

New records of fossil deep-sea shark teeth from the Lillebælt Clay (Early–Middle Eocene) of Denmark

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This study describes for the first time a number of distinct fossil teeth documenting several deep-sea shark species from the Eocene, which were previously not recorded from the North Sea Basin, including *Apristurus* sp., *Orthechinorhinus* cf. *pfeili*, *Deania* cf. *angouneensis*, *Squaliolus* sp., *Etmopterus* cf. *cahuzaci* and *Paraetmopterus nolfi*. Our findings significantly increase the deep-sea shark diversity documented from this area so far. Despite the fact that the North Sea Basin had already lost direct connections to the neighbouring marine areas in the Eocene, the fauna shows highest similarities with documented Eocene deep-sea faunas of France, Austria and northern Morocco using cluster analysis.

Keywords: Chondrichthyes; Echinorhinidae; Squaliformes; Pentanchidae; North Sea Basin.

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The North Sea persists since the Late Cretaceous when the uplift of the British Isles forced the separation of the basin from the North Atlantic Realm. Since then, this predominantly shallow sea, today with an average depth of 90 m and a maximum depth of 700 m (European Maritime Spatial Planning Platform 2023), has existed almost continuously between the Fennoscandian Shield and the British Isles. It was connected to adjacent basins during several time intervals, for example, to the southwest with the Paris Basin during the Late Paleocene (Thanetian to Early Eocene, middle Ypresian), to the southeast with the Paratethys Sea, or to the south with the Tethys Ocean (Late Oligocene, middle Chattian) (Gibbard & Lewin 2016; Palcu & Krijgsman 2023).

Today, Palaeogene sediments of this basin are mainly exposed along the south-eastern coast of Great Britain as well as along the Belgian, Dutch, German and Danish North Sea coasts. Retrieving information from a keyword-based query (keywords *Place* defined

as ‘United Kingdom, Netherlands, Denmark, Belgium, Germany’ and *Time* defined as ‘Paleocene, Eocene’) from the bibliographic database www.shark-references.com (Pollerspöck & Straube 2022) resulted in 107 scientific publications on this topic. Some notable contributions are, for example, the Eocene elasmobranch and osteichthyes faunas of South-East England (London Clay) monographically studied by Casier (1966), supplemented and extended by works of e.g. Cappetta (1976), Cappetta & Ward (1977) and Ward (1979, 1984). The Palaeogene sediments exposed on the European mainland (Belgium), were also intensively studied, see for example Herman (1974a, 1974b, 1977, 1979, 1982a, 1982b, 1984, 1986). Considerable amounts of sediment of the Danish Lillebælt Clay (Kirstinebjerg) were also analysed in the course of this study. However, Palaeogene deposits of Denmark were not in focus of research until the 21st century (e.g. Hansen *et al.* 2013; Carlsen & Cuny 2014; Adolfssen & Ward 2015; Shimada & Ward 2016; Adolfssen *et al.* 2017; Myrvold *et al.* 2018).

To date, only a few characteristic deep-sea shark taxa have been recorded within all the aforementioned studies. Typical taxa are, for example, Pentanchidae of the genus *Apristurus* or Squaliformes in general. The following species have been hitherto documented from the Danish Paleocene deposits only: *Squalus gabrielsoni*, *Squalus* sp., *Squaliodalatias* sp., *Centroscymnus praecursor* (Adolfsson & Ward 2015; Adolfsson *et al.* 2017). Only two squaliform species were recorded from Danish Eocene deposits: *Centrophorus* aff. *granulosus* and *Isistius trituratorus* (Carlsen & Cuny 2014).

In this study we describe new Eocene deep-sea shark taxa based on tooth fossils from a Danish Ypresian succession and characterise the available fauna by comparing diversity indexes from other described Eocene faunas. Our findings include several new records contributing to the understanding of the deep-water shark diversity during the Ypresian in the North Sea Basin.

Geographical and geological settings

The fossil shark teeth described in this paper were collected at Kirstinebjerg (GPS coordinates: 09°48'09.03"E, 55°35'52.6"N), Trelde Næs, a peninsula in eastern Jylland, Denmark (Fig. 1). The exposed succession was divided into six lithological layers L1 to L6 (Lillebælt Clay Formation) by Heilmann-Clausen *et al.* (1985). All shark teeth analysed herein derive from layer L2 representing a Late Ypresian age. For a detailed geo-

logical description, we refer to Heilmann-Clausen *et al.* (1985) and Carlsen & Cuny (2014).

Material and methods

Sampling procedures

During a period of 3 years, approximately 6000 kg of material was disintegrated and sieved on the shore of Trelde Næs. Two preparation procedures were applied. The first procedure involved the following steps: soft clay samples of 15 kg were placed in a plastic bucket (20 L) and ocean water was added. Mechanically stirring of the mixture was obtained by using an electric screwing machine (Flake 18V, 35 Nm) fitted with a paddle mixer. The dissolved material was poured through double nylon stockings (Denim 20). The process was repeated for 5850 kg in total until all the material was dissolved and poured through the double nylon stockings (Denim 20). Generally, three buckets (approximately 45 kg) of material were reduced each to 1–2 kg before the nylon stocking was replaced.

The second procedure involved collecting bulk material (approximately 150 kg) on the shore of Lillebælt. The collected material was divided into smaller pieces (5 cm) and submerged under water in large plastic containers (30 × 45 × 70 cm). Regular mechanical stirring (once in 24 hours) was maintained until most of the material was dissolved. After approximately one week the material was sieved through a large DIY

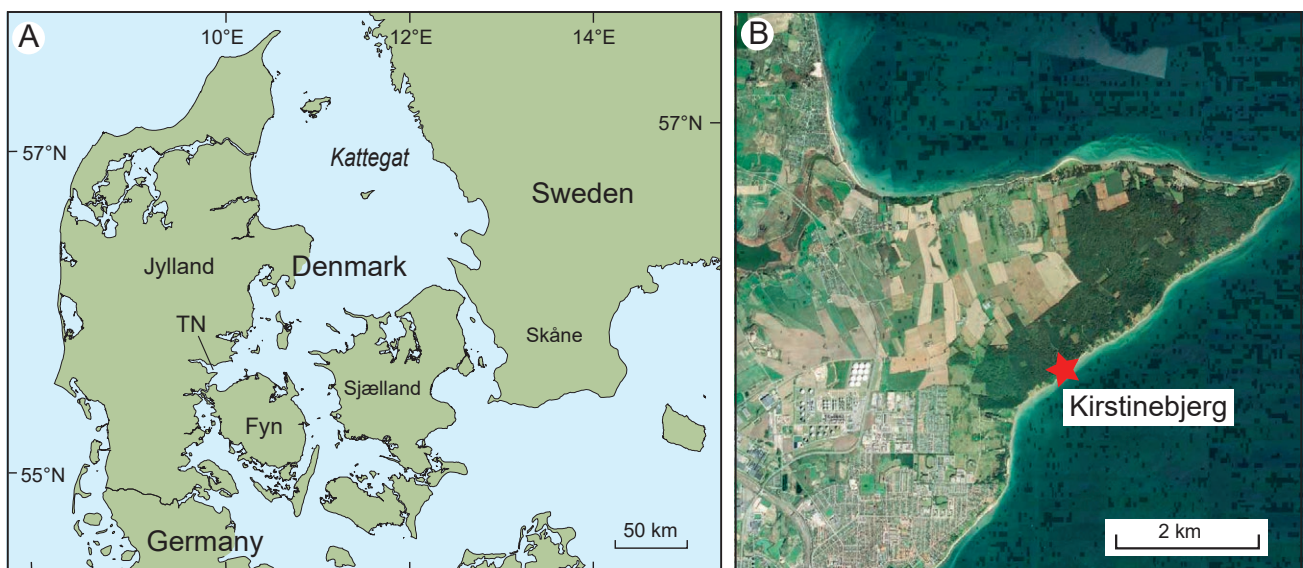


Fig. 1. A, Map of Denmark showing the location of Trelde Næs (TN), a peninsula in eastern Jylland. B, Google Earth image of the Trelde Næs area, showing the location of Kirstinebjerg (KB; GPS coordinates: 09°48'09.03"E, 55°35'52.6"N).

sieve (30 × 50 cm, mesh 7 = 3 × 3 mm) and rinsed with plenty of water. The dissolved material was poured through double nylon stockings (Denim 20). The remaining undissolved material was left submerged under water for another week with regular mechanical stirring (once a day) and processed when dissolved.

The reduced material from both procedures was further processed in the following steps. The material was first rinsed with cold water while gently massaging the nylon stocking until clear water was leaving the nylon stocking (approximately 15 min). The material was then rinsed with lukewarm water (5 min) before dish soap (approximately 5 ml) was added while gently massaging the nylon stocking (2 min). After soaking for 15 min, cold water was used to remove the excess soap. The material was then transferred to a large (7 × 20 × 30 cm) plastic container and water was added. The floating organic material was given a stir to ensure that no inorganic material (sand and fossils) was attached. The organic material was then slowly decanted out of the plastic container. This process was repeated until all the organic material was removed. The remaining water was decanted out of the container before the material was dried in an oven at 90 degrees (15 min or until completely dry). The final pure material was sorted using a binocular microscope (*efix*). Within the context of this study, a total of 413 fossil teeth were analysed.

Images were taken using automatic photo stacking. A full frame camera (Canon EOS RP) was mounted on a vertical stand holding a WeMacro focus stacking rail (100 mm). The camera was equipped with a Raynox DCR 150 tube lens system and either a Mitutoyo M Plan Apo (10X / 0.28) or a Mitutoyo M Plan Apo (20X / 0.42). Light was provided by custom led lights (3 X MJ58 Led). Helicon remote was used to control the photo stacking rail and Helicon Focus 7 to render (Method C (pyramid), Smoothing 2) the photos.

The dental terminology and systematic scheme employed here largely follow those of Cappetta (2012).

Statistical analysis and fossil fauna comparisons

Data for statistical analysis were obtained from the bibliographic database www.shark-references.com (Pollerspöck & Straube 2022). We collected data to assemble a presence/absence matrix of fossil shark species. A query targeting the database www.shark-references.com directly was written in SQL searching the database entries for records of species in fossil fauna inventories. In a first step, all database records containing 'Eocene' as time-dependent keyword were assembled and combined with the database columns 'reference' (including information on author, year,

title, journal), 'described species' and if necessary 'valid species', 'keyword time', 'keyword place' and 'keyword content'. In a next step, database entries containing information on sharks were extracted. Further, all works dealing with other stratigraphic units besides Eocene sedimentary sites were removed. The resulting dataset contained a list of publications from sites of interest and allowed for extracting a list of all Eocene deep-sea shark records on genus level. This full list was applied to different Eocene palaeogeographic regions and an absence/presence-matrix was constructed. The matrix also allowed to gain insights of regional Eocene diversity. For gauging the similarity and diversity of the selected 30 faunas, four different indexes (Dice (1945), Jaccard (1912), Kulczynski (1927) and Ochiai (1957)) were calculated and two different versions of the matrix were created. One version of the matrix contains all occurring taxa, the second version was restricted to typical deep-sea taxa. Dataset details can be found in the Supplementary Material Part 1.

These four coefficients were presented by Hurbalek (1982) as the most useful coefficients for the analysis of absence/presence data sets. They measure the similarity between two sets of binary data. The Jaccard index is the quotient of the number of shared taxa to the total number of taxa. This means that missing taxa in both samples are ignored. The Dice index is similar to the Jaccard index, but normalised with respect to the average and not to the total number of taxa in two given samples. Ochiai and Kulczynski coefficients are also similarity indexes for binary data. The underlying formulae of the four coefficients are listed in the Supplementary Material Part 2.

These four indexes are used to calculate the levels of similarities of different faunas documented from different localities or similar habitat conditions of the different localities (Biriukov 2021; Guinot 2013; Guinot *et al.* 2014; Marramà *et al.* 2021; Höltke *et al.* 2022). The software package PAST 4.12 (Hammer *et al.* 2001) was used to perform the cluster analysis applying the four indexes from Kulczynski, Jaccard, Ochiai and Dice using the unweighted pair group method with arithmetic mean (UPGMA). The analysis was not constrained by groups or stratigraphy. PAST was further used to visualize the results.

For further characterization of the documented diversity, we generated a Sankey diagram comparing the four different faunas showing highest similarities in the cluster analysis. The diagram was made with SankeyMATIC (<https://sankeymatic.com/>).

All teeth from Kirstinebjerg are deposited in the Natural History Museum of Denmark (NHMD), Universitetsparken 15, DK-2100 Copenhagen, collection numbers NHMD-1201349–1201382.

Results

Systematic palaeontology

Order Carcharhiniformes

Family Pentanchidae Smith, 1912a

Genus *Apristurus* Garman, 1913

Type species. *Scylliorhinus indicus* Brauer, 1906, type by original designation.

Apristurus sp.

Figs 2A–B

Material. 1 tooth, NHMD-1201349.

Description. The tooth consists of a main cusp, three mesial and one distal lateral cusplets (Figs 2A–B). The main cusp is clearly inclined distally, has a straight distal and a strongly convex curved mesial crown edge. The three lateral cusplets decrease in height in mesial direction. The distal lateral cusplet is only about one third as high as the main cusp. The enameloid of the distal cusplet is strongly ornamented labially and lingually with the characteristic reticulate pattern of *Apristurus*, which continues on the labial crown base towards the

mesial crown edge (Figs 2A–B, arrows). Additionally, the main cusp and the mesial cusplets possess enameloid folds on both faces. The thin, translucent and very sharp cutting edges of the main cusp and the mesial lateral cusplets are damaged and therefore appear to be serrated. The distal cusplet lacks a well-pronounced cutting edge. The root is not well preserved.

Remarks. The genus *Apristurus* is one of the most diverse extant shark genera with currently 41 valid species (Pollerspöck & Straube 2022). Detailed morphological studies with a focus on dental characters, however, are only available for a single extant species (Herman *et al.* 1990, *A. laurussoni*). Without further knowledge on the inter- and intraspecific morphological variations of different species, we refrain from an identification to species level.

Distribution. Teeth of the genus *Apristurus* are scarce in the fossil record and only known from the Eocene of France (*Apristurus sereti* Adnet, 2006, middle Lutetian, Angoumé, France (Adnet 2006)), the Upper Marine Molasse (*Apristurus* sp., lower Ottnangian, Mitterdorf, Bavaria, Germany (Pollerspöck & Straube 2017); *Apristurus* sp., Ottnangian, Allerding, Upper Austria, Austria (Pollerspöck *et al.* 2022)), from the Pacific (*Apristurus* sp., Langhian, Japan (Nishimatsu 2019; Nishimatsu & Ujihara 2020)), and from the Pliocene of Italy (*Apristurus* sp., lower-middle Pleistocene, Fiumefreddo, Sicily, Italy (Marsili 2007)). The specimen

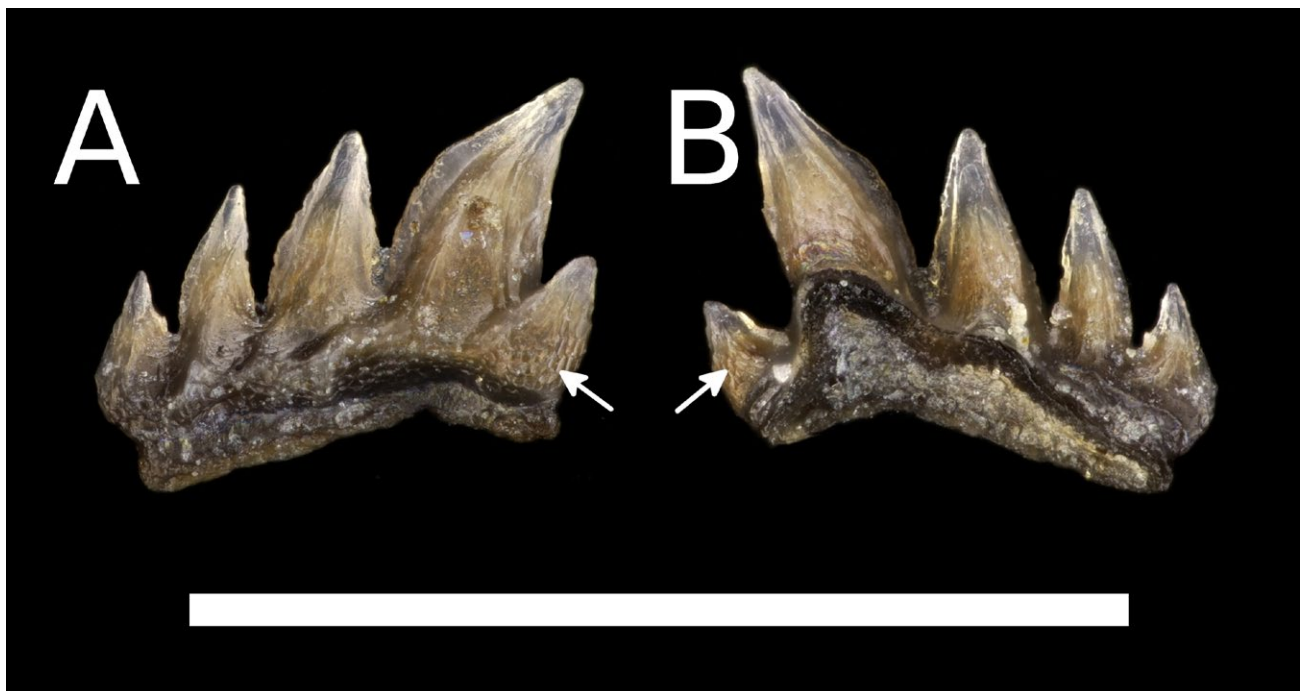


Fig. 2. A–B, *Apristurus* sp. Lateral tooth, NHMD-1201349. A, labial view; B, lingual view. Scale bar: 1 mm. Explanation of arrows is given in the text.

from this study shows most similarities with the specimen from the lower Ottnangian of Bavaria figured in Pollerspöck & Straube (2017; figs 4–5) but differs in the less pronounced enameloid folds and the presence of ornamentation on the distal lateral cusplet. This single tooth is the first record of this genus for Denmark and the North Sea Basin.

Order Echinorhiniformes

Family Echinorhinidae *incertae sedis*

Genus *Orthechinorhinus* Adnet, 2006

Type species. *Orthechinorhinus pfeili* Adnet, 2006, type by original designation.

Orthechinorhinus cf. *pfeili* Adnet, 2006

Figs 3A–G

Material. 3 teeth, NHMD; 1201350 (Figs 3A–C), NHMD-1201351 (Figs 3D–E), NHMD-1201352 (Figs 3F–G).

Description. The two anterior-lateral mono-cuspid teeth (Figs 3A–E) possess an erect, labio-lingually compressed, triangular crown. The crown height of the anterior-lateral teeth is 2.1 mm (Figs 3A–C) and 1.6 mm (Figs 3D–E) respectively. The cusp has a weakly pronounced sigmoid contour in mesial or distal view (Fig. 3B). The labial crown face is weakly convex, the lingual crown face is strongly convex. The mesial and distal cutting edges are well-developed but smooth and reach the base of the crown. Mesially, the cutting

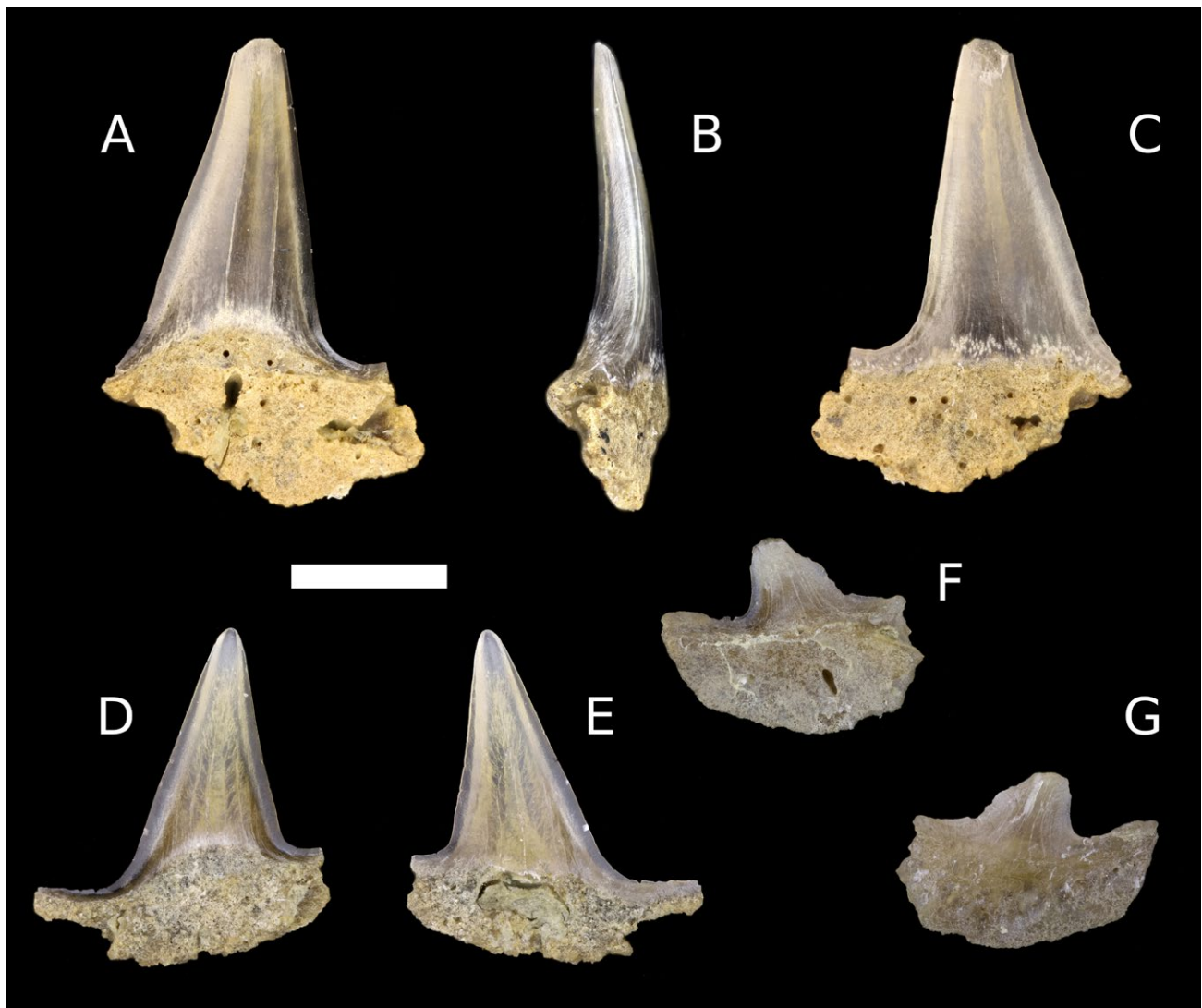


Fig. 3. A–G, *Orthechinorhinus* cf. *pfeili*. NHMD-1201350–NHMD-1201352. A,D,F, lingual view; B, profile view; C,E,G, labial view. Scale bar: 1 mm.

edge extends further down and continues towards the mesial heel. Distally, the cutting edge terminates slightly more upwards and continues towards the shorter distal heel. Thus, the teeth appear asymmetrical and the cusp is displaced distally. The teeth possess a smooth crown surface without folds or visible ornamentation. A central pulp cavity is visible (Figs 3C, D, E). The labio-lingually compressed root is only fragmentarily preserved in both teeth. The basal face of the root is lingually separated from the crown by a narrow but robust transverse bulge, which is centrally pierced by a medio-lingual foramen. In one tooth several small foramina are visible above the transverse bulge (Fig. 3A), and in two teeth is a rudimentary nutritive groove developed below the bulge (Figs 3D and F). The single latero-posterior tooth (Figs 3F–G) shows a similar morphology. The tooth differs from antero-lateral teeth in a lower crown height (0.8 mm), has a proportionally wider crown base and slightly distally inclined crown. Although the basal root is not well-preserved, the root edge appears convex. No tooth-interlocking device is visible. The labial root face possesses numerous small foramina, which open below the crown-root junction (Fig. 3G) and the lingual face of the root developed a central, elongated foraminal opening (Fig. 3F). All described teeth lack an apron (Figs 3C, E, F).

Remarks. To date, only two valid species are known. The type species *Orthechinorhinus pfeili* from the Eocene of southern France and *O. davidae* Welton, 2016b from the Oligocene of Oregon, USA. Adnet (2006) already highlights the unusual morphological characters of this tooth type in his description. Due to the root morphology for the family Echinorhinidae, Adnet (2006) concluded that the taxonomic position of this genus cannot be clearly determined. For this reason, Adnet (2006) placed the taxa in the family Echinorhinidae *incertae sedis*. Subsequently, Welton (2016b) assigned the genus to the squaliform family Etmopteridae based on the tearing-type dentition. He also pointed out that the species *O. davidae* possesses an orthodont cusp histology with a central pulp cavity in contrast to recent *Echinorhinus* teeth. As a result, he concluded that the morphological characters that led Adnet (2006) to place the genus in the Echinorhinidae ('labio-lingually flattened teeth, absence of dignathic heterodonty, absence of tooth imbrication in the lower dentition, presence of a simple unicuspid crown, numerous foramina and grooves on the labial root face, poorly defined and short apron, and a flat lingual root face') also occur in the etmopterid genus *Trigonognathus*.

The teeth described here strongly resemble the teeth illustrated and described by Adnet (2006).

The opinion of Welton (2016b) that the presence of a central pulp cavity does not allow an assignation to Echinorhinidae is not supported, as teeth of the extant species *Echinorhinus brucus* possess such a pulp cavity (Herman *et al.* 2003). For this reason, we follow the opinion of Adnet (2006) and place the genus in the family Echinorhinidae.

Distribution. Denmark, Late Ypresian to Middle Lutetian (this study); France, Ypresian/Lutetian-Bartonian (Adnet 2006); Austria, Lutetian (Adnet *et al.* 2021), Oregon, USA, early Oligocene (Welton 2016b). The described teeth represent the first record of this genus and species from Denmark, and the first record from the North Sea Basin.

Order Squaliformes

Family Centrophoridae Bleeker, 1859

Genus *Centrophorus* Müller & Henle, 1837

Type species. *Squalus granulatus* Bloch & Schneider, 1801, type by monotypy.

Centrophorus sp.

Figs 4A–J

Material. 6 teeth, NHMD-1201353 (Figs 4A–B), NHMD-1201354 (Figs 4C–D), NHMD-1201355 (Figs 4E–F), NHMD-1201356 (Figs 4G–H), NHMD-1201357 (Figs 4I–J), NHMD-1201358 (Figs 4K–L).

Description. The dental material described in this study comprises teeth of all jaw positions of the genus *Centrophorus* (Fig. 4). All examined teeth show the typical morphological characters of *Centrophorus*. The lower teeth (Figs 4A–F) show a strong labio-lingual compression and a distally bent cusp. The distal heel is convex and a serrated mesial cutting edge is present. A weakly developed and short lingual uvula is visible (Fig. 4A, arrow). A central infundibulum is placed at the lingual bulge (Fig. 4A, arrows). The long and well-developed apron narrows towards the root base. The root shows a concave contour and a clear lingual depression area is located below the distal heel.

The upper teeth show a strong disjunct monognathic heterodonty. The parasymphyseal and anterior teeth are triangular, symmetrical with a straight crown (Figs 4I–J). The antero-lateral teeth become more asymmetrical (Figs 4K–L) and the lateral to posterior teeth resemble lower teeth but differ in having a more erected cusp.

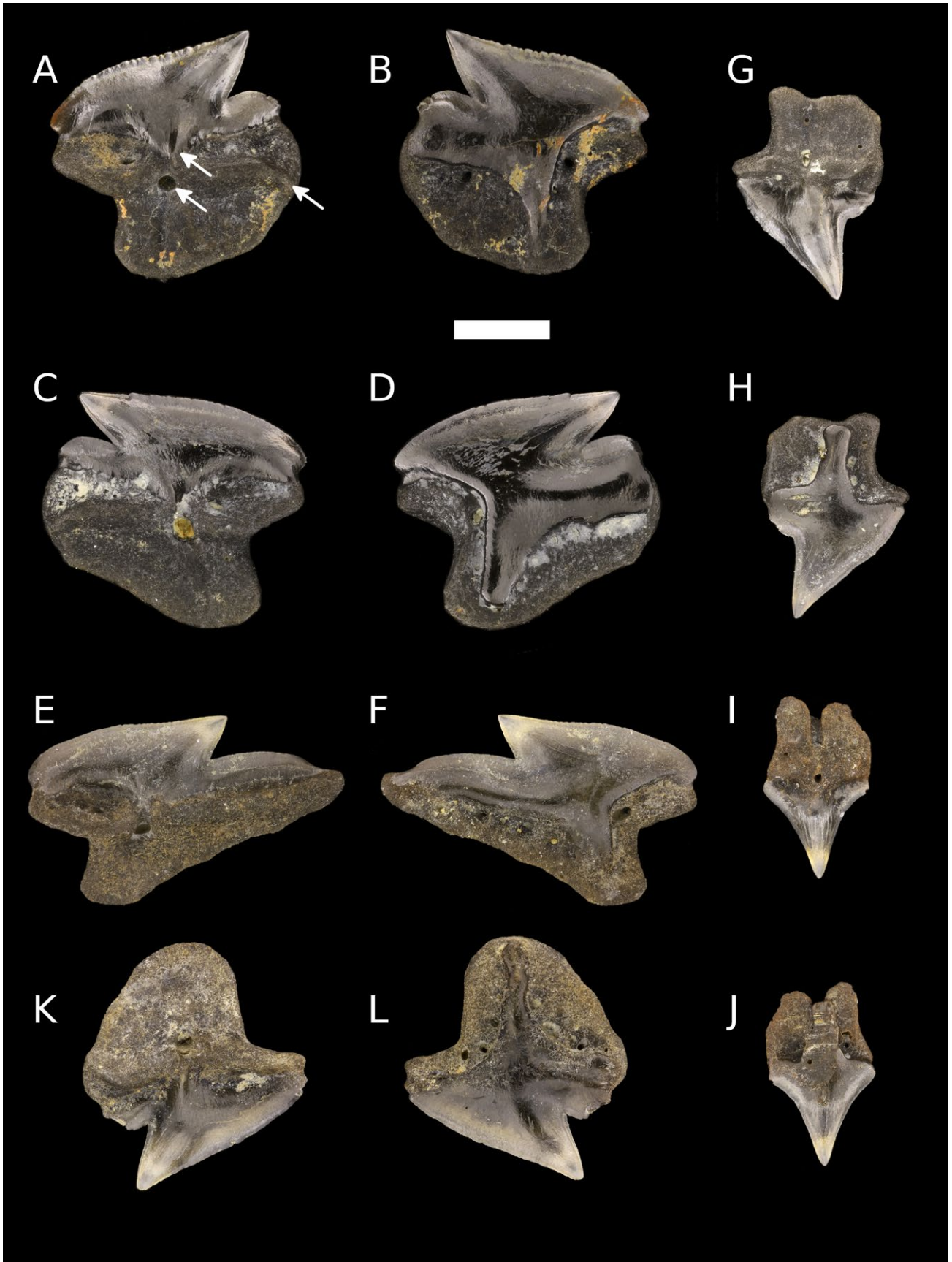


Fig. 4. A–L, *Centrophorus* sp. NHMD-1201353–NHMD-1201358, A–F, lower teeth, A,C,E, lingual view; B,D,F, labial view; G–L, upper teeth, G,I,K, lingual view; H,J,L, labial view. Scale bar: 1 mm. Explanation of arrows is given in the text.

Remarks. The genus was already documented by Carlsen & Cuny (2014) and described as *Centrophorus* aff. *granulosus*. The authors noted the morphological similarities of the teeth illustrated by Adnet (2006) from the Eocene of France and Cappetta (2012) from the Langhian, middle Miocene, southern France.

The usage of the species name '*granulosus*' for a large number of fossil teeth of the genus *Centrophorus* is based on the studies of Ledoux (1970, 1972) and Herman *et al.* (1989). However, it must be considered in this context that the specimen of a 97 cm female (Plate 11) illustrated by Herman *et al.* (1989) under the name *C. granulosus* was taken from the Mediterranean Sea. However, recent studies have shown that the species *C. granulosus* does not occur in the Mediterranean and that the species in question is *C. uyato* (White *et al.* 2022).

Both the lower tooth illustrated by Carlsen & Cuny (2014), and the lower teeth illustrated by Adnet (2006) reach widths of 3–4 mm. So far, no such large teeth have been found in the course of our study. The largest specimens reach widths of about 2 mm (Figs 4A–D). Further collection efforts, not analysed herein, resulted in numerous well-preserved teeth from all tooth positions. A detailed study will analyse potential morphological differences between the Eocene, Miocene and extant species of *C. uyato*.

Genus *Deania* Jordan & Snyder, 1902

Deania eglantina Jordan & Snyder, 1902, type by monotypy.

Deania cf. *angoumeensis* Adnet, 2006

Figs 5A–N

Material. 7 teeth, NHMD-1201359 (Figs 5A–B), NHMD-1201360 (Figs 5C–D), NHMD-1201361 (Figs 5E–F), NHMD-1201362 (Figs 5G–H), NHMD-1201363 (Figs 5I–J), NHMD-1201364 (Figs 5K–L), NHMD-1201365 (Figs 5M–N).

Description. The assemblage contains teeth of all jaw positions of the genus *Deania* (Fig. 5). All figured teeth show the typical morphological characters of *Deania*. The lower teeth (Figs 5A–H) are strongly labiolingually compressed with an oblique cusp, which is inclined in distal direction. A convex distal heel, a smooth or weakly serrated mesial cutting edge, and a narrow developed lingual uvula are present. On the root a displaced central foramen and a medio-lingual foramen are developed (Figs 5A, C, arrows). A nutritive groove is present on the labial face of the root. The root is low and wider than high, with a rectangular

outline. A well-developed apron is developed.

The upper teeth show a strong disjunct monognathic heterodonty. The parasymphyseal tooth is triangular, symmetrical with a straight crown (Figs 5K–L). The antero-lateral teeth become more asymmetrical (Figs 5I–J) and the lateral to posterior teeth resemble lower teeth but differ in having a more erected cusp (Figs 5M–N).

Remarks. Teeth of the genus *Deania* are rare in the fossil record and have only been found at few sites. A detailed description of the palaeogeographical distribution can be found in Pollerspöck *et al.* (2022), regarding the morphological differences to *Centrophorus*, we refer to Ledoux (1970, 1972), Herman *et al.* (1989) and Cappetta (2012). From the Eocene, the genus is so far only known from northern France (*Deania angoumeensis*, Adnet 2006). The teeth analysed herein differ only in size from *D. angoumeensis*. All teeth discovered have a width of less than 2 mm, whereas *D. angoumeensis* reaches a width of up to 3 mm (Adnet 2006). For this reason, the species is provisionally listed in open nomenclature.

Family Dalatiidae Gray, 1851

Genus *Squaliolus* Smith & Radcliffe, 1912 in Smith, 1912b

Type species. *Squaliolus laticaudus* Smith & Radcliffe, 1912 in Smith, 1912b, type by original designation.

Squaliolus sp.

Figs 6A–T

Material. 10 teeth, NHMD-1201366 (Figs 6A–B), NHMD-1201367 (Figs 6C–D), NHMD-1201368 (Figs 6E–F), NHMD-1201369 (Figs 6G–H), NHMD-1201370 (Figs 6I–J), NHMD-1201371 (Figs 6K–L), NHMD-1201372 (Figs 6M–N), NHMD-1201373 (Figs 6O–P), NHMD-1201374 (Figs 6Q–R), NHMD-1201375 (Figs 6S–T).

Description. The monocuspid upper teeth are small and do not exceed a total height of 2.0 mm (Figs 6O–T). The erect, approximately triangular cusps are more or less symmetrical in anterior files (Figs 6O–P) and slightly inclined distally in lateral teeth (Figs 6Q–T). The lingual crown face is convex and faint enameloid folds are developed (Figs 6P, R and T). These irregular folds extend from the base to almost the tip of the cusp. All upper teeth show a well-developed and sharp cutting edge, which continues from the pointed apex

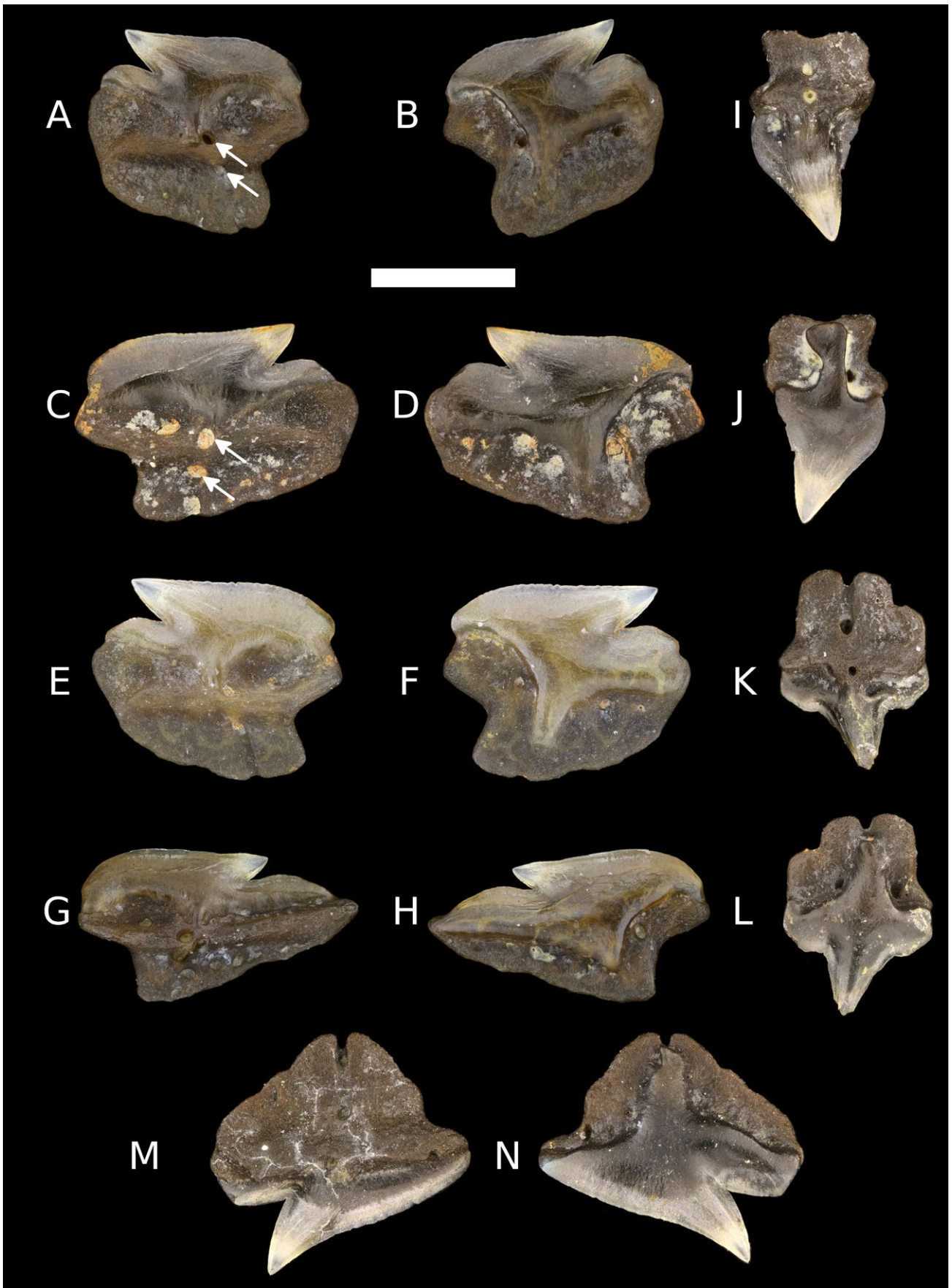


Fig. 5. A–N, *Deania* cf. *angoumeensis*. NHMD-1201359–NHMD-1201365, A–H, lower teeth, A,C,E,G, lingual view; B,D,F,H, labial view; I–N, upper teeth, I,K,M, lingual view; J,L,N, labial view. Scale bar: 1 mm. Explanation of arrows is given in the text.

down to the crown base. The labial face of the crown is flatter compared to the lingual side and teeth of anterior positions possess a distinct enameloid fold running from the apex of the crown down to the

lower end of the apron (Fig. 6O). In lateral teeth this fold is not developed (Figs 6 Q, S). The bilobed root has a single small to medium-sized medio-lingual foramen. The mesial root lobe is always longer than

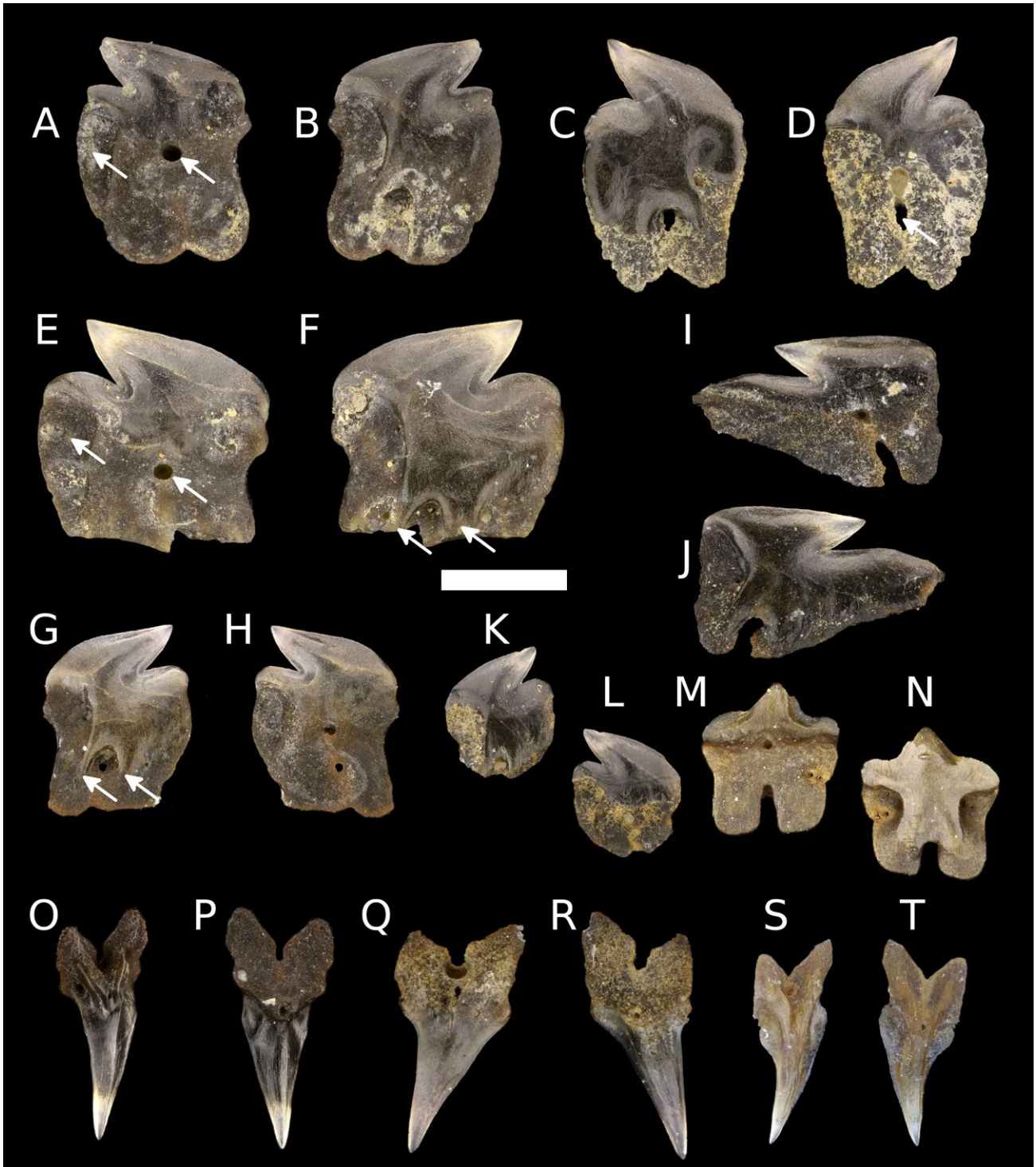


Fig. 6. A–T, *Squaliolus* sp. NHMD-1201366–NHMD-1201375. A–H, lower teeth, A,D,E,H, lingual view; B,C,F,G, labial view; I–J, lower commissural tooth, I, lingual view, J, labial view; K–L, lower (?juvenile) lateral tooth, K, labial view, L, lingual view; M–N, lower symphyseal tooth, M, lingual view, N, labial view; O–T, upper teeth, O,Q,S, labial view, P,R,T, lingual view; Scale bar: 1 mm. Explanation of arrows is given in the text.

the distal one. The lingual root face is flat and lacks a nutritive groove. On the labial side of the root a very narrow, clearly prominent bilobed apron is developed. The large medio-labial foramen is situated centrally between the two lobes of the apron. Anterior teeth possess an additional foramen, which is situated directly below the crown-root junction distally of the apron.

The small monocuspid, labio-lingually compressed lower teeth reach a height up to 2.1 mm and a width of 1.9 mm (Figs 6A–N). The strongly distally inclined cusp is smooth, shows no ornamentation and is flanked by a distal heel. In anterior teeth, the tip extends to the distal edge of the tooth; in lateral teeth, the tip ends well in front of it. The mesial cutting edge is sharp, not serrated and slightly convex or sigmoidally curved. The distal cutting edge is slightly convex. The distal heel is in anterior and lateral teeth well rounded, in commissural teeth straight and elongated (Figs 6I–J). The tooth interlocking devices are well-developed and extend down to the middle or lower third of the root (Figs 6A, E, arrows). The distal root contour is strongly convex, the lower end straight with only a small notch in the middle. A nutritive groove is absent. Lingually there is only one central foramen present (Figs 6A, E, arrows) but sometimes a button-hole is developed (Fig. 6D, arrow). Labially, a well-developed bilobed apron is present (Figs 6F, G, arrows), which is pierced by a large medio-labial foramen. Additional labial foramina, which are variable in size, are situated mesially to the apron in the tooth-interlocking surface. On the distal side of the root, the enameloid extends down to the height of the central foramen.

Remarks. The family Dalatiidae currently includes four monotypic genera (*Dalatius*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*) and three genera with two species each (*Isistius*, *Mollisquama*, *Squaliolus*). Considering the tooth morphology, the ten species can be divided into two groups: species with lower teeth with almost vertically erect main cusps (*Dalatius*, *Isistius*, *Euprotomicroides*, *Mollisquama*) and species with lower teeth that have a distinct distally inclined main cusp (*Euprotomicrus*, *Heteroscymnoides*, *Squaliolus*) (Pollerspöck & Straube 2019). The following fossil taxa also qualify for the inclusion in the second group: *Angoumeius* Adnet, Cappetta & Reynders, 2006, *Eodalatias* Engelbrecht, Mörs, Reguero & Kriwet, 2017, *Eosqualiolus* Adnet, 2006, *Oligodalatias* Welton, 2016a, *Squaliodalatias* Adnet, Cappetta & Reynders, 2006, *Squaliomicrosus* Suzuki, 2015. The fossils described herein are assigned to the second group. The lower teeth of the fossil taxa differ from *Eodalatias* in having smooth cutting edges and a smooth distal heel (vs. cutting edges and distal heel coarsely serrated). The teeth from this study differ from *Angoumeius* in show-

ing more strongly inclined crowns and considerably smaller medio-lingual and medio-labial foramina. Furthermore, they can be distinguished from *Squaliodalatias* by smaller medio-labial foramina and narrower as well as higher lower and upper teeth. The new dental material differs from *Eosqualiolus* in more strongly inclined crowns and, from *Oligodalatias* due to the much smaller teeth (<3.00 mm vs maximum tooth height 7.95 mm in *Oligodalatias*) and in having a bilobate apron (vs non-bilobate apron). Teeth of *Squaliomicrosus* are generally wider than high and thus, differ from the teeth of this study, which are higher than wide.

From the two extant taxa *Euprotomicrus* and *Heteroscymnoides* the fossil taxa can be distinguished on the basis of the following characters: from *Euprotomicrus* by an enlarged distance between both labial apron lobes, which covers a third of the root. Furthermore, the mesial lower part of the apron is distinct, conical and clearly separated from the root (Pollerspöck *et al.* 2022). The teeth from this study differs from *Heteroscymnoides* in having a convex to sigmoidal mesial cutting edge (vs. straight cutting edges) and a smaller medio-labial foramen.

Fossil teeth of the genus *Squaliolus* are generally rare in the fossil record. *Squaliolus gasconensis* Adnet, 2006 from the Eocene of France and *Squaliolus schaubi* (Casier, 1958) from Miocene deposits are the only extinct valid species of this genus. The teeth of the fossils analysed herein differ from *S. gasconensis* in showing more distally inclined crowns, and thicker, more pronounced aprons and roundish basal root outlines. The fossils differ from the neogene species *S. schaubi* by a distinctly smaller medio-labial foramen. Furthermore, the distal part of the labial apron is more pronounced and clearly separated from the adjacent enameloid surface (see Underwood & Schlögl 2013, Figs A1, D, E1 and F1).

The teeth described herein represent the first record of the genus from the North Sea Basin. The fossil teeth will be the focus of a more detailed study as they most probably represent an undescribed form. The genus was also recorded in the Eocene in southern France (Atlantic, Adnet 2006) and in the North-western Tethyan Realm (Adnet *et al.* 2021).

Family Etmopteridae Fowler, 1934

Genus *Etmopterus* Rafinesque, 1810

Type species. *Etmopterus aculeatus* Rafinesque, 1810, type by monotypy.

Etmopterus cf. cahuzaci Adnet, 2006

Figs 7A–D

Material. One lower NHMD-1201376 (Figs 7A–B), one upper tooth NHMD-1201377 (Figs 7C–D).

Description. The main cusp of the incomplete lower tooth is very strongly inclined distally. The mesial cutting edge is sigmoidally curved, whereas the distal one is clearly convex. The distal heel is low and relatively elongated. Lingually, the lower crown edge is slightly wavy and below the crown-root junction are several small foramina present. Labially, the apron extends down to the lower third of the tooth. Several foramina are present at the labial root junction with some of them considerably larger (Fig. 7B).

The upper tooth is incompletely preserved. The crown is distinctly convex lingually and only slightly convex labially. On the mesial side, only one very slender, dagger-shaped lateral cusp is present, reaching to the middle of the main cusp. Two other lateral cusps are broken off. On the distal side of the main cusp, both lateral cusps are broken off. The mesially preserved lateral cusp is sigmoidally curved in labial or lingual views and inclined mesially, contrary to the main cusp, which is slightly inclined distally. Lingually, two large central foramina are present. The root is bilobed. (Figs 7C–D).

Remarks. The upper tooth (Figs 7C–D) corresponds to the teeth illustrated in Adnet (2006, pl. 8 figs 2–4), the lower tooth (Figs 7A–B) appears narrow and high due to the mesial fragmentation of the root. The lower tooth from this study differs from the teeth of the type series mainly by the slightly raised tip in the upper part of the crown and the somewhat stronger

arched curvature of the labial enameloid edge. Due to the limitation of only two incomplete teeth found so far, it cannot be definitively clarified whether it is the species mentioned. Based on the great similarity of the upper teeth with the type material, both teeth are tentatively assigned to *Etmopterus* cf. *cahuzaci*.

Family Etmopteridae *incertae sedis*
sensu Adnet 2006 or Somniosidae sensu
Pollerspöck *et al.* 2023 (this study)

Genus *Paraetmopterus* Adnet, 2006

Type species. *Paraetmopterus nolfi* Adnet, 2006, type by original designation.

Paraetmopterus nolfi Adnet, 2006

Figs 8A–J

Material. Two upper NHMD-1201378 (Figs 8A–B), NHMD-1201379 (Figs 8C–D), three lower teeth NHMD-1201380 (Figs 8E, H), NHMD-1201381 (Figs 8F, I), NHMD-1201382 (Figs 8G, J).

Description. The upper teeth are small (maximum height 1.6 mm), have a slender and slightly distally inclined crown and a pair of lateral cusplets. The two slender lateral cusps reach about half of the main cusp (Figs 8A–D). The lingual face of the crown is convex, the labial side is flatter. The main and lateral cusps of the upper teeth show well-developed and sharp cutting edges, which run from the pointed apex down to the base of the crown. The cutting edges of the

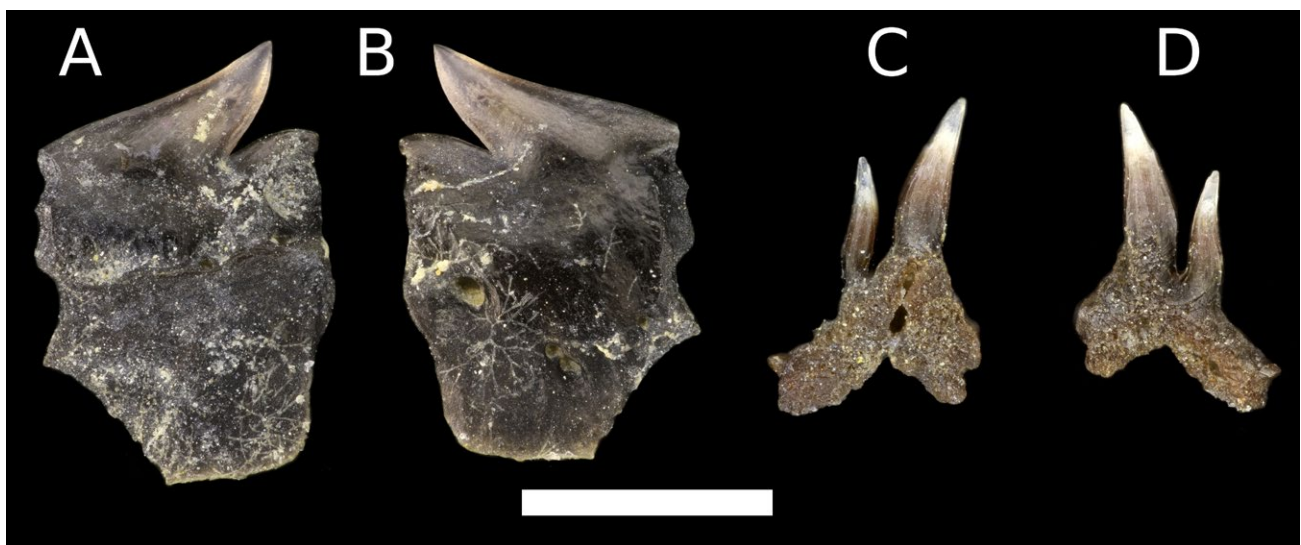


Fig. 7. A–D, *Etmopterus* cf. *cahuzaci*. NHMD-1201376–NHMD-1201377. Lower anterior-lateral tooth. **A**, lingual view; **B**, labial view; upper lateral tooth. **C**, lingual view; **D**, labial view; Scale bar: 1 mm.

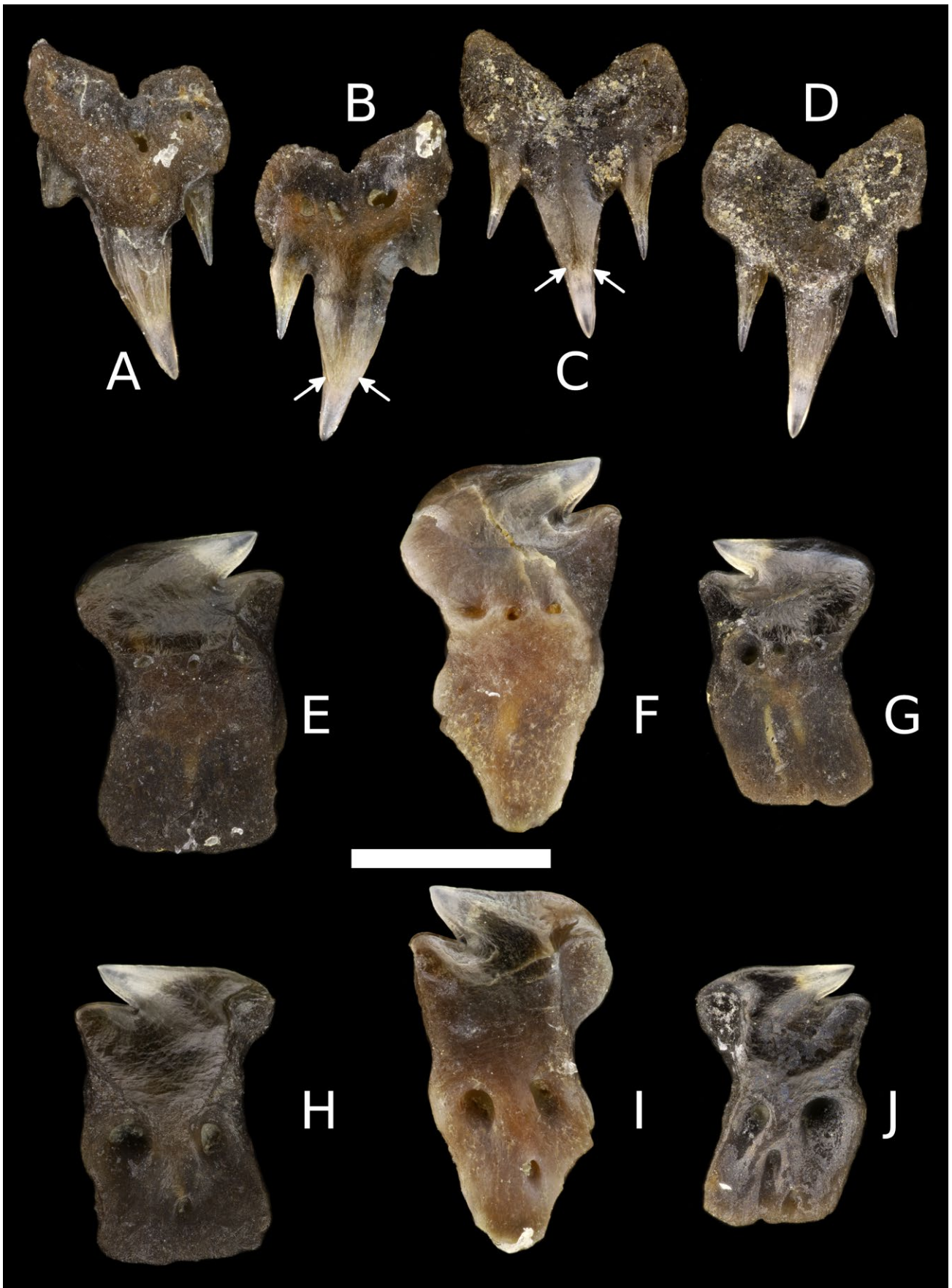


Fig. 8. A–J, *Paraetmopterus nolfi*. NHMD-1201378–NHMD-1201382. upper lateral tooth. A,D, lingual view; B,C, labial view; lower lateral teeth. E,F,G, lingual view; H,I,J, labial view; Scale bar: 1 mm. Explanation of arrows is given in the text.

main cusp split in the upper third of the cusp and continue as a clear enameloid ridge towards the apex (Figs 8B–C, arrows). The bilobed root has a single small to medium-sized medio-lingual foramen. The mesial root lobe is always longer than the distal one. The lingual face of the root is flat and bears a short nutritive groove. This groove ends in a notch between the two root lobes. The labial crown-root transition is smooth and lacks an apron. Additionally, several foramina, some of them very large (Fig. 8B), are developed directly below the lower crown edge.

The small monocuspid, labio-lingually compressed lower teeth possess a height up to 1.8 mm and a width of 1.0 mm. In the illustrated teeth, the ratio of crown height to root height is 1:2.5–2.8 (Figs 8E–G). The strongly distally inclined cusp is smooth and flanked by a distal heel (Figs 8E–J). The mesial cutting edge is sharp, not serrated and straight to slightly convex or sigmoidally curved. The distal cutting edge is slightly convex. The distal heel is low, almost straight and elongated. The tooth interlocking devices are small and only formed as a triangular depression area in the crown-root junction region (Fig. 8E–G). The distal root contour is strongly convex, the lower end is straight and the mesial side slightly curved. A labial nutritive groove is absent. Lingually, three foramina are pre-

sent, which are located along the bulge between the crown and the root. Labially, a well-developed apron is present accompanied by two or three large foramina.

Remarks. We consider the present material conspecific with the material described by Adnet (2006) from France (Lutetian-Bartonian) with respect to both the upper and lower teeth. Only teeth with a distinctly erect crown, as illustrated by Adnet (2006, tab. 10, figs 1 and 2), have not yet been found in Kirstinebjerg, Denmark. As to its tentative placement in the family Etmopteridae, we rather propose a classification of the genus *Paraetmopterus* as a member of the family Somniosidae. Adnet's (2006) tentative placement is based on the multicuspid upper teeth, a character distinctive for the extant genus *Etmopterus*, but not Etmopteridae *per se*. This led Adnet (2006) to suggest an origin of the Eocene *Paraetmopterus* in the Maastrichtian, multicuspid *Proetmopterus* Siverson, 1993 which also shows similarities in lower tooth characters (Herman 1982c; Siverson 1993; Adolfssen & Ward 2014; Feichtinger *et al.* 2023). However, Adnet (2006) pointed out that lower teeth of *Paraetmopterus* show morphological characters of Somniosidae, of the genus *Centroscymnus* in particular. Fossil lower teeth carrying somniosid characters were also documented



Fig. 9. A–B, *Paraetmopterus* sp., lower lateral tooth, collection no. NHMW/2023/0070/0001, A, labial view; B, lingual view; Upper Cretaceous, Campanian/Maastrichtian, near Bergen, Upper-Bavaria, Germany; Scale bar: 1 mm.

from Miocene and Oligocene sediments (Germany: Barthelt *et al.* 1991; Austria: Bracher & Unger 2007; Schultz 2013; Pollerspöck *et al.* 2018; Filek *et al.* 2021; Czech Republic: Tomanová Petrová *et al.* 2018; Slovakia: Underwood & Schlögl 2013; Spain: Martínez-Pérez *et al.* 2018; Japan: Takakuwa 2007; Nishimatsu 2019; Nishimatsu & Ujihara 2020) for which the somniosid genus *Palaeocentroscymnus* was erected (Pollerspöck *et al.* 2018).

Newly discovered Campanian/Maastrichtian fossil teeth of Upper Bavaria now also challenges the origin of *Paraetmopterus* in *Proetmopterus*. Figure 9 shows a lower tooth tentatively assigned to ?*Paraetmopterus* (Collection No. NHMW/2023/0070/0001). These lower teeth show a combination of characters of both *Paraetmopterus* and *Palaeocentroscymnus*. However, they are distinct from *Proetmopterus*, i.e., this tooth type co-existed with *Proetmopterus*. Even though no extant somniosids are known showing multicuspid upper teeth, the possibility of ancestral occurrence of this character state in Somniosidae is currently under investigation.

Statistical analysis

Multivariate Clustering - indexes after Kulczynski, Jaccard, Ochiai and Dice

The matrix generated for the cluster analysis includes 30 different geographical locations of Eocene deposits and a total number of 108 genera. Of these, 49 genera were classified as deep-sea sharks based on the predominant lifestyle of their modern ancestors. The result of the cluster analysis suggests that the fauna of Kirstinebjerg, Denmark (this study) analysed here has the greatest faunistic similarity with the fauna of North Morocco (Noubhani & Cappetta 1997; Supplementary Material Part 2).

Performed cluster analysis for both matrices (all taxa versus deep sea taxa) result in similar clusters in all eight analyses (Figs 10A and B, Supplementary Material). The cluster analysis with focus on deep-sea taxa only shows highest similarity to faunas described from northern Morocco (Ypresian) (Noubhani & Cappetta 1997) and northern France (Ypresian/Lutetian) (Adnet 2006). Within this cluster, the sister fauna of the Lillebælt Clay fauna cannot be estimated with confidence. Sister taxa are variable throughout the different analysis which is further reflected in low bootstrap node support (Supplementary Material). Depending on the Index matrix underlying the clustering analysis, the Lillebælt Clay fauna is sister to northern Morocco (Ypresian; Kulczynski, Ochiai) or northern

France (Ypresian/Lutetian; Dice, Jaccard). This cluster, however, is sister to northern Morocco in two of the four cluster analysis only (Jaccard and Dice indexes underlying the analysis), while it is sister to the fauna of the Caribbean (Mexico), using the Kulczynski index and to the fauna of France (Ypresian/Lutetian) using the Ochiai index (Supplementary Material). Comparing the clusters supported in three of the four analyses (Figs 10A and B; Supplementary Material), we find that of 24 deep-sea genera known to date from the Lillebælt Clay (France: 18, Morocco: 11), seven genera occur in all three localities (*Fountizia*, *Echinorhinus*, *Heptranchias*, *Hexanchus*, *Striatolamia*, *Hypotodus*, *Odontaspis*). Five genera (*Apristurus*, *Weltonia*, *Anomotodon*, *Woellsteinia*, *Isistius* and *Paraetmopterus*) are found in at least one other location outside the Lillebælt Clay (northern Morocco or France). All three sites that were compared have in common that extensive material was sieved (this study approximately 6000 kg, France: 2500 kg, Morocco: kg not specified, but 3 years field campaign, several 10,000 teeth). Based on the high amount of sediment processed, the cluster analyses in relation to these three sites were not influenced by the sample size. The Sankey diagram (Fig. 10C) shows a typical deep-sea composition of the three compared faunas (Lillebælt Clay, this study; northern Morocco, Ypresian (Noubhani & Cappetta 1997) and France, Ypresian/Lutetian (Adnet 2006).

Discussion

At the deposition time of Lillebælt Clay site Layer 2, there were apparently no direct geographical connections to the adjacent genus-rich deep-water shark faunas documented from the Tethyan Realm (southern France, Austria), the Mediterranean or the Pacific Ocean (Gibbard & Lewin 2016, fig. 4)). Therefore, the high number of genera (25) of the Lillebælt Clay representing orders dominated by deep-sea shark species, i.e. Carcharhiniformes (families Pentanchidae and Scyliorhinidae), Lamniformes (families Mitsukurinidae and Odontaspidae), Squaliformes, Hexanchiformes, Pristiophoriformes and Echinorhiniformes is noteworthy, as the documented deep-sea shark diversity of geographically adjacent sites (the North Sea Basin in Belgium, the Netherlands, southern England and northern Germany) is significantly lower. For example, only the four genera *Hexanchus*, *Weltonia*, *Isistius* and *Squalus* were recorded from the London Clay sites analysed in Cooper (1977) and Rayner *et al.* (2009); only two genera (*Isistius* and *Squalus*) were documented from the Belgian sites (Van den Eeckhaut & De Schutter 2009; Iserbyt & De Schutter 2012),

and none were actually documented from northern Germany (Diedrich 2012). The higher diversity of the Lillebælt Clay can likely be explained with an average water depth of 100–350 m (Schnetler & Heilmann-

Clausen 2011, Carlsen & Cuny 2014), comparatively notably deeper to adjacent depositions (e.g. London Clay less than 100 m depth (Friedman *et al.* 2016)). The sites analysed herein represent those localities depos-

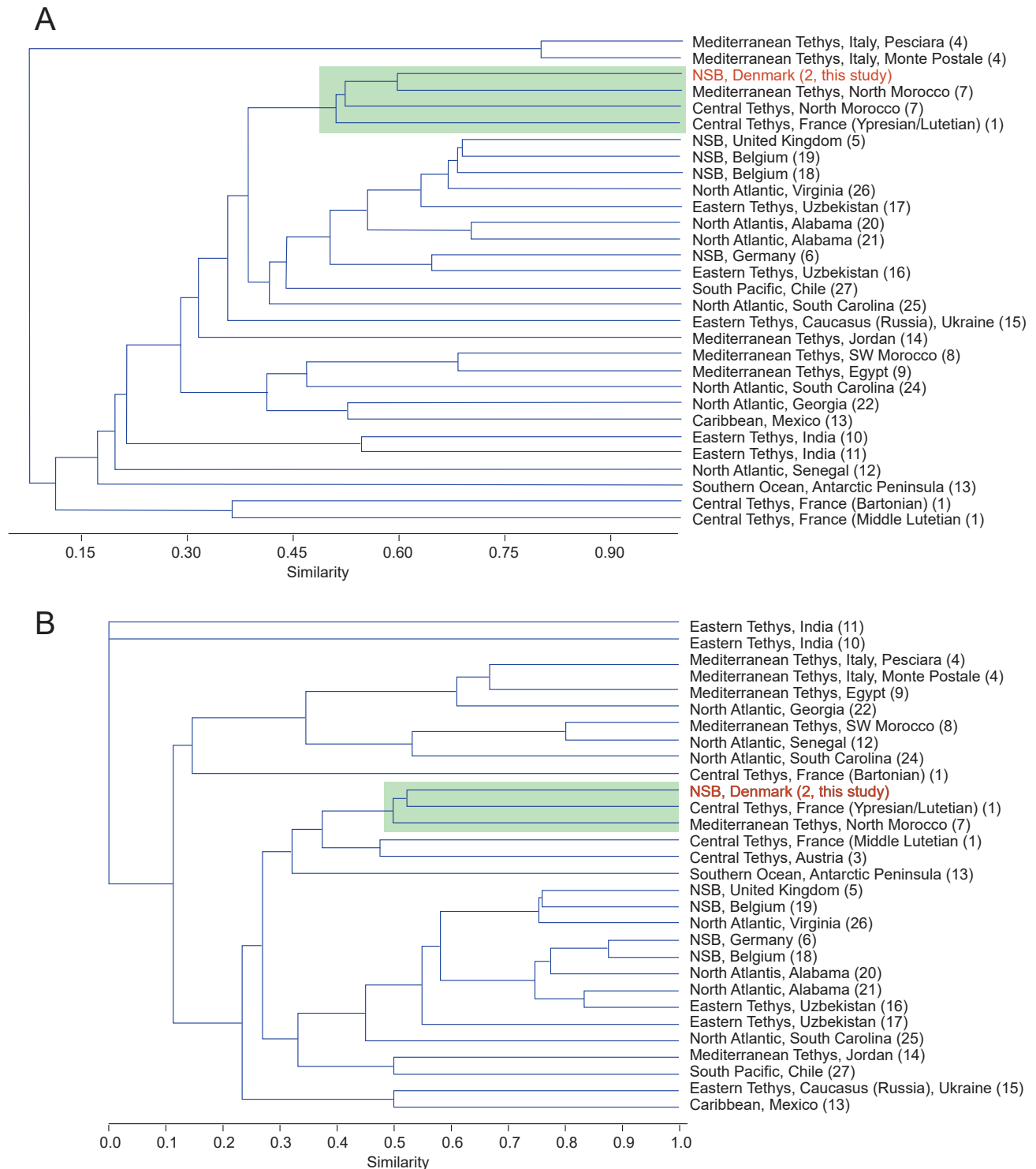


Fig. 10. Cluster analysis of the 30 Eocene faunas. **A,B,** Dendrogram based on incidence (presence/absence) data showing results based on the Dice index (three more dendrograms were obtained with the Kulczynski, Jaccard and Ochiai indices (see Supplementary Material), **A,** all taxa; **B,** only deep-sea taxa.

ited at the largest water depths within the North Sea Basin during the Early Eocene (late Ypresian) (Gibbard & Lewin 2016). Schwarzahns (2007) studied the otolith fauna of the Lillebælt Clay. He found a large number of otoliths of the deep-water taxon *Gephyroberyx*, but none of the typically shallow-water elements found in the Belgian Eocene. From this result he concluded that the water depth of the Lillebælt Clay deposits must have been deeper than in Belgium and probably also in southern England (London Clay). Our findings are complementary with Schwarzahns' (2007) conclusion adding numerous deep-sea shark species to the recorded fauna.

All four calculated indexes suggest a sister-group relationship of the Lillebælt Clay with other Atlantic and Mediterranean Tethyan faunas (Fig. 10A; Sup-

plementary Material). Although the fauna of northern Morocco (Mediterranean Sea, Tethys) represents taxa characteristic for shallow shelf ecosystems with additional pelagic and deep-water elements (Noubhani & Cappetta 1997), the relationship to the Lillebælt Clay deep-water fauna is probably due to genera of the order Hexanchiformes (3) and the families Odontaspidae (2), Mitsukurinidae (1), Echinorhinidae (1) and Scyliorhinidae (1). In contrast, the order Squaliformes, which comprises today almost exclusively deep-water species, is of minor impact with only one similarity (genus *Isistius*, Fig. 10C). Fossil teeth of *Isistius* are widespread (Pollerspöck *et al.* 2022) and often found in nearshore environments, such as the shallow water deposits of the London Clay or the Eocene of Belgium (Cooper 1977; Rayner *et al.* 2009; Van den Eeckhaut. &

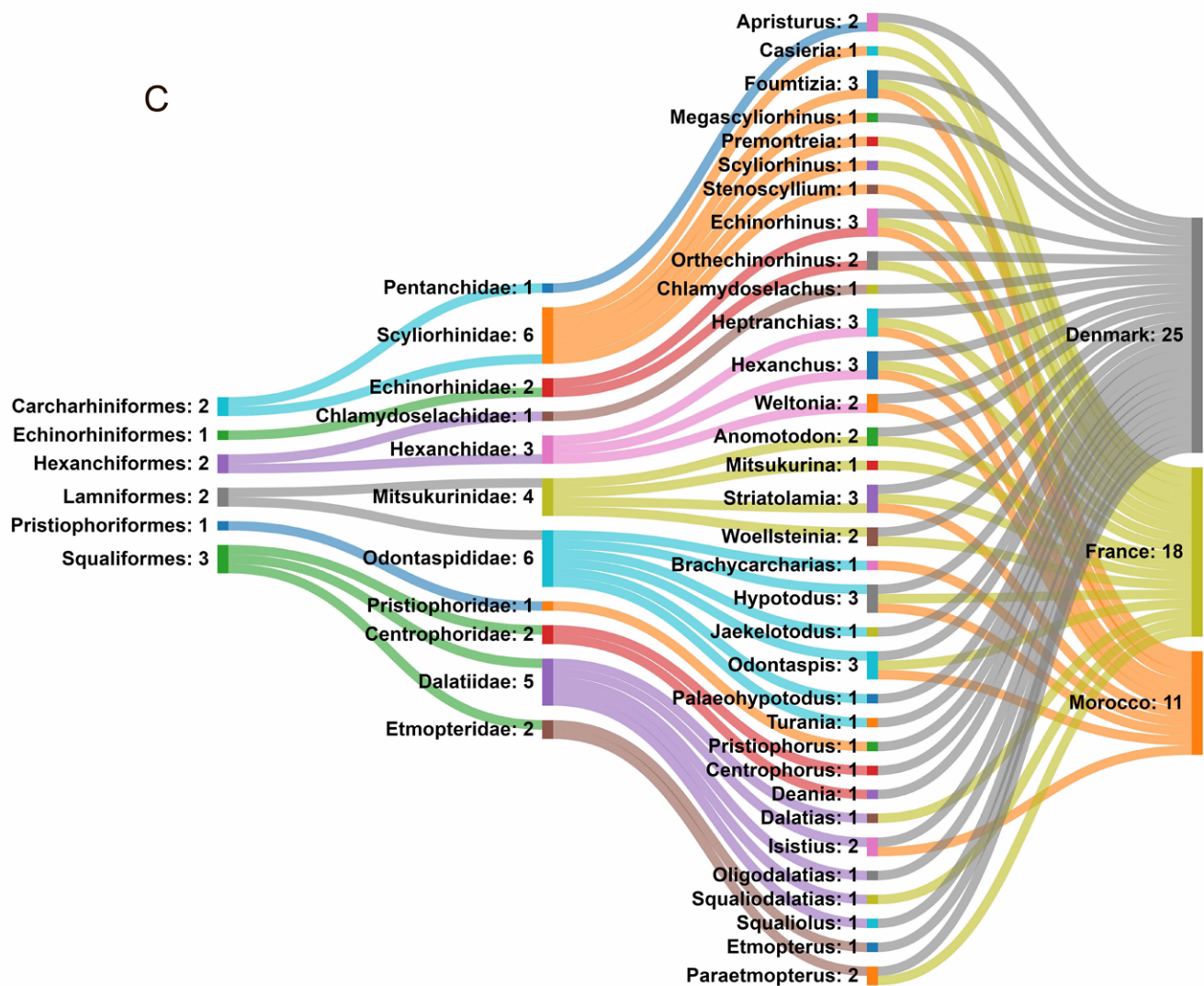


Fig. 10 continued. C, Diversity comparison of the three sites clustering in the Dice index cluster analysis (this study, France, northern Morocco). Left: the recorded orders with the number of different families; second column: the recorded families with the cumulative number of genera (the given value corresponds to the sum of genera per site), third column: the recorded genera with the cumulative number of records, right: the number of (deep-sea) genera of the three sites.

De Schutter 2009; Iserbyt & De Schutter 2012). Comparing the sites of France, which represent a typical deep-sea sediment (Adnet 2006), already 12 deep-sea taxa (*Apristurus*, *Fountizia*, *Echinorhinus*, *Orthechinorhinus*, *Heptranchias*, *Hexanchus*, *Anomotodon*, *Striatolamia*, *Woellsteinia*, *Hypotodus*, *Odontaspis*, *Paraetmopterus*) co-occur (Fig. 10C). However, the sister-group relationships should be re-evaluated in future analyses based on denser sampling.

Comparing the tooth sizes of some of the taxa documented in this study (e.g., *Centrophorus*, *Deania*, or *Paraetmopterus*) with published material from southern France (Adnet 2006), teeth analysed herein are on average smaller in size. Several options may qualify as explanation, such as genetic barrier (Catarino *et al.* 2016) or nursery areas. However, estimation of a likely scenario causing this are subject to future studies, as a sampling artefact cannot be ruled out. This might also be the reason for the lack of recorded deep-water sharks in a first evaluation of the Lillebælt Clay shark fauna (Carlsen & Cuny 2014).

Conclusion

In this study, we describe a number of distinct fossil teeth for the first time documenting deep-sea shark species from the Eocene, which were previously unknown from the North Sea Basin. Documented species are *Apristurus* sp., *Orthechinorhinus pfeili*, *Deania* cf. *angoumeensis*, *Squaliolus* sp., *Etmopterus* cf. *cahuzaci* and *Paraetmopterus nolfi*. This significantly extends the diversity hitherto known from this area. Cluster analysis shows that the fauna shows highest similarities with documented deep-sea shark faunas of France, Austria and northern Morocco even though the North Sea Basin had already lost direct connections to the neighbouring marine areas in the Eocene.

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