modern genera with which they have most in common. This is, however, not always desirable, besides having genera ranging for more than 60 Myr, and in the case of *Scyliorhinus* 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 morphology close to a modern genus. Either solution is undesirable and has taxonomic repercussions. We

have here continued to use the Recent genus *Scyliorhinus* in its wide, traditional palaeontological sense, but in quotation marks, rather than to erect new fossil genera prematurely. This problem was aired by Müller and Diedrich (1991) who saw the use of *Scyliorhinus* as a last resort rather than to be a desirable solution.

“*Scyliorhinus*” *elongatus* (Davis, 1887)

Fig. 8A–F.

Material.—41 teeth from the Ce of Stevns Kridtbrud (MGUH 29861–29866, GMV2012-71 [batch number]), 35 specimens

from the Br1 of Kulstirenden (GMV2012-72 [batch number]), and a few in a private collection from the Br2 of Faxe. The majority are fragmentary.

Description.—Teeth with a high degree of monognathic heterodonty. Anterior teeth are robust, taller than wide with a prominent main cusp flanked by a pair of cusplets. Lateral teeth are lower and wider. The main cusp is biconvex and with a convex labial face and a very strongly convex lingual face. The cusplets are acute and converging towards the main cusp. Anterior teeth have vertical folds on the cusplets and on the lingual face of the main cusp, whereas lateral teeth also carry vertical folds on the main cusp, both labial and lingual. The crown-root boundary of the main cusp is labially indented. The root is low labially and bilobed with a flat basal face. The lingual face of the root is more prominent than the labial with a strong protuberance with a median foramen. Lingually, below the cusplets, is a foramen present. Posterior teeth are low crowned with up to two pairs of cusplets covered with vertical folds. There is no indentation at the median crown-root junction and in general the posterior teeth are more mesio-distally elongated than teeth from other jaw positions. Teeth reaching 2.4 mm in height and 2.0 mm in width.

Remarks.—Cappetta (1980), in his re-description of the fossils from Sahel Alma (Lebanon), had several specimens at different ontogenetic stages, but he did not mention teeth with more than one pair of cusplets. However, female and juvenile teeth of the Recent *S. canicula* frequently have more than one pair of cusplets in more lateral files (Ellis and Shackley 1995). This can also be observed in *S. stellaris* (JSA, personal observation). *S. elongatus* is long ranging both from a stratigraphical and a geographic point of view and may represent a species group rather than a single species, much in the same way as *Cretalamna appendiculata*.

Stratigraphic and geographic range.—Late Cretaceous: Santonian of Lebanon (Davis 1887; Cappetta 1980), Campanian of England, France, and Belgium (Herman 1977; Vullo 2005; Underwood and Ward 2008) to the late Maastrichtian Morocco (Noubhani and Cappetta 1997) and the Danian (early Paleocene) of Denmark.

“*Scyliorhinus*” *biddlei* Halter, 1995

Fig. 8G–I.

1995 *Scyliorhinus biddlei* sp. nov.; Halter 1995: 77, pls. 1–5, text-figs. 8–10.

Material.—22 specimens from the Ce of Stevns Kridtbrud (MGUH 29867, MGUH 29868, GMV2012-73 [batch number]) and six from the Br1 at Kulstirenden (MGUH 29869, GMV2012-74 [batch number]).

Description.—Teeth belonging to this species display monognathic heterodonty. Anterior teeth have an elongated biconvex main cusp slightly inclined towards the commissure. The labial face is smooth and convex with some short folds below the shoulders at the crown-root junction. The base of the crown overhangs the root and is deeply indented

medially. The shoulders are both inclined labially. The lingual face of the crown is strongly convex and carries folds almost up to the apex of the main cusp, with the most prominent folds being below the shoulders. Roots are missing in all anterior teeth.

Lateral teeth have a prominent elongate main cusp declining towards the commissure and a small distal cusplet. The labial face is convex and smooth, with the exception of the crown-root junction and at the shoulders, which carries short strong vertical folds. The crown overhangs the root. The lingual face of the crown is strongly convex and carries several longitudinal folds on the main cusp and a more reticulated ornamentation on the shoulders. The labial face of the root is low with multiple foramina. The root is bilobed with a flat basal face and a prominent lingual protuberance. There are multiple foramina below the shoulders on the lingual face of the root and foramina in the lingual protuberance. Teeth reaching up to 1.2 mm in height and 1.2 mm in width.

Remarks.—In his description of the type, Halter (1995) states that young individuals have lingual folds on their crowns reaching almost the apex, which is the case for many of our specimens and they are also in general smaller than the specimens described by Halter (1995) (2 mm high and 1.5 mm wide). This suggests that the specimens from Stevns Kridtbrud may have been from juveniles to sub-adults. Interestingly enough, anterior teeth are almost always missing the root, whereas this is not the case of the laterals.

Stratigraphic and geographic range.—*Scyliorhinus biddlei* is known from the Maastrichtian (Late Cretaceous) of Belgium (Eben-Emael) and the Netherlands (Halter 1995) and the Maastrichtian (Late Cretaceous) and, Danian (early Paleocene) of Denmark.

Genus *Crassescyliorhinus* Underwood and Ward, 2008

Type species: *Scyliorhinus germanicus* Herman, 1982; Maastrichtian, Hemmoor Zement AG quarry, North-West Germany.

Crassescyliorhinus germanicus (Herman, 1982)

Fig. 9J, K.

1977 *Scyliorhinus elongatus* (Davis); Herman 1977: 252, pl. 11: 1H.

1982 *Scyliorhinus germanicus* sp. nov.; Herman 1982: pl. 2: 10, pl. 4: 4, 5.

1989 *Scyliorhinus germanicus* Herman; Müller 1989: 47, pl. 11: 5, pl. 12: 1–4.

2001 *Scyliorhinus* sp.; Cappetta in Cappetta and Odin 2001: 651, pl. 1: 8a, b.

2008 *Crassescyliorhinus germanicus* (Herman); Underwood and Ward 2008: 512, pl. 2: 10–18.

Material.—14 teeth from the Ce of Stevns Kridtbrud (MGUH 29870, GMV2012-75 [batch number]), 10 from the Br1 at Kulstirenden (MGUH 29871, GM2012-76 [batch number]), and one from the Br2 at Faxe (GMV2012-77).

Description.—Teeth displaying some monognathic and ontogenetic heterodonty. Low crowned robust teeth with a short

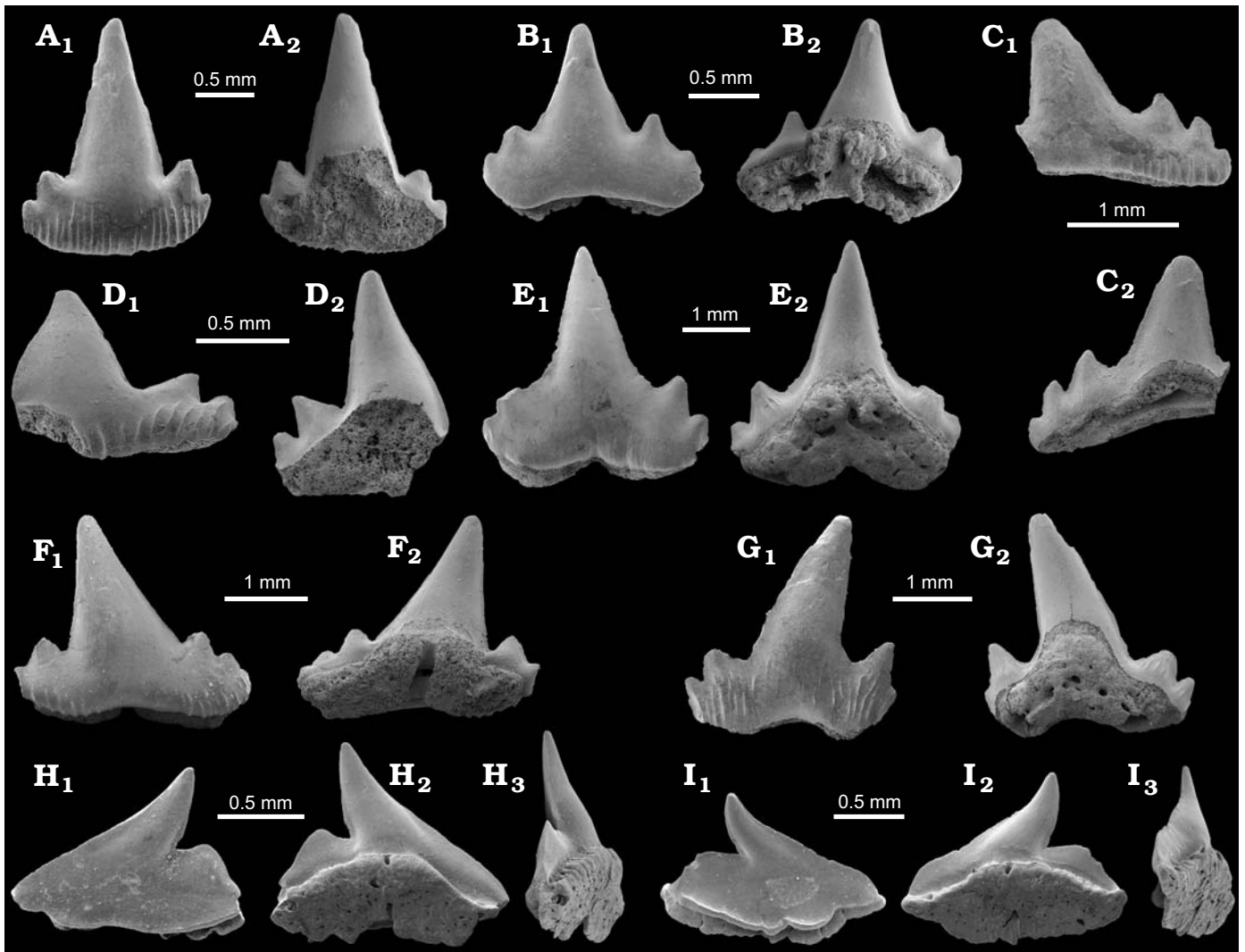


Fig. 9. Carcharhiniformes from the Danian of Stevns Kridtbrud and Kulstirenden and Faxe kalkbrud. **A–F.** *Palaeogaleus* aff. *faujasi* (Geyn, 1937). **A.** MGUH 29872 (Ce) anterior tooth in labial (A₁) and lingual (A₂) views. **B.** MGUH 29873 (Ce) lateral tooth in labial (B₁) and lingual (B₂) views. **C.** MGUH 29874 (Br1) posterior tooth in labial (C₁) and lingual (C₂) views. **D.** MGUH 29875 (Br1) anterior tooth in labial (D₁) and lingual (D₂) views. **E.** MGUH 29876 (Br1) anterior tooth in labial (E₁) and lingual (E₂) views. **F.** MGUH 29877 (Br1) lateral tooth in labial (F₁) and lingual (F₂) views. **G.** Triakidae sp., MGUH 29878 (Br1) tooth in labial (G₁) and lingual (G₂) views. **H, I.** *Paratriakis curtirostris* (Davis, 1887). **H.** MGUH 29879 (Ce) anterior tooth in labial (H₁), lingual (H₂), and distal (H₃) views. **I.** MGUH 29880 (Ce) lateral tooth in labial (I₁), lingual (I₂), and mesial (I₃) views.

massive conical main cusp and two pairs of cusplets diminishing in size from the main cusp. Anterior teeth are more symmetrical than lateral teeth. The labial face of the crown is flat with strong ornamentation in smaller teeth and less so in larger teeth. The ornamentation consists of three to six vertical folds on the main cusp bifurcating into a reticulate pattern in the basal part of the crown. The crown strongly overhangs the root and the median part of the basal edge of the crown is indented in anterior and lateral teeth. The lingual face is strongly convex and carries fine vertical or reticulated folds. Larger teeth lack most of the labial ornamentation, and posterior teeth are lower crowned and more mesio-distally elongated. The root is missing in almost all specimens. Teeth reaching a width of 3.0 mm and 2.5 mm in height.

Remarks.—Herman (1982) argued that the ornamentation of the teeth is a function of age and jaw position. This appears

to be supported by the teeth sampled at Stevns Kridtbrud, as larger teeth appear to lack the labial ornamentation, whereas smaller teeth are strongly ornamented. Posterior teeth are always ornamented regardless of size.

Stratigraphic and geographic range.—Late Cretaceous: late Coniacian to early Campanian of Southern England (Underwood and Ward 2008), middle Campanian of France (Vullo 2005), to the late Maastrichtian of Northern Germany (Herman 1982) and the middle Danian (early Paleocene) of Denmark.

Family Triakidae Gray, 1851

Genus *Palaeogaleus* Gurr, 1963

Type species: *Galeocерdo vincenti* Daimeries, 1888; Thanetian, Orp-le-Grand, Belgium.

Palaeogaleus aff. *faujasi* (Geyn, 1937)

Fig. 9A–F, ?G.

Material.—16 teeth from the Ce of Stevns Kridtbrud (MGUH 29872, MGUH 29873, GMV2012-78 [batch number]) and four from Kulstirenden (Br1) (MGUH 29874–29877).

Description.—Teeth displaying moderate degree of monognathic heterodonty. Anterior teeth are symmetrical and narrow with a large elongated triangular main cusp that is flanked by two pairs of small triangular cusplets diminishing in size outwards. Lateral teeth are wider, but still retain a more or less symmetrical shape with an erect main cusp whereas in posterior teeth the main cusp is declined towards the commissure. The labial face of the crown is convex and in general smooth, but may carry strong short folds below the shoulders in some specimens. In anterior teeth the basal edge of the crown is convex, whereas lateral and posterior teeth have a median indented basal edge. The labial face strongly overhangs the root. The lingual face is smooth and convex. The root is missing in most specimens, but some remnants indicate a low bilobed root with a flat basal face and a deep median groove. One of the specimens (Fig. 9G) has a more narrow crown and more robust labial folds. It may represent an extreme variant or an undescribed species. For the moment is best referred to as Triakidae sp.

Teeth reaching 2.0 mm in height and 2.5 mm in width.

Remarks.—Several Cretaceous and Paleocene species of *Palaeogaleus* have been described from Europe, North Africa, and North America all of which show a marked degree of intraspecific variation. The Danish material is more similar to the Maastrichtian *P. faujasi* of the Netherland (Geyn 1937b) than the Paleocene *P. vincenti* of Belgium (Daimeries 1888), as the apex of the cusplets in *P. vincenti* is more blunt than observed in *P. faujasi*. Additionally some tooth positions in *P. vincenti* can have a heavily folded labial crown base. Cvancara and Hoganson (1993: fig. 3Z–AA) depicted two incomplete specimens which they referred to as *P. vincenti*, but could as well be conspecific with the Danish material.

Stratigraphic and geographic range.—Late Cretaceous: late Campanian of France (Vullo 2005), Maastrichtian of the Netherlands (Geyn 1937b; Herman 1977) and Spain (Cappetta and Corral 1999) to the Danian (early Paleocene) of Denmark.

Genus *Paratriakis* Herman, 1977

Type species: *Paratriakis bettrechiensis* Herman, 1977; Bettrechies, Turonian of France.

Stratigraphic and geographic range.—Late Cretaceous: Cenomanian of Lebanon (Davis 1887) to the Campanian of Belgium (Herman 1977) to the Danian (early Paleocene) of Denmark.

Paratriakis curtirostris (Davis, 1887)

Fig. 9H, I.

Material.—45 specimens teeth from the Ce of Stevns Kridt-

brud (MGUH 29879, MGUH 29880, GMV2012-79 [batch number]) and one from the Br2 at Faxø (GMV2012-80).

Description.—Teeth displaying little monognathic heterodonty. Strongly labio-lingually compressed teeth and all wider than high. Teeth with a single cusp strongly inclined towards the commissure. The mesial cutting edge is straight at an angle of 40 to 50° to the basal edge of the crown, but turning upwards at the apex of the main cusp. The distal cutting edge of the cusp is convex, joining the distal shoulder in a notch. The distal shoulder is at a near right angle to the distal edge of the crown in anterior teeth, but somewhat less in lateral teeth. The apex of the cusp never protrudes further distally than the distal edge of the crown. The labial face of the cusp is smooth and convex, but is at an angle with the body of the crown, creating a small mesio-distal trough. The basal edge of the crown strongly overhangs the root and creates a ledge. The lingual face of the crown is convex and smooth. The labial face of the root is very low with multiple foramina; the basal face of the root is flat and tapering at both ends. The basal edge of the roots has a deep median notch. The lingual face of the root is low and with a median protuberance and a median foramina. Anterior teeth have a smaller height to width ratio than lateral and posterior teeth. Teeth reaching up to 1.3 mm in height and 2.5 mm in width.

Remarks.—Body fossils of *P. curtirostris* are known from Sahel Alma in Lebanon (Davis 1887; Cappetta 1980), so the dentition in this particular species is well known, although our knowledge of intraspecific variability is limited.

Unidentified material

In addition to the material described and illustrated above, several large unidentifiable fragments of selachian teeth >15 mm were also collected, indicating that larger sharks were more numerous than the identifiable teeth may indicate. Furthermore, numerous osteichthyan bones, jaws, vertebrae and teeth all less than 4 mm in length were recovered.

Concluding remarks

The species recovered from the early to middle Danian limestone rocks in Denmark are shown in Table 1.

The results from the early Danian *Cerithium* Limestone reveal a fauna mainly consisting of small Carcharhiniformes and Squaliformes but also large sharks, such as *Cretalamna appendiculata*, *Chlamydoselachus* sp., and *Palaeohypotodus* aff. *bronni*. The occurrence of *Chlamydoselachus* sp. is the earliest record of Chlamydoselachidae in Europe. This and the occurrence of species of Dalatiidae and Scymnorhinidae casts some doubt on whether the *Cerithium* Limestone really was deposited in shallow water (Hansen 1990), as modern relatives of these families tend to be deep water dwellers. The preferred habitats of these families may have been affected by factors like oceanic oxygenation, productivity and tem-

Table 1. Distribution of fossil shark taxa collected from the *Cerithium* Limestone (Ce) and the bryozoan limestone (Br1 and Br2). 17 species have been found in the early Danian *Cerithium* Limestone, 8 species in the lowermost part of the bryozoan limestone at Kulstirenden and further 17 species at the Quarry at Faxe. +, rare to; +++, abundant.

	early Danian		middle Danian
	Ce	Br1	Br2
<i>Synechodus faxensis</i> (Davis, 1890)			+
<i>Sphenodus lundgreni</i> (Davis, 1890)			+++
<i>Hexanchus microdon</i> (Agassiz, 1843)	+		+++
<i>Gladioserratus</i> sp.			+
<i>Notidanodon brotzeni</i> Siverson, 1995			+
<i>Heptranchias howelli</i> Reed, 1946			+++
<i>Chlamydoselachus</i> sp.	+		
<i>Squalus gabrielsoni</i> Siverson, 1993b	++	++	+
<i>Squaliodalatias</i> sp.	+		
<i>Centroscymnus praecursor</i> Müller and Schöllmann, 1989	+		
<i>Squatina</i> sp.	+		+
<i>Parasquatina cappetta</i> Herman, 1982	+		
<i>Hemiscyllium hermani</i> Müller, 1989	+++	++	
<i>Pararhincodon groessenssi</i> Herman, 1982	++		
<i>Pararhincodon</i> sp.		+	
<i>Delipotocyllium planum</i> (Davis, 1890)			+
<i>Heterodontus rugosus</i> (Agassiz, 1843)	++		
<i>Heterodontus</i> sp.			++
<i>Carcharias</i> aff. <i>gracilis</i> (Davis, 1890)	+		+
<i>Palaeohypotodus</i> aff. <i>bronni</i> (Agassiz, 1843)	+	+	
<i>Odontaspis speyeri</i> Dartevelle and Casier, 1943			++
<i>Striatolamia cederstroemi</i> Siverson, 1995			+++
<i>Cretalamna appendiculata</i> (Agassiz, 1843)	+		+++
“ <i>Scyliorhinus</i> ” <i>elongatus</i> (Davis, 1887)	+++	+++	+
“ <i>Scyliorhinus</i> ” <i>biddlei</i> Halter, 1995	+++	++	
<i>Crassescyliorhinus germanicus</i> (Herman, 1982)	+++	++	+
<i>Palaeogaleus</i> aff. <i>faujasi</i> (Geyn, 1937b)	++	+	
Triakidae sp.		+	
<i>Paratriakis curtirostris</i> (Davis, 1887)	+++		+

perature from the warm Paleogene to the cooler Neogene, but we regard this as unlikely.

During the deposition of the bryozoan limestone the fauna changes from one dominated by small Carcharhiniformes and Squaliformes to one dominated by Hexanchiformes and Lamniformes. In particular, *Cretalamna* and *Striatolamia* become very common and the synechodontiform *Sphenodus* becomes abundant. The Hexanchiformes are represented by no fewer than four species in the bryozoan limestone of Faxe and include the oldest record of *Heptranchias howelli*. Whereas the teeth of *Hexanchus* and *Heptranchias* are common, comparably few teeth of *Notidanodon* and *Gladioserratus* have been found. What attracted so many species of hexanchiform to this habitat is unknown, but there were several other large shark species present, so it was not due to a lack of other top predators.

The fauna from the early Danian limestone is an im-

poverished Cretaceous fauna lacking among others the large Anacoracidae which became extinct at the end of the Cretaceous. The fauna did, however, contain a many species that were present in the late Maastrichtian and survived across the K–T boundary and well into the Danian. The fauna from the bryozoan limestone (Faxe Formation) is, however, very different from the late Maastrichtian–early Danian fauna, and is characterized by diverse hexanchids and very numerous *Cretalamna* and *Sphenodus* specimens. This change in faunal composition has been linked to a change in environment, from a warm to a cool water environment.

This study suggests that the Boreal Sea acted as a refuge for Cretaceous species, as it did with ammonites (Machalski and Heinberg 2005). The only major comparable study on sharks and rays is that of Noubhani and Cappetta (1997) on Moroccan materials, in which they recorded only two species in common either side of the K–T boundary. Just as this Danish study is to an extent extreme; deep cool water and a short span, the Moroccan situation is the opposite, warm shallow water and probably a long temporal hiatus. It is evident that many groups of sharks not present in this study also survived the K–T boundary elsewhere. The lack of rays at the Danish localities could be attributed to bathymetry, as rays, particularly Rajiformes, may not have been adapted to deep cool water in the early Paleogene.

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